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LEGADO DA HISTÓRIA DA PAISAGEM NA ESTRUTURA DAS COMUNIDADES DE RIACHOS

EDINEUSA PEREIRA DOS SANTOS

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de doutor em Ecologia e Biodiversidade.

Agosto - 2019

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Orientador: Prof. Dr. Tadeu de Siqueira Barros

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TÍTULO DA TESE: Legado da história da paisagem na estrutura das comunidades de riachos

AUTORA: EDINEUSA PEREIRA DOS SANTOS
ORIENTADOR: TADEU DE SIQUEIRA BARROS
COORIENTADOR: SILVIO FROSINI DE BARROS FERRAZ

Aprovada como parte das exigências para obtenção do Título de Doutora em ECOLOGIA E BIODIVERSIDADE, especialidade: Biodiversidade pela Comissão Examinadora:

Prof. Dr. TADEU DE SIQUEIRA BARROS
Departamento de Ecologia / UNESP - Instituto de Biociências de Rio Claro - SP

Profa. Dra. PAULA KOELER LIRA
Departamento de Biologia / Pontifícia Universidade Católica do Rio de Janeiro - RJ

Profa. Dra. LILIAN CASATTI
Departamento de Zoologia e Botânica / UNESP - Câmpus de São José do Rio Preto - SP

Prof. Dr. LUIS MAURÍCIO BINI
Departamento de Biologia Geral / Universidade Federal de Goiás, Instituto de Ciências Biológicas - Goiânia / GO

Prof. Dr. VICTOR SATORU SAITO
Centro de Ciências Biológicas e da Saúde - Departamento de Ciências Ambientais / Universidade Federal de São Carlos / SP

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À tia Lia (in memoriam)

Por mudar o endereço e

A perspectiva de vida

Da garotinha magricela

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"if I have seen further, it is by standing on the shoulders of giants"

Letter to Robert Hooke, by Isaac Newton, Feb 5, 1675

"The Answer to the Great Question… […] is… […] Forty-two! […] So once you do know what the question actually is, you'll know what the answer means"

The Hitchhiker's Guide to the Galaxy, Douglas Adams

"[…] both the past and the future are simply "there", laid out as part of four-dimensional space-time, some of which we have already visited and some not yet."

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RESUMO

Esta tese busca entender a estruturação de comunidades de riachos em paisagens modificadas enquanto contabiliza possíveis assincronias entre ambas. Logo, ela questiona os pressupostos de que (i) é necessário incluir características das paisagens passadas para alcançar uma abordagem mais completa dos fatores estruturadores das comunidades atuais e (ii) alternativamente, de que lapsos temporais nas respostas das comunidades devem ser considerados para compreender a total magnitude dos efeitos de uma dada mudança da paisagem. Além disso, são explorados condicionantes relacionados à caracterização do histórico da paisagem, ao tipo de descritor da comunidade e à complexidade do sistema ecológico. Em seu primeiro manuscrito, esta tese confirma tais pressupostos enquanto apresenta o primeiro registro de respostas tardias de insetos aquáticos em região tropical. Nele, eu demonstro que padrões nas comunidades poderiam ser mais bem compreendidos quando o histórico é descrito com mais de uma característica (e.g., média histórica e trajetórias de perda e ganho de cobertura florestal) e que a detecção de respostas tardias varia de acordo com os descritores de comunidades estudados. Em seu segundo manuscrito, um modelo teórico foi testado admitindo múltiplas relações simultâneas e, predominantemente, indiretas para o sistema de estudo. Neste, além daqueles pressupostos, foram confirmados caminhos causais pelos quais a cobertura florestal e usos dos solos estruturam as comunidades. Com os caminhos são fornecidas evidências empíricas de que a montagem das comunidades de insetos aquáticos é afetada pela quantidade de floresta remanescente através da regulação das condições ambientais locais dos riachos e pelo arranjo recente e pretérito dos fragmentos florestais conforme sua influência sobre a conectividade espacial ao longo dos riachos. Assim, além de acrescentar elementos à ecologia de comunidades e à interpretação de distúrbios antropogênicos, tais achados abrem uma janela de oportunidade para tomadores de decisão. Pois, de um lado, eles assinalam a possibilidade para interromper futura perda de espécies decorrente de modificação recente da paisagem em sistemas fluviais e, de outro, alertam para a influência do histórico das paisagens para o sucesso de atividades de restauração.

Palavras-chave: conectividade, crédito de imigração, débito de extinção, equações estruturais, filtros ambientais, insetos aquáticos, lapso temporal, usos do solo

ABSTRACT

This thesis aims to understand the assembly of stream communities in modified landscapes by accounting for possible asynchronies between the two. In this way, it questions the assumptions that (i) it is necessary to include past landscape characteristics to reach a more complete approach of the structuring factors of current communities, and that (ii), alternatively, one should consider time lags in community responses to encompass the magnitude of the effects of a certain landscape change. In addition, drivers related to the characteristics of landscape history, the type of community descriptor and the complexity of the ecological system are questioned. In its first manuscript, this thesis confirms those assumptions and shows the first record of delayed responses of aquatic insects in the tropical region. In that, I show that patterns in communities could be better understood when landscape history is described with more than one characteristic (e.g., historical mean and loss and gain trajectories of forest cover) and that the detection of delayed responses varies according to the community descriptors. In its second manuscript, a theoretical model was tested admitting multiple simultaneous, and predominantly, indirect relationships in the study system. Then, in addition to the previous assumptions, causal pathways by which forest cover and land uses structure communities were confirmed. With the paths, empirical evidence that aquatic insect community assembling is affected by the amount of forest remaining via instream condition regulation and by the arrangement of the recent and past forest fragments according to their influence on the connectivity along the channels were provided. Thus, in addition to including elements to community ecology and the interpretation of anthropogenic disturbances, such findings open a window of opportunity for decision makers. Because, in a way, they indicate the possibility of interrupting future species loss due to recent landscape modification in river systems and, in another one, they alert to influence of landscape history on the success of restoration activities.

Keywords: connectivity, immigration credit, extinction debt, structural equation model, environmental filter, aquatic insect, time lag, land use

LISTA DE ILUSTRAÇÕES

Figura 1.1 Diagrama e equações ilustrando as relações entre variáveis observadas e latentes em um modelo de equações estruturais (adaptado de Grade et al. 2006, pag.193) 19

Figure 2.1 Location of the studied watersheds in the Corumbataí river basin, São Paulo state, Brazil 32

Figure 2.2 Mean and standard deviation of forest cover proportion of the catchments of each trajectory. Colors red and green represent the trajectories of forest loss and gain, respectively, and gray represents general trajectory of all catchments.....35

Figure 2.3 Standardized beta coefficient of estimated recent rarefied richness (above) and abundance (below) according to forest cover (%) at each observed year (1962-2011) in a linear mixed model...36

Figure 2.4 Predicted rarefied richness, abundance and Tsallis diversity by interaction between the trajectories of forest loss and gain (values: -30 and 30 respectively) and mean forest cover (a, b, c), variation of accumulated forest cover (d, f) and total accumulated forest cover (e) 37

Figure 3.1 – Spatial scales (catchment and riparian) at which land uses and forest cover were assessed. The catchment scale comprised the entire area upstream the sampled site. The riparian scale comprised an upstream buffer from the sample site (30-m width at both stream sides) 55

Figure 3.2 – General theoretical model relating landscape characteristics and spatial scales to stream conditions, habitat connectivity, and local community structure. LUFC = Land use and forest cover. Local forest canopy cover and topographic constraints are single variables; all others are latent variables that include some observed indicators. Variables with term 'history' have indicators varying along time (1962, 1972, 1978, 2003, 2011) 58

Figure 3.3 – Structural equation models showing the pathways by which landscape modification affects local community diversity. Arrow thickness is proportional to the estimated standardized effect size (single headed) or correlation to other variables (double headed), and their values are indicated over the arrows. Cycles contain the standard errors associated to all significant estimates, except correlation. Red arrows indicate negative values. Dashed arrows indicate marginally significant effects. Dotted arrows indicate non-significant effects and gray arrows show indicators of the reflective latent variables. Only significant correlations ($P < 0.05$) are shown for simplicity. R^2 indicates the proportion of variation of endogenous factor (from the rightmost) explained by exogenous factors (from the leftmost), except for latent variables represented by the ellipse 66

LISTA DE TABELAS

Table 1. Description of the latent variables that underpin processes (dispersal and niche selection) affecting directly aquatic insects in freshwater systems and their indicators.....59
Table 2. Description of exogenous and endogenous latent variables and their indicators 61

SUMÁRIO

INTRODUÇÃO GERAL 12

A história da paisagem e as comunidades fluviais 12

A ecologia de riachos e a modelagem de equações estruturais 16

Objetivo geral e estrutura dos manuscritos 20

REFERÊNCIAS 21

LEGACY OF HISTORICAL LANDSCAPE CHANGE ON TROPICAL STREAM COMMUNITIES 28

Abstract 28

Introduction 29

Methods 31

Results 34

Discussion 38

References 42

Supplementary material 48

SPATIAL CONNECTIVITY AND INSTREAM CONDITIONS MEDIATE THE LEGACY OF LANDSCAPE HISTORY IN RIVERINE COMMUNITIES 50

Abstract 50

Introduction 51

Methods 53

Results 64

Discussion 67

References 70

Supplementary material 80

CONCLUSÃO 88

Referências 90

INTRODUÇÃO GERAL

A história da paisagem e as comunidades fluviais

A interação entre paisagens modificadas e comunidades de águas correntes tem um longo histórico, porém, a influência deste histórico nas comunidades ao longo do tempo só começou a ser investigada muito recentemente – especificamente em 1998 (HAIDVOGL, 2018). No decorrer deste extenso lapso temporal, muitas ideias, conceitos e ferramentas surgiram e ajudaram a embasar e impulsionar um crescente interesse pelo que se tem denominado de 'legado do histórico das paisagens'.

Os primórdios da relação da modificação antrópica da paisagem com os organismos aquáticos remontam ao estabelecimento das primeiras civilizações nas margens dos rios, como a civilização egípcia no rio Nilo há mais de 5000 anos (HASSAN, 2011; MAYS, 2008; SCHMUTZ; MOOG, 2018). Naquela época, um impacto incipiente sobre a biodiversidade de água doce decorria de fatores locais ou regionais envolvendo os açudes e desvios dos cursos dos rios (HAIDVOGL, 2018; SCHMUTZ; MOOG, 2018). A partir de século XVIII, com a revolução industrial e, simultaneamente, a expansão urbana e agrícola, houve aceleração na modificação das paisagens naturais bem como aumento no grau e alcance dos impactos (HAIDVOGL, 2018). No entanto, apenas quando esse conjunto de fatores pôs em risco a saúde humana por meio da poluição dos rios é que aspectos ecológicos desses ecossistemas passaram a ter visibilidade (CAIRNS; PRATT, 1993). Entre os registros mais emblemáticos das condições dos rios a partir daquele período estão a distribuição de lençóis encharcados de vinagre pelo parlamento inglês para amenizar o odor fétido e nauseante do rio Tâmisa (CAIRNS; PRATT, 1993) e a fatídica morte de centenas de milhares de pessoas devido a pandemia de cólera ao longo do século XIX (SANTOS, 2011).

Em meados do século XIX, as comunidades de água doce despertariam grande interesse científico fomentado pela busca de indicadores da saúde desses sistemas. Os trabalhos dos cientistas Kolenati (1848) e Cohn (1853) foram precursores desta fase ao registrarem que os organismos que ocorriam nas águas poluídas diferiam dos de águas limpas (DE PAUW; VANHOOREN, 1983). A despeito de já serem estudados fatores físicos, químicos e bacteriológicos para fins agrícolas, domésticos e industriais, Pratt e Coler (1976) argumentavam que a inclusão de comunidades aquáticas era necessária quando o valor da água se estendia para dimensões estéticas, recreativas e ecológicas. Tal inclusão já havia sido iniciada na Alemanha com registros de ocorrência de microrganismos das comunidades planctônicas e perifíticas (sistema sapróbio, Kolkwitz and Marsson 1908). Posteriormente, métodos com foco na presença e ausência de macroinvertebrados surgiram nos

Estados Unidos e logo se espalharam por quase toda a Europa (METCALFE, 1989). Além de fatores pragmáticos como abundância e ubiquidade, o enorme interesse pelos invertebrados visíveis emergiu das características ecológicas que também contribuíam para seu potencial bioindicador, tais como (*i*) a sensibilidade a poluentes de vários tipos; (*ii*) o hábito relativamente sedentário que os tornam representativos das condições locais; (*iii*) a expectativa de vida longa o suficiente para fornecer um registro da qualidade ambiental e (*iv*) a reunião de representantes filogeneticamente distantes – o que significa que ao menos alguns deles reagem a uma mudança específica nas condições ambientais (DE PAUW; VANHOOREN, 1983; METCALFE, 1989; PRATT; COLER, 1976). Além do mais, o fato de tais invertebrados ocuparem diversos níveis tróficos em redes tróficas de riachos sugeria o seu uso para inferir sobre a base alimentar (algas, folhas) e sobre o status de conservação de toda a comunidade aquática (CAIRNS; PRATT, 1993). Outros fatores que contribuiriam para o entendimento de como a diversidade dessas comunidades se relacionaria com as mudanças da paisagem terrestre vieram no século XX.

Avanços teóricos e empíricos sobre interações entre componentes bióticos e abióticos dos riachos estiveram até então concentrados na dimensão longitudinal destes sistemas, o que deu suporte a teoria do rio contínuo (VANNOTE et al., 1980). Tal teoria propunha uma mudança gradual na estrutura e funcionamento dos ecossistemas fluviais decorrente de processos intrinsecamente ligados ao aumento da hierarquia dos rios (seguindo sua extensão longitudinal) e às mudanças dos componentes nas interfaces – por exemplo, o sombreamento e a insolação. Com o potencial de elucidar alguns padrões ao longo das redes fluviais, essa teoria ocupou o interesse de muitos pesquisadores por longo tempo (ELLIS; JONES, 2013; JIANG et al., 2011). Esta, no entanto, já considerava a importância da dimensão lateral – a qual incorpora o meio terrestre – para também explicar estruturas e processos dentro dos canais fluviais. Um primeiro passo nessa direção foi dado por Leopold et al. (1964), cujo livro inovava o estudo da geomorfologia ao explicar o desenvolvimento de formas de relevo com processos associados às águas correntes. Contudo, a ideia de que os corpos fluviais são governados pelos vales que os acompanham foi mesmo primeiramente apresentada por Hynes (1975). Este não só considerou fenômenos físicos, como a inundação, como também a contribuição do vale com material orgânico para as redes tróficas fluviais. Naquela época já se esperava que as relações com o meio terrestre tenderiam a ser mais fortes nos rios de cabeceiras considerando o baixo quociente entre a área do canal e sua respectiva área de drenagem (KARR; SCHLOSSER, 1978). Tais considerações também justificavam o uso dos rios e riachos como indicadores apropriados da saúde ambiental de bacias hidrográficas (ALLAN; ERICKSON; FAY, 1997).

A dimensão lateral ampliou as escalas espaciais de observação dos processos que atuam nos sistemas de riachos e, por sua vez, também aumentou a escala de tempo necessária para a compreensão destes processos (LOTSPEICH; PLATTS, 1982; WARD, 1989). As múltiplas escalas espaciais foram, depois, hierarquizadas considerando que as mais elevadas restringiam à manifestação das demais (FRISSELL et al., 1986; LEVIN, 1992). Ao olhar sob diferentes escalas, também já se observava que a influência de características do meio terrestre era mais forte quanto mais próximo estivessem do leito (ALLAN; ERICKSON; FAY, 1997; KING et al., 2005). Por consequência, uma faixa adjacente às margens dos rios denominada de zona ripária passou a receber especial atenção nos trabalhos científicos. Inicialmente, experimentos de curta duração indicavam que a remoção da vegetação nesta faixa aumentava o volume dos rios uma vez que evitava perda com a evapotranspiração da vegetação (DUNFORD; FLETCHER, 1947; HOOVER, 1944). Posteriormente, novos estudos demonstraram a necessidade de manter a vegetação ripária por proporcionar (i) a estabilidade do canal e fluxo com os troncos caídos no leito (HEEDE, 1972), (ii) o controle da temperatura e da produção primária devido ao sombreamento (HANSMANN; PHINNEY, 1973), (iii) uma fonte de material orgânico para detritívoros (FISHER, 1977) e (iv) a filtragem de nutrientes e sedimentos carreados em bacias agrícolas (KARR; SCHLOSSER, 1978; LOWRANCE et al., 1984). Assim, com a adição da dimensão lateral foram incluídos novos fatores associados a paisagem que poderiam afetar indiretamente comunidades de riachos. E, paralelamente a ela, outros fatores estavam sendo agregados por meio das contribuições que a teoria da biogeografia de ilhas deu a ecologia de comunidades e da paisagem.

