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Drivers of spatio-temporal dissimilarity in community composition: temporal changes in land use and environmental heterogeneity

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2020

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Tese apresentada ao Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais do Departamento de Biologia, Centro de Ciências Biológicas da Universidade Estadual de Maringá, como requisito parcial para obtenção do título de Doutor em Ciências Ambientais.
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Orientadora: Dr.^a Carla Simone Pavanelli

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'The Answer to the Great Question...
Of Life, the Universe and Everything...Is...Forty-two.'

Douglas Adams

Determinantes da dissimilaridade espaço-temporal na composição de comunidades: mudanças temporais no uso da terra e heterogeneidade ambiental

RESUMO

A biodiversidade está constituída por múltiplos aspectos ou facetas que mudam no espaço e tempo. Ante um cenário de perda de diversidade em resposta a impactos antropogênicos é urgente determinar quais aspectos da biodiversidade estão sendo alterados e os determinantes de tais mudanças. Usando informação de abundância de espécies, suas relações evolutivas e características ecológicas, determinamos como a dissimilaridade da composição entre comunidades de peixes é influenciada por mudanças no uso da terra ao longo do tempo e mudanças da heterogeneidade ambiental no espaço. Na primeira abordagem, podemos ver que ao longo do tempo as mudanças no uso da terra afetam principalmente a substituição de linhagens evolutivas e características ecológicas. Na segunda abordagem, encontramos evidência de que as comunidades estão sendo homogeneizadas taxonômica e funcionalmente ao longo do tempo, provavelmente devido à perda de diversidade em características relacionadas ao uso de *habitat*. Ademais, encontramos que as características ecológicas contribuem de forma diferente para as mudanças na composição funcional e apresentam diferenças na resposta à heterogeneidade ambiental. Esses resultados suportam evidências de que impactos antropogênicos estão levando a mudanças nas comunidades biológicas, as quais estão tendendo a perder diversidade mediante homogeneização taxonômica e funcional.

Palavras-chave: Peixes de água doce. Uso do solo. Heterogeneidade. Homogeneização. Diversidade beta

Drivers of spatio-temporal dissimilarity in community composition: temporal changes in land use and environmental heterogeneity

ABSTRACT

Biodiversity encompasses multiple aspects or facets changing in space and time. Before a loss of biodiversity in response to anthropogenic impacts it is of the utmost importance to determine what facets of biodiversity are altered and the determinants of such changes. By using information from species abundance, their evolutionary relatedness, and ecological traits we determine how the dissimilarity in composition of fish communities is influenced by temporal changes in land use and changes in environmental heterogeneity across space. In the first approach, we can see that changes in land use over time affected mainly the substitution of evolutionary lineages and functional traits. In the second approach, we find evidence of taxonomic and functional homogenization over time, likely following a decrease in diversity of traits related to habitat use. Furthermore, we found that ecological traits contributed differently to the changes in functional composition as well in their response to environmental heterogeneity. These results support recently evidence showing that anthropogenic impacts are driving changes in biological communities through a taxonomic and functional homogenization.

Keywords: Freshwater fish. Land use. Heterogeneity. Homogenization. Beta diversity.

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1 GENERAL INTRODUCTION

Some controversy rests on the scientific status of a human-driven geological era: the Anthropocene (Lewis & Maslin, 2015; Millette et al., 2019). Yet, evidence points out that species distributions and abundance are changing in response to anthropogenic impacts (Benning et al., 2002; Steinbauer et al., 2018). The introduction of non-native species, habitat loss, changes in land use and climate change are the main threats triggering a biodiversity crisis (Barnosky et al., 2011; Frishkoff et al., 2014; Reid et al., 2019). In a scenario of diversity loss, the adoption of strategies for protecting biodiversity depends on the understanding of how and why diversity is changing (Ceballos et al., 2015; Socolar et al., 2016).

Given the multiplicity of biodiversity features, there is still unclear at which aspects (alpha, beta, gamma) and facets (genetic, phylogenetic, functional, species) of diversity are undergoing changes in response to anthropogenic impacts (Benedetti et al., 2019). This multifaceted organization of biodiversity has led to the detection of contrasting patterns of diversity change, where communities may not loss species nor individuals but are still losing diversity becoming more similar in composition across space (Benedetti et al., 2019; Buisson et al., 2013). Moreover, although it is intuitive to expect the same species can occur at the same places over time, communities also undergo temporal changes (Magurran et al., 2019).

Compositional changes across space have been studied more extensively than temporal changes in composition. The spatial dissimilarity in composition among communities (β -diversity) results from an interplay between dispersal limitation, environmental heterogeneity and spatial extent contributing to species turnover and species gains and losses (Gianuca et al., 2017; Heino, Melo, Siqueira, et al., 2015). However, it is still unclear how colonization history and environmental

variability drive changes in the abundance of species, the identities of dominant and rare species, as well as their contribution to other dimensions of communities' temporal β -diversity (e.g. phylogenetic, traits compositional changes).

Here we used fish communities to investigate the drivers of temporal and spatio-temporal changes in composition. First, we investigated for the direct and indirect effects of changes in land use over time on taxonomic, phylogenetic and traits temporal β -diversity. As temporal changes in composition can result from substitution of the identity of dominant species, we investigated whether effects of land use on β -diversity were mediated by the contribution to phylogenetic and traits diversity of dominant species over time. Second, we investigated whether changes in taxonomic β -diversity resulted in changes in traits composition and which traits were associated to such shifts in composition.

Overall, our results show that changes in composition across space and over time can respond to environmental factors, mainly resulting in the replacement of species, lineages and traits. Also, that taxonomic β -diversity is related to changes in traits composition, but not to all the set traits. Traits associated to habitat-use had a stronger relationship with changes in species identity, as well as a higher effect of environmental heterogeneity. Finally, comparing spatial β -diversity over time showed that communities tended to become more similar, a possible loss of diversity by homogenization. These findings highlight the importance of integrating spatial and temporal changes in composition, as well as the crucial contribution of long-term ecological research to understand how diversity is changing in multiple dimensions.

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2 CHANGES IN LAND USE DRIVE TEMPORAL B-DIVERSITY IN FRESHWATER FISH COMMUNITIES

ABSTRACT

Aim: Biodiversity changes over time and its multiple facets can respond to anthropogenic impacts in different ways. Albeit changes in land use have led to shifts in diversity across space, the limited availability of temporal data has prevented a more complete understanding of the effects of land use over time. Here, we investigate the effect of temporal shifts in land use on the temporal changes in composition of several widespread freshwater fish communities.

Location: North America (North temperate Lakes, Upper little Tennessee River basin, Kansas River Basin), South America (Upper Paraná River basin) and Oceania (Waikato River).

Methods: Using path analysis, we investigated for direct and indirect effects of land use on temporal compositional changes in taxonomic, phylogenetic and traits diversity in ten temporal series of freshwater fish communities. Total β -diversity was decomposed on its replacement and differences in richness components. Since changes in the abundance of dominant species influence the β -diversity, we measured the indirect effect of land use on β -diversity via the contribution of the most abundant species through time.

Results: Temporal changes in land use drove the replacement of species, lineages and traits over time, showing stronger positive effects on traits and phylogenetic β -diversity. At the same time, the effects of land use on the contribution of dominant species to abundance, traits and phylogenetic diversity varied across sites. Although we found that communities had lower to moderate compositional changes, for most sites the changes in composition over time were explained by temporal changes in land use.

Main conclusions: Our results show that temporal changes in composition respond to shifts in land use. As the taxonomic, phylogenetic and traits β -diversity were strongly correlated, it is likely that land use affects the species composition through niche processes, acting on species traits.

Keywords: land cover, temporal β -diversity, functional diversity, phylogenetic diversity, SCBD, path analysis.

2.1 Introduction

A great portion of the Earth environments has experienced some degree of human intervention (Geldmann et al., 2014). Freshwater ecosystems face the impacts resulting from the human population growth, agriculture, disruption of water flow and connectivity by impoundments, introduction of non-native species, overexploitation, and the interactions of these threats with climate change (Reid et al., 2019; Vörösmarty et al., 2010). By 2010, it was estimated that 65% of the habitats associated with continental waters were under moderate to high threat (Vörösmarty et al., 2010). Moreover, the intensity of human activity has been growing at some regions (Geldmann et al., 2014), and new threats to freshwater systems that derived from human activities have appeared on the scene (e.g. species e-commerce, pollution from pharmaceutical products) (Reid et al., 2019). Several of these human-driven pressures are directly or indirectly linked to changes in land use (Domenech et al., 2005; Spear et al., 2013).

Changes in land use affect physical and biotic properties of freshwater systems (Bostanmaneshrad et al., 2018; Hester & Doyle, 2011). The replacement of primary vegetation for urbanized structures has been found to negatively affect water quality by increasing soil erosion (Asselman et al., 2003; Nearing et al., 2017). In addition, the reduction of the riparian vegetation may increase the water temperature in streams (Rutherford et al., 2004). Even in large rivers which are more resilient to variability in temperature, have shown increases in temperature as a response to anthropogenic impacts (Webb & Nobilis, 1994). Erosion, changes in temperature and land cover have been found to be drivers of shifts in diversity and community composition, resulting in decreases of biomass and species richness (Dodson et al., 2005; Wantzen, 2006), and facilitating the colonization by non-native species (Von Holle & Motzkin, 2007). Furthermore, the interaction between land use and climate change can drive the dissimilarity in composition between communities (β -diversity) via complementary effects, where changes in land use promote the substitution of species, whereas the climate change results in species gain or loss (Ferber et al., 2017).

A long-standing question in ecology is at which level of spatial and temporal organization the changes in diversity occur (Whittaker, 1972), and which are the mechanisms underlying patterns of local (α) and among habitats dissimilarity in composition (β) (Fukami et al., 2005; Magurran et

al., 2019). Besides the organization of biodiversity across spatial and temporal scales, the diversity can be measured on different facets (genetic, species, traits and evolutionary history), which exhibit, in different degrees, the signature of niche and stochastic processes (Fukami et al., 2005; Gianuca et al., 2018). However, before a biodiversity crisis (Ceballos et al., 2015), it remains unclear what aspects of biodiversity change or show resilience to anthropogenic pressures (Millette et al., 2019). For instance, the expected loss of diversity, as the reduction in the number of species over time, sometimes does not show a relationship with human-driven impacts (Gotelli et al., 2017; Hillebrand et al., 2018). Instead, the species richness can stay unchanged through time or show a rapid recovery from disturbances, although the communities undergo changes in the identity of species (Dornelas et al., 2014; Gotelli et al., 2017). Then, shifts or loss of diversity as a response to human impacts seem more likely to be manifested as changes in the species identities and traits composition, in which the communities get more dissimilar or similar through time (Fukami et al., 2005; Hillebrand et al., 2018).

Biological communities exhibit trajectories over time determined by the influence of stochastic and niche processes on the occurrence and abundance of species (Fukami et al., 2005; Steiner, 2014). Thus, temporal compositional changes can occur by the influence of shifts in the identities of dominant and rare species (Christensen et al., 2018; Legendre & De Cáceres, 2013), and show different or converging trends for the species and traits composition (Fukami et al., 2005). Since the species identities change over time, looking at temporal β -diversity can bring out information on whether communities are converging or diverging from an initial state, and whether these changes occur at the multiple facets of diversity (e.g. genetic, phylogenetic and functional) (Gianuca et al., 2018; Magurran et al., 2019; Socolar et al., 2016). Furthermore, the relationship between the changes in the species composition and traits composition may indicate the influence of neutral and niche processes on community assembling (Leibold & Chase, 2018).

Here we explore the response of temporal changes in freshwater fish communities to land use. We focused on investigating two main questions: first, we investigated whether the temporal change in land use explained the temporal β -diversity and, second, we explored whether the effects of changes in land use on β -diversity were mediated by the contribution of species to beta diversity. That is, we searched whether the changes in land use had direct effects on β -diversity, as well as for indirect effects via changes in the contribution to the phylogenetic and traits

diversity of the species with higher contribution to changes in the taxonomic composition. We had three main expectations: i) that communities were dissimilar, over time, as a response to the changes in land use, that is, communities at the end of temporal series would be different from the initial communities. Moreover, since forested and uncovered habitats can hold different sets of species and traits, but the effects of niche processes on the functional composition tend to be higher (Arantes et al., 2018), we also expected that: ii) the traits β -diversity would exhibit higher effects of land use than taxonomic β -diversity. And, since highly human-impacted systems showed the loss of functionally divergent or specialized species (Buisson et al., 2013; McKinney, 2006), we expected that iii) the changes in land use would lead to a higher contribution to β -diversity of species at the center of the functional space (more general combination of traits).

2.2 Methods

2.2.1 Temporal series

We considered ten temporal series from five long-term ecological research projects, where the sampling periods ranged from 12 to 32 years. The earliest temporal series was sampled between 1962 and 1974 (Whitaker & Gummer, 1975), and the most recent, between 2000 and 2018. Here, we updated and added data to the temporal series that have already been curated and compiled by Dornelas et al. (2018) (<http://biotime.st-andrews.ac.uk/home.php>). The sites encompassed small streams, lakes and floodplain systems from Midwestern United States, South Brazil and north New Zealand (Fig. S1). A description of the sampling methods is available at the LTER's websites (<http://lter.konza.ksu.edu/>; <https://lter.limnology.wisc.edu/about/overview>; <https://coweeta.uga.edu/>; <https://niwa.co.nz/>). In order to deal with data series sampled with multiple capture gears (electrofishing, gill nets, fyke nets, trammel nets, seines), the Multi Gear Mean Standardization (MGMS) approach proposed by Gibson-Reinemer et al. (2017) was employed.

2.2.2 Land use change

Information on the temporal change in land use was obtained from Chini et al. (2014), measuring the proportion of land cover type (primary vegetation, secondary vegetation, pasture, cropland, and urban cover) at a spatial resolution of 0.5 degree (~50 km). For each year, cover types were averaged for the grid cells adjacent to the main channel for rivers and lake basin for lakes. The temporal data series encompasses historical data for the period of 1500-2005 (Chini et al., 2014),

while the data from 2006 on are future projections based on four land-cover change models. For temporal series with data after 2005, the temporal series in land use was completed with the projections continuing the trend of change since 1900. In this case, the data for 2006-2016 came from the AIM model based on the RCP6 climate scenario of moderate emission of greenhouse gases and mitigation actions taken late in the 21st century for temporal series in the United States and New Zealand, and from MapBiomas data (MapBiomas, 2019) for temporal series in Brazil.

2.2.3 Species traits

Fourteen traits for 333 species (Appendix S1) were considered to account for species niche dimensions related to habitat use and life history. The values of traits consisted of information from multiple sources, including the temporal series data, the species taxonomic and ecological descriptions and FishBase (Froese & Pauly, 2018). Body length, shape factor, swim factor, eye size and snout length were the morphological traits regarded as indicative of the habitat use. The body length and body shape are proxies to the swimming ability and the habitats frequented by the species (e.g. migratory behavior, range of distribution, use of structural complex habitats) (Blake, 2004). The eye size is related to diel activity, visual acuity and habitat type (e.g. smaller eyes in fishes in murky or deep habitats) (Caves et al., 2017), whereas the type of prey and diet can relate with fishes' snout length (Marrero & Winemiller, 1993). The body length was measured from temporal series when the data on the species size was available. Otherwise, and also for the eye size and shape factor, the values were those reported in the species original descriptions and FishBase (Froese & Pauly, 2018). As measures on the caudal fin depth are generally never reported in taxonomic descriptions, the swimming factor was calculated using photographs and illustrations taken from taxonomic descriptions. For this, the software 'tpsDIGs' (Rohlf, 2017) was used to place landmark points on the caudal fin and the caudal peduncle in the picture of each species, and to calculate the distances between the landmarks that were used to obtain the swimming factor. The position in the water column, diel activity and trophic position (from FishBase) were also descriptors of habitat use.

Life-history traits consisted of those traits associated with the reproduction and offspring investment. Reproductive guild followed Balon (1975), and indicated if the species are open substrate spawners, guarders (internal or external guarding of eggs or juveniles), nesters (build nests), hidiers (hide brood without building a nest) or livebearers. Parental care accounted for

monoparental (female or male) and biparental investment in offspring care (Mank et al., 2005), and spawning migration for the presence and absence of the five types of reproductive migration exhibited by the sampled species (potamodromous, anadromous, amphidromous, catadromous, and non-migrators). To compute traits β -diversity, traits dissimilarity between each pair of species was calculated using the Gower dissimilarity coefficient. This pairwise ecological dissimilarity matrix also was used to generate functional groups by hierarchical clustering through ‘Complete’, ‘Average’, ‘Median’ and ‘Ward’ algorithms. The best clustering scheme was selected by majority rule (higher performance over 21 indices), evaluated by the ‘NbClust’ function (Charrad et al., 2014). The selected clustering scheme (four groups) explained 41.3% of traits dissimilarity between species and was related mainly to differences in life-history traits.

2.2.4 Phylogeny

The time-calibrated molecular phylogeny for ray-finned fishes of Rabosky et al. (2018) was the backbone to reconstruct the phylogenetic relationships for 333 fish species. The phylogeny was accessed through the ‘fishtree’ package (Chang et al., 2019) and contained 86% of the sampled species. Species in the occurrence matrices, but absent in the phylogeny, were added in two steps. First, we edited ‘by hand’ the species not included in Rabosky et al., (2018) but with relationships that were already published, for example, some relationships in Characiformes and Siluriformes (Calegari et al., 2019; Ramirez et al., 2017), and non-ray-finned fishes (Betancur-R et al., 2013). After this ‘by hand’ reconstruction, 5% of the species were still missing from the phylogeny. These species were added as polytomies at the root of each clade, and then the polytomies resolved using a birth–death polytomy resolver through a Bayesian approach (Kuhn et al., 2011). The package ‘phytools’ (Revell, 2012) in R 3.6.1 (R Core Development Team, 2019) was used for phylogenetic tree editing, and BEAST (Bouckaert et al., 2014) and BEAGLE (Ayres et al., 2012) for resolving polytomies. To account for phylogenetic uncertainty, calculations using phylogenetic information were done by sampling 1000 trees from the generated phylogenies.

2.2.5 Temporal changes in composition (β -diversity)

Shifts in composition occur through replacement (substitution) and by changes in richness among sites in space or samplings over time (Baselga, 2010; Carvalho et al., 2012). For taxonomic, phylogenetic and traits composition, we calculated the temporal β -diversity within each site

following the approach proposed by Carvalho et al. (2012). This approach differs from Baselga (2010) in the cases when two communities without common species show a contribution of difference in richness (all species are replaced, but one community has higher richness, which, under Baselga's (2010) approach, will lead to β -diversity determined only by replacement). Thus, the replacement (Brepl; changes in the species identity, composition of traits and lineages composition) and differences in richness (Brich; gain or loss of species, traits and lineages), were calculated from abundance data and through the Jaccard dissimilarity index. Phylogenetic β -diversity was computed from the cophenetic distances generated for 1000 trees. For traits β -diversity, first a dendrogram was generated from the species dissimilarity matrix using hierarchical clustering. This dendrogram was employed for β -diversity calculation. Finally, the Mantel test was performed to test the correlations between changes in phylogenetic and traits composition with taxonomic β -diversity. Calculations of β -diversity and their correlations were done using the packages 'BAT' (Cardoso et al., 2018) and 'vegan' (Oksanen et al., 2016) in R (R Core Development Team, 2019).

2.2.6 Data analysis

The changes in land use over time was summarized using a PCA for each site. Then, to test whether the change in land use explained the changes in the communities composition, the first two axes of the land use PCA were utilized as explanatory variables in a constrained ordination (CAP, Anderson & Willis, 2003) of the total temporal β -diversity for each site and each aspect of diversity (taxonomic, phylogenetic and traits). The significance of the axes of the canonical ordination was tested by Anova (999 permutations). Secondly, the Legendre & De Cáceres (2013) approach was employed to determine the contribution of each species to taxonomic β -diversity (SCBD). Species with higher SCBD are those with higher abundance variation over time. After the calculation, for each site, only the species with SCBD higher than the third SCBD quantile were selected (25% of species for each site; usually the most dominant species in terms of abundance). For these species, their yearly contributions (as proportions) to abundance, phylogenetic diversity and traits diversity were computed. As β -diversity was calculated for dendrograms then, the contribution of the species with the highest SCBD was calculated as the proportion of the total distances (both ecological and phylogenetic) among species accounted by the selected 25% of species.

