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The Ecological Memory of Fish Assemblages in Tropical Agroecosystems With Different History of Landscape Changes

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ABSTRACT

1. Environmental changes can have persistent effects on the local and regional dynamics of multispecies assemblages. However, the extent of historical legacies on current diversity patterns may depend on the trajectory and intensity of the environmental change. Here, we investigate how persistent decadal land use and land cover (LULC) changes are related to the taxonomic and functional structure of present-day fish assemblages in regions with distinct histories of land use transformation.
2. We selected streams in Brazilian river basins where the LULC change has started more than 150 years ago (state of São Paulo), in the 1970s (state of Rondônia), and more intensively in the 2000s (state of Mato Grosso). We used a dataset comprising 219 streams, 240 species, 13 instream variables and 13 variables describing past LULC changes. We used varying-coefficient models (VCM) to test how instream habitat and past land use are related to taxonomic and functional fish richness and rarity.
3. Although diversity metrics were slightly better explained by instream variables, we found stronger landscape legacy effects on fish diversity in RO and MT, where LULC changes have occurred more recently. We did not detect landscape legacy effects or strong biodiversity–environment relationships in the region that experienced deforestation earliest (SP), probably because fish assemblages are now dominated by generalist species that are more resistant to further environmental change.
4. Our results indicate that landscape legacies may leave more detectable signals in stream communities in regions where the first major LULC changes happened not too long ago. Thus, the influence of past processes on current fish assemblage diversity and structure may decline with increasing time since the initial LULC change.
5. Our study shows that past LULC changes can shape present-day biodiversity patterns, and that differences in species pool and landscape change histories can lead to different assemblage–environment relationships. Incorporating historical land use variables, especially in recent deforested regions, can therefore improve our understanding of current patterns of biodiversity. Our findings highlight the importance of preserving and restoring riparian corridors to prevent species loss locally and regionally, because, even in long-altered regions, streams with riparian cover may still support rare species. Overall, integrating land use history and regional context is crucial for effective conservation and biodiversity monitoring in ecosystems, especially those ones under the first major LULC changes.

1 | Introduction

Environmental changes can have persistent effects on the local and regional dynamics of biological assemblages because some species can take some time to respond to the new conditions (Turner 2005; Brejão et al. 2018). Delayed responses are the result of different processes at the individual (e.g., survival rates at different life cycles), population (e.g., size and structure), metapopulation (e.g., extinction and colonisation rates; Hylander and Ehrlén 2013), community (e.g., biotic interactions; Barret et al. 2021) and metacommunity (e.g., dispersal) levels. Also, the magnitude, trajectory (Jung et al. 2019; Santos et al. 2020; Camana et al. 2022) and duration of the events that change the environment (Brejão et al. 2018; Jung et al. 2019) operate synergistically with these ecological processes to determine the chronology of the delayed responses. In fact, some biodiversity patterns are better explained by past than current environmental conditions (Bommarco et al. 2014; Duplisea et al. 2016; Noh et al. 2019; Löffler et al. 2020; Santos et al. 2020). For example, Tabi et al. (2025) found that historical landscape composition was the only landscape metric explaining stream insect richness patterns, where richer assemblages were found in catchments with the historical land use classes distributed more evenly. However, there should be a timeframe in which past disturbance events still affect communities, either because most of the local extinctions are completed after some time (Halley et al. 2016) or because the local community composition is dominated by widespread generalists that respond weakly to further environmental change (Baselga et al. 2015; Zeni et al. 2017; Newbold et al. 2018; Betts et al. 2019). Thus, the persistent effect of past environmental change on community dynamics may be linked to the type and time since the major event of change happened. Incorporating historical processes in ecological models may provide a better understanding of current biodiversity patterns and how they are affected by environmental change (Hylander and Ehrlén 2013).

In the Anthropocene, land use and land cover (LULC) changes are the primary cause of biodiversity loss (Davison et al. 2021). South America has experienced one of the largest LULC changes in the last 30 years, where natural land cover has been significantly replaced by cropland (Liu et al. 2020). Regions historically occupied by pasture in Brazil have been quickly replaced by commodity croplands (e.g., sugarcane, cotton, corn, soybean), while pushing forward the deforestation frontier throughout the Amazon, where native forests have been increasingly converted into new pastures (Souza et al. 2020). Two distinct processes of LULC change are currently happening in Brazil, one that represents the first conversion from native forest to an agroecosystem (mostly pasture) and another that represents a switch between different land covers (i.e., pasture to sugarcane) in areas that had been previously changed to agroecosystems (Souza et al. 2020). Three Brazilian regions fit this scenario and thus represent a good opportunity to investigate the response of biodiversity to past LULC changes. The first region is the Northwest of the state of São Paulo (SP), where the first conversion from native forest to an agroecosystem happened more than 150 years ago and after successive LULC changes another major conversion from pasture to sugarcane occurred more recently. The second region is the East of the state of Rondônia (RO), and the last one is the North of the state of Mato Grosso (MT), where the first conversion from native forest to pasture started in the 1970s in both regions, but more intensively in the 2000s in MT (Figure 1).

