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# The ecological memory of landscape complexity shapes diversity of freshwater communities

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Land use change affects the biodiversity of terrestrial landscapes as well as of the freshwater systems they surround, and thereby numerous ecosystem services that are essential for human well-being. Previous research suggests that freshwater systems show delayed responses to abrupt disturbances such as deforestation, however less is known about whether there is a memory effect of landscape history on freshwater communities under a long history of land use change. We addressed this research gap here by first quantifying the historical complexity of landscapes, including natural and agricultural formations, in terms of their composition and configuration in 26 tropical catchment areas surrounding 101 streams over a 30-year period. We identified clear evidence for a memory effect of past events, whereby higher historical landscape complexity, measured as the information entropy of landscape composition, led to higher freshwater biodiversity. Finally, using a causal discovery approach, we showed that species richness was causally related to landscape complexity only when historical values were incorporated. Our results corroborate previous work on the positive effect of landscape complexity on biodiversity, and also confirm the role of historical contingencies in predicting future ecological outcomes.

Keywords: causal discovery, information entropy, landscape composition, landscape configuration, spatial entropy

## Introduction

Land use change has become one of the main causes of biodiversity loss around the world (Newbold 2018, Marques et al. 2019). Human activities have been transforming landscapes for thousands of years, destroying natural habitats and causing species extinctions (Ellis 2021). The historical dependence of biodiversity on land use change has been demonstrated in many systems (Kardol et al. 2007, Perry et al. 2008), including forests (Nuttle et al. 2011) affected by various human activities (Harding et al. 1998, Foster et al.

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2003, Cuddington 2011, Santos et al. 2020). These ecosystem responses to past events and conditions – also called ecological memory – are crucial for increasing future resistance and resilience of ecological systems (Bengtsson et al. 2003).

The conversion of natural land use to intensive land uses, such as agriculture, forestry and pasture, affects both terrestrial and riverine communities at different spatial and temporal scales (Allan 2004, Barbosa and Siqueira 2023). That is because the hierarchical structure of riverine networks, which are embedded in terrestrial drainage basins, make them both receivers and transmitters of materials and organisms. They receive sediment, nutrients, contaminants, and organisms from the surrounding landscape and from upstream; they process and transmit these downstream (Dudgeon 2019). In riverine communities, invertebrates include species that are sensitive to environmental change and that play pivotal, diverse roles in food web dynamics. While random demographic events and density independent and dependent processes shape the species composition of aquatic invertebrates at the local scale, dispersal plays a major role in distributing individuals among localities within the catchment area (Malmqvist 2002, Tabi et al. 2023). Dispersal of riverine invertebrates occur via two main pathways: the aquatic stages disperse through watercourses, while winged adults disperse along and across riparian vegetation (Jurača et al. 2019). Thus, the structural complexity of the surrounding landscape, including its composition and spatial configuration, should play a major role in the assembly of riverine biodiversity.

Previous empirical studies on ecological memory have focused mainly on the effects of abrupt conversion of one type of natural land use (e.g. natural forest) to one anthropogenic land use type (e.g. pasture) (Rosa et al. 2016, Brejão et al. 2018, Frainer and McKie 2021). However, most landscapes have a long history of land use change and exist as complex mosaics comprising both natural and modified formations. Capturing the complexity of these mixed landscapes is not an easy task because biological and physical properties and processes in a landscape interact simultaneously between its parts (Green et al. 2020). Recent studies have measured landscape complexity as the percentage of natural elements in the landscape (Cormont et al. 2016), using metrics based on Shannon information entropy (Nelson and Burchfield 2021), or various metrics to measure spatial configuration of land use types (Cushman 2018, Zhao and Zhang 2019, Nelson and Burchfield 2021). Overall, these studies indicate that higher landscape complexity leads to higher biodiversity in agricultural landscapes (Estrada-Carmona et al. 2022) and to an increased provision of ecosystem services such as water quality, pollination, pest regulation, carbon storage (Duarte et al. 2018), and crop production (Nelson and Burchfield 2021). However, less is known about to what degree the historical complexity of landscapes shape biodiversity in areas with a long history of land use change. Freshwater invertebrates are sensitive to past landscape changes due to their delayed ecological responses (Santos et al. 2020), and quantifying these memory effects properly is important for explaining current biodiversity patterns that might otherwise appear stochastic or driven by unmeasured contemporary factors.

Ecological memory has been previously quantified using weight functions, which determine the functional form of discounting past values, such as hyperbolic or exponential decay. For instance, the hyperbolic and exponential decay functional form has been used in psychology to model forgetting – known as Jost's Second Law of forgetting (Jost 1897, Rachlin 2006), and in economics, to explain future consumer choices (Laibson 1997, Tabi 2013). Other more flexible frameworks such as Bayesian hierarchical models (Itter et al. 2019), stochastic antecedent modelling (Ogle et al. 2015), or random forests (Benito et al. 2020), estimate the relative importance (weight) of past time points of the explanatory variables on the target variable with predefined time lags.