Até a primeira metade do século XX, a montagem das comunidades biológicas era investigada considerando apenas o processo de seleção de espécies através de filtros ambientais e interações entre elas (VELLEND, 2010). Nesse meio tempo, MacArthur and Wilson (1967) assinalaram – com a dinâmica de colonização e extinção de espécies ao longo de um conjunto de ilhas – a importância da dispersão para que populações de ilhas menores e relativamente próximas fossem mantidas. A ecologia de comunidades tomou, então, a dispersão como um processo chave na montagem de comunidades locais (SHURIN, 2000; WINEGARDNER et al., 2012). Além disso, como a dinâmica de uma comunidade passava a depender da dispersão e do conjunto de comunidades vizinhas, esta passou a ser estudada sob o conceito de '*meta'comunidade* (LEIBOLD et al., 2004). À luz da ecologia de metacomunidades, padrões ecológicos observados em ambientes antropizados poderiam ser mais bem compreendidos. Por exemplo, uma improvável elevada diversidade de insetos em um riacho com condições ambientais adversas seria, então, possível quando houvesse elevada dispersão de indivíduos dos riachos menos impactados do entorno (efeito de massa, Heino 2013). Enquanto isso, no meio

terrestre, a ecologia da paisagem tomou as relações espaciais das ilhas oceânicas como modelo de estudo para as manchas de vegetação natural que passavam pelo processo de fragmentação (FAHRIG, 2013; HAILA, 2002). Tal como nas ilhas, os tamanhos e formas dos fragmentos naturais e a distância entre eles (configuração espacial) deveriam afetar processos ecológicos das comunidades terrestres. A dispersão entre comunidades locais, por exemplo, poderia reduzir com o distanciamento entre manchas florestais – ou menor conectividade – decorrente da fragmentação da paisagem (STRATFORD; STOUFFER, 1999). Adicionalmente, os fragmentos florestais poderiam ser envoltos por diferentes atividades agrícolas que, por sua vez, também afetariam a dispersão de acordo com seu grau de permeabilidade ao deslocamento das espécies (STAMPS; BUECHNER; KRISHNAN, 1987). Com a adoção de conceitos da biogeografia de ilhas e a emergência de outros novos voltados para o meio terrestre, houve maior demanda da quantificação de vários atributos da paisagem. Oportunamente, novas tecnologias em sensoriamento remoto e ciência da computação passaram a fornecer imagens e a melhorar o tratamento e análises dos dados de paisagem, respectivamente (JOHNSON; GAGE, 1997). Desde então, além das características das paisagens contemporâneas, tornava-se interessante e possível buscar explicações para as estruturas das comunidades atuais nas características das paisagens passadas.

O primeiro registro de que comunidades de riachos respondem a condição da paisagem passada veio com Harding et al. (1998) ao verificar que a diversidade de macroinvertebrados e peixes era explicada pela cobertura florestal e atividade agrícola de 40 anos antes. Antes, Diamond (1972) já havia introduzido o conceito de dilatação temporal (*time relaxation*) ao se referir ao intervalo de tempo necessário para que a diversidade de espécies retomasse o valor de equilíbrio considerando o novo tamanho de habitat após sua redução – atualmente designado como *time lag*, em inglês. Neste caso, o número de espécies que seriam extintas de maneira tardia em decorrência da perda do habitat formava o que foi posteriormente denominado por Tilman et al. (1994) de débito de extinção. O oposto deste foi apresentado por Hanski (2000) como crédito de espécies (ou de imigração por JACKSON; SAX, 2010), referindo-se ao número de espécies que retornariam se medidas fossem tomadas para, neste caso, aumentar a área de habitat. Ambos, débito de extinção e crédito de imigração, têm implicações práticas para a conservação da biodiversidade (FOSTER et al., 2003). No primeiro, por exemplo, o número de espécies efetivamente ameaçadas tende a ser subestimado (HANSKI; OVASKAINEN, 2002). Também, a persistência das espécies previstas para serem extintas tende a ser um indicativo de que ainda há tempo para implementar medidas que evitem futuras extinções (HANSKI, 2000).

Em face ao volume de estudos mostrando o risco de extinção de espécies em todo o mundo e a contribuição das mudanças na paisagem para isso – mais frequentemente da perda de habitats florestais – (ANDRÉN, 1994; BROOKS et al., 2002; GARDNER et al., 2009; NEWBOLD et al., 2015), muitos pesquisadores têm olhado para o passado para saber onde é possível evitar perdas de espécies e em quais grupos taxonômicos (CHEN; PENG, 2017; HALLEY et al., 2016). Embora haja mais investigações das zonas temperadas (KUUSSAARI et al., 2009), tal interesse tem se estendido também para as tropicais, principalmente envolvendo sistemas terrestres e grupos de vertebrados. E, apesar das regiões tropicais serem caracterizadas, de maneira geral, pela maior velocidade com que processos ecológicos operam (BRUDER et al., 2014), respostas tardias foram observadas para aves, mamíferos, anfíbios e peixes (BREJÃO et al., 2018; CHEN; PENG, 2017; LIRA et al., 2012; METZGER et al., 2009). Logo, respostas tardias poderiam também ser encontradas em comunidades aquáticas tal como em Harding et al. (1998). De outro lado, também se tornou necessário entender o que faz as comunidades responderem tardiamente, ou, em outras palavras, apresentarem tais legados (HYLANDER; EHRLÉN, 2013). Entre os possíveis motivos, sugere-se que certas características das espécies, especialmente as associadas a longevidade (LINDBORG, 2007), levariam a lapsos temporais, mas, respostas tardias têm sido encontradas em quase todos os grupos taxonômicos (BOMMARCO et al., 2014; KUUSSAARI et al., 2009). Também, a conectividade espacial entre conjuntos de comunidades e as características do próprio distúrbio – no que tange ao nível de fragmentação e sua duração – têm sido evidenciadas entre possíveis razões (SHACKELFORD et al., 2016).

Em suma, dadas as evidências de que comunidades ecológicas apresentam um legado das condições passadas da paisagem, novas pesquisas não poderiam compreender sua estrutura se olhassem apenas para fatores contemporâneos. No caso das comunidades de riachos, isso implica em não só incluir dados do histórico daquela dimensão lateral – como a composição das feições antrópicas e naturais da paisagem, mas também considerar mais atributos dentre os que emergem na ecologia da paisagem. Além disso, como todos estes fatores estão fora dos riachos e atuam nas comunidades, em grande parte, indiretamente, também é preciso desvendar os mecanismos pelos quais eles operam sobre essas comunidades.

A ecologia de riachos e a modelagem de equações estruturais

Investigar mecanismos responsáveis pela montagem de comunidades fluviais com dados observacionais requer, inevitavelmente, que se avalie a influência de diversas variáveis. A maioria dos

estudos busca soluções em análises multivariadas descritivas e exploratórias, como as análises de agrupamentos e componentes principais, e em algumas passíveis de se estabelecer relações causais diretas, tal como a MANOVA (do inglês, *Multivariate Analysis of Variance)* (GRACE, 2006). Entretanto, grande parte das variáveis em questão afeta as comunidades fluviais indiretamente – principalmente quando se inclui aquelas associadas ao meio terrestre – o que não é contemplado por tais análises. Além disso, as diversas relações entre os pares de variáveis que emergem de tais análises e que são confirmadas experimentalmente se encerram como múltiplos pedaços de teorias. Logo, torna-se evidente a falta de uma reunião dos pedaços numa teoria única capaz de explicar as interações entre todos eles e, consequentemente, de explicar o sistema de estudo (GRACE, 2006; SHIPLEY, 2000). Tais problemas foram inicialmente enfrentados por Wright (1920), que, então, desenvolveu um modelo capaz de lidar com relações indiretas: o modelo de caminhos. Este modelo propunha o encadeamento de efeitos através de uma sequência de variáveis, de modo que uma dada variável (variável endógena) que é explicada pela sua predecessora (variável exógena), também poderia ser preditora da variável posterior. Em meio a proeminência dos testes estatísticos baseados nas variâncias das variáveis, o relacionamento entre elas, isto é, a covariância, foi tomado como evidência estatística dos caminhos (sequência) previstos nos modelos hipotéticos. No limite oposto, a independência probabilística de duas variáveis também poderia ser confirmada quando a covariância da população fosse zero (SHIPLEY, 2000).

Na área biológica, o modelo de caminhos foi ignorado, e rejeitado, por um longo período em decorrência da atenção dada às análises univariadas após as contribuições de Karl Pearson, tais como o coeficiente de correlação, e Robert Fisher, como a randomização de amostras e testes de hipóteses usando a teoria de probabilidades (SHIPLEY, 2000). Enquanto isso, outras áreas de estudo adotaram o modelo de Wright e atualizaram suas técnicas. Utilizando dados da economia e psicologia, Jöreskog (1970), por exemplo, introduziu a estimação dos coeficientes dos caminhos por máxima verossimilhança. O uso da máxima verossimilhança permitiu que a sequência de equações que descrevia o processo causal hipotético fosse testada em relação aos dados para verificar se os condicionantes de tal sequência (coeficientes de correlação parcial e outros) concordavam com as observações. Essa técnica permitiu falsear a estrutura causal hipotetizada (hipótese nula), que antes era assumida de maneira dedutiva por Wright, possibilitando que esta pudesse ter suas consequências estatísticas testadas (JÖRESKOG, 1970; SHIPLEY, 2000). Da psicometria vieram as variáveis latentes e a análise fatorial confirmatória (SPEARMAN, 1904). A primeira se refere a uma variável que não pode ser mensurada diretamente, mas pode ser representada por um vetor cujos valores (como por

exemplo as variâncias das amostras) têm origem em outras variáveis, citadas como 'indicadores'. Estes últimos, por sua vez, foram realmente observadas e contribuirão com uma dada proporção (peso/carga fatorial) na derivação da variável latente (SÁNCHEZ, 2013). Um dos primeiros e mais figurativos exemplos de variável latente foi apresentada por Spearman (1904) com o precursor do atual quociente de inteligência (QI). O autor presumia que a propriedade latente da inteligência geral existia, mas não havia maneira direta de observá-la. Logo, ela só poderia ser avaliada indiretamente estimando seus efeitos. As medidas observadas da inteligência das pessoas, obtidas a partir de testes com perguntas sobre a capacidade verbal, matemática e raciocínio analítico, por exemplo, seriam os indicadores de uma capacidade intelectual geral latente que variava de pessoa para pessoa. Com essas reformulações, e mais frequentemente alcunhado por modelo de equações estruturais (SEM em inglês), o modelo de caminhos retornou a biologia. Dessa vez, dada a persistência de antigas lacunas relacionadas a uma teoria geral envolvendo a relação indireta e de múltiplas variáveis, o SEM disseminou-se por diversos campos desta área incluindo a ecologia (FAN et al., 2016; GRACE, 2006).

As reformulações dos modelos de equações estruturais permitiram que eles assumissem estruturas extremamente complexas. Entretanto, tais modelos podem ser identificados por alguns componentes básicos. Na figura 1.1 apresentamos um diagrama de um modelo SEM e o conjunto de equações que o descrevem. Como ocorre nesses modelos, as variáveis latentes estão representadas com uma elipse, as variáveis observadas ou manifestas com retângulos, os erros do modelo com círculos e as relações causais com setas unidirecionais. Também podem ser utilizadas setas bidirecionais para demonstrar correlações quando houver. Neste modelo todas as variáveis observadas são indicadores de variáveis latentes, mas elas poderiam compor modelos onde seriam diretamente uma variável explanatória ou resposta. A variável latente (ξ) resulta de uma combinação de possíveis cargas (λ) que representam a proporção de variação necessária para explicar o grau de covariância entre as variáveis observadas (equação detalhada em Grace). As variáveis latentes são calculadas com análise fatorial confirmatória (em inglês, CFA) e buscam representar as causas subjacentes não mensuradas da variação comum entre as variáveis observadas (SHIPLEY, 2000). A análise CFA é similar a análise de componentes principais (PCA, em inglês) quanto ao objetivo de criar preditores que representem as correlações entre as variáveis mensuradas usando um conjunto reduzido de variáveis e quanto ao fato de não apresentarem erro para esses preditores (GRACE, 2006). No entanto, ao contrário da PCA, na CFA são admitidos erros para os indicadores e correlação entre os fatores. Assim, como não há exigência de ortogonalidade entre os fatores (variáveis latentes) também não se usa a rotação da nuvem de dados para maximizar a variação comum entre todos os indicadores quando estes fatores são

extraídos. Além disso, os conjuntos de indicadores são predeterminados de acordo com relações previstas no modelo teórico, o qual é construído previamente baseado na literatura. Por isso, posteriormente, o método de máxima verossimilhança é usado para chegar a ponderações que satisfaçam o modelo e para permitir a avaliação de expectativas baseadas no modelo teórico.

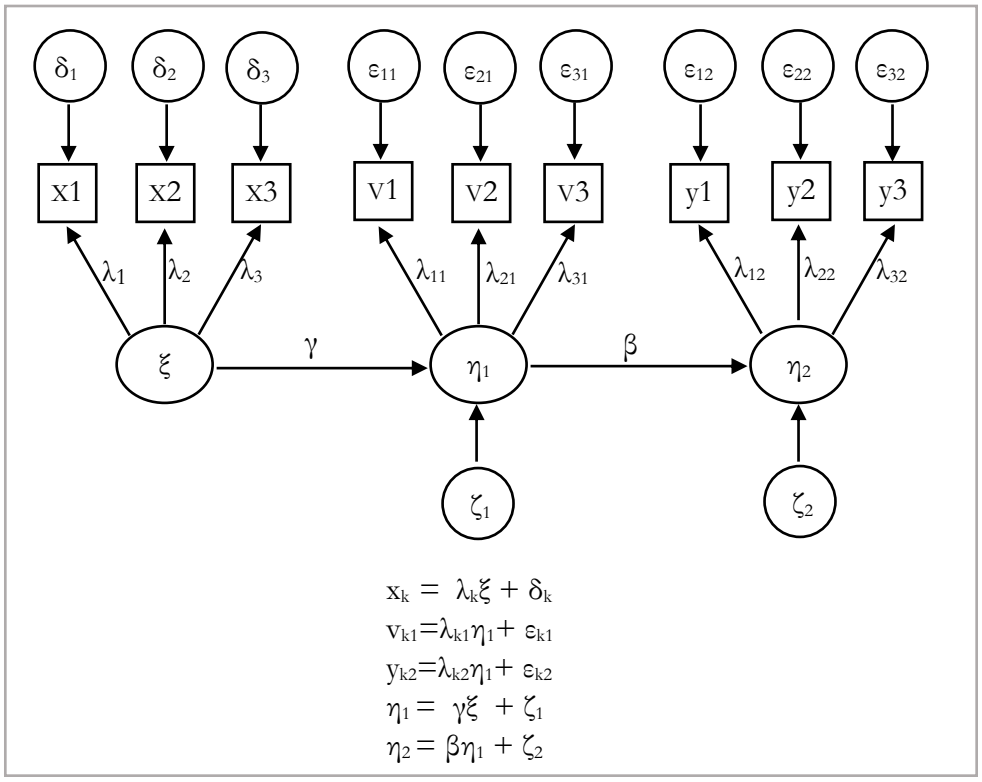

Figura 1.1 – Diagrama e equações ilustrando as relações entre variáveis observadas e latentes em um modelo de equações estruturais (adaptado de Grace et al. 2006, pag.193).

