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Beyond the Local Catchment: Influence of Regional Context and Land Use Legacy on Current Stream Fish Diversity in Agricultural Systems

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ABSTRACT

Land use poses a major threat to global biodiversity, impacting ecosystems across various spatial and temporal scales. Recent studies suggest that past land use changes influence the observed contemporary diversity patterns in stream fish assemblages more strongly than current land use. However, these studies often focus on limited spatial scales, and it remains unclear whether the influence of historical land use holds true when analysing broader regional contexts. In this study, we address how historical

changes in local (upland catchment) and regional (broader watershed) land use interactively affect stream fish diversity using fish community data from 366 streams in Brazil, sampled from watersheds with varied agricultural land use histories. We found that local species richness (alpha diversity) was influenced by both current and historical land uses at regional extent, while beta diversity was more influenced by current regional land use than by historical land use. Additionally, we mapped the status of regional watersheds for fish diversity conservation, identifying areas with lower or more recent land use. The results indicate that local catchment land use and fish diversity relationships may not be evident in catchments immersed in heavily modified regional contexts or in regions that have faced long historical land use changes. Our findings highlight the importance of the regional context and past land use legacy for the management and conservation of aquatic ecosystems.

1 | Introduction

Land use change is currently one of the most prevalent threats to biodiversity globally, resulting in substantial losses in species and functional diversity across different ecosystems (Newbold et al. 2015, 2016; Maxwell et al. 2016; Miiller et al. 2021). These impacts are particularly relevant for freshwater ecosystems, where land use change interacts with other stressors such as channel modifications and altered erosion-sedimentation dynamics (Auerswald and Geist 2018; Bierschenk et al. 2019; Mueller et al. 2020), with significant consequences for aquatic biodiversity and ecosystem services (Auerswald et al. 2025). The effects of land use occur at multiple and interacting spatial and temporal scales (Townsend et al. 2003; Thuiller et al. 2004; Faleiro et al. 2013; Guttery et al. 2017; Pelicice et al. 2017; Moraga et al. 2019; Shew et al. 2019). While most research on stream community ecology focuses on the influence of current land use, some recent studies have investigated the influence of past land use on aquatic communities (Harding et al. 1998; Maloney et al. 2008; Brejão et al. 2018; Santos et al. 2020; Camana et al. 2022). These studies have found that past land use can be important for understanding current communities and how they changed over time, as ecological responses (e.g., local extinctions) may not occur immediately after land use change (Kuussaari et al. 2009; Jackson and Sax 2010; Magalhães et al. 2025). For instance, similar landscapes may differ in species diversity because their historical trajectory of land use change was different (Ernoult et al. 2006; Uezu and Metzger 2016). However, the consistency of these effects across wide spatial extents and in which spatial scales these historical processes influence local communities remains to be studied. Understanding these dynamics is not only relevant from a theoretical standpoint, but also crucial for informing conservation strategies that seek to preserve or restore aquatic biodiversity under ongoing and legacy land use pressures (Hermoso et al. 2009; Leal et al. 2020).

Multiscale approaches to study the influence of land use on stream communities often include local habitat, riparian and catchment scales (Carroll and Jackson 2008; Herringshaw et al. 2011; Barbosa et al. 2019; Roa-Fuentes et al. 2019), but not a wider regional scale. This gap is also highlighted in studies such as Bierschenk et al. (2019) and Mueller et al. (2020), which emphasise the importance of considering broader landscape configurations, but these approaches have not yet been applied to tropical streams with different climatic, geomorphological and biogeographic conditions, as addressed in our study. Because streams are connected dendritic systems, environmental change at different parts of the stream network, including neighbouring catchments within a larger drainage basin (regional scale), can also influence local communities (Poff 1997; Dunn and Angermeier 2019; Firmiano et al. 2021). For example, different species pools from connected watercourses may influence the response of local communities to local environmental gradients (Sousa et al. 2023). In fact, in regions with a long history of degradation at watershed scale, the environmental signal of local deforestation in stream fish assemblage is weaker than in watersheds with recent human disturbances (Teresa and Casatti 2017). This effect is probably due to species pool depletion in watersheds more heavily degraded (Zeni et al. 2019; Magalhães et al. 2025), affecting rates of dispersion, recolonisation and local extinction in communities (a view consistent with metacommunity theory; Leibold et al. 2004; Heino et al. 2015). Considering that dispersal processes operate at larger spatial scales than are often studied (e.g., local catchment vs. regional hydrographic system), it is essential to better understand how landscape changes (regional context) affect aquatic communities.

It is well known that catchment land use (i.e., a sub-basin within a larger hydrographic system) affects local stream communities (Allan 2004; Hughes et al. 2019; Knott et al. 2019; Alvarenga et al. 2021). These effects may stem from specific causes, such as the input of pesticides and pollutants into aquatic ecosystems (Whittier and Van Sickle 2010; Hassett et al. 2018), or processes leading to the alteration and homogenisation of in-stream habitat through various pathways (Sciera et al. 2008; Leitão et al. 2018) such as, for example, increased transport of fine sediments to aquatic environments (Naiman et al. 2010; Cunico and Gubiani 2017; Mueller et al. 2020). In addition, the impact of land use on fish communities in a particular catchment may depend on species dispersal from adjacent catchments under better land cover conditions (i.e., a regional scale effect), consequently allowing the recolonisation of degraded areas (Dunn and Angermeier 2019). This supports the idea that understanding how processes involved in community assembly are affected by land use at the regional scale is a crucial step for understanding fish community diversity patterns and supporting management at the basin-level scale (Fausch et al. 2002).

The effect of land use on the structure of local stream communities results from an interaction between changes in local catchments and regional watersheds (Edge et al. 2017; da Silva Almeida et al. 2022). We illustrate in Figure 1 how land use at multiple spatial scales may influence the diversity of stream fish communities. The figure shows six hypothetical sampling sites (white dots), each with its own upstream catchment (Figure 1A,B, black lines), all exhibiting similar levels of local land use. Catchment land use produces changes in-stream habitat structure, such as substrate homogenisation (Casatti et al. 2009; Cunico and Gubiani 2017) and water eutrophication (Dala-Corte et al. 2016; Ishiyama et al. 2021), which may result in local extinction of sensitive species, reducing

