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Dissertação de Mestrado

Trajetórias de uso da terra e seus efeitos sobre comunidades de peixes de riacho no Pampa

[Land use trajectories and their effects on stream fish communities in Pampa]

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Porto Alegre, março de 2020

Trajetórias de uso da terra e seus efeitos sobre comunidades de peixes de riacho no Pampa

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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Este trabalho dedico ao tempo, que nunca deixa de avançar.
Traz-me pessoas, experiências e conhecimentos que me
auxiliam a compreender e aproveitar o máximo presente
e orientar-me para o futuro.

Time flies over us, but leaves its shadow behind –
The Marble Faun, Nathaniel Hawthorne

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Resumo

A perda de cobertura vegetal nativa em bacias hidrográficas afeta as comunidades de peixes de riacho. No entanto, as comunidades de peixes podem não responder imediatamente após a mudança na cobertura da terra, de modo que algumas respostas serão detectáveis apenas anos após a mudança na cobertura da terra. Além disso, os padrões atuais das comunidades aquáticas podem depender não apenas de eventos específicos do passado, mas também do histórico desses eventos ou de algum limiar cumulativo. Neste estudo, investigamos como as trajetórias históricas (1985-2017) da perda de vegetação nativa em bacias hidrográficas afetam as comunidades de peixes em 60 riachos no Pampa. Primeiramente, avaliamos se a riqueza e a composição atuais dos peixes de riacho estão mais relacionadas à cobertura vegetal do passado ou recente da vegetação natural. Em seguida, definimos trajetórias de perda de vegetação como trajetórias de distúrbio da paisagem e testamos se diferentes atributos (frequência, magnitude e duração do distúrbio) afetaram espécies e grupos funcionais de comunidades de peixes em riachos. Construímos trajetórias de perda de vegetação usando dados anuais de uso da terra do Projeto MapBiomas. Descobrimos que a riqueza e composição atual das espécies estão mais relacionadas ao passado (10 a 20 anos antes da amostragem das comunidades) do que à cobertura vegetal na época das coletas. No entanto, também observamos que as respostas de determinadas espécies e grupos funcionais foram dependentes de atributos específicos da trajetória de perturbação. Concluímos que as características atuais da comunidade de peixes podem responder não apenas às condições passadas da bacia, mas também à forma como as condições da bacia mudaram ao longo do tempo (suas trajetórias históricas). Explorar as trajetórias de uso da terra parece uma abordagem promissora para melhorar a compreensão dos efeitos da paisagem na ecologia dos riachos, bem como a previsibilidade do atual gerenciamento e planejamento da paisagem nas comunidades de peixes dos riachos.

Palavras-chave

Dívida de extinção, limiares, gestão de bacias hidrográficas, comunidades de água doce, tendências de longo prazo, MapBiomas

Abstract

Loss of native vegetation cover in the watershed affects stream fish communities. However, fish communities may not respond immediately after land cover change takes place, so that some responses will be apparent only years after land cover change. Furthermore, present aquatic community patterns may depend not only on specific events from the past, but on the history of these events or some cumulative threshold. In this study, we investigated how a ca. 30-year (1985-2017) historical trajectory of native vegetation loss in watersheds affected fish communities in 60 streams in the southern Brazilian Pampa. Firstly, we evaluated whether current richness and composition of stream fish are more related to past or to recent natural vegetation cover. We then defined trajectories of vegetation loss as trajectories of landscape disturbance and tested whether different attributes of disturbance (frequency, magnitude and duration) affected particular species and functional groups of stream fish communities. We constructed vegetation loss trajectories using annual land use data from the MapBiomas Project. We found that current species richness and composition were more related to past (10 to 20 years before communities were sampled) than to current vegetation cover. However, we also observed that responses from particular species and functional groups were dependent on specific trajectory attributes. We concluded that present fish community characteristics may respond not only to past watershed conditions, but to how watershed conditions changed over time. Exploring land use trajectories seems a promising approach for improving understanding of landscape effects on streams, as well as the predictability of present landscape management and planning on stream fish communities.

Key-Words

Extinction debt, thresholds, watershed management, freshwater communities, long term trends, MapBiomas

Sumário

Introdução Geral

Efeitos da perda de vegetação nativa e a dívida de extinção

A perda de cobertura de vegetação nativa nas bacias hidrográficas, devido à conversão para agricultura e infraestruturas urbanas, afeta as comunidades de peixes de riacho em todo o mundo. A mudança no uso da terra na bacia hidrográfica afeta as comunidades aquáticas por vias abióticas que propagam distúrbios terrestres, modificando o habitat no interior dos riachos, por exemplo, aumentando a entrada de sedimentos finos da erosão do solo, redução da qualidade e complexidade do habitat e aumento da produção primária devido ao aporte de nutrientes utilizados na agricultura. Assim, medir a cobertura da terra em escala de bacia hidrográfica é importante para uma melhor compreensão dos padrões nas comunidades aquáticas locais e para prever os resultados do gerenciamento da paisagem dos rios e da regulamentação do uso da terra.

No entanto, as comunidades aquáticas e terrestres podem não responder imediatamente após as mudanças na paisagem, e diferentes paisagens podem ser submetidas a diferentes históricos de uso da terra. Portanto, não apenas as condições passadas de uma bacia podem ter um legado nos padrões ecológicos atuais, mas também as suas trajetórias históricas. Como as mudanças no uso da paisagem no passado ainda podem afetar os ecossistemas atuais, as extinções locais podem possuir um atraso. Portanto o efeito da mudança de habitat na perda de espécies pode ser detectado somente após algum tempo; este processo é conhecido como dívida de extinção. De fato, compreender o papel de fatores históricos foi recentemente apontado como um desafio importante para um melhor entendimento das influências da paisagem nos habitats e biota de água doce atuais e futuros. Nesse sentido, o uso recente da cobertura vegetal nativa para prever as características atuais da comunidade, como riqueza e composição de espécies, pode ter uma capacidade preditiva limitada, pois as paisagens atualmente semelhantes podem ter passado por trajetórias históricas muito diferentes do uso da terra.

Séries temporais em estudos ecológicos e o MapBiomas

Até muito recentemente, a pouca acessibilidade a séries temporais de dados de uso da terra obtidos, tratados e disponibilizados de uma forma padronizada, dificultava seu amplo uso em pesquisas em ecologia e biodiversidade. Estas usualmente restringiam-se a análise entre uso da terra no presente e uma ou poucas datas do passado. Entretanto, a criação da Plataforma MapBiomas tornou efetivamente possível para a comunidade científica investigar e analisar trajetórias de mudança de uso da terra e cobertura vegetal no território brasileiro, em uma escala de tempo com extensão (>30 anos) e resolução (anual) relevante para muitos fenômenos ecológicos.

Neste trabalho utilizamos dados do projeto MapBiomas abrangendo a região do bioma Pampa para o período 1985-2017 para 60 pequenas bacias hidrográficas onde amostramos peixes. A partir dos dados da plataforma, nos foi possível estimar atributos das trajetórias que captam importantes aspectos das séries temporais e que dialogam com uma abordagem fundamental em ciência ecológica, conhecida como Ecologia do Distúrbio, mas que usualmente compreende escala espacial de menor extensão. Assim, com os dados anuais, pudemos extrair valores que sintetizam as trajetórias a partir de atributos representando a frequência, a magnitude e a duração da perda de vegetação nativa.

Esses atributos foram importantes para captar diferentes aspectos das paisagens, uma vez que ao longo das bacias hidrográficas avaliadas, encontramos áreas que sofreram conversão há mais de 30 anos (baixa frequência e magnitude, mas altos valores para duração), com alta constância (alta frequência e magnitude e média duração) ou acentuada nos últimos anos (baixa frequência, alta magnitude e baixa duração). Essa perspectiva associada à Ecologia de Distúrbio pode ser útil para estudos em áreas amplas, com históricos de uso heterogêneo ao longo do território, como o bioma Pampa. Em sentido mais amplo, esses resultados indicam a importância de compreender como certos atributos ecológicos se comportam em relação a distintas trajetórias de mudança do uso da terra, o que pode ter implicações para o monitoramento de biodiversidade, para a projeção futura de efeitos de manejo, de restauração ecológica e de políticas ambientais.

Capítulo 1 – Assessing the legacy of land use trajectories on stream fish communities of southern Brazil*

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Introduction

Loss of native vegetation cover in watersheds due to conversion to agriculture and urban land use affects stream fish communities worldwide (Allan, 2004; Clapcott et al., 2012; Dala-Corte et al., 2016; Brejão et al., 2018; Wilkinson et al., 2018; Joy et al., 2019; Tóth et al., 2019). Land use change in the watershed affects aquatic communities via abiotic pathways that propagate terrestrial disturbances, modifying in-stream habitat (Burcher et al., 2007), *e.g.*, by increasing input of fine sediments from soil erosion (Naiman et al., 2010; Wagenhoff et al., 2012), reduction of habitat quality and complexity (Wang et al, 1997), and increase of primary production owing to input of nutrients used in agriculture (Burrell et al., 2013). Thus, measuring land cover at watershed scale became important for a better understanding of patterns in local aquatic communities (*e.g.* Leal et al., 2016) and for predicting the outcomes of riverscape management and land use regulation (Infante et al., 2019).