Além das relações entre variáveis latentes e seus indicadores, as quais formam blocos denominados de modelos de mensuração, também há as relações destas com outras variáveis latentes que compõem o modelo estrutural. As relações entre variáveis latentes podem ser apresentadas com equações lineares onde se descreve uma variável endógena em função de variáveis exógenas e com uma variável endógena em função de outras endógenas – e assim sucessivamente seguindo a orientação das setas nos modelos estruturais. Embora possa ser representada com uma estrutura similar as dos modelos lineares, a modelagem SEM se baseia em análises de covariâncias em vez de observações individuais. Também, todos os coeficientes estruturais (γ, β) são estimados simultaneamente com o método de máxima verossimilhança. De maneira simplista, este método é utilizado para estimar os

coeficientes (lineares) do modelo teórico proposto e a partir dele gerar uma matriz de covariância esperada que seja tão similar a matriz de covariâncias observada que as mínimas diferenças encontradas sejam devido ao processo de amostragem de uma população com distribuição normal. O desenvolvimento desta abordagem e dos cálculos que lhe dão suporte pode ser acompanhado no trabalho de Jöreskog (1970). Tal como em outros modelos, os valores de parâmetros individuais ainda possuem incertezas, as quais estão associadas aos erros padrão presentes, e podem ser avaliados usando valores p (GRACE, 2006). O ajuste do modelo também é avaliado com um teste qui-quadrado que parte da hipótese nula de igualdade entre a matriz de covariância dos dados e a matriz de covariância estimada. Além deste, nos softwares e em pacotes para o ambiente R de programação (como o *lavaan*) são disponibilizados diversos índices que complementam a avaliação do ajuste dos modelos (FAN et al., 2016; ROSSEEL, 2012).

Objetivo geral e estrutura dos manuscritos

Diante das muitas evidências de que há lapsos temporais nas respostas de comunidades aos distúrbios nos sistemas ecológicos, esta tese *busca compreender padrões atuais de biodiversidade de insetos aquáticos e mecanismos que estruturam essas comunidades sob a influência do histórico de mudanças da paisagem ribeirinha*. Nas próximas duas seções deste documento apresento os manuscritos cujas investigações possibilitam atender a este objetivo.

O primeiro manuscrito focou na identificação e compreensão de respostas tardias explorando características do histórico da paisagem e descritores da comunidade de insetos aquáticos. O segundo manuscrito focou na corroboração de caminhos causais pelos quais a história da cobertura florestal e usos dos solos estruturam as comunidades.

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LEGACY OF HISTORICAL LANDSCAPE CHANGE ON TROPICAL STREAM COMMUNITIES

Edineusa Pereira Santos[1*], Helene H. Wagner[2], Sílvio F. B. Ferraz[3], Tadeu Siqueira[1]

[1]Institute of Biosciences, São Paulo State University (Unesp), Rio Claro, Brazil
[2]Department of Ecology and Evolutionary Biology, University of Toronto, Canada
[3]Department of Forest Sciences, Luiz de Queiroz College of Agriculture, University of São Paulo, Brazil

[*]Corresponding author: edineusa.eco@gmail.com

Abstract

Evidence indicating that some ecological communities show delayed responses to landscape modifications has raised the need to better understanding the role landscape history can play in determining current biodiversity patterns. Here, we investigated how stream communities were related to both recent and past land use in tropical riverine networks. We modeled rarefied species richness, local abundance and Tsallis diversity as a function of the within-catchment forest cover proportion in 1962, 1972,1978, 2003 and 2011, and of the loss or gain trajectories of forest cover. Local abundance showed a more delayed response to landscape change than rarefied richness, whereas Tsallis diversity was not related to forest cover of any year. We found that stream communities were positively related with the historical mean of forest cover only when conditioned by (loss or gain) trajectories. Among catchments with the lower mean values of forest cover, we found higher rarefied richness in catchments that lost forest cover than those where forest cover was more constant through time, which suggests a surplus of species to be lost later. In contrast, community descriptors were high in catchments with a forest gain trajectory when forest cover was also high. We provide the first evidence of delayed responses of stream insect communities to forest cover history in tropical riverine landscapes. Our findings indicate that the maintenance of large amounts of remaining forest patches underpins positive reforestation effects on biodiversity. We also suggest new attributes of forest cover history that complement the identification and improve the interpretation of delayed responses in riverine systems.

Key Words

Aquatic insects, deforestation, extinction debt, forest recovery, freshwater systems, immigration credit, species richness

Introduction

Current levels of landscape modification worldwide have led to alarming consequences for biodiversity and ecosystem functioning (DÍAZ et al., 2019; GARDNER et al., 2009; NEWBOLD et al., 2015). More than affecting current biodiversity patterns and processes, landscape changes can have persistent, long-term impacts that propagate over time, from years to decades (HALLEY et al., 2016; KUUSSAARI et al., 2009; MORENO-MATEOS et al., 2017). Delayed responses to landscape history are rarely taken into account in ecological studies, which directly affect our perception about how communities are assembled in modified landscapes (BLONDER et al., 2017; HYLANDER; EHRLÉN, 2013; MOUQUET et al., 2011). Neglecting delayed responses can affect conservation strategies and management decisions (SANG et al., 2010). For example, extinction debts and restoration targets are more accurately quantified when time lag responses are considered (KITZES; HARTE, 2015; WEARN; REUMAN; EWERS, 2012). Therefore, a current challenge for community and applied ecologists is to elucidate the factors that lead communities to show delayed responses (KITZES; HARTE, 2015; LIRA; LEITE; METZGER, 2019).

Previous evidence indicates that delayed responses of communities depend on the extent, frequency and intensity of landscape change (HYLANDER; EHRLÉN, 2013; SHACKELFORD et al., 2016). Most studies have investigated these facets of change in forested ecosystems, considering that delayed responses are related to a history of change in forest cover, specifically forest loss and gain (JACKSON; SAX, 2010; KUUSSAARI et al., 2009), and their consequences to biodiversity – e.g., extinction debts and immigration credits, respectively. Extinction debt refers to the difference between the number of species observed in a remaining habitat compared with a continuous habitat of the same area, or estimated for a different area based on the species-area relationship (KUUSSAARI et al., 2009; VELLEND et al., 2006). Similarly, forest gain leads to an immigration credit that refers to the number of species lacking in the restored habitat compared to natural habitats with the same area (JACKSON; SAX, 2010). Delayed community responses have received support from theoretical models (HANSKI; OVASKAINEN, 2002) but remains less investigated in hyperdiverse tropical systems empirically

(BREJÃO et al., 2018). For example, if forest loss had been very extensive and resulted in small, disconnected patches, the time for half the species number to be extinct (i.e., half-life) would be short (HALLEY et al., 2016; HYLANDER; EHRLÉN, 2013). Since forest loss does not completely disrupt spatial connectivity and colonization-extinction dynamics, the delay in species loss can be long lasting due to rescue effects (HYLANDER; EHRLÉN, 2013; LINDBORG; ERIKSSON, 2004).

Beyond the dichotomous classification of forest loss versus gain commonly adopted in many ecological studies, landscape history tends to be more complex and dynamic (CLAUDINO; GOMES; CAMPOS, 2015; LIRA et al., 2012). If a given landscape accumulates multiple events of forest loss over time, it could be expected that for each new deforestation event, some species would be immediately lost and another set of surplus species would be lost later (KITZES; HARTE, 2015). Then, current communities may be related to any, or multiple, past events (LINDBORG; ERIKSSON, 2004; LIRA et al., 2012; METZGER et al., 2009). As multiple forest loss events increase the risk of local extinction, community responses may relate more strongly to recent landscape characteristics (e.g., Lira *et al.*, 2012). However, it still remains poorly understood how overall characteristics of landscape history, such as mean forest cover, variation of forest cover and the amount of forest cover maintained over a certain period of time contribute to delayed responses (FERRAZ; VETTORAZZI; THEOBALD, 2009).

Delayed responses of biological communities to past landscape changes are also expected to vary across taxa and life histories (LINDBORG, 2007; VELLEND et al., 2006). To date, most of the communities studied were terrestrial, including plants, mammals, birds, amphibians, but rarely insects (HALLEY et al., 2016; KUUSSAARI et al., 2009). Aquatic communities, such as aquatic invertebrates in streams, also show strong relationships with the amount of forest cover in the surrounding landscape, even though they are often affected indirectly (ALLAN, 2004; KING et al., 2005; LEITÃO et al., 2017; PEASE et al., 2015; SIQUEIRA; LACERDA; SAITO, 2015). For example, forest loss within stream the riparian zone reduces the input of litter and debris to riverbeds and thus affects water quality and in-stream spatial heterogeneity (PALMER et al., 2000; PAULA et al., 2013, 2018; QUINN et al., 1997). Also, deforestation in the riparian zone can disrupt dispersal colonization dynamics, as aquatic insects with an adult flight stage disperse predominantly along the stream channel (HUGHES, 2007; LANCASTER; DOWNES, 2017). Although there are good reasons to expect that stream communities also show delayed responses to landscape history, only few studies have investigated this issue (e.g., Harding et al. 1998, Brejão et al. 2018). While the pioneering study by Harding et al. (1998)

showed that present-day stream diversity was better predicted by watershed land use decades before, Brejão et al. (2018) showed that fish in Amazonian streams respond to deforestation events sooner after they take place. Given that land use modification has been identified as a major threat to freshwater ecosystems (DUDGEON et al., 2006), investigating factors that may lead communities to show delayed responses in riverine landscapes is urgently needed.

In this study, we examined some attributes of forest cover change history and relate them to descriptors of current aquatic insect communities with the aim of estimating long-term effects of forest cover change in tropical riverine landscapes. We quantified temporal variation in forest cover maps (from 1962 to 2011) from an heterogeneous river basin in southeastern Brazil to address the following question: How do current community patterns relate to past forest cover? We identified catchments with two opposite trajectories, forest loss and forest gain, and tested for interactions of these trajectories with overall characteristics of forest cover history to answer a second question: Do the attributes of landscape history drive the delayed responses of aquatic insect communities?

Methods

Landscape history descriptors

We mapped forest cover from the Corumbataí river basin (São Paulo State, southeastern Brazil) from panchromatic aerial photographs in 1962, 1972 and 1978, and from LandSat-7 TM and ETM scenes in 2003 and 2011 (30 m spatial resolution) provided by the Brazilian Institute for Space Research (INPE). LandSat scenes were geo-referenced based on topographic maps at a 1:10,000 scale, and digital images from other years were spatially registered to the 2011 scene, which was used as reference (FERRAZ et al., 2014). The river basin comprises an area of 170,000 ha, and the natural vegetation was originally dominated by semi-deciduous forest with patches of Savanna (Cerrado) (RODRIGUES, 1999; VALENTE; VETTORAZZI, 2003). This region experienced initial deforestation at beginning of 19th century through logging, followed by expansion of pasture and cropland (mainly sugarcane), which reduced the natural vegetation into small fragments. Along the last five decades, natural vegetation recovery on abandoned agricultural land has led to an increase of forest cover (FERRAZ et al., 2014). Given that remaining patches of Savanna are very small, and that shrubs and trees commonly compose vegetation along the riparian zones even for the non-forest biomes, we decided to treat the entire natural vegetation as forest cover.

Within the Corumbataí river basin area, watersheds were delineated through SWAT modeling (Soil and Water Assessment Tool) in ArcGIS 10.3 (Environmental System Research Inst., Redlands, CA,

USA), using a Digital Elevation Model (DEM) derived from SRTM (Shuttle Radar Topography Mission, 30m resolution; Figure 2.1). Considering the need for finer scale details, we used 1:10,000 scale topographic maps and delineated manually the reach contribution areas within catchments. We selected catchments out of urban development perimeter and where access was feasible.

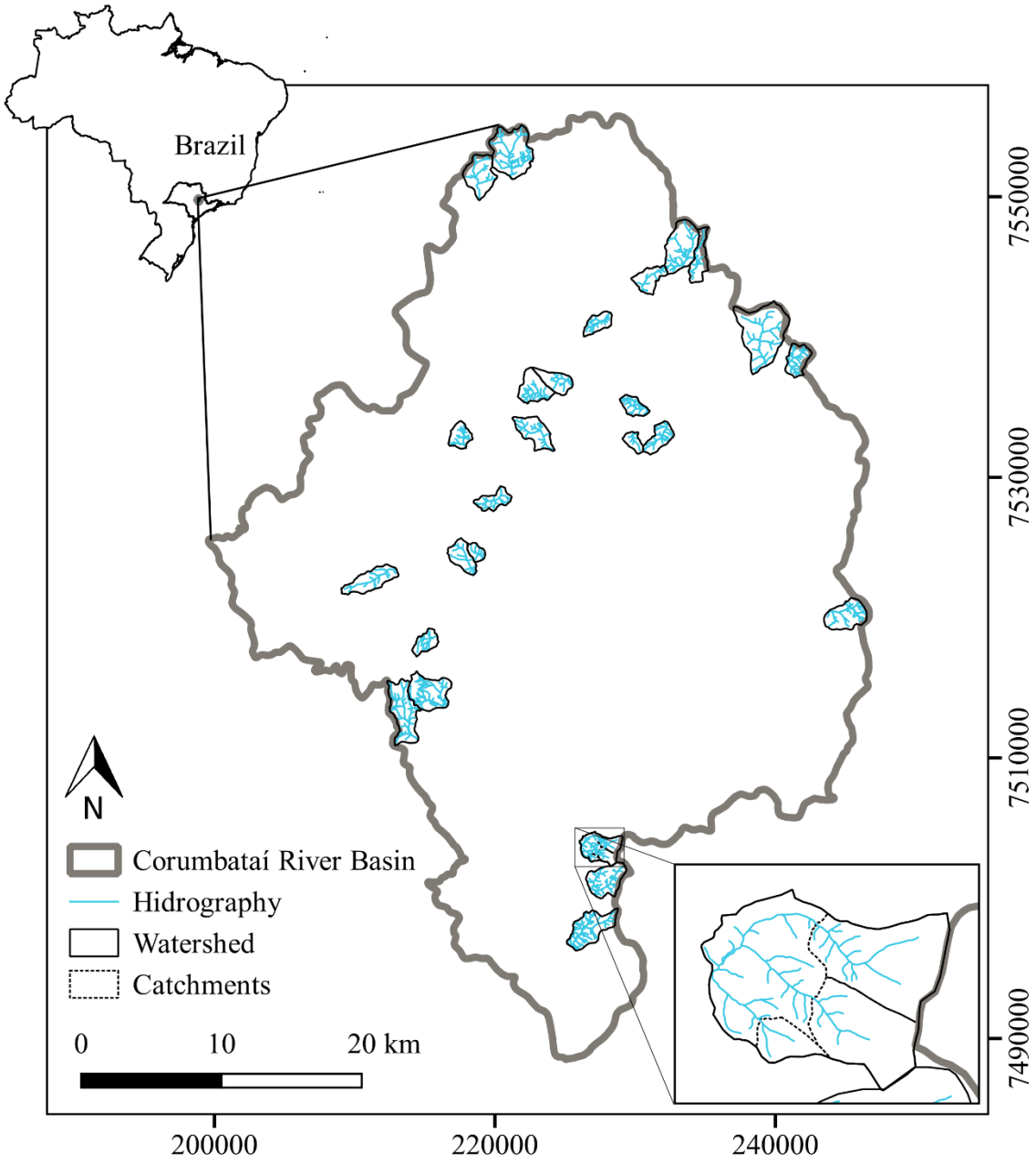

Figure 2.1 – Location of the studied watersheds in the Corumbataí river basin, São Paulo state, Brazil.

We determined the percentage of forest cover within catchment at each year, which were used to derive the following descriptors of landscape history: mean and the standard deviation of forest proportion (%). Landscape history also was characterized by a combination of the proportion and persistence of remaining forest. Therefore, for each catchment, we calculated some measures considering the persistence of remaining forest through the accumulated forest proportions along time intervals. Each accumulated forest proportion was calculated by tallying the proportional area of new forests formed during each time interval (1962:1972, 1972:1978, 1978:2003, 2003:2011). Then, we used these accumulated proportion values to estimate the total accumulated forest cover proportion, the mean accumulated forest cover proportion and variation of accumulated forest cover proportion for each catchment (Figure S1). We also considered the direction (signal) of forest cover change for the entire time length and within each catchment as descriptors of landscape history. We interpreted the catchments as either following a 'loss' (i.e., forest loss) trajectory, when the recent forest cover percentage was less than that of the oldest period (negative values), or a 'gain' (i.e., recovery) trajectory, when the recent forest cover percentage was larger than that of the oldest period (positive values).