Finally, we use path analysis to determine the direct and indirect effects of land use on β -diversity. As time is unidirectional, temporal β -diversity was taken as the dissimilarity from the first sampled year to posterior years. The yearly contributions to diversity of the 25% of species with high SCBD were considered as mediators: annual percentage of abundance for taxonomic β -diversity, the percentage of phylogenetic distances for phylogenetic β -diversity and the percentage of traits dissimilarity for traits β -diversity. Taking land use as the proportion of land covered by the summation of urban, cropland and pasture covers, we investigated the direct and indirect effects of land use on each component (B_{total} , B_{repl} and B_{rich}) and facet of temporal β -diversity. Direct effects accounted for the predictability of β -diversity from changes in land use. Indirect effects accounted for changes in composition (β -diversity) caused by the effect of land cover on the contributions of the species with higher SCBD to abundance, phylogenetic diversity and traits diversity. The purpose of using the contributions of a subset of species (those with higher SCBD) is founded in the possibility that land use causing shifts in habitats conditions may result in the increase, decrease or fluctuation in the abundance of some species and, consequently, in shifts in the representation of their traits and lineages in the communities (Arantes et al., 2018; Dodson et al., 2005). Since all variables were proportions, most of them had a right-skewed distribution. Then, path models were fitted by correcting the chi-square using the Satorra-Bentler test statistic, which has been found to be effective for non-normal variables (Curran et al., 1996). To get a measure of the effect of land use on β -diversity, the effect sizes across models were summarized using the ‘rma’ function of the ‘metafor’ package (Viechtbauer, 2010). The path models were fitted using the “Lavaan” package (Rosseel, 2012).

2.3 Results

2.3.1 Relationship between land use and β -diversity

The changes in land use showed different tendencies among the sites. Two out of ten sites were already almost 100% covered by cropland, pasture and urban types, or by secondary vegetation at the sampled period, showing no change over time (gaining or losing less than 1% of cropland, pasture and urban cover). Seven sites showed an increase in land use (cropland + urban + pasture), ranging between 2% and 9% over the sampling period (Fig. S1; Fig. S2). For most sites, CAP analysis shows that the total (B_{total}) taxonomic, phylogenetic and traits temporal changes in composition are explained by changes in land use (Fig. 1). These three aspects of diversity had

similar amount of explained variance (ranging between 9.1% and 35.3%). However, traits β -diversity did not show a higher explained variance, as expected.

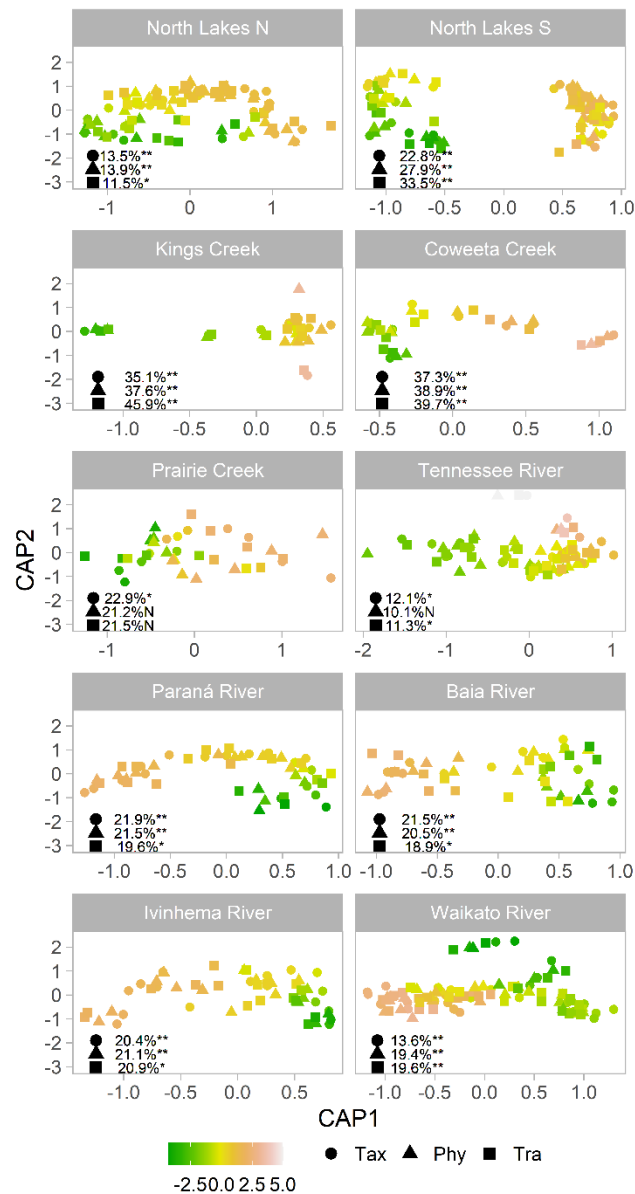


Fig. 1. Constrained ordination (CAP) of temporal changes in composition (Btotal) for ten freshwater fish communities. Color scale is given by the loadings of each year on the PCA1 for land use: lower values for higher proportions of primary and secondary vegetation. Tax: taxonomic; Phy: phylogenetic; Tra: traits. Significance: N(non-significant); *(<0.05); **(<0.001).

2.3.2 Contribution of species to β -diversity

The communities had low to moderate temporal changes in composition ($B_{total} = 0.47 \pm 0.15$, 0.28 ± 0.08 and 0.26 ± 0.09 for species, phylogenetic and traits β -diversity). The decomposition of β -diversity into replacement (B_{repl}) and differences in richness (B_{rich}) showed that the replacement drove temporal changes in taxonomic diversity (60%-88% of B_{total}). Phylogenetic and traits β -diversity had contributions of both replacement and differences in richness (Fig. S3). The changes in phylogenetic and traits composition were related to shifts in the species composition in all sites, but the Mantel correlation test found stronger relationships between phylogenetic and taxonomic β -diversity (mean $M_r = 0.92$) than between the changes in traits composition and species composition (mean $M_r = 0.85$) (Fig. S4; Fig. S5). In addition, β -diversity had a positive relationship with time, that is, late communities differed from initial communities (Fig. S5).

The 25% of the species with higher SCBD contributed with 62.5% to 94.8% of the taxonomic β -diversity. The abundance of these species varied among the sites: increasing, decreasing or fluctuating over time. Nonetheless, for all sites, these species contribute largely to the abundance (Fig. 2) and traits diversity ($57.1\% \pm 11.7$ of traits dissimilarity among species; Fig. S6). Species with higher SCBD belonged to all functional groups, reflecting the distribution of numbers of species across groups. Species of Group 1 (sedentary benthopelagic species with small body size, large eyes and no parental care; Fig. S7) were dominant in eight of the ten temporal series. Although Group 1 was dominant, for some temporal series it was replaced by species exhibiting an equilibrium strategy (Group 3 and Group 4. Species with parental care, medium body size; Fig. 2a and b).

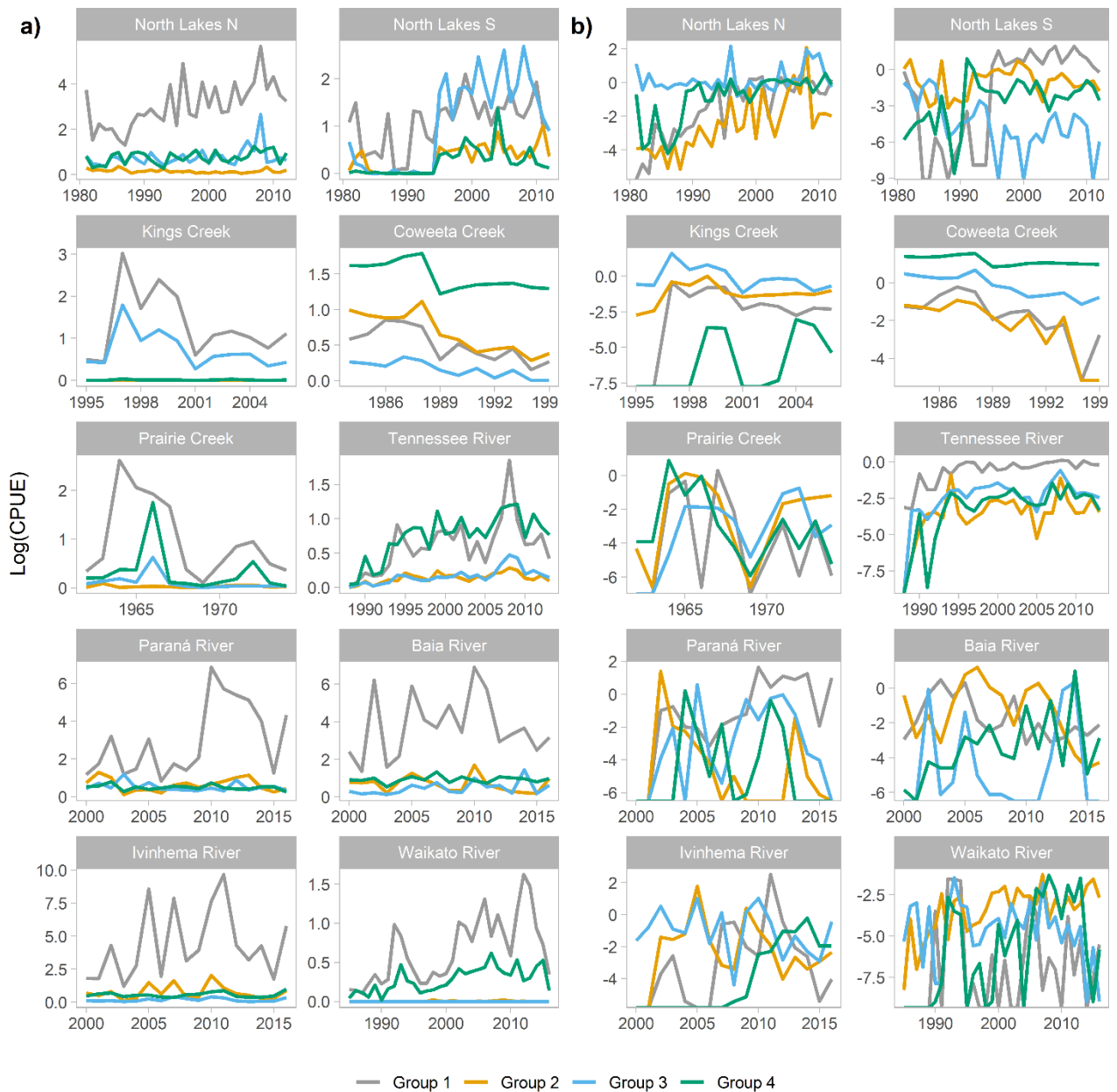


Fig. 2. a) total abundance (CPUE) of functional groups. b) Abundance of the top 4 species with higher contributions to species β -diversity (SCBD). Group 1: small to middle size body, without parental care, no spawning migrations (186 species); Group 2: large body size, spawning migrations (48 species). Group 3: parental care (mouthbrooding), deep body (38 species); Group 4: parental care (bearers, external brooders and brood hiders), vertically compressed body (61 species).

2.3.3 Effects of land use on β -diversity

Taxonomic, phylogenetic and traits temporal β -diversity were affected directly by land use (Fig. 3.; Appendix S2). Eight out of ten temporal series showed a tendency to a positive direct effect of land use on total β -diversity, with significant effect size (mean effect sizes: 0.19, 0.13 and 0.10, for taxonomic, phylogenetic and traits Btotal). All the mean effect sizes for the Brich component were not significantly different from zero. The replacement component had the highest positive effect sizes (mean effect sizes: 0.31, 0.42 and 0.39, for taxonomic, phylogenetic and traits replacement) and were significantly different from zero. That is, land use contributes to temporal changes in composition through replacement.

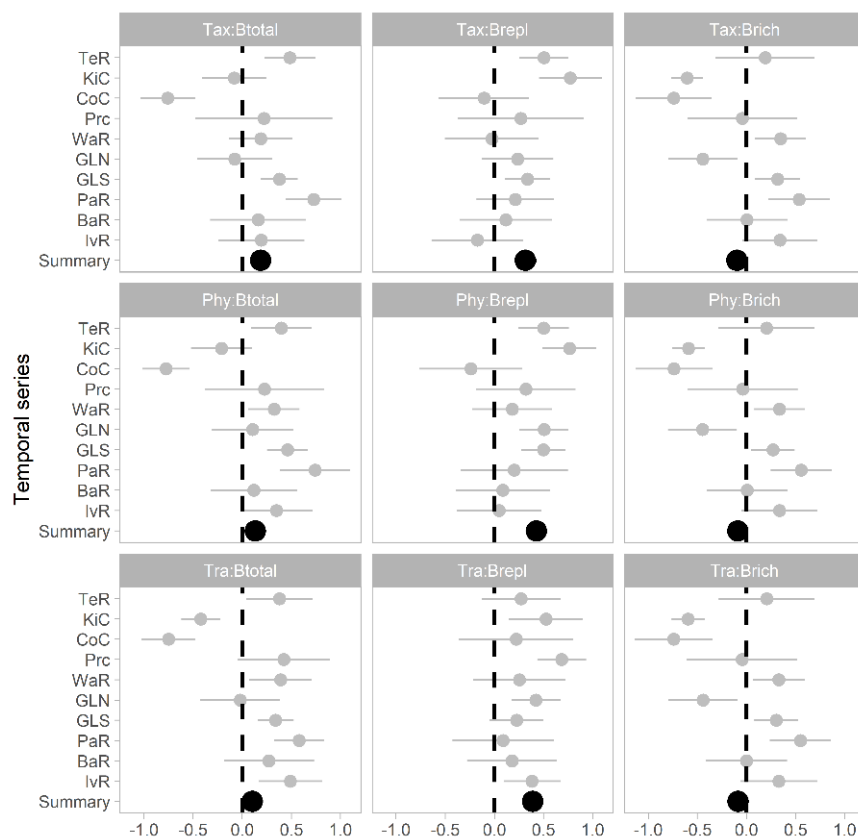


Fig. 3. Effect sizes for direct effects of land use on taxonomic (Tax), phylogenetic (Phy) and traits (Tra) β -diversity ($n=219$; 10 temporal series). Btotal: total β -diversity; Brepl: replacement; Brich: difference in richness. Land use was measured as the sum of percentage of urban, cropland and pasture cover for each year at each locality. **TeR**: Tennessee River; **KiC**: Kings Creek; **CoC**: Coweeta Creek; **PrC**: Prairie Creek; **WaR**: Waikato River; **NLN**: North Temperate Lakes (North); **NLS**: North Temperate Lakes (South); **PaR**: Paraná River; **BaR**: Baia River; **IvR**: Ivinhema River.

The effects of land use on the dominant species varied across sites. Land use affected positively and negatively the abundance (-0.60 - 0.52), the portion of phylogenetic diversity (-0.66 - 0.72)

and traits diversity (-0.60 - 0.52) associated with the species with high SCBD (Fig. S8). Consequently, the indirect effects of land use via the yearly contributions of species with higher SCBD varied among the sites and the mean effect sizes were not significantly different from zero, although they tended to be positive for all the facets and components of β -diversity (Fig. 4; Appendix S2).

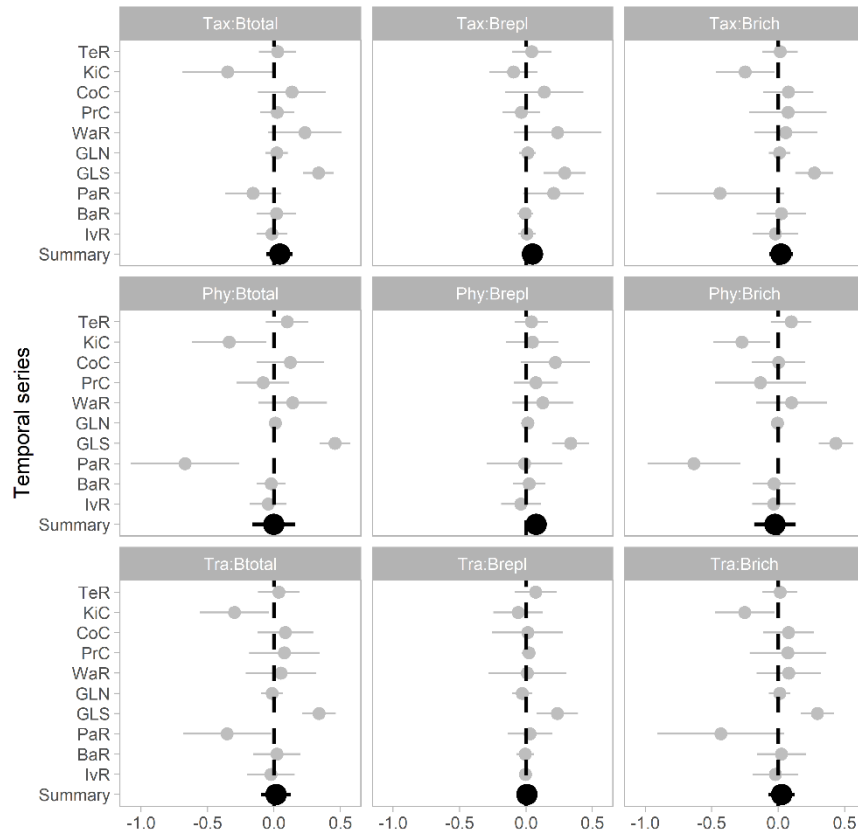


Fig. 4. Effect sizes for indirect effects of land use on taxonomic (Tax), phylogenetic (Phy) and traits (Tra) β -diversity ($n=219$; 10 temporal series). Btotal: total β -diversity; Brepl: replacement; Brich: difference in richness. Land use was measured as the sum of percentage of urban, cropland and pasture cover for each year at each locality. **TeR:** Tennessee River; **KiC:** Kings Creek; **CoC:** Coweeta Creek; **PrC:** Prairie Creek; **WaR:** Waikato River; **NLN:** North Temperate Lakes (North); **NLS:** North Temperate Lakes (South); **PaR:** Paran River; **BaR:** Baia River; **IvR:** Ivinhema River.

2.4 Discussion

Overall, our results show that changes in land use drove the compositional shift of fish communities at taxonomic, phylogenetic, and functional levels. The species with higher contributions to taxonomic β -diversity experienced positive and negative effects of land use, findings that seem to support that some aspects of alpha diversity may display some contrasting

responses to anthropogenic impacts and disturbance (Hillebrand et al., 2018; Magurran et al., 2018). Yet, the effect of land use on β -diversity was consistent over these widespread fish communities and stronger on the replacement component of the phylogenetic and traits composition. The changes in composition were driven by the changes in abundance of opportunistic and equilibrium species, which have ecological traits in the opposite of a gradient of life-history strategies: opportunistic species favored by high environmental variability, and the equilibrium ones by highly homogenous environments.

2.4.1 Contribution of species to β -diversity

Species with higher contribution to species β -diversity (SCBD) exhibited different habitat use and life-history strategies. That is, the species with high SCBD were scattered over the functional space (Fig. S7) and not clustered, as expected. However, most of the species classified here as ‘Group 1’ dominated the communities and are characterized by exhibiting an intermediate to generalist strategy, classified as opportunistic strategists (Olden et al., 2006; Winemiller, 1989): omnivores with small to intermediate size, no parental care nor spawning migrations (e.g. *Serrasalmus* spp, *Serrapinnus* spp, *Notropis* spp and *Cyprinella* spp). Opportunistic species can reproduce rapidly, have short life spans, are favored by fluctuating or rapidly changing environmental conditions (Olden et al., 2006; Winemiller, 1989), and their occurrence has been found to be bolstered by shifts in the land cover across the space (Arantes et al., 2018; Teresa & Casatti, 2012). The species with the highest SCBD are generally the dominant species in each community (Legendre & De Cáceres, 2013), but their contribution can be associated to the different types of behavior of the abundance through time: fluctuating or staying stable within each community. Fluctuations might lead to the substitution of the predominant group of species and in changes within groups. Over time, transitions between groups of species or changes in the regime of dominance can be rapid, involving the species occurrence, abundance and traits composition (Christensen et al., 2018). These transitions can occur when the abundance of some species decreases to very low numbers, liberating other species of negative interactions (Armitage & Jones, 2019; Chesson, 2000) by leaving empty niche spaces after a disturbance, resulting in a re-assembly of the community (Fukami, 2015), or by the influence of the order of the species colonization and environmental conditions (Steiner, 2014). For instance, the introduction of piscivores to control planktivores, mass fish mortality at mid-1980’s due to

environmental variability (Vanni et al., 1990) and habitat degradation (Lyons, 1989), associated with anthropogenic pressures, led to the observed replacement of dominant species at the North Lakes communities (Fig. 2, top panels). Similarly, the dam construction in the Paraná River was followed by the introduction of non-native species that appeared at the top 4 species with high SCBD (e.g. *Hemiodus orthonops*, *Cichla kelberi*) (Agostinho et al., 2015). Furthermore, the habitat degradation and shifts of hydrological regimes of the ecosystems can be linked to the changes in land use (Dupouey et al., 2002; Hester & Doyle, 2011; Nearing et al., 2017).