Nonetheless, aquatic and terrestrial communities may not respond immediately after landscape changes (Harding et al., 1998), and different landscapes can be subjected to different histories of land use (Ernoult et al., 2006; Maloney & Weller, 2011), so that biological responses may also change depending on how land use changed through time. Past conditions not only may have a legacy on present ecological patterns (*e.g.* Harding et al., 1998; Surasinghe & Baldwin, 2014; Uezu & Metzger, 2016; Zeni et al., 2014), but their historical trajectory towards a current state is important (Brejão et al., 2018). As past landscape use change may still affect current ecosystems (Lunt & Spooner, 2005), local extinctions may be delayed, so the effect of habitat change on species loss may be detected only after some time, a process known as extinction debt (Tillman et al., 1994; Kuussaari, 2006; Figueiredo et al., 2019). In fact, addressing the role of historical factors has been recently pointed as an important challenge for a better understanding of landscape influences on current and future freshwater habitats and biota (Infante et al., 2019). In this sense, using recent native vegetation cover for predicting present community characteristics, such as species richness and composition, may have a limited predictive capability (Brejão et al., 2018), as landscapes that are currently similar may have undergone very different historical trajectories of land use (Ernoult et al., 2006, Ferraz et al., 2009) (Fig. 1).

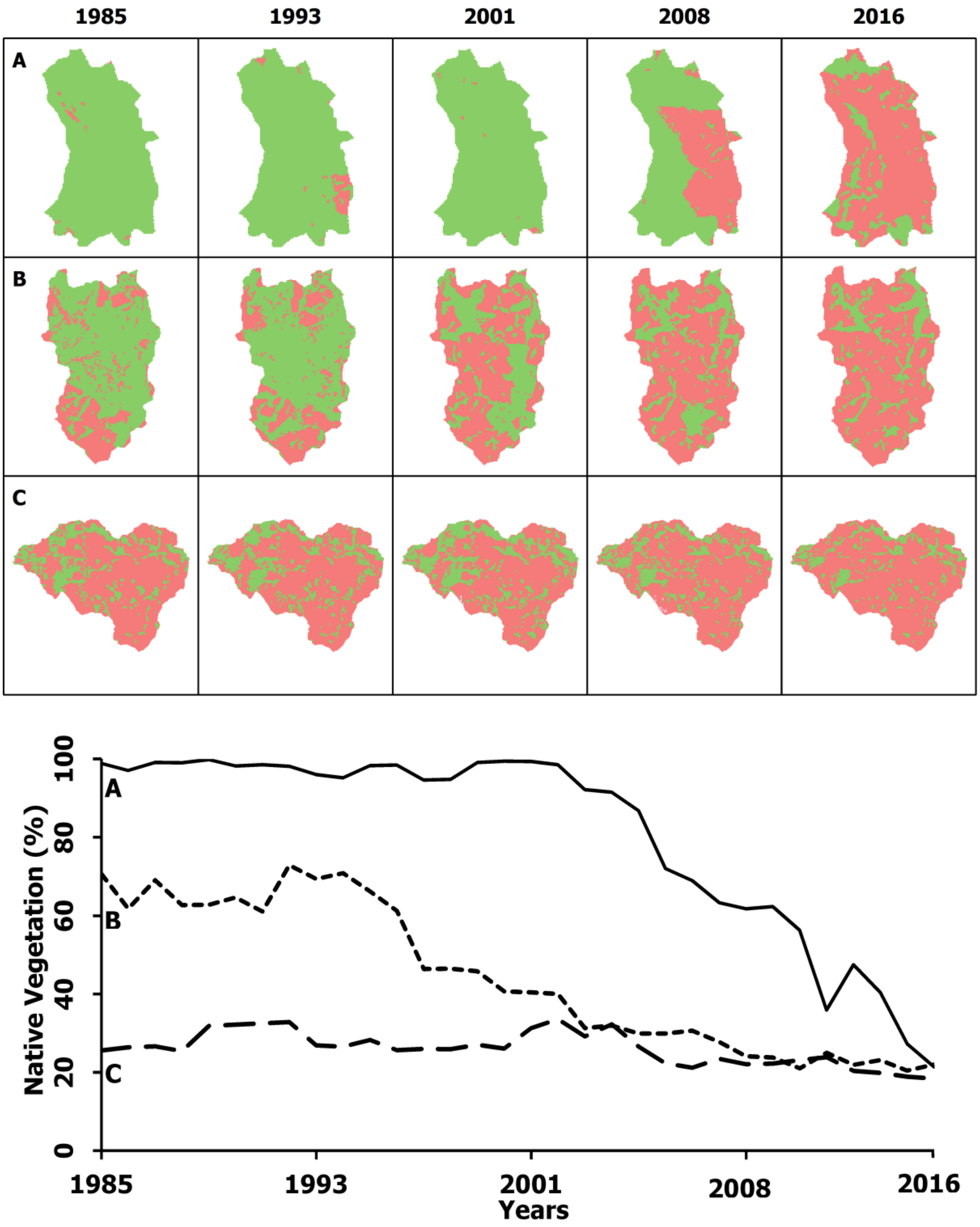

Fig. 1. Three watersheds (A, B and C) of the Brazilian Pampa with similar proportions (~25%) of current (2016) land use, but showing distinct historical trajectories of change in vegetation cover along the last 30 years. Maps represent change in natural vegetation (green) and other cover (red) between 1985 and 2016. Graphs show trajectories of annual change in native vegetation cover. Data from MapBiomas Project (2019). The sizes of watershed A, B and C are 22, 10 and 27 km², respectively.

Species can vary greatly in their responses to land use. Some may show negative linear declines in their populations, some may be favored and increase their abundance and occurrence, while others decline abruptly following minor losses of native vegetation (King & Baker, 2010). Also, responses may be nonlinear, so that it is important to define thresholds, breakpoints, and nonlinear responses for the communities under study (Dodds et al., 2010; see Brejão et al., 2018), as different biological groups in a given site may show distinct responses to environmental change gradients (Hanski & Hovaskainen, 2002). These differences may occur due to distinct habitat use, life history traits, and the measure of diversity considered (Ewers & Didham, 2006; Chase et al, 2018). In this sense, identifying individual response of species and functional groups, as well as relevant attributes of land use trajectories, may be more effective in capturing effects of land use on local communities (Statzner & Beche, 2010).

For a given landscape, different attributes can be used to describe the history of environmental change, including trajectory of land use. Moreover, land use change can be considered a type of disturbance, and disturbance ecology has traditionally described ecosystem change as a function of frequency, magnitude, and duration of disturbances (Stanley et al., 2010). Resistant species can tolerate stronger disturbances (magnitude), but the recurrence of a disturbance event (frequency) or its secondary effects that occur after a given period (duration) may preclude their persistence in streams (Resh et al., 1988; Capra et al., 1995; Simon & Klimetz, 2008). For instance, in a previous study on amazonian stream fish, the timing of response to conversion of 60% of the native vegetation in the landscape varied between 0 and 16 years for different groups (Brejão et al., 2018). After analyzing five studies of plant species richness in temperate grasslands, Cousins (2009) found that areas with <10% of natural cover in the landscape lead to rapid local extinction of sensitive species. In another example, Uezu & Metzger (2016) found that forest bird can persist up to 25 years in mildly fragmented landscapes, but when conversion intensity was too high, the time required for local extinction was substantially reduced. These examples show that measuring only current conditions is not enough to understand how communities change in response to land use, nor to predict futures scenarios (Newbold et al., 2015).

In this study, we used a 33-year annual series of land cover satellite images to investigate the historical effects of native vegetation loss on current stream fishes in 60 watersheds of the Pampa grasslands, in southern Brazil. Our first objective was to evaluate whether current species richness and composition are more related to past or current land uses. We expected that past land cover would provide a relevant explanation to models of present species richness, supporting the hypothesis that current fish community characteristics result also from past land cover (land use legacy). Secondly, we tested how different land use trajectory attributes affect fish species and functional groups. Our hypothesis was that different species and functional groups would be sensitive to particular attributes of vegetation loss trajectories, supporting the importance of using land use trajectory attributes in ecological studies. Trajectory attributes are important for understanding the legacy of past environments and their history on present ecological patterns, but also to improve predictive ability of present environmental policy and management decisions or to build potential future scenarios for ecological restoration or conservation.