Sampling procedures and community descriptors

We sampled immature aquatic insects in 101 streams (from 26 watersheds) predominantly during the dry period between May and August of 2015 (Figure 2.1). The number of streams per watershed varied between three to five. We used a kick-net, with $1m^2$ area and 250 μm mesh, to collect a generous sample in each stream by gently kicking the stony substrate in four riffles for a total of two minutes in each stream. Samples were preserved in 80% ethanol and packed for examination in the laboratory. Aquatic insects of the Ephemeroptera, Plecoptera, Trichoptera and Odonata orders were identified to species or morphotype based on identification keys (DOMÍNGUEZ et al., 2006; DOMÍNGUEZ; FERNÁNDEZ, 2009; HECKMAN, 2006) and original descriptions. For each catchment, we calculated total local abundance of insects and estimated rarefied species richness using 100 individuals as the minimum sample size. We also calculated the Tsallis diversity index, which is very similar to the Shannon index but minimizes biases caused by sample size given that each community receives a specific weighting of the relative abundance of species by the lowest possible evenness of each community (MENDES et al., 2008).

Statistical analyses

To investigate the relationship between landscape change history and aquatic insect communities and estimate long-term effects of forest cover change, we fitted linear mixed models

using the package lme4 (BATES et al., 2015) in R (R Core Team, 2016). More specifically, we modeled each community descriptor (rarefied richness, abundance and Tsallis diversity) individually and used watershed as a random factor, given that catchments belonging to same watershed tend to show more ecological similarities. As abundance showed a Poisson distribution, we used generalized linear mixed models (GLMM).

First, we modeled each community descriptor as a function of forest cover in 1962, 1972, 1978, 2003 and 2011 as fixed effects. We did not include the catchments with constant forest cover over time in the analysis – i.e., a variation of forest proportion lower than 10% of maximum variation – as biodiversity patterns in these catchments cannot be explained by differences in the forest cover between the years.

We also modeled each community descriptor as a function of landscape history descriptors, which included time intervals (total, mean and variation of accumulated forest cover proportion), interacting individually with trajectory. We first removed variables that were strongly correlated ($r > 0.70$). Then, we started with a full model containing all remaining uncorrelated variables and used a backwards model selection to reach the minimum adequate model. We used the corrected Akaike's Information Criterion, AICc (BURNHAM; ANDERSON, 2002) to compare models. For the model selection, we analyzed delta AICc values, then interpret the model weights as the amount of evidence there was for each model, given all other models in the set. We inspected residuals plots for all models visually and found no violation of linear modeling assumptions. We extracted pseudo R-squared values of fixed and random effects using the package MuMIn (BARTÓN, 2009). We estimated standardized beta coefficients to assess effect size of the predictors, including interaction terms, and used confidence intervals of 95% to interpret only those parameters whose confidence intervals did not include zero. We considered there was as time-delayed response when a community descriptor was related to any landscape history descriptor but the most recent forest cover (2011). All statistical analyses were performed in R (R Core Team, 2018).

Results

We counted a total of 37,205 individuals distributed among 72 morphospecies. We found 36 catchments with forest loss trajectory and 48 with forest gain trajectory. Even the catchments on a forest loss trajectory showed slight forest gains during the last time interval (2003-2011, Figure 2.2). Overall, the catchments showed a mean (SD) number of morphospecies, individuals and Tsallis

diversity similar between forest loss (richness: 17.6 ±4.4, abundance: 448.2 ±343.3, Tsallis diversity: 2.7 ±0.9) and gain trajectories (17.0 ±4.9; 412.5 ±304.5; 2.4 ±0.8).

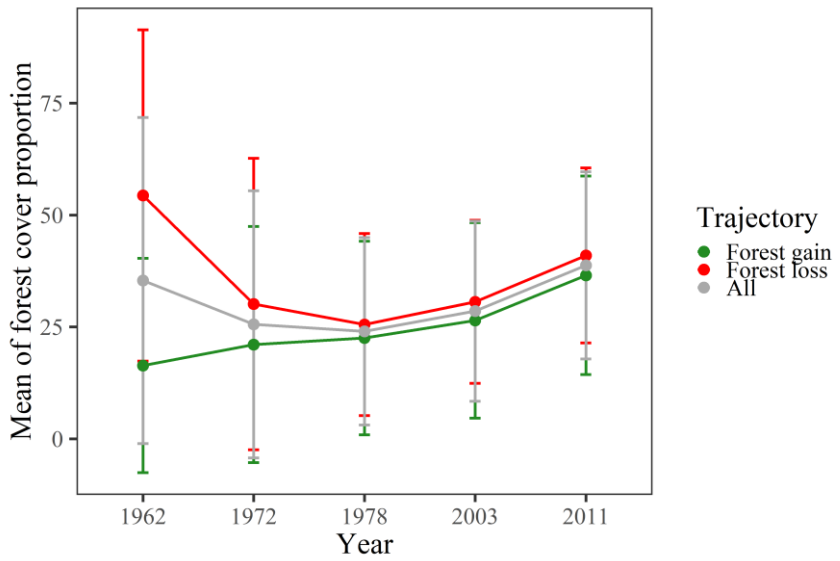

Figure 2.2 – Mean and standard deviation of forest cover proportion of the catchments of each trajectory. Colors red and green represent the trajectories of forest loss and gain, respectively, and gray represents general trajectory of all catchments.

How does current community patterns relate to past forest cover?

The linear mixed model including forest cover at each of the five time-steps as fixed effects and watershed as random factor explained 20% of rarefied richness, with 8% explained only by the fixed effects (AICc= 358.63, df= 65). Rarefied richness had a positive relationship with forest cover in 2003 and a negative relationship with forest cover in 2011, but no statistically significant relationship with forest cover further back in time (1962, 1972, or 1978; Figure 2.3). For total local abundance, the fixed effects explained 4% of the variation of abundance, while the random factor explained 15% of the variation (AICc= 7481.08, df= 67). Total local abundance had a positive relationship with forest cover in 2011, 2003 and 1972 and a negative relationship with forest cover in 1962 and 1978 (Figure 2.3). Forest cover did not explain variation in Tsallis diversity in any of the studied years.

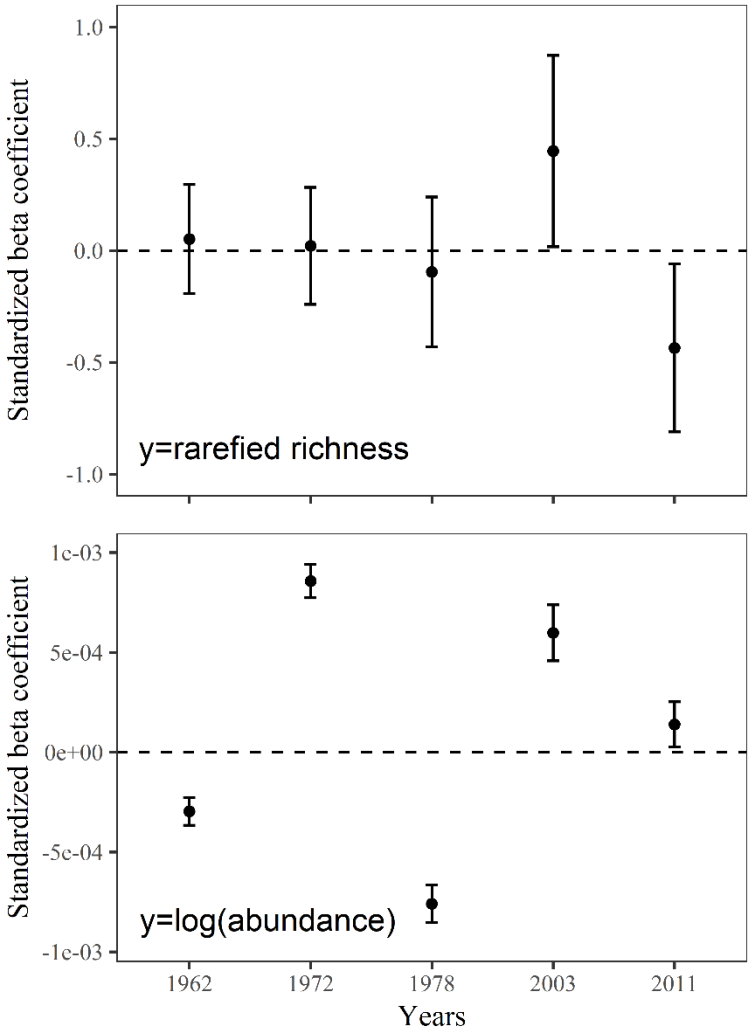

Figure 2.3 – Standardized beta coefficient of estimated recent rarefied richness (above) and abundance (below) according to forest cover (%) at each observed year (1962-2011) in a linear mixed model.

Do the attributes of landscape history drive the delayed responses of aquatic insect communities?

The best linear mixed models including the overall characteristics of forest cover history resulted in the same fixed effect for all response variables: the interaction between mean forest cover proportion and forest cover trajectory. The fixed effect explained 7% of a total of 21% of the variation of rarefied richness explained by the model (AICc= 413.44 and df=79), 5% of a total of 30% of the variation of abundance (AICc= 9367.9 and df=80), and 10% of a total of 22% of the variation of Tsallis diversity (AICc=218.5 and df=79). Rarefied richness, total local abundance and Tsallis diversity all had a positive relationship with the interaction between the mean forest cover proportion and forest cover trajectory (Table S2, β =0.320 and CI=0.08:0.5; β=0.001 and CI=0.00093:0.0010; β=0.351 and

CI=0.116:0.587, respectively). The interaction between mean forest cover and trajectory indicated that rarefied richness was higher in catchments that lost forest cover and had low mean cover and also in those with a trajectory of forest gain and high mean forest cover (Figure 2.4). Catchments with more consistent forest proportion over time showed intermediate values of rarefied richness compared to those found in catchments with forest loss and gain trajectories (Figure 2.4).

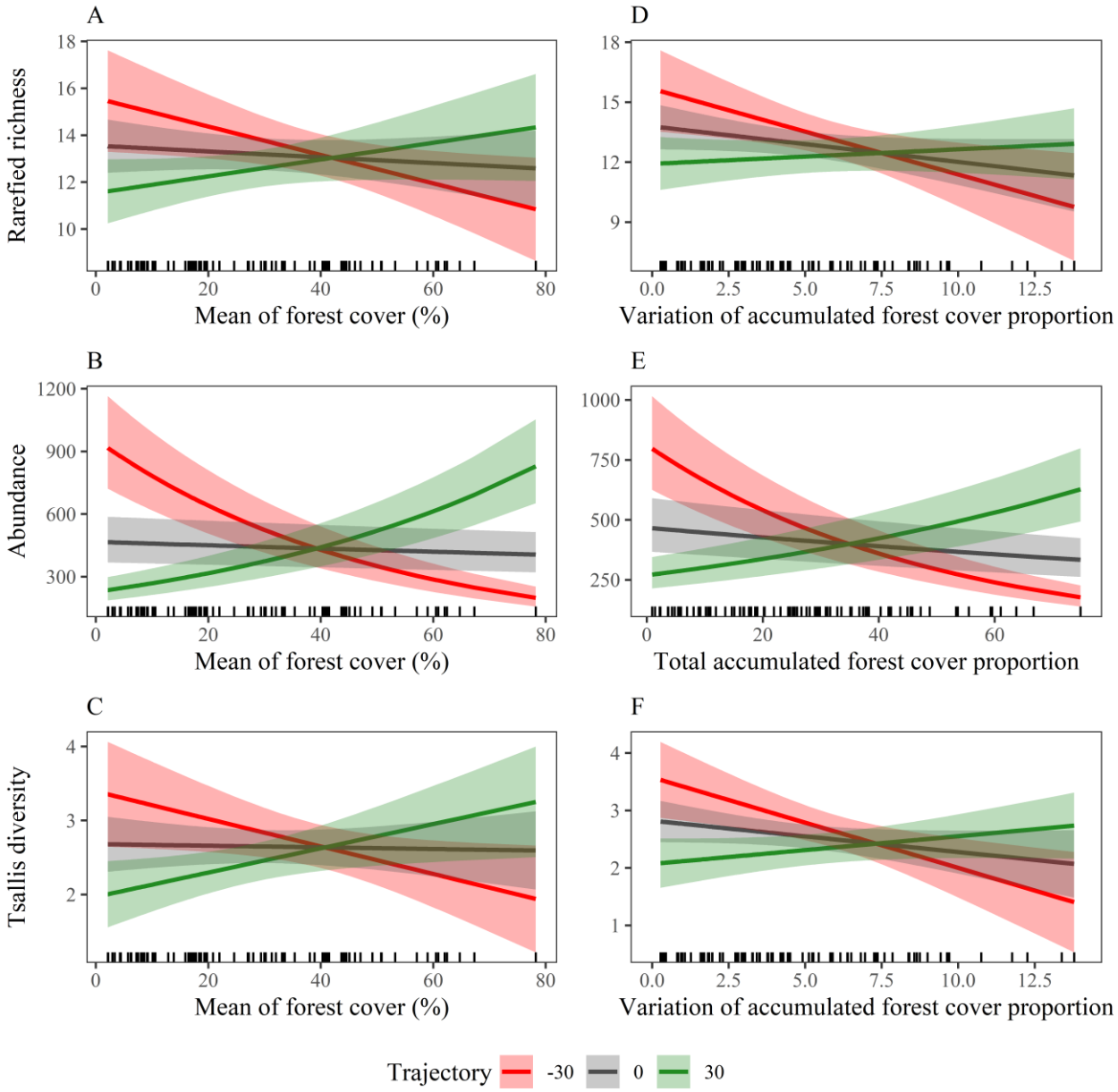

Figure 2.4 – Predicted rarefied richness, abundance and Tsallis diversity by interaction between the trajectories of forest loss and gain (values: -30 and 30 respectively) and mean forest cover (a, b, c), variation of accumulated forest cover (d, f) and total accumulated forest cover (e).

The best linear mixed models that included explanatory variables describing accumulated forest proportion by time intervals had the same fixed effects for rarefied richness and Tsallis diversity. For rarefied richness, 7% of the variation was explained by the fixed effects and 20% by the full model (AICc= 413.2, df=79). Rarefied richness had a positive relationship with the interaction between the variation of accumulated forest cover proportion and trajectory (β =0.353 and CI=0.0962:0.609). This implies that rarefied richness was higher in the catchments with a higher variation of forest cover and a forest gain trajectory. Among the catchments with low variation of accumulated forest cover, those with a forest loss trajectory showed higher rarefied richness than the catchments with forest gain trajectory or those with little change between last and previous forest cover. For Tsallis diversity, 12.6% of the variation was explained by the fixed effects and 25% by the full model (AICc= 216.0029, df=79). Tsallis diversity was explained by the same explanatory variables (fixed effect) as rarefied richness and showed a similar linear relationship (β =0.439 and CI=0.187:0.691).

For total local abundance, the best linear mixed model included total accumulated forest cover proportion and trajectory as fixed effects, which explained 4% of variation of abundance, with 27% explained by the full model (AICc= 216, df=79). Total local abundance had a negative relationship with each predictor individually, i.e. with accumulated forest (β =-0.00013 and CI=-0.00018:-0.000083) and with trajectory (β =-0.00044 and CI=-0.00049:-0.00039), where the highest abundance values were related mainly to catchments with forest loss, while other values were distributed among both trajectories. Total local abundance also had a positive relationship with the interaction between these variables (β =0.00089 and CI=0.00083:0.00095). Catchments with large proportion of forest accumulated over time showed higher abundance when on a forest gain trajectory and a lower abundance when on a forest loss trajectory (Figure 2.4). As for the previous models, we found an opposite relationship for catchments with small total accumulated forest cover proportion.

Discussion

How does current community patterns relate to past forest cover?