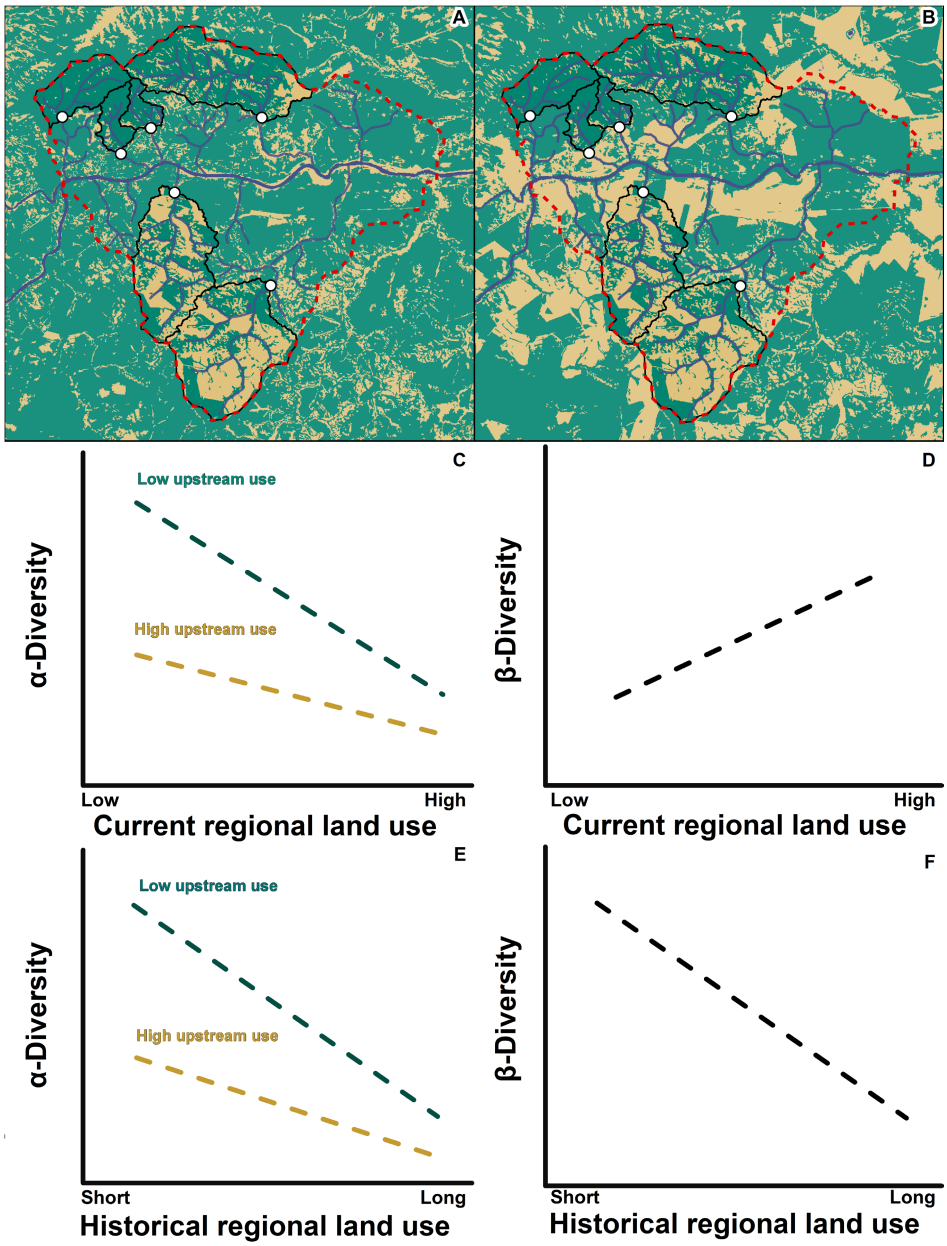

FIGURE 1 | Hypothetical illustration of six sampling sites (white dots) and their corresponding upstream catchments inserted in a regionally conserved (A) and a degraded (B) land cover context. All local upstream catchments (black lines) have similar levels of land use (yellow = anthropogenic land use; green = native vegetation), but differ in the broader regional context (red dashed lines = regional watersheds). Expected relationships of alpha and beta diversity with current regional land use: sites with low local land use show higher variability in α-diversity (C), while β-diversity (D) decreases with increasing regional land use, and with historical land use (E,F): sites with longer exposure to land use change ('Long') are expected to show stronger responses, while sites recently exposed ('Short') may retain higher diversity due to delayed biotic responses.

species richness (alpha diversity) (Astorga Roine et al. 2022). However, these catchments are embedded in broader regional watersheds (red dashed lines) that differ in their overall degree of anthropogenic land cover (Figure 1A,B, red lines). At the regional scale, native vegetation loss prevents dispersion and recolonisation of degraded streams by species sensitive to land use that have already suffered regional extinction or population size reduction, affecting alpha diversity locally (Figure 1C) and contributing to differentiation among communities, increasing regional beta diversity (Gering and Crist 2002; Krynak et al. 2019; Magalhães et al. 2021, 2025). Therefore, understanding the influence of land use changes at a spatial extent broader than just the upstream catchment is crucial. This broader perspective helps clarify how the landscape or regional context affects stream biological communities, which has been rarely explored by other studies (Infante et al. 2019).

Using a countrywide fish community data compilation for Brazil, we investigated the interacting effect of local (upstream catchment) and regional (watershed) scales of land use, combined with current and historical land use change, on fish diversity patterns. We hypothesised that the effects of land use at the upstream catchment on fish communities

are influenced by the surrounding regional context, both present and historical (Figure 1). We predicted that alpha diversity should decrease with regional land use, both in catchments with high and low anthropogenic cover, but that the decrease in alpha diversity should be larger when upstream catchment cover has also been depleted. This means that the lowest species richness (alpha diversity) should be expected in communities of streams with degraded upstream catchments that are also immersed in degraded regional contexts (Figure 1C). We additionally predicted that a degraded regional context should affect beta diversity. More specifically, recently converted watersheds may still harbour sensitive species that have not been locally extirpated, increasing beta diversity among streams, because variations in land use across the watershed may lead to an increase in the differentiation of local communities. Alternatively, a negative effect of anthropogenic land use on beta diversity would be expected if the persistent species in degraded catchments tend to be the same all over the regional watershed, which may result in homogenisation (Figure 1D). Furthermore, we predicted that, in comparison to current regional land use, the past land use at the regional scale would have a stronger effect (a historical legacy) on both alpha and beta diversities (Figure 1E,F). Finally, we demonstrate how our results can be applied to conservation by producing a watershed conservation value map that spatially projects threshold values of current and historical land use, identifying watersheds likely to harbour the least degraded stream fish communities in Brazil. This map can support conservation planning, monitoring and research efforts.

2 | Material and Methods

2.1 | Study Sites and Data Selection

We used stream fish community data sets from samples distributed throughout Brazil and obtained between 2000 and 2018 (see further details in Dala-Corte et al. 2020). The sampled watersheds encompassed various land use histories and extents, mostly agricultural, with distinct historical patterns of alteration and streams no wider than 10 m (Camana et al. 2025; Table S1). The datasets were derived from different field campaigns conducted by independent research teams, and although sampling methods were not fully standardised, all surveys targeted wadeable streams and used active techniques such as electrofishing, seine nets, and hand nets. Most sites were sampled during the dry season, typically for 1 to 3 h, covering stream reaches between 50 and 150 m in length. In general, sites were sampled only once and were not revisited. We adopted a selection criterion to reduce noise in the analyses by excluding data points as follows: (a) catchments with $>5\%$ urban area, because processes and thresholds in agricultural and urban land use can be significantly different (Chen and Olden 2020), (b) catchments containing large dams, because barriers can influence the movement of individuals between sites (Stoczynski et al. 2021), (c) catchments with less than two sampling sites in the regional context (Hydroshed scale 9; see definition below), to enable the measurement of beta diversity. The screening process resulted in 366 sites distributed across 15 datasets (Figure S1).