In this study, we present a nonlinear, nonparametric framework to quantify discrete memory effects of landscape complexity on freshwater biodiversity using observational data on 101 tropical freshwater communities across 26 river catchments in Brazil, combined with annual historical land use type data between 1985 and 2015. By using this approach, we aimed to identify past events with major impacts on current diversity without having a predefined time lag or weight function. Furthermore, we present a causal discovery analysis to map the causal links between landscape complexity metrics, diversity and other biotic and abiotic factors that potentially affect diversity.

## Material and methods

### Study sites and data

We compiled landscape data by analyzing maps of land use types from the Corumbataí River basin, state of São Paulo, southeastern Brazil (Fig. 1). This basin comprises an area of 1700 km$^2$, and its natural vegetation was originally dominated by semi-deciduous forests and with patches of Savanna (Rodrigues 1999). Initial deforestation in the basin began in the early 18th century with farming, followed by an expansion of pasture land and crop land, mainly sugar cane, which modified the natural vegetation to small fragments (Ferraz et al. 2014). More recently, the amount of native forest has been increasing due to natural vegetation recovery in abandoned agricultural lands (Ferraz et al. 2014, Molin et al. 2017). Within the Corumbataí River basin, we delineated 26 catchments using a SWAT model (soil and water assessment tool), based on a digital elevation model (DEM) that was obtained from SRTM (Shuttle Radar Topography Mission, 30 m of spatial resolution). We used MapBiomas 8.1 with 30 m of spatial resolution (Souza et al. 2020). We quantified the land use classes (in m$^2$) yearly between 1985 and 2015.

We surveyed 101 streams distributed within 26 catchments, in which we collected immature aquatic insects predominantly in the dry season between May and August 2015. We used a kick-net, with 1-m$^2$ area and 250 µm mesh, to collect a generous sample in each stream by gently kicking the stony substrate of four riffles for a total of two minutes (30 s each). In each of the four riffles, we sampled aquatic insects. The identification of the collected specimens to



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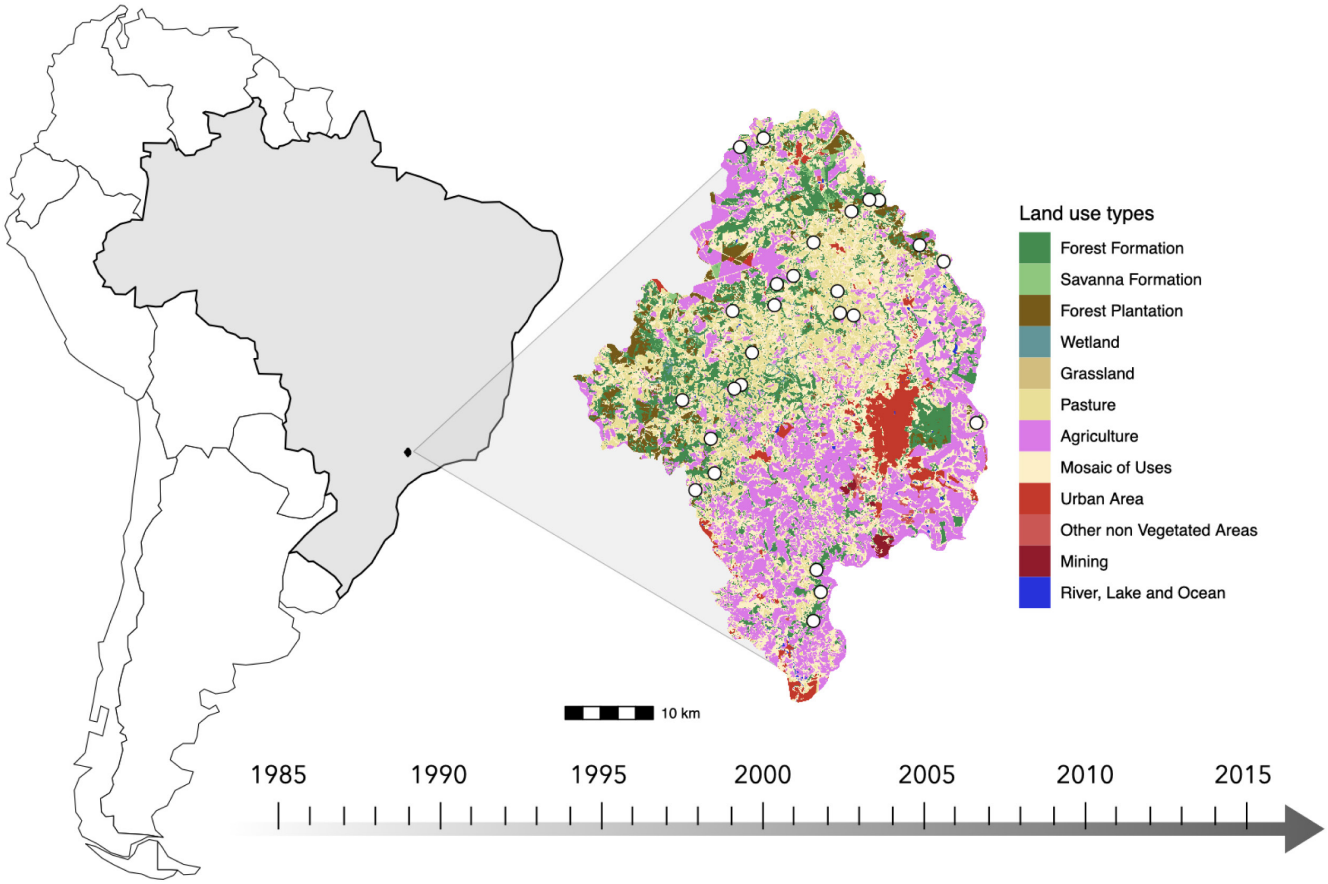


