Human land-use intensification threatens stream biodiversity and ecosystem functioning

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Abstract

Human land-use is changing Earth's surface, causing a decline in biodiversity and altering ecosystem functioning. However, most of the empirical evidence of land-use impacts in the Neotropics comes from studies investigating isolated land-use types, and the pathways by which intensified land-uses affect ecosystem functioning are largely unknown. Using a database from 61 streams spanning two hyperdiverse Neotropical regions, we demonstrate that intensive human land-uses (agriculture, urbanization, pasture, and afforestation) strongly affect stream biodiversity and functioning. We showed negative associations of agriculture, pasture and urbanization with taxonomic richness, functional diversity, and diversity of trait categories (recruitment and life-history, resource and habitat-use, and body size) of fish, arthropod, and macrophyte. The impacts of intensive land-uses on standing biomass were negative and driven by direct and indirect effects mediated by declines in taxonomic and functional diversities. Our findings highlight that human land use can reshape stream biodiversity, with multiple negative consequences on ecosystem functioning.

INTRODUCTION

Global biodiversity is declining continuously in the Anthropocene (Dirzo et al., 2014), which has been widely attributed to conversion from natural landscapes to agriculture, pastures and urban settlements (Foley et al., 2005; Newbold et al., 2016). Recent findings revealed that intensive human land-uses cause species losses and filter specific sets of functional traits, with homogenizing effects on entire biotic communities (Gámez-Virués et al., 2015; Newbold et al., 2015, 2020). This has severely altered ecosystem functioning, which largely relies on biodiversity (Soliveres et al., 2016; Barnes et al., 2017). Although biodiversity decline is broadly attributed to intensive land-uses, current evidence of land-use impacts is mostly based on studies focused on isolated land-use types, such as urbanization (Monteiro-Júnior et al. 2014), agriculture (Gossner et al., 2016), or pasture (Wang et al., 2018). Consequently, most studies fail to capture the complexity of biodiversity responses to intensive cover of multiple land-uses that operate simultaneously in multiple ways.

Recent evidence shows that taxonomic richness responses to intensive human land-uses differ among trophic groups (Allan et al., 2014; Le Provost et al., 2021), suggesting that using taxonomic richness alone hinders generalizing overall biodiversity responses of entire communities to land-use changes. For improved clarity herein, we define 'community' as all the biota of an ecosystem, and 'assemblage' as any taxonomic subset of the ecosystem (e.g., fish, arthropods, macrophytes; Fauth et al. 1996). The problem of focusing on taxonomic richness can be mitigated by using trait-based approaches, and empirical evidence has shown that different biotic assemblages sharing similar traits often respond similarly to intensive land-use (Gámez-Virués et al., 2015; Newbold et al., 2020). For instance, intensive land-use impacts may be stronger for large apex consumers, as they are disproportionately vulnerable to human pressures (Estes et al., 2011; Enquist et al., 2020). Moreover, biodiversity changes at the level of one assemblage may cascade to other assemblages. For example, there is evidence that changes in plant diversity have strong bottom-up effects on the diversity of arthropods (Scherber et al., 2010). Similarly, subtle shifts in diversity of apex consumers (e.g., fish) may exert cascading effects on the diversity of primary consumers (Duffy et al., 2007; Antiqueira et al. 2018). Such intensive land-use impacts on the diversity of plants and apex consumers likely alter the structure of entire communities with negative consequences for ecosystem functioning.

Human land-uses have severely altered ecosystem functioning through direct and biodiversity-mediated indirect pathways (Barnes et al., 2017). Direct effects involve changes in environmental quality. This is particularly true in aquatic ecosystems where loss of riparian vegetation, decrease in depth, depletion in oxygen availability and increased nutrient inputs cause deterioration in water quality and compromised ecosystem functioning (Walker & Walters 2019). Indirect effects are more difficult to predict because they manifest via multiple biodiversity facets such as taxonomic and functional diversities (Le Provost et al., 2020; Moi & Teixeira de Mello, 2022). Given that both taxonomic richness and functional traits underlie the ability of ecosystems to maintain their functions (Leitão et al., 2018; Le Bagousse-Pinguet et al., 2019), a joint evaluation of these two facets of biodiversity is essential to understanding how intensive human land-use alters ecosystem functioning. Human land-use may weaken the linkages between organisms, threatening, in turn, the capacity of biodiversity to promote ecosystem functioning (Eisenhauer et al., 2019). Recent analyses revealed that the indirect effects of intensive human land-uses could be as strong as associated direct effects (Moi & Teixeira de Mello, 2022). Thus, there is an urgent need to disentangle the direct and indirect effects of human land-uses on ecosystem functioning.

Here, we tested how the intensification of multiple human land-uses types affects taxonomic and functional diversities of three stream assemblages (fish, arthropods and macrophytes). We further investigate the direct and indirect (biodiversity-mediated) effects of intensive land-use cover on ecosystem functioning (Figure S1). We used a database of 61 stream sites dispersed across an area of 507,003 km^2 in two Neotropical areas (Amazonia and Uruguay; Figure 1) that harbor exceptionally high levels of biodiversity (Antonelli et al. 2018). We sampled streams spanning different cover of land-use types: agriculture, pasture, urbanization, and afforestation (Figure 1b,c). Those four human land-uses have expanded globally, largely due to the rapid expansion of commercial monocultures such as soybean and cereals, as well as livestock grazing, cities, and eucalyptus, pine and oil palm plantations (Grimm et al., 2008; Gossner et al., 2016; Maloney et al., 2020). We decomposed functional diversity into three independent trait categories: (i) recruitment and life-history, (ii) resource and habitat use, and (iii) body size, all of which can mediate cross-assemblage responses to intensive land use (Gámez-Virués et al., 2015; Benejam et al., 2016). As a measure of ecosystem function, we focused on standing fish biomass, which is a commonly used metric of ecosystem functioning, underpinning ecosystem services, such as fisheries production and food supply (Benkwitt et al., 2020).

We accounted for the effects of climate (temperature and precipitation), local environmental factors (sediment heterogeneity and water quality deterioration), and stream morphology (depth) to test the hypothesis that taxonomic richness, functional diversity, and diversity of trait categories are negatively affected by intensive human land-use types. We also predicted that (i) fish, arthropod, and macrophytes assemblages would respond differently to different land-use types (Hughes et al., 2009); (ii) apex consumers (fish and arthropods) would be more strongly affected by intensive land-uses than primary producers (macrophytes); (iii) negative effects of intensive human land-uses on plant diversity would have cascading effects on arthropod and fish diversities, leading to declines in standing fish biomass; and (iv) indirect (biodiversity-mediated) effects of intensive land-uses on standing fish biomass would be as strong as the direct effects. Our findings suggest that intensive agriculture, pasture, and urbanization had consistently negative effects on taxonomic and functional diversities of fish, arthropod, and macrophyte assemblages, as well as declines in standing fish biomass, through both direct and indirect effects.