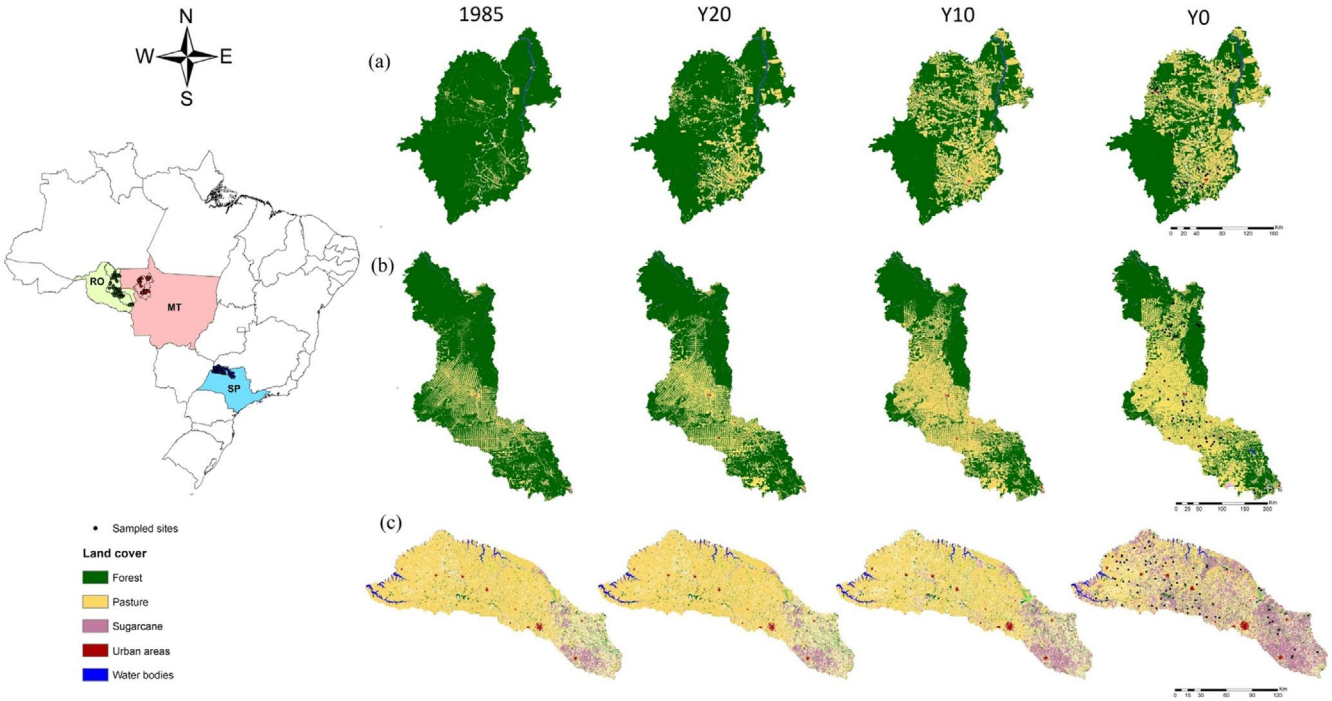

FIGURE 1 | Land cover in 1985, Y20 (20 years before the sampling), Y10 (10 years before the sampling) and Y0 (sampling year) in the three study areas: (a) Aripuanã and Juruena River basins in the Northwest part of the state of Mato Grosso (MT); (b) The Machado River basin, East part of the state of Rondônia (RO) and (c) São José dos Dourados River and the Turvo-Grande River basins, in the Northwest of the state of São Paulo (SP). Black dots in the sampling year (YO) represent sampled stream reaches. In RO, some stream reaches were inside of protected areas (i.e., large green areas in the superior part of the basin).

LULC changes have been affecting not only terrestrial but also aquatic organisms, especially those inhabiting small streams (Leitão et al. 2018). Streams are intrinsically bonded with terrestrial landscapes because of their geographical position and their hierarchical dendritic organisation, which allows the input, runoff and transport of allochthonous material along the river network (Allan and Castillo 2007). In forested biomes, extensive and dense riparian buffers help maintain water quality (Paula et al. 2025), reduce siltation, increase channel stability and the availability of allochthonous structures (e.g., woods, roots, litter), which can act as micro and mesohabitats for shelter, nursery and fish foraging (Lo et al. 2020). Thus, the loss of these structures—a common pattern after converting naturally heterogeneous systems into agroecosystems (Leitão et al. 2018; Lo et al. 2020)—has the potential to locally extirpate species, especially fish species that co-evolved with these allochthonous structures from the terrestrial environment. For example, conversion from forest to pasture can increase unconsolidated substrate and marginal grasses and, consequently reduce benthonic species associated with rocky substrate (e.g., Siluriformes: Loricariidae, Heptapteridae) and litter banks (e.g., *Gymnorhamphichthys*) (Zeni et al. 2019). However, instream habitat changes following LULC changes often occur with a delay (Paula et al. 2013), and fish assemblages tend to respond slowly to these changes (Brejão et al. 2018; Camana et al. 2022). For example, species-specific responses are shaped by the magnitude and frequency of LULC change, as well as the duration that a specific threshold has been exceeded over time (Camana et al. 2022). Thus, landscape legacy, as defined as the long-lasting influence of landscape past events on biodiversity, can play a crucial role in current biodiversity patterns and must be considered in ecological studies (Bürgi et al. 2017).

We investigated how past LULC changes since 1985 (the earliest year with available data) and current instream features relate to stream fish assemblages in Brazilian river basins that have undergone different historical trajectories of LULC change. We tested the hypothesis that fish biodiversity in the regions with the first and more recent major LULC changes is strongly affected by landscape legacies. We expected that fish assemblages in RO and MT would show signs of the first major LULC change and thus would be characterised by the loss of specialist species (e.g., usually rare species) and unique traits related to complex microhabitats. Thus, taxonomic and functional richness should be strongly related to environmental predictors both at the local and the landscape scale in MT and RO. On the other hand, because fish assemblages in SP have already gone through the first LULC major change more than a century ago and are composed mainly of generalist and resistant species (Zeni et al. 2017), we expected that current biodiversity patterns should be weakly related to environmental predictors.

2 | Methods

2.1 | Study Regions

We used a dataset that comprises three different regions in Brazil with different processes of past LULC change. The Aripuanã and Juruena River basins, in the Northwest of the state of Mato Grosso (MT; Figure 1a), were originally covered by the Amazon Tropical Rainforest. Deforestation in the region started around late 1970s due to road expansion, but more intense deforestation events occurred in the mid-2000s driven by the increase of livestock grazing to sustain beef exportation (DeFries et al. 2013). Despite the main land use conversion being native forest to pasture, the region has two patterns of deforestation: a disorderly one, especially in the northern portion of the basins, and the 'large property' one in the southern portion, characterised by abrupt, large deforestation events (Geist and Lambin 2001). Currently, the Aripuanã River basin has 36.4% of native forest, while Juruena has 54.9%, mainly in protected areas.

The Machado River basin, in the east of the state of Rondônia (RO; Figure 1b) is also in the Amazon region. LULC changes have started around 1970 also due to a main road expansion (BR-364) (Alves et al. 1998) and through government-sponsored settlement programmes for small farmers (Fearnside and Salati 1985). The small farms along the roads gradually converted the native forest to pasture for livestock grazing leading to a deforestation pattern known as 'fish-bone' (Geist and Lambin 2001). Nowadays, around 50% of the basin's area has been converted to pasture with the remaining forest patches concentrated in protected areas (Brejão et al. 2018).

The São José dos Dourados and the Turvo-Grande River basins, in the Northwest of the state of São Paulo (SP; Figure 1c), have been modified for agricultural development for more than a century and have gone through several cycles of LULC changes including logging, coffee beans, citrus and pasture (Victor et al. 2005). More recently, pasture has been replaced by sugarcane for biofuel production (Lapola et al. 2014). According to Caldarelli and Gilio (2018), the area with sugarcane crops in São Paulo increased more than 125% from 2000 to 2015, especially in the Northwest. Because of these successive changes, less than 4% of the original land cover (Semi-Deciduous Forest, a type of Atlantic Forest) remains in small and isolated fragments under strong edge effects (Nalon et al. 2008). Streams in this region reflect long-term human-induced changes and are mostly physically and biologically homogeneous (Casatti et al. 2009, 2015; Molina et al. 2017) and the effects of the recent conversion from pasture to sugarcane on fish assemblages range from non-significant to barely detectable (Zeni et al. 2017, 2020; Roa-Fuentes et al. 2019, 2022). All three regions have tropical climate and two well-defined seasons: a dry one, from May to September and a wet one, from October to April.

2.2 | Fish Sampling

We sampled 84, 75 and 60 stream reaches in SP (2013), RO (2011–2012) and MT (2017–2018), respectively, during the dry seasons. Sampling permits were provided by the Chico Mendes Biodiversity Conservation Institute (ICMBio) (SISBIO numbers 3604-1/2011, 4355-1/2012, 5580-1/2013, 8894-1/2017, 9630/2018). In the three regions, fish sampling was conducted using upstream and downstream block nets, with three collectors sampling for 1 h. In SP, stream reaches were 75 m long, while in RO and MT they were 80 m long. We chose the most appropriate method to sample fish according to stream features (i.e., conductivity and instream habitat). In SP, we used two techniques

of electrofishing: alternate current generator (220 V, 50–60 Hz, 3.4–4.1 A, 1000 W) and a Smith-Root backpack (model LR-24, 500 V DC) with dip net (0.5 × 0.8 m, 2 mm mesh). In RO and MT, we used a hand sieve (1.5 × 2 m, 2 mm mesh) and a dip net (0.5 × 0.8 m, 2 mm mesh). Contrary to SP, in Amazonian streams (RO and MT), water conductivity is naturally low and channels have a myriad of different forest structures (e.g., tree roots, tree branches) that taken together can significantly jeopardise the effectiveness of the electrofishing. In this scenario, sampling with a hand sieve and net were our best choices. Thus, we are confident that using the same methods (e.g., electrofishing) in all regions would be inappropriate to characterise species composition. Sampled specimens were anaesthetised using a 100 mg L^{-1} clove oil solution (Brazilian Normative Resolution no. 37, February 15th 2008—CONCEA) fixed in a 10% formaldehyde solution, and after 72 h, they were transferred to a 70% ethanol solution. We identified 60 species in SP (11,724 individuals), 135 species in RO (22,860 individuals) and 129 species in MT (18,557 individuals) (Table S1).