Figure 1. Land use types and sampling sites. Our study site is the Corumbataí River basin, state of São Paulo, southeastern Brazil. We collected landscape data by analysing maps of land use types from 26 catchments between 1985 and 2015, where we surveyed 101 streams for aquatic insects in 2015.

species or morphotype was based on taxonomic keys and original descriptions (Dominguez et al. 2006, Domínguez and Fernández 2009). To estimate body size, we averaged the size of the three largest specimens of each species. The feeding strategy of each species was collected from literature (Cummins et al. 2005, Poff et al. 2006, Tomanova et al. 2006). In each stream, we also obtained measurements of turbidity, conductivity and dissolved oxygen with a multiparameter YSI 556 MPS probe (YSI Inc., Ohio). Stream width, water temperature and flow velocity were measured as well. In each stream, we took water samples that were analysed for total nitrogen and total phosphorus, following national standards for Brazil (Golterman et al. 1978). We also visually estimated the proportion of organic detritus (small litter patches) intercepted by rocks in the stream riffles and the proportion of shading.

### Measuring landscape complexity and memory effects

We used three entropy metrics to quantify landscape complexity of each catchment area. First, we calculated the normalised Shannon information entropy to calculate compositional complexity of the different land use types in each catchment area:

$$\mathrm{LCS} = -\sum_{i=1}^{S} P_i \log[P_i]/\log S$$

where $P_i$ is the relative area of land use type $i$. The values of landscape composition vary from 0 to 1, with zero representing landscapes dominated by a single land use type (low entropy) and with 1 representing landscapes with equally distributed land use types. Then, we used two spatial entropy metrics; the Boltzmann approach and the Wasserstein distance (Zhao and Zhang 2019, Zhang et al. 2020), to capture the configurational entropy of the landscape mosaics (Cushman 2018, 2021b).

The Boltzmann entropy approach (hereafter LCB), based on the thermodynamics concept of entropy, quantifies the configurational entropy of a landscape. For landscape mosaic, it calculates the total length along edges of cells where two different land use types touch (Cushman 2021b). First, a landscape mosaic is spatially permuted 5000 times, producing a distribution of randomized landscape mosaic patterns. Then, the total edge length is calculated for the landscape and for the permuted patterns representing the possible microstates. The entropy ($S_B$) is calculated from the fitted log-normal distribution of microstates (Cushman 2021b). Then, we normalised



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Boltzmann entropy as $\mathrm{LCB} = 1 - \frac{S_B}{S_{B,\min}}$, where $S_{B,\min}$ is the entropy of the theoretical minimal edge length (Sciaini et al. 2018). The Wasserstein metric-based Boltzmann entropy (hereafter LCW) calculates the configurational entropy of land use types by taking into account the spatial repetition of adjacent cells of the same land use type. Thus, LCW captures both the compositional and configurational information of landscape mosaic such that $\mathrm{LCW} = (1 - W_c) \times (1 - W_s)$, where $W_c$ is the distance between frequency of states (land use types) and a reference distribution (Dirac delta distribution) and $W_s$ is the distance between the repetition of spatial configuration and reference state (Dirac delta distribution). Both $W_c$ and $W_s$ are normalized between [0,1] by the number of cells (Zhao and Zhang 2019). We also quantified the relative co-occurrences of the agricultural land (ACO) and forest (FCO) as the number of directions, in which cell adjacencies are considered as neighbours (eight possible directions) divided by the total sum of all occurrences.