2.2 | Land Use Data

For each sampling site, we defined two spatial scales of analysis (depicted in Figure 1). We defined two spatial scales of analysis to assess land use effects on fish communities. The first scale, the upstream drainage areas of each sampling site (local catchments), is a widely recognised unit of analysis with documented influence on aquatic communities. These catchments were delineated using digital elevation models (30×30 m resolution; Valeriano 2004) and hydrological modelling tools in QGIS.org (2023). The second scale corresponds to the regional watershed, obtained from HydroSHEDS level 9 (Lehner 2024), which represents a spatial extent comparable to those used in studies evaluating site-level comparisons across broader landscapes (Urban et al. 2006; Dala-Corte, Sgarbi, et al. 2019). For each scale, we extracted land use for each year from 1985 until the precise year in which fish samples were taken. Land use data were obtained from the MapBiomas project, collection 8.0 (Souza et al. 2020; 30×30 m pixels). We reclassified each original MapBiomas class into 'native vegetation' and 'land use'. Native vegetation included forest formation, savanna formation, grassland, wetlands, and rocky outcrop. Land use included pasture, soybean, sugarcane, rice, other temporary crops, coffee, citrus, other perennial crop, and other non-vegetated areas. Operations were performed in ArcGIS 10.5 (Esri 2016). To assess the historical trajectory of land use, we applied three thresholds (30%, 50% and 70%) to define the duration (D30, D50, D70) of native vegetation loss at the regional watershed scale. These thresholds were selected because there is no strong consensus in the literature regarding a single definitive value to represent land use impacts on stream biodiversity. This approach follows previous studies that used multiple thresholds to assess land use effects on aquatic communities (e.g., Camana et al. 2022; Brejão et al. 2018). Applying multiple thresholds enables the detection of whether ecological responses are consistent across different levels of native vegetation loss, rather than depending on a single arbitrary cutoff. Additionally, we applied a model selection approach using delta AIC to compare the explanatory power of different thresholds, ensuring that the results were not dependent on a single arbitrary cutoff. Similar approaches are commonly used in ecological studies, including those assessing hydrological impacts (e.g., Tonkin et al. 2016). Annual land use values and duration were not collinear ($r < 0.6$).

2.3 | Data Analysis

To investigate the relationship between land use at the local (hereafter, local catchment) and regional (hereafter, regional watershed) spatial scales, as well as current and past native vegetation loss on alpha and beta diversity, we employed multiple linear mixed regression models (LMMs). Species richness and beta diversity were used as response variables in the LMMs. We used species richness as a metric of alpha diversity, which represents the number of species per sampling site (each site has an independent local catchment area). We computed beta diversity from community composition dissimilarities between sites within a regional watershed, based on the Sørensen dissimilarity index; we used the function *beta.pair*

in 'betapart' package in R statistical environment (Baselga et al. 2018). We also extracted the local contribution to beta diversity (LCBD) to assess how much individual sites contribute to the overall beta diversity of each regional watershed (Legendre and De Cáceres 2013).

The explanatory variables in the LMM models were as follows: (i) local scale current land use (%), representing the proportion of anthropogenic cover in the upstream catchment directly draining to each sampling site; (ii) regional scale current land use (%), calculated for the broader watershed (HydroSHEDS level 9) where each site is located; (iii) number of years after the region exceeded the 30% land use threshold (D30); (iv) number of years after exceeding the 50% threshold (D50); and (v) number of years after exceeding the 70% threshold (D70). For alpha diversity and LCBD, we constructed four models, each consisting of the local current land use variable (i) interacting with one of the four variables as described above (ii-v). For total beta diversity, we created models with only one explanatory variable each, utilising the variables ii-v described above. We did not include local catchment land use (i) in the beta diversity models because we had only a single value per watershed, as we calculated beta diversity as the dissimilarity between sites within each watershed (regional context). For the models with alpha diversity, we used the regional watershed in which the sites were located as a random effect, whereas for the beta diversity models, we used the dataset corresponding to the sites as a random effect. Each dataset corresponds to a distinct sampling campaign, typically conducted under a unified methodology and institutional team. Differences among datasets may include sampling methods, spatial coverage and taxonomic resolution. Therefore, including datasets as a random effect variable allowed us to account for potential methodological heterogeneity across data sources. Additionally, we tested an alternative modelling approach for alpha diversity, using the sampling dataset as a random effect instead of the regional watershed; both dataset and regional watershed could not be included as random effect variables in the models simultaneously because they are somewhat redundant and because of the low number of sites within the regional watershed (results from this second approach are presented in supplementary material, Table S3, Figures S2 and S3). These random effect variables were included to account for potential variation among sampled contexts, such as differences in climate, topography and species richness.

In addition to the four models for alpha and four models for beta diversity, we also constructed a null model fitted with the intercept only, and all five models were compared and ranked using the Akaike information criterion (AIC). All the models were compared against the null model. Although models with $\Delta AIC \leq 2$ are typically considered equally plausible (Burnham and Anderson 2002), we also considered models with slightly higher ΔAIC values that outperformed the null model and presented biologically meaningful predictors (Arnold 2010). This approach allowed us to identify the most significant models for explaining the observed variations in alpha and beta diversity. Analyses were conducted in the R statistical environment (R Core Team 2023) using the 'vegan', 'lme4' and 'betapart' packages (Bates et al. 2015; Baselga et al. 2018; Oksanen et al. 2008). All data and scripts to run the analyses are available online in Camana et al. (2025).

2.4 | Mapping Watershed Conservation and Restoration Value

Based on the results obtained from the analyses of land-use effects at different spatial and temporal scales on fish diversity, we developed a watershed conservation value map. This mapping aimed to synthesise the main variables associated with the maintenance of regional (alpha and beta) diversity, identifying areas with different priorities for conservation and restoration. For this, we used both current and historical land-use values that showed significant relationships with fish diversity, as indicated by the analyses described above. Watersheds were classified according to three main criteria: (i) current percentage of native vegetation cover; (ii) time since the vegetation cover dropped below the 50% native vegetation cover threshold, which was identified as an important cutoff in our analyses (more conservative results for 30% threshold are shown in supplementary material); and (iii) the spatial scale of the regional context (level 9 basins from HydroSHEDS; Lehner 2024). This approach allowed us to identify watersheds in different stages of conservation, restoration or prolonged degradation.