We used the iNEXT package to estimate species richness based on size (i.e., computes diversity estimates for rarefied and extrapolated samples up to an appropriate size) and coverage (i.e., computes diversity estimates for rarefied and extrapolated samples based on a standardised level of sample completeness) (Hsieh et al. 2016). For SP, size-based and coverage-based estimates were 65.8 and 70.3 species, respectively. For RO, 142.3 and 147.0 species were estimated and for MT 137.4 and 154.7 species. Thus, our sampling coverage in all regions varied from 85% to 95%. Fish specimens were deposited in the fish collection of the Department of Biological Sciences, São Paulo State University (DZSJRP), São José do Rio Preto, São Paulo, Brazil.

2.3 | Instream Variables

In all three regions, instream conditions were measured in situ using a standardised protocol (Zeni et al. 2017). We estimated substrate composition along the stream reach by visually quantifying the proportion of unconsolidated (silt, clay and sand) and consolidated (gravel, cobble, rock and slab) elements. We also visually quantified the proportion of the stream bottom occupied by litter and wood debris from the adjacent terrestrial environment. For hydrological variables, we quantified the mean of water velocity, depth and width through several measures along at least three transects in the stream reach. To assess streambank and riparian area variables, we visually quantified the proportion of both banks occupied by grass (i.e., from nearby cultivated pastures), fine and large roots, exposed bank (i.e., without any vegetation) and trees and shrubs.

2.4 | Past Land Use Variables

For all regions, we obtained the land cover classification since 1985 (oldest year available) up to the sampling year (SP: 2013; RO: 2012 and MT: 2017) from the MapBiomas project (MapBiomas 2021), collection 5.0. The land cover classification provided by MapBiomas is based on Landsat satellite images with 30-m resolution. Temporal land cover series included 28 years (1985–2013), 27 years (1985–2012) and 32 years (1985–2017) for SP, RO and MT, respectively. We obtained land cover information at catchment and riparian buffer area scales. To do this, we used the georeferenced coordinates of each sampled stream to delimit the catchment boundaries with a digital elevation model (DEM 90 × 90 m^2 resolution; ASTER GDEM 2011) and the SWAT hydrological model (Soil and Water Assessment Tool: Neitsch et al. 2011) for ArcGIS 10.5. To generate the riparian scale, we delimited a 100-m buffer at each streamside along the entire network drainage. For each stream, we obtained the proportion (from 0 to 1) of the catchment and riparian area occupied by native forest (primary and secondary native forest), pasture and sugarcane (only present in streams in SP).

We estimated predictor variables to represent temporal trends in LULC change at three temporal intervals: (i) (All), (ii) T20 and (iii) T10, where variables were estimated considering the entire period since 1985, 20 and 10 years before sampling, respectively. We also estimated some variables independent of these previously determined intervals (e.g., thresholds, extreme events) and included land use cover for 1985 (YI), 20 (Y20) and 10 (Y10) before sampling. Variables were distributed into the following categories:

2.4.1 | Land Cover

Composed of the proportion of each land cover (forest, pasture and sugarcane) at YI, Y20 and Y10. Varies from 0 (i.e., where none of the catchment and riparian area are composed of the specific land cover) to 1 (i.e., all the surface area in catchment and riparian area are composed of the specific land cover).

2.4.2 | LULC Changes (%)

Composed of the percentage of each land cover changes during the intervals. This category was obtained by the formula: $\left[\frac{\text{Land cover in the sampling year} \times 100}{\text{Land cover in YI;Y20;Y10}}\right] - 100$. Negative and positive values indicate loss and gain of the specific land cover, respectively.

2.4.3 | LULC Magnitude

Composed of the magnitude of each land cover change in the intervals. This category was obtained by subtracting the proportion of the specific land cover in YI, Y20 and Y10 from the same land cover in the sampling year. Values vary from −1, where the catchment or riparian area in the past was composed only of the specific land cover (e.g., forest = 1.0) and during the analysed interval it was completely lost (e.g., forest = 0.0) to +1, where land cover was not observed in the catchment and riparian area in the past (e.g., forest = 0.0) and nowadays dominates the entire area (e.g., forest = 1.0).

2.4.4 | Metrics

Composed of the mean, the standard deviation and the coefficient of variation of each land cover in the intervals.

2.4.5 | Events

Frequency of events with more than 0.05 of forest loss and gain in the intervals. These variables measure the number of events between 2 years where the magnitude of forest loss and gain was higher than 0.05 in the catchment and riparian area.

2.4.6 | Extreme Events

Composed of the time (years since) and the magnitude (proportion) of the biggest event of forest loss and sugarcane gain in the entire temporal series.

2.4.7 | Thresholds (Years)

Composed of the time since the thresholds of 10%, 20% and 40% of forest loss were reached and the time since the thresholds of 10%, 20%, 40% and 60% of sugarcane gain were reached.

2.4.8 | Regeneration

Composed by variables that quantify the magnitude (proportion) and time (years) since of the lowest forest proportion was registered in the time series. We also quantified the total regeneration (i.e., forest gain since the lowest forest proportion in the catchment and riparian area; [Forest proportion in the sampling year − the lowest forest proportion]) and mean of regeneration (i.e., [Total Regeneration/Time since the lowest forest proportion]).

2.4.9 | Land Use Intensity (LUI)

An index that quantifies the trajectory of the LULC changes in a given area (see MTD in Ferraz et al. 2009). According to Ferraz et al. (2009), LUI quantifies the extent, duration and persistence of LULC changes within a given area. It ranges from 0 to 1, where 0 indicates no LULC changes, values close to 0 indicate smaller and more recent changes, while values approaching 1 indicate larger and older changes. Intermediate values reflect a spectrum of LULC change histories, such as small but older and persistent changes or larger changes that occurred more recently.

2.4.10 | Distance

Composed by the environmental distance of each stream in the intervals. We used the proportion of catchment and riparian land covers in the past (YI, Y20 and Y10) and sampling year in a principal component analysis (PCA). With the scores from the same stream in the past and sampling year, we calculated the Euclidean distance based on the Pythagorean theorem.

Apart from 'Distance', all past land use variables were obtained for catchment and riparian area scales (Table S2).

2.5 | Assemblage Diversity and Structure

To describe fish assemblage diversity and structure, we estimated taxonomic and functional richness and rarity separately for SP, RO and MT. Since taxonomic richness is highly sensitive to sampling effort, we used the approach proposed by Chao et al. (2014). In this approach, we can identify the effective number of species (i.e., Hill numbers) based on a specified level of sample coverage (i.e., completeness). Firstly, we assessed the mean of sample coverage across streams in each region using abundance data. For SP the mean was 0.94 (±0.11), RO was 0.96 (±0.04) and MT was 0.97 (±0.02). After that, we chose a common sample coverage (0.94) to generate rarefaction curves for all three regions using $q = 0$. Briefly, streams below 0.94 of sample coverage had the species richness extrapolated (i.e., increased), while streams above this value had their species richness interpolated (i.e., decreased). Despite not directly comparing species richness among regions (or any other response variable), by using this approach we were able to reduce the influence of the sampling effort on our results.