In order to detect the memory effect of landscape complexity on species richness in riverine communities, we used a stochastic local search algorithm called *threshold accepting* (TA) (Gilli et al. 2019). The memory weights were constrained as $\sum_{i=1}^{n} w_i = 1$, where $n$ is the number of time points. The algorithm maximized the Spearman's correlation coefficient between diversity and the sum of the weighted landscape complexity time series ($\mathrm{LC} = \sum_{i=1}^{n} w_i \mathrm{LC}_i$). The advantage of stochastic optimization techniques over other similar algorithms, such as simulated annealing (SA), is that depending on the choice of the threshold it does not get stuck in local minima due to its different acceptance rules (Dueck and Scheuer 1990). TA accepts every new configuration as long as it is not much worse than the old one, whereas SA accepts worse solutions with very small probabilities. On average, TA provides better solutions with shorter computational time compared to SA. We ran the algorithm 500 times for each case in order to obtain a distribution of correlation coefficients. Each time the algorithm was run for $5 \times 10^5$ iterations. Then, we calculated the average weight values and confidence intervals.

### Discovery of causal structure

In the causal discovery analysis we included the measured species richness in 101 streams, community-weighted species traits (predation and body size), locally measured variables (organic detritus in stream, shading, temperature and stream width), and the three landscape complexity metrics. We also tested for the spatial autocorrelation of species richness between study sites due to their nested structure into catchment areas. We did not find evidence for spatial autocorrelation in the data before or after removing the effect of catchments (Supporting information).

The construction of a graphical causal model, i.e. DAG (directed acyclic graph), is referred to as causal discovery (Pearl 2009). We apply the IC (*inductive causation*) algorithm (Pearl and Verma 1995, Pearl 2009) that is based on conditional independence testing (or constraint-based approaches). First, we find the skeleton (i.e. undirected causal graph) for each pair of variables $(A,B) \in \vec{V}$, IC searches for a set $V$ such that $(A \perp\!\!\!\perp B|V)$. We start with a fully undirected graph with edges between all nodes (variables). Second, we conduct conditional independent tests between each pair of variables $A$ and $B$ conditioned on the combinations of the set of other variables $S$. We used partial correlation tests to test for independence; if $A$ and $B$ variables are independent given $V$ $(A \perp\!\!\!\perp B|V)$, the edge between $A$ and $B$ should be removed. Repeating this process, the skeleton of the causal graph is generated. In the next step, we search for colliders (i.e. nodes that receive edges from at least two other nodes) by checking for conditional dependencies between independent variables where $A \perp\!\!\!\perp B$, but $A \not\perp\!\!\!\perp B|V$. Lastly, we orient the remaining undirected edges (if possible) by consistency with already-oriented edges (Pearl and Verma 1995, Pearl 2009). We also tested these models by setting across different significance levels ($\alpha$ [0.01, 0.1]) of the conditional independence tests.

## Results

Overall, ten land use categories including natural and non-natural formations between 1985 and 2015 were identified and measured within the catchment areas of the Corumbataí river basin, southeastern Brazil (Supporting information). All catchments had a long history of land use modification to various degrees (Supporting information). The temporal changes in landscape composition measured as the Shannon information entropy increased during the study period, which was mostly driven by changes in agricultural land use expansion (Fig. 2D). Natural forest was temporally stable during over the 30-year period. The spatial co-occurrence of agricultural land use and forest was calculated as well, however they were very highly correlated with the land use values. Changes in landscape configuration were quantified by two spatial entropy metrics; Wasserstein (LCW) and Boltzmann (LCB) entropy. Wasserstein entropy captures the distribution of composition and patch sizes, and was strongly correlated with landscape composition. Boltzmann entropy, which measures the length of the overall perimeter of land use types, showed no strong trend across the study period (Fig. 2C). The two spatial entropy metrics exhibited no association. The analysis showed that landscape composition had the strongest effect on diversity, with the highest average memory weight in 2012 (Fig. 3A). Using the concurrent value (i.e. the value from the year 2015) of landscape composition, the effect is significantly lower ($\rho = 0.22$) compared to incorporating the effect of historical values. Similarly, landscape configuration calculated as the Wasserstein metric, showed the importance of 2012, however its overall effect on biodiversity was lower