Materials and methods

Study area

To evaluate the effect of land cover and land use trajectory on stream fish communities we sampled 60 independent streams in natural grassland landscapes of the Brazilian Pampa (Fig. 2), the northern part of the Uruguayan Savanna terrestrial ecoregion (Olson, 2001). The Brazilian Pampa has been historically used for cattle ranching, but strong expansion of monocultural agriculture took place in the last three decades, mainly for soybean, rice and maize crops (Overbeck et al., 2007). However, there is a large variation in the rate of grassland conversion across the territory, with some areas covered mainly by native vegetation (grasslands and riparian forests), predominantly used for cattle ranching, such as the Southeastern Mountains, while other areas have been highly converted, such as the Central Western Plateau (Andrade et al., 2015).

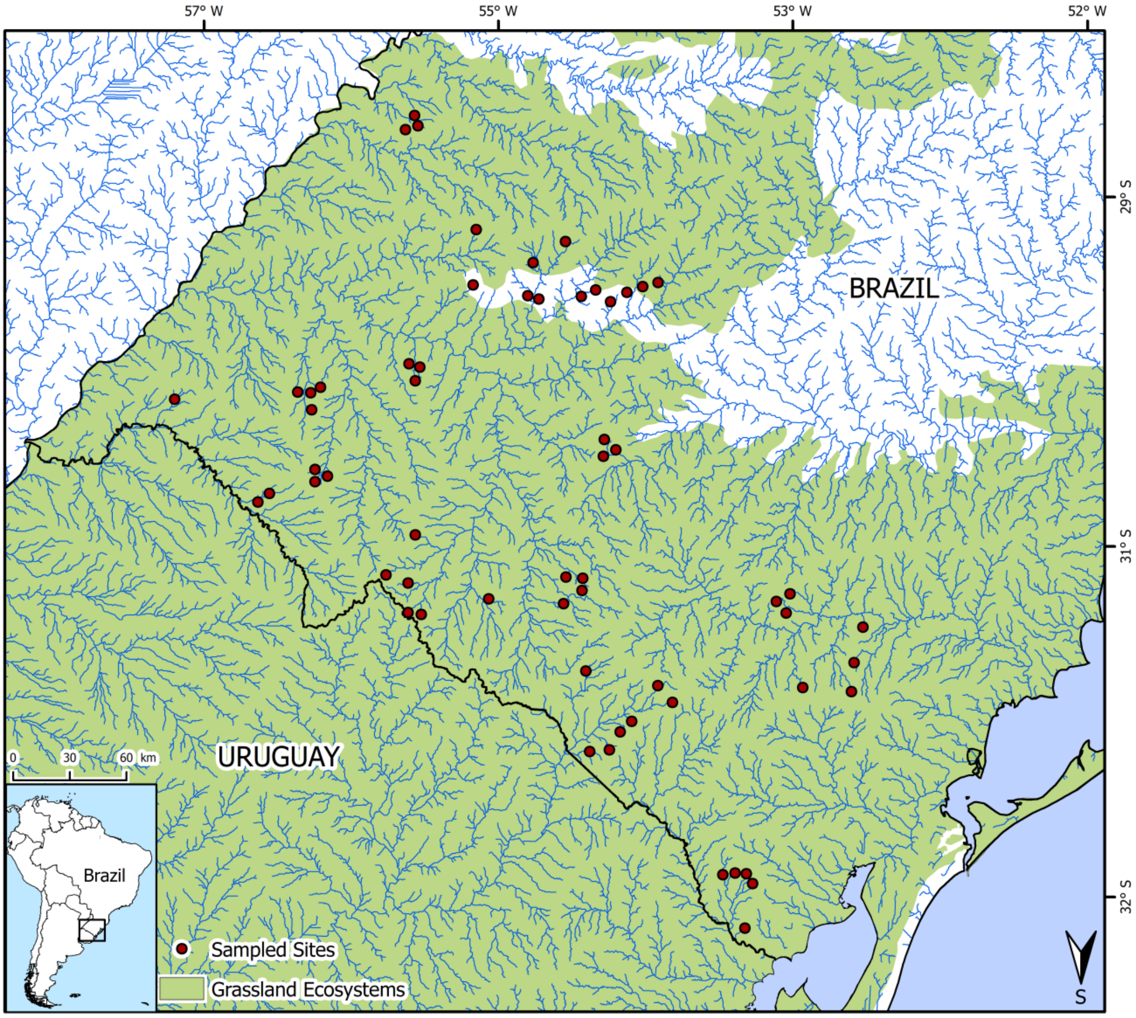

Fig. 2. Location of the study area and fish sampling sites (n = 60). Sampling sites are located in the natural grassland landscapes of the Brazilian Pampa.

Fish sampling was carried out in second (24), third (30) and fourth (6) Strahler order streams. Each sampled stream site comprised a single and independent catchment area (*i.e.*, sites were never located either downstream or upstream from each other). Catchment areas ranged from 1.46 to 134.35 km² (mean = 20.03, SD = 19.52). Water depth ranged between 10 cm and 150 cm [mean = 30.1, standard deviation (SD) = 3.32] and width between 3.6 and 13 m (mean = 4.6, SD = 2.28). Current native vegetation cover ranged from 20.4 to 99.6% of the catchment area upstream the sampling site (mean = 78.8, SD = 21.73). The streams were located in the following freshwater ecoregions (Abell et al., 2008): Laguna dos Patos (18) e Lower Uruguay (42). Both ecoregions harbor relatively similar taxonomic fish groups, with the predominance of Characidae and Loricariidae (Bertaco et al., 2016), but a higher richness is found in the Lower Uruguay.

Fish sampling

Fish sampling was carried out only once per site, in the summer and spring of 2013, 2014, 2015 e 2019. We sampled fish communities across 150-m stream reaches with single-pass electrofishing (EFKO model GmbH FEG 1500), performing a zig-zag route towards upstream. All habitats found along the 150-m stream reaches were sampled. During sampling, the sample reach limits were blocked with gillnets (1.2 cm bar mesh). Sampling was performed by a 4-person team (one operating the electrofishing backpack; three collecting fish) and each site was submitted to approximately 3h electrofishing. Fish specimens were euthanized with clove oil and preserved in 10% formaldehyde solution for later identification in laboratory. All fish samples have been stored at the ichthyological collection of the Zoology Department, UFRGS (http://www.splink.org.br/).

Land use data

For each catchment, we extracted yearly land use data, for a *ca*. 30-year time interval, from 1985 until the precise year of fish sampling (2013 – 2019, see above). Land use data were obtained from the MapBiomas project, collection 3.1 (Projeto MapBiomas, 2019). We reclassified the original MapBiomas land cover and land use classes into only two classes: “native cover” and “other cover”. Native vegetation cover included grasslands, riparian forest, wetlands and rocky outcrops. “Other cover” comprised agriculture, agriculture-pasture mosaic, urban, reservoirs and other non-vegetated areas (*e*. *g*. bare soil, assumed to be agricultural soil). Using these data, we calculated Native Vegetation Loss (NVL) for each catchment, as the proportional area without native vegetation ($A_{\text{other cover, km}^2}$) for the entire catchment upstream from the sampled reach ($A_{\text{catchment}}$, km^2): NVL = 100($A_{\text{other cover}}$)/($A_{\text{catchment}}$).

We defined landscape change trajectories as the series of annual native vegetation percent cover for each catchment (60 trajectories). We then obtained three different attributes to describe these trajectories, based on ecological disturbance ecology and landscape ecology (White & Pickett, 1985; White & Jentsch, 2001; Watson et al., 2014): i) frequency, ii) magnitude and iii) duration of vegetation loss. Frequency was estimated as the number of events in which native vegetation cover declined along the study period (1985 to the year of sampling), regardless of the time span of each decline. Magnitude was estimated as the total vegetation loss (in % catchment area), considering the whole study period. Finally, duration was estimated as the number of years at which the NVL exceeded two different thresholds, that is, 20% or 40% of total catchment area. These threshold values for duration were defined based on Dala-Corte et al. (*submitted*), which observed thresholds for stream bioindicator decrease around 25.9 and 48.5% of native vegetation loss in Brazil.

Species traits and functional groups

We characterized each species according to four categorical traits: typical individual position at the water column (benthic; nektonic), main diet (carnivore; detritivore; herbivore; insectivore; invertivore; parasite; piscivore; omnivore), food origin (allochthonous; autochthonous), and ecomorphological group (Online Resource I). The first three traits were based on published scientific literature, while ecomorphological groups were obtained from Dala-Corte et al., (2016). Fish species were then allocated to functional groups, which were generated by a cluster analysis (UPGMA) on the species abundance-by-traits matrix using Gower distance. The definition of 35 functional groups (FG) was based on the silhouette method (Rousseeuw, 1987). Mean species number per FG was four (SD = 5). The abundance of each FG was calculated as the sum of all individuals of the species contained in each group. This analysis was conducted with the phytools (Revell, 2012) and ggtreer (Yu et al., 2017) package for R environment (R Core Team, 2019).