For rarity, we used the *rr* index, proposed by Maciel (2021), which combines three aspects of a species rarity: geographic range, habitat specificity and the size of the population. The index is generated per species and accounts for the inverse of the geographic range (i.e., the range of the two extreme latitude and longitude points of a species occurrence), the maximum number of habitats that the species occurs in, and the maximum population size anywhere. These three aspects were extracted from our dataset (i.e., geographical coordinates and species abundance per stream). The *rr* index is the mean of the geographic range, habitat specificity and size of the population values. The index varies from 0 to 1, where species with restricted geographic range, habitat occupancy and small population size are close to 1 and represent rarer species, while species close to 0 are the common ones. Because of the biogeographical differences in faunal composition, we calculated the *rr* index within each of the three regions. To obtain a rarity index for each stream, we summed the *rr* value for each species in each assemblage and standardised by the local richness. Thus, streams with values close to 1 were those with rarer species compared to streams with values close to 0.

We used ecomorphological traits related to body size, habitat preference and swimming ability to generate functional diversity indexes. To do this, we randomly chose 1–15 adult individuals from each species with well-preserved body structures (e.g., complete fins without alterations in their form) and obtained linear measures and areas of body, fins (dorsal, pectoral, caudal), head, eyes and mouth. We then calculated 15 ecomorphological attributes (Oliveira et al. 2010; Zeni et al. 2017). After that, we used the total functional diversity (FD-Q) proposed by Chao et al. (2014). The authors generalised Hill numbers to a distance-based functional Hill number, which quantifies the effective number of equally abundant and functionally equally distinct species. We used $q = 0$ to generate FD-Q, which is the product of the functional Hill number and the mean functional diversity per species (i.e., the effective sum of functional distances between a fixed species and all other species) and represents the effective total

distance between species of the assemblage. Larger values of FD-Q indicate assemblages with more functionally distinct species, while lower values can indicate more functionally similar assemblages.

To represent functional rarity, we used functional uniqueness, which describes the functional distance of a given species to the nearest neighbour (or neighbours) within the regional species pool (Violle et al. 2017). We chose functional uniqueness because it measures how rare one species is based on its set of traits compared to all species sampled in a region. According to Violle et al. (2017) rarer species are those with no functional equivalent in the regional pool. This metric results in an index for each species that ranges from 0 to 1, where values close to 1 indicate rare species with a more unique set of traits (i.e., no functional redundancy) compared to the other species of the pool. To obtain a value of functional uniqueness per stream, we summed the values for each species in a specific assemblage and standardised by local richness. To do this, we used species composition and the distance matrix based on the standardised Euclidean distance (e.g., all distances divided by the maximum distance observed to create a range from 0 to 1) for functional attributes. High values of uniqueness (close to 1) indicate assemblages composed of species with a rarer set of traits.

To obtain taxonomic richness and rarity, we used the 'iNEXT' (Hsieh et al. 2016) and the 'rrindex' (Maciel 2021) packages, respectively. For FD-Q and uniqueness, we used the 'hillR' (Chiu and Chao 2014) and the 'funrar' (Grenié et al. 2017) packages. All analyses were done in R, version 4.0.3.

2.6 | Data Analysis

We ran several rounds of variable selection to reduce the dimensionality of our past land use matrix. First, we standardised all variables (decostand function on 'vegan' package), conducted principal component analysis (PCAs) separately for each group of variables (as described in Table S2) and excluded variables with similar patterns along the first two axes. For the PCA, we kept the variables with higher eigenvectors. After that, we examined pairwise correlations among the remaining variables within each group and excluded variables with correlation superior to |0.70|. For this step, we removed those variables with a higher number of correlations with other variables. Finally, we used a correlation test (based on Pearson's r) between all the remaining past land use variables and removed those whose r values were associated with p-values < 0.05. A similar process was made to reduce the number of local instream variables. Firstly, we ran a PCA with all variables and removed the variables that graphically presented the same pattern along the first two axes. After that, we ran correlation test (based on Pearson's r) and removed those whose r values were associated with p-values < 0.05.

After that, we used Generalised Additive Models (GAMs) to model each response variable (species richness, FD-Q, rarity and functional uniqueness) as a function of past LULC change and instream predictor variables (Table 1) separately. Since we identified an interaction between region and the predictors, we fitted models that contain different smoothers for each predictor variable in each region. Models like this are constructed using the 'by' argument and have been referred to as Varying-Coefficient Models (VCM; Hastie and Tibshirani 1993). The inclusion of a factor with the 'by' command ('mgcv' package) sets up a model matrix that can use a separate smoother for each level of the factor (region with 3 levels [MT, RO, SP], in this case) and allows the interactions between smoothers and factors (Wood 2017). According to Gelfand et al. (2003), VCM is adequate to construct models to explain a response variable that is spatially structured. Our approach is partially exploratory in the sense that we did not build a model entirely based on previous knowledge or evidence, especially because this is one of the first attempts to relate current biodiversity patterns with past land use variables. We did, however, include only variables that appear to make sense considering our experience working in these regions. Thus, we were able to assess the number of significant predictor variables for each region (which we used to infer how responsive to environmental changes the assemblages were) and the effect of each predictor variable on assemblage response within each region. Since all our response variables were continuous, we used Gaussian GAMs. Because our models are complex, with a relatively large number of explanatory variables, we tested for potential overfitting by checking model singularity with the function check_singularity in the R package performance. None of our models were singular and thus we are confident that overfitting was not an issue in our analysis. We also assessed independence and correlation on the model's residuals by using the 'performance' package (Nakagawa et al. 2017).

3 | Results

The general pattern of past LULC changes was different among regions. For Amazonian streams (MT and RO), we observed a decrease of native forest followed by an increase of pasture. There was also a tendency for forest regeneration in MT in the last 10 years before sampling. In SP, while native forest was consistently low over time, sugarcane increased over pasture, especially in the last 10 years before sampling.

Residuals in all models were independent and not autocorrelated (p-value > 0.05). Based on the analysis of R^2 values, overall, we found that diversity metrics were slightly better explained by instream variables than variables describing past LULC change (Table 2). Species richness and functional diversity were better explained by predictor variables than rarity and functional uniqueness (Table 2). RO was the region with the highest number of different predictor variables regarded as important to biodiversity response (21 in total, considering all models), largely due to the high number of instream variables associated with species richness, FD-Q and rarity (13) (Table 3; Table S3). In MT, the number of different predictor variables selected as important was similar to RO (19; Table 3), however past LULC change was related only to species richness and FD-Q (12; Table 3; Table S4). Four out of the five past land use variables related to FD-Q were important in both MT and RO. SP had fewer explanatory variables regarded as important for explaining variation in biodiversity metrics and most of them were variables describing instream habitat conditions (Table 3; Table S3). Past LULC changes only explained variation in rarity and functional uniqueness in SP streams (Table 3; Table S4).

TABLE 1 | Code and description of the past land use changes and instream habitat variables used as predictors for the diversity patterns.

