

# The past is never dead: legacy effects alter the structure of benthic macroinvertebrate assemblages

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## ABSTRACT

### The past is never dead: legacy effects alter the structure of benthic macroinvertebrate assemblages

Land use is the most common and widespread threat to lotic ecosystem health and freshwater biodiversity conservation. The legacy effects of past anthropogenic land use and cover may also affect the structure and functioning of current lotic ecosystems. Therefore, the aim of this study was to use benthic macroinvertebrate assemblages to evaluate the potential legacy effects of anthropogenic land use on headwater streams in the Neotropical Savanna. We tested three hypotheses. (1) The legacy effects on macroinvertebrates of the riparian zone are more important than those of the entire catchment. (2) Recent deforestation has a stronger effect on the current taxonomic structure of benthic macroinvertebrate assemblages than historical deforestation. (3) Sensitive taxa respond more readily than tolerant taxa to historical deforestation. To test these hypotheses, we estimated deforestation over the last 30 years for 97 stream sites in 5 hydrological units and tested it against benthic macroinvertebrate abundance, taxa richness, EPT abundance, EPT richness, Shannon-Wiener diversity, and Simpson diversity. The two first hypotheses were corroborated, as Shannon-Wiener and Simpson diversity indices were significantly correlated with deforestation in the riparian zone ( $p < 0.05$ ) and these diversity variables were positively correlated with older deforestation, meaning that such sites tended to recover their diversity over time after a deforestation event. The third hypothesis was only partially supported because EPT (sensitive taxa) did not represent most taxa with significant correlations with historical deforestation at catchment scale, but were the only taxa to do so at the 200 m riparian buffer. We conclude that recent deforestation has more significant effects, but past deforestation still plays a significant role in the structure and functioning of lotic ecosystems.

**Key words:** land use, lotic ecosystems, riparian vegetation, bioindicators, sensitive taxa

## RESUMO

### O passado não morre: efeito legado altera a estrutura de assembleias de macroinvertebrados bentônicos

O uso antropogênico do solo é a ameaça mais comum à conservação da biodiversidade de água doce. Os efeitos do legado do uso antropogênico do solo também podem afetar a estrutura e o funcionamento dos atuais ecossistemas lóticos. Portanto, o objetivo deste estudo foi utilizar assembleias de macroinvertebrados bentônicos para avaliar os potenciais efeitos legados do

*uso antropogênico do solo. Para tanto testamos três hipóteses. (1) Os efeitos do legado na zona ripária sobre os macroinvertebrados são mais importantes do que aqueles em toda a bacia; (2) O desmatamento recente tem efeito mais forte na estrutura taxonômica atual das assembleias de macroinvertebrados bentônicos do que o desmatamento histórico; (3) Táxons sensíveis respondem mais prontamente ao desmatamento histórico. Para testar essas hipóteses, estimamos o desmatamento nos últimos 30 anos para 97 sítios amostrais (riachos) em cinco unidades hidrológicas e testamos contra abundância de macroinvertebrados bentônicos, riqueza de táxons, abundância de EPT, riqueza de EPT, diversidade de Shannon-Wiener e diversidade de Simpson. As duas primeiras hipóteses foram corroboradas, pois os índices de diversidade de Shannon-Wiener e Simpson foram significativamente correlacionados com o desmatamento na mata ciliar ( $p < 0.05$ ) e essas variáveis de diversidade foram positivamente correlacionadas com o desmatamento mais antigo, significando que tais locais tenderam a recuperar sua diversidade ao longo tempo após um evento de desmatamento. A terceira hipótese foi parcialmente corroborada, porque os EPT (taxóons sensíveis) não representaram a maioria dos táxons com correlações significativas com o desmatamento histórico na escala de estudo, mas foram os únicos táxons a fazê-lo no buffer de 200 m de cada riacho. Concluímos que o desmatamento recente tem efeitos mais significativos, mas o desmatamento passado ainda desempenha um papel significativo na estrutura e funcionamento de ecossistemas lóticos.*