Effect of native vegetation loss on fish species richness and composition

To test whether species richness and composition were more related to past or current native vegetation loss, we used multiple linear regression models (LM) and redundancy analysis (RDA). The response variable for the LM was species richness. In RDA, we used a species abundance matrix. Abundance data were log-transformed to reduce the weight of very abundant species ($log\ x_{+1}$). Both analyses had the same explanatory variables: i) NVL annual values from 1985 to 2013 (% catchment area); ii) catchment area (km^2) for each fish sampling site (to control for the species-area effect); and iii) the aquatic ecoregion where the site is located, as the two encompassed freshwater ecoregions contain distinct species numbers and a few unique species. Models were built separately for each year of land use (*i.e*. 28 models for each of the 60 sampled streams). We then assessed the effect size of NVL in each year: for the LM, we used the standardized regression slope (std-*b*) value, and for the RDA we used the adjusted r^2 (adj-r^2). The effect sizes of NVL in each year were compared to assess whether current/recent or past NVL had a larger effect on species richness. Analyses were conducted in R software (R core team, 2019) using the vegan package (Oksanen et al., 2007).

Effect of vegetation cover trajectory on fish species and functional groups

To evaluate how attributes of land use trajectory affected changes in particular species and functional groups, we followed the approach of Brejão et al. (2018), using threshold indicator taxa analysis (TITAN, Baker & King, 2010). With this analysis, we intended to determine sensitive species and functional groups, but mostly, we intended to explore how they would respond to trajectory attributes and whether there are thresholds of response to these attributes. The response variables in these analyses were species and FG abundances. Abundance data were log-transformed to reduce the weight of very abundant species ($logx_{+1}$). Predictor variables were 1993 and 2013 NVL, as well as the frequency, magnitude, and duration of %vegetation trajectories. Year 1993 was set as reference because it is when we observed the highest effect size of vegetation loss on fish species richness (as found with LM) and composition (RDA), while 2013 represents current state of native vegetation cover (see Results).TITAN was run separately for each trajectory attribute. As a requirement of TITAN, we used only species and FG with three or more occurrences in the analyses, totaling 91 species and 31 FGs. Species and FG response thresholds to trajectory attributes were estimated based on 1000 bootstraps. This analysis was ran using the TITAN2 package (Baker & King, 2010) in R software (R Core Team, 2019).

Results

A total of 144 fish species was sampled in 60 streams. Mean species number per stream was 20 (SD = 7). From the 18 families recorded, Characidae, Loricariidae and Cichlidae were the most species-rich, with 54, 28 and 20 species, respectively. The most frequent species were small benthic fish: *Heptapterus mustelinus* (present in 93.3% of all sampling sites), *Bryconamericus iheringii* (91.6%), *Characidium pterostictum* and *Rineloricaria stellata*, both with 63.3% (Online Resource I). All sampled species are native to the study region.

Both species richness and species composition were more related to past than to current land use (NVL) (Fig. 3), supporting our first hypothesis. Effect size for species richness was generally strong (*ca*. 0.25) before 2004, and ceased to be significant after 2004 (Fig. 3a). For composition, effect size was generally weak but significant up to 2001 (Fig. 3b). The largest effect size was observed for 1993 NVL data, both for richness (std-b = 0.39; p = 0.008; df = 3, 56), and for composition (adj-r^2 = 0.049; p = 0.037; df = 3, 56). Interestingly, current land use (2013) was neither related to species richness (std-b = 0.16; p = 0.250; df = 3, 56) nor to species composition (adj-r^2 = 0.038; p = 0.346; df = 3, 56).

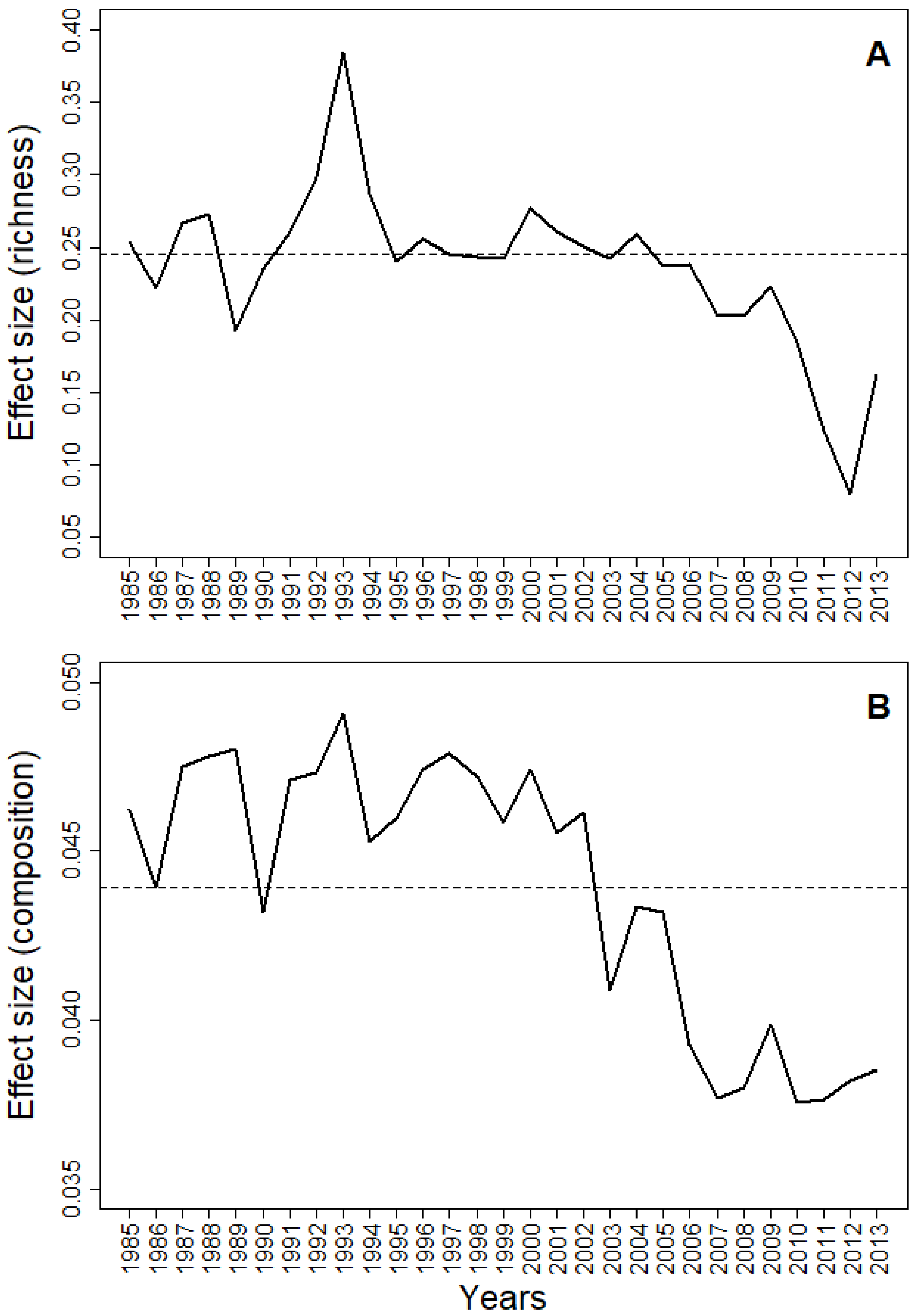

Fig. 3. Effect size of native vegetation loss (NVL) at the catchment scale on current species richness (A) and composition of stream fishes. For species richness (A), effect size was obtained from multiple linear regression models and is represented by standardized slope coefficient (std-b). For species composition (B), effect size is the explanation proportion (adj-r^2) resulting from redundancy analysis (RDA). Fish community responses were more related (largest effect size) to past land use, with maximum effect size in 1993, while the most recent significant effect size was in 2004 for current richness and in 2001 for current community composition. Areas below the dashed line represents relations whit $p>0.1$ values, except year 1995 in A.

Effects of land use trajectories were found also at the species and functional group level. All tested attributes describing trajectories of vegetation loss were related to the sensibility of at least one species or functional group (Table I). NVL values (total vegetation loss up to 1993 and up to 2013) and Frequency of vegetation loss events affected fish either positively or negatively, depending on species or functional group, whereas Magnitude and the two measures of Duration presented only negative influence on fish (Table I).

Thirteen fish species (14.3%) and six functional groups (19.4%) were identified as responsive to watershed vegetation loss. Eleven species showed negative thresholds (*z*-), meaning they decrease in abundance and occurrence along the land use trajectory (Fig. 4). Only two species showed positive thresholds (*z*+) in response to trajectory attributes (Fig. 4), meaning they increase in occurrence and abundance. Five functional groups responded negatively (*z*-) and just one responded positively (*z*+) to attributes of land use trajectory (Fig. 5). Values of individual species and functional group thresholds are presented in Online Resource II.