	Code	Description
Past land use variables	ForC_Y20	Proportion of forest in the catchment 20 years before the sampling
	ForB_Y10	Proportion of forest in the buffer 10 years before the sampling
	ForCChange_T20	Percentage of forest change in the catchment in the last 20 years
	MagForBChange_All	Magnitude of forest change in the riparian buffer since 1985
	RegeForB	Regeneration of the forest in the riparian buffer
	TimeBigForCLoss	Time since the biggest event of forest loss in the catchment
	MagBigForCLoss	Magnitude of the biggest event of forest loss in the catchment
	DurLost40	Time since the threshold of 40% of forest loss in the catchment was reached
	MeanPasC_T20	Mean of pasture in the catchment 20 years before the sampling
	MagPasBChange_T10	Magnitude of pasture change in the riparian buffer in the last 10 years
	AveSugC_T10	Mean of sugarcane in the catchment in the last 10 years
	MagBigSugWGain	Magnitude of the biggest event of sugarcane gain in the catchment
	LUI_C	Land Use Intensity for the catchment
	Dis_all	Environmental distance since 1985
Instream habitat variables	Unconsolidated	Percentage of the unconsolidated substrate (silt and sand) in the stream reach
	Consolidated	Percentage of the consolidated substrate (peddle, rock) in the stream reach
	Litter	Percentage of the litter (leaves, small branches) in the stream reach
	Woods	Percentage of the wood debris (trunks and branches) in the stream reach
	Fine_roots	Percentage of the streambank occupied by fine roots
	Large_roots	Percentage of the streambank occupied by large roots
	Grasses	Percentage of the streambank occupied by grasses
	Exposed_soil	Percentage of the streambank occupied by exposed soil
	Water_velocity	Water velocity mean (cm/s)
	Width	Width mean (cm)
	Depth	Depth mean (cm)
	Shrubs	Percentage of the 10-m stripe riparian area occupied by shrubs
	Trees	Percentage of the 10-m stripe riparian area occupied by trees

TABLE 2 | *R* squared adjusted (*R*-sq. adj) and deviance explained (DE) for past land use and instream habitat models for richness, rarity, total functional diversity (FD-Q) and uniqueness.

	Past land use		Instream habitat	
	***R*-sq.(adj)**	**DE**	***R*-sq.(adj)**	**DE**
Richness	0.474	61.6%	0.534	64.2%
Rarity	0.198	36.4%	0.427	56.4%
FD-Q	0.582	70.3%	0.646	74.5%
Uniqueness	0.290	44.9%	0.316	46.6%

Environment–assemblage relationships were highly variable, especially for instream habitat and biodiversity patterns (Table 3). However, we identified some similar responses to past land use in Amazonian streams. Species richness was higher in streams with higher mean pasture proportion in the last 20 years (MeanPasC_T20) and lower in sites where the biggest event of forest loss was more recent (TimeBigForCLoss), despite the pattern of decreased species richness in RO when the event is older than 20 years, not observed in MT (Figure 2). For functional diversity, streams with higher mean pasture proportion in the last 20 years (MeanPasC_T20) and lower Land Use Intensity (LUI) showed higher FD-Q (Figure 3). Despite these similarities, some local variables had opposite

TABLE 3 | Past land use and instream habitat variables and their estimated relationships with species richness, functional diversity, rarity and functional uniqueness from MT, RO and SP streams. The direction of the arrow indicates the direction of the relationship. The first arrow represents the direction of the explanatory variable and the second one, the estimated effect on the response variable. For example, the first variable '↑ AvePasC_T20 ↑' indicates that an increase in the mean of pasture in the catchment 20 years before sampling led to an increase in species richness in MT. Variables included in this table had p-values > 0.05.

	MT		RO		SP	
	Past land use	**Instream habitat**	**Past land use**	**Instream habitat**	**Past land use**	**Instream habitat**
Richness	↑ MeanPasC_T20 ↑ ↑ MagBigForCLoss ↓ ↑ Rege_ForB ↑ ↓ ForCChange_T20 ↑ ↑ MagPasBChange_T10 ↓ ↑ ForC_T20 ↑ ↓ Dur40Loss ↓ ↓ TimeBigForCLoss ↓ ↑ Dis_all ↓	↑ Large_roots ↓ ↑ Exposed_soil ↓	↑ MeanPasC_T20 ↑ ↑ LUI ↓ ↑ TimeBigForCLoss ↑ ↑ MagBigForCLoss ↓	↑ Woods ↑ ↑ Fine_roots ↑ ↑ Grasses ↑ ↑ Large_roots ↑ ↑ Exposed_soil ↑ ↑ Consolidated_subs ↓ ↑ Shrubs ↑ ↑ Trees ↑	No variables were filtered	↑ Grasses ↓ ↑ Trees ↑ ↑ Depth ↑ ↑ Exposed_soil ↓
FD-Q	↑ ForB_T10 ↑ ↓ TimeBigForCLoss ↓ ↑ MeanPasC_T20 ↑ ↑ MagForBChange_all ↑ ↑ LUI ↓	↑ Litter ↓ ↑ Fine_roots ↓ ↑ Trees ↓	↑ MagBigForCLoss ↓ ↑ LUI ↓ ↑ MagForBChange_all ↑ ↑ MeanPasC_T20 ↑ ↑ ForB_T10 ↑	↑ Width ↑ ↑ Shrubs ↑ ↑ Litter ↑ ↑ Unconsolidated_subs ↑ ↑ Fine_roots ↑ ↑ Trees ↑ ↑ Large_roots ↑	No variables were filtered	↑ Trees ↑
Rarity	No variables were filtered	↑ Woods ↓	↑ Dis_all ↓	↑ Trees ↑ ↑ Depth ↑ ↑ Fine_roots ↑ ↑ Exposed_soil ↑ ↑ Large_roots ↑ ↑ Grasses ↑ ↑ Water_velocity ↑	↑ ForB_T10 ↑	↑ Unconsolidated_subs ↓ ↑ Woods ↑ ↑ Depth ↑
Uniqueness	No variables were filtered	↑ Large_roots ↑ ↑ Exposed_soil ↑ ↑ Shrubs ↑ ↑ Grasses ↑ ↑ Fine_roots ↑	↓MagPasBChange_T10 ↑ ↑ ForB_T10 ↑ ↑ ForCChange_T20 ↑	No variables were filtered	↑ ForCChange_T20 ↓ ↓MagPasBChange_T10 ↑ TimeBigForCLoss[a]	↑ Shrubs ↓ ↑ Width ↓ ↑ Depth ↓ ↑ Consolidated_subs ↑

[a]High values for both recent and old events.