**Palavras chave:** *uso do solo, ecossistemas lóticos, vegetação ripária, bioindicadores, táxons sensíveis*

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## INTRODUCTION

Streams and rivers are among the most anthropogenically altered ecosystems because historically human populations have tended to live disproportionately close to them, changing the surrounding landscapes and compromising their health (Death & Collier, 2009). Where humans dominate, natural vegetation is replaced by anthropogenic land uses, such as agriculture, silviculture forestry, livestock grazing and urbanization. Headwater streams are tightly linked to their surrounding terrestrial ecosystems, forming meta-ecosystem complexes, linked by biotic and abiotic processes (Callisto *et al.*, 2019). Thus, the ecological health of adjacent terrestrial ecosystems has been reported to be important factors in the structure and functioning of lotic ecosystems globally (Chen & Olden, 2020; Dala-Corte *et al.*, 2020; Mello *et al.*, 2020; Riis *et al.*, 2020).

Anthropogenic land use is a widespread and common threat to lotic ecosystem health (Allan, 2004; Reid *et al.*, 2019; Vitousek, 1997). The linkages of contemporary land use and in-stream processes have been studied since the latter half of the last century (Allan *et al.*, 1997; Allan, 2004; Castro-López *et al.*, 2019; Ferreira *et al.*, 2014; Maloney & Weller, 2011). However, anthropogenic land use and cover can have effects lasting long after it has ceased (Maloney *et al.*,

2008). The legacy effect of past anthropogenic land use likely has substantial effects on the structure and functioning of lotic ecosystems (Allan, 2004; Baumgartner & Robinson, 2015) because sites that are minimally disturbed at present could have poor assemblage health because of past poor environmental conditions (Harding *et al.*, 1998).

In recent years, analyses of the dynamics of past land use and cover and its impacts on current biodiversity, have been gaining more and more attention in the study of freshwater communities (e.g., Camana *et al.*, 2020; Cosentino & Brubaker, 2018; Sheppard & MacKay, 2018). The study of possible effects of past land use on present taxonomic and functional structure of biological assemblages is called *legacy effect* (Allan, 2004). Some studies have shown that lotic ecosystems draining areas currently covered by forest vegetation, but that have a history of past agricultural use, have biodiversity comparable to the basins in which agricultural use currently predominates (Greenwood *et al.*, 2012; Harding *et al.*, 1998; Surasinghe & Baldwin, 2014).

To monitor the environmental quality of lotic ecosystems, precise measures of how their structure and functioning respond to natural and anthropogenic changes are necessary (Jørgensen, 2007; van Rees *et al.*, 2021). Among aquatic organisms used as bioindicators, benthic macroinvertebrates

have been increasingly studied (Bonada et al., 2006; Reid et al., 2019). They stand out as good biological indicators because of their wide distribution, taxonomic richness, varying tolerances to anthropogenic disturbances, relative abundance, limited mobility, relatively long life cycles and ease of collection (Huryn & Wallace, 2000; Resh, 2008; Verissimo et al., 2012).

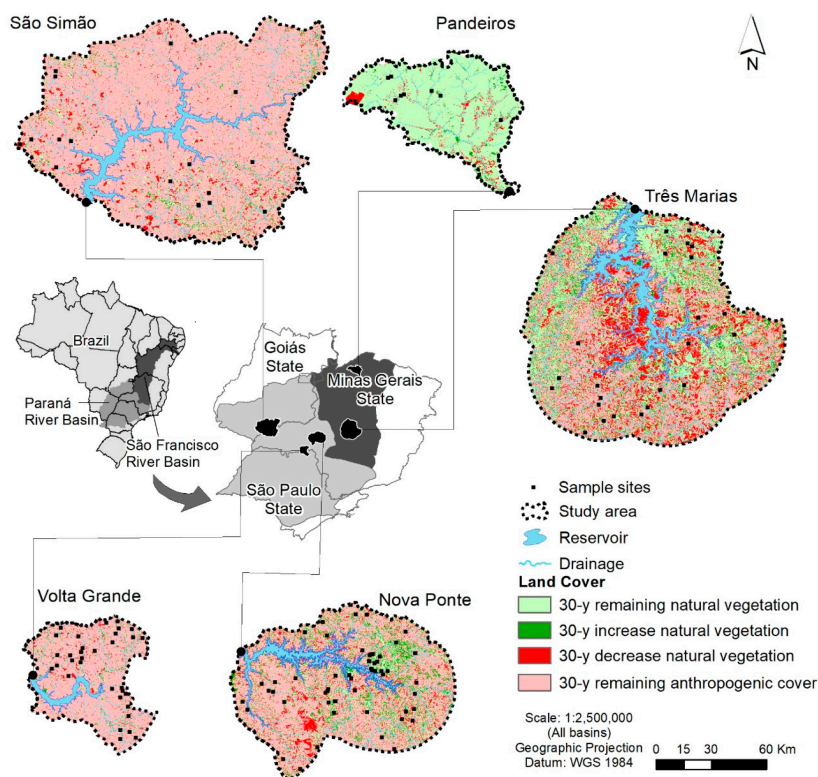
Therefore, the aim of this study was to use benthic macroinvertebrate assemblages to determine the legacy effects of anthropogenic land use on headwater streams in the Neotropical Savanna (Cerrado biome). To do so we tested three hypotheses. Firstly, we expected that the legacy effects of riparian zone deforestation on macroinvertebrates would be more important than would that of the entire catchment. Secondly, we predicted that more recent catchment and riparian zone deforestation would have a greater effect on the benthic macroinvertebrate metrics than his-