Table I. Observed (obs) community level thresholds (and percentile confidence intervals, 5th e 95th) for changes in fish species (taxonomic) and functional groups in response to change in attributes of land use trajectory.

	Taxonomic			Functional		
Gradient	obs	5th	95th	obs	5th	95th
Native vegetation loss in 1993						
TITAN sum(*z*-)	2.99	1.78	8.15	2.96	2.97	8.15
TITAN sum(*z*+)	8.61	1.93	27.91	-	-	-
Native vegetation loss in 2013						
TITAN sum(*z*-)	-	-	-	5.97	2.8	32.22
TITAN sum(*z*+)	17.53	6.29	62.08	19.85	1.96	62.08
Frequency						
TITAN sum(*z*-)	9.0	7.5	10.0	-	-	-
TITAN sum(*z*+)	9.5	8.5	10.0	-	-	-
Magnitude						
TITAN sum(*z*-)	31.74	22.56	37.22	98.79	31.73	98.79
TITAN sum(*z*+)	-	-	-	-	-	-
Duration <40%						
TITAN sum(*z*-)	-	-	-	0.0	0.0	28.0
TITAN sum(*z*+)	-	-	-			
Duration <20%						
TITAN sum(*z*-)	0.0	0.0	14.0	28.0	22.0	30.0
TITAN sum(*z*+)	-	-	-	-	-	-

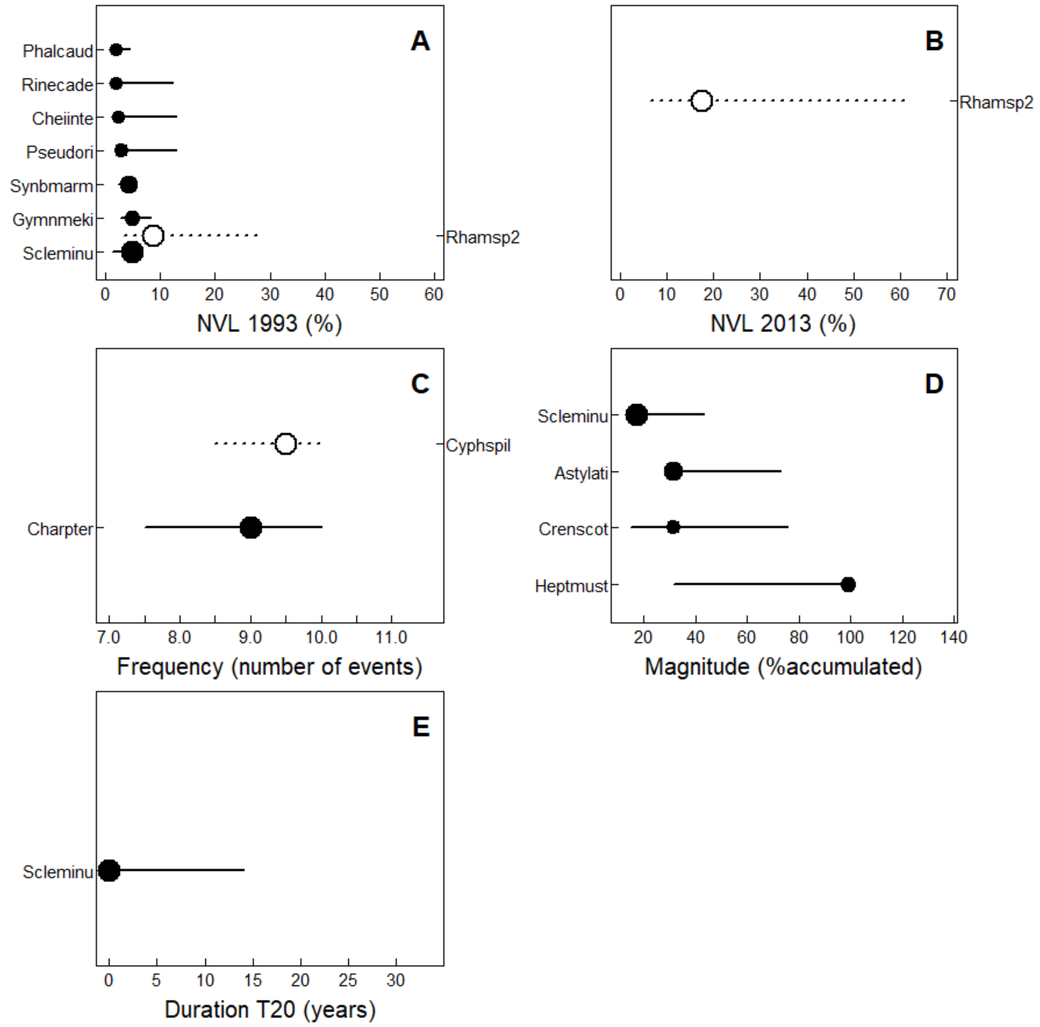

Fig. 4. Thresholds for indicator species response to land use trajectories and Native Vegetation Loss (NVL), measured as proportional area without native vegetation cover in the catchment area in 1993 and 2013. Frequency is the number of events of NVL; Magnitude is the summed percentage of NVL across the years; Duration is the number of years which native vegetation cover declined below 20% (T20) of total catchment area. Black circles are negative responses and open circles are positive responses to trajectory attributes. Circle size is proportional to *z* score, which indicates how strong is the threshold for each species. The horizontal line indicates variation around the threshold value. Species abbreviations are *Astyanax laticeps* (astylati), *Characidium pterostictum* (charpter), *Cheirodon interruptus* (cheiint), *Crenicichla scottii* (crensco), *Cyphocharax spilotus* (chypspil), *Gymnogeophagus mekinos* (gymnmeki), *Heptapterus mustelinus* (heptmust), *Phalloceros caudimaculatus* (phalcaud), *Pseudocorynopoma doriae* (pseudori), *Rhamdia* sp2 (rhamsp2), *Rineloricaria cadeae* (rinecade), *Scleronema minutum* (scleminu), *Synbranchus marmoratus* (symbmarm).

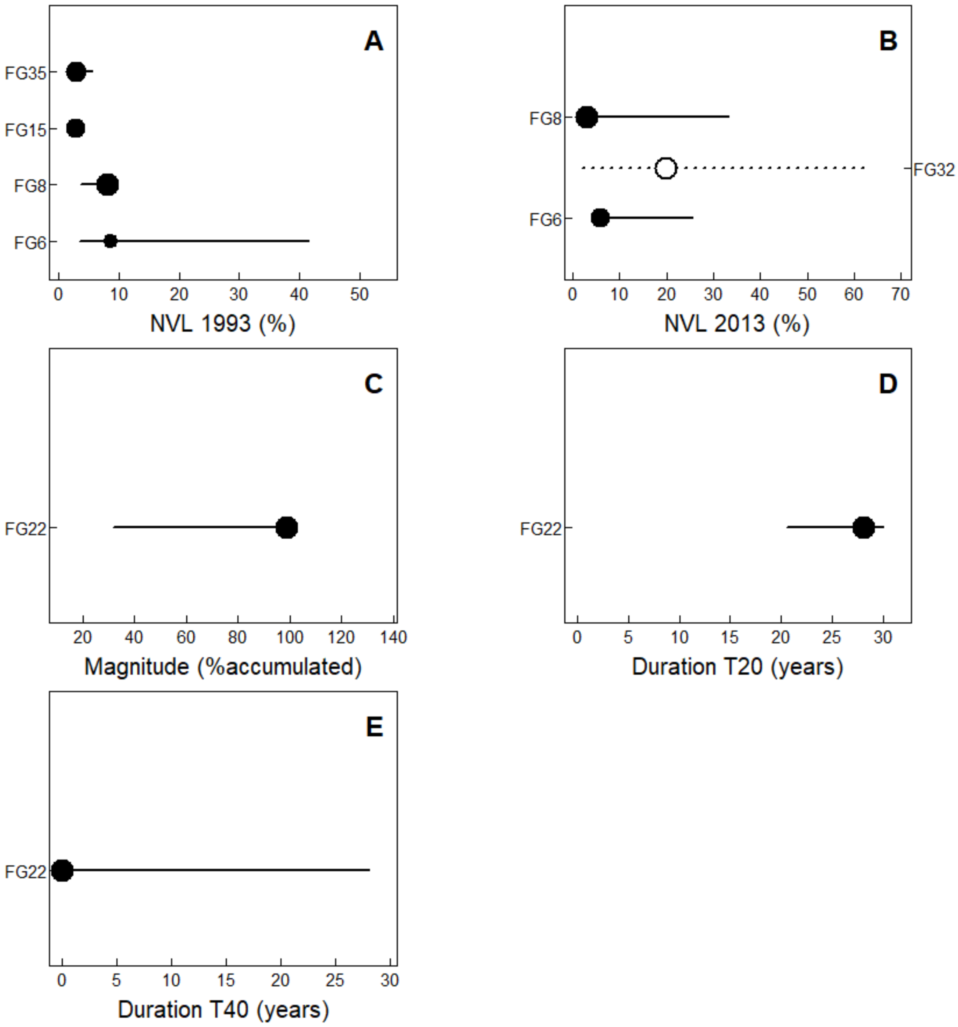

Fig. 5. Thresholds for each functional group (FG) in response to land use trajectories and Native Vegetation Loss (NVL) measured as proportional area without native vegetation cover in the catchment area, using satellite images in 1993 and 2013. Frequency is the number of events of NVL; Magnitude is the summed percentage of NVL across the years; Duration is the number of years in which native vegetation cover declined below 20% (T20) or below 40% (T40) of total catchment area. Black circles are negative responses and open circles are positive responses to trajectory attributes. Circle size is proportional to *z* score, which indicates how strong is the threshold for each FG. The horizontal line indicates variation around the threshold value. Species in each FG are listed in Online Resource I.