MATERIALS AND METHODS

Study area

We conducted this study in 61 stream sites distributed across two different Neotropical areas (31 in Amazonia and 30 in Uruguay), which are characterized by different climatic conditions. Amazonia has a tropical climate with a mean annual temperature of 26.8ºC and mean precipitation of 2136.8 mm year^{-1}. Uruguay has a subtropical climate, with a mean annual temperature of 17.4ºC and mean precipitation approximately 1203.3 mm year^{-1}. In both Amazonia and Uruguay, land-use types were monitored yearly at the stream site scale. All survey campaigns followed standardized sampling protocols (see sampling of biotic communities in Supporting Information), including fish, arthropods, macrophytes, and regular measurements of in-stream environmental conditions. Specifically, each stream was sampled twice, during a dry and rainy season, totaling 122 sampling events (between 2017 and 2019).

Intensive human land-use cover

The selected stream sites covered a wide range in percentages of agriculture, pasture, urbanization and afforestation, from nearly pristine (natural forest in Amazonia and grasslands in Uruguay) to highly altered areas (e.g., streams with high cover of land-use; Figure 1b,c). The intensive cover of each land-use was quantified based on percentage of the total upstream catchment of each stream site. To do so, each catchment area was delimited using geographical information system (GIS) databases with flow direction and digital elevation, running on QGIS (v. 3.6). The upstream percentages of agriculture, pasture, urbanization, and afforestation were visually assessed using satellite images and digital topographic maps from Google Earth (http://earth.google.com). The cover of each land-use was estimated at a resolution of 30m pixel in the upstream catchment, during the sampling periods (see, Figure 1 b and c).

In addition to the cover of the single land-uses, we created an index of intensive land-use cover (ILUC), which synthesizes the four land-uses (i.e., agriculture, pasture, urbanization, and afforestation) into a single combined land-use intensity measure. In this index, each land-use was standardized relative to its mean cover across all stream sites in each region. The ILUC index was then estimated by summing all standardized land-use types. This ILUC index is analogous to the land-use intensity index developed by Blüthgen et al. (2012), which has been commonly used in recent studies, as it provides a robust estimate of the impact of land-use intensity on biodiversity and ecosystem functioning (Allan et al., 2015; Gossner et al., 2016). The ILUC index is robust and positively correlated with agriculture, pasture and urbanization, thereby reflecting the simultaneous intensity in the cover of these land-uses (Figure S2). The ILUC can be considered 'low' when the catchment is occupied by a low percentage of agriculture, pasture, and urbanization (i.e., low land-use degradation). Conversely, ILUC is considered 'high' and 'very high' when these land-uses occupy more than 40% and 90% of the total catchment, respectively.

Taxonomic richness of fish, arthropod, and macrophyte assemblages

We sampled fish, arthropod and macrophyte assemblages at each stream site. Those three assemblages were selected because they represent diverse biotic components of stream communities, and are associated with key ecosystem processes, such as standing biomass (Moi et al., 2021). All fish were identified to species; arthropods and macrophytes were identified to species or genus. We recorded 141 fish species, 321 arthropod taxa, and 43 macrophyte taxa across the two study areas. Importantly, taxonomic richness of the assemblages did not differ markedly between Amazonia and Uruguay stream sites (see, Figure 1d). However, to account for possible differences in population densities and sampling effort among sites, we estimated taxonomic richness as the Chao index with abundance-based data using the R package iNEXT (Hsieh et al., 2016). The Chao index is based on rarefaction and extrapolation of Hill numbers. It provides an unbiased estimate of asymptotic taxonomic richness, thus enabling comparisons among areas with different potential levels of assemblage richness.

Functional diversity and traits measurements

We selected functional traits related to three major categories: (1) recruitment and life-history, (2) resource and habitat use, and (3) body size (see functional trait measurements in Supplementary Information). We selected eight traits for fish, six for arthropods, and nine for macrophytes (Table 1). All traits were measured by us (e.g., body length) or by using published literature sources (see Table S1). For each trait in each stream, the assemblage abundance-weighted trait variances (CWV) were calculated by following Bernard-Verdier et al. (2012) and Enquist et al. (2015). Importantly, the CWV was computed for each assemblage separately (Table 1). CWV is a measure of trait dispersion within a given assemblage weighted by the abundance of each individual taxon and is considered a measure of functional trait diversity of a given community assemblage (Enquist et al., 2015).

We also calculated a multivariate index of functional diversity based on trait dispersions for each assemblage, i.e., functional dispersion (FD; Laliberté & Legendre, 2010). Functional diversity of the three assemblages had similar values between Amazonia and Uruguay streams sites (Figure 1d). Moreover, to analyze whether intensive human land-uses have similar effects on different traits categories, we calculated the average indices for each trait component using average standardized assemblage community variance values (CWV). For body size, we used maximum length (fish and arthropods) and vegetative plant height (macrophytes). For recruitment and life-history traits, we used traits related to the persistence and reproduction mode of each assemblage, and for resource and habitat use, we selected those traits that are closely related to feeding modes of fish and arthropods, and growth form, and nutrient acquisition to macrophytes (Table 1). Importantly, we did not compare the traits across assemblages, but instead considered the traits individually for each assemblage (see Table S1).

Environmental and climatic covariates

At each 50-m long stream site, a line was drawn perpendicular to the channel every 10 m and at every 25 centimeters of the line, we took sediment samples for later analysis in the laboratory. The sediments were identified according to grain size following the Wentworth scale (Wentworth, 1922). We identified four sediment classes: (i) mud (< 0.00006 mm), (ii) silt (>0.0039 mm and <0.0625 mm), (iii) sand (>0.0625 mm and <2 mm), and (iv) gravel (>2 mm). We measured the percentage of each sediment class in each site. We then used the percentage of sediment classes to estimate the sediment heterogeneity in each site, which was calculated using the coefficient of variation (CV, the ratio between the standard deviation SD and the mean µ [SD/µ]) οφ τηε περςενταγε οφ τηε σεδιμεντ τψπες (Στειν & Κρεφτ, 2015). Ιν αδδιτιον, ωε μεασυρεδ τηε δεπτη οφ εαςη στρεαμ σιτε (μ) ιν σιτυ βψ υσινγ α ρυλερ. Δεπτη ωας μεασυρεδ ατ τηε σαμε ποιντς ας ωε σαμπλεδ συβστρατε.

Το δετερμινε σιτε ωατερ χυαλιτψ, ωε μεασυρεδ δισσολεδ οξψγεν (ΔΟ, μγ Λ^{-1}), τοταλ πηοσπηορυς (ΤΠ, µg L^{-1}), total nitrogen (TN, µg L^{-1}), and conductivity (uS/cm). The sampling method for each variable is provided in the Supplementary Methods. To evaluate patterns of water quality variation, we used a principal component analysis (PCA) approach (Monteiro-Júnior et al., 2014). The first PCA axis synthesized the major source of variation in the original four variables (55.8%), and this axis was negatively correlated with DO (Spearman correlation; $r = –0.560$), and positively correlated with TP ($r = 0.510$), TN ($r = 0.531$), and conductivity ($r = 0.377$; Figure S3). Thus, the distribution of samples along the first PCA axis indicates that as nutrients and conductivity increased, dissolved oxygen decreased, representing a proxy for water quality deterioration.