torical land uses. Finally, we expected that highly sensitive taxa (Ephemeroptera, Plecoptera and Trichoptera families) would comprise the majority of the taxa with significant negative correlations with deforestation.

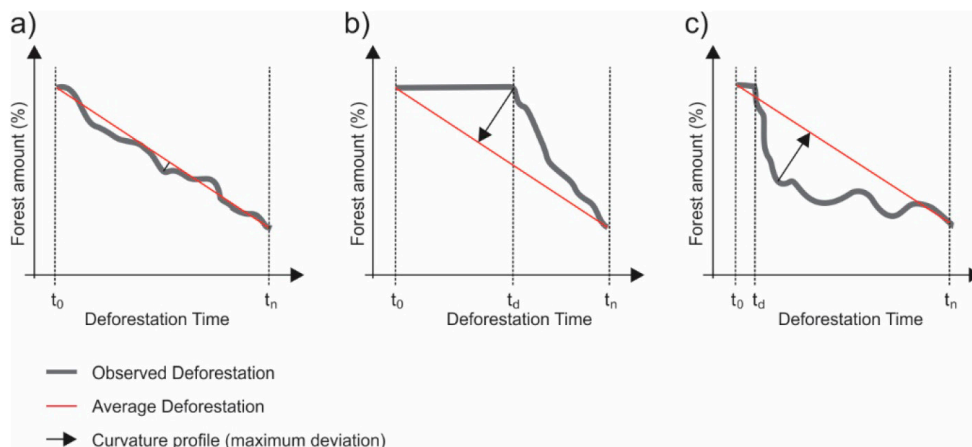
## METHODOLOGY

### Study Area

We sampled 97 wadeable stream sites in the Cerrado biome of southeastern Brazil. The sites were defined at a 1:100 000 scale, and selected via a spatially dispersed random survey design (Macedo et al., 2019; Macedo et al., 2014). The sites occurred in five hydrological units, defined as drainage areas within 35 km upstream of each of the hydropower reservoirs of Três Marias, Volta Grande, São Simão, Nova Ponte, and Pandeiros (Fig. 1). Sampling was conducted in September



**Figure 1.** Locations of sampled sites in five hydrological units and last 30-y land cover changes. *Localização de sítios amostrais em cinco unidades hidrológicas e mudanças no uso do solo nos últimos 30 anos.*



**Figure 2.** Model representation of natural cover profile change represented by the Deforestation Profile Curvature: a) constant deforestation deviation rate (values near zero); b) deforestation deviation concentrated in more recent years (negative values); c) deforestation deviation concentrated in earlier years (positive values).  $t_0$  = start monitoring time,  $t_n$  = last monitored year;  $t_d$  = time of major deforestation. Modified from Ferraz et al. (2009). *Modelo de representação da mudança do perfil de cobertura natural representada pela Curvatura de Perfil de Desmatamento: a) taxa de desvio de desmatamento constante (valores próximos de zero); b) desvio de desmatamento concentrado em anos mais recentes (valores negativos); c) desvio do desmatamento concentrado em anos anteriores (valores positivos).  $t_0$  = tempo de início de monitoramento,  $t_n$  = último ano monitorado;  $t_d$  = tempo de maior desmatamento. Modificado de Ferraz et al. (2009).*

(Três Marias, 2010; Volta Grande, 2011; São Simão, 2012; Nova Ponte, 2013; Pandeiros, 2016), ensuring that sampling occurred at the end of the low flow (dry) season. Site lengths were 40 times the mean wetted channel width or a minimum of 150 m (Hughes & Peck, 2008; Kaufmann et al., in press; Peck et al., 2006).