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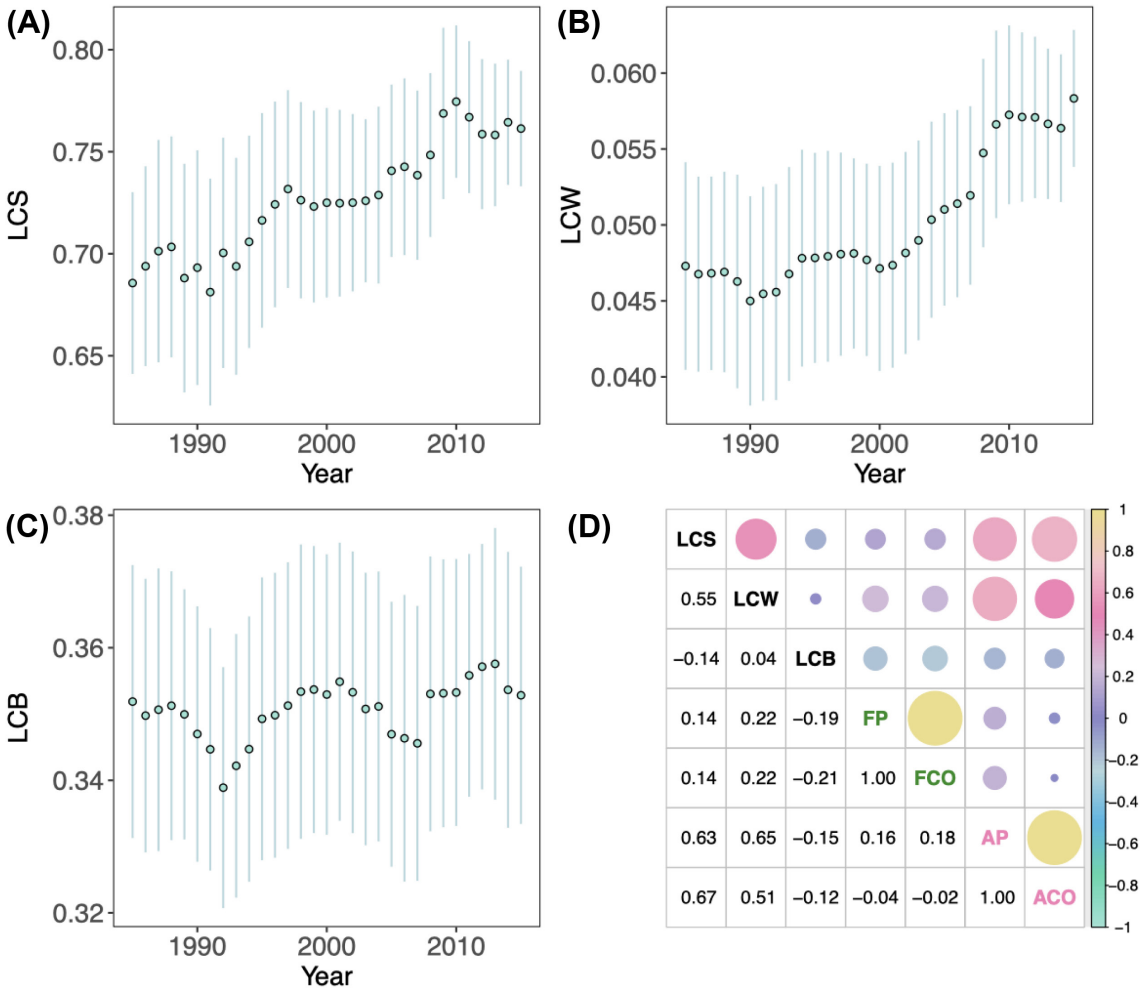


Figure 2. Measuring landscape complexity in river catchments. (A–C) Time series of landscape complexity metrics (Shannon (LCS), Wasserstein (LCW) and Boltzmann (LCB) entropy). Calculated annually over a 30-year period in each catchment (colors). (D) shows the Spearman's correlation between landscape complexity metrics and proportion of agricultural land use (AP) and co-occurrence (ACO) and forest proportion (FP) and co-occurrence (FCO) time series.

than landscape composition (Fig. 3B). The effect of landscape configuration calculated as the Boltzmann metric remained very low after the optimisation (Fig. 3C). We also analysed the effect of agricultural land use on biodiversity, however we did not recover memory effect of the year 2012. The concurrent correlation value between agricultural use and diversity was higher than the optimised values (Supporting information).

Observational data are naturally confounded. So, in order to establish causality between species richness and landscape complexity, and to confirm a true memory effect, we conducted a causal inference analysis. For this analysis, in addition to the three landscape complexity metrics, we included community-weighted traits (predation and body size) and site-specific variables (organic detritus in stream, shading, water temperature and stream width) (Supporting information). We tested the causal graph at different significance levels with and without incorporating the optimised historical landscape complexity metrics. Then, we identified the threshold at which the focus link between species richness and landscape complexity appeared in the causal structure. When we estimated the causal structure with concurrent values (Fig. 4A), landscape complexity did not have a causal effect on diversity or any other variables. However, the inclusion of historical landscape metrics resulted in a different causal structure. We found that historical landscape composition was the only landscape metric that directly affected species richness (Fig. 4B). Higher values of landscape composition, representing more evenly distributed land use classes, increased species richness. The only abiotic variable that directly influenced species richness was the amount of organic detritus, whereby higher amounts of organic detritus in streams contributed to higher diversity. Predators, being on average larger-bodied species, were the most important biotic factor in our analysis that decreased species richness.