3 | Results

3.1 | Effects of Land Use at the Upstream Catchment and Regional Scales on Diversity

In general, the results supported the hypothesis that the effects of upstream catchment land use on fish communities are influenced by the surrounding regional context. We compared candidate models using AIC, where models with lower AIC values are considered more parsimonious. Additionally, higher Akaike weights indicate stronger relative support among the set of candidate models. For alpha diversity, the most supported model was the one including an interaction between local catchment anthropogenic cover and the number of years since the regional watershed exceeded 50% anthropogenic cover (duration 50%, D50) (Model 3, $R^2 = 0.47$; Akaike weight = 0.59; $\Delta AIC = 0$; Table 1), followed by the model containing an interaction between local and regional land use (Model 1, $R^2 = 0.49$; Akaike weight = 0.37; $\Delta AIC = 0.92$; Table 1). Models incorporating alternative thresholds (duration 30% and 70%) showed poor performance and had higher AIC values than the null model, indicating that they were less supported than the other candidate models when using a modelling approach with the regional watershed as a random effect variable. Alternatively, to assess potential biases related to sampling heterogeneity among datasets, we repeated the alpha diversity models using dataset as a random effect variable instead of regional watershed. Although the models ranked slightly different (model using duration 30% [D30] ranked slightly better than D50), results were consistent with those using regional watershed as the random effect variable (Table S3, Figures S2 and S3). Therefore, we focused on the less conservative results (D50) in the main text and further discussed a more conservative alternative (D30).

Our prediction that alpha diversity should decrease with regional land use both in degraded and undisturbed upstream catchments was only partially supported (Figure 2). As expected, local diversity tended to decrease with increasing

TABLE 1 | Linear models for alpha diversity using the Akaike information criterion (AIC). Model, models; ΔAIC, difference between the models; w_i, weight; df, degrees of freedom; Marginal r^2, variation explained by fixed predictors; Conditional r^2, variation explained by both fixed predictors and random effects; Parameters, predictor variables; Effect, effect size of independent variables; CI, 95% confidence intervals; *p* value, significance value.

Model	ΔAIC	w_i	df	Marginal r^2	Conditional r^2	Parameters	Effect	CI	*p*
Model 3	0.00	0.59	6	0.14	0.47	Upstream	−0.07	−0.22–0.09	0.397
						D50	−0.14	−0.31–0.03	0.103
						Upstream:D50	0.23	0.09–0.36	0.001
Model 1	0.92	0.37	6	0.13	0.49	Upstream	−0.03	−0.19–0.14	0.758
						Regional	−0.19	−0.38–0.01	0.059
						Upstream: Regional	0.18	0.04–0.31	0.012
Model 2	5.91	0.03	6	0.09	0.49	Upstream	−0.19	−0.33– −0.06	0.005
						D30	0.06	−0.11–0.23	0.484
						Upstream:D30	0.18	0.06–0.29	0.003
Model 4	10.81	0.00	6	0.08	0.48	Upstream	−0.12	−0.30–0.05	0.162
						D70	−0.12	−0.30–0.06	0.194
						Upstream:D70	0.13	−0.04–0.29	0.123
Null	11.19	0.00	3	0.00	0.52	Intercept	0.04	−0.12–0.20	0.613

anthropogenic cover in regional watersheds. However, decreasing alpha diversity occurred, in general, when regional watersheds had crossed the 50% threshold value less than 20 years ago (Figure 2A), and when upstream catchments had less than 50% anthropogenic land cover (Figure 2B). Additionally, the effect of past land use on species richness was not apparent in sites for which anthropogenic cover in the upstream catchment was over 50% (Figure 2B), suggesting that most local species losses take place before the 50% anthropogenic cover threshold. The 20-year threshold was determined by the nature of the available data and represents a temporal scale where effects on biodiversity become more evident. Importantly, the 50% land use threshold and the 20-year time frame are independent (not correlated) metrics, allowing us to interpret their effects separately and in combination.

Regarding current land use, there was a significant interaction between upstream catchment and regional watershed land use (Model 1, Table 1). The negative relationship between land use and species richness was only evident when either local catchment or regional watershed anthropogenic cover was below 50% (Figure 2C,D), while these relationships approached neutral effects when land use covered more than 50% of the regional or the local catchment area. Rather than applying a strict ΔAIC ≤ 2 threshold, we considered models to be plausible if they had lower AIC values than the null model and included ecologically meaningful predictors, following the guidance by Arnold (2010). This allowed us to highlight informative models with strong biological support even when ΔAIC values were slightly above 2.

For total beta diversity, results were consistent with the alpha diversity models, with similar models being the most plausible (Table 2; Figure 3) and supported the hypothesis that beta diversity tends to increase with regional anthropogenic cover. The model for current regional land use (Model 1, $R^2 = 0.33$; weight = 0.36; ΔAIC = 0; Table 2) was slightly better supported, but the model considering historical land use 50% threshold (Model 3, $R^2 = 0.27$; weight = 0.26; ΔAIC = 0.24) also received similar support (ΔAIC < 2), indicating that both models are equally plausible in explaining the patterns in beta diversity (Table 2).

These results indicate that beta diversity tends to be higher when vegetation cover at both regional and local catchment scales is >50% (Figure 3A). Moreover, this effect tends to get stronger with accumulating years under low vegetation cover (Figure 3B). The interaction between native vegetation cover and the time since its loss is key to our interpretation of the models, as both factors influence the observed patterns of diversity. There was no significant relationship between LCBD and any predictor variable (Table S2).

3.2 | Spatial Classification of Watershed Conservation Value

The previous results suggested that higher alpha diversity is sustained in the long run but only in catchments with >50% natural vegetation that are contained in regional watersheds with <50% anthropogenic land cover. Moreover, we found that in regions with lower levels of vegetation cover, alpha diversity tends to decrease even in local catchments with high vegetation cover, suggesting a regional extinction debt effect. These results highlighted the importance of considering three key landscape attributes in conservation planning: current catchment land use, regional land use, and the time elapsed since vegetation loss exceeded 50% cover (D50). Therefore, after defining the current and historically related values of land use significantly associated