### Historical Changes in Land Cover

To assess the anthropogenic land cover change, we first estimated the current (considering the above-mentioned sampling years, i.e., 2010 to 2016) and then the past nearly 30-y cover represented by natural forest and savanna. To estimate the current catchment and riparian land cover for each site, we used Mapbiomas data (<http://mapbiomas.org>). The data were based on 30-m resolution maps and were produced from the pixel-per-pixel classification of Landsat satellite images by extensive machine learning algorithms through the Google Earth Engine platform. It shows 35 years (1985 to 2019) of annual land cover (Souza et al., 2020). The percentages of the natural cover were estimated in 1985, 1990,

1995, 2000, 2005, 2010 and in the year in which each site was sampled. For our tests, we selected sites that showed natural vegetation loss (deforestation) between 1985 and its sampling date, resulting in 97 stream sites. We then extracted the deforestation data (Supplementary information, Table S1, available at <http://www.limnetica.net/en/limnetica>) for (1) the entire catchment upstream of each site and (2) for a riparian zone represented by a 200 m riparian zone buffer upstream of each site (Morley & Karr, 2002).

To assess the natural cover change, we calculated Deforestation Profile Curvatures (Ferraz et al., 2009). For that we used the percentages of the natural cover estimated for 1985, 1990, 1995, 2000, 2005, 2010 and in the year in which each site was sampled. This index (Deforestation Profile Curvature) represents the maximum deviation of the deforestation curve (i.e., natural cover loss) relative to a straight line between the initial and final natural forest vegetation proportions (Ferraz et al., 2009). Positive values represent deforestation concentrated in early years of the measured interval; negative values represent deforestation concentrated in recent years. Values near zero

represent constant deforestation rates over the time interval studied (Fig. 2).

### Benthic Macroinvertebrate Data

We sampled benthic organisms through use of a D-frame kick net (30 cm aperture, 250  $\mu\text{m}$  mesh). Sampling was conducted in September (Três Marias, 2010; Volta Grande, 2011; São Simão, 2012; Nova Ponte, 2013; Pandeiros, 2016), ensuring that sampling occurred at the end of the local low flow (dry) season. Eleven sub-samples were taken at each site following a systematic zig-zag trajectory along the site (Peck et al., 2006). In the laboratory, samples were washed in a 250  $\mu\text{m}$  sieve and then stored in 70 % alcohol. We identified the benthic macroinvertebrates to family level using taxonomic keys and the subsamples were composited to represent each site. More details about sampling strategy and taxa identification may be found in Castro et al. (2018). All specimens were deposited in the reference collection of benthic macroinvertebrates of the Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais. To characterize the taxonomic structure of the benthic macroinvertebrate assemblages we estimated six biological metrics: total abundance, total richness, Shannon-Wiener diversity index, Simpson diversity index, EPT abundance and EPT richness for each site.

### Data Analyses

To test if the legacy effect from the riparian zone was more important than that from the catchment (hypothesis 1), and whether more recent land use changes had a stronger effect than older changes (hypothesis 2), we ran generalized linear models (GLMs). In doing so, we used the macroinvertebrate response variables versus the deviations from the Deforestation Profile Curvatures for the whole catchment and for the 200 m riparian zone buffer of each site as explanatory variables. The GLMs used Gaussian distribution (for Shannon-Wiener, Simpson diversity indices) and Quasi-poisson distribution (for abundance, richness, EPT abundance, EPT richness). To determine if the variables showed positive or negative correlations from the deviations from the Deforestation Profile Curvatures, we then calculated Pearson correlations ( $r$ ) for all models. All analyses were done using R software version 3.5.1 (R Core Team, 2020).