Discussion

Our findings support that the history of native vegetation conversion in the watersheds can significantly affect current stream fish communities. The studied fish communities were influenced both by a legacy of past vegetation cover at the watershed scale (delayed response in richness and composition change) and by specific trajectory attributes along a 28-year history of native vegetation loss (response in species and functional group occurrence and abundance). A significant proportion of current species richness and composition was explained by past native vegetation cover (<2006), while current values were not significant, *i.e.*, current community features were unrelated to recent land use. Our results suggest that characteristics of stream fish communities of Pampa grasslands were partially influenced by watershed land cover existent 20-10 years before these communities were actually sampled.

We observed that the species loss or substitution (the native invasion hypothesis, Scott & Helfman, 2001; Dala-Corte et al., 2019) have a delayed response to native vegetation conversion, a phenomenon known as extinction debt (Tilman et al., 1994; Kuussaari et al., 2009). As a consequence of such delay, watersheds that present similar amounts of native vegetation cover (*e.g.*, Fig. 1) may harbor distinct species richness and composition. This is not surprising, because communities not always respond immediately to habitat loss (Hanski & Ovaskainen, 2002; Brejão et al., 2018), and similar landscapes may have very distinct histories (Ernoult et al., 2006). Nevertheless, native vegetation conversion has been often measured using land cover maps a few years displaced from stream condition measures (Allan, 2004), or even taken precisely in correspondence with fish sampling year, and the relation to fish communities is not always significant or strong (Meador & Goldstein, 2003; Dala-Corte et al., 2016). However, few studies have used historical data of land cover, but they found a significant contribution of past cover to current diversity of aquatic invertebrates and fish (Harding et al., 1998; Burcher et al., 2008; Brejão et al., 2018). Accordingly, our findings reinforce the importance of measuring past vegetation cover to investigate the relation between land use and stream fish communities. This seems particularly important when analysis of current landscape characteristics yields no relation with the current state of fish communities, what could be erroneously interpreted as local habitat only being important, although some species or functional groups may in fact be sensitive only to local or to riparian characteristics (e.g. Brejão et al., 2018; Dala-Corte et al., 2016).

We observed that some fish community responses were dependent on particular trajectory attributes. Therefore, not just a particular condition in the past may influence present communities (*e.g*. native vegetation cover in 1993), but also the specific paths of land use change (trajectories) and their properties (frequency, duration, magnitude) matter. All land use trajectory attributes we tested were somehow related to at least some species or functional groups. However, few taxa or functional groups responded to more the one trajectory attribute, and when this happened, the threshold was considerably distinct. For instance, FG22, composed by benthic species with elongated body shape (including *Scleronema*, *Heptapterus* and *Ituglanis*), which has previously been considered sensitive to land use (Cruz et al., 2013; Brejão et al., 2018), had a low threshold only to Duration T40 (responded immediately, 0 years, after NVL exceeded 40% of the catchment area), meaning that the species is very sensitive to a 40% vegetation loss at the watershed scale. In contrast, for Magnitude and Duration T20, FG22 had higher threshold values, showing a delayed response to these land use attributes, taking more than 20 years to decline in response to NVL when vegetation loss is smaller (up to 20%). This result suggests that predicting local extinctions is a complex matter that depends not only on the amount of vegetation cover *per se*, but on the trajectory of vegetation change. For a given FG (as FG22 in this study), long periods under small amount of vegetation loss (Duration T20) or short periods after large amount of vegetation loss (Duration T40) may have similar effects.

It is known that the effects of habitat loss may depend on life history and ecological function of species, and also on the way that the trajectories are interpreted and measured (Ewers & Didham, 2006; Stanley et al., 2010). This could explain why most of the indicator species and FGs in our study responded only to one trajectory attribute, and the threshold level varied greatly depending on which attribute was considered. We suggest there is wide opportunity for exploring the effect of land use trajectories on stream communities. Looking carefully at trajectory attributes may be important. For instance, we tested delayed response for only two years (1993 and 2013, T40 and T20), but response delay probably differs for distinct species and functional groups, and should probably be checked across the whole time series available (in this study, 28-33 years).

Although land use legacy may have strong effects on the current ecosystem conditions (Lunt & Spooner, 2005), in our study only 13 species (14.3%) and six FGs (19.4%) were identified as sensitive to land use trajectories. Detecting stronger or more prevalent relations between stream communities and land use change might depend on testing ecologically meaningful functional attributes and functional groups (Teresa & Casatti, 2017). Another possible reason for this result is the spatial scale in which we assessed vegetation loss. Stream fish communities are known to be sensitive to change of vegetation at the riparian scale or at stream banks (Brejão et al., 2018; Leal et al., 2016; Molina et al., 2017; Leitão et al., 2018; Montag et al., 2019). Also, land use values obtained for the entire catchment area can sometimes be independent of local or riparian scale areas (Casatti et al., 2009; Casatti et al., 2012; Zeni & Casatti, 2013). A relevant perspective for future studies would then be to assess the interplay between spatial scale of land use (local, network riparian, watershed) and their temporal change trajectories.

Past watershed cover has been widely recognized as important for understanding present fish community characteristics (Harding et al., 1998b; Allan, 2004), however, it is still a challenge to stream ecology research (Infante et al., 2019). In this study, we assessed past land use effects on stream fish communities and demonstrated that land use trajectories matter. We employed a disturbance ecology perspective (White & Pickett, 1985; White & Jentsch, 2001; Watson et al., 2014) to assess vegetation loss as a temporally recurrent disturbance, characterized by frequency, magnitude and duration. This perspective is commonly used to assess effects of flow disturbance in stream ecosystems (McCabe & Gotelli, 2000; Winemiller et al., 2010), but not to explore the influence of landscape change. We suggest that progress in understanding the effects of land use trajectories could be gained from using disturbance ecology perspective, and by testing *a priori* and empirical hypotheses about the pathways of stream community response (*e.g.* Burcher et al., 2007; Maloney & Weller, 2011; Dala-Corte et al., 2016; Brejão et al., 2018; Leitão et al., 2018) to landscape change trajectories.

In summary, we observed that past land use can be an important driver of the current and future state of stream fish communities. We found evidence that this effect may occur as a delayed response of species, with large negative effects occurring mostly around 10 to 20 years after watershed vegetation loss events, leading to local extinction debts. Most interestingly, we observed that sensitivity to watershed vegetation loss varied between species and functional groups, but that actually detecting these responses depends on the trajectory attributes (frequency, magnitude and duration). Exploring land use trajectories seems thus a promising approach for improving understanding of landscape effects on stream ecology.

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Considerações Finais

O tempo e os peixes

Nossos resultados mostraram que a riqueza e composição das comunidades de peixes dos riachos apresentam relação significativa com características da cobertura de vegetação em um intervalo de tempo anterior a 10 e 20 anos em relação ao presente. Isso significa que há um lapso de tempo entre a resposta biológica dos peixes e os o impacto do uso da terra, caracterizando o efeito da dívida de extinção. Além disso, vimos que características específicas de trajetória de mudança na cobertura (frequência, duração, magnitude), e não apenas um momento particular da cobertura no passado, apresentam efeitos sobre os peixes de riacho. Essa análise de trajetórias de uso da terra (>30 anos, com resolução anual) nos permitiu observar e caracterizar respostas biológicas à mudança de uso da terra que foram pouco exploradas cientificamente.