To estimate the key climatic predictors for each stream site, we determined mean annual temperature [MAT] and mean annual precipitation [MAP]. Both MAT and MAP data were obtained from the WorldClim 2.0

database (http://www.worldclim.org) at a 1-km^2 spatial resolution. MAT and MAP are the most common climatic metrics used in ecological studies and are known to be corrected with biodiversity variation (Patrick et al., 2019; García-Girón et al., 2021).

Ecosystem function: standing biomass

We used standing fish biomass, which is a commonly used aquatic ecosystem function metric (Benkwitt et al., 2020). Fish biomass is also directly related to important ecosystem services, such as fish production and food security (Benkwitt et al., 2020). To estimate standing fish biomass, most fish individuals were weighed on a microbalance (0.01 g precision). For species not weighed on microbalance, we calculated the biomass by using published species-specific length–weight relationships (e.g., Froese & Pauly, 2018). The standing biomass of the entire fish assemblage (g m^{-2}) was then quantified by summing the weight of all individuals at each site and dividing by the site area.

Data analyses

In the first step of our analysis, we investigated the relationships between the intensive cover of agriculture, pasture, urbanization, afforestation, environmental (sediment heterogeneity and water quality deterioration), stream morphology (depth), biogeographical (latitude of stream sites) and climatic variables (MAT and MAP) and (i) taxonomic richness, (ii) functional diversity, and (iii) diversity of three trait categories (recruitment and life-history, resource and habitat use, and body size). To do so, we employed linear mixed-effects models (LMM) in the R 'nlme' package (Pinheiro et al., 2013). The two seasonal sampling periods were nested within each site that was nested within each study area (Amazonia and Uruguay) as a random effect. In the models of functional diversity, we included taxonomic richness as a predictor to account for confounding effects of the local species pool (Mayfield et al., 2010; see the Table S2). Using a stepwise regression procedure all the models were reduced to select the best model (i.e., the model with better predictors for each biodiversity attribute of each assemblage) with the lowest Akaike's Information Criterion corrected for small sample size (AICc). With the best selected models, we then performed a model-averaging procedure based on AICc selection ([?]AICc < 2) to determine parameter coefficients for the best final subset of predictors for each response variable (Tables S2 and S3). This procedure was performed using the dredge function in the MuMIn package (Bartoń, 2014). Visual inspection of residuals using graphical diagnostics (QQ plots and residual plots) revealed that the assumptions of normality and homoscedasticity were met. We assessed the multicollinearity of each predictor variable within models by calculating the variance inflation factor (VIF), and we removed all variables with VIF > 3 (here, latitude). All other variables had VIF < 3, indicating they were not highly correlated (Figure S4 and Table S3). *A priori* , we standardized all predictors (z-scored: centered to mean and divided by the SD) to interpret slope estimates on a comparable scale (Schielzeth, 2010). To infer the relative importance of each predictor on different biodiversity components, we computed the percentage of variance each explained according to Le Provost et al. (2020). To do so, we compared the absolute value of their standardized coefficients with the sum of all standardized regression coefficients of all predictors considered in the best models. This approach is analogous to a variance partitioning analysis because all predictors were previously transformed to z-scores (Le Bagousse-Pinguet et al., 2019).

We also applied structural equation models (SEM) to disentangle the direct and biodiversity-mediated indirect pathways by which intensive land-use cover (ILUC) influenced standing biomass. We fitted separate SEMs to taxonomic richness and functional diversity. Environmental (water quality, heterogeneity), stream morphology (depth), and climate (temperature and precipitation) covariates were also included in SEMs, and all paths specified were theoretically supported (Figure S1). For simplicity, we only use the ILUC, as it is strongly related to agriculture, pasture, and urbanization (Figure S2). To evaluate whether the ILUC effects differed between Amazonia and Uruguay, we constructed SEMs using multi-level analysis considering the two areas separately (results presented in supplementary material, Figure S5, Table S10). This approach allowed us to implement a model-wide interaction and to test each path interaction within the model. To reduce the number of predictors, we performed a model selection based on Akaike's Information Criteria corrected for small sample size (AICc). In this selection, the full model (including all predictors) was compared with the reduced model using AICc ($\mathrm{AIC}_{\mathrm{fullmodel}} - \mathrm{AIC}_{\mathrm{reducedmodel}}$). We considered $\Delta\mathrm{AICc} > 2$ units as distinguishing between the full and the reduced models. Notably, the full and reduced final models differed in ΔAICc > 10 (Table S8). The lack of direct or indirect effect on standing biomass was used as a criterion to remove predictors. SEMs were constructed with the same random factor design as previous LMMs using linear mixed effects models (Pinheiro et al., 2018) with the 'psem function' from the 'piecewiseSEM' package (Lefcheck, 2016). We present the standardized coefficient for each path and estimated the indirect effects by coefficient multiplication. Path significance was obtained by maximum likelihood, and model fit was evaluated using Shipley's test of d-separation through Fisher's C-statistic ($p > 0.05$ indicates no missing path). All analyses were conducted in R version 4.1.1. (R Core Team, 2021).

RESULTS

Human land-uses drive assemblage taxonomic & functional diversities

Despite considering environmental and climate-related biodiversity predictors, intensive human land use was a key driver, accounting for 83%, 66% and 83% of the explained variance in taxonomic richness for fish, arthropod, and macrophyte, respectively (Figure 2). Intensive human land use also accounted for 74%, 36%, and 26% of the explained variance in functional diversity for fish, arthropods, and macrophytes (Figure 2). In particular, agriculture, pasture, and urbanization were significantly and negatively related with taxonomic richness and functional diversity of the three assemblages (Figure 3a, Table S6). However, land-use types had contrasting effects on diversity components of fish, arthropod and macrophyte. For instance, agriculture and urbanization were most strongly associated with fish taxonomic richness, whereas pasture and urbanization were most strongly associated with arthropod and macrophyte taxonomic richness (Figure 3b). Similarly, agriculture, pasture, and urbanization were most strongly associated with fish functional diversity, whereas urbanization was most strongly associated with functional diversity of arthropods, and agriculture was most strongly associated with functional diversity of macrophytes (Figure 3c).

Intensive human land use was also important in explaining the diversity of the three trait categories (Table S7). Human land-use accounted for 43%, 24%, and 39% of the explained variance for recruitment and life-history of fish, arthropod, and macrophyte respectively (Figure 4). Similarly, human land-use explained 60%, 60%, and 26% of the variance in diversity of resource and habitat-use for fish, arthropod, and macrophyte (Figure 4). Lastly, human land-use explained 34%, 20% and 43% of the variance in diversity of body size for fish, arthropod, and macrophyte (Figure 4). In general, agriculture and urbanization were negatively associated with diversity of recruitment and life-history, resource and habitat-use, and body size of three assemblages. Afforestation was positively related with diversity of resource and habitat-use of fish and arthropods (Figure 5a). Diversities of trait categories of fish, arthropod, and macrophyte were also significantly related to different land-use types (Figure 5b-d).