Our study provides the first empirical evidence that stream insect communities show delayed responses to forest cover history in tropical riverine landscapes. Such delayed responses are indicated by the observed relationships between past forest cover and community descriptors. Local insect abundance was related to catchment forest cover of all studied years, but more negatively related to forest cover in 1962 and 1978. This indicates that the time lag length for total local abundance extended over 49 years. Given that changes in abundance precede changes in species richness, one could expect

that local abundance describes a more immediate community response (WITH, 2007). However, a delayed response of local community abundance but not of species richness to landscape modification has been observed previously for other taxonomic groups (LIRA et al., 2012; METZGER et al., 2009). In these studies, it was suggested that the delayed response of local abundance resulted from wide delay variation among individual species responses, some of which were not even delayed. Indeed, we found a negative relationship between rarefied species richness and recent forest cover (2011), opposite to the direction expected a priori and observed in studies with aquatic insects (ALLAN, 2004; RODRIGUES et al., 2016). Additionally, because rarefied species richness was only explained by forest cover of 2003, surprisingly this suggests a shorter delay (eight years) for species richness than for local abundance.

Regarding forest change history, we observed a general increase in the mean proportion of forest cover in 2011, even in the catchments on a forest loss trajectory. Thus, the negative relationship between species richness and recent forest cover could indicate that communities are responding to forest increase, which may have triggered, via direct or indirect pathways, a dominance effect in local communities. In this scenario, some specific groups (e.g., r-strategists) become abundant and outcompete others, decreasing local richness and diversity (HILLEBRAND; BENNETT; CADOTTE, 2008). In line with previous evidence (DALA-CORTE et al., 2016), we found that more deforested catchments have higher total abundance than more forested catchments, which may be associated with an increment in primary production (e.g., periphyton and macrophyte) and nutrient loading (in case of agriculture landscapes) in open canopy riparian zones (LORION; KENNEDY, 2009). Additionally, previous studies also suggested that such negative relationship between forest cover and community abundance might last for long periods of time. For example, Harding et al. (1998) found that total fish abundance was significantly greater in streams with agricultural past (lasting 40 years) than in those with forested past. Brejão et al. (2018) also found that some fish may respond positively to major deforestation events that occurred more than 10 years before. Accordingly, our results confirm that historical land use change have subsequent effects on current biodiversity patterns that are more complex than initially thought.

What aspects of landscape history lead aquatic communities to show delayed responses?

Our approach to quantify landscape history by weighting landscape changes according to the order and duration they occurred supports and complements the hypothesis that current community patterns emerge from the legacy of multiple combined historical landscape changes (KITZES;

HARTE, 2015). In addition to the classic, widely used "snapshot" representation of past forest cover, we show that time-delayed biotic responses vary according to landscape temporal trajectory, intensity of forest cover changes, and mean and accumulated amount of remaining forest. Moreover, some patterns emerged from the interactions between these variables and trajectories. For example, the type of delayed response, which has been predicted as the extinction debt and species credit, seemed to fit only for the lower values of these variables, except trajectory. This finding adds empirical evidence that the emergence of delayed responses may depend on the levels of landscape changes. In this same sense, Cousins et al. (2009) observed that landscapes with <10% of remaining grassland cover had plant species richness more related to contemporary landscape characteristics, while landscapes with >10% of grassland cover showed extinction debt. Also, when comparing the extension of deforestation and time since landscape changes to investigate thresholds, Brejão et al. (2018) reported that Amazonian fish showed a negative threshold response to the lowest deforestation levels (<20%) and soon after forest loss (<10 years), and a positive and less-consistent threshold response at >70% deforestation and >10 years after forest loss. Although our study did not focus on identifying thresholds, our findings are consistent with such thresholds reported elsewhere (BREJÃO et al., 2018; ROQUE et al., 2018). More importantly, we suggest that the current percentage of vegetation cover per se, which is usually the main predictor targeted in studies on tipping points (e.g., Roque et al. 2018), may strongly depend on how forest coverage changed historically, emphasizing the importance to incorporate temporal trajectories to explain current and predict future biodiversity patterns.

Community descriptors (i.e., rarefied species richness, total local abundance and Tsallis diversity) were lower in catchments on a forest gain trajectory than in those on a forest loss trajectory. This relationship was especially stronger in more deforested catchments, i.e., with small final forest cover even after forest recovery. Considering that diversity and abundance in catchments with small changes in forest cover (i.e., more stable temporal trajectories) were lower than in catchments with a forest loss trajectory, it is possible that some species will be lost in the future (i.e., extinction debit). This potential species surplus may be associated with the (1) persistence of species with longer life cycles, (2) a rescue effect due to the aerial (via flying adults) and, mainly, aquatic dispersal (drift dispersal), and (3) the fact that forest changes affect aquatic organisms indirectly. Otherwise, some pathways that link stream communities to landscape change have shown a legacy of past landscape characteristics, such as those related to water chemistry (MALONEY; WELLER, 2011; MARTIN et al., 2017) and physical stream habitat characteristics (WHITE et al., 2017). Rarefied richness, total local abundance and Tsallis diversity were lower in catchments on forest gain trajectories than in those close

to a stable trajectory (previous and latter forest cover proportion very similar), when the catchments showed low values of any explanatory variable describing landscape history. This possible number of species lacking could be considered a species credit in these catchments (KUUSSAARI et al., 2009). With a similar response pattern, Greenwood et al. (2012) argued that the severity and extension of landscape changes would lead to local modifications in streams and long-lasting species credit. For example, sedimentation caused by slash and burn agriculture kept the total abundance and diversity of stream communities lower where the riparian forest was previously affected than where the primary riparian forest had remained (IWATA; NAKANO; INOUE, 2003). Additionally, if such landscape changes affect the regional species pool, full community recovery will not be reached even after full forest or habitat restoration (STOLL et al., 2014; TONKIN et al., 2014) – i.e., the species credit will not be fully paid (LIRA et al., 2012).

Finally, we observed that all community descriptors increased from trajectories of forest loss to forest gain in catchments with high values of any descriptor of forest history. This indicates that more forested catchments have higher diversity (richness and Tsallis diversity) and total abundance if they were on a forest gain trajectory than those that were on a forest loss trajectory. Also, beyond the relative amount of forest cover, our results support previous expectations that the magnitude of forest cover change, mediated by trajectory, is an important driver of delayed responses. We show that under severe forest loss trajectory (i.e., a large negative temporal variation), the final amount of forest cover in catchments is very low, which results in both a higher immediate loss of species and a larger set of species doomed for future extinction (HYLANDER; EHRLÉN, 2013; KUUSSAARI et al., 2009). These results suggest that the conservation of long-lasting large riparian zones may help natural forest regeneration to play a more successful role in the maintenance and even recovery of aquatic insect diversity. This is because, even under a forest gain trajectory, stream communities continue responding to past landscapes changes depending on how extensive and intensive changes were (HARDING et al., 1998).

Taken together, our findings indicate that stream communities responses to historical changes in forest cover can be investigated by two manners: one describing the traditional extinction debt and species credit (for low values of the landscape history descriptor), and another where surplus or lacking species are not evidenced (for high values of the landscape history descriptor). Thus, we raise potential concerns about trends to overestimate community diversity and abundance in watersheds where forest has been replaced by other land uses over previous decades. Therefore, our findings indicate that time-delayed biotic responses may blur our ability to properly quantify biodiversity in altered landscapes,

emphasizing the relevance of considering landscape history in conservation planning and decision making.

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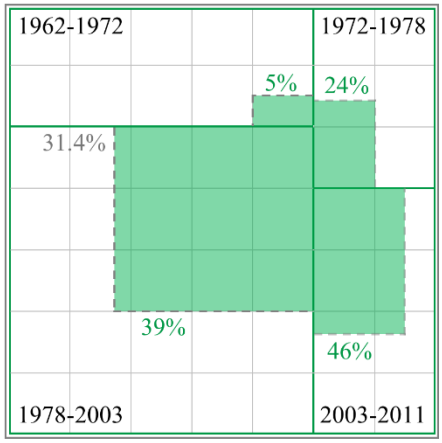
Supplementary material



S1-Illustration of the mean proportion of the forest cover in a catchment over time intervals (e.g., 1962: 1972) and the proportion considering the entire period studied (1962:2011). The mean proportion of forest cover within intervals is represented in green (e.g., 5%, 24%) and the total accumulated forest proportion (dashed line) along entire period (gray square) is represented in gray (i.e., 31.4%). Means and standard deviations were calculated considering green patches as fractions within their respective time intervals and as fractions of entire time period (gray square).

S2- Estimate, standard error (SE), Degrees freedom (Df), t-value and p-value, standardized beta coefficient (beta) and confidence interval (CI) of the linear mixed models that included trajectory (forest gain and loss) as fixed effect. Random effects are shown for simplicity. For abundance as the response variable, z-values are shown due the use of generalized linear models.

Response variable	Fixed effect	Estimate (SE)	Df	t	beta	CI
Rarefied richness ~	Intercept	13.12(0.33)	23.75	39.24	--	--
	Mean of forest cover	-0.11(0.29)	83.95	-0.39	-0.04	-0.25: 0.17
	Trajectory	-0.67(0.33)	83.02	-2.02	-0.25	-0.5: 0.01
	Mean of FC: trajectory	0.94(0.36)	80.56	2.64	0.32	0.08: 0.56
Rarefied richness ~	Intercept	12.85(0.31)	19.31	41.1	--	--
	Variation of accumulated forest cover (VAFC)	-0.46(0.29)	83.9	-1.58	-0.17	-0.39: 0.04
	Trajectory	-0.71(0.34)	77.34	-2.11	-0.27	-0.51: -0.02
	VAFC: Trajectory	0.83(0.31)	77.58	2.69	0.35	0.1: 0.61
Tsallis diversity	Intercept	2.62(0.11)	32.3	23.9	--	--
	Mean of forest cover	0.02(0.09)	83.9	0.25	0.03	-0.18: 0.24
	Trajectory	-0.22(0.11)	83.4	-2.01	-0.25	-0.49: -0.01
	Mean of FC: trajectory	0.34(0.12)	81.8	2.9	0.35	0.11: 0.59
Tsallis diversity	Intercept	2.52(0.1)	29.7	24.6	--	--
	Mean of forest cover	-0.13(0.09)	83.9	-1.38	-0.15	-0.36: 0.06
	Trajectory	-0.27(0.11)	80.7	-2.5	-0.31	-0.55: -0.07
	Mean of FC: trajectory	0.34(0.1)	80.6	3.41	0.44	0.19: 0.7
Response variable	**Fixed effect**	**Estimate**	**z**	**p**	**beta**	**CI**
Abundance	Intercept	6.07(0.118)	51.3	<0.01	--	--
	Mean of forest cover	0.01(0.008)	1.6	0.11	3.8e-5	-9e-6:8.6e-5
	Trajectory	-0.2(0.01)	-21.0	<0.01	-6.9e-4	-6.7e-4: -5.6-e4
	Mean of FC: trajectory	0.36(0.011)	32.3	<0.01	9.9e-4	9.3e-4:1e-3
Abundance	Intercept	6.01(-0.14)	49.9	<0.01	--	--
	Total of accumulated forest cover (TAFC)	-0.04(0.01)	-5.3	<0.01	-1.3e-4	-1.8e-4: -8.3e-4
	Trajectory	-0.14(0.01)	-16.4	<0.01	-4.3e-4	-4.8e-4: -3.8e-4
	TAFC: Trajectory	0.3(0.011)	29.1	<0.01	8.9e-4	8.3e-4:5.5e-4

SPATIAL CONNECTIVITY AND INSTREAM CONDITIONS MEDIATE THE LEGACY OF LANDSCAPE HISTORY IN RIVERINE COMMUNITIES

*Edineusa Pereira Santos[1], Sílvio F. B. Ferraz[2], Tadeu Siqueira[1]

[1]Institute of Biosciences, São Paulo State University (Unesp), Rio Claro, Brazil

[2]Department of Forest Sciences, Luiz de Queiroz College of Agriculture, University of São Paulo, Brazil

*Corresponding author: edineusa.eco@gmail.com

Abstract

The conversion of natural vegetation for anthropogenic land uses has negatively affected freshwater biodiversity. Previous evidence suggests that modifications in the landscapes surrounding streams affect riverine communities mainly through pathways representing local niche selection. However, biological communities should respond direct and indirectly to a myriad of mechanisms operating at different spatiotemporal scales. Here, we rely on previously described relationships among landscape variables, stream conditions, spatial connectivity and community structure to build a theoretical path model. Then, we analyzed direct and indirect effects of land use and forest cover (LUFC) history, and topographic heterogeneity on riverine communities. Finally, we identify the relevance of pathways either involving niche selection and spatial connectivity to elucidate patterns related to local and regional spatial scales. We find that LUFC history indirectly affected riverine communities by altering instream characteristics, specially by reducing/increasing the amount of leaf litter and phosphorus in streams, mainly at the catchment scale. Alterations in spatial connectivity due to past and recent land uses strongly affected riverine communities via the length of streams uncovered by forests. Our results indicate that sustaining the diversity and abundance of riverine communities requires the maintenance of: (i) continuous forest patches along the riparian zone for long periods, as they maintain the spatial connectivity among communities; and (ii) large forest patches beyond the riparian zone because they support instream conditions. Our analyses provide empirical evidence of the role forest fragments and their spatial arrangement play within catchments, and how the incorporation of spatial connectivity variables is pivotal for freshwater bioassessment.

Key Words

Structural equation modeling, niche selection, connectivity, pathways, landscape legacy

Introduction

Most ecosystems on earth were or have been affected by disturbances related to human activities (SALA et al., 2000; SONG et al., 2018; VITOUSEK et al., 1997). In riverine networks, such as streams and rivers in watersheds, the conversion of natural land cover to intensive land uses (e.g., agriculture, forestry and pasture) interacts with both the terrestrial and aquatic parts of landscapes to structure aquatic communities (ALLAN, 2004). For example, steep slopes strength the effects of land use intensification on aquatic organisms by mediating stream sedimentation in deforested catchments (ALLAN; CASTILLO, 2007). Land use intensification that occurs near the stream has presumably more influence on aquatic communities than those occurring on a distant part of the catchment (KING et al., 2005; STRAYER et al., 2003). Accordingly, many studies have investigated the response of aquatic communities to disturbances occurring (i) in the immediate area surrounding the sampled site (i.e., local scale), (ii) in the area extending beyond and along the stream reach (i.e., riparian scale), and (iii) in the area extending the whole drainage natural boundaries (i.e., catchment scale; ALLAN, 2004; SPONSELLER; BENFIELD; VALETT, 2001). A complete understanding about how riverine communities are assembled and respond to anthropogenic disturbances demands that attributes describing the surrounding landscape be examined simultaneously with those inherent to stream systems (KING et al., 2005; MALONEY; WELLER, 2011). Also, although some studies have investigated the explanatory power of models describing community responses within different spatial scales, few have tried to understand the direct and indirect pathways by which deforestation and land use intensification affect riverine communities (ALLAN, 2004; TOWNSEND; RILEY, 1999).

Increasingly, ecological studies have been using path modelling to address questions that are inherently multi-scale (MALONEY; WELLER, 2011; MUSSEAU et al., 2015). Path models allow the analysis of complex relationships by organizing variables along cause-effect pathways (SHIPLEY, 2016). For example, Dala-Corte et al., (2016) found, through path modelling, that agricultural activities along stream margins led to a decline in fish diversity by decreasing coarse organic matter supply. In this case, the effect of a landscape variable on the biota could only be understood through an indirect pathway and a mediator variable (MALONEY; WELLER, 2011); e.g., agriculture activity in the catchment → organic matter in the stream (mediator variable) → fish diversity. Instream conditions, such as water and substrate characteristics, besides being sensitive to land uses (CASTILLO et al.,

2012; LEAL et al., 2016; LEFEBVRE et al., 2007) and acting in the assembly of local communities (MATTHAEI; PIGGOTT; TOWNSEND, 2010; PIGGOTT et al., 2012), have also been suggested as good mediator variables in path models that include landscape variables (STRAYER et al., 2003; TOWNSEND; RILEY, 1999). Thus, causal relationships should emerge from pathways describing how deforestation at the catchment scale affects communities by modifying instream habitat structure, and from pathways describing how catchment level deforestation affects communities directly (ALLAN; ERICKSON; FAY, 1997).