Perspectivas

As principais perspectivas que criamos a partir deste estudo têm relação com a forma de avaliar a perda histórica de vegetação nativa e seu efeito sobre as comunidades aquáticas a partir de diferentes escalas espaciais, dos diferentes limiares para diferentes grupos e do tipo de conversão da terra. Existem efeitos sobre comunidades locais que são resultado de alterações em diferentes escalas espaciais (*e. g.* invasão nativa), não medidas neste projeto, como a zona ripária e áreas em regiões de toda a bacia, tanto à jusante dos sítios amostrados como em sub-bacias adjacentes. Aqui, vimos que diferentes grupos tiveram respostas específicas para cada atributo das trajetórias, porém, delinear os gradientes de resposta é uma importante contribuição para a compreensão das comunidades aquáticas. Por fim, ao agrupar as classes de uso como "*other cover*", deixamos de considerar possíveis diferenças entre os efeitos de distintos usos da terra, como agrícola e urbano. Assim, várias novas perspectivas para a compreensão das mudanças no uso da terra e seu efeito sobre comunidades aquáticas se abrem com este projeto.

Anexos

Anexo I

Lista de espécies de peixes, abreviação do nome, grupo funcional gerado por análise de agrupamento (UPGMA) e respectivos atributos: posição na coluna de água (bent, bentônico; nekt, nectônico), dieta (carn, carnívoro; detr, detritívoro; herb, herbívoro; inse, insetívoro; inve, invertívoro; para, parasita; omni, onívoro; pisi, piscívoro), fonte de recurso (auto, autóctone; allo, alóctone), morfologia (ver Dala-Corte et al., 2016). Para algumas espécies, consideramos duas classes para alguns atributos, a primeira (antes do ponto) como principal e a segunda (após o ponto) como secundária. F é a frequência de ocorrências para cada espécie.

Espécies	Abreviação	Grupo Funcional	Hábito	Dieta	Recurso	Morfologia	F
Acestrorhynchus pantaneiro	Acespant	FG01	nekt	pisc.carn	auto	B	1
Ancistrus brevipinnis	Ancibrev	FG02	bent	detr.inse	auto	C	7
Ancistrus taunayi	Ancitaun	FG02	bent	detr.inse	auto	C	31
Apareiodon affinis	Aparaffi	FG03	nekt.bent	herb.inse	auto	A	1
Aphyocharax anisitsi	Aphyanis	FG04	nekt	carn.inve	auto	A	6
Apistogramma commbrae	Apiscomm	FG03	nekt.bent	inse.herb	auto	A	1
*Astyanax*aff. *fasciatus*	Astyfasc	FG05	nekt	herb.inse	allo.auto	B	3
Astyanax aramburui	Astyaram	FG06	nekt	inse.herb	allo.auto	A	5
Astyanax cremnobates	Astycrem	FG06	nekt	inse.herb	allo.auto	A	1
Astyanax dissensus	Astydiss	FG06	nekt	herb.inse	allo.auto	A	15
Astyanax douradilho	Astydour	FG06	nekt	inse.herb	allo.auto	A	1
Astyanax eigenmanniorum	Astyeige	FG06	nekt	inse.herb	auto.allo	A	24
Astyanax fasciatus	Astyfasc.1	FG05	nekt	herb.inse	allo.auto	B	2
Astyanax henseli	Astyhens	FG05	nekt	herb.inse	allo.auto	B	24
Astyanax lacustris	Astylacu	FG05	nekt	inse.herb	allo.auto	A	32
Astyanax laticeps	Astylati	FG05	nekt	inse.herb	auto.allo	B	28
Astyanax paris	Astypari	FG06	nekt	inse.herb	allo.auto	A	2
Astyanax procerus	Astyproc	FG05	nekt	herb.inse	allo.auto	B	6
Astyanax saguazu	Astysagu	FG05	nekt	inse.herb	auto.allo	B	3
Astyanax sp1	Astysp1	FG05	nekt	inse.herb	allo.auto	B	2
Astyanax sp2	Astysp2	FG05	nekt	inse.herb	allo.auto	B	3
Astyanax stenohalinus	Astysten	FG05	nekt	inse.herb	allo.auto	B	5
Astyanax xiru	Astyxiru	FG05	nekt	inse.herb	allo.auto	B	11
Australoheros acaroides	Austacar	FG07	nekt.bent	inse	auto	B	4
Australoheros facetus	Austface	FG08	nekt.bent	carn.detr	auto	B	2
Australoheros minuano	Austminu	FG07	nekt.bent	inse.herb	auto	B	14
Australoheros scitulus	Austscit	FG07	nekt.bent	inse.herb	auto	B	6
Australoheros sp.	Austsp	FG07	nekt.bent	inse.herb	auto	B	1
Brachyhypopomus bombilla	Bracbomb	FG09	nekt.bent	carn.inve	auto	D	5
Bryconamericus iheringii	Bryciher	FG03	nekt.bent	inse.herb	auto	A	55

Espécies	Abreviação	Grupo Funcional	Hábito	Dieta	Recurso	Morfologia	F
Bryconamericus sp.	Brycsp	FG03	nekt.bent	inse.herb	auto	A	1
Bryconamericus ytu	Brycytu	FG03	nekt.bent	inse.herb	auto	A	2
Bunocephalus doriae	Bunodori	FG10	bent	inse	auto	C	4
Callichthys callichthys	Callcall	FG11	bent	detr.inse	auto	B	3
Characidium aff. *zebra*	Charzebr	FG12	nekt.bent	inse	auto	A	15
Characidium occidentale	Charocci	FG12	nekt.bent	inse	auto	A	18
Characidium orientale	Charorie	FG12	nekt.bent	inse	auto	A	5
Characidium pterostictum	Charpter	FG12	nekt.bent	inse	auto	A	38
Characidium rachovii	Charrach	FG12	nekt.bent	inse	auto	A	4
Characidium tenue	Chartenu	FG12	nekt.bent	inse	auto	A	12
Charax stenopterus	Charsten	FG13	nekt.bent	carn.inve	auto	A	12
Cheirodon ibicuhiensis	Cheiibic	FG03	nekt.bent	herb.inse	auto	A	2
Cheirodon interruptus	Cheiinte	FG03	nekt.bent	herb.inse	auto	A	31
Cichlasoma dimerus	Cichdime	FG14	bent	inse.herb	auto.allo	C	3
Cnesterodon decemmaculatus	Cnesdece	FG15	nekt.bent	detr.herb	auto	D	6
Corydoras longipinnis	Corylong	FG16	bent	inse.herb	auto	B	10
Corydoras paleatus	Corypale	FG16	bent	inse.herb	auto	B	13
Corydoras sp.	Corysp	FG16	bent	inse.herb	auto	B	1
Corydoras undulatus	Coryundu	FG16	bent	inse.herb	auto	B	3
Crenicichla cf *scottii*	Crenscot	FG07	nekt.bent	inse.pisc	auto	B	2
Crenicichla lepidota	Crenlepi	FG17	nekt.bent	pisc.inse	auto	B	35
Crenicichla punctata	Crenpunc	FG07	nekt.bent	inse.pisc	auto	A	3
Crenicichla scottii	Crenscot.1	FG07	nekt.bent	inse.pisc	auto	B	20
Cyanocharax itaimbe	Cyanitai	FG18	nekt	inse	auto	A	1
Cyanocharax uruguayensis	Cyanurug	FG18	nekt	inse	auto	A	3
Cyphocharax saladensis	Cyphsala	FG19	nekt.bent	detr.herb	auto	B	3
Cyphocharax spilotus	Cyphspil	FG19	nekt.bent	detr.herb	auto	B	13
Cyphocharax voga	Cyphvoga	FG19	nekt.bent	detr.herb	auto	B	14
Diapoma alburnum	Diapalbu	FG06	nekt	inse	allo.auto	A	1
Diapoma alegretensis	Diapaleg	FG06	nekt	inse	allo.auto	A	19
Diapoma speculiferum	Diapspec	FG06	nekt	inse	allo.auto	A	2
Diapoma terofali	Diaptero	FG06	nekt	herb.inse	auto	A	14
Diapoma thauma	Diapthau	FG06	nekt	inse	allo.auto	A	3
Diapoma uruguayensis	Diapurug	FG06	nekt	inse	allo.auto	A	6
Eigenmannia trilineata	Eigetril	FG20	nekt.bent	carn.herb	auto	D	4
Gymnogeophagus gymnogenys	Gymngymn	FG08	nekt.bent	carn.detr	auto	B	6
Gymnogeophagus labiatus	Gymnlabi	FG07	nekt.bent	inse.detr	auto	B	1
Gymnogeophagus mekinos	Gymnmeki	FG08	nekt.bent	carn.detr	auto	B	20
Gymnogeophagus meridionalis	Gymnmeri	FG08	nekt.bent	carn.detr	auto	B	5
Gymnogeophagus pseudolabiatus	Gymnpseu	FG08	nekt.bent	carn.detr	auto	B	1