To test if sensitive taxa responded more readily to deforestation time (hypothesis 3), we performed Threshold Indicator Taxa Analysis (TITAN) to detect change points in the macroinvertebrate taxa responses to the deviations from the Deforestation Profile Curvature. TITAN combines change point and indicator species analyses to detect abrupt changes in the abundance and

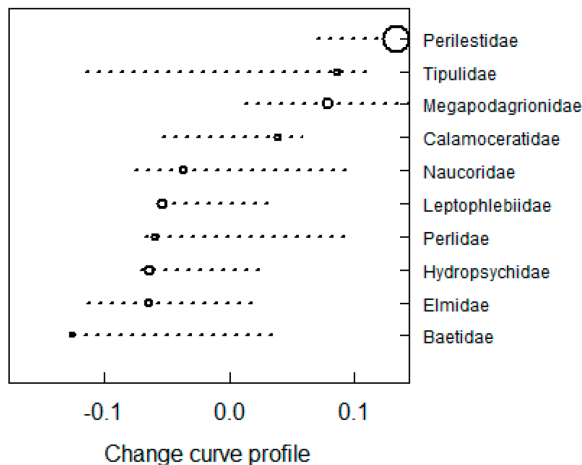
**Table 1.** Significance of correlations (GLM) between benthic macroinvertebrate assemblage metrics and the Deforestation Profile Curvature in the catchment and 200 m riparian zone buffer. Degrees of Freedom (DF); bold (significant correlation at  $p < 0.05$ );  $r$  (Pearson correlation). *Correlações significativas entre as métricas da assembleia de macroinvertebrados bentônicos e a Curvatura de Perfil de Desmatamento na bacia hidrográfica e zona ripária de 200 m. Graus de liberdade (DF); negrito (correlação significativa em  $p < 0.05$ );  $r$  (correlação de Pearson).*

| Variable             | p    | Catchment |    |      | r           | 200m Riparian Zone Buffer |           |             |
|----------------------|------|-----------|----|------|-------------|---------------------------|-----------|-------------|
|                      |      | F         | DF | p    |             | F                         | DF        | r           |
| Abundance            | 0.06 | 3.64      | 95 | 0.19 | 0.63        | 0.23                      | 95        | -0.05       |
| Richness             | 0.27 | 1.26      | 95 | 0.11 | 0.75        | 0.10                      | 95        | 0.03        |
| Shannon-Wiener Index | 0.21 | 1.61      | 95 | 0.13 | <b>0.01</b> | <b>6.78</b>               | <b>95</b> | <b>0.26</b> |
| Simpson Index        | 0.24 | 1.37      | 95 | 0.12 | <b>0.01</b> | <b>7.66</b>               | <b>95</b> | <b>0.27</b> |
| EPT Abundance        | 0.12 | 2.49      | 95 | 0.16 | 0.23        | 1.47                      | 95        | 0.12        |
| EPT Richness         | 0.26 | 1.27      | 95 | 0.12 | 0.29        | 1.13                      | 95        | 0.11        |

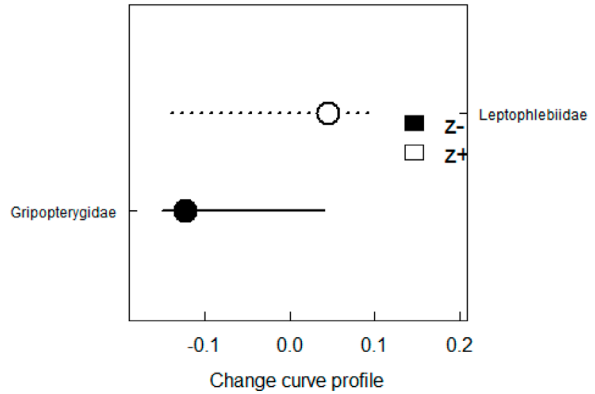
frequency of taxa along the Deforestation Profile Curvature, and uses bootstrap resampling (1000 permutations) to create 95 % confidence intervals (Baker & King, 2010). Change points indicate where along the continuum of a disturbance variable that various taxa in a response assemblage begin to appear (z+) or disappear (z-).