Besides in-stream and landscape features, spatial connectivity has also been suggested as a major driver of community dynamics in riverine systems (FULLER; DOYLE; STRAYER, 2015; SIQUEIRA; DURÃES; ROQUE, 2014; TONKIN et al., 2018; VALENTE-NETO et al., 2018). The connectivity among streams depends on factors such as discharge frequency and volume, drainage density and the number of confluences (FULLER; DOYLE; STRAYER, 2015; HEINO et al., 2017; TONKIN et al., 2018). Land use intensification can modify such factors and add physical barriers to dispersal via watercourses as the building of dams and roads (FULLER; DOYLE; STRAYER, 2015). Although aquatic organisms tend to disperse mainly through watercourses, some aquatic insects disperse actively as winged adults along stream corridors and overland (SMITH; ALEXANDER; LAMP, 2009; TONKIN et al., 2018). In this sense, forest-to-land use conversion reduces terrestrial permeability to aerial dispersal due to the increase of wings' desiccation and predation risk, and the reduction of stepping-stones and stream corridors (CARLSON et al., 2016; HEINO et al., 2017; PETERSEN et al., 2004; SMITH; ALEXANDER; LAMP, 2009). As dispersal is a process occurring over time – i.e., it cannot be described only as the distance individuals can move in one dispersal event during one generation (SAITO et al., 2015), past disturbance events that altered spatial connectivity and other landscape characteristics may have persistent, long-term impacts on communities that propagate over time (KUUSSAARI et al., 2009).

Biological communities show delayed responses to landscape history (KUUSSAARI et al., 2009). While Harding et al. (1998) showed that present-day stream diversity was better predicted by watershed land use decades before, Brejão et al. (2018) showed that fish in Amazonian streams responded to deforestation events sooner after they take place. As stream communities respond indirectly to landscape features, it is expected that mediator variables in path models also show delayed responses (HAMILTON, 2012; MALONEY; WELLER, 2011). In a study with lakes, for example, water chemical conditions showed legacies of past land uses in which the more apparent ones were supported by the longest pathways (MARTIN et al., 2017). Reduced spatial connectivity can also delay

responses of some communities after disturbances (SHACKELFORD et al., 2016). Overall, the increase in the amount and availability of remotely sensed data have allowed researchers to compose landscape history and use broader spatial variables such as connectivity to advance the understanding of current biodiversity patterns (PETERSON et al., 2011; TURNER; GARDNER, 2015).

Here, we gathered variables related to landscape, stream conditions, connectivity and community structure (functional and taxonomic diversity) and, then, inventoried relationships previously described among them to build a path model in order to respond the following questions: What are the direct and indirect effects of land use and forest cover (LUFC) history and topographic heterogeneity on the structure of tropical stream communities? Does landscape history change affect stream communities via spatial connectivity as strongly as via local niche selection? Do the pathways by which land use and forest cover affect stream insect communities diverge between riparian and catchment scales?

Methods

Land use and forest cover (LUFC) history

We compiled landscape data by analyzing maps of land use and land cover from the Corumbataí River Basin, São Paulo State, southeastern Brazil, from 1962, 1972, 1978, 2003 and 2011. The Corumbataí River Basin comprises an area of 1,700 Km^2, and its natural vegetation cover was originally dominated by semi-deciduous forest and with patches of Savanna (RODRIGUES, 1999). Initial deforestation in the basin began in the early 18th century with subsistence farming followed by an expansion of pastureland and cropland, mainly sugarcane, which modified the natural vegetation cover to small fragments (FERRAZ et al., 2014; VICTOR et al., 2005). More recently, the amount of native forest cover has been increasing due to natural vegetation recovery in abandoned agricultural lands (FERRAZ et al., 2014; MOLIN et al., 2017). The natural forests that covered 12% of the basin area in 2000 (VALENTE; VETTORAZZI, 2003) increased to 32% in 2011, as mapped in the present study. Meanwhile, the dominant land use, pasture, has reduced from 44% in 2000 to 30% in 2011. The second most dominant land use, sugarcane, increased from 26% to 28% in the same period. Land use and land cover were mapped from panchromatic aerial photographs in 1962, 1972 and 1978, and from LandSat TM and ETM scenes in 2003 and 2011 (30 m of spatial resolution) provided by the Brazilian Institute for Space Research (INPE). LandSat scenes were georeferenced based on topographic maps at a 1:10,000 scale, and digital images from other years were spatially registered to the 2011 scene, which was used as reference. Among the classes of landscape features, we chose the predominant ones

over the years: native forest, pasture and sugar cane. The landscape data also included altitude (meters) and slope (percentage) maps of the Corumbataí River Basin obtained from Digital Elevation Model (DEM), which was elaborated with SRTM (Shuttle Radar Topography Mission, resolution of 30 m).

Within the Corumbataí River Basin, we selected watersheds that were delineated in a SWAT model (Soil and Water Assessment Tool), based on a Digital Elevation Model (DEM), which was obtained from SRTM (Shuttle Radar Topography Mission, resolution of 30 m). We followed criteria that allowed the delineation of 2nd and 3rd order watersheds, with an approximate mean area of 400 hectares. Then, we selected the most upstream watersheds in order to avoid the influence of land use from surrounding ones. We identified the tributaries of each watershed and delineated manually their drainage area using 1:10,000 scale topographic maps. The drainage areas will be referred as catchments in this study and used as the largest spatial scale. For the riparian scale, we created buffers for the stream network upstream from the sampled sites and with a width of 30 m on each side of the watercourse (Figure 3.1). This strip width represents the permanent protection area for all ≤10 m wide streams according to the current Brazil's Native Vegetation Protection Law (Law Number 12,651/2012). We calculated the coefficient of variation of the altitude and the mean of the slope within each catchment to composite a variable representing topographic heterogeneity. The proportion of land uses (pasture and sugar cane) and forest cover was calculated within each catchment and riparian buffer. We also considered the stream reach where aquatic insects were sampled as the smallest scale. Local forest canopy cover was assessed within the stream reach and was represented by the mean of visually estimated shading (%) in three sites along the sampled stream reach (ca. 7 m).

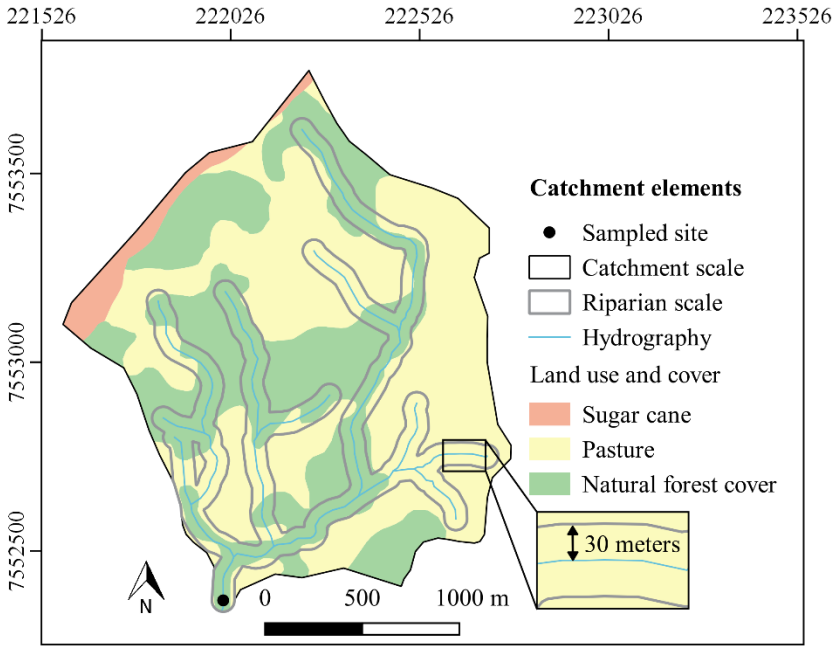


Figure 3.1 – Spatial scales (catchment and riparian) at which land uses and forest cover were assessed. The catchment scale comprised the entire area upstream the sampled site. The riparian scale comprised an upstream buffer from the sample site (30-m width at both stream sides).

Terrestrial and aquatic connectivity

Connectivity was estimated by considering the dispersal of aquatic insects through three routes: watercourses, stream corridors and overland. To represent watercourse dispersal, we considered factors that naturally affect the drift of immature aquatic insects and an anthropogenic barrier: the total length (meters) of the drainage upstream the sampled site and the number of dams, respectively (Table 1). To represent dispersal through stream corridors, we considered the length of the stream downstream the sampled site to the outlet of its catchment (Table 1). Given that riparian forests support such corridors, we also calculated the proportion of that length that was uncovered by forests as a measure of disconnectedness (Table 1). To represent factors that affect overland dispersal, we included variables describing landscape permeability to insect movement according to natural and anthropogenic factors. Natural resistance to dispersal was examined considering the dispersal of insects from the surrounding area to the sampled site. We calculated mean cost distance at a radius of 300 m around the sampled site considering the slope map as a resistance surface. In this case, a cost distance surface was generated with the sum of the resistance of each pixel – i.e., pixel slope value, to insect movement among watercourses. Then, we calculated the mean cost surface values within 300 m around the sampled site (Table 1). This radius value was based on a meta-analysis in aquatic insect

dispersal and represents half of the maximum distance from the channel in which such insects were captured (MUEHLBAUER et al., 2014). Landscape permeability also was calculated considering the classes of land uses and forest cover. We attributed weights to such classes to indicate their resistance to insect movement considering the risk of desiccation of their wings, predation and the provision of probable stepping stones (CARLSON et al., 2016; DIDHAM et al., 2012; SMITH; ALEXANDER; LAMP, 2009). Based on the differentiation among the classes for these criteria, forest cover, reforestation, sugar cane, pasture and urban area received the respective weights: 1, 2, 3, 5 and 8. The resistance surface resulting from land use classes and forest cover was used to calculate the mean cost distance following the same steps that we used with slope. We estimated each of the described variables separately for 1962, 1972, 2003 and 2011. All connectivity measurements were estimated using ArcGis 9.3 (Environmental System Research Inst., Redlands, CA, USA).

Field sampling

We surveyed 101 streams distributed among 26 watersheds, in which we collected immature aquatic insects predominantly in the dry period between May and August 2015. We used a kick-net, with 1 m^2 area and 250 μm mesh, to collect a generous sample in each stream by gently kicking the stony substrate of four riffles for a total of two minutes (30 seconds each). Samples were preserved in 80% ethanol and packed for examination in the laboratory. The identification of the collected specimens to species or morphotype was based on taxonomic keys and original descriptions (DOMÍNGUEZ et al., 2006; DOMÍNGUEZ; FERNÁNDEZ, 2009; HECKMAN, 2006). We also measured the size of the three largest specimens of each species and used its mean as a measure of body size (Table S3). Other traits, such as body shape, shape and number of gills and wing length, were obtained from original descriptions, while rheophily and feeding strategy were gathered from articles on functional ecology and reviews (CUMMINS; MERRITT; ANDRADE, 2005; POFF et al., 2006; TOMANOVA; GOITIA; HELEŠIC, 2006).

We included three variables describing insect communities in our path models (see details below): community structure, and taxonomic and functional diversity. We considered total local abundance as a descriptor of community structure. For taxonomic diversity, we estimated rarefied richness using 100 individuals as the minimum sample size and also calculated diversity indices based on Tsallis entropy. The family of indices derived from Tsallis entropy minimizes biases caused by sampling size given that each community receives a specific weighting of the relative abundance of species by the lowest possible evenness of each community (MENDES et al., 2008). Furthermore,

such indices may mimic traditionally used diversity indices, such as Simpson (D, dominance), Evenness (E) and Shannon-Wiener (H). Tsallis dominance, evenness and diversity index were calculated with the *eventstar* function of the *vegan* package (OKSANEN et al., 2018) in R (R Core Team, 2018).

Functional diversity indices were based on 23 morphological and behavioral traits (Table S3, S4 and S5). We gathered traits related to environmental adaptation/ecological niche and dispersal capacity, and calculated functional richness, dispersion, evenness and divergence indices with functions in the package FD (LALIBERTÉ; LEGENDRE; SHIPLEY, 2014). We grouped descriptors of taxonomic and functional diversity to form sets with high redundancy within and, consequently, low redundancy between them. For example, functional evenness and functional divergence consider different dimensions of a community trait matrix (MOUCHET et al., 2010). Specifically, Functional Divergence (Fdiv) assesses the species deviance from the mean distance to the center of gravity weighted by relative abundance, whereas Functional Evenness assesses the sum of branch lengths of the minimum spanning tree that links all the points contained in a trait-dimensional space, which is also weighted by relative abundance (VILLÉGER et al., 2008).

In each stream reach, we also obtained nine measurements of turbidity, temperature, pH, conductivity, dissolved oxygen and superficial velocity. Habitat physical heterogeneity was estimated by measuring the proportion of inorganic substrates (boulder, pebbles, gravel and sand) and by measuring channel width and water-column depth in each of the four riffles we sampled within each stream reach. We visually estimated the proportion of small litter patches (organic substrate) intercepted by rocks in the stream riffles in relation to inorganic substrate.

Path models

Model description

Based on previous empirical evidence (Table 1), we built a general conceptual model, *a priori* specifying the direct and indirect effects of LUFC history and topographic heterogeneity on spatial connectivity, instream habitat characteristics, taxonomic and functional diversity, and local abundance (Figure 3.2, Table 2).

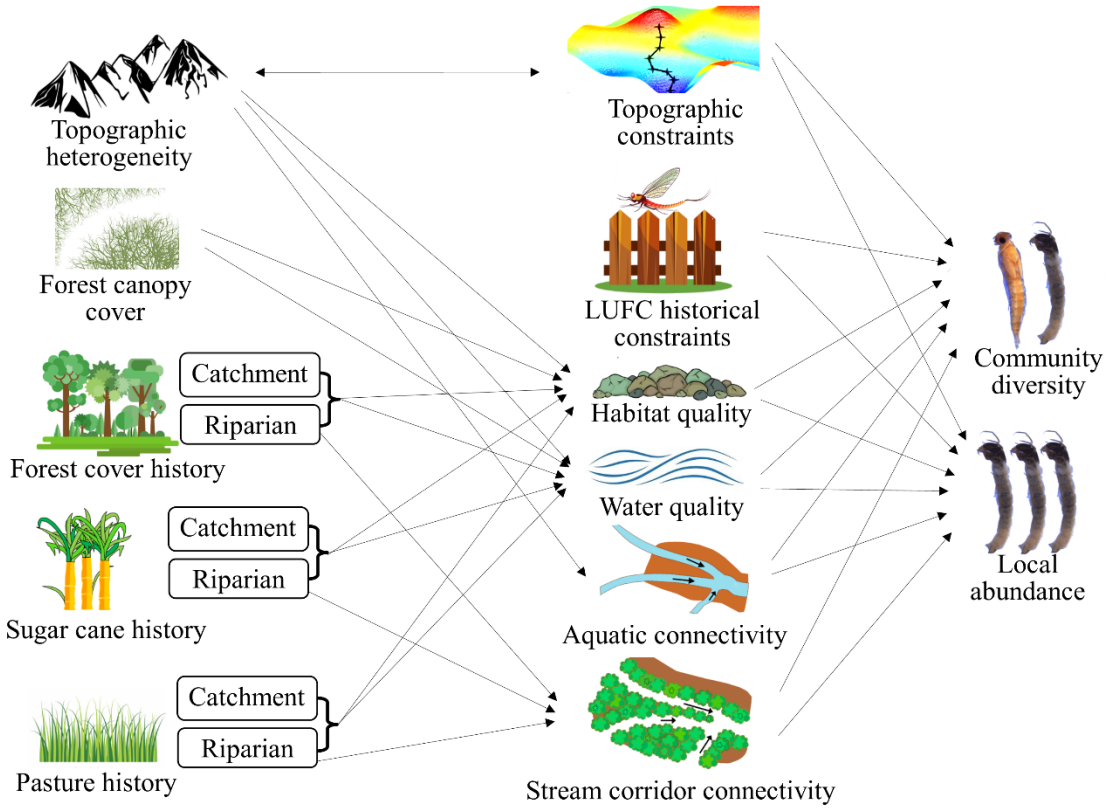


Figure 3.2 – General theoretical model relating landscape characteristics and spatial scales to stream conditions, habitat connectivity, and local community structure. LUFC = Land use and forest cover. Local forest canopy cover and topographic constraints are single variables; all others are latent variables that include some observed indicators. Variables with term 'history' have indicators varying along time (1962, 1972, 1978, 2003, 2011).