Espécies	Abreviação	Grupo Funcional	Hábito	Dieta	Recurso	Morfologia	F
Gymnogeophagus rhabdotus	Gymnrhab	FG08	nekt.bent	carn.inse	auto	B	12
Gymnogeophagus spn	Gymnspn	FG08	nekt.bent	carn.detr	auto	B	6
Gymnogeophagus terrapurpura	Gymnterr	FG08	nekt.bent	carn.detr	auto	B	1
Gymnotus carapo	Gymncara	FG21	nekt	inse	auto.allo	D	2
Gymnotus cuia	Gymncuia	FG21	nekt	inse	auto.allo	D	3
Hemiancistrus chlorostictus	Hemichlo	FG02	bent	detr.herb	auto	C	4
Hemiancistrus fuliginosus	Hemifuli	FG02	bent	detr.herb	auto	C	5
Hemiancistrus punctulatus	Hemipunc	FG02	bent	detr.herb	auto	C	1
Heptapterus exilis	Heptexil	FG22	bent	inse	auto	D	4
Heptapterus mustelinus	Heptmust	FG22	bent	inse	auto	D	56
Heptapterus sympterygium	Heptsymp	FG22	bent	inse	auto	D	1
Heterocheirodon yatai	Heteyata	FG03	nekt.bent	inse.herb	auto	A	8
Hisonotus armatus	Hisoarma	FG23	bent	herb.detr	auto	D	1
Hisonotus charrua	Hisochar	FG23	bent	herb.detr	auto	D	10
Hisonotus laevior	Hisolaev	FG23	bent	herb.detr	auto	D	8
Hisonotus notopagos	Hisonoto	FG23	bent	herb.detr	auto	D	3
Hisonotus ringueleti	Hisoring	FG23	bent	herb.detr	auto	D	3
Homodiaetus anisitsi	Homoanis	FG24	bent	para	auto	D	1
Hoplias aff. *malabaricus*	Hoplmala	FG17	nekt.bent	pisc	auto	B	19
Hoplias lacerdae	Hopllace	FG17	nekt.bent	pisc	auto	B	5
Hyphessobrycon anisitsi	Hyphanis	FG25	nekt	herb.omni	auto	A	6
Hyphessobrycon luetkenii	Hyphluet	FG25	nekt	herb.omni	auto	A	24
Hyphessobrycon meridionalis	Hyphmeri	FG25	nekt	herb.omni	auto	A	9
Hyphessobrycon togoi	Hyphtogo	FG25	nekt	herb.omni	auto	A	2
Hypobrycon sp.	Hyposp	FG12	nekt.bent	inse	auto	A	2
Hypostomus aspilogaster	Hypoaspi	FG02	bent	detr	auto	C	6
Hypostomus spiniger	Hypospin	FG23	bent	detr.herb	auto	D	8
Hypostomus uruguayensis	Hypourug	FG26	bent	detr	auto	D	1
Imparfinis mishky	Impamish	FG27	nekt.bent	inse	auto	D	3
Ituglanis australis	Itugaust	FG22	bent	inse	auto	D	1
Ituglanis inusitatus	Ituginus	FG22	bent	inse	auto	D	2
Laetacara dorsigera	Laetdors	FG08	nekt.bent	carn.detr	auto	B	1
Loricariichthys melanocheilus	Lorimela	FG02	bent	detr.inse	auto	C	1
Macropsobrycon uruguayanae	Macrurug	FG28	nekt.bent	carn.inve	auto	A	1
Microglanis cottoides	Micrcott	FG27	nekt.bent	inse	auto	D	11
Microglanis malabarbai	Micrmala	FG27	nekt.bent	inse	auto	D	3
Mimagoniates inequalis	Mimaineq	FG29	nekt.bent	inse	allo.auto	A	5
Moenkhausia bonita	Moenboni	FG28	nekt.bent	carn.inve	auto	A	2
Moenkhausia dichroura	Moendich	FG28	nekt.bent	carn.inve	auto	A	1
Odontostilbe pequira	Odonpequ	FG03	nekt.bent	herb.inse	auto	A	1

Espécies	Abreviação	Grupo Funcional	Hábito	Dieta	Recurso	Morfologia	F
Oligosarcus jacuiensis	Oligjacu	FG01	nekt	pisc.carn	auto	B	1
Oligosarcus jenynsii	Oligjeny	FG01	nekt	pisc.carn	auto	B	21
Oligosarcus oligolepis	Oligolig	FG30	nekt	carn.inve	auto	B	5
Oligosarcus robustus	Oligrobu	FG01	nekt	pisc	auto	B	1
Oligosarcus sp.	Oligsp	FG01	nekt	pisc.carn	auto	B	1
Otocinclus arnoldi	Otocarno	FG23	bent	detr.herb	auto	D	2
Otocinclus flexilis	Otocflex	FG23	bent	detr.herb	auto	D	2
Phalloceros caudimaculatus	Phalcaud	FG15	nekt.bent	herb.detr	auto	D	25
Pimelodella australis	Pimeaust	FG09	nekt.bent	carn.inve	auto	D	25
Pseudobunocephalus iheringii	Pseuiher	FG10	bent	inse	auto	C	3
Pseudocorynopoma doriae	Pseudori	FG06	nekt	inse	allo	A	33
Pseudohemiodon laticeps	Pseulati	FG31	bent	herb.omni	auto	C	1
Rhamdella eriarcha	Rhameria	FG27	nekt.bent	inse	auto	D	4
Rhamdella longiuscula	Rhamlong	FG27	nekt.bent	inse	auto	D	7
Rhamdia sp1	Rhamsp1	FG32	nekt.bent	pisc.carn	auto	C	9
Rhamdia sp2	Rhamsp2	FG32	nekt.bent	pisc.carn	auto	C	19
Rineloricaria anitae	Rineanit	FG02	bent	detr.inse	auto	C	2
Rineloricaria cadeae	Rinecade	FG02	bent	detr.inse	auto	C	11
Rineloricaria longicauda	Rinelong	FG02	bent	detr.inse	auto	C	1
Rineloricaria microlepidogaster	Rinemicr	FG02	bent	detr.inse	auto	C	6
Rineloricaria sanga	Rinesang	FG02	bent	detr.inse	auto	C	1
Rineloricaria stellata	Rinestel	FG02	bent	detr.inse	auto	C	38
Rineloricaria strigilata	Rinestri	FG02	bent	detr	auto	C	2
Rineloricaria zaina	Rinezain	FG02	bent	detr.inse	auto	C	1
Scleronema cf. *minutum*	Scleminu.1	FG22	bent	inse	auto	D	2
Scleronema minutum	Scleminu	FG22	bent	inse	auto	D	13
Scleronema operculatum	Scleoper	FG22	bent	inse	auto	D	3
Scleronema sp3	Sclesp4	FG22	bent	inse	auto	D	2
Scleronema sp4	Sclesp5	FG22	bent	inse	auto	D	6
Scleronema sp5	Sclesp3	FG22	bent	inse	auto	D	2
Serrapinnus calliurus	Serrcall	FG33	nekt.bent	herb	auto	A	2
Steindachnerina biornata	Steibior	FG34	nekt	detr	auto	A	11
Steindachnerina brevipinna	Steibrev	FG34	nekt	detr	auto	A	2
Synbranchus marmoratus	Synbmarm	FG35	bent	carn.inve	auto	D	30

Anexo II

Limiares ambientais de resposta na análise TITAN para cada gradiente de trajetória de uso da terra.

	Grupos de Resposta	+/-	Native vegetation loss 1993 (%)	Native vegetation loss 2013 (%)	Magnitude (%acumlada)	Frequency (anos)	Duration T40 (anos)	Duration T20 (anos)
Taxonômico	astylati	z-	-	-	31.74	-	-	-
	charpter	z-	-	-	-	9.0	-	-
	cheiint	z-	2.36	-	-	-	-	-
	crensco	z-	-	-	31.74	-	-	-
	gymnmeki	z-	4.82	-	-	-	-	-
	heptmust	z-	-	-	98.79	-	-	-
	phalcaud	z-	1.77	-	-	-	-	-
	pseudori	z-	2.82	-	-	-	-	-
	rinecade	z-	1.78	-	-	-	-	-
	scleminu	z-	4.82	-	17.19	-	-	0.0
	symbmarm	z-	4.20	-	-	-	-	-
	chypspil	z+	-	-	-	9.5	-	-
	rhamsp2	z+	8.60	17.53	-	-	-	-
Funcional	FG6	z-	8.61	5.97	-	-	-	-
	FG8	z-	8.15	2.85	-	-	-	-
	FG15	z-	2.98	-	-	-	-	-
	FG22	z-	-	-	98.79	-	0.0	28.00
	FG35	z-	2.82	-	-	-	-	-
	FG32	z+	-	19.85	-	-	-	-