Direct and indirect effects of ILUC on ecosystem functioning

The SEM indicated a consistent negative effect of ILUC on standing fish biomass (Table S10). Overall (including Amazon and Uruguay streams) the total effect of ILUC on standing fish biomass was composed of a direct negative path from ILUC (–0.126; Figure 6a,b) and indirect paths. The indirect paths were mediated by negative effects on fish and macrophyte taxonomic richness (Figure 6c; SEM: fish richness: –0.063, macrophyte richness: –0.110) and fish functional diversity (Figure 6d; SEM: fish functional diversity: –0.150). Therefore, indirect effects of ILUC on ecosystem functioning were as strong as direct effects. Notably, there were strong positive links among the three assemblages – manifested through positive effects of macrophytes on arthropod and fish taxonomic richness and functional diversity (Figure 6). Similarly, arthropod taxonomic richness and functional diversity positively affected fish taxonomic richness and functional diversity (Figure 6). Comparing the results of SEM between the two study regions (Amazonas and Uruguay separately), we observed stronger links among taxonomic richness and functional diversity of fish, arthropod, and macrophyte in Amazonia than in Uruguay streams (Figure S5, Tables S8 and S9).

DISCUSSION

Our results revealed that the intensive cover of human land use (i.e., agriculture, pasture, and urbanization) is negatively associated with multiple biodiversity facets of three different stream assemblages. Although our survey did not encompass all possible local environmental factors (e.g., habitat size, drainage area, riparian condition), it showed that impacts of human land use on taxonomic and functional diversities of fish, arthropod, and macrophyte were consistent even accounting for environmental, stream morphology, and climate predictors. These results are robust and represent the first spatially extensive analysis of the response of multiple biodiversity facets across entire aquatic communities to intensive human land-use in the Neotropics. Our finding is in line with previous analyses from the terrestrial realm (Newbold et al., 2015; Gossner et al., 2016), showing the negative impacts of intensive human land-use also on hyperdiverse aquatic systems. Because diversity of fish, arthropod and macrophyte assemblages responded to different human land-use types, we believe that those different land uses may act in concert to drive biodiversity patterns across multiple assemblages. Consequently, the focus on isolated land-use types likely hinders our ability to understand and manage biodiversity response to human activities across landscapes worldwide. More studies should focus on the combined impacts of multiple human stressors if we are to effectively mitigate biodiversity losses and safeguard ecosystem functioning (e.g., Benkwitt et al., 2020)

Trait diversity has been reported to decline with increasingly intensive human land-use (Newbold et al., 2020). We demonstrated significant declines in diversity of recruitment and life history, resource and habitat use, and body size of different assemblages to intensive covers of agriculture, pasture, and urbanization. Those land uses often degrade stream environmental conditions by (i) reducing habitat and resource availability; (ii) increasing over-exploitation, mainly of large individuals; and (iii) compromising water quality via excessive inputs of nutrients, pesticides, fertilizers and sewage (Allan et al., 2005; Walker & Walters, 2019; Marques et al., 2021). Here, there was a marked decline of sediment heterogeneity, stream depth, and water quality with increasingly intensive land-uses. These human-induced stressors act as filters selecting traits affecting organism resistance to disturbance, thereby reshaping biotic community composition (Williams et al., 2020). Lower habitat availability (due to sediment simplification) and stream depth both reduce availability of feeding niches (Leitão et al., 2018, Price et al., 2019), which favors generalist consumers and filters out specialized consumers including many apex predators (Walker & Walters, 2019; Cantanhêde et al., 2021). Consequently, there was a drastic reduction in the diversity of traits related to resource and habitat-use. Environmental degradation also restricts the phenology of organisms, including life histories (Morellato et al., 2016). We found that organisms with long life spans and small geographical ranges could not persist in streams with intensive agriculture, pasture, or urbanization. Consequently, the diversity of life history traits decreased. Intensive human land-use has disproportionately strong impacts on large-sized organisms because they are more vulnerable to loss of habitat and need a greater diversity of resources, which are scarcer under high land-use intensity (Newbold et al., 2015). This is in agreement with the strong declines in body size of fish and arthropods, and macrophytes, in streams experiencing intensive agriculture, pasture and urbanization catchment coverage. Our findings suggest a loss of trait diversity in human-altered ecosystems that is likely to impair ecosystem functioning (Frainer et al., 2017; Le Bagousse-Pinguet et al., 2021).

The structural equation modelling revealed that increased cover of human land-use affected ecosystem functioning through direct and biodiversity-mediated, indirect pathways. The two pathways were consistent regardless of the study area (Amazonia and Uruguay), suggesting a broad-scale decline of standing fish biomass resulting from human land-use intensification. The direct effect of ILUC on standing biomass is intuitive because fish biomass often declines in human-dominated systems as a result of fishing pressure, pollution and eutrophication (Duffy et al., 2016). Importantly, however, intensive land-use cover had a strong negative effect on taxonomic richness and functional diversity, particularly of fish and macrophytes, which ultimately resulted in net negative effects on standing fish biomass. Considering the trophic roles of macrophytes (primary producers) and fish (apex consumers), this indicates that intensive land-use can disrupt the bottom-up and top-down control of ecosystem biomass production. Bottom-up control of biomass production has been widely reported because macrophytes are basal organisms that structure habitats and enhance biomass production (Teixeira de Mello et al., 2015; Marsh et al., 2021). Fish are major apex consumers in aquatic ecosystems, and they can maintain high biomass despite relatively high human pressures (Duffy et al., 2016). Arthropods enhanced fish taxonomic and functional diversities, which indirectly increased standing fish biomass. This suggests that arthropods indirectly affected stream functioning through fish biodiversity. Arthropods are important food resources for fish, and their diversity is often linked to greater production of fish biomass (Correa & Winemiller, 2018). Although intensive human land use had negative effects on biodiversity, this did not break down positive biodiversity-ecosystem functioning relationships. This finding suggests that biodiversity can buffer ecosystem functioning against human pressures (Isbell et al., 2015). Thus, preserving high levels of biodiversity, including both taxonomic and functional components, is essential to maintain healthy ecosystem functioning in light of increasing human pressures.

By decomposing SEM results between study areas (Amazonia and Uruguay), we found stronger associations between diversity of different assemblages in Amazonia than in Uruguay. In general, the positive association between fish and arthropod diversity was stronger in Amazonia. This can be partly explained by the higher macrophyte diversity in Amazonia, which likely facilitates coexistence between fish and arthropods via increasing habitat heterogeneity (García-Girón et al., 2020; Monato et al., 2021). The taxonomic richness and functional diversity of macrophytes were 51% and 18% higher in Amazonia (29 species; FD= 2.8) than in Uruguay (14 species; FD= 2.3). Combined with the fact that the positive association between macrophyte on arthropod diversity was also stronger in Amazonia, these findings imply a strong bottom-up effect from the primary producers, favoring positive relationships between fish and arthropod assemblages diversities.