Table 1. Description of the latent variables that underpin processes (dispersal and niche selection) affecting directly aquatic insects in freshwater systems and their indicators.

Latent variable	Indicator	Unit	Specification	Reasoning	Reference
Aquatic connectivity	Dams	count	Number of dams and roads upstream the sampled site	Physical barriers to drift	JANUCHOWSKI-HARTLEY et al., 2013; SINGER; GANGLOFF, 2011
	Length of drainage upstream	meter	Upstream each sampled habitat	Maintenance of stream flow to the individual drift.	IRWIN; WHITELEY, 2010; JAMES; DEWSON; DEATH, 2008
Stream corridor connectivity	Length of drainage downstream	meter	Distance between the river outlet and sampled site upstream following the watercourses	Distance along stream corridor for aerial dispersal.	DIDHAM et al., 2012; SMITH; ALEXANDER; LAMP, 2009
	Uncovered stream length	proportion	Proportion of length of riparian gap along the network downstream each sampled site	Continuity of the riparian corridor affects upstream dispersal.	CHAPUT-BARDY et al., 2008; LANDEIRO et al., 2012
No latent variable	Topographic constraints	score	Mean cost of movement of individuals coming from surroundings, considering slope	Slope affects route and costs to aerial dispersal.	CARLSON et al., 2016; HEINO et al., 2017

Continua

Latent variable	Indicator	Unit	Specification	Reasoning	Reference
LUFC historical constraints	Mean cost distance in 1962, 1972, 1978, 2003, 2011	score	Mean cost of movement of individuals coming from surroundings, considering land use	Resistance to individual movement over a given surface.	HEINO et al., 2017; KÄRNÄ et al., 2015
Habitat quality	Depth and width. Sand, gravel, pebble, cobble, boulder, leaf litter	cm proportion	Mean depth and width measured in three sites along stream reach. Mean of proportion of each substrate inorganic and organic component measured in three sites along stream reach	Depth and width reflect habitat size. Substrate components reflect habitat complexity. Leaf litter is also a food source to aquatic insects.	MATTHAEI; PIGGOTT; TOWNSEND, 2010; PALMER; MENNINGER; BERNHARDT, 2010; PIGGOTT et al., 2012; WAGENHOFF; TOWNSEND; MATTHAEI, 2012
Water quality	Temperature, turbidity, conductivity, dissolved oxygen, salinity, total phosphorus, total nitrogen, acidity		Degrees Celsius, NTU, mS/cm, mg/L, percentage, µg/L, mg/L, pH	Low oxygen and high temperature increase stress. Increased nutrient concentrations leads to high primary productivity and herbivory.	CHASE, 2010; PIGGOTT et al., 2012

Table 2. Description of exogenous and endogenous latent variables and their indicators.

Latent variable	Indicator	Unit	Specification	Reasoning	Reference
Forest cover history, Pasture history and Sugar cane history	Each feature class in 1962, 1972, 1978, 2003, 2011	Proportion (%)	Proportion of each feature class (forest, pasture and sugar cane) within each catchment in 1962, 1972, 1978, 2003 and 2011 was used to form the history of that class	The conversion of forest cover to land uses often reduces coarse organic material delivery and increase organic nutrient input and siltation in streams modifying local filters	KAUFMANN; LARSEN; FAUSTINI, 2009; NEILL et al., 2009; PAULA et al., 2013
No latent variable	Forest canopy cover	Proportion (%)	Proportion of forest canopy cover upper sampled stream reach	Forest canopy reduction increases temperature and light input leading to an increased primary productivity	BURRELL et al., 2014; DOHET et al., 2015
Topographic heterogeneity	Altitude variation, slope mean	Score, percentage	Coefficient of variation, mean of slope	Valley topography relates to physical structure of stream habitats. Highlands and steep slope areas contribute with low temperature and high oxygenation of water	JACOBSEN; SCHULTZ; ENCALADA, 1997; MONTGOMERY ; MACDONALD, 2002
Functional diversity	Functional richness, dispersion, evenness and divergence	score	Functional indices that vary in the weights given the number of traits and trait frequency across species and individuals and that consider the variation between types and values of traits.	Functional approach in modified landscape is supported by the natural selection of species traits according to resource use, sensitivity to physicochemical deterioration and persistence to disturbances.	DOLÉDEC; STATZNER; BOURNARD, 1999; SAITO; SIQUEIRA; FONSECA-GESSNER, 2015

Continua

Latent variable	Indicator	Unit	Specification	Reasoning	Reference
Taxonomic diversity	Rarefied richness, Tsallis diversity index, Tsallis dominance, Tsallis evenness	Count, score	Number of species according to sample size.	As with functional traits, the community descriptors based on species number and abundance provide consistent responses across ecoregions even when taxonomic composition changes.	MAGURRAN; BRIAN, 2011; MENDES et al., 2008

In this model, we considered forest cover, pasture and sugar cane history observed in the catchment and riparian scales as explanatory (or exogenous) latent variables. Each latent variable summarizes five observed variables, which represent the proportion of forest cover, pasture and sugar cane in 1962, 1972, 1978, 2003 and 2011. For the local scale, we assessed only forest canopy cover, which remained as an isolated explanatory variable. Topographic heterogeneity also represented an exogenous latent variable in which the coefficient of variation of altitude and the mean of slope were the indicators. Instream habitat characteristics were compiled as two latent variables: (i) habitat quality, which summarized inorganic and organic substrate composition, and width and depth of the stream reach; and (ii) water quality, which summarized the chemical and physical characteristics of water. The indicators of connectivity by watercourses, stream corridors, and overland were represented by the following latent variables: aquatic connectivity, stream corridor connectivity, and LUFC historical constraints. Overland connectivity, which assessed topographic constraints, was used as a single variable, i.e., it was not represented by a latent variable and their indicators. All latent variables related to the local characteristics of the streams and some variables describing connectivity (aquatic and stream corridor connectivity) represented mediator (intermediate) variables, i.e., they explain community variables as well as are predicted by landscape characteristics. The descriptors of community diversity were summarized as two endogenous (response) latent variables: functional diversity and taxonomic diversity. Local abundance remained as an isolated response variable.

Model analysis

The relationships predicted in the general conceptual model were examined with a structural equation modeling approach – SEM (BOOMSMA, 2000; GRACE, 2006). SEM considers the covariance structure among the variables to fit a path model using the maximum likelihood (ML) estimation (BOOMSMA, 2000; the set of covariances is available in S4). We used the package *lavaan* to carry out the analysis (ROSSEEL, 2012). This package includes functions that allow the expected model paths to be informed with one or many multiple regressions and, in addition, adds a z-test with p-value for coefficient estimates. We used standardized coefficients that relate each pair of variables as a direct effect size and multiplied the standardized coefficients obtained along a path to find the indirect effects of exogenous variables on the endogenous ones via mediator variables (ROSSEEL, 2012). Latent variables were built using confirmatory factor analysis, as a step of path model itself, and among their observed indicators we kept those whose estimates had positive residual variances and correlation not exceeding 1. We used the package MVN to exam skewness and normality for

multivariate data (KORKMAZ; GOKSULUK; ZARARSIZ, 2014) and applied the correction of Satorra-Bentler to the ML fit, which is recommended for small samples (SATORRA; BENTLER, 1994). Considering a probable spatial autocorrelation due to the spatial proximity between streams belonging to same watershed, we applied a correction of sample sizes and standard errors of the endogenous variables of the fitted model using the function *lavSpatialCorrect*. This correction employs Moran's *I* statistics using geographic coordinates of the sampled sites and returns new adjusted standard errors and test statistics of the coefficient estimates of the model. The goodness-of-fit of the global model was verified with a chi-square test that assesses the magnitude of discrepancy between the observed data and the hypothesized model (HU; BENTLER, 1999). A good model should present a low value of chi-square and a P value higher than 0.05.

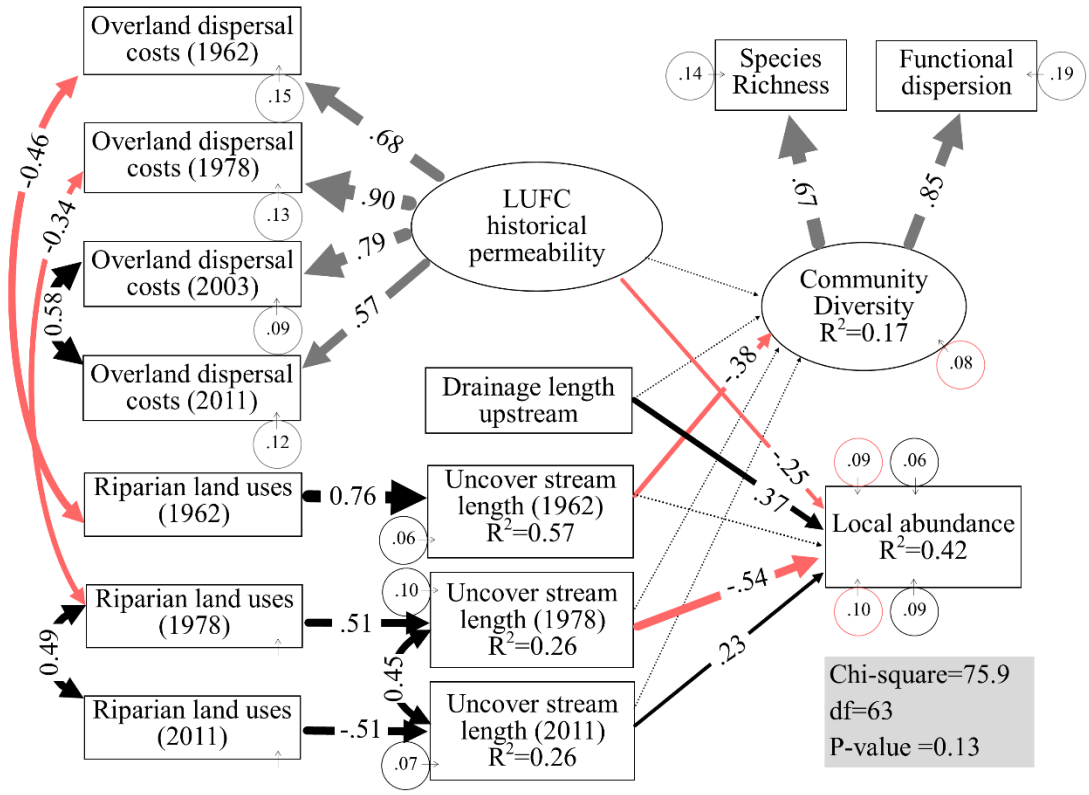
Results

Path models

Our final models showed fewer latent variables than predicted in the general theoretical model (Table 1 and 2 vs. Figure 3.3). Variables representing local niche selection (habitat and water quality), connectivity (aquatic connectivity) and others representing landscape characteristics (LUFC history) were not good indicators of their respective latent variables (P $|z| > 0.05$).Thus, we re-specified the previous model taking these variables individually, i.e., removing only latent variables, in order to confirm their relevance as direct or indirect predictors of community structure and diversity. We kept forest cover history (catchment scale) and LUFC historical constraints as latent variables and with almost all indicators previously included. In addition, we summarized the indicators of functional and taxonomic diversity into the latent variable 'community diversity' due to the covariance between them (Figura S6), and kept species richness and functional richness as indicators because they showed significant variance (P $|z| >0.05$, Figure 3.3).

Also, we observed no overlap between variables and paths involving connectivity and instream characteristics in the global model (no explanatory variable shared by models, Figure 3.3). Thus, we reorganized the global model in two sub-models: an instream habitat path model (IHPM) and a connectivity path model (CPM). We found support for the two models ($P > 0.05$, Figure 3). The IHPM explained 33% of the variation in community diversity and 28% of the variation in local abundance. The CPM explained 17% of the variation in community diversity and 42% of the variation in local abundance.

a) Connectivity path model (CPM)



b) Instream habitat path model (IHPM)

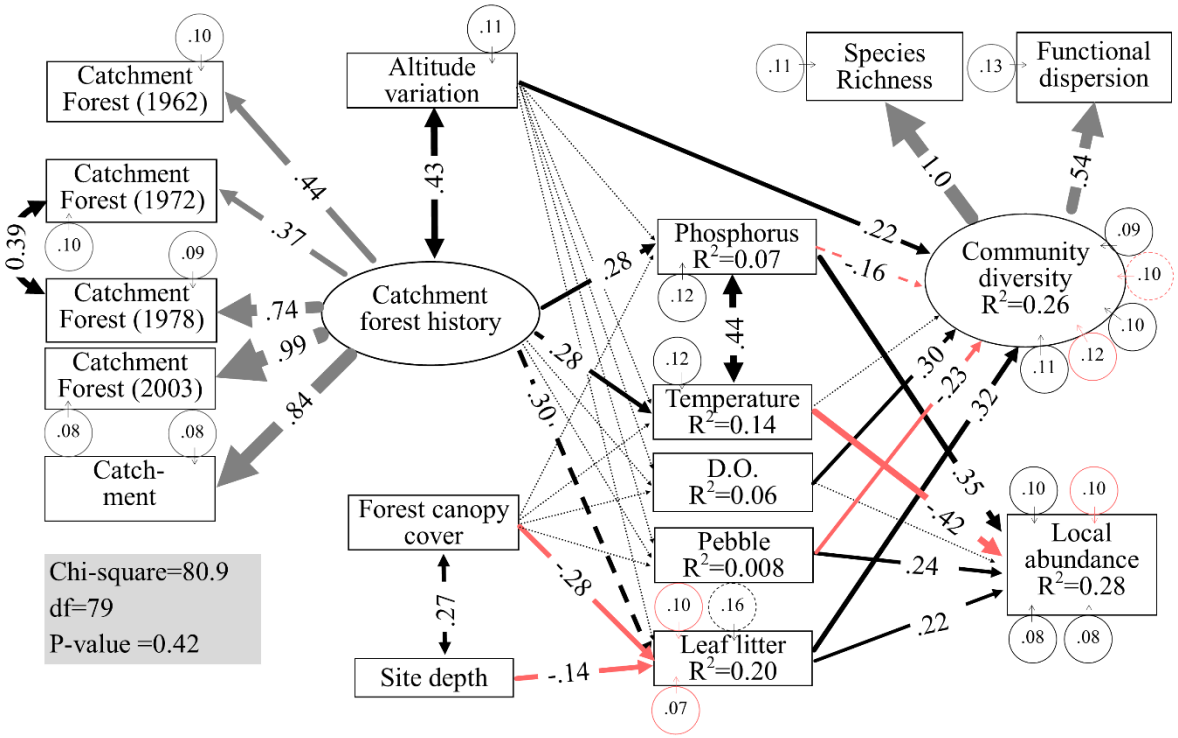


Figure 3.3 – Structural equation models showing the pathways by which landscape modification affects local community diversity. Arrow thickness is proportional to the estimated standardized effect size (single headed) or correlation to other variables (double headed), and their values are indicated over the arrows. Cycles contain the standard errors associated to all significant estimates, except correlation. Red arrows indicate negative values. Dashed arrows indicate marginally significant effects. Dotted arrows indicate non-significant effects and gray arrows show indicators of the reflective latent variables. Only significant correlations ($P < 0.05$) are shown for simplicity. R^2 indicates the proportion of variation of endogenous factor (from the rightmost) explained by exogenous factors (from the leftmost), except for latent variables represented by the ellipse.

Direct and indirect effect of landscape history

We found more indirect (IE) than direct effects (DE) in both models. In the IHPM, we found a positive direct effect of altitude variation on community diversity (DE = 0.22). Altitude variation also showed a strong positive correlation with catchment forest history. All other exogenous variables affected community diversity and local abundance indirectly. Forest cover history in the catchment had a positive effect on community diversity and on local abundance by increasing the amount of litter in streams (IE = 0.1 and IE = 0.06), and a negative effect on community diversity (IE = -0.04) and a positive effect on local abundance by increasing total phosphorus concentration (IE = 0.1). We also found a negative effect of forest cover history on local abundance by increasing water temperature (IE = -0.12). Total phosphorus and temperature showed a strong positive correlation.