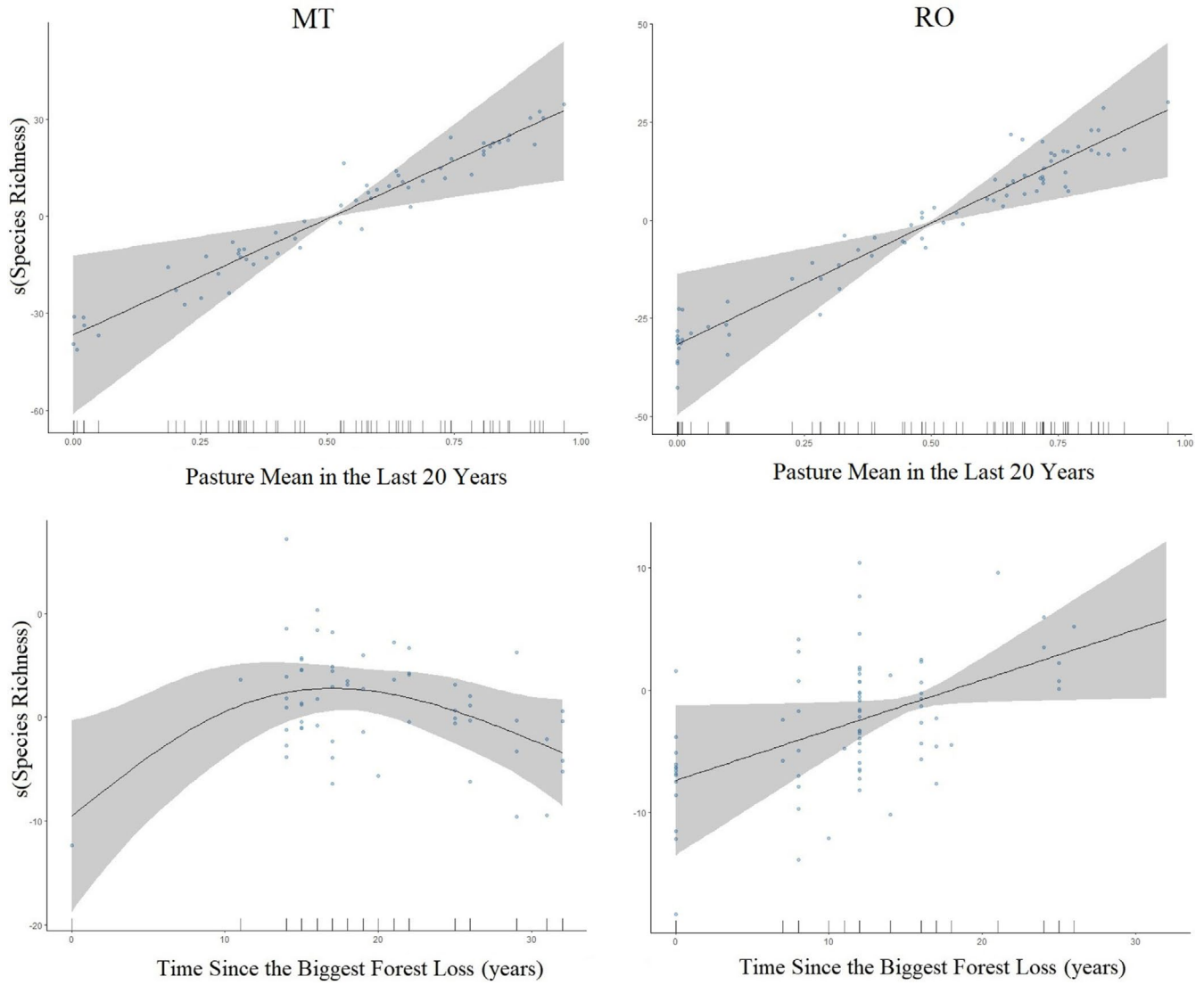

FIGURE 2 | The estimated effect of pasture mean in the last 20 years (proportion) and time since the biggest forest loss in the catchment (years) on species richness (s(Species Richness)) in MT and RO fish assemblages.

relationships with biodiversity metrics in these regions. For example, instream variables usually related to forested stream margins (e.g., litter, fine and large roots) were positively related to richness and FD-Q in RO but negatively related to them in MT (Figure 4a,b).

Streams in SP were unique compared to the other regions. Past LULC changes explained only variation in taxonomic and functional rarity. Streams with higher native riparian forest proportion 10 years before sampling (ForB_Y10) had more rare species (Figure 5). Although weak, functional uniqueness was negatively associated with the increase of the native forest change in the catchment throughout the previous 20 years (ForCChange_T20) and the magnitude of the pasture loss in the last 10 years in the riparian area (MagPasBChange_T10) (Table 3; Table S4). Despite some instream variables having been selected for SP streams (Table 3), most of them had a very weak relationship with biodiversity metrics (Table S3), except for woods and unconsolidated substrate that were positively and negatively associated with taxonomic rarity, respectively (Figure 5).

4 | Discussion

Our findings provide partial support for the hypothesis that historical land use serves as a legacy filter shaping fish assemblages, especially in areas where deforestation occurred more recently or was followed by persistent agricultural expansion. The region where major events of forest conversion to agriculture were more recent, occurring mainly after 2000 (Mato Grosso; MT), had the highest number of predictor variables describing past LULC changes regarded as important for explaining assemblage diversity metrics. The second region in this regard was Rondônia (RO), where major events of forest conversion to pasture have been occurring since the 1970s. In São Paulo (SP), where the first and major event of forest conversion to agriculture happened more than 150 years ago, only a few variables describing past LULC change explained variation in rarity and functional uniqueness, and none explained variation in species richness and functional diversity. Taken together, these results suggest that the importance of past processes driving fish assemblage diversity and structure may be a negative function of the time since the first LULC change.

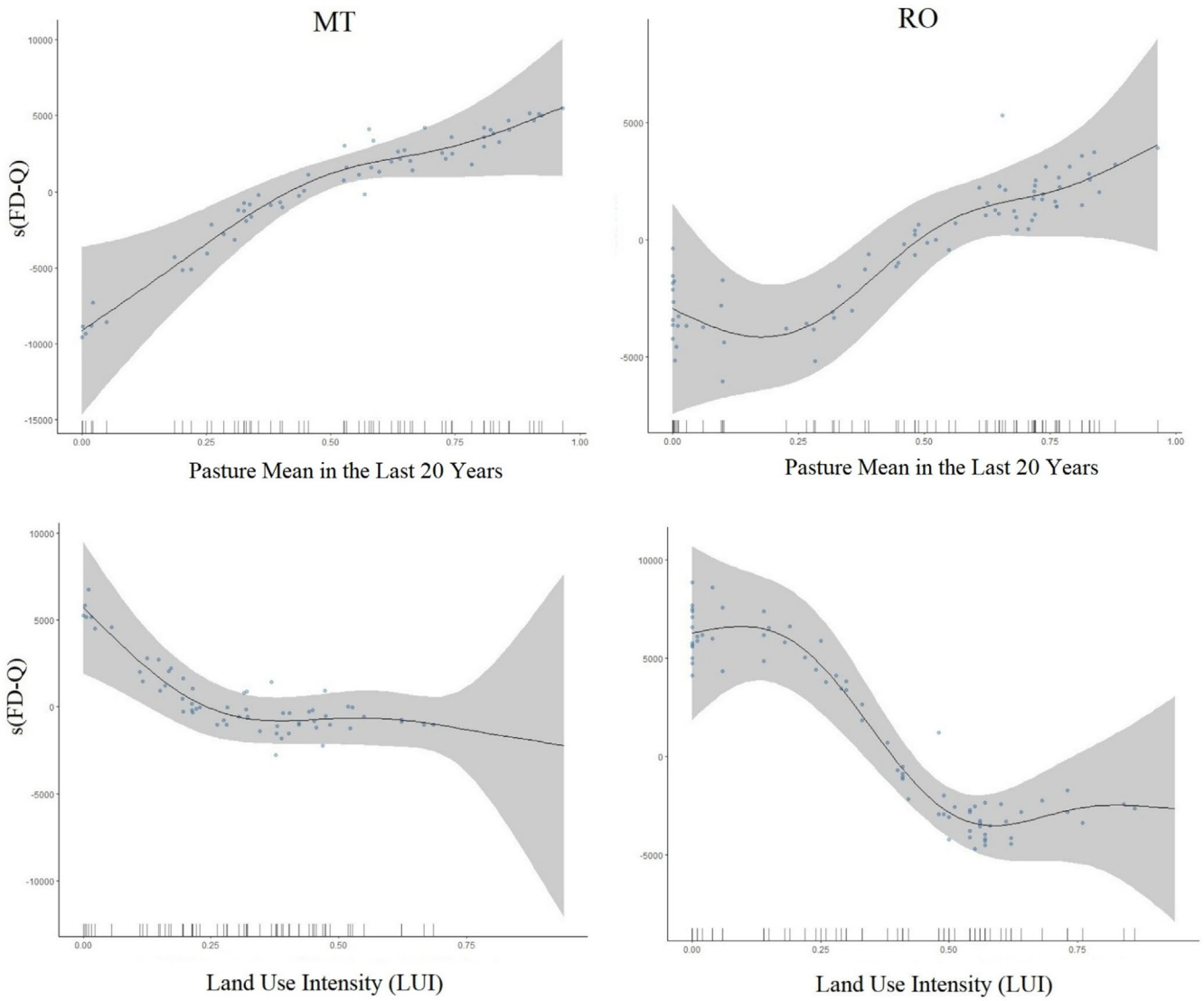

FIGURE 3 | The estimated effect of pasture mean in the last 20 years (proportion) and Land Use Intensity (LUI) in the catchment on functional diversity (s(FD-Q)) in MT and RO fish assemblages.