## Discussion

Our findings confirmed the presence of memory effects of historical landscape complexity on the biodiversity of tropical



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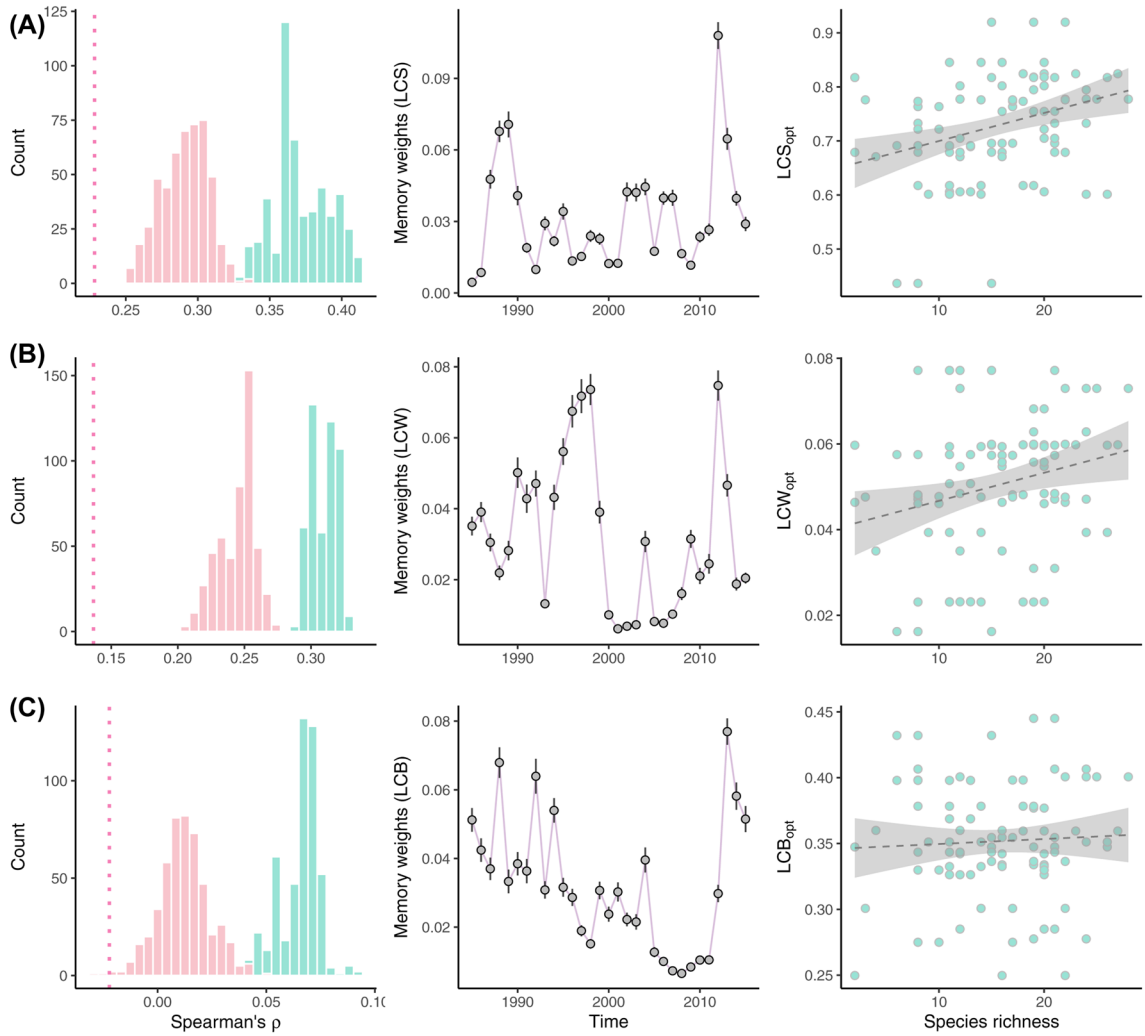


Figure 3. Estimated average memory weights. Memory weights were estimated using a stochastic optimisation approach for the Spearman's ρ between diversity and the three landscape complexity metrics. On the left hand side, the distribution of the values with optimised (blue) and values with random memory weights (pink) of Spearman's ρ are depicted. The vertical dotted line shows the concurrent correlation value. In the middle, the ensemble average of memory weights by year are shown. On the right hand side, the relationship is plotted between the optimised landscape entropy metrics and species richness.

riverine systems. More specifically, historical landscape composition, measured as Shannon information entropy, had a strong influence on species richness. Furthermore, we identified the most relevant point in time when compositional change in land use affected species richness. The analysis revealed that agricultural land expansion drove changes in landscape composition on average, however, the importance of historical agricultural land use did not peak in the same years as the historical landscape composition. The other major changes in many locations around this time period can be attributed to the increase in forest plantations (Supporting information), a pattern that mirrors observations for the entire Atlantic Forest Biome (Joly et al. 2014, Lacerda Silva et al. 2018, Tavares et al. 2019). This simultaneous land use change over time highlights the need for landscape entropy metrics that are able to capture the complex nature of such structural changes in landscapes. Structural changes can happen gradually or abruptly over time, which is reflected in the ecological memory of the community. This means that nonparametric approaches are the most suitable for detection of memory in ecological system Ogle et al. (2015), Benito et al. (2020) opposed to continuous decay functions Khalighi et al. (2022).