2.4.2 Effects of land use on β -diversity

The temporal changes in land use directly affected species, phylogenetic and traits composition. A direct positive effect of land use on β -diversity indicates that the communities changed in the direction of temporal shifts of land use (Fig. 1). The replacement component of β -diversity showed the larger positive effects, mainly for the phylogenetic and traits composition (Fig. 3). Since shifts at the different facets of diversity were correlated, it suggests that niche processes are driving changes in composition (Leibold & Chase, 2018; Meynard et al., 2011). It is likely that, analogous to the substitution of species and functional groups across spatial gradients of land use (Arantes et al., 2018; Ferger et al., 2017), shifts in the land cover act as drivers of compositional changes over time (Smart et al., 2006). However, it is also probable that what was here considered as a direct effect of land use is acting via other environmental factors over time, such as alterations on water quality, species introductions and water flow modifications (Johnson et al., 2008; McKnight et al., 2017; Vörösmarty et al., 2010).

The non-significant indirect effects of land use (via the species with high SCBD) on the phylogenetic and traits diversity can result from the contrasting patterns of effect sizes displayed across sites. Although the mean effect of land use on the contribution to the abundance and traits diversity of dominant species was significant and negative, land use had positive effects for some communities (KiC, CoC, PaR; Fig. S9). Land use has been found to negatively affect aspects of functional alpha diversity (Laliberté et al., 2010; Wantzen, 2006). However, as measures of alpha diversity relying on species richness and abundance can remain stable over time and unrelated to changes in β -diversity (Hillebrand et al., 2018; Magurran et al., 2018), species with high SCBD might not show a direction in the effect of land use. Moreover, as some species are favored by the changes in land use (Arantes et al., 2018; Teresa & Casatti, 2012), even sites at the same basin

showed contrasting patterns, reinforcing findings on the dependence of temporal trends of the properties of alpha diversity on the taxa and metrics surveyed (Magurran et al., 2018). For instance, the species with high SCBD displayed different temporal trends, sometimes remaining dominant and sometimes being replaced by species from other ecological groups. At some sites, dominant species were substituted by species with similar traits and phylogenetically related, as species of Characidae (*Astyanax* spp, *Moenkhausia* spp) in the Parana River; species of Galaxiidae and Eleotridae, in the Waikato River; and species of Leuciscidae (*Notropis* spp, *Cyprinella* spp) and Centrarchidae, in North Temperate Lakes (Fig. 2). This could also explain the similar contribution of replacement and differences in richness to the traits and phylogenetic β -diversity (Villéger et al., 2013): communities changed by the replacement of species and individuals among dominant species which might be phylogenetically closely related species with similar traits.

Regarding the patterns exhibited by phylogenetic β -diversity, some criticism has arisen against the use of birth-death models to resolve polytomies for synthesis phylogenies. However, the approach is especially problematic when more than 30% (vs $\approx 5\%$ here) of the sampled species are absent from the phylogeny (Rabosky, 2015). Besides, synthesis phylogenies produce diversity measures highly correlated with those calculated from phylogenies built from data (molecular, morphological) for all species (Li et al., 2019). Moreover, the effects of land use on phylogenetic and traits replacement were consistent on these widespread fish communities. That is, the integration of the multiple facets of diversity, where changes in taxonomic, phylogenetic and functional composition are strongly associated, allows to infer that environmental processes drove changes in the composition (Gianuca et al., 2018; Tucker et al., 2018).

Although land use was found to lead to compositional changes, there are multiple environmental factors linked to land use that can act as mediators of its effect on diversity (Ferber et al., 2017). Despite findings showing an influence of land use on changes in the composition of fish communities, we are aware that temporal changes in land use likely affect aquatic communities via factors that were not considered here (e.g. water temperature, erosion, climate change) (Ferber et al., 2017; Hester & Doyle, 2011). Besides, it remains unclear how land use affects aspects of alpha diversity that can influence β -diversity. Thus, although our results allowed the uncovering of changes in abundance, valuable for explaining temporal changes in composition,

by giving emphasis on the dominant species, we could underestimate the contributions of rare species (in terms of abundance and traits or functions) (Leitão et al., 2016). Furthermore, as human activity becomes more intense in some regions, especially in developing countries (Vörösmarty et al., 2010), we need to fill the gap of knowledge on the functional role of species, and how dominant and rare species contribute to ecosystem processes. These will be helpful to determine if systems are resilient to perturbations and to clarify the consequences of species and traits loss and replacement on ecosystem services. Overall, our findings highlight that species, lineages and traits are replaced over time in response to human-driven impacts. Such widespread fish communities, in habitats with different characteristics (lakes, streams, rivers), share similar responses to land use and seem to share similar patterns of replacement and gains and losses of individuals and species.

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APPENDIX A - Land use changes for the ten surveyed sites.

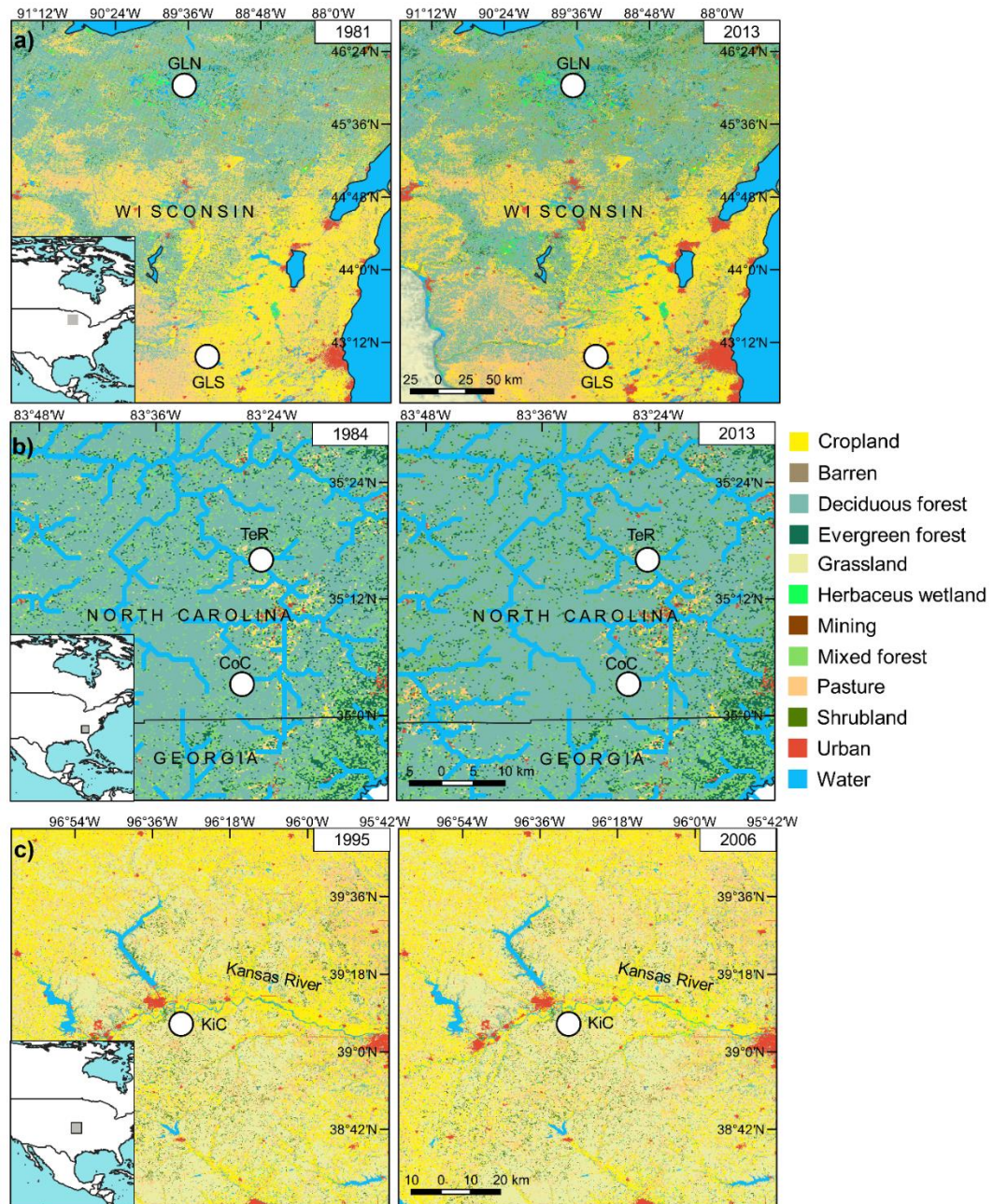


Figure S 1. Land use changes for the ten surveyed sites. **a)** North Temperate Lakes LTER; **b)** Coweeta LTER (Upper Little Tennessee); **c)** Konza Prairie LTER.

APPENDIX A - (continued). Land use changes for the ten surveyed sites.

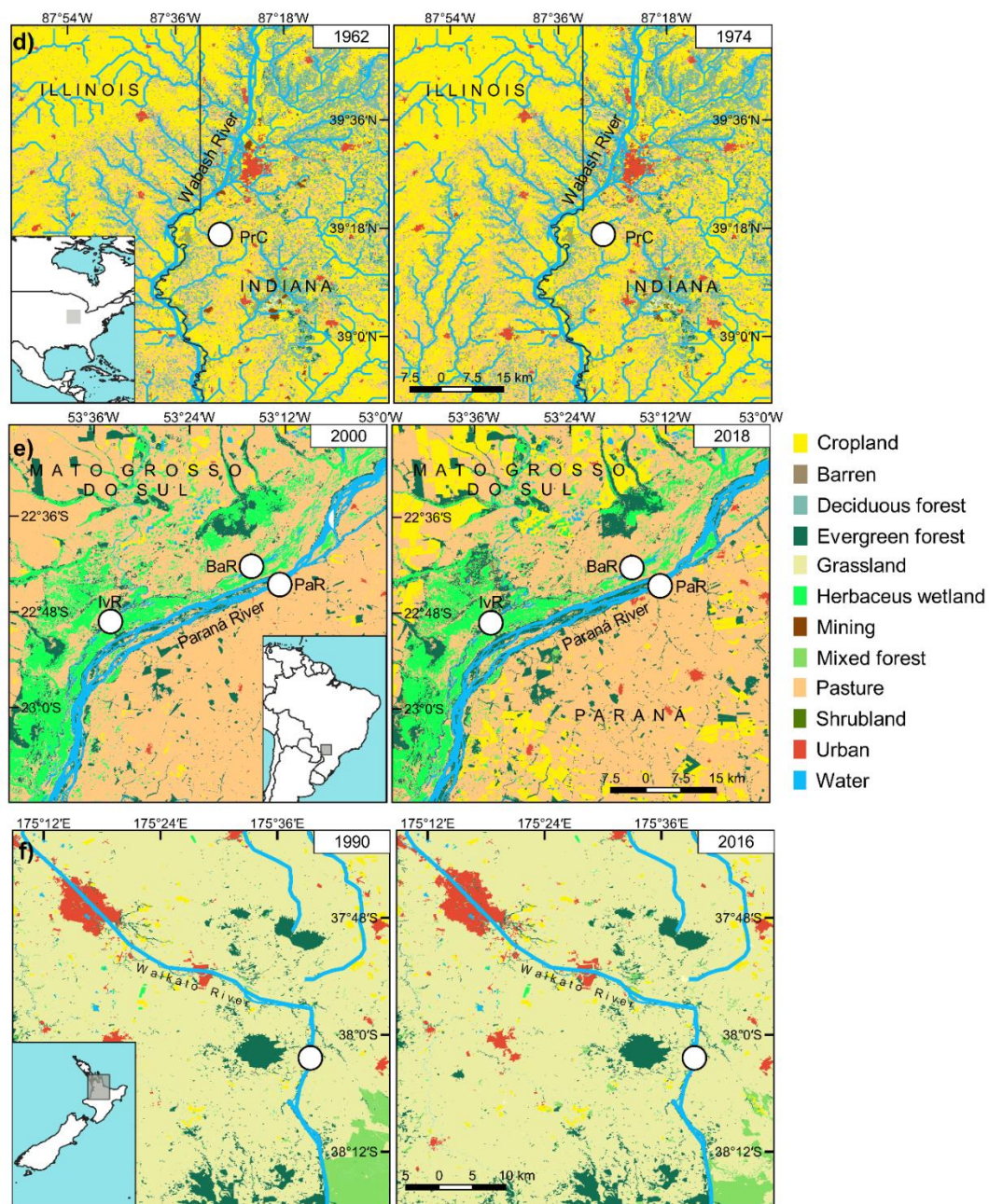


Figure S 1 (continued). Land use changes for the ten surveyed sites. **d)** Prairie Creek; **e)** PELD site 6 (Upper Paraná River); **f)** Waikato River.

APPENDIX B - Land use over time for ten sites.

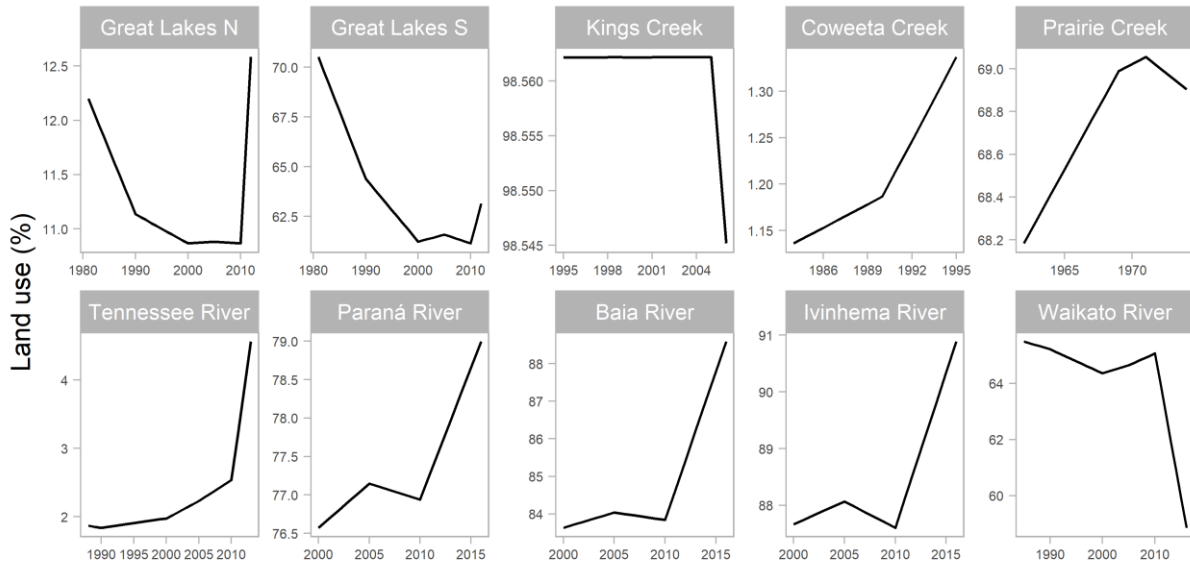


Figure S 2. Land use over time for ten sites. Land use is the total percentage from the summation of cropland, pasture and urban cover in at ~50km resolution.

APPENDIX C - Decomposition of temporal β -diversity into replacement and richness differences.

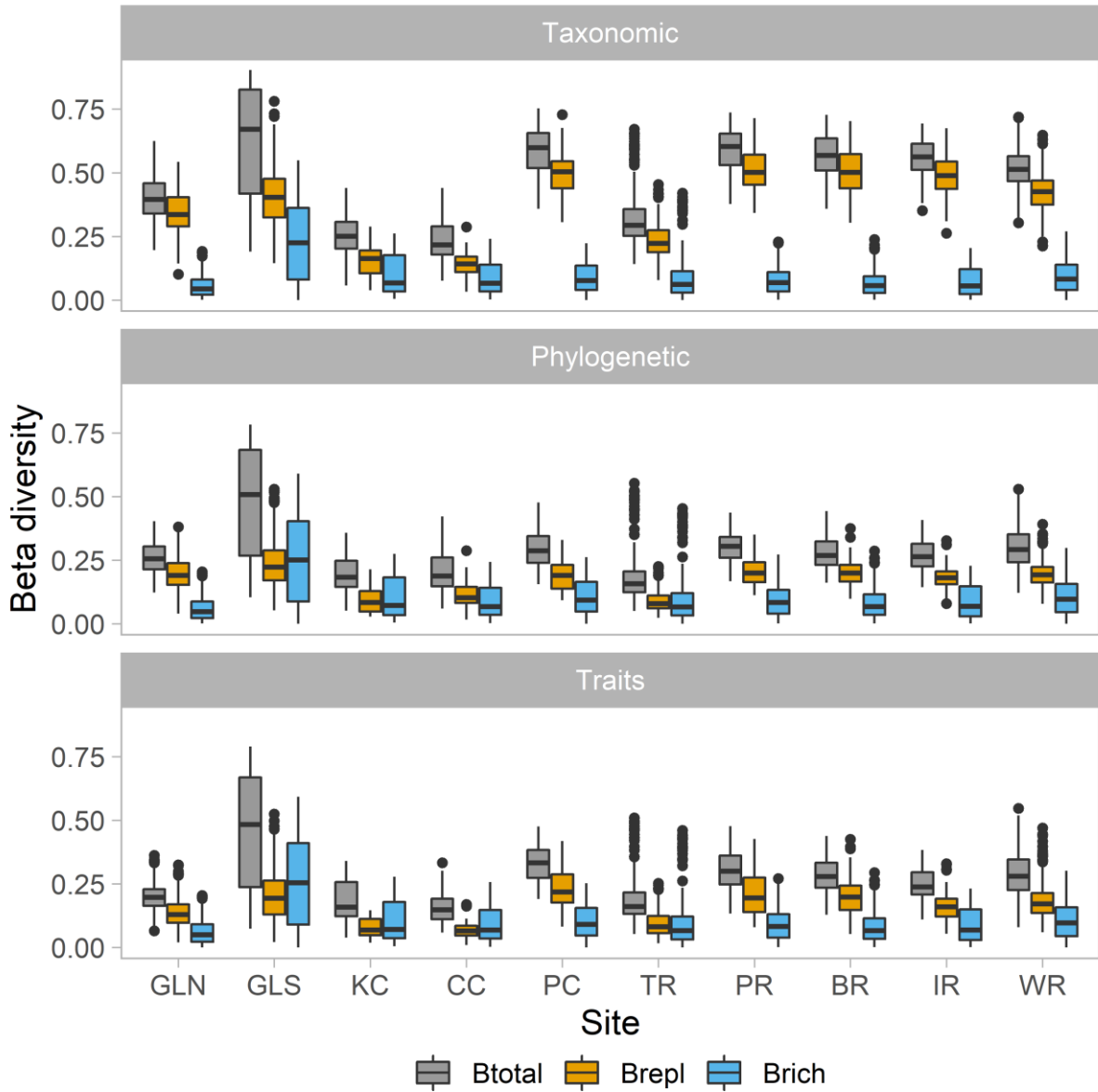


Figure S 3. Decomposition of temporal β -diversity (Btotal) into replacement (Brepl) and richness differences (Brich).

APPENDIX D - Relationship between phylogenetic and traits temporal β -diversity with changes in species composition.