## RESULTS

We found that two of the response variables (Shannon-Wiener and Simpson diversity) showed significant positive correlations with the Deforestation Profile Curvature deviation at the catchment and riparian extents (Table 1). The Deforestation Profile Curvature deviation in the 200 m riparian zone buffer showed significant correlations with Shannon-Wiener diversity ( $F = 6.78$ ;  $r = 0.26$ ;  $p = 0.01$ ) and Simpson diversity ( $F = 7.66$ ;  $r = 0.27$ ;  $p = 0.007$ ). Positive Deforestation Profile Curvature deviations represented deforestation concentrated in the earlier years of the measured interval (see Fig. 2). Our tests incorporating the 97 deforested sites showed a positive correlation be-



**Figure 3.** Robust indicator taxa identified by TITAN in response to the Deforestation Profile Curvature in the catchments. Lines (solid or dashed) represent 95 % confidence intervals of observed change points (open or black circles). *Táxons indicadores robustos identificados pela TITAN em resposta à Curvatura do Perfil de Desmatamento em bacias hidrográficas.* As linhas (sólidas ou tracejadas) representam intervalos de confiança de 95 % dos pontos de mudança observados (círculos abertos ou pretos).

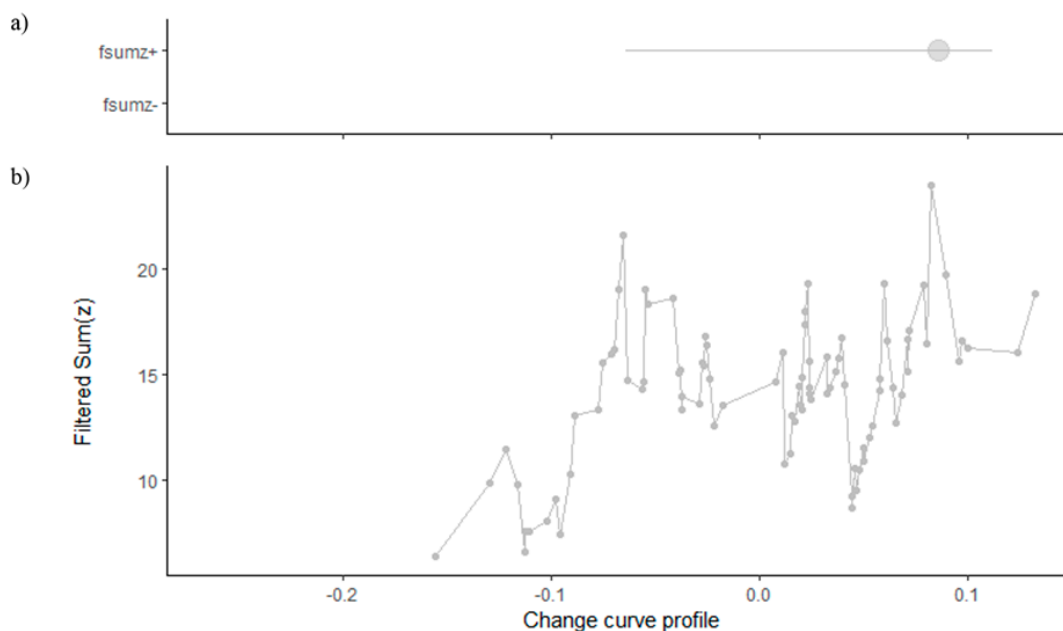


**Figure 4.** Robust indicator taxa identified by TITAN in response to the Deforestation Profile Curvature in the riparian buffers. Lines (solid or dashed) represent 95 % confidence intervals of observed change points (open or black circles). *Táxons indicadores robustos identificados pela TITAN em resposta à Curvatura de Perfil de Desmatamento na zona ripária.* As linhas (sólidas ou tracejadas) representam intervalos de confiança de 95 % dos pontos de mudança observados (círculos abertos ou pretos).

tween the positive Deforestation Profile Curvature deviation and the diversity variables (Shannon-Wiener and Simpson indices) at the 200 m riparian buffer, meaning that the more positive the former, the greater the latter. Because more positive Deforestation Profile Curvature deviation values indicate earlier deforestation events and more negative Deforestation Profile Curvature deviation values indicate recent deforestation events (Fig. 2), earlier deforestation events are associated with sites having higher diversities (and some recovery), whereas recent deforestation events result in sites with lower diversity.