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Assemblage functional diversity increased with assemblage taxonomic richness, indicating relatively low functional redundancy in the study ecosystems. The low functional redundancy suggests that fish, arthropod, and macrophyte are mostly composed of taxa with sets of different traits. This agrees with the low functional redundancy that is predicted by biogeographical hypotheses for the Neotropics (see, Leitão et al., 2016; Rodrigues-Filho et al., 2018). This implies that Neotropical biodiversity is particularly vulnerable to human pressures — species loss will likely be closely accompanied by declines in functional diversity. In addition, consistent positive associations between diversities of different assemblages highlight that biodiversity is closely related in these streams. Therefore, the diversity loss of any taxonomic group would result in cascading effects on the diversity of other taxonomic groups. We draw this conclusion based on the evidence that the negative effect of intensive land-use on macrophyte diversity indirectly affected fish and arthropod diversities, which likely unraveled the interactions between these consumers (Figure 6). We argue that preserving biodiversity requires mutual conservation of different facets of biodiversity across multiple Neotropical assemblages.

The conversion of natural landscapes for human use is a global problem that has transformed Earth‘s surface (Foley et al., 2005). Our dataset revealed how intensive cover of human land-use types differentially affect the taxonomic and functional diversities of three key stream assemblages. We demonstrated that taxonomic richness, functional diversity, and diversity of trait categories of fish, arthropod and macrophyte strongly declined with intensive cover of agriculture, pasture and urbanization. Our findings indicate that biodiversity conservation strategies should focus on joint management of multiple pressures at the catchment level. Biodiversity conservation will become even more challenging in the coming decades given projected increases in human population and climate chaos (United Nations 2018). We have shown that intensive human land uses reduce standing fish biomass, which occurs both directly and indirectly (mediated by taxonomic and functional diversities), by reducing the levels of biodiversity needed to maintain this function. This illustrates that intensive human land use impairs ecosystem function through multiple biodiversity facets, which suggest that biodiversity conservation alone is unlikely to suffice for sustaining ecosystem functions if underlying human pressures are not reduced.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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Table 1. Traits considered in this study were grouped into three broad categories: (i) recruitment and life-history traits, (ii) resource and habitat use traits, and (iii) body size traits.

Assemblage	**Trait diversity category**	**Traits**	**Units**
Fish	Body size	maximum length	cm
	Recruitment and life-history	eggs parental care	(i) yes, (ii) no
		larval parental care	(i) yes, (ii) no
		reproduction mode	(i) viviparous, (ii) oviparous
		fecundity mode	(i) internal, (ii) external
	Resource and habitat use	feeding modes	(i) piscivore, (ii) omnivore, (iii) detritivore, (iv) herbivore, (v) insectivore, (vi) invertivore
		mouth position	(i) subterminal, (ii) terminal, (iii) superior, (iv) low
		position in water	(i) pelagic, (ii) benthopelagic, (iv) benthic
Arthropods	Body size	maximum length	cm
	Recruitment and life-history	respiration mode	(i) air, (ii) branchial, (iii) integumentary, (iv) plastron, (v) stigmata
		reproduction cycle	(i) univoltine, (ii) semivoltine, (iii) plurivoltine
		refuge use	(i) networks, (ii) sand and debris, (iii) wood, (iv) builders, (v) no refuge
	Resource and habitat use	feeding mode	(i) shredders, (ii) predators, (iii) scrapers, (iv) collector-gatheres, (v) collector-filtering, (vi) piercers
		habitat use	(i) burrowers, (ii) climbers, (iii) skaters, (iv) skaters, (v) sprawlers, (vi) swimmers
Macrophytes	Body size	plant vegetative height	m
	Recruitment and life-history	seed dry mass	mg

Assemblage	Trait diversity category	Traits	Units
		propagation mode	(i) seed/ spore, (ii) mostly by seed/spore, also vegetatively, (iii) by seed/spore and vegetatively, (iv) mostly vegetatively, also by seed/spore, (v) vegetatively
		main dispersal agent	(i) passive, (ii) wind, (iii) water, (iv) animals (v) wind+water, (vi) wind+animals, (vii) water+animals, (viii) wind+water+animals
		plant phenology	(i) perennial, (ii) annual/short-lived perennial
	Resource and habitat use	growth form	(i) submerged, (ii) emergent, (iii) free-floating, (iv) rooted-floating
		leaf compoundness	(i) simple, (ii) compound
		leaf area	mm^2/mg^{-1}
		specific leaf area	mm^2/mg^{-1}

FIGURE CAPTIONS

Figure 1. Map representing (a) the study area in Amazonia and Uruguay, (b) intensive land-use cover of Amazon stream catchments, (c) intesive land-use cover of Uruguay stream catchments, and (d) taxonomic richness and functional diversity of the three assemblages (fish, arthropods, macrophytes). Land use information was extracted from MapBiomas (https://mapbiomas.org/colecoes-mapbiomas-1?cama_set_lan.). Importantly, study sites included two river basins in Amazonia and almost the entire territorial aea of Uruguay. Whereas Amazonia is dominated by dense tropical forest, Uruguay is dominated by grassland. Note that both study areas are strongly influenced by human land use, including agriculture and pasture (strong yellow), urbanization (red), and afforestation by non-native pine and eucalyptus (faint green). Finally, taxonomic and functional diversities of the three assemblages do not differ markedly between the two study regions, although Amazonia supports slightly higher taxa richness, especially for arthropods and macrophytes.

Figure 2. Relative importance of intensive human land-use types, local environmental variables, stream morphology (depth), climatic variables, and the regional taxa pool in explaining variation in taxonomic richness and functional diversity of fish, arthropod and macrophyte assemblages across the Neotropical stream sites studied. Explained variance (relative effect, % R^2) was calculated for each group of predictors using a model averaging procedure. All predictors were z-standardized to facilitate interpretation of parameter estimates on a comparable scale. Importantly, the contribution of stream morphology is not shown in the graph because depth was removed during model selection (AICc).