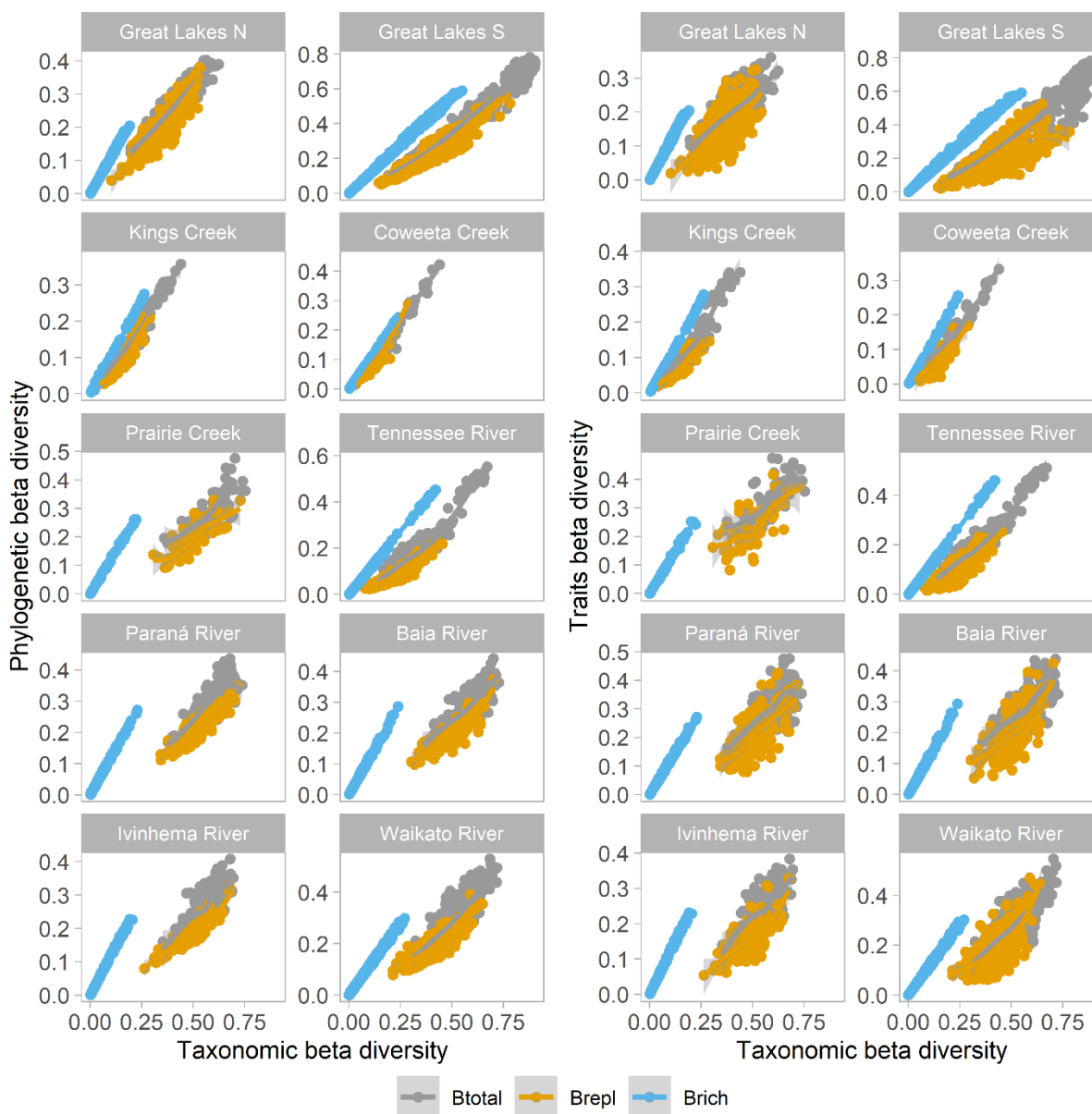


Figure S 4. Relationship between phylogenetic and traits temporal β -diversity with changes in species composition.

APPENDIX E - Correlation between β -diversity and temporal distance in years.

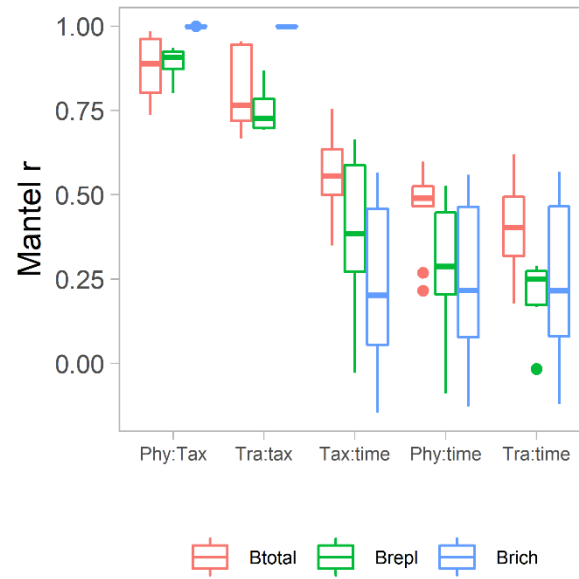


Figure S 5. Mantel test. Phy:Tax and Tra:Tax for Mantel correlations between taxonomic β -diversity and phylogenetic and traits β -diversity. Tax:time, Phy:time and Tra:time for correlation between β -diversity and temporal distance in years.

APPENDIX F – Contribution of species to alpha diversity.

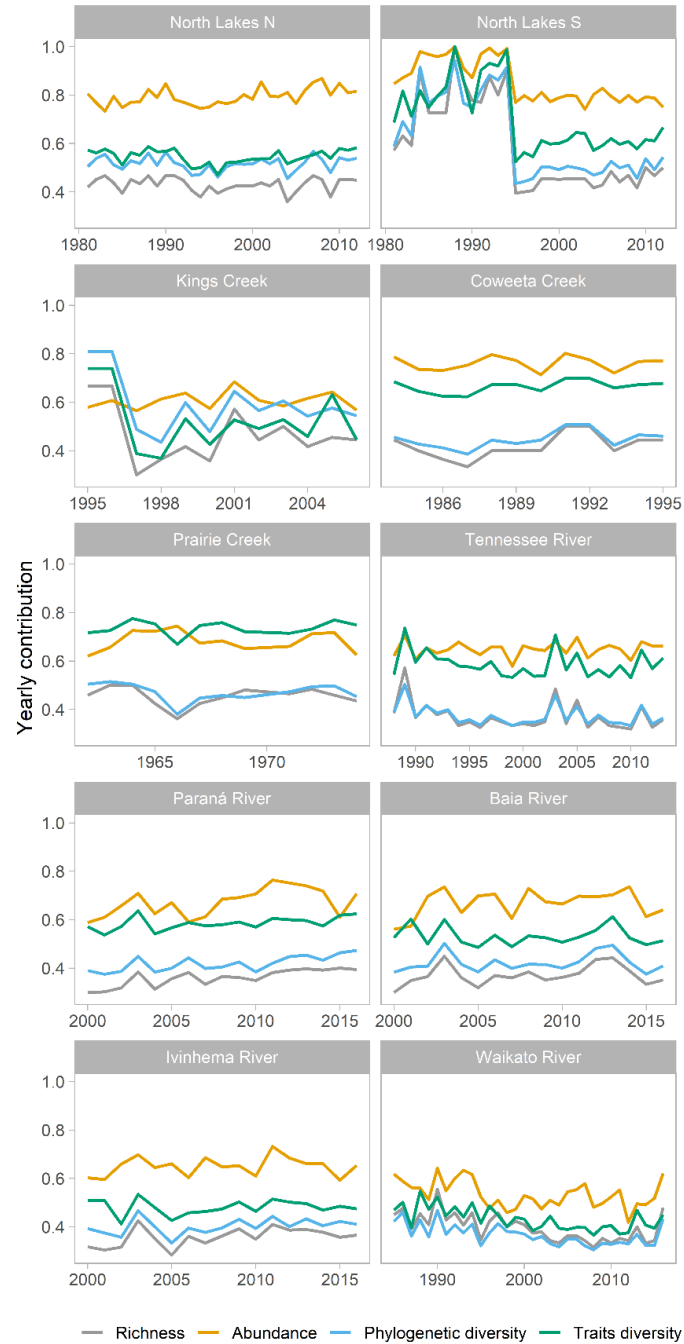


Figure S 6. Yearly contribution of the 25% of species with high SCBD as percentage of abundance, phylogenetic diversity and traits diversity.

APPENDIX G - Trait space occupied by 334 species from 10 temporal series.

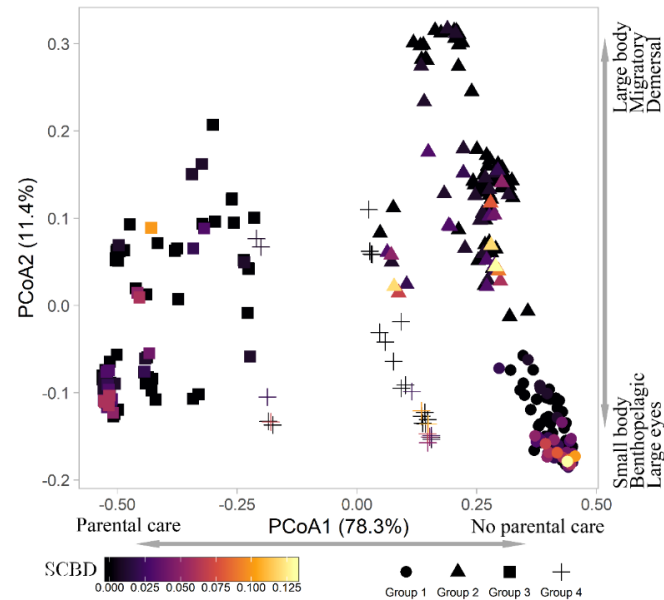


Figure S 7. Trait space occupied by 334 species from 10 temporal series. Color scale shows SCBD values for each species. Species with higher SCBD values were those with higher abundance variation through time. Groups were generated by hierarchical clustering (11 out of 21 indices suggested four groups) and explained 41.3% of traits dissimilarity between species.

APPENDIX H – Effect sizes for the relationship between land use and the contribution of species to alpha diversity.

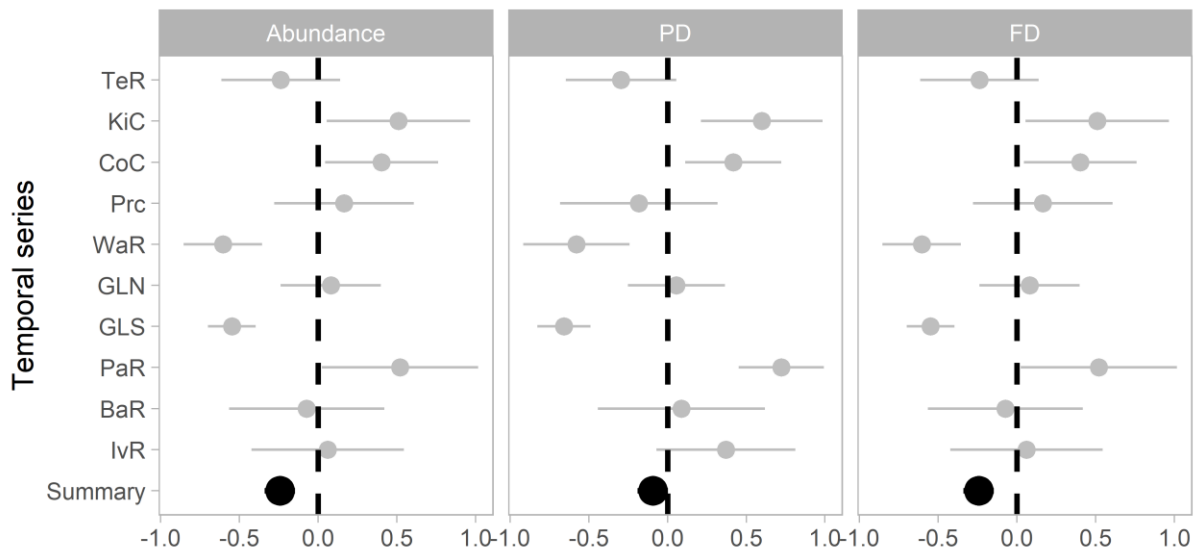


Figure S 8. Effect sizes for the effect of land use on the contribution to abundance, phylogenetic diversity (FD) and traits diversity (FD) of the species with higher SCBD (n=219; 10 temporal series). Land use was measured as the sum of percentage of urban, cropland and pasture cover for each year at each locality.

3 HABITAT-USE TRAITS LEAD TEMPORAL TRAJECTORIES OF TRAITS BETA DIVERSITY IN FISH ASSEMBLAGES

ABSTRACT

1. Human-driven pressures are leading to temporal changes in composition which can result in increases and decreases of dissimilarity among communities. Since traits can differ in their response to niche and stochastic processes, it is crucial to investigate which traits contribute to temporal changes in composition. We aimed to investigate: i) whether changes in taxonomic composition lead to changes in traits composition; ii) which traits were related to shifts in composition and iii) the effects of environmental heterogeneity on taxonomic and traits β -diversity.
2. Freshwater fish communities for 23 sites on four systems were used to investigate for the relationship between taxonomic and traits β -diversity. First, we investigated for changes (or no changes) of β -diversity among sites over time. Second, we tested the contribution of habitat-use and life-history traits to traits β -diversity. Third, the effects of environmental heterogeneity and spatial isolation on the facets and components of β -diversity were determined.
3. Taxonomic and traits homogenization and differentiation were strongly related. Habitat-use traits showed higher contributions to traits β -diversity and was strongly related with changes in species composition. While the effects of spatial isolation varied among sites, environmental heterogeneity contributes positively to species and traits replacement, mainly habitat-use traits replacement.
4. Our results show that although changes in species and traits composition can be related, not all traits are contributing equally to changes in composition. Environmental

variability, instead, structure community's composition by acting on different combinations of traits.

Keywords: trajectory analysis; life-history traits; beta diversity; functional dissimilarity

3.1 Introduction

Understanding the mechanisms driving community changes over space and time has been a long-lasting pursuit for ecologists. Communities change across multiple scales: locally (α) where local environmental fluctuation and biotic interactions drive species numbers and abundance; among sites or habitats (β), where dispersion and environmental gradients determine the dissimilarity in species composition, and regionally (γ) where speciation, extinction and colonization shape diversity patterns (Alexander Pyron & Wiens, 2013; Whittaker, 1972). Since measures of α -diversity appeared as more intuitive, the number and abundance of species has received more attention for detecting shifts in composition. However, communities can regulate species richness and abundance showing high stability (Gotelli et al., 2017), while species and traits composition may display rapid changes. These changes in species identities can result in a changes (loss and gains) of diversity not seen in trends of species richness and abundance (Dornelas et al., 2014; Hillebrand et al., 2018). That is, across space and time communities may maintain a constant number of species while losing diversity due to biotic homogenization, for example (Winter et al., 2009). Thus, the understanding on how diversity change across space and over time can resides on the explanation of patterns of beta diversity (Magurran et al., 2019).

Over the last three decades, the availability of functional and phylogenetic information has allowed ecologist to investigate how multiple facets of diversity respond to environmental changes, the influence of assembly processes and the relationships among compositional changes at multiple levels of diversity (Narwani et al., 2013, 2015; Nathan et al., 2016; Tucker et al.,

2018). There has been found, albeit with a large variability among studies, that functional or ecological traits and phylogenetic composition exhibit higher effects of niche processes (Bishop et al., 2015; Comte et al., 2014; Dehling et al., 2014). Using functional and taxonomical information also has allowed to investigate whether gains and losses of species occur simultaneously in these two facets of diversity (Naaf & Wulf, 2012), that is, whether decreases in species diversity leads to decreases in functional diversity. For some systems, the influence of anthropogenic pressures introducing species and modifying habitats has resulted in taxonomic and functional homogenization (Buisson et al., 2013; Vanni, Luecke, Kitchell, & Magnuson, 1990; Villéger et al., 2014). These losses of diversity via the reduction of dissimilarity among communities is a concern because habitats varying in traits composition may support different ecosystems functions (Mouillot et al., 2011; Van Der Plas et al., 2016).

Furthermore, the effect of environmental processes can vary among traits, with some traits showing the influence of abiotic factors (Matthews et al., 2010) while others are affected by biotic interactions or are neutral (Botta-Dukát & Czúcz, 2016; Sterck et al., 2011). Within communities, the variability in the influence of environmental processes on traits results in contrasting patterns of traits diversity: higher diversity than expected for some traits and lower diversity for others (Ackerly & Cornwell, 2007; Saito et al., 2016; Šímová et al., 2015). When freshwater fishes are studied from a functional perspective, a typical set of ecological traits comprised descriptors of multiple niche dimensions (*i.e.* trophic, defense, life-history, morphological) (Olden et al., 2006; Winemiller et al., 2015). Findings show that environmental factors explain the variation in abundance and richness of functional groups based on habitat-use traits (Arantes et al., 2018; Ibañez et al., 2009). Moreover, environmental factors also act on life-history traits, favoring species with high offspring investment, low fecundity and aseasonal

reproduction (equilibrium strategists) on environmentally stable habitats (Mims & Olden, 2013; Santos et al., 2017). Therefore, there is a need to establish which traits had higher contribution to changes in composition or whether traits are responding differently to niche and stochastic processes (Dianye Zhang et al., 2019).

Moreover, the above mentioned findings come mainly from surveys across spatial scales while an understanding on whether traits contribute differently to changes in traits composition over time is still emerging (Magurran et al., 2019). Compositional changes of communities over time can be pictured as trajectories on an ordination space, where communities diverge from or converge to an initial state (De Cáceres et al., 2019; Fukami et al., 2005). For example, after starting with different traits composition, communities may converge over time (decreasing traits β -diversity) when exposed to similar environmental conditions and still maintaining high species β -diversity (Fukami et al., 2005). Then, changes in species composition can lead or not to changes in traits composition. That is, if niche processes are operating then species traits may influence the chance of a species to enter into a community, and species and traits trajectories over time to be related (Leibold & Chase, 2018). Otherwise, if dispersal, drift and trait redundancy are high, taxonomic and traits composition would show no relationship (Leibold & Chase, 2018; Spasojevic et al., 2014).

Considering that traits can differ in the signature of environmental factors and that temporal changes in composition can be depicted as trajectories of community states (De Cáceres et al., 2019), we investigated for the drivers of spatio-temporal changes in habitat-use and life-history traits in freshwater fish communities. We aimed to test the following predictions: i) taxonomic homogenization leads to traits homogenization. We predicted that communities became more similar over time, exhibiting traits and taxonomic homogenization with decreases in taxonomic

β -diversity leading to decrease in traits β -diversity. ii) Taxonomic and traits β -diversity are driven by spatial and environmental factors in different degrees. We predicted that environmental heterogeneity would have a higher effect on traits β -diversity, while spatial isolation would be a driver of taxonomic β -diversity.

3.2 Material and methods

3.2.1 Temporal series

We considered 23 sites from four temporal series from United States, New Zealand, and Brazil. From the North Temperate Lakes LTER (<https://lter.limnology.wisc.edu/about/overview>) we took data between 1981-2012 for nine lakes, five lakes at the northern region (46°2'45.96" N - 89°40'30.36" W) and four lakes at the south (43°3'10.7994" N - 89°25'29.99" W). Fishes were capture through seven sampling gears (electric fishing, gillnets, seine nets, minnow traps, etc.), and species number in each site range between 6-29 species each year. From New Zealand four main rivers (46°26'6.56"S - 169°7'6.91"E; 37°55'30.43"S - 175°32'20.03"E) were sampled by electric fishing between 1985-2016, capturing 2-18 species each year (<https://nzffdms.niwa.co.nz/>). Finally, a floodplain system from the Southeast Brazil (22° 45' 48.0594"S - 53° 21' 53.676"W) comprising nine sites (three main rivers, three connected and three isolated lakes) and sampled between 2000-2018 using gillnets and seine nets. Sites at this floodplain showed 24 to 73 species annually. The Multi Gear Mean Standardization (MGMS) suggested by Gibson-Reinemer et al. (2017) was employed to standardize abundance (CPUE) data from data sampled using multiple capture devices.

3.2.2 Environmental heterogeneity and spatial isolation

Monthly measurements for North Temperate Lakes (although depending on winter conditions) and New Zealand rivers, and quarterly measurements from Upper Parana, of turbidity (NTU),

dissolved oxygen (ppm and μgL^{-1}), water temperature ($^{\circ}\text{C}$) and pH were used to calculate an annual average for each variable. Then, a PERMDISP on the Euclidean distance for log-transformed and standardized variables was performed for each temporal series. The distance of each site to the year centroid was taken as a measure of environmental heterogeneity (Anderson et al., 2006).