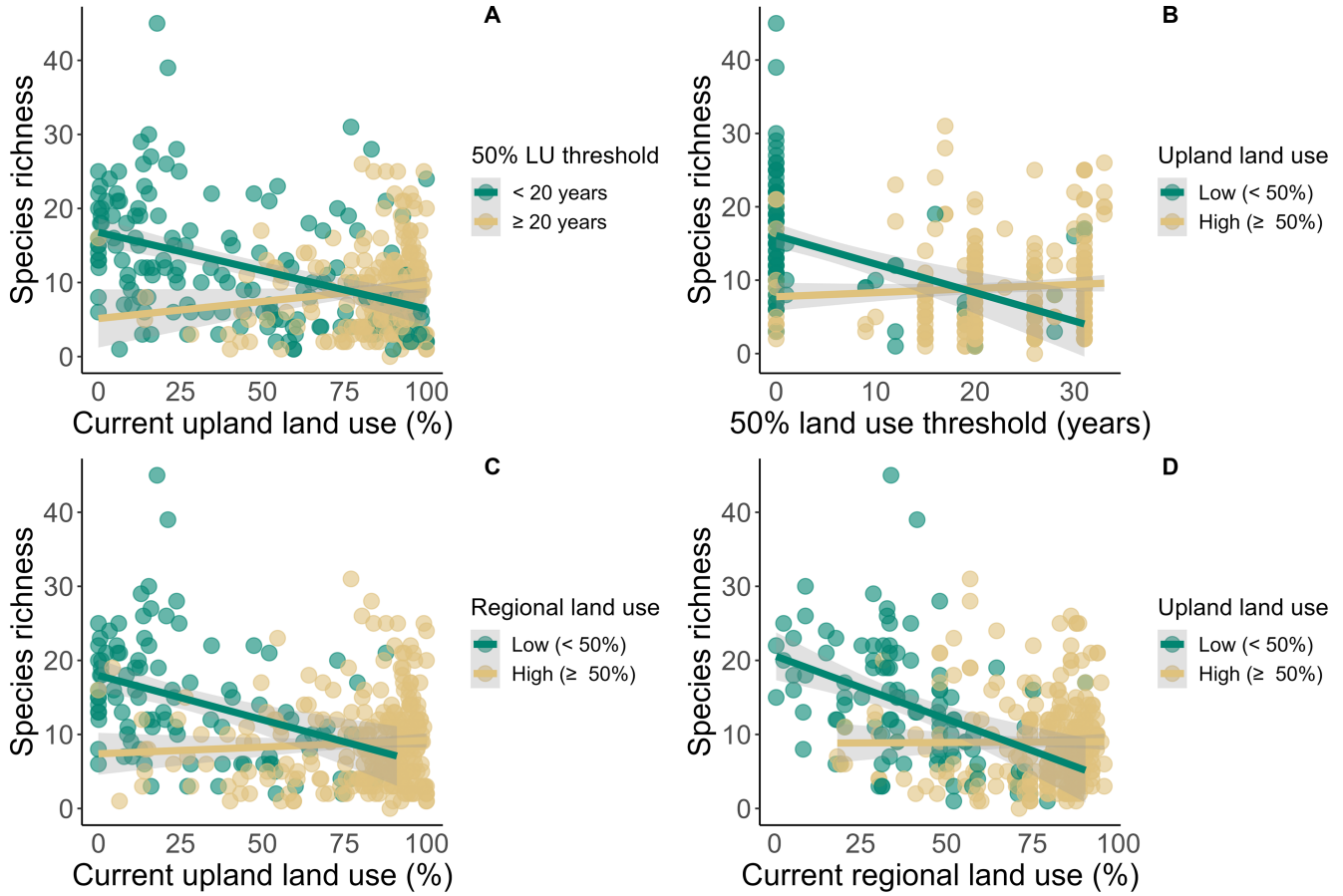

FIGURE 2 | Results from the most parsimonious linear models based on model selection using AIC, showing the interacting effect of current and historical land use, at local catchment and regional scale, on fish species richness (alpha diversity). (A) Current local catchment land use, considering the time since the watershed surpassed 50% anthropogenic cover < 20 years (green) or ≥ 20 years (yellow). (B) Years since the regional watershed surpassed 50% anthropogenic cover, differentiating upstream catchment areas with less than 50% (green) and more than 50% (yellow) current anthropogenic cover. (C) Current anthropogenic cover in local catchments, regional watersheds with less than 50% (green) or more than 50% anthropogenic land cover (yellow). (D) Current anthropogenic cover in the regional watershed, considering local catchment areas with less than 50% (green) or more than 50% (yellow) land use. Each point in the plots represents observed data, while the lines represent modelled trends. For visualisation purposes, we categorised continuous predictors based on thresholds derived from the literature.

TABLE 2 | Results of the comparison of linear models for beta diversity using the Akaike information criterion (AIC). Model, models; ΔAIC, difference between the models; w_i, weight; df, degrees of freedom; Marginal r^2, variation explained by fixed predictors; Conditional r^2, variation explained by both fixed predictors and random effects; Parameters, predictor variables; Effect, effect size of independent variables; CI, 95% confidence intervals; *p* value, significance value.

Model	ΔAIC	w_i	df	Marginal r^2	Conditional r^2	Parameters	Effect	CI	*p*
Model 1	0.00	0.36	4	0.10	0.33	Regional	0.33	0.07–0.59	0.014
Model 3	0.24	0.26	4	0.10	0.27	D50	0.33	0.08–0.58	0.009
Model 2	1.16	0.18	4	0.08	0.25	D30	0.29	0.06–0.52	0.015
Null	4.10	0.15	4	0.00	0.34	Intercept	0.05	−0.24–0.33	0.743
Model 4	5.93	0.02	3	0.00	0.35	D70	−0.04	−0.42–0.34	0.830

with alpha and beta diversity, we conducted an analysis of land use status for all the regional watersheds (Lehner 2024), generating a regional extent watershed conservation value map for the entire Brazil (Figure 4). Initially, we assessed the amount of current land use in the basin, using a threshold value of 50% (Figure 4A). For those exceeding this threshold, we evaluated (at 5-year intervals) how many years ago this threshold had been crossed (Figure 4B). Finally, we created three categories of conservation value, where basins with less than 50% land use presented a higher conservation priority (19,459 basins; 62%), those with more than 50% land use but exceeding this threshold less than 20 years ago, showing restoration priority (2101; 7%),

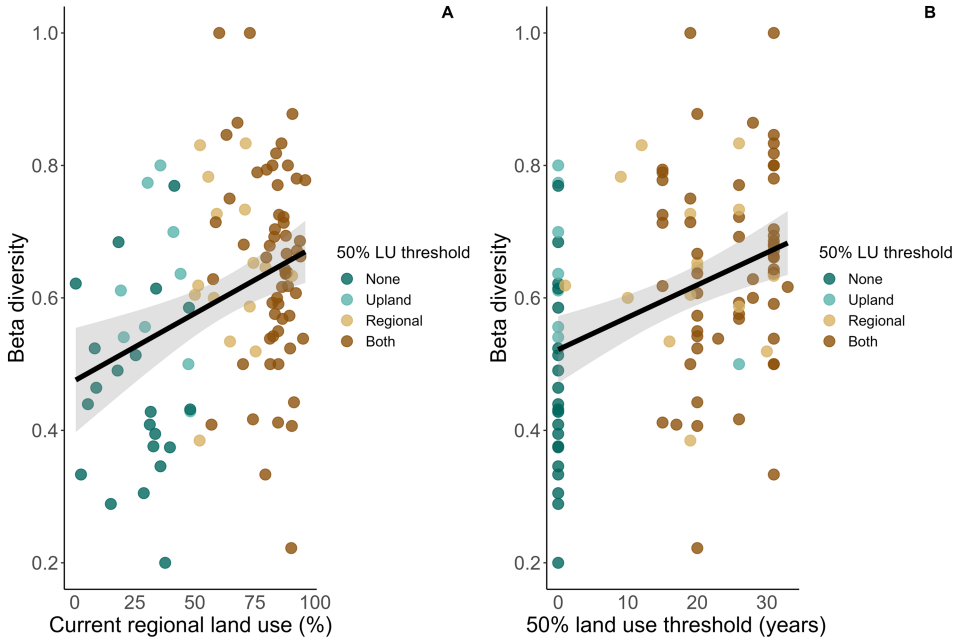

FIGURE 3 | Results from the most parsimonious linear models based on model selection using AIC showing the relationship between current and historical land use at the regional and local catchment scales and beta diversity. Point colours represent whether the land use threshold exceeded 50% for local catchment and regional anthropogenic land cover (brown), only regional (yellow), only local watershed (light green) or neither of them (dark green).