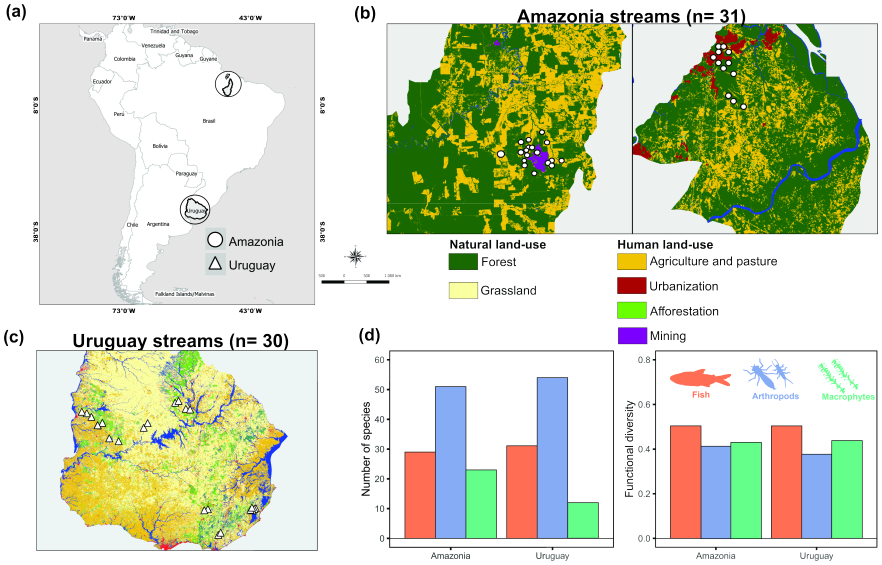
Figure 3. Responses of fish, arthropod and macrophyte assemblage taxonomic richness and functional diversity to human land-use types. (a) Effects of best predictors, including land-use types (agriculture,

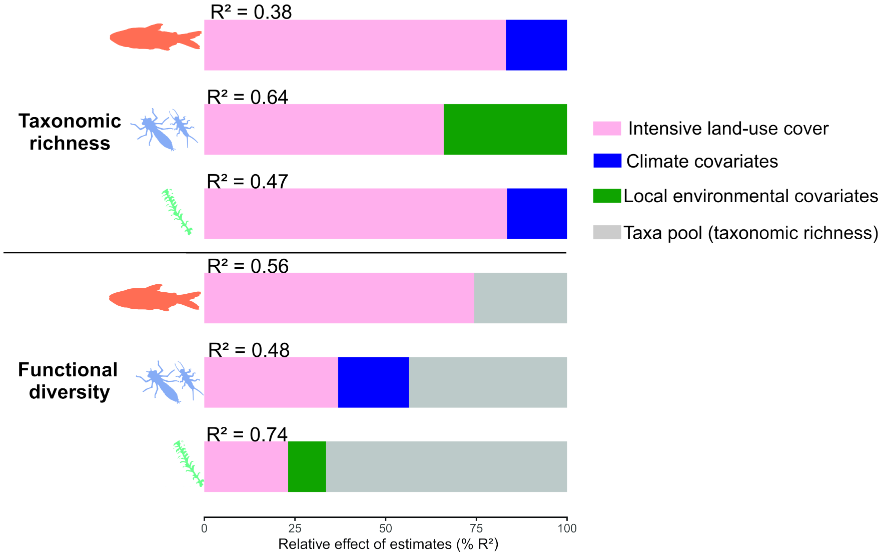
pasture, and urbanization), climate and local environmental variables on taxonomic richness and functional diversity of fish, arthropod, and macrophyte assemblages. Effect sizes were adjusted using linear mixed-effects models. Colors represent different assemblages: orange (fish), blue (arthropods), and green (macrophytes). See Supplementary Table S6 for the model output summaries. Relationships of the land-use types selected during backward selection with (b) taxonomic richness and (c) functional diversity of the assemblages. Lines show model fits and colored shaded areas correspond to the 95% confidence interval from linear mixed effect models (LMM). Model predictions were calculated using a model averaging procedure (see Methods). Land-use types were scaled to interpret parameter estimate on a comparable scale. *P* -values of the best predictors for each model are displayed. Symbols (n = 122) correspond to observed data and their shape indicates the region: circle (Amazonia) and triangle (Uruguay).

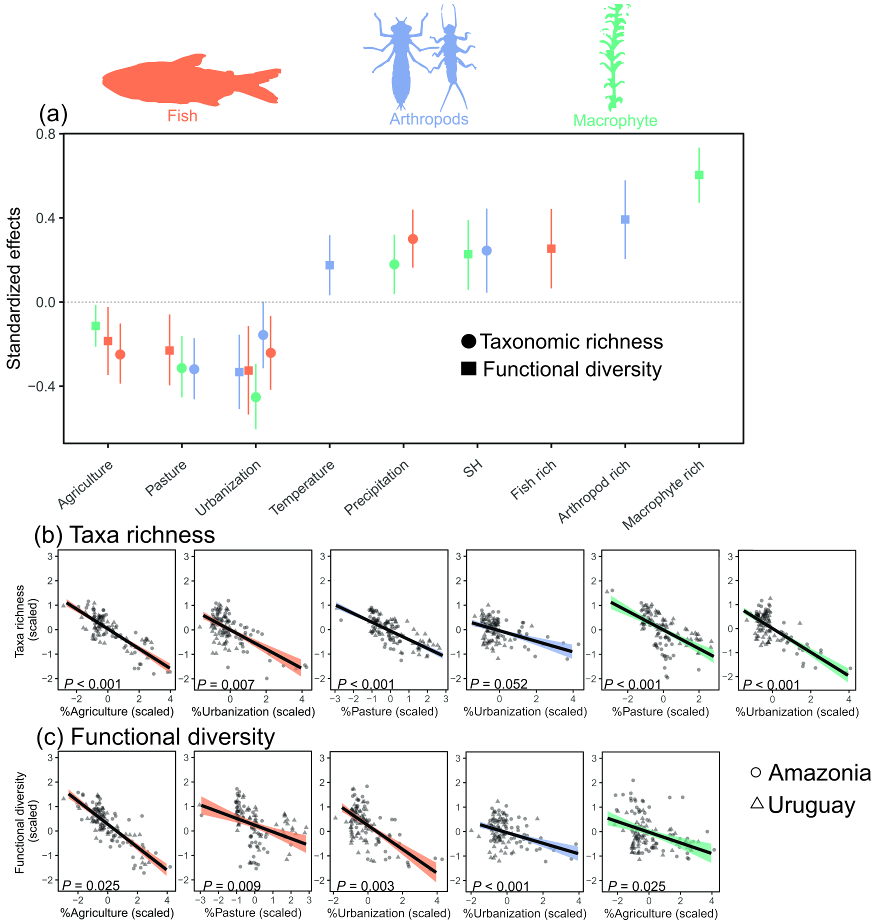
Figure 4. Relative importance of human land-use types, local environmental variables, stream morphology (depth), climate variables, and the regional taxa pool in explaining the diversity trait category (i.e., recruitment and life-history, resource and habitat use, and body size) of fish, arthropod, and macrophyte assemblages across the study sites. Explained variance (relative effect, % $\mathbf{R^2}$) was calculated for each group of predictors, resulting from the model averaging procedure. All predictors were z-standardized to allow the interpretation of parameter estimates on a comparable scale. Importantly, the contribution of stream morphology is not shown in the graph because depth was removed during model selection (AICc).