Since temporal series comprised habitats with different characteristics, spatial isolation was calculated separately. Spatial isolation was measured based on sites geographic coordinates, connectivity (only for Paraná temporal series) and area (for lakes). For Paraná temporal series which consisting of rivers, connected and disconnected lakes, and ordinal measure of connectivity was used (0: isolated lakes, 1: connected lakes; 2: for rivers). Lakes area was converted to an ordinal variable ranging from 1-6, then a value of seven was assigned to rivers. For New Zealand rivers, spatial isolation was based only on geographic coordinates. The first axis of a principal component analysis (63.16% - 99.23% of explained variance) was taken as the measure of spatial isolation.

3.2.3 Species traits

Eleven traits for 295 species were considered to account for species niche dimensions related to habitat-use and life history. Traits information was taken from multiple sources including the species original descriptions, temporal series data, ecological descriptions and FishBase (Froese & Pauly, 2018). Seven traits were considered as proxies to habitat-use: shape factor, swim factor, eye size, snout length, mouth position, habitat preference as position in the water column and diel period of most activity. Body shape and swim factor are proxies to swimming ability and the habitats frequented by species (Blake, 2004). Habitat preferences, diel activity and predation can be determined by eye size (Caves et al., 2017), whereas type of prey and diet can relate with

snout length (Marrero & Winemiller, 1993). Body length was measured from temporal series when data on species size was available. Otherwise, and also for eye size and shape factor, values were those reported on species original descriptions and FishBase (Froese & Pauly, 2018).

The life-history traits set (four traits) consisted of those traits associated with life span (body size), reproduction and offspring investment. In the case of offspring investment, besides the presence or absence of a parental care, parents investment on offspring followed the classification of Winemiller (1989). Thus, offspring investment was measured as the summation considering the presence/absence of the reproductive strategies exhibited by species: i) placement of zygotes (0-1); ii) bearing (0-1); iii) guarding (0-1); iv) mouthbrooding (0-1); v) stage of offspring when parental care is ended (eggs = 1; larval = 2; young = 3); vi) contribution of parents (monoparental = 1; biparental = 2; monoparental or biparental = 1.5); vii) prolonged gestation = 8 (only for *Potamotrygon* species) (Olden et al., 2006; Winemiller, 1989). The presence /absence of internal fertilization and spawning migrations completed the life-history traits set.

3.2.4 Beta diversity and temporal trajectories

The decomposition of total β -diversity (B_{total}) in its replacement (B_{repl}) and richness difference (B_{rich}) components was employed following (Carvalho et al., 2012). Using abundance data and the Jaccard dissimilarity index, the components of β -diversity were calculated for species, the entire set of traits, and for each subset comprising habitat-use and life-history traits. The dissimilarity matrices for each component of β -diversity were used were to calculate a delta of compositional change ($\Delta\beta$ -diversity) between time 1 (T1) and the last sampled period (T2) (Baiser & Lockwood, 2011; Villéger et al., 2014). The $\Delta\beta$ -diversity was calculated as the difference between the spatial β -diversity at T2 and the β -diversity in T1. If $\Delta\beta$ -diversity > 0 , sites in T2 were more dissimilar in composition, indicating differentiation in composition. If $\Delta\beta$ -

diversity < 0 , then late communities (T2) were compositionally more similar, suggesting homogenization. The same procedure was conducted for individual traits (Baiser & Lockwood, 2011) with the purpose of investigating the relationship between the temporal changes of individual traits and the $\Delta\beta$ for the entire set of traits.

On an ordination space, temporal changes in composition can exhibit geometric properties (i.e. frequency, length, speed, divergence, convergence) giving information on the quantity of change, the resilience to disturbances and regime shifts in ecological systems (De Cáceres et al., 2019; Ryo et al., 2019). Thus, the community trajectory analysis approach (CTA; De Cáceres et al., 2019) was performed to investigate the relationship between temporal trajectories in habitat-use and life-history traits. For CTA analysis, the trajectory of each site (23 sites) is based on a projection of the communities on an ordination space (PCoA) built from the lingoes corrected β -diversity dissimilarity matrices. The coordinates of each community are their states over time. The trajectory of a community is determined by its initial and end points (beginning and end of the sampled period), and the geometric characteristics of the temporal change: its total length can inform on how much change a community experienced through time; the length of the segments connecting states (points in the ordinations space) shows the quantity of change there was among adjacent samplings in time (large lengths means large change), and the angles between sampling points inform us on the direction of the trajectory. For example, trajectories can converge or diverge over time indicating increases and decreases on β -diversity (Fukami et al., 2005). Here we took the lengths of segments between sampling points (year) as descriptors of the degree of change between adjacent points in time. These lengths were used to investigate the relationship between changes in habitat-use traits, life-history traits and the entire set of traits. Calculations of

beta diversity and temporal trajectories were done using the packages ‘BAT’ (Cardoso et al., 2018) and ‘vegclust’ (de Cáceres et al., 2010) in R.

3.2.5 Data analysis

First, using the $\Delta\beta$ for traits as response and the taxonomic $\Delta\beta$ as explanatory, linear models were fitted to test whether the increase and decrease of species β -diversity explained changes in traits β -diversity. Linear models also were fitted to determine the amount variance in the $\Delta\beta$ for the complete set of traits explained by changes in habitat-use traits, life-history traits and individual traits. To test whether temporal trajectories in trait composition for individual sites were most related to habitat-use or life-history traits, generalized linear models (GLM) were fitted. GLM’s considered as response variable the lengths of each segment (from T_i to T_{i+1}) describing the temporal change in traits composition for each site in each sampled system (23 sites). The explanatory variables were the trajectories for habitat-use and life history in separated models. The adjusted coefficient of determination (R^2_{adj}) was considered as the measure of the explained variance in temporal changes in traits composition associated to habitat-use traits and life-history traits. Finally, using the β -diversity dissimilarity matrices (12 matrices for each site), their distance to the centroid was calculated through a PERMDISP. These distances were used as a measure of β -diversity (Anderson et al., 2006). Then for each system, GLMs were fitted using spatial isolation and environmental heterogeneity as explanatory variables, with the aim to investigate for their effects on taxonomic and traits β -diversity and their components. The R^2_{adj} for GLM models were computed through the ‘rsq’ package (Dabao Zhang, 2017).

3.2.6 Trait sensitivity

We determined whether results depended on the number and identity of traits (Mouillot et al., 2014), and the relationship among trajectories was influenced by the unequal sizes of the habitat-use (seven traits) and life-history (four traits) sets. Thus, 220 matrices of three traits were generated and the beta diversity and trajectories calculated for each matrix. Then, the relationship between trajectories of species and traits change was explored using linear models. If results are determined by the size of the traits subsets, then habitat-use and life-history matrices of equal size would show similar contribution $\Delta\beta$.

3.3 Results

3.3.1 Temporal changes in spatial β -diversity

Overall, the comparison ($\Delta\beta$) between early (T1) and late (T2) fish communities showed both homogenization and differentiation on species and traits composition. Late communities had a slightly higher portion of taxonomic homogenization (47.8% vs 46.2%, of the comparisons for species and traits composition). Approximately 16% of the comparisons showed no change, while 35.4% and 38.1% exhibited taxonomic and traits differentiation, respectively. All sites experienced taxonomic and habitat-use traits (HU) homogenization, while differentiation in life-history traits (LH) occurred in two temporal series (Table 1). Although, we expected a higher homogenization, the number of comparisons exhibiting a decrease in β -diversity only exceeded the number of comparisons showing differentiation by $\approx 8\%$. Overall and as expected, the increase and decrease of traits β -diversity were related to changes in species composition for all components of β -diversity (Figure 3).

Table 1. temporal change ($\Delta\beta$) in the B_{total} (B_{repl}) components of taxonomic (Tax) and traits (Tra) β -diversity. T1 and T2 refer to the mean for B_{total} at the first and last year of sampling, respectively. HU: habitat-use traits; LH: life-history traits.

	GLN		GLS		BRA		NWZ	
	$\Delta\beta$	T1 T2	$\Delta\beta$	T1 T2	$\Delta\beta$	T1 T2	$\Delta\beta$	T1 T2
Tax	-0.016 (0.08)	0.60-0.58	-0.01 (-0.07)	0.49-0.48	-0.013 (-0.03)	0.52-0.51	-0.024 (-0.09)	0.87-0.84

Tra	-0.017 (0.00)	0.43-0.41	-0.022 (-0.04)	0.37-0.34	-0.003 (-0.01)	0.35-0.35	0.017 (-0.05)	0.61-0.63
Tra(HU)	-0.019 (0.03)	0.44-0.42	-0.015 (-0.05)	0.39-0.37	-0.008 (-0.01)	0.35-0.35	-0.014 (-0.09)	0.66-0.64
Tra(LH)	-0.035 (-0.05)	0.31-0.27	-0.085 (-0.06)	0.32-0.21	0.026 (0.05)	0.17-0.2	0.043 (-0.03)	0.38-0.44

Regarding the subsets of traits, the $\Delta\beta$ -diversity for habitat-use had stronger relationships with species $\Delta\beta$ -diversity ($R^2_{\text{ajd}} = 0.67-0.90$ vs $R^2_{\text{ajd}} = 0.0-0.53$ for life-history traits) (Figure S 7). Besides, habitat-use traits individually were highly related to the temporal change ($\Delta\beta$) in the entire set of traits. Morphological variables and position in the water column explained between 68.9% and 72.8% of the changes in the entire set of traits, whereas life-history traits explained 9.6% to 69.6% of traits $\Delta\beta$ -diversity (Figure S 8). We evaluated *a posteriori* the relationship between $\Delta\beta$ -diversity and a delta of environmental dissimilarity between sites, founding significant relationship for habitat-use traits ($r = 0.39$) and no relationship for life-history traits in one of the temporal series (Figure S 9).

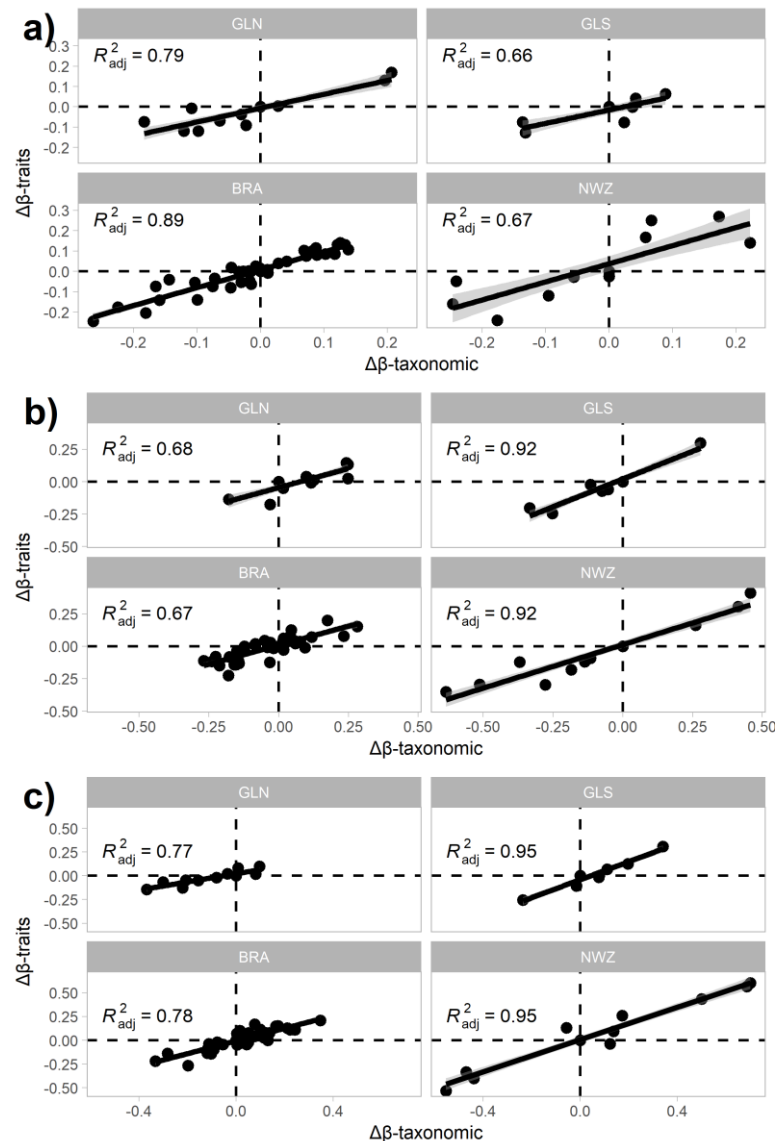


Figure 3. Relationship between temporal change ($\Delta\beta$) in traits and taxonomic composition for **a)** the Btotal, **b)** replacement components and the **c)** difference in richness components of β -diversity. Values of $\Delta\beta$ higher than zero indicate that communities in time T2 had higher dissimilarity in composition. Values lower than zero show that communities in time T2 had more similar composition (loss of diversity).

3.3.2 Trajectories of habitat-use and life-history traits

Overall, the trajectory analysis showed that taxonomic changes were larger (mean lengths = 0.59 ± 0.13) than changes in traits composition (mean lengths = 0.48 ± 0.13) (Figure 4), with habitat-use and life-history traits differing in the magnitude of changes. The change from one year to the

next of the habitat-use traits were similar to temporal changes in the entire set of traits (mean lengths = 0.48 ± 0.12), whereas the composition on life-history traits changed less over time (mean lengths = 0.37 ± 0.14). Accordingly, the analysis of the replacement component shows that the substitution of habitat-use traits was higher (0.34 ± 0.15 vs 0.22 ± 0.14 ; $F = 147.4$, $P < 0.001$) (Figure 2b). Moreover, generalized linear models showed that temporal changes in traits composition had a stronger relationship with changes in habitat-use traits (Figure 4d, Figure S 8), showing a 15% higher explanatory power than life-history traits trajectories (mean $R^2_{\text{adj}} = 0.89 \pm 0.07$ and 0.74 ± 0.16 , respectively). Sensitivity analysis (220 set of three traits), showed similar patterns in the relationship between the subsets of traits and taxonomic trajectories: habitat-use traits trajectories had a stronger relationship with changes in species composition (mean $R^2_{\text{adj}} = 0.42 \pm 0.10$ vs 0.23 ± 0.04 , for habitat-use and life-history traits; Figure S 10).

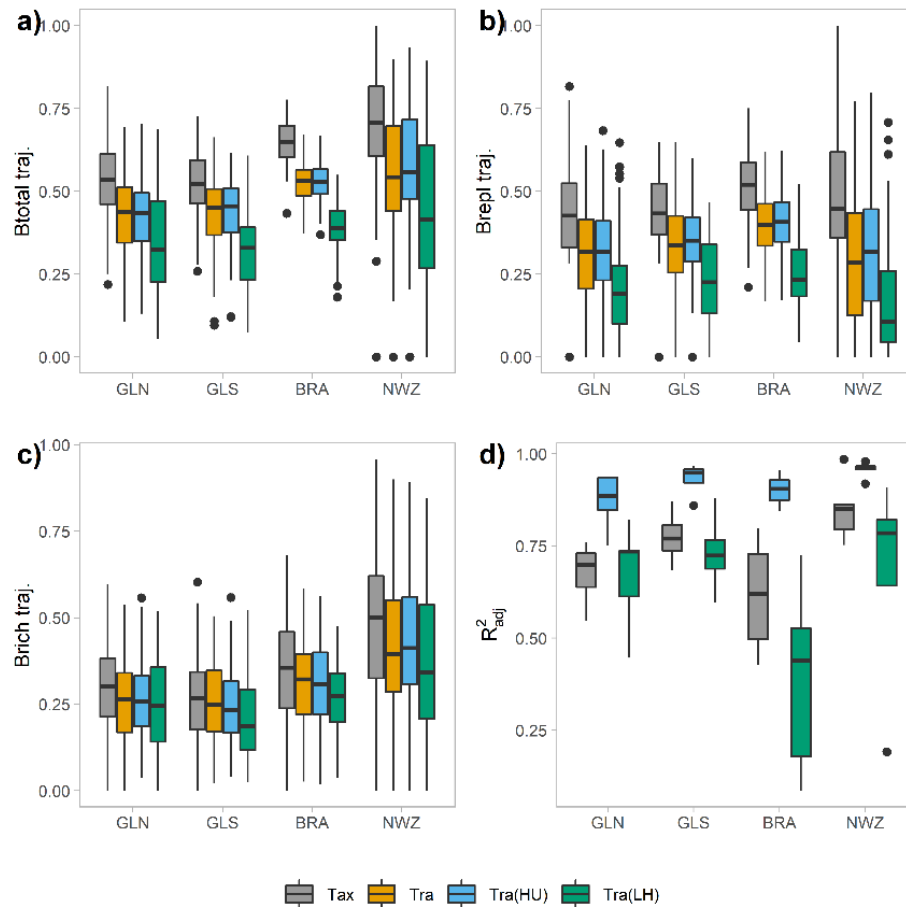


Figure 4. Trajectory lengths describing temporal changes in composition for 23 sites **a)** total β -diversity (Btotal); **b)** Replacement (Brepl); **c)** Richness difference (Brich); **d)** Relationship between temporal changes in habitat-use, life-history traits and species composition with the entire set of traits. Tax: taxonomic; Tra: traits; HU: habitat-use traits; LH: life-history traits.

3.3.3 Relationship between environmental heterogeneity and β -diversity

Environmental heterogeneity (EH) explained changes in composition across space (Figure 5). As expected, changes in both habitat-use and life-history traits were related to environmental heterogeneity. However, habitat-use only showed higher mean effect of EH on the replacement component (0.24 ± 0.09 ; 0.15 ± 0.06 , for habitat-use and life-history respectively), while total life-history traits β -diversity (Btotal) showed the highest mean effects (0.28 ± 0.08). The effect of spatial isolation were significant for temporal series with isolated sites (New Zealand rivers and Great Lakes), but mean effect size was not significantly different from zero.

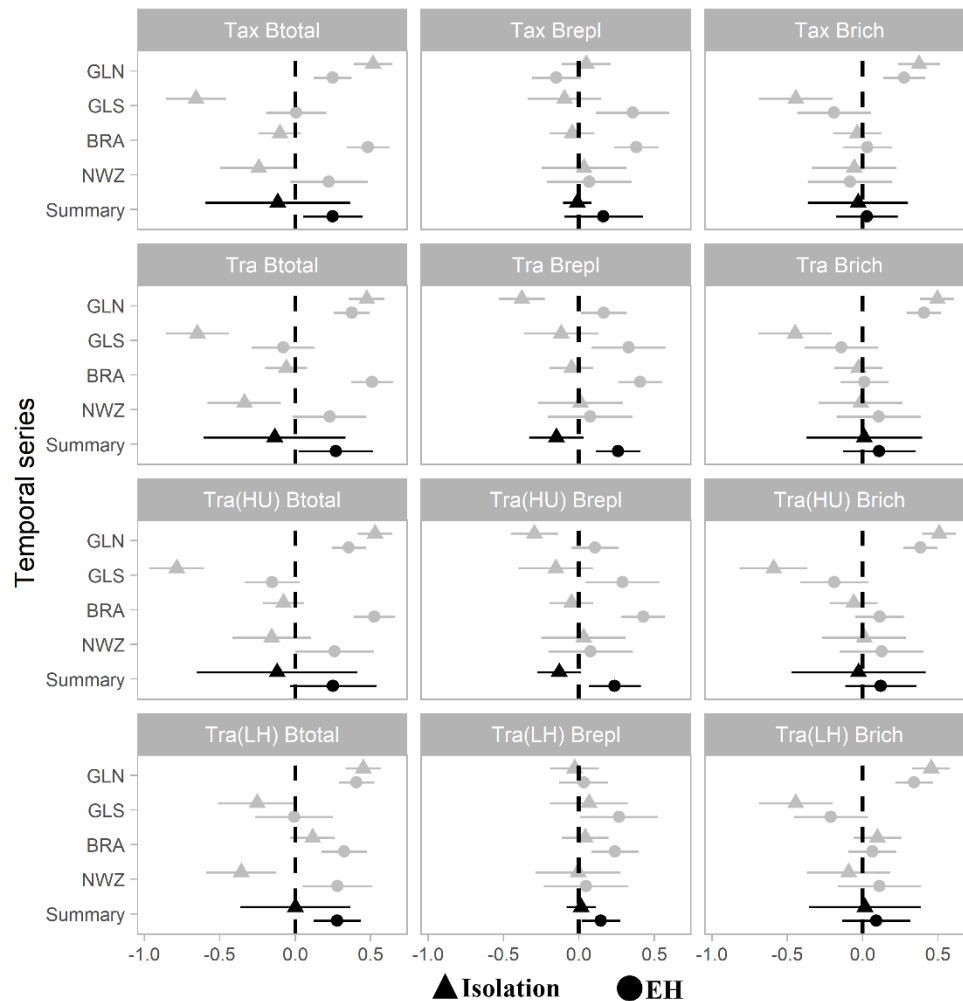


Figure 5. Effect size of the relationship between spatial β -diversity and environmental heterogeneity (EH) and spatial isolation. Tax: taxonomic; Tra: traits; HU: habitat-use traits; LH: life-history traits.