4.1 | The Strength and Timing of Land Use Legacies

Assemblages in regions dominated by old long-lasting agricultural lands are likely to go through successive and different assembly cycles since the first major deforestation event, which should sequentially favour widespread generalist species if environmental changes are severe (Baselga et al. 2015; Zeni et al. 2017; Newbold et al. 2018). Species in these regions are expected to exhibit low sensitivity to additional environmental changes (Betts et al. 2019). Thus, catchments with a history of intense LULC change can have higher present-day thresholds for changes in species composition and richness (Chen and Olden 2020). That means that even more intense subsequential LULC changes would be necessary to cause further compositional changes in these regions. In SP, the most recent major landscape conversion (from pasture to sugarcane cultivation) occurred 10 years prior to fish sampling. At that time, the conversion intensity was still relatively low, with a mean increase in sugarcane cover of 11% of the per-catchment area. Thus, either local instream characteristics and fish assemblages had not yet responded to LULC changes due to time lags in habitat and population dynamics (e.g., habitat availability, birth and mortality rates), or the magnitude of those changes was too small to drive further changes in biodiversity. Interestingly, the strongest relationships in SP involved taxonomic rarity. Areas with more rare species had greater riparian forest cover 10 years before sampling and more instream woody structures. Riparian forests are responsible for providing allochthonous structures that increase habitat heterogeneity to streams (Saraiva et al. 2023) and usually can be used for many fish species (Nagayama et al. 2012). Species associated with instream wood may be rare in SP assemblages precisely because these allochthonous structures are uncommon in the region (Casatti et al. 2006). In this context, streams with some riparian forest and instream wood may serve as refuges for rare species, such as certain catfish (e.g., Pseudopimelodidae and Pimelodidae).

It is noteworthy to mention that assemblages in old and highly modified agroecosystems, such as those in SP, can be related to even older landscape changes that are difficult to capture. We included LULC changes from 30 years before the sampling. On the other hand, river basins in RO and MT are likely still going

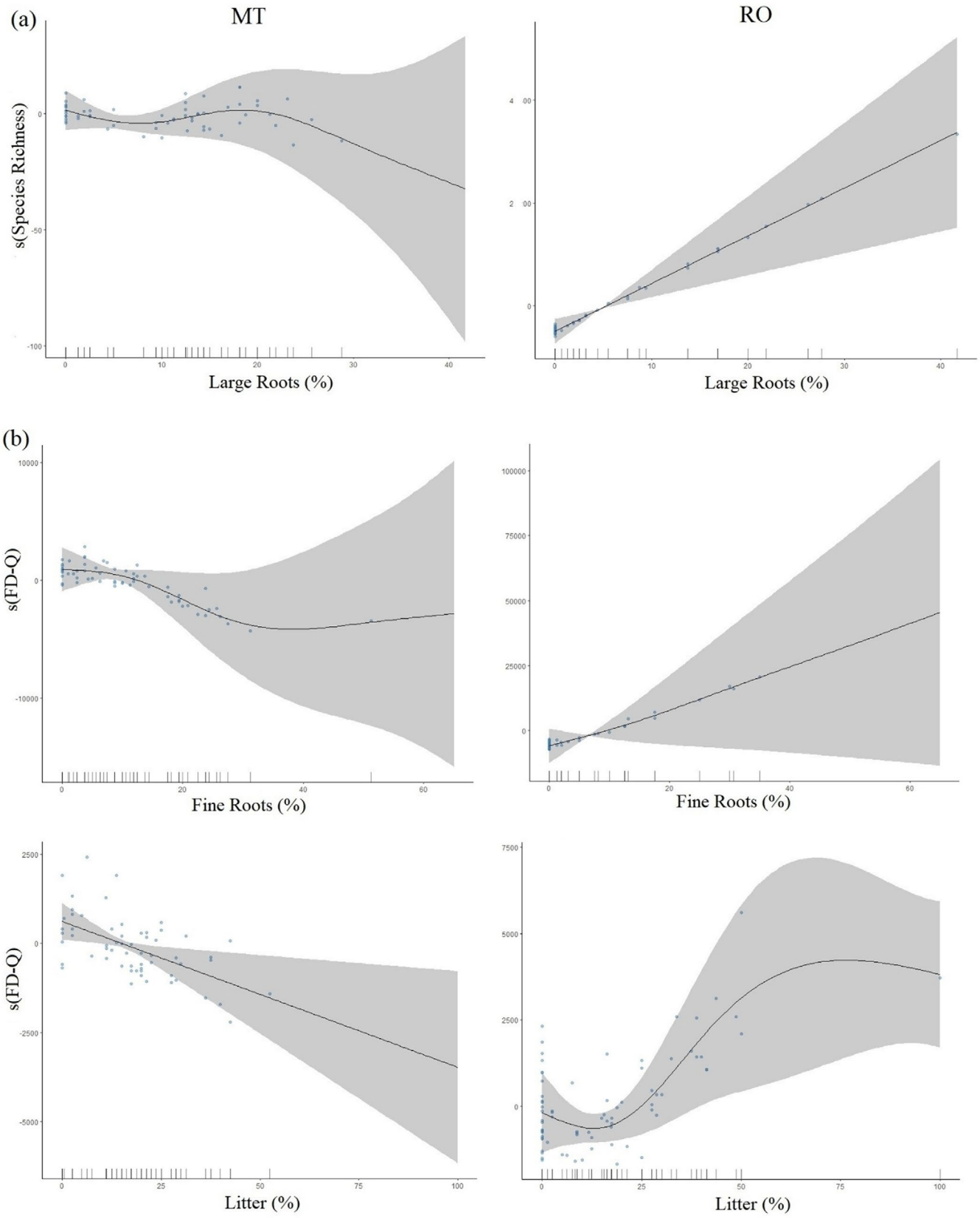

FIGURE 4 | The estimated effect of (a) large roots (%) on species richness (s(Species Richness)) and (b) fine roots (%) and litter (%) on functional diversity (s(FD-Q)) in MT and RO fish assemblages.