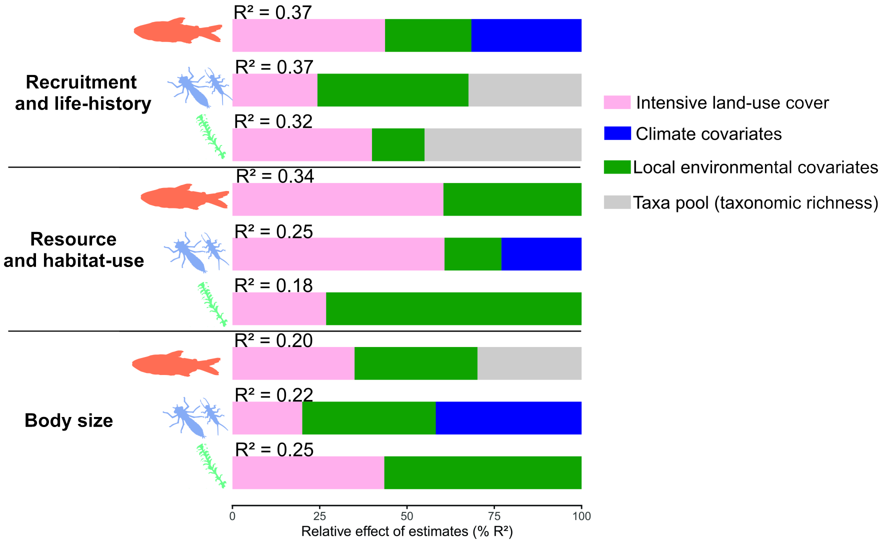
Figure 5. Responses of fish, arthropod and macrophyte trait diversity to human land-use types. (a) Effects of best predictors, including land-use types, climatic and local environmental variables on recruitment and life-history, resource and habitat-use, and body size of fish, arthropods, and macrophytes. Effect sizes were adjusted using linear mixed-effects models. Colors represent assemblages: orange (fish), blue (arthropods), and green (macrophytes). See Supplementary Table S7 for the model output summaries. Relationships of the land-use types selected during backward selection with (b) recruitment and life-history, (c) resource and habitat-use, and (d) body size. Lines show the best model fits and colored shaded areas correspond to the 95% confidence interval from linear mixed effect models (LMM). Model predictions were calculated using a model averaging procedure (see Methods). Land-use types were scaled to interpret parameter estimate on a comparable scale. *P* -values of the best predictors for each model are displayed. Symbols (n = 117) correspond to observed data and their shape indicates the region: circle (Amazonia) and triangle (Uruguay).

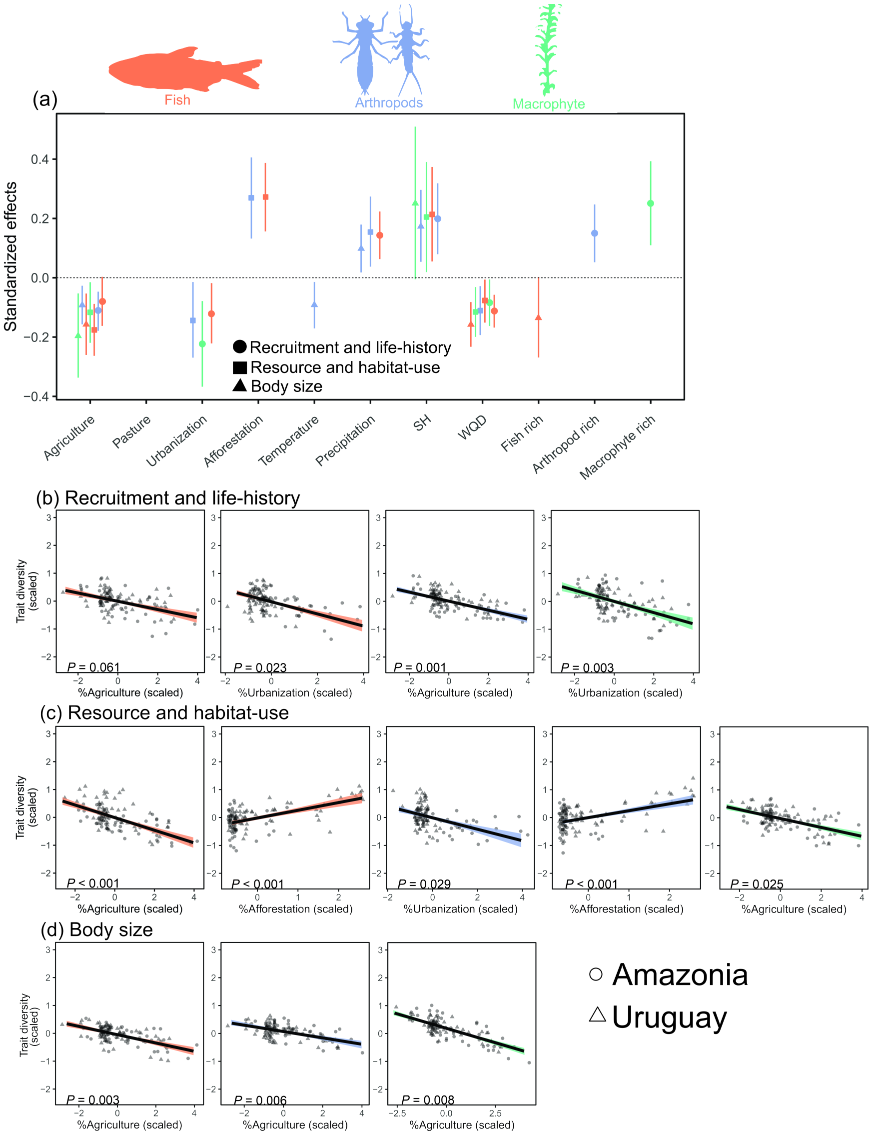
Figure 6. Structural equation models (SEMs) showing the overall (Including both Amazonia and Uruguay streams) direct and cascading effects of intensive land-use cover on standing fish biomass mediated by (a) taxonomic richness and (b) functional diversity of fish, arthropod, and macrophyte. Models accounted for local environmental and climate predictors. Model selection and simplification steps using Akaike Information Criteria (AIC) are available in Supplementary Information, Table S8. The full model fitted well to the data for both (a) species richness (Fisher's C = 1.739, $P = 0.419$) and (b) functional diversity (Fisher's C = 3.307, $P = 0.508$) models. Results for the multi-group approach (i.e., Amazonia and Uruguay separately) are provided in Supplementary Information, Table S10. Solid black arrows are significant pathways (P [?] 0.05, piecewiseSEM), whereas the thickness of the arrows represent the magnitude of the standardized regression coefficient. Numbers in the arrows are the standardized path coefficients of the relationship, and R^2 values for each model are given in the boxes of the variables. Significance levels of each predictor are $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. (c) and (d) show the standardized indirect effects of the ILUC on fish standing biomass mediated by taxonomic richness and functional diversity, respectively. Effects are derived from the SEMs, and standardized effect is computed based on multiplication of coefficients. Significance of indirect effects is calculated based on significance of direct effects. Importantly, water quality parameters (nutrient, oxygen, and conductivity) and stream morphology (depth) were removed during model selection (AICc; see Table S8). Although precipitation was selected (AICc) for modeling taxa richness, temperature was selected for modeling functional diversity.