Our analysis identified 2012 as a critical period when compositional shifts in land use coincided with changes in species richness. The landscape changes around this period primarily reflected an increase in agricultural use. This trend may have been accelerated by the introduction of Brazil's Native Vegetation Protection Law (NVPL, Law no. 12 651/2012), which relaxed environmental requirements in three key ways: 1) reducing Legal Reserve restoration obligations for pre-July 2008 deforestation on small and medium properties (≤ 4 fiscal modules); 2) permitting limited low-impact activities (e.g. agroforestry, subsistence farming) exclusively for smallholders



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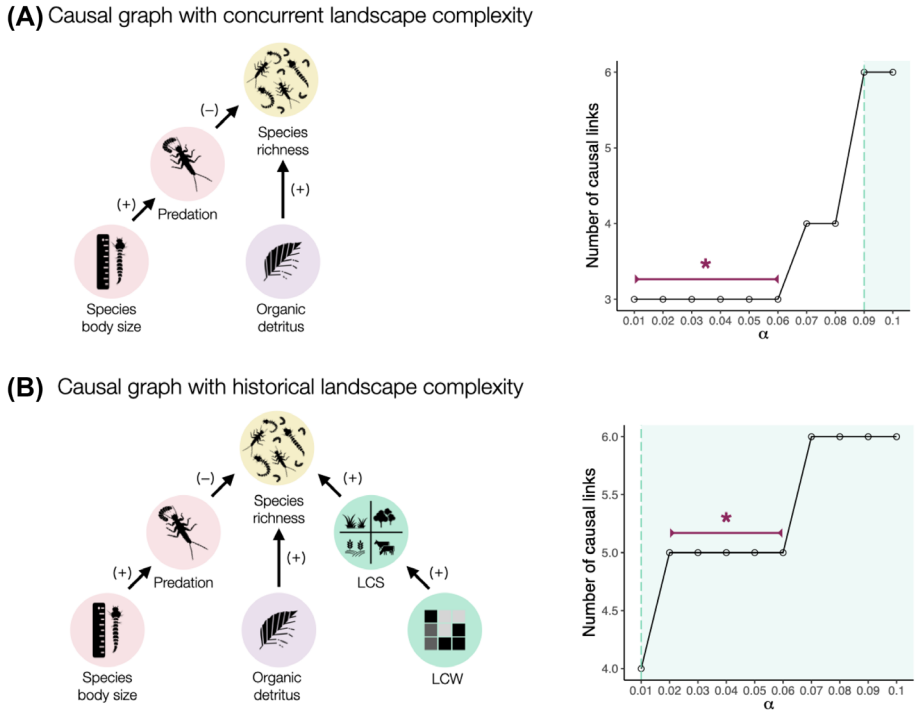


Figure 4. Causal structure. (A) The number of causal links resulted from the causal discovery analysis with concurrent landscape entropy values increased with the significance level (α) of conditional independence tests, where the green dashed line indicates the threshold, where the link between species richness and landscape composition first appeared. (B) The causal structure including historical landscape complexity metrics shows that species richness of freshwater communities is directly affected by historical landscape composition, predation and organic detritus in stream.

in protected areas of permanent preservation (APPs); and 3) offering conditional amnesty for fines tied to illegal deforestation pre-2008, provided landowners enrolled in environmental registries and committed to partial restoration (Brancalion et al. 2016). Notably, the protracted legislative debate over these changes (2009–2012) created expectations of reduced future compliance costs and penalties, particularly for pre-2008 violations. This likely incentivized preemptive clearance by landowners seeking to legalize post-2008 deforestation under the anticipated, more lenient framework. For instance, Nunes et al. (2019) documented elevated deforestation rates in riparian zones relative to non-riparian areas in 2012, suggesting that landowners may have prioritized clearing these ecologically vulnerable areas ahead of the NVPL's implementation.

The structural consequences of such changes likely altered community dynamics in ways that persisted beyond 2012. Riparian forests, which play a disproportionate role in stabilizing microclimates, filtering pollutants and supplying organic matter to aquatic ecosystems (Dala-Corte et al. 2020, Ferreira et al. 2023), are particularly sensitive to land use change (Dias et al. 2010). Reduced riparian forest accelerates soil erosion, amplifying sedimentation that smothers benthic microhabitats critical for many species. These physicochemical shifts homogenize instream conditions, favoring generalist species that thrive in disturbed environments while excluding specialists dependent on cool, shaded and structurally complex habitats (Rosa et al. 2016, Brejão et al. 2018). Such legacy effects, like cumulative sedimentation or delayed extinctions of remnant populations, can create a 'memory' in the system (Harding et al. 1998, Foster et al. 2003, Cuddington 2011, Santos et al. 2020), where species richness reflects prior landscape degradation (e.g. pre-2012 deforestation) long after the initial disturbance.