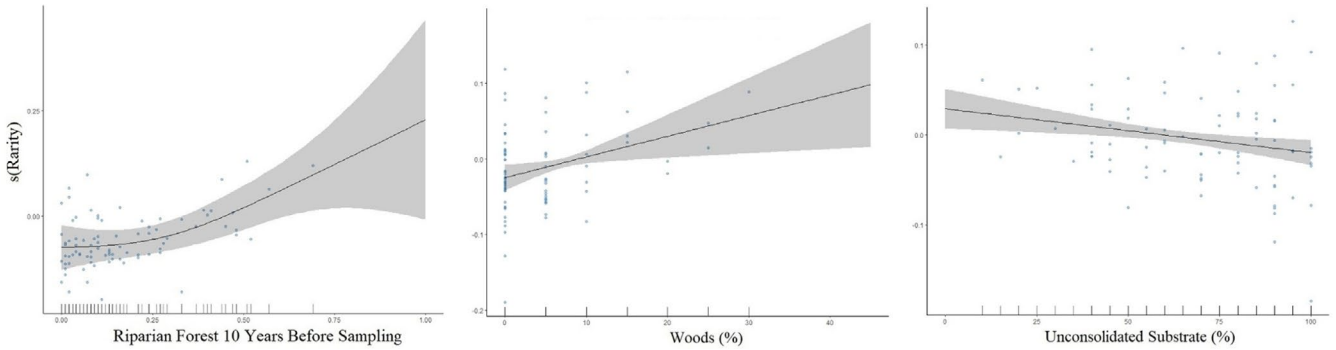

FIGURE 5 | The estimated effect of riparian forest 10 years before sampling (proportion), woods (%) and unconsolidated substrate (%) on rarity (s(Rarity)) in SP fish assemblages.

through the first major event of LULC change (from native forest to pasture) and assemblages with sensitive species (Betts et al. 2019) are going through the first human-induced environmental filter. In this context, a short-term threshold is expected to happen, which makes landscape legacy more detectable in these recently deforested regions.

4.2 | The Filtering of Assemblages and Ecological Thresholds

Species richness and functional diversity in MT and RO were similarly related to common past LULC change, whereas local instream variables had opposite effects. For example, the increase of pasture lands in these regions during the last 20 years has created new habitat in streams (e.g., marginal grasses) without completely wiping out the ones associated with forested streams (e.g., wood and roots in RO and riffles in MT). Thus, recent LULC changes have favoured some species that are able to colonise those modified streams, while part of the original fish composition has been kept (Brejão et al. 2021). According to Brejão et al. (2018), the abundance of sensitive fish in Amazon streams decreases at low levels of deforestation (< 20%) and soon after a major deforestation event (0–10 years). On the other hand, the abundance of more tolerant species starts increasing after around 70% of forest loss and more than 15 years after the major deforestation event (Brejão et al. 2018). Thus, major recent deforestation events probably are driving the local extinction of some sensitive species in RO and MT, while increasing species richness due to the colonisation and establishment of native tolerant species. Given the > 30-year LULC timeframe and recent deforestation in MT and RO, we are likely observing the early stages of assemblage shift. Continuous loss of allochthonous structures and increased siltation in pasture streams may lead to lower species richness and novel assemblages, with most benthic and structure-dependent species already excluded (Leitão et al. 2018).

While the presence of allochthonous structures (e.g., large roots, fine roots, litter) increased species richness in RO streams, they were associated with a lower richness in MT. Streams in MT drain the ancient crystalline basement of the Brazilian Shield (Amazonian highlands) and are characterised by large amounts of riffles. These characteristics have led to high levels of fish endemism compared to the rest of the Amazon (Dagosta and De Pinna 2019), mainly Loricariidae species (mostly *Hypostomus* spp. and *Ancistrus* spp.) associated with the stream bottom and consolidated substrate. On the other hand, streams in RO drain Amazonian lowlands (Dagosta and De Pinna 2019) and have a fish composition more typical of the Amazon, with a high abundance of Characiformes, Siluriformes (other families aside from Loricariidae), and Gymnotiformes, species related to more complex habitats, such as structures from adjacent forest (i.e., roots, woods) and litter in the substrate. Thus, we suggest that while LULC changes drive general patterns of stream fish assemblages in regions with more recent conversion (i.e., contemporary events), regional idiosyncrasies are also expected to happen because they depend on the regional species pool (i.e., historical events).

Contrary to our expectations, taxonomic and functional rarity (i.e., functional uniqueness) were not related to past LULC changes in the region with the most recent conversion (MT). This is interesting first because of the high number of rare species usually found in any community and, second, because previous evidence indicates that LULC changes negatively affect rare species occurrence (Newbold et al. 2018). Weak or absent relationships between rare species and environmental predictors often stem from low sample sizes, which reduce model accuracy and inflate uncertainty (Barbet-Massin et al. 2012). High zero-inflation and imperfect detectability can further mask true environmental associations, since many rare species go undetected or are undercounted in standard surveys (Martin et al. 2005). Finally, spatial biases in presence-only data, where sampling is clustered in accessible areas, can obscure genuine signals by over-representing particular habitats (Phillips et al. 2009). Notwithstanding the numeric importance of rare species in communities, some studies have demonstrated that common species are responsible for most of the spatial variation in species richness (Lennon et al. 2004, 2011; Bregović et al. 2019) and for the relationship among assemblages and environmental and spatial features (Brasil et al. 2020; but see Siqueira et al. 2012). Therefore, the species that are responding to historical changes in the landscape in MT are probably the common species with wide geographical and habitat ranges. Despite evidence that both common and rare species often respond primarily to environmental variation (Siqueira et al. 2012; Alahuhta et al. 2014; Pérez-Mayorga et al. 2017), spatial processes can play a key role in shaping rare fish dynamics in Amazonian streams (Benone et al. 2022). In recently deforested streams, rare species may be

more limited by their dispersal ability, whether to colonise or move among streams, than by local environmental conditions. The low variation in rarity explained by our models may reflect the absence of key predictors related to past LULC changes in the spatial configuration of the river basins, such as temporal changes in small reservoirs for cattle watering, which are common in pasture areas. Future studies should examine how such spatial changes influence community dynamics.

4.3 | Implications and Future Directions

Although the strength of landscape legacies typically diminishes over time, we suggest that initial conversion from forest to agriculture plays a crucial role in shaping these legacy effects. Testing this hypothesis would benefit from historical community data collected before major LULC changes happened. However, such data are rarely available in developing countries like Brazil, and in many cases, human impacts had already eroded biodiversity before records were even made. In this context, our study brings important information about how past LULC changes can affect current biodiversity patterns and indicates that fundamental differences in the species pool and unique landscape change histories can lead to different assemblage–environment relationships. Thus, understanding how stream biodiversity responds to both historical and recent changes at local and regional scales would benefit from long-term ecological research (LTER) that generates time series data on compositional changes linked to landscape changes. This is especially important in Neotropical regions, where the rates of LULC change are high (Song et al. 2018) and fish assemblages account for over three-quarters of the world's fish functional diversity (Toussaint et al. 2016). The joint knowledge from the monitoring of landscapes and assemblages can help create and apply more effective conservation and restoration measures before biotic homogenisation becomes irreversible.

In summary, our results reveal that historical land use legacies on fish biodiversity vary across tropical regions and are strongest where deforestation is relatively recent (< 30 years) and followed by ongoing land use intensification. These recently deforested areas offer a window of conservation opportunity, as species that are both taxonomically and functionally rare and are more prone to extinction (Chichorro et al. 2019) are still regionally present. In MT, streams with greater riparian forest cover a decade before sampling supported more diverse and functionally rare assemblages. Preserving and restoring riparian corridors may therefore be particularly effective in preventing species loss both locally and regionally. This also applies for long-altered regions like SP, where tropical streams with higher historical riparian cover still harbour many rare species. Together, our findings underscore the need to incorporate temporal land use history and regional context into conservation planning and biodiversity monitoring.

Author Contributions

Conceptualisation: J.O.Z. Developing methods: J.O.Z. and T.S. Data analysis: J.O.Z. and T.S. Preparation of figures and tables: J.O.Z. Conducting the research, data interpretation, writing: J.O.Z., T.S., G.L.B. and L.C.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The datasets and R code used in this study are available from the corresponding author on reasonable request. Moreover, we shared our response and explanatory variables on Zenodo (https://doi.org/10.5281/zenodo.7337844).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** fwb70139-sup-0001-AppendixS1.docx.