and those that exceeded this threshold more than 20 years ago, classified as no priority (62,270; 31%) (Figure 4C). To further evaluate the sensitivity of our prioritisation map to the choice of land use threshold, we repeated this classification using the more conservative 30% land use threshold (D30), which was also supported in alternative model structures (Table S3). The resulting prioritisation map for this more conservative threshold is provided as Figure S3.

4 | Discussion

We found that local species richness of stream fish is influenced not only by land use in the local catchment upstream of the sampling site, but also by both contemporary and historical land uses at the regional scale. Interestingly, streams with both conserved and converted catchment basins (i.e., catchments where more than 50% of the native vegetation has been replaced by anthropogenic land uses such as agriculture, pasture, or urban areas) presented similar richness when they were situated in heavily converted regional contexts (>50% native vegetation cover loss). Furthermore, we show that beta diversity increases with regional land use, but, contrary to our expectation, we did not find support for the hypothesis that this pattern is more related to the historical than the current land use.

Our results support that land use in the regional spatial scale significantly contributes to structuring local stream communities. However, this effect is shared with the land use conditions at the more restricted scale of upstream catchments, demonstrating a multiscale spatial effect (Wagner and Fortin 2005; Jackson and Fahrig 2015). Streams with either upland or regional land use below the 50% land use cover threshold showed a more evident and negative relationship between land use and species richness, and such relationship becomes neutral when such threshold was already crossed (Figure 2C,D). This suggests that the stability of local richness depends not only on the local environmental integrity, but also on inputs from the regional species pool (Leibold et al. 2004; Li et al. 2012; Henriques-Silva et al. 2013), and that conservation actions and land use management for fish in lotic ecosystems should be prioritised and implemented at broader spatial scales to effectively guide conservation decision-making and promote biodiversity preservation (Abell et al. 2007). Hence, we bring a new perspective to the regional scale concept for aquatic systems, echoing other studies that highlight the importance of assessing freshwater conservation at broader spatial delineations (Castello et al. 2012; Edge et al. 2017; Stoczynski et al. 2021). It is also important to note that these patterns may not solely result from the depletion of the regional species pool, but could also arise from other processes, such as reduced hydrological connectivity (Estrada and Bodin 2019) or the presence of dispersal barriers (Favaro et al. 2014) at the regional scale. This highlights the need for conservation and management strategies that address both local and regional drivers of biodiversity loss.

Land use history is an additional component for understanding the effects of changing landscapes on local fish species richness, where a delayed or a long-lasting effect of land use is observed, suggesting an extinction debt process (Tillman et al. 1994; Kuussaari et al. 2009; Jackson and Sax 2010; Santos et al. 2020). We found that watersheds that have similar current land use, but distinct land conversion trajectories, did not exhibit the same diversity. Other studies also found delayed effects on the diversity of both terrestrial and freshwater environments, including plants (Guardiola et al. 2013), insects (Cusser et al. 2018), birds (Allen et al. 2019) and mammals (Lira et al. 2012). Our findings indicate that diversity decreases with regional land use primarily where vegetation loss has been more recent, suggesting

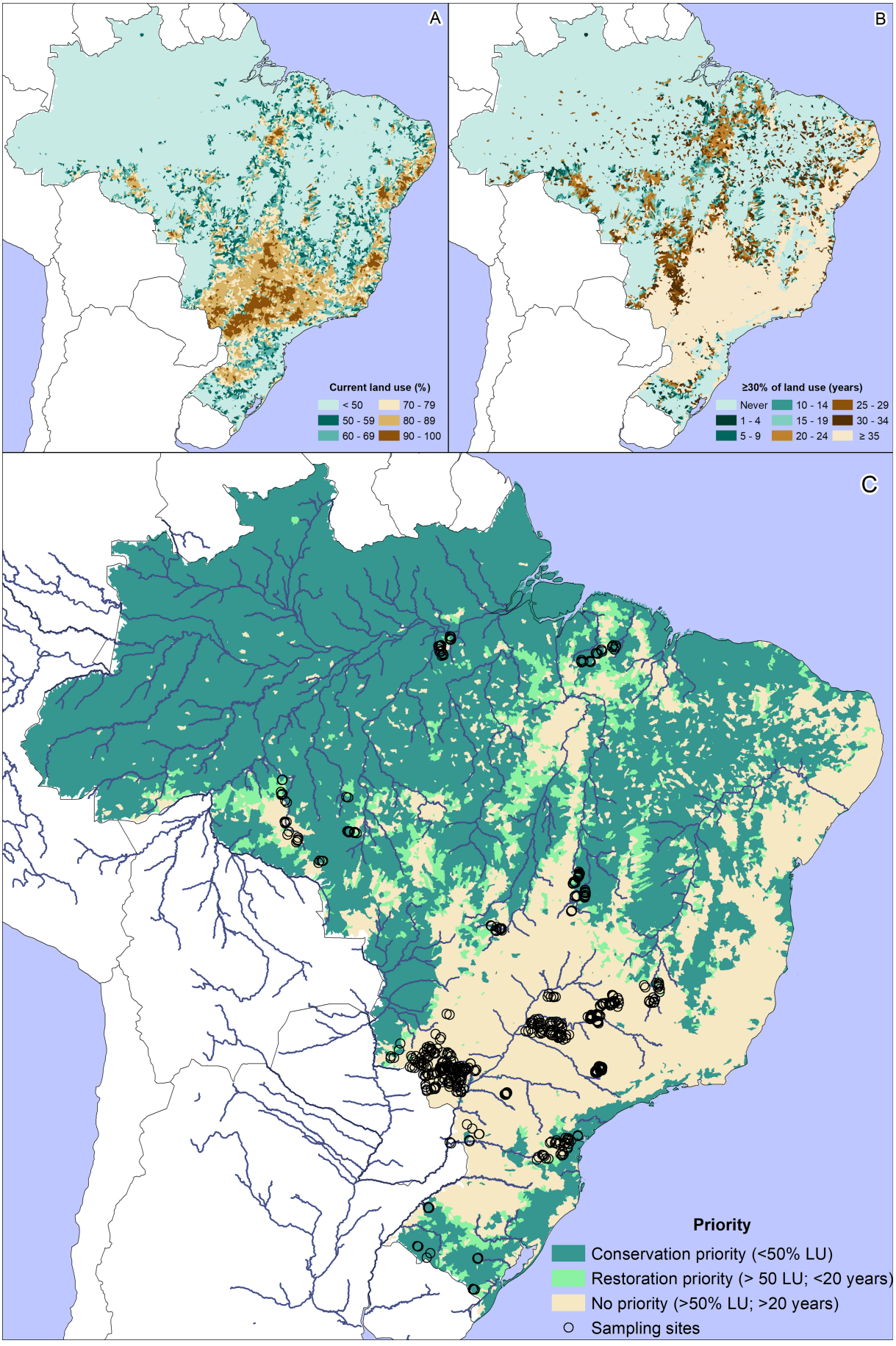

FIGURE 4 | Legend on next page.