TITAN detected 10 insect families with a significant response (purity and reliability  $\geq 0.95$ ) to the Deforestation Profile Curvature deviation for the whole catchment, with 4 families belonging to the EPT (Baetidae, Calamoceratidae, Hydropsychidae and Leptophlebiidae) (Fig. 3). All families with significant results had increased abundance (Z+) with the Deforestation Profile Curvature deviation at this spatial extent.

In the 200 m riparian zone buffer, only 2 families responded significantly to the Deforestation Profile Curvature deviation (Fig. 4), both being EPT (Leptophlebiidae and Gryptopterygidae).



**Figure 5.** Total assemblage change point thresholds for the 200 m riparian zone buffer (a) and total fitted sums (b). *Limiares do ponto de inflexão da assembleia de macroinvertebrados bentônicos para a zona ripária (200 m) (a), e somas totais ajustadas (b).*

Leptophlebiidae increased their abundance with the deviation. Gripopterygidae decreased abundances ( $Z^-$ ) with the Deforestation Profile Curvature deviation in the 200 m riparian zone buffer.

The total assemblage change-point thresholds in the riparian zone (Fig.5;  $z^-$  0.06,  $z^+$  0.11) were slightly lower to  $z^-$  and higher to  $z^+$  than those for the entire catchment (Fig. 6;  $z^-$  0.07,  $z^+$  0.09), further suggesting that the assemblages were slightly more sensitive to deforestation events in the riparian zone.

## DISCUSSION

Our first hypothesis, that legacy effects in the riparian zone are more important than those in the entire catchment, was corroborated because only the Deforestation Profile Curvature deviations for the 200 m riparian zone buffers showed significant positive correlations with the two diversity indices than that in the catchments (Table 1). Our second hypothesis, that more recent land use changes have a stronger negative effect on the taxonomic

structure of benthic macroinvertebrate assemblages than earlier land use changes, was also corroborated. Our third hypothesis, that EPT taxa will respond more readily to historical changes in land use, was partially corroborated. This is because while EPT families were not the majority of the taxa that responded negatively to the Deforestation Profile Curvature deviation at catchment scale, they were the only ones that showed significant correlation at the 200 m buffer scale.

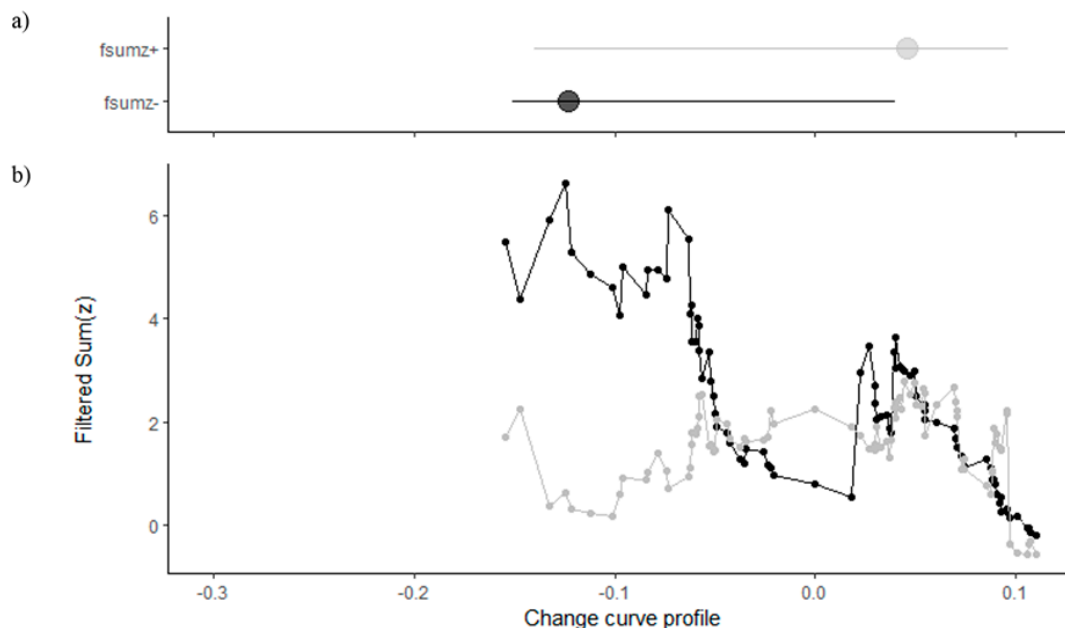
Riparian land use is an important factor affecting the structure and function of lotic ecosystems (Espinoza-Toledo et al., 2021; Gregory et al., 2007; Kaufmann et al. 2022; Tonkin, 2014). Riparian vegetation regulates the quantity and quality of the energy available to lotic ecosystems and also buffers anthropogenic disturbances from the nearby landscape (Linares et al., 2018; Martins et al., 2018; Rezende et al., 2016; Santos et al., 2019). Anthropogenic disturbances in the riparian zone act as environmental filters; therefore, riparian deforestation is reflected in macroinvertebrate assemblages (Castro et al., 2018; Firmiano et al.,