Our findings align with a previous study in the same region that demonstrated that freshwater insect communities exhibit delayed responses to landscape history, but mediated by the trajectory of forest cover change (Santos et al. 2020). They found that catchments undergoing forest loss showed declining biodiversity even when forest cover temporarily persisted, whereas forest gain trajectories supported recovery. In our study, the 2012 peak in memory effect may thus reflect both the immediate effects of agricultural expansion and the delayed consequences of pre-2012 deforestation (e.g. riparian zone degradation, sediment accumulation), which (Santos et al. 2020) linked to extinction debt. Altogether, these results suggest that Shannon entropy's increase driven by agricultural mosaics does not capture the ecological functionality of retained native vegetation (e.g. stable riparian forests), which likely buffered biodiversity losses despite ongoing degradation. For instance, even fragmented riparian buffers in agricultural catchments may sustain dispersal pathways or organic matter inputs, as seen in Santos et al.'s forest-gain catchments, whereas purely anthropogenic configurations



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lack these elements. We thus suggest that the positive effect of historical complexity on species richness may arise from the interaction between native vegetation and agriculture (e.g. stable forest patches alongside farmland), not agricultural expansion itself.

This distinction between mathematical and ecological complexity underscores the challenges of using entropy metrics to capture biodiversity-relevant landscape features. Capturing the heterogeneity of land use types has been a primary challenge in understanding the interactions between landscapes and underlying ecological processes. The use of different entropy metrics to describe the complexity of landscape mosaics, however, has been deeply rooted in landscape ecology (Vranken et al. 2015, Cushman 2021a). The lack of importance of spatial configuration as a driver of species richness suggests that landscapes are highly structured, rendering configurational information that is redundant in explaining biodiversity patterns. This result suggests that the applied spatial entropy metrics did not capture the most relevant feature of spatial heterogeneity with regard to species richness, as it has been shown before (Nelson and Burchfield 2021). This also aligns with Santos et al.'s (2020) conclusion that delayed biodiversity responses depend on the trajectory of forest cover change, a factor not captured by spatial entropy metrics, which ignore temporal dynamics.

Our causal analysis confirmed that landscape composition was not only associated but also causally related to species richness, and most importantly not confounded by any other factors. Species richness was also directly related to local biotic and abiotic factors, such as predation and amount of organic detritus in streams, respectively. In line with previous studies (Tabi et al. 2023), predation had a negative effect on species richness, a relationship that has been suggested to be particularly stronger in the tropics (Freestone et al. 2011). In the context of freshwater macroinvertebrates, both predatory fish and predatory invertebrates have shown strong effects on prey density. In this study we only took the effect of invertebrate predation into consideration, which has, according to previous studies, more negative effect on the prey invertebrate density and consequently diversity (Wooster 1994).

Body size, which is considered a master trait that scales with many other species traits and interactions (Kleiber 1932), was causally-related to predation, whereby predators tended to have larger body sizes (Woodward and Warren 2007). A higher accumulation of organic detritus in streams contributed to higher species richness. A major proportion of the organic detritus in streams comes from terrestrial areas (Fisher and Likens 1973). However, landscape complexity metrics were not causally connected to species traits, nor to the amount of organic detritus in streams. Because landscape complexity metrics were based on a 30-m resolution of land use types, we may have underestimated the role of riparian buffers of native vegetation, which, even when narrow, are the major contributors of organic matter inputs into streams (Pozo et al. 1997).

Our research demonstrated that discrete historical events of landscape change impose constraints on freshwater biodiversity. This agrees with previous work on biological legacies as part of the ecological memory of communities (Bengtsson et al. 2003). We also confirmed that composition is an essential feature of landscapes to explain species richness in tropical riverine systems. Following a causal inference approach, we showed how landscape complexity and other biotic and abiotic factors influence local freshwater biodiversity. Although more research is needed to explore the connection between biodiversity and landscape complexity and how it varies across different scales and contexts, our research indicates a strong role of landscape-level historical contingencies in predicting freshwater biodiversity.

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### Author contributions

**Andrea Tabi**: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Edineusa Pereira Santos**: Data curation (lead); Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Gabriel Lourenço Brejão**: Data curation (lead); Writing – review and editing (supporting). **Tadeu Siqueira**: Conceptualization (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

### Data availability statement

Data are available on Zenodo: https://doi.org/10.5281/zenodo.15584199 (Tabi et al. 2025).

### Supporting information

The Supporting information associated with this article is available with the online version.

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