FIGURE 4 | Different land use conditions for Brazilian watersheds. In (A), the current proportion of land use (2020). In (B), the amount of time since the basin exceeded 50% of anthropogenic land cover. In (C), conservation value considering the two indicators. The analyses were based on level 9 Hydrosheds (Lehner 2024). The black dots represent the sampling sites used in the analyses.

that the extinction debt tends to have been 'paid' approximately 20 years after the 50% native vegetation cover threshold was surpassed (but notice we also had support for models suggesting this threshold value could be even earlier, around 30%, if we use a more conservative threshold; Table S3). This timeframe aligns with empirical evidence from different ecosystems, where delayed biodiversity responses to land conversion were also observed within similar temporal scales. For example, Lira et al. (2012) demonstrated that functional shifts in stream fish assemblages in the Brazilian Cerrado became evident roughly two decades after major deforestation events. Likewise, Le Provost et al. (2020) found that multiple trophic levels in terrestrial landscapes exhibited strong legacy effects tied to land use changes occurring around 20 years prior, while Camana et al. (2022) provided evidence that historical deforestation continues to affect stream fish communities for at least two decades. These studies suggest that the 20-year period may represent a biologically meaningful window during which ecological debts manifest in tropical and subtropical landscapes, although this may also be contingent on the availability of satellite imagery data. While our statistical models directly estimate the effects associated with the 50% land use threshold, this temporal reference was guided by this consistent body of empirical evidence. Although alternative thresholds such as 30% land use were also tested and yielded plausible models (see Table S3), we focused on the less conservative 50% threshold due to its broader applicability for prioritising conservation and restoration actions across a larger number of watersheds. Lower thresholds would result in excluding many areas that still retain conservation or restoration potential. Moreover, this indicates that biodiversity responses to habitat loss are not immediate but follow the inertia of extinction debt processes, where species extinctions and community shifts materialise years or decades after habitat degradation. Thus, although the 50% threshold value may be useful to set conservation targets, the optimal threshold value for each watershed may be likely variable and dependent on several other environmental conditions not assessed in our study.

Contrary to our expectations, we observed a positive relationship between beta diversity and regional-scale land use, but the model with current land use had a slightly better fit than the ones with historical land use. However, the AIC difference between these models was small ($\Delta AIC < 2$), indicating similar support. This differs from our prediction, as we expected a greater negative effect of land use history (Figure 1F). Regional land use can increase overall beta diversity across the watershed for at least two plausible reasons. Firstly, increased land use at regional scale may be related to increased stream network fragmentation (e.g., higher density of stream road-crossings and dams), which can hinder species movement and recolonisation of converted areas (Edge et al. 2017; Krynak et al. 2019), so that local species losses are less likely compensated by dispersal from adjacent catchments. A second explanation would be that stream habitat altered by land use could lead to processes of random local extinction (i.e., extirpation) and colonisation that are regionally heterogeneous among different streams, particularly if they are spatially distant in the watershed, increasing overall beta diversity (Dala-Corte, Sgarbi, et al. 2019). These processes may also be driven by the spread of opportunistic native species, such as *Poecilia reticulata* and *Laetacara araguaiae* (Casatti et al. 2015), which often originate from larger streams and rivers, a phenomenon known as native invasion (Scott and Helfman 2001; Dala-Corte, Melo, et al. 2019). The increased beta diversity we observed becomes more evident when comparing beta diversity where both local upstream catchment and regional watershed were highly converted (i.e., more than 50% land use) in contrast to streams where both local upstream catchment and regional anthropogenic cover were less than 50% (Figure 3). Therefore, we suggest caution when interpreting higher beta diversity as an indicator of conservation value, because high values of beta diversity are not always a desirable conservation outcome (Socolar et al. 2016; Kramer et al. 2023). Furthermore, although contemporary land use had a stronger effect on beta diversity than historical land use, past land use still provided plausible models for explaining the current diversity patterns, reinforcing the importance of integrating spatial and temporal scales in biodiversity assessments (Cusser et al. 2018; Allen et al. 2019; Lawson et al. 2024).

We detected the effect of land use on a broad spatial scale and the legacy of time on the taxonomic response of alpha and beta diversity of stream fish communities. Intensified land use can drive eutrophication processes and long-term declines in dissolved oxygen levels, which in turn affect fish species composition and abundance (Piatka et al. 2021). These alterations may exacerbate competitive imbalances among species, favouring tolerant generalists over habitat-specialist taxa and contributing to shifts in community structure over time. This perspective also can be extended to other biological attributes. For example, species loss in converted sites may be associated with specific functional groups, such as bottom-dwelling armoured catfishes and nektobenthic gymnotids, which are particularly sensitive to habitat alterations in substrate heterogeneity (Terui et al. 2021; Seabra et al. 2022; Magalhães et al. 2025). Moreover, recent studies indicate that such habitat alterations can interact synergistically with climate change, exacerbating biodiversity loss through combined effects of altered flow regimes, higher temperatures, and reduced habitat complexity (Wild et al. 2024; Auerswald et al. 2025). Although we found that a 50% loss of native vegetation occurring more than 20 years ago may be a critical point for communities, we emphasise that this loss may not be linear, and each group may have different responses along the gradient, requiring a deeper evaluation of thresholds, breakpoints, and nonlinear responses (Dodds et al. 2010). It is also noteworthy the fundamental role played by connectivity in shaping beta diversity of aquatic species, so we recommend the use of metrics such as site position in the network (Heino et al. 2015; Loyola-Bartra et al. 2023), the presence of natural and anthropic barriers (Mozzaquattro et al. 2020; Tsuboi et al. 2020) and channel slope (Caetano et al. 2021).

4.1 | Implications for Conservation and Conclusions

Based on our results, we then mapped the conservation status of Brazilian watersheds according to land use cover percentage and time since conversion (see Figure 4). The resulting map can be interpreted to identify valuable areas for conservation and recovery, including potential reference sites (Stoddard et al. 2006). In this sense, mapped regional watersheds with less than 50% land use have a greater chance of harbouring fish communities that still maintain species diversity near the original condition. In addition, watersheds that crossed the 50% threshold more recently offer a greater chance for land cover restoration before experiencing high levels of community modification (species loss; native invasion, Dala-Corte, Melo, et al. 2019). One promising management strategy for these habitats would be the implementation and/or restoration of wide and continuous native vegetation riparian buffers so that the total native vegetation cover in these watersheds stays above the 50% threshold.