3.4 Discussion

3.4.1 Temporal changes in spatial β -diversity

The loss of diversity via a decrease in biotas dissimilarity (e.g. β -diversity) is a concern due to its effects on ecosystems viability by reducing the functionality and capability of response of communities to environmental change (Van Der Plas et al., 2016). Biotic homogenization has been registered mainly over large spatial extents, with species loss leading to functional homogenization (Buisson et al., 2013; Villéger et al., 2014). For west Europe freshwater fishes, Villéger et al. (2014) found that 53% of the comparisons among assemblages showed no change

or differentiation. Likewise, we found that the dissimilarity in composition between late communities exhibited both species and traits homogenization (46% of comparisons) and differentiation (38% of comparisons). These findings highlight that even communities on intermediate spatial extents and over short time frames (18 – 32 years) exhibit decreases in species and traits β -diversity (Lambdon et al., 2008).

Diversity loss in the surveyed systems may be related to the introduction of non-native species and human impacts affecting habitats quality over the last four decades (Daga et al., 2015; Vanni, Luecke, Kitchell, Allen, et al., 1990). The introduction of species has been recorded as one of the major causes of biotic homogenization, reducing the dissimilarity among sites over large spatial scales (Devictor et al., 2008). Both life-history (Liu et al., 2017) and habitat-use traits had been found to determine the success of invasive species (McKnight et al., 2017). Nevertheless, the invasion success of non-native species might not depend on exhibiting niche differences from natives. That is, invaders exhibiting high niche similarity with natives can colonize successfully, and even the number of native congeneric species may facilitates the colonization by non-natives (Diez et al., 2008).

Traits and functional homogenization also has been found to result from the effects of anthropogenic pressures and climate change leading to the loss of specialized species (Buisson et al., 2013; Devictor et al., 2008). For fish communities high disturbed habitats can be environmentally homogeneous favoring species with similar life-history traits (Santos et al., 2017) or create patches of habitats differing in quality where the composition of both life-history and habitat-use traits are determined by environmental variability (Arantes et al., 2018; Villéger et al., 2010). Accordingly, we found that environmental heterogeneity promotes the replacement

of species and traits, though larger effects on habitat-use traits was observed (Figure 5, Figure S 9).

3.4.2 Trajectories of habitat-use and life-history traits

Our results showed that habitat-use traits had a stronger relationship with changes at the whole set of traits and with changes in species composition. A relationship between changes in taxonomic and traits β -diversity suggest that niche processes are driving changes in composition where species on different habitats are dissimilar in their traits (Chesson, 2000; Leibold & Chase, 2018). Besides, since the replacement of habitat-use traits was higher than for life-history traits, it seems that the niche processes selected species according the way they use the resources, hence species on different habitats are dissimilar in their traits.

Although traits can respond differently to the processes driving community composition (Ackerly & Cornwell, 2007; Chesson, 2000; Saito et al., 2016), there is also a lack of information on life-history traits for many species. As more detailed information on life-history can be obtained it may be possible to detect their response to environmental factors and their contribution to species composition and ecosystem processes (King et al., 2015; Olden et al., 2006). For instance, although species mobility for foraging can influence community composition and ecosystem properties (Guzman et al., 2019; Massol et al., 2017), little is known on the spatial extents on which dispersal and foraging of most of freshwater fishes occur. Yet, our results suggest that niche processes can be acting on both life-history and habitat-use traits, but in a larger extent on traits associated on how species obtain food and occupy habitats (Figure 5; Figure S 7).

3.4.3 Relationship between environmental heterogeneity and β -diversity

Processes leading to changes in composition occur in a gradient of dispersal and environmental variability (Gianuca et al., 2017; Heino, Melo, & Bini, 2015). The observed positive relationship between replacement and environmental variability can result from sites differing in environmental conditions, but also from spatially structured environmental variation (Hill et al., 2017; Tonkin et al., 2018). Where sites were isolated (e.g. Great Lakes), or over large spatial extents (e.g. New Zealand rivers) it is more likely that both spatial isolation and environmental heterogeneity to drive β -diversity (Heino, Melo, Siqueira, et al., 2015). Moreover, for organisms restricted to aquatic environments spatial isolation and dispersal limitation would have a greater influence on the dissimilarity of communities composition (Tonkin et al., 2018).

Besides the observed mean effects of environmental heterogeneity, increases and decreases of environmental variability between sites might lead to the homogenization and differentiation of communities (Figure S 9). Although this was an *a posteriori* finding and limited to the temporal series with large number of sites, there is evidence supporting that reduction of environmental variability can lead to the suppression of traits and functions (Bishop et al., 2015; Gámez-Virués et al., 2015). The decrease of environmental variability across space and time through urbanization (Marchetti et al., 2006; McKinney, 2006), land use (Benning et al., 2002) and flow impoundments (Vitule et al., 2012) had been found to lead to more similar communities. For freshwater fishes highly homogeneous environments can lead to the substitution of species with seasonal behavior by equilibrium strategist with aseasonal behavior and high offspring investment (Mims & Olden, 2013; Santos et al., 2017).

Although both life-history and habitat-use traits replacement were affected by environmental heterogeneity, the effect was almost twice for habitat use traits. Using reproductive and trophic functional groups Arantes et al.(2018) found a higher influence of environmental factors on the

variation in composition of trophic guilds. Turbidity, substrate and water temperature has been observed as drivers of changes in composition for freshwater fishes (Peláez & Pavanelli, 2019; Zbinden & Matthews, 2017). Environmental factors can determine the composition of habitat use traits, for instance, deterring or favoring visual predators along turbidity gradients (Caves et al., 2017; Santos et al., 2018), or leading to spatial and diel partitioning of resources (Crow et al., 2010).

Overall, our results showed that compositional changes in traits diversity had a stronger relationship with changes in habitat-use traits. Communities displayed a degree of homogenization slightly higher than differentiation, losing species and traits diversity when comparing initial and late communities. The observed relationship between changes at taxonomic composition and habitat-use traits may indicate that homogenization and differentiation can be due to the loss and gains of ecological and morphological traits rather than to the loss of life-history traits. Moreover, the mean effect of environmental heterogeneity was higher on the replacement of habitat-use traits across space probably indicating that niche processes are driving changes in composition. These results highlight and support findings showing that traits may differ on the signature of effects of processes driving community composition, with the conclusions depending on the selected traits.

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APPENDIX A - Relationship between temporal change ($\Delta\beta$) in composition.

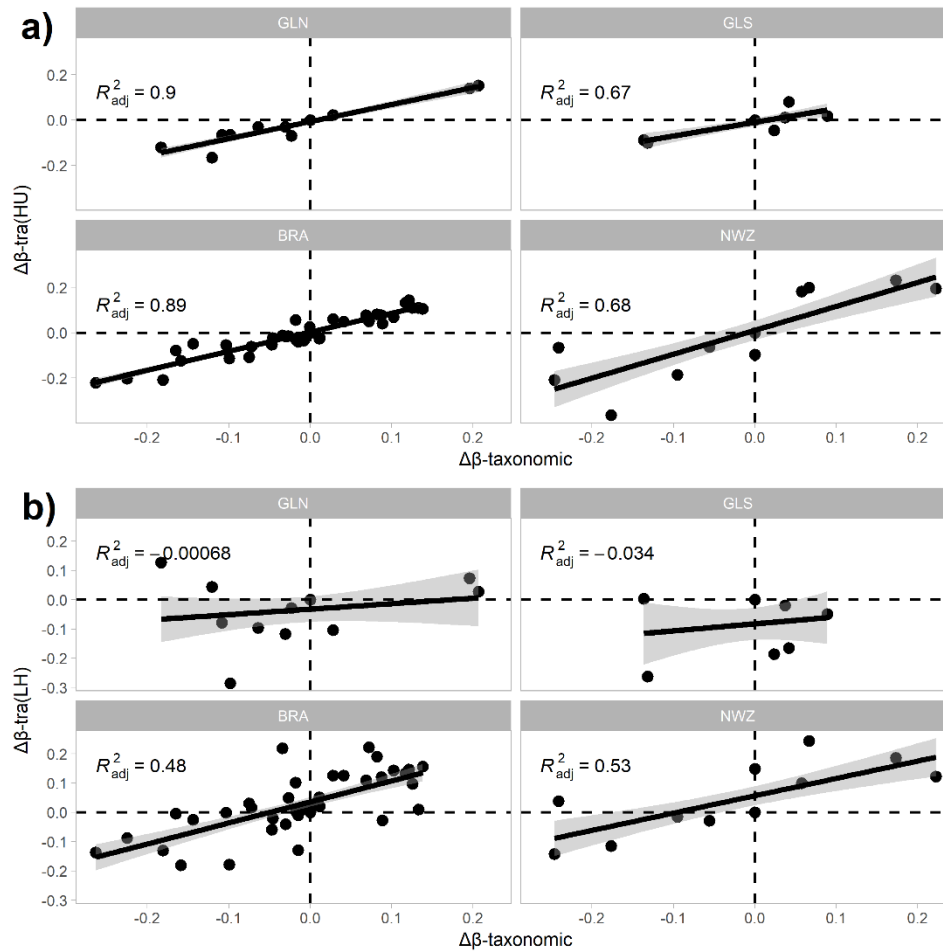


Figure S 7. Relationship between temporal change ($\Delta\beta$) in **a)** habitat-use traits and **b)** life-history traits with changes in taxonomic composition.

APPENDIX B - Relationship between temporal change at individual traits and the changes at the entire set of traits $\Delta\beta$ -traits

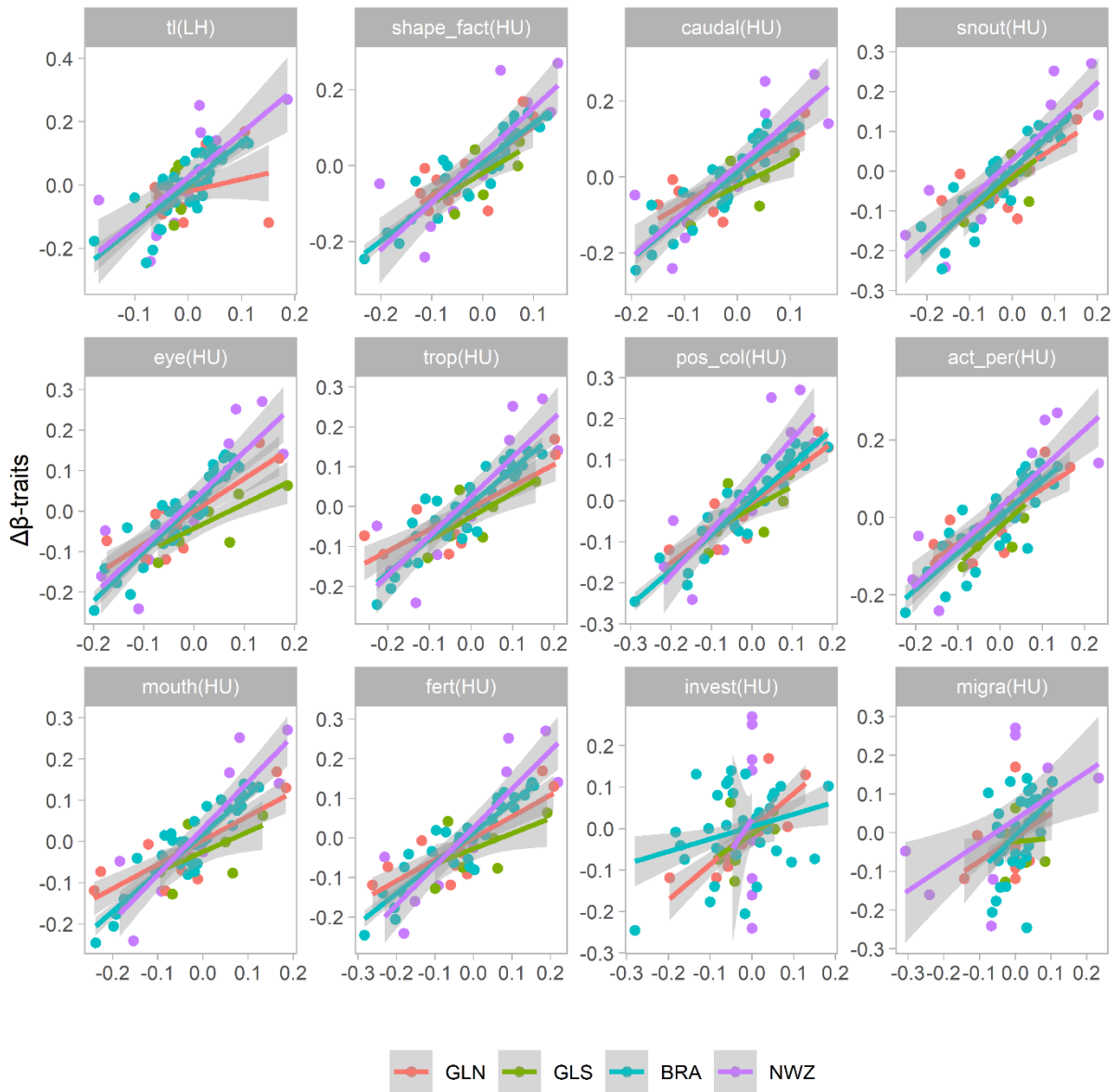


Figure S 8. Relationship between temporal change at individual traits and the changes at the entire set of traits $\Delta\beta$ -traits. HU: habitat-use traits; LH: life-history traits.

APPENDIX C - Relationship between a delta of environmental dissimilarity and changes in composition for life history and habitat use traits.

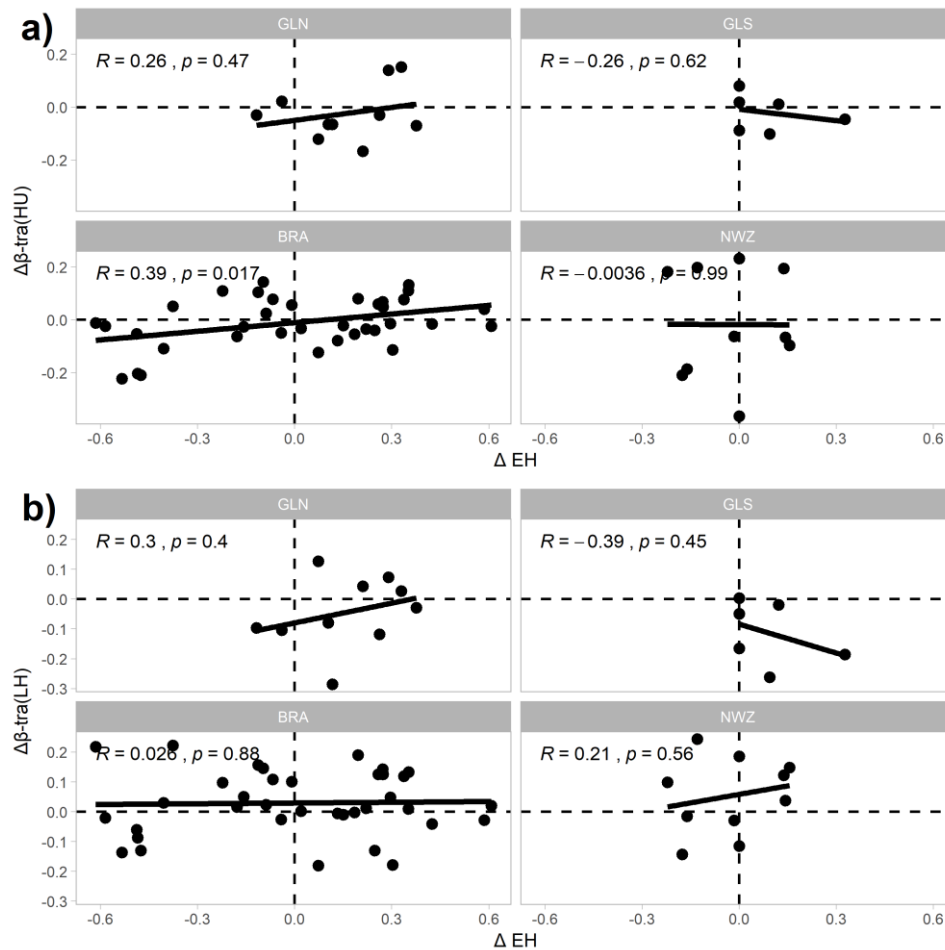


Figure S 9. Relationship between a delta of environmental dissimilarity and ($\Delta\beta$) for **a)** habitat-use traits and **b)** life-history traits. The delta for environmental dissimilarity was calculated as the difference between the environmental dissimilarity between sites in T2 minus the environmental dissimilarity between sites in T1.

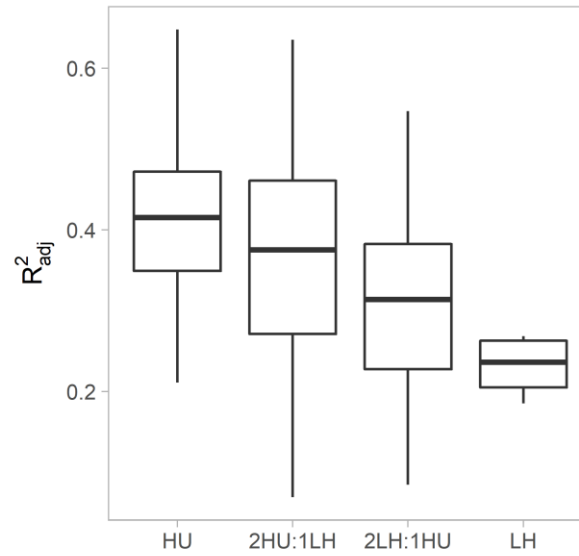
APPENDIX D - Sensitivity analyses.

Figure S 10. Sensitivity analyses. The relationships between the trajectories for habitat-use and life-history traits with changes in species composition were tested for 220 matrices of three traits. **HU**: for matrices of three habitat-use traits; **LH**: for matrices of three life-history traits.

APPENDIX E - Mean effect size of environmental heterogeneity (EH) and spatial isolation (ISO) on spatial β -diversity

Table S 1. Mean effect size of environmental heterogeneity (EH) and spatial isolation (ISO) on spatial β -diversity. Tra: entire set of traits; Tra(LH): life-history traits; Tra(HU): habitat-use traits; Tax: taxonomic β -diversity.

Facet	Component	var	Mean Effect	se	zval	pval	ci.lb	ci.ub
Tra	Btotal	EH	0.271	0.126	2.144	0.032	0.023	0.518
	Btotal	ISO	-0.136	0.24	-0.567	0.571	-0.606	0.334
	Brepl	EH	0.26	0.076	3.429	0.001	0.111	0.409
	Brepl	ISO	-0.149	0.092	-1.611	0.107	-0.33	0.032
	Brich	EH	0.11	0.122	0.901	0.368	-0.13	0.35
	Brich	ISO	0.011	0.196	0.056	0.955	-0.374	0.396
Tra(LH)	Btotal	EH	0.28	0.08	3.516	0	0.124	0.437
	Btotal	ISO	0.001	0.187	0.006	0.995	-0.364	0.367
	Brepl	EH	0.147	0.065	2.262	0.024	0.02	0.274
	Brepl	ISO	0.015	0.049	0.297	0.766	-0.082	0.112
	Brich	EH	0.091	0.115	0.792	0.428	-0.135	0.318
	Brich	ISO	0.014	0.189	0.075	0.94	-0.357	0.386
Tra(HU)	Btotal	EH	0.253	0.146	1.73	0.084	-0.034	0.539
	Btotal	ISO	-0.12	0.271	-0.44	0.66	-0.652	0.413
	Brepl	EH	0.238	0.088	2.7	0.007	0.065	0.411
	Brepl	ISO	-0.131	0.074	-1.771	0.077	-0.277	0.014
	Brich	EH	0.121	0.121	1.003	0.316	-0.116	0.359
	Brich	ISO	-0.027	0.227	-0.119	0.905	-0.473	0.419
Tax	Btotal	EH	0.251	0.1	2.502	0.012	0.054	0.447
	Btotal	ISO	-0.116	0.245	-0.472	0.637	-0.597	0.365
	Brepl	EH	0.164	0.133	1.233	0.218	-0.096	0.424
	Brepl	ISO	-0.012	0.048	-0.243	0.808	-0.106	0.082
	Brich	EH	0.029	0.105	0.275	0.783	-0.176	0.234
	Brich	ISO	-0.031	0.17	-0.18	0.857	-0.363	0.302

APPENDIX F – Species functional traits.