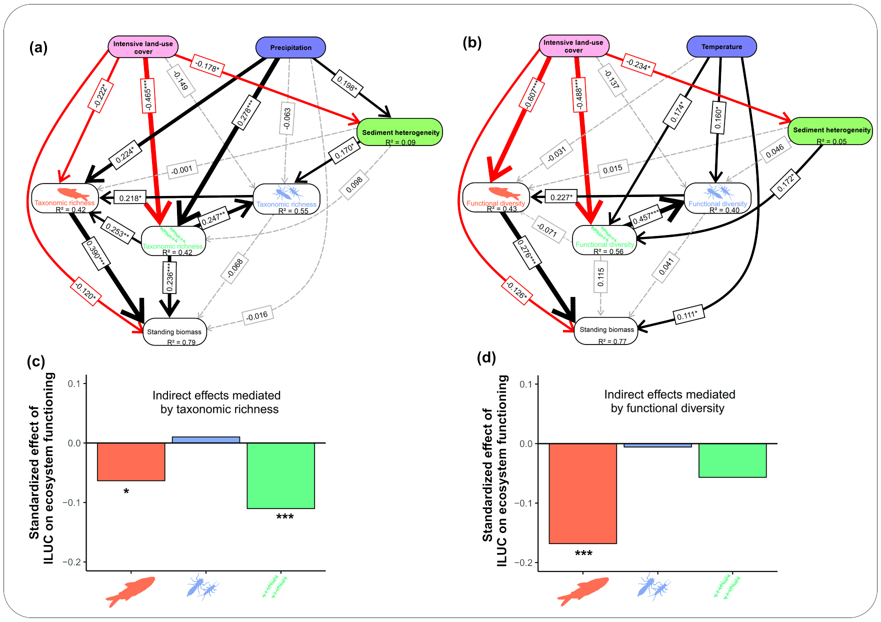

(a)
73°0'W
43°0'W
8°0'S
38°0'S
Panamá
Trinidad and Tobago
Venezuela
Guyana
Guyane
Colombia
Ecuador
Perú
Brasil
Bolivia
Paraguay
Chile
Argentina
Uruguay
Falkland Islands/Malvinas
Amazonia
Uruguay
(b)
Amazonia streams (n= 31)
Natural land-use
Forest
Grassland
Human land-use
Agriculture and pasture
Urbanization
Afforestation
Mining
(c)
Uruguay streams (n= 30)
(d)
Number of species
0
10
20
30
40
50
60
Amazonia
Uruguay
Functional diversity
0.0
0.2
0.4
0.6
0.8
Fish
Arthropods
Macrophytes
Amazonia
Uruguay


R^2 = 0.38
R^2 = 0.64
R^2 = 0.47
R^2 = 0.56
R^2 = 0.48
R^2 = 0.74
Taxonomic richness
Functional diversity
Intensive land-use cover
Climate covariates
Local environmental covariates
Taxa pool (taxonomic richness)
0
25
50
75
100
Relative effect of estimates (% R^2)


Fish
Arthropods
Macrophyte
(a)
Standardized effects
0.8
0.4
0.0
−0.4
● Taxonomic richness
■ Functional diversity
Agriculture
Pasture
Urbanization
Temperature
Precipitation
SH
Fish rich
Arthropod rich
Macrophyte rich
(b) Taxa richness
Taxa richness (scaled)
P < 0.001
%Agriculture (scaled)
P = 0.007
%Urbanization (scaled)
P < 0.001
%Pasture (scaled)
P = 0.052
%Urbanization (scaled)
P < 0.001
%Pasture (scaled)
P < 0.001
%Urbanization (scaled)
(c) Functional diversity
Functional diversity (scaled)
P = 0.025
%Agriculture (scaled)
P = 0.009
%Pasture (scaled)
P = 0.003
%Urbanization (scaled)
P < 0.001
%Urbanization (scaled)
P = 0.025
%Agriculture (scaled)
○ Amazonia
△ Uruguay


Recruitment and life-history
R² = 0.37
R² = 0.37
R² = 0.32
Resource and habitat-use
R² = 0.34
R² = 0.25
R² = 0.18
Body size
R² = 0.20
R² = 0.22
R² = 0.25
Intensive land-use cover
Climate covariates
Local environmental covariates
Taxa pool (taxonomic richness)
0
25
50
75
100
Relative effect of estimates (% R²)


Fish
Arthropods
Macrophyte
(a)
Standardized effects
0.4
0.2
0.0
−0.2
−0.4
● Recruitment and life-history
■ Resource and habitat-use
▲ Body size
Agriculture
Pasture
Urbanization
Afforestation
Temperature
Precipitation
SH
WQD
Fish rich
Arthropod rich
Macrophyte rich
(b) Recruitment and life-history
Trait diversity (scaled)
P = 0.061
%Agriculture (scaled)
P = 0.023
%Urbanization (scaled)
P = 0.001
%Agriculture (scaled)
P = 0.003
%Urbanization (scaled)
(c) Resource and habitat-use
Trait diversity (scaled)
P < 0.001
%Agriculture (scaled)
P < 0.001
%Afforestation (scaled)
P = 0.029
%Urbanization (scaled)
P < 0.001
%Afforestation (scaled)
P = 0.025
%Agriculture (scaled)
(d) Body size
Trait diversity (scaled)
P = 0.003
%Agriculture (scaled)
P = 0.006
%Agriculture (scaled)
P = 0.008
%Agriculture (scaled)
○ Amazonia
△ Uruguay


(a)
Intensive land-use cover
Precipitation
Sediment heterogeneity
R² = 0.09
-0.178*
0.198*
-0.222*
-0.465***
-0.149
0.278***
-0.063
0.224*
-0.001
0.170*
0.098
Taxonomic richness
R² = 0.42
0.218*
Taxonomic richness
R² = 0.55
0.247**
0.253**
Taxonomic richness
R² = 0.42
0.390***
0.236***
-0.068
-0.016
-0.120*
Standing biomass
R² = 0.79
(b)
Intensive land-use cover
Temperature
Sediment heterogeneity
R² = 0.05
-0.234*
-0.607***
-0.488***
-0.137
0.174*
0.160*
-0.031
0.015
0.046
0.172*
Functional diversity
R² = 0.43
0.227*
Functional diversity
R² = 0.40
0.457***
-0.071
Functional diversity
R² = 0.56
0.276***
0.115
0.041
-0.126*
0.111*
Standing biomass
R² = 0.77
(c)
Standardized effect of ILUC on ecosystem functioning
0.1
0.0
-0.1
-0.2
Indirect effects mediated by taxonomic richness
*
***
(d)
Standardized effect of ILUC on ecosystem functioning
0.1
0.0
-0.1
-0.2
Indirect effects mediated by functional diversity
***