2021). Apparently, riparian areas with recently recovered vegetation cover still lack assemblages with biological integrity because of the difficulty of the macroinvertebrate recovery process, which is driven by colonization barriers in surrounding areas (Bond & Lake, 2003). Our results further indicate that past and present deforestation in the riparian zone have significant direct effects on aquatic insect assemblage structure. Finally, our results show that assessing legacy effects can provide important insights in linking local environmental conditions with aquatic biota, especially when those linkages cannot be explained by current conditions (Maloney *et al.*, 2008).

The lack of correlation between the aquatic insect assemblages and the Deforestation Profile Curvature deviation in the whole catchment than in the riparian zone can be explained by the lack of direct connections between catchment land use and benthic macroinvertebrate assemblage structure (Mwajengo *et al.*, 2020). Anthropogenic activities in the catchment generally affect structure and processes in riparian ecosystems, and riparian

ecosystems are also responsible for directly affecting in-stream structures and processes (Firmiano *et al.*, 2021; Sponseller *et al.*, 2001). However, both recent and historical catchment deforestation can degrade aquatic assemblages as a result of complex interactions among direct and indirect pathways and latent effects (Betts *et al.*, 2021; Leitão *et al.*, 2018).

Positive correlation between aquatic insect diversity and the Deforestation Profile Curvature deviation in the catchment indicates that catchment deforestation also influences instream biotic condition. In fact, we identified more families (10) with a significant response to the Deforestation Profile Curvature deviation at the catchment scale (Fig. 2), than those at the 200 m riparian zone buffer (2 families). Others have also found that the threshold change point for assemblages was lower for catchment deforestation than for riparian deforestation (Brito *et al.*, 2020; Martins *et al.*, 2021), contrary to what we found (Fig. 4). It is important to remember that the relative importance of riparian versus catchment deforestation



**Figure 6.** Total assemblage change point thresholds for the catchment scale (a), and total fitted sums (b). *Limiares do ponto de inflexão da assembleia de macroinvertebrados bentônicos para a bacia hidrográfica (a), e somas totais ajustadas (b).*



is a function of their ecoregional setting and the relative amounts of deforestation in each (Wang et al., 2006a, b) as well as their rates of change.

Although EPT families were not particularly affected by the pattern of historical deforestation at catchment scale, a Plecoptera family (Gryopterigidae) and an Ephemeroptera family (Leptophlebiidae) were the only taxa that were significantly affected by the Deforestation Profile Curvature deviation at the riparian 200 m buffer, with Leptophlebiidae showing significant results at both scales. Gryopterigidae however, increased in abundance along the deforestation gradient, contrary to their classification as sensitive indicators of disturbance, as has been reported in previous studies (Firmiano et al., 2020, 2021). These differing results suggest that the timing of deforestation, the type of deforestation and recovery, and the level of taxonomic identification can influence observed faunal responses (Barlow et al., 2016; Martins et al., 2021).

## CONCLUSIONS

Our results show that the legacy effects of deforestation are an important factor for structuring aquatic insect assemblages in the Neotropical Savanna, albeit less important than recent impacts. They also highlight the importance of the ecological health of both the catchment and the riparian zone for the structure and functioning of headwater ecosystems.

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