Species	tl	sh_fc	sw_fc	snout	eye	trop	pos_col	act_period	mouth_pos
<i>Acestrorhynchus lacustris</i>	30.2	0.23	0.22	0.35	0.17	4.2	benthopel	1	T
<i>Acestrorhynchus pantaneiro</i>	26.6	0.24	0.28	0.34	0.19	4.3	benthopel	1	T
<i>Acipenser fulvescens</i>	150	0.18	0.28	0.48	0.09	3.3	demersal	3	I
<i>Aequidens plagiozonatus</i>	13	0.44	0.72	0.3	0.29	3.2	benthopel	1	T
<i>Ageneiosus inermis</i>	55.5	0.2	0.63	0.56	0.13	4	pelagic	2	ST
<i>Ageneiosus militaris</i>	37	0.2	0.5	0.36	0.1	3.7	pelagic	2	ST
<i>Ageneiosus ucayalensis</i>	30.4	0.19	0.54	0.46	0.11	3.7	pelagic	2	ST
<i>Aldrichetta forsteri</i>	40	0.24	0.37	0.22	0.18	2.5	demersal	1	T
<i>Ambloplites rupestris</i>	32.67	0.42	0.42	0.27	0.26	3.28	demersal	3	T
<i>Ameiurus brunneus</i>	29	0.25	0.52	0.23	0.1	3.4	demersal	3	T
<i>Ameiurus melas</i>	60.5	0.33	0.54	0.29	0.14	3.81	demersal	3	T
<i>Ameiurus natalis</i>	31.2	0.19	0.51	0.23	0.1	3.3	demersal	3	T
<i>Ameiurus nebulosus</i>	54.45	0.23	0.57	0.26	0.12	3.41	demersal	3	T
<i>Ameiurus platycephalus</i>	29	0.23	0.47	0.43	0.3	3.4	demersal	3	T
<i>Amia calva</i>	78.7	0.23	0.65	0.22	0.16	3.8	demersal	1	T
<i>Anguilla australis</i>	106.5	0.08	1	0.2	0.08	3.89	benthopel	3	T
<i>Anguilla dieffenbachii</i>	110	0.09	1	0.21	0.08	3.75	demersal	3	T
<i>Apareiodon affinis</i>	15.7	0.18	0.47	0.31	0.28	2.2	demersal	1	ST
<i>Aphyocharax anisitsi</i>	6.6	0.32	0.4	0.28	0.31	3.2	pelagic	1	T
<i>Aphyocharax dentatus</i>	5.4	0.23	0.39	0.26	0.32	3.2	pelagic	1	T
<i>Apistogramma commbrae</i>	4.6	0.33	0.89	0.24	0.33	3.2	benthopel	1	T
<i>Aplodinotus grunniens</i>	95	0.33	0.39	0.23	0.3	3.4	demersal	1	T
<i>Apteronotus caudimaculosus</i>	21.7	0.18	0.9	0.23	0.15	3.3	demersal	3	T
<i>Apteronotus ellisi</i>	22.4	0.17	0.9	0.34	0.12	3.3	demersal	3	T
<i>Astronotus crassipinnis</i>	32.3	0.52	0.7	0.21	0.27	3	benthopel	1	T
<i>Astyanax fasciatus</i>	11.5	0.34	0.36	0.22	0.34	3	benthopel	1	T
<i>Astyanax lacustris</i>	13.5	0.33	0.36	0.16	0.39	2.8	benthopel	1	T
<i>Astyanax paranae</i>	9.3412	0.32	0.51	0.25	0.31	2.8	benthopel	1	T
<i>Astyanax schubarti</i>	10.8	0.3	0.34	0.21	0.4	3.1	benthopel	1	T
<i>Auchenipterus osteomystax</i>	33.8	0.2	0.66	0.26	0.29	3.6	benthopel	2	ST
<i>Brachyhypopomus gauderio</i>	17.8	0.11	1	0.26	0.11	3.1	demersal	3	ST
<i>Brycon hilarii</i>	28.89	0.29	0.33	0.24	0.23	2	benthopel	1	T
<i>Brycon orbignyanus</i>	61	0.3	0.34	0.21	0.27	2.5	benthopel	1	T
<i>Bryconamericus exodon</i>	4.2	0.26	0.37	0.22	0.38	2.7	benthopel	1	T
<i>Bryconamericus stramineus</i>	7.5	0.33	0.38	0.28	0.4	2.7	benthopel	1	T
<i>Callichthys callichthys</i>	15.5	0.2	0.69	0.26	0.14	3.3	demersal	3	ST
<i>Campostoma anomalum</i>	17	0.24	0.24	0.36	0.12	2	benthopel	1	T
<i>Carassius auratus</i>	41.14	0.34	0.37	0.29	0.23	2	benthopel	1	T
<i>Carpiodes carpio</i>	64	0.3	0.3	0.25	0.19	2	demersal	1	ST
<i>Carpiodes cyprinus</i>	64	0.35	0.37	0.24	0.22	2.6	demersal	1	ST
<i>Catathyridium jenynsii</i>	26	0.5	0.67	0.37	0.09	3.3	demersal	2	T

<i>Catostomus commersonii</i>	64	0.21	0.34	0.42	0.21	2.98	demersal	1	ST
<i>Cetopsorhamdia iheringi</i>	11.1	0.19	0.59	0.37	0.1	3.04	demersal	3	T
<i>Characidium zebra</i>	6	0.22	0.51	0.25	0.23	3.5	benthopel	1	T
<i>Cheimarrichthys fosteri</i>	9.2	0.2	0.41	0.41	0.22	3.2	demersal	3	I
<i>Chrosomus eos</i>	4.84	0.2	0.47	0.22	0.27	2.51	demersal	1	T
<i>Chrosomus erythrogaster</i>	5.8	0.25	0.46	0.34	0.26	2.5	demersal	1	T
<i>Chrosomus neogaeus</i>	6.171	0.24	0.5	0.23	0.28	2.63	demersal	1	T
<i>Chrosomus oreas</i>	5.5	0.25	0.41	0.26	0.28	2	demersal	1	T
<i>Cichla kelberi</i>	72.6	0.26	0.42	0.33	0.18	4.4	benthopel	1	T
<i>Cichla piquiti</i>	48.5	0.26	0.43	0.32	0.15	4.2	benthopel	1	T
<i>Cichla sp</i>	28.5	0.27	0.41	0.33	0.17	4.2	benthopel	1	T
<i>Cichlasoma paranaense</i>	15.7	0.38	0.52	0.27	0.27	3.2	benthopel	1	T
<i>Clarias gariepinus</i>	90.4	0.15	0.61	0.21	0.12	3.8	benthopel	3	T
<i>Clinostomus funduloides</i>	6.7	0.2	0.38	0.26	0.31	2.7	benthopel	1	T
<i>Colossoma macropomum</i>	44.8	0.45	0.3	0.16	0.14	2.02	benthopel	1	T
<i>Coregonus artedi</i>	57	0.24	0.25	0.21	0.21	3.4	pelagic	2	T
<i>Coregonus clupeaformis</i>	52	0.25	0.29	0.24	0.21	3.09	demersal	2	T
<i>Corydoras aeneus</i>	7.5	0.38	0.59	0.47	0.23	3	demersal	1	T
<i>Cottus bairdii</i>	15	0.22	0.4	0.26	0.18	3.3	demersal	2	T
<i>Cottus cognatus</i>	10.1	0.17	0.43	0.3	0.19	3.4	demersal	2	T
<i>Crenicichla britskii</i>	26.6	0.28	0.66	0.25	0.24	3.1	benthopel	1	T
<i>Crenicichla haroldoi</i>	14.2	0.18	0.55	0.36	0.23	3.2	benthopel	1	T
<i>Crenicichla jaguarensis</i>	23	0.23	0.46	0.31	0.22	3.2	benthopel	1	T
<i>Crenicichla niederleinii</i>	13.5	0.18	0.48	0.34	0.15	3.2	benthopel	1	T
<i>Culaea inconstans</i>	9.68	0.21	0.33	0.21	0.28	3.18	demersal	1	T
<i>Curculionichthys insperatus</i>	4	0.18	0.57	0.46	0.19	2	demersal	3	I
<i>Cyphocharax modestus</i>	17	0.3	0.39	0.24	0.34	2.2	benthopel	1	T
<i>Cyphocharax nagelii</i>	20.5	0.28	0.4	0.27	0.34	2.2	benthopel	1	T
<i>Cyprinella galactura</i>	15	0.21	0.34	0.29	0.21	3.2	benthopel	1	T
<i>Cyprinella lutrensis</i>	9	0.3	0.38	0.29	0.3	2.8	benthopel	1	T
<i>Cyprinella spiloptera</i>	6.3	0.26	0.42	0.31	0.25	2.84	benthopel	1	T
<i>Cyprinus carpio</i>	145.2	0.4	0.44	0.28	0.18	2.63	benthopel	1	T
<i>Diapoma guarani</i>	4.5	0.26	0.54	0.25	0.42	2.9	benthopel	1	T
<i>Dorosoma cepedianum</i>	57	0.38	0.37	0.21	0.2	2.4	pelagic	1	T
<i>Eigenmannia trilineata</i>	30.5	0.11	1	0.22	0.2	3.1	demersal	3	T
<i>Eigenmannia virescens</i>	36.5	0.1	1	0.27	0.17	3.2	demersal	3	ST
<i>Erimyzon oblongus</i>	37.6	0.32	0.42	0.47	0.19	3	demersal	1	ST
<i>Erythrinus erythrinus</i>	24.6	0.2	0.75	0.19	0.12	3.7	demersal	2	T
<i>Esox americanus</i>	37.6	0.17	0.34	0.42	0.17	3.7	demersal	1	T
<i>Esox lucius</i>	157.3	0.18	0.33	0.4	0.16	4.2	demersal	1	T
<i>Esox masquinongy</i>	187	0.21	0.27	0.43	0.18	4.24	demersal	1	T
<i>Etheostoma blennioides</i>	17	0.17	0.37	0.36	0.22	3.4	benthopel	1	T
<i>Etheostoma caeruleum</i>	8	0.24	0.38	0.24	0.23	3.3	benthopel	1	T

<i>Etheostoma chlorobanchium</i>	11	0.24	0.68	0.22	0.28	3.4	benthopel	1	T
<i>Etheostoma exile</i>	4.8	0.18	0.56	0.15	0.25	3.52	benthopel	1	T
<i>Etheostoma flabellare</i>	9.5	0.2	0.58	0.2	0.24	3.2	benthopel	1	T
<i>Etheostoma nigrum</i>	7.5	0.16	0.36	0.73	0.27	3.2	demersal	1	ST
<i>Etheostoma spectabile</i>	7.4	0.23	0.43	0.27	0.17	3.3	benthopel	1	T
<i>Etheostoma vulneratum</i>	8.1	0.23	0.59	0.21	0.22	3.3	benthopel	1	T
<i>Etheostoma zonale</i>	8.1	0.18	0.63	0.31	0.23	3.3	benthopel	1	T
<i>Farlowella amazonum</i>	22.5	0.06	0.15	0.84	0.09	2.3	demersal	3	I
<i>Fundulus diaphanus</i>	11	0.22	0.47	0.27	0.27	3.2	benthopel	1	SP
<i>Fundulus notatus</i>	8	0.21	0.55	0.31	0.28	3.1	benthopel	1	T
<i>Galaxias anomalus</i>	6.8	0.15	0.49	0.18	0.23	3.2	benthopel	3	T
<i>Galaxias argenteus</i>	40	0.15	0.57	0.21	0.16	3.2	demersal	3	T
<i>Galaxias brevipinnis</i>	13.068	0.13	0.44	0.23	0.2	3.45	benthopel	3	SP
<i>Galaxias cobitinis</i>	6.7	0.11	0.53	0.3	0.19	3.2	benthopel	3	T
<i>Galaxias depressiceps</i>	10	0.15	0.61	0.18	0.23	3.2	benthopel	3	T
<i>Galaxias divergens</i>	6.8	0.13	0.57	0.27	0.25	3.2	demersal	3	T
<i>Galaxias eldoni</i>	8.4	0.18	0.55	0.19	0.21	3.2	benthopel	3	T
<i>Galaxias fasciatus</i>	25.3	0.18	0.55	0.26	0.16	3.3	demersal	3	T
<i>Galaxias gollumoides</i>	15	0.16	0.55	0.23	0.29	3.2	benthopel	3	T
<i>Galaxias macronasus</i>	7	0.11	0.77	0.24	0.23	3.2	demersal	3	T
<i>Galaxias maculatus</i>	10.285	0.17	0.37	0.28	0.23	3.16	benthopel	3	T
<i>Galaxias paucispondylus</i>	10.1	0.12	0.61	0.32	0.2	3.1	benthopel	3	T
<i>Galaxias postvectis</i>	26	0.21	0.5	0.2	0.22	3.3	demersal	3	T
<i>Galaxias prognathus</i>	9.1	0.13	0.55	0.28	0.18	3.1	benthopel	3	T
<i>Galaxias pullus</i>	11.85	0.17	0.38	0.35	0.2	3.2	benthopel	3	T
<i>Galaxias vulgaris</i>	12	0.17	0.54	0.27	0.21	3.1	benthopel	3	T
<i>Galeocharax knerii</i>	25.7	0.34	0.28	0.24	0.27	4.3	benthopel	2	T
<i>Gambusia affinis</i>	5.082	0.3	0.8	0.29	0.29	3.22	benthopel	2	SP
<i>Gambusia holbrooki</i>	7.26	0.32	0.72	0.34	0.27	3.1	benthopel	2	SP
<i>Geophagus sveni</i>	28	0.42	0.54	0.38	0.28	2.3	demersal	1	T
<i>Geotria australis</i>	72.6	0.04	1	0.31	0.06	4.5	demersal	3	I
<i>Gobiomorphus alpinus</i>	6.844	0.21	0.52	0.17	0.29	3.2	demersal	3	T
<i>Gobiomorphus basalis</i>	9	0.19	0.67	0.25	0.22	3.2	demersal	3	T
<i>Gobiomorphus breviceps</i>	9.23	0.28	0.61	0.3	0.16	3.24	demersal	3	T
<i>Gobiomorphus cotidianus</i>	6.8	0.22	0.74	0.24	0.22	3.28	demersal	3	T
<i>Gobiomorphus gobioides</i>	17.4	0.26	0.64	0.28	0.16	3.3	demersal	3	T
<i>Gobiomorphus hubbsi</i>	6.1	0.2	0.57	0.25	0.17	3.2	demersal	3	T
<i>Gobiomorphus huttoni</i>	12	0.19	0.56	0.24	0.15	3.3	demersal	3	T
<i>Gymnorhamphichthys britskii</i>	70.6	0.09	1	0.5	0.08	3.2	benthopel	3	T
<i>Gymnotus inaequilabiatus</i>	79	0.12	1	0.29	0.11	3.4	benthopel	3	SP
<i>Gymnotus pantanal</i>	49	0.11	1	0.34	0.07	3.3	benthopel	3	SP
<i>Gymnotus paraguensis</i>	79.5	0.11	1	0.3	0.04	3.3	benthopel	3	SP
<i>Gymnotus sylvius</i>	73	0.16	1	0.26	0.08	3.2	benthopel	3	T

<i>Hemigrammus marginatus</i>	5.1	0.34	0.27	0.2	0.49	2.8	benthopel	2.8	T
<i>Hemigrammus ora</i>	5.1	0.37	0.66	0.2	0.42	3	benthopel	2	T
<i>Hemiodus orthonops</i>	37.9	0.22	0.26	0.24	0.28	2.6	benthopel	2	T
<i>Hemisorubim platyrhynchos</i>	60	0.16	0.29	0.41	0.1	4.5	demersal	3	SP
<i>Hoplerythrinus unitaeniatus</i>	30	0.23	0.77	0.18	0.21	3.4	benthopel	2	T
<i>Hoplias intermedius</i>	48.5	0.21	0.86	0.18	0.16	3.5	benthopel	2	T
<i>Hoplias mbigua</i>	79.5	0.2	0.61	0.17	0.17	3.5	benthopel	2	T
<i>Hoplias sp2</i>	45	0.24	0.62	0.14	0.15	3.5	benthopel	2	T
<i>Hoplias sp3</i>	47.5	0.22	0.64	0.21	0.16	3.5	benthopel	2	T
<i>Hoplosternum littorale</i>	28	0.3	0.61	0.32	0.13	2.7	demersal	3	T
<i>Hybognathus hankinsoni</i>	9.7	0.22	0.48	0.3	0.18	3.1	demersal	1	T
<i>Hybognathus nuchalis</i>	18	0.21	0.46	0.27	0.26	3.1	benthopel	1	T
<i>Hypentelium nigricans</i>	61	0.18	0.46	0.54	0.14	3.3	demersal	1	ST
<i>Hyphessobrycon anisitsi</i>	13.2	0.36	0.42	0.26	0.31	3	benthopel	1	T
<i>Hyphessobrycon eques</i>	8.4	0.41	0.35	0.16	0.4	3.1	benthopel	1	T
<i>Hypophthalmus oremaculatus</i>	46	0.22	0.35	0.34	0.14	2.9	pelagic	1	T
<i>Hypostomus albopunctatus</i>	36	0.2	0.5	0.55	0.12	2.2	demersal	3	I
<i>Hypostomus ancistroides</i>	27.6	0.21	0.5	0.44	0.18	2.3	demersal	3	I
<i>Hypostomus cochliodon</i>	41.6	0.27	0.5	0.46	0.17	2.3	demersal	3	I
<i>Hypostomus commersoni</i>	39.5	0.22	0.48	0.5	0.13	2.3	demersal	3	I
<i>Hypostomus hermanni</i>	21	0.2	0.65	0.52	0.21	2.3	demersal	3	I
<i>Hypostomus iheringii</i>	23	0.22	0.51	0.44	0.17	2.3	demersal	3	I
<i>Hypostomus regani</i>	42.7	0.19	0.38	0.51	0.19	2.3	demersal	3	I
<i>Hypostomus strigaticeps</i>	45.5	0.2	0.54	0.45	0.17	2.3	demersal	3	I
<i>Ichthyomyzon greeleyi</i>	20	0.08	1	0.34	0.06	4.2	demersal	3	I
<i>Ichthyomyzon unicuspis</i>	39.2	0.08	1	0.42	0.07	4.5	demersal	3	I
<i>Ictalurus punctatus</i>	121	0.23	0.3	0.3	0.13	3.76	demersal	3	ST
<i>Ictiobus bubalus</i>	112	0.36	0.55	0.23	0.21	3	demersal	1	ST
<i>Ictiobus cyprinellus</i>	123	0.31	0.42	0.19	0.16	3.1	demersal	1	T
<i>Ictiobus niger</i>	123	0.35	0.51	0.21	0.17	3.4	demersal	1	ST
<i>Iheringichthys labrosus</i>	34	0.17	0.34	0.37	0.21	2.9	demersal	1	ST
<i>Imparfinis mirini</i>	7.986	0.18	0.52	0.36	0.16	3.24	demersal	3	T
<i>Imparfinis schubarti</i>	13.13	0.16	0.52	0.36	0.2	3.1	demersal	3	T
<i>Knodus moenkhausii</i>	6.5	0.29	0.4	0.21	0.39	2.6	benthopel	1	T
<i>Labidesthes sicculus</i>	13	0.12	0.4	0.35	0.29	3.4	pelagic	1	ST
<i>Laetacara araguaiae</i>	9	0.44	0.6	0.23	0.33	3.1	demersal	1	T
<i>Lepisosteus osseus</i>	180	0.08	0.41	0.7	0.07	4.2	demersal	3	T
<i>Lepomis auritus</i>	13.2	0.45	0.36	0.18	0.18	3.23	demersal	1	T
<i>Lepomis cyanellus</i>	12.7	0.41	0.44	0.25	0.2	3.5	benthopel	1	T
<i>Lepomis gibbosus</i>	19	0.55	0.52	0.28	0.19	3.48	benthopel	1	T
<i>Lepomis gulosus</i>	28	0.39	0.5	0.27	0.19	3.4	demersal	1	T
<i>Lepomis humilis</i>	15	0.4	0.41	0.23	0.25	3.6	benthopel	1	T
<i>Lepomis macrochirus</i>	19	0.48	0.41	0.24	0.2	3.4	benthopel	1	T