Conservation strategies should then be conceived at different spatial scales, including local, riparian, upstream catchment scales (see Hermoso et al. 2009; Leal et al. 2018; Dala-Corte et al. 2020) and, as shown here, at the regional watershed scale. Prioritising catchments under a regional context not only optimises the allocation of resources for environmental restoration but also maximises the effectiveness of actions in mitigating biodiversity loss, emphasising the crucial role of managing land use at the regional scale to preserve overall aquatic biodiversity. Considering the varying effectiveness of different mitigation measures across spatial scales, the integration of broader conservation strategies at the watershed level can ensure a more holistic approach, which aligns with the integrative concept of freshwater biodiversity conservation (Geist 2011). Prioritising larger, ecologically connected areas for restoration can amplify the resilience of ecosystems to land use pressures, particularly in regions where legacy effects of past land use are still influential.

Reference systems are important elements in setting priorities for the conservation and management of large-scale environments (Goebel et al. 2005; King et al. 2005; Martins et al. 2018; Agra et al. 2019). For example, identifying reference catchments with low levels of land use and high ecological integrity can help set realistic targets for restoration and serve as benchmarks for biodiversity assessments (Stoddard et al. 2006). Furthermore, the compartmentalisation of high conservation value areas within regional watersheds seems to be an interesting strategy, integrating terrestrial and aquatic aspects (Hermoso et al. 2011; Leal et al. 2018, 2020). These watersheds can be used as an information layer to guide conservation policies and decision-making (Briassoulis 2001; Cowell and Owens 2006), in addition to other factors such as endangered species, endemism, connectivity, gaps in the protected area network, and environmental pressure (Moilanen et al. 2008; Nogueira et al. 2010; Hermoso et al. 2015; Howard et al. 2018). Specifically, the mapped categories can inform spatial prioritisation in restoration programs, environmental licensing procedures, and land-use planning by identifying watersheds at risk or with high potential for biodiversity recovery (Margules and Pressey 2000). This allows decision-makers to act preemptively, especially in areas where land conversion is recent but ecological degradation is already underway.

In summary, we found that the local diversity of stream fish communities is influenced not only by changes in land use in their local upstream catchments but also on a broader regional watershed scale, highlighting the need for multiscale assessments of biological diversity and the importance of considering the complex interplay between land use at different spatial and temporal scales. Additionally, we show that richness responses were mediated by land use legacy, suggesting that the extinction debt effect can influence preserved catchments embedded in a degraded regional context. These findings have an impact on both past and future studies, as past studies may not have detected an effect of land use on diversity in highly modified regions or with a long land use history. They can also be used as a benchmark for study design, for prioritisation of areas to search for new species in taxonomic studies, and as an important guidance for regional conservation plans. Conservation of stream biodiversity depends on setting regional scale conservation aims, not only on individual catchment conservation.

Author Contributions

Mateus Camana: conceptualisation, methodology, data curation, writing – original draft, visualisation, project administration. **Renato Bolson Dala-Corte:** conceptualisation, data curation, formal analysis, writing – review and editing. **Jean M. Freitag Kramer:** methodology, visualisation, writing – review and editing. **Almir Cunico:** data curation, methodology, writing – review and editing. **André Magalhães:** data curation, methodology, writing – review and editing. **Cecília Gontijo Leal:** data curation, methodology, writing – review and editing. **Dilermando Pereira Lima-Junior:** data curation, methodology, writing – review and editing. **Éder André Gubiani:** data curation, methodology, writing – review and editing. **Fabrício Barreto Teresa:** data curation, methodology, writing – review and editing. **Fagner Junior M. Oliveira:** data curation, methodology, writing – review and editing. **Gabriel Lourenço Brejão:** data curation, methodology, writing – review and editing. **Jean Vitule:** data curation, methodology, writing – review and editing. **Lilian Casatti:** data curation, methodology, writing – review and editing. **Luciano Lima:** data curation, methodology, writing – review and editing. **Luciano Montag:** data curation, methodology, writing – review and editing. **Paulo S. Pompeu:** data curation, methodology, writing – review and editing. **Rafael Leitão:** data curation, methodology, writing – review and editing. **Vinícius Abilhoa:** data curation, methodology, writing – review and editing. **Yzel Rondon Suarez:** data curation, methodology, writing – review and editing. **Fernando Gertum Becker:** conceptualisation, methodology, supervision, writing – review and editing.

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Ethics Statement

No ethical approvals or permits were required for the research conducted in this study.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and analyses supporting the findings of this study have been deposited in Zenodo and are publicly available under the DOI: 10.5281/zenodo.11551526 (Camana et al. 2025). This repository contains the full dataset on stream fish diversity, land use legacy and all associated analyses used in the study. We encourage the reuse of this data for further research.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Summary table of current and historical land use values for each data frame used in the study. 'Current LU' presents values in % and 'Duration' presents values in years. **Figure S1:** Map showing the sampling sites distributed across the 15 data frames used in the analyses. **Table S2:** Linear models for local contribution to beta diversity (LCBD) using the Akaike information criterion (AIC). Model, models; ΔAIC, difference between the models; wi, weight; df, degrees of freedom; Marginal r2, variation explained by fixed predictors; Conditional r2, variation explained by both fixed predictors and random effects; Parameters, predictor variables; Effect, effect size of independent variables; CI, confidence intervals; p value, significance value. **Table S3:** Summary of linear models for alpha diversity using the Akaike information criterion (AIC), with dataset identity included as a random effect. Model, models; ΔAIC, difference between the models; wi, weight; df, degrees of freedom; Marginal r2, variation explained by fixed predictors; Conditional r2, variation explained by both fixed predictors and random effects; Parameters, predictor variables; Effect, effect size of independent variables; CI, 95% confidence intervals; p value, significance value. **Figure S2:** Results from the most parsimonious linear model (based on AIC) showing the interacting effect of current and historical land use at local catchment and regional scales on fish species richness (alpha diversity). (A) Current local catchment land use, considering the time since the regional watershed surpassed 30% anthropogenic cover: < 20 years (green) or ≥ 20 years (yellow). (B) Years since the regional watershed surpassed 30% anthropogenic cover, differentiating upstream catchment areas with less than 30% (green) and more than 30% (yellow) current anthropogenic cover. **Figure S3:** Different land use conditions for Brazilian watersheds. (A) Current proportion of land use (2020). (B) Time since the watershed exceeded 30% anthropogenic land cover. (C) Conservation value based on the two indicators. Analyses were based on HydroSHEDS level 9 (Lehner, 2024). Black dots represent sampling sites used in the analyses.