<i>Lepomis megalotis</i>	9.4	0.42	0.36	0.27	0.21	3.6	benthopel	1	T
<i>Lepomis microlophus</i>	19.2	0.39	0.38	0.27	0.18	3.5	demersal	1	T
<i>Leporellus vittatus</i>	23.6	0.29	0.41	0.34	0.2	3.2	benthopel	1	ST
<i>Leporinus friderici</i>	41.1	0.33	0.3	0.29	0.21	3.3	benthopel	1	T
<i>Leporinus lacustris</i>	59	0.38	0.59	0.28	0.27	3.7	benthopel	1	ST
<i>Leporinus octofasciatus</i>	23	0.25	0.42	0.33	0.3	2	benthopel	1	T
<i>Leporinus striatus</i>	25.2	0.26	0.38	0.42	0.22	2	benthopel	1	T
<i>Lepthoplosternum pectorale</i>	10	0.25	0.91	0.44	0.18	3	demersal	2	T
<i>Loricaria cataphracta</i>	32.5	0.11	0.24	0.4	0.16	2.2	demersal	3	I
<i>Loricariichthys platymetopon</i>	38.3	0.12	0.19	0.36	0.16	2.5	demersal	3	I
<i>Loricariichthys rostratus</i>	29.2	0.11	0.25	0.53	0.16	2.6	demersal	3	I
<i>Lota lota</i>	40	0.14	0.82	0.31	0.12	3.54	demersal	3	T
<i>Luxilus chrysocephalus</i>	8.3	0.25	0.46	0.22	0.3	3.3	demersal	1	T
<i>Luxilus coccogenis</i>	14	0.22	0.36	0.28	0.3	3	pelagic	1	T
<i>Luxilus cornutus</i>	10.1	0.27	0.35	0.28	0.28	2.98	demersal	1	T
<i>Lythrurus umbratilis</i>	8.8	0.23	0.36	0.25	0.26	3	benthopel	1	T
<i>Macrhybopsis storeriana</i>	22.2	0.22	0.34	0.33	0.29	3.6	demersal	2	ST
<i>Megalancistrus parananus</i>	52.7	0.19	0.4	0.54	0.23	2	demersal	3	I
<i>Megaleporinus macrocephalus</i>	63.5	0.31	0.44	0.3	0.18	2.5	benthopel	1	ST
<i>Megaleporinus obtusidens</i>	49	0.28	0.31	0.32	0.24	3.2	benthopel	1	ST
<i>Megaleporinus piavussu</i>	54	0.32	0.4	0.29	0.23	2.5	benthopel	1	ST
<i>Melanorivulus apiamici</i>	2.4	0.24	0.52	0.2	0.33	3.1	benthopel	1	SP
<i>Metynnis lippincottianus</i>	20	0.56	0.25	0.14	0.31	2.9	pelagic	1	T
<i>Micropterus dolomieu</i>	50.5	0.32	0.35	0.27	0.15	3.64	benthopel	2	T
<i>Micropterus punctulatus</i>	63.5	0.28	0.36	0.24	0.17	3.6	demersal	2	T
<i>Micropterus salmoides</i>	78.65	0.33	0.42	0.2	0.15	3.81	benthopel	2	T
<i>Minytrema melanops</i>	32.67	0.25	0.28	0.25	0.18	3.4	demersal	2	ST
<i>Moenkhausia bonita</i>	23.3	0.29	0.31	0.23	0.23	3.3	benthopel	1	T
<i>Moenkhausia forestii</i>	5.1	0.31	0.35	0.18	0.4	3.2	benthopel	1	T
<i>Moenkhausia gracilima</i>	5.3	0.25	0.37	0.23	0.47	3.3	benthopel	1	T
<i>Moenkhausia intermedia</i>	10.5	0.36	0.34	0.2	0.38	2.7	benthopel	1	T
<i>Moenkhausia sanctaefilomenae</i>	6.5	0.4	0.35	0.21	0.43	3	benthopel	1	T
<i>Mola mola</i>	363	0.77	1	0.44	0.2	3.3	pelagic	1	ST
<i>Morone chrysops</i>	36	0.38	0.41	0.21	0.2	4	benthopel	2	T
<i>Morone mississippiensis</i>	46	0.4	0.56	0.22	0.2	4.1	demersal	3	T
<i>Moxostoma anisurum</i>	49.2	0.27	0.33	0.42	0.2	3	demersal	3	ST
<i>Moxostoma breviceps</i>	62	0.25	0.35	0.45	0.19	3.1	demersal	2	ST
<i>Moxostoma carinatum</i>	77	0.26	0.37	0.39	0.25	3.6	demersal	2	ST
<i>Moxostoma duquesnii</i>	51	0.26	0.33	0.41	0.19	3	demersal	2	ST
<i>Moxostoma erythrurum</i>	78	0.25	0.45	0.43	0.21	3	demersal	2	ST
<i>Moxostoma macrolepidotum</i>	75	0.25	0.44	0.45	0.19	3.1	demersal	2	ST
<i>Moxostoma valenciennesi</i>	80	0.28	0.44	0.4	0.18	3.3	demersal	2	ST
<i>Mugil cephalus</i>	96.8	0.23	0.37	0.19	0.22	2.5	benthopel	1	T

<i>Myloplus tiete</i>	26.2	0.54	0.23	0.25	0.36	3	benthopel	1	T
<i>Neochanna apoda</i>	11	0.15	0.74	0.22	0.12	3	benthopel	3	T
<i>Neochanna burrowsius</i>	8.5	0.15	0.61	0.21	0.15	3.39	demersal	3	T
<i>Nocomis biguttatus</i>	26	0.21	0.46	0.28	0.21	3	demersal	2	T
<i>Nocomis micropogon</i>	33	0.25	0.41	0.27	0.33	3.2	demersal	2	T
<i>Notemigonus crysoleucas</i>	36.7	0.36	0.31	0.21	0.23	2.84	demersal	2	T
<i>Notropis atherinoides</i>	13	0.18	0.45	0.27	0.32	2.8	benthopel	3	T
<i>Notropis blennioides</i>	13	0.2	0.47	0.28	0.31	2.7	benthopel	3	T
<i>Notropis boops</i>	9	0.21	0.38	0.25	0.39	3.2	benthopel	3	T
<i>Notropis buccatus</i>	9.8	0.2	0.47	0.3	0.26	3.1	benthopel	3	T
<i>Notropis heterodon</i>	7.1	0.2	0.35	0.18	0.34	3	benthopel	3	T
<i>Notropis heterolepis</i>	9.8	0.17	0.45	0.23	0.31	2.8	benthopel	3	T
<i>Notropis hudsonius</i>	10.1	0.18	0.37	0.28	0.3	2.6	benthopel	3	T
<i>Notropis leuciodus</i>	8.2	0.22	0.35	0.27	0.33	2.9	benthopel	3	T
<i>Notropis lutipinnis</i>	7.2	0.23	0.36	0.31	0.28	2.9	benthopel	3	T
<i>Notropis micropteryx</i>	8	0.17	0.38	0.26	0.33	2.9	benthopel	3	T
<i>Notropis photogenis</i>	14.3	0.17	0.37	0.34	0.29	3.3	pelagic	3	T
<i>Notropis rubellus</i>	9	0.28	0.45	0.35	0.3	3.1	benthopel	3	T
<i>Notropis spectrunculus</i>	7.9	0.18	0.3	0.25	0.33	2.9	benthopel	3	T
<i>Notropis stramineus</i>	8.2	0.21	0.42	0.2	0.28	2.4	benthopel	3	T
<i>Notropis telescopus</i>	11.5	0.16	0.36	0.24	0.4	2.8	benthopel	3	T
<i>Notropis volucellus</i>	5	0.22	0.35	0.25	0.31	3.02	benthopel	3	T
<i>Noturus exilis</i>	15	0.15	0.65	0.36	0.17	3.4	demersal	3	T
<i>Noturus flavus</i>	13.2	0.14	0.67	0.32	0.19	3.2	demersal	3	T
<i>Noturus miurus</i>	13.2	0.23	0.63	0.3	0.21	3.5	demersal	3	T
<i>Odontostilbe avanhandava</i>	9.3	0.27	0.4	0.15	0.46	2.3	benthopel	1	T
<i>Oligosarcus pintoii</i>	7.5	0.32	0.32	0.25	0.34	4.2	pelagic	1	T
<i>Oncorhynchus mykiss</i>	121	0.25	0.38	0.27	0.21	3.5	benthopel	1	T
<i>Oncorhynchus nerka</i>	55.5	0.29	0.31	0.38	0.1	3.65	pelagic	1	T
<i>Oncorhynchus tshawytscha</i>	102.85	0.24	0.33	0.3	0.1	4.4	benthopel	1	T
<i>Osmerus mordax</i>	21.5	0.15	0.25	0.27	0.27	3.3	pelagic	1	T
<i>Ossancora eigenmanni</i>	13	0.31	0.38	0.39	0.23	2.8	demersal	2	ST
<i>Otothyropsis marapoama</i>	5	0.19	0.49	0.44	0.22	2.3	demersal	2	I
<i>Otothyropsis polyodon</i>	3.7	0.14	0.52	0.49	0.15	2.3	demersal	2	I
<i>Pamphorichthys hollandi</i>	3.8	0.25	0.64	0.19	0.41	3	pelagic	1	SP
<i>Parodon nasus</i>	10.7	0.25	0.49	0.25	0.25	2.3	benthopel	2	ST
<i>Perca flavescens</i>	14.036	0.28	0.39	0.24	0.2	3.33	benthopel	1	T
<i>Perca fluviatilis</i>	72.6	0.3	0.35	0.24	0.21	3.68	demersal	1	T
<i>Percina aurantiaca</i>	18	0.2	0.49	0.23	0.22	3.5	benthopel	1	T
<i>Percina caprodes</i>	18	0.16	0.44	0.28	0.24	3.4	benthopel	1	T
<i>Percina evides</i>	9.6	0.2	0.38	0.28	0.22	3.4	benthopel	1	T
<i>Percina maculata</i>	11	0.19	0.54	0.19	0.24	4	benthopel	1	T
<i>Percina squamata</i>	13	0.18	0.41	0.26	0.16	3.4	benthopel	1	T

<i>Percopsis omiscomaycus</i>	15	0.22	0.35	0.32	0.25	3.4	demersal	1	T
<i>Phalloceros harpagos</i>	3.4	0.27	0.82	0.22	0.37	3	pelagic	1	SP
<i>Phenacobius crassilabrum</i>	11.2	0.21	0.44	0.36	0.24	3	demersal	1	ST
<i>Phenacobius mirabilis</i>	12.2	0.2	0.55	0.43	0.2	3	demersal	1	ST
<i>Phenacorhamdia tenebrosa</i>	10	0.15	0.34	0.32	0.07	3.4	demersal	3	T
<i>Piabina argentea</i>	8.3	0.28	0.42	0.19	0.29	3	benthopel	1	T
<i>Piaractus mesopotamicus</i>	59	0.56	0.31	0.13	0.29	2	benthopel	1	T
<i>Pimelodella avanhandavae</i>	26.5	0.15	0.38	0.3	0.23	3.4	benthopel	2	T
<i>Pimelodella gracilis</i>	26	0.15	0.38	0.28	0.25	3.2	benthopel	2	T
<i>Pimelodella taenioptera</i>	23.5	0.16	0.48	0.32	0.26	3.5	benthopel	2	T
<i>Pimelodus maculatus</i>	41.9	0.3	0.39	0.4	0.24	2.8	demersal	3	T
<i>Pimelodus microstoma</i>	26.5	0.24	0.37	0.42	0.24	3.3	demersal	2	T
<i>Pimelodus misteriosus</i>	28.7	0.31	0.27	0.41	0.21	2.8	demersal	3	T
<i>Pimelodus ornatus</i>	37	0.18	0.29	0.35	0.14	3.3	demersal	3	T
<i>Pimephales notatus</i>	6.4	0.2	0.4	0.25	0.24	2.92	demersal	1	T
<i>Pimephales promelas</i>	6.05	0.22	0.46	0.23	0.29	2.43	demersal	1	T
<i>Pinirampus pirinampu</i>	69	0.2	0.42	0.36	0.09	4.5	demersal	3	T
<i>Plagioscion squamosissimus</i>	55.2	0.27	0.42	0.25	0.14	4.4	demersal	1	T
<i>Platanichthys platana</i>	4.8	0.33	0.47	0.26	0.25	3	pelagic	1	T
<i>Platydoras armatulus</i>	19	0.25	0.51	0.29	0.21	2.2	demersal	3	T
<i>Poecilia reticulata</i>	6.05	0.29	0.52	0.23	0.35	3	benthopel	1	SP
<i>Pomoxis annularis</i>	20	0.44	0.47	0.23	0.19	4.11	demersal	3	T
<i>Pomoxis nigromaculatus</i>	25	0.44	0.42	0.29	0.18	3.77	benthopel	3	T
<i>Potamotrygon amandae</i>	58	0.08	1	1	0.1	3.2	demersal	1	I
<i>Potamotrygon falkneri</i>	81.5	0.08	1	1	0.1	3.2	demersal	1	I
<i>Prochilodus lineatus</i>	61.3	0.34	0.32	0.3	0.19	2.2	demersal	1	T
<i>Proloricaria prolixa</i>	36.2	0.1	0.26	0.48	0.1	3	demersal	3	I
<i>Psellogrammus kennedyi</i>	6.7	0.48	0.26	0.17	0.42	3.1	pelagic	2	T
<i>Pseudopimelodus mangurus</i>	102.8	0.26	0.27	0.25	0.07	3.9	demersal	3	T
<i>Pseudoplatystoma corruscans</i>	125.4	0.16	0.29	0.44	0.05	4.5	demersal	3	ST
<i>Pseudoplatystoma reticulatum</i>	39.5	0.19	0.27	0.43	0.04	4.2	demersal	3	ST
<i>Pterodoras granulosus</i>	71	0.26	0.29	0.23	0.13	2.6	demersal	3	T
<i>Pterygoplichthys ambrosettii</i>	65.5	0.24	0.42	0.47	0.13	2.3	demersal	3	I
<i>Pungitius pungitius</i>	7.744	0.22	0.17	0.29	0.24	3.3	benthopel	1	T
<i>Pyloodictis olivaris</i>	140	0.24	0.43	0.27	0.1	3.79	demersal	3	T
<i>Pyrrhulina australis</i>	4.2	0.27	0.42	0.22	0.37	3.2	benthopel	1	SP
<i>Retropinna retropinna</i>	9.5	0.16	0.26	0.31	0.22	3.2	demersal	2	T
<i>Rhamdia quelen</i>	29	0.22	0.64	0.31	0.13	3.9	benthopel	3	T
<i>Rhamphichthys hahni</i>	100	0.06	1	0.56	0.03	3.2	demersal	3	T
<i>Rhaphiodon vulpinus</i>	64	0.18	0.35	0.2	0.29	4.5	pelagic	1	SP
<i>Rhinelepis aspera</i>	50.6	0.24	0.73	0.46	0.12	2.5	demersal	2	I
<i>Rhinichthys atratulus</i>	12.4	0.21	0.44	0.29	0.21	3.1	demersal	1	ST
<i>Rhinichthys cataractae</i>	17.8	0.2	0.45	0.35	0.2	3.2	demersal	3	ST

Rhinodoras dorbignyi	24.4	0.21	0.2	0.27	0.14	2.7	demersal	2	I
Rhombosolea retiaria	25	0.54	0.48	0.2	0.14	3.2	demersal	3.2	T
Roebooides descavadensis	10.8	0.35	0.28	0.2	0.4	3.3	benthopel	1	T
Salminus brasiliensis	77.2	0.27	0.35	0.22	0.11	3.8	benthopel	2	T
Salminus hilarii	38	0.28	0.28	0.21	0.15	2.6	benthopel	2	T
Salmo salar	121	0.22	0.32	0.39	0.12	4.5	benthopel	3	T
Salmo trutta	157.3	0.24	0.44	0.24	0.16	3.4	pelagic	3	T
Salvelinus fontinalis	102.85	0.29	0.48	0.26	0.24	3.3	benthopel	2	T
Salvelinus namaycush	121	0.21	0.35	0.29	0.13	4.29	benthopel	2	T
Sander vitreus	54	0.18	0.38	0.25	0.2	4.39	demersal	3	T
Satanoperca pappterra	27.5	0.37	0.57	0.34	0.38	2.8	benthopel	1	T
Scaphirhynchus platyrhynchus	80	0.11	0.23	0.56	0.1	3.5	demersal	2	I
Scardinius erythrophthalmus	42.35	0.35	0.38	0.18	0.29	2.9	benthopel	1	T
Schizodon altoparanae	33.7	0.24	0.43	0.29	0.27	2.5	benthopel	1	T
Schizodon borellii	43.9	0.25	0.4	0.2	0.32	2.4	benthopel	1	T
Schizodon nasutus	40.2	0.21	0.46	0.34	0.24	2.8	demersal	1	ST
Sebastes maliger	44	0.4	0.48	0.23	0.22	3.84	demersal	1	T
Semotilus atromaculatus	19.1	0.21	0.38	0.23	0.21	4	demersal	1	T
Serrapinnus calliurus	5.6	0.36	0.33	0.19	0.36	2.4	benthopel	1	T
Serrapinnus heterodon	4.3	0.25	0.37	0.17	0.44	2.5	benthopel	1	T
Serrapinnus notomelas	5.7	0.34	0.36	0.17	0.42	2.2	benthopel	1	T
Serrapinnus sp2	3.9	0.32	0.33	0.18	0.41	2.4	benthopel	1	T
Serrasalmus maculatus	30.1	0.63	0.25	0.18	0.25	4.1	pelagic	1	T
Serrasalmus marginatus	41.4	0.5	0.25	0.15	0.25	3.6	benthopel	1	T
Sorubim lima	60.6	0.17	0.32	0.37	0.07	4.1	demersal	3	I
Steindachnerina brevipinna	17.2	0.32	0.37	0.19	0.32	2.1	demersal	1	ST
Steindachnerina insculpta	17.3	0.32	0.41	0.19	0.33	2.1	demersal	1	ST
Sternopygus macrurus	55	0.12	1	0.26	0.09	3.2	demersal	3	T
Synbranchus marmoratus	59.5	0.04	1	0.19	0.1	2.8	demersal	3	T
Tinca tinca	72.6	0.35	0.44	0.29	0.14	3.78	demersal	3	T
Trachelyopterus galeatus	30.5	0.29	0.52	0.2	0.15	3.1	demersal	2	T
Trachydoras paraguayensis	23	0.36	0.36	0.16	0.24	2.7	demersal	1	I
Umbra pygmaea	14.52	0.24	0.63	0.23	0.26	3.3	demersal	1	T
Zungaro zungaro	73.5	0.19	0.39	0.51	0.05	4.5	demersal	3	T

4 CONCLUDING REMARKS

The two works presented here have two main findings: 1) that *temporal changes in land use contributed to the turnover* component of phylogenetic and functional composition. And 2) that ecological traits related differently to changes in taxonomic composition: *habitat use traits had a stronger relationship with changes in species composition than life history traits*. These results

show that fish communities are undergoing compositional changes in response to anthropogenic activities, resulting mostly on the taxonomic and functional homogenization of fish faunas in temperate and subtropical regions. That is, although it is expected that communities change over time, it is an interesting finding to observe that earlier communities were more different than later communities. The implication of such changes in functional composition is that by having less variation in ecological traits ecosystem functionality could be compromised. For instance, functionally diverse systems might have a higher chance to respond to the variability in environmental conditions, resist to species introductions and maintain a broader set of ecosystem services (e.g. fisheries, recreation, stability and resilience of trophic webs).

Showing that habitat use traits are related to changes in species composition can be indicative that deterministic processes (e.g. filtering) are driving community assembly over time. However, it does not mean that life history traits are not responding to environmental change. Instead, the gaps of information on species life history might lead to the observed weak relationship between life history β -diversity and species β -diversity. Filling the lack of knowledge on fish ecological traits (e.g. fecundity, growth rate, nutrients intake) will increase the chance to disentangle the effects of changes in environmental conditions on the functionality of fish communities, as well as to an understanding on how fish functions alter ecosystem properties.