Local forest canopy cover did not affect water temperature, but had a negative effect on accumulated leaf litter in the stream bed (Figure 3.3). However, local forest canopy cover was correlated with stream depth, which in turn also had a negative effect on accumulated leaf litter. The proportion of pebble and the amount of dissolved oxygen had a positive effect on local abundance and community diversity, respectively, but neither acted as mediator variables of any of the tested exogenous variables. The amount of accumulated leaf litter was the variable with the most important role as a meditator of landscape changes on community structure given the number of links in which it was involved (Figure 3.3).

In the CPM, land use and forest cover historical constraints remained as latent variables including the cost distances of all years, except 1972, and had a significant negative effect on local abundance (Figure 3.3). Considering connectivity by stream corridors, we found that the downstream land uses of 1962 had a negative effect on community diversity by increasing the length of streams uncovered by forest (IE = 0.29), and the downstream land uses of 1978 had a negative effect on local abundance by increasing the length of streams uncovered by forest (IE = 0.28). The length of streams uncovered by forest in 1978 showed the strongest effect of a mediator variable on community diversity

(Figure 3.3). On the other hand, the more recent land uses (2011) had a weak positive effect on local abundance (IE = 0.12). Although connectivity by watercourses did not remain as a latent variable, nor their indicators acted as mediators of any tested exogenous variables, the length of upstream drainage showed a positive effect on local abundance.

Relevance of connectivity and local variables to the path models

Together, variables representing spatial connectivity and those representing local niche selection had a similar strong effect on community structure (R^2=0.59). Pathways involving stream local variables and connectivity included the same number of variables (five), but the former comprised more links (eight versus five). Most connectivity variables explained local abundance (four links). In addition, the mean regression coefficients by link was higher for connectivity variables related to both community diversity (mean=0.38) and local abundance (mean=0.35) than for instream variables (means of 0.26 and 0.31, respectively).

LUFC history had a greater effect on community structure via connectivity variables (sum of IE and DE = 0.94) than via stream variables (sum of IE=0.32). Their effects involved only three of the five stream variables, and five links between these and community variables.

Community responses at different scales

Overall, we found predominately indirect relationships between landscape variables – at all studied scales, even those nearest to stream sampled site (forest canopy cover) – and community structure (Figure 3.3). Instream habitat characteristics were explained by variables at catchment and local scales, but not at the riparian scale (Figure 3.3). In contrast, connectivity variables with a strong effect on community variables were those taken predominantly at the riparian scale and long back in time (four links, Figure 3.3).

Discussion

Due to the complexity of the processes structuring stream communities (ALLAN, 2004; LEPS et al., 2015), empirical investigations have increasingly sought to understand the direct and indirect effects of such processes on communities (DALA-CORTE et al., 2016; LEITÃO et al., 2017; MALONEY; WELLER, 2011; VILLENEUVE et al., 2018). Here, we identify the effects of land use and forest cover change along decades, and topographic heterogeneity on stream communities by disentangling how explanatory variables related to each other and with response variables across

different spatial scales. Path models revealed that recent and past conditions of the surrounding landscape affect current riverine communities by altering instream characteristics and by disrupting spatial connectivity among local patches.

Our expectations that forest cover at riparian scale would explain variation in communities by controlling instream conditions and, therefore, would mitigate land use effects through these pathways were not confirmed. On the contrary, our results agree with idea that land uses that extent to large proportions and/or involve intense management can aggravate their effects on streams at a level that overwhelms the mitigating effects of riparian forests (LEPS et al., 2015; WAHL; NEILS; HOOPER, 2013). Extensive land uses were common in the catchments we studied. The proportion of forest converted to agricultural activities reached 100% in 64% of the catchments. A previous study carried out in this region (Corumbataí River Basin) showed that even with the increase of forest cover offsetting the increase of sugar cane (which increased from 11% to 33% along the studied period) across catchments, the high concentration of nitrate in streams indicated that riparian forests were not wide enough to prevent surface runoff from cultivated fields (MORI et al., 2015). Also, it should be emphasized that the riparian zone we investigated is very narrow compared to those from other studies (around 100 meters; e.g., SWEENEY; NEWBOLD, 2014, but represents the current Brazil's Native Vegetation Protection Law (Law Number 12,651/2012), which states that landowners in all biomes must permanently protect a minimum of 30-m wide riparian zones on both sides of streams that are smaller than 10-m wide. Our study, therefore, adds evidence that only preserving vegetation in a narrow riparian zone is not enough to protect instream conditions in catchments dominated by agriculture.

Our path model indicated that maintaining large long-lasting forest patches beyond the riparian zone increases leaf litter supply to the streams and, consequently, the diversity and the abundance of aquatic insects. Often, over 90% of the organic matter in small streams comes from terrestrial forested areas (RICHARDSON; BILBY; BONDAR, 2005), which usually is of better quality as food resources to aquatic insects (MIGLIORINI; SRIVASTAVA; ROMERO, 2018) compared to the input from agricultural lands (FERREIRA et al., 2016; HART; HIBBS; PERAKIS, 2013). Likewise, empirical studies have confirmed that the decline of coarse particulate organic matter due to deforestation and agricultural activities has led to a decline in fish diversity (DALA-CORTE et al., 2016; LEITÃO et al., 2017). An experiment examining leaf litter colonization along reaches downstream pasture lands demonstrated a negative effect of such land use on the local abundance of shredder insects (ENCALADA et al., 2010). Our study advances the understanding of such relationships by finding a rare evidence that leaf litter supply also affects stream insect diversity. Our analyses support the role

forest canopy cover plays on leaf litter input, but in an opposite direction to that we expected. This is probably because such a role is involved in complex relationships including stream depth. Considering other stream conditions, we also found that maintaining large forest patches for a long period in the catchments increases local abundance via phosphorus supply. Although the major input of phosphorus to streams is from anthropogenic activities, natural components in the surrounding area may also contribute to small phosphorus loads, including natural vegetation cover (MAINSTONE; PARR, 2002). Phosphorus may increase the abundance of aquatic insects in streams because it supports primary production and, in turn, herbivory in this system whose dissolved nutrient concentrations are naturally low (MAINSTONE; PARR, 2002).

Contrary to previous path models that were restricted to examining environmental factors (but see LEITÃO et al., 2017), we show that the variation in spatial connectivity due to natural characteristics and modifications of landscapes also structures stream communities. Among the results with direct pathways, for example, we found a positive effect of upstream drainage length on local abundance. This suggests that the position of a community within the drainage network affects its local structure (MILESI; MELO, 2014). Although another study has found a positive relationship between invertebrate drift and upstream length (MARCH et al., 1998), little progress has been made in relation to underlying mechanisms that influence the displacement of those organisms. Greater stream extension upstream a certain focal site should indicate the existence of many tributaries and, therefore, indicates the maintenance of a steady flow to support dispersal through drift. Another direct pathway included reduced local abundance due to LUFC historical constraints on insect dispersal coming from the surroundings. This finding suggests that the conversion of natural vegetation lands to agricultural activities decreases local abundance by limiting the overland movement of aquatic insects with a winged adult stage, as dispersal costs should be higher along intense land uses. This emerges as a new avenue to applying functional connectivity to overland dispersal by the use of (i) a buffer with a maximum distance around focal sites, instead of assuming arbitrary origins or destinations along streams (HEINO et al., 2017; TONKIN et al., 2018) and (ii) weights to land use classes and forest cover considering their permeability to aquatic insects with a flying adult stage (SMITH; ALEXANDER; LAMP, 2009).

Indirect pathways using connectivity variables also represent a novel finding of our study. These pathways clarified new mechanisms, apart from those occurring in streams, by which riparian deforestation history affect local communities and illustrate delayed responses by these communities. The strongest indirect effect shows a decrease in local abundance due to the increased land uses of

1978 at within riparian areas, which in turn lead to an increase in the length of streams uncovered by forests. Considering the scarcity of empirical evidence supporting the effects of riparian deforestation on community structure via spatial connectivity (but see, DOWNES et al., 2017; RAWI et al., 2013), our findings are paramount to confirm such expectations. The use of uncovered stream length as a proxy for spatial connectivity provides a mean to establish a causal link between riparian forest changes and dispersal of winged stream insects, as it is related to processes that can limit the movement of individuals, such as: (i) wing desiccation (CARLSON et al., 2016), (ii) females being attracted by other reflecting surfaces instead of the stream (SMITH; ALEXANDER; LAMP, 2009), and (iii) individuals being carried by wind currents away from the upstream route (HEINO et al., 2017; PETERSEN et al., 2004). Exceptionally, a positive association between the fragmentation of stream corridors and recent riparian land use with local abundance could result from a dominance effect of species with high dispersal abilities. For example, larvae of the caddisfly genus *Smicridea* were the most abundant among all genera, with a total of 6,852 individuals; a number thirteenfold higher than the mean abundance per taxon. Caddisfly adults are known to be able to fly long distances even through overland dispersal (MUEHLBAUER et al., 2014). This might also be related to land uses of 1962 being negatively related to community diversity, as it might take longer for disturbances to reduce species richness through changes in abundance (LIRA et al., 2012). This finding also indicates that some effects of stream corridor fragmentation on aquatic communities might only be recognized while considering time lags.

Our findings confirm that variation in local stream structure is a major driver of local community structure. However, we must emphasize that leaf litter was supported by a set of forest patches maintained over time. Therefore, landscape history needs to be also considered to understand the support of local characteristics to communities. Finally, we must also highlight that habitat connectivity history was as important as environmental filtering for the dynamics of stream communities. We suggest that the role of habitat connectivity in riverine systems can be investigated by measuring simple variables, such as the length of stream uncovered by riparian forest, that can be incorporated in future studies about community assembly as well as in freshwater bioassessment.

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Supplementary material

S3- Mayfly traits from Corumbataí River Basin, São Paulo. Collector, shredder, scrapper and filterer encompass the feeding habit of mayflies using a fuzzy code where we provide an affinity (between 0 and 3) of each species for each trait level. The number of gills is a discrete trait. The larvae size is a continuous trait.

	Collector	Shredder	Scraper	Filterer	Predator	Larvae size	Gill number
A. longetron	3	1	2	0	0	7.1	12
A. alphus	3	1	2	0	0	5.6	12
Baetodes sp.1	3	0	3	0	0	4.1	10
Baetodes sp.2	3	0	3	0	0	3.3	10
Caenis chamie	3	1	1	0	0	5.5	8
Caenis pflugfelderi	3	1	1	0	0	5.3	8
Callibaetis sellacki	3	1	2	1	0	7.8	28
Cloeodes maracatu	2	0	1	0	0	5.1	14
Farrodes sp.	2	1	1	1	0	6.3	28
Paracloeodes sp.	2	0	3	1	0	4.1	14
Traverhyphes edmundisi	3	1	2	0	0	5.0	28
Tricorythopsis sp.	3	1	3	0	0	2.2	32
Zelusia sp.	3	0	2	1	0	4.0	12
Thraulodes sp.	0	3	0	1	0	8.5	28
Hylister sp.	1	0	2	3	0	11.0	24
Leptohyphes sp.	3	1	3	0	0	6.1	42
Hagenulopsis sp.	2	1	1	1	0	6.3	28
Waltzoyphius sp.	2	0	3	1	0	3.4	14
Miroculis sp.	2	1	1	1	0	5.0	28
Ulmeritoides sp.	0	3	1	1	0	10.0	28
Apobaetis sp.	3	1	2	1	0	6.9	14
Tricorythodes sp.	3	0	1	1	0	5.2	28
Anacroneuria sp.1	1	1	0	0	3	11.6	15
Anacroneuria sp.2	1	1	0	0	3	13.6	15
Anacroneuria sp.3	1	1	0	0	3	18.7	15
Anacroneuria sp.4	1	1	0	0	3	11.3	15
Gripopteryx sp.1	1	3	0	0	0	9.0	51
Gripopteryx sp.2	1	3	0	0	0	9.0	51
Tupiperla sp.	1	3	0	0	0	6.4	51
Kempnya sp.1	0	0	0	0	3	14.6	23
Kempnya sp.2	0	0	0	0	3	11.9	23
Contulma sp.	0	0	3	0	0	3.6	0
Xiphocentron sp.	3	0	0	0	0	6.0	0
Itauara sp.	3	0	3	0	0	1.9	0
Atopsyche sp.	0	1	0	0	3	11.8	0
Leptonema sp.	0	1	0	3	1	21.3	44

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	Collector	Shredder	Scraper	Filterer	Predator	Larvae size	Gill number
Alisotrichia sp.	0	0	3	0	3	9.1	0
Blepharopus sp.	2	0	0	2	0	13.0	68
Cernotina sp.	0	1	0	0	3	13.8	0
Wormaldia sp.	0	1	0	3	0	15.5	5
Chimarra sp.1	0	1	0	3	0	16.5	5
Chimarra sp.2	0	1	0	3	0	14.5	5
Phylloicus sp.	1	3	0	0	0	16.6	42
Smicridea sp.1	0	1	0	3	1	8.0	50
Smicridea sp.2	0	1	0	3	1	8.9	50
Smicridea sp.3	0	1	0	3	1	6.0	50
Helicopsyche sp.	0	0	3	2	0	7.1	0
Polyplectropus sp.1	0	0	0	0	3	10.6	0
Metricia sp.	3	0	2	0	0	2.2	0
Neotrichia sp.1	1	1	3	0	0	1.8	0
Hydroptila sp.	2	0	3	0	0	4.0	0
Neotrichia sp.2	1	1	3	0	0	2.1	0
Marilia sp.1	3	1	3	0	1	3.7	52
Marilia sp.2	3	1	3	0	1	2.3	32
Marilia sp.3	3	1	3	0	1	8.3	32
Oecetis sp.	0	0	0	0	3	3.6	0
Triplectides sp.	2	3	0	0	0	17.9	36
Austrotinodes sp.	3	0	0	0	0	9.9	0
Archeogomphus sp.1	0	0	0	0	3	5.6	0
Brechmorhoga sp.	0	0	0	0	3	10.0	0
Perithemis sp.	0	0	0	0	3	13.2	0
Argia sp.1	0	0	0	0	3	10.6	3
Oxiagrion sp.1	0	0	0	0	3	13.3	3
Hetaerina sp.	0	0	0	0	3	16.6	3
Neuraeschna sp.	0	0	0	0	3	50.0	0
Heteragrion sp.	0	0	0	0	3	34.2	3

S4. Mayfly traits from Corumbataí River Basin, São Paulo. Gill shape trait (flat gill, sharp gill, gill fringes and opercular gill) and the absence of gills are coded as binary variables. Gill number according to body position (dorsal, lateral, ventral and caudal) is a discrete trait.

	Gill number				Gill shape					
	dorsal	lateral	ventral	caudal	flat	sharp	fringes	opercular	branched	No gill
A. longetron	0	12	0	0	1	0	0	0	0	0
A. alphus	0	12	0	0	1	0	0	0	0	0
Baetodes sp.1	0	10	0	0	1	0	0	0	0	0
Baetodes sp.2	0	10	0	0	1	0	0	0	0	0
Caenis chamie	0	8	0	0	1	0	1	1	0	0
Caenis pflugfelderi	0	8	0	0	1	0	1	1	0	0
Callibaetis sellacki	0	28	0	0	1	0	0	0	0	0
Cloeodes maracatu	0	14	0	0	1	0	0	0	0	0
Farrodes sp.	0	28	0	0	0	1	0	0	0	0
Paracloeodes sp.	0	14	0	0	1	0	0	0	0	0
Traverhyphes edmundisi	0	28	0	0	1	0	0	1	0	0
Tricorythopsis sp.	0	32	0	0	1	0	0	1	0	0
Zelusia sp.	0	12	0	0	1	0	0	0	0	0
Thraulodes sp.	0	28	0	0	1	0	0	0	0	0
Hylister sp.	0	24	0	0	1	0	1	0	0	0
Leptohyphes sp.	0	42	0	0	1	0	0	1	0	0
Hagenulopsis sp.	0	28	0	0	0	1	0	0	0	0
Waltzoyphius sp.	0	14	0	0	1	0	0	0	0	0
Miroculis sp.	0	28	0	0	0	1	0	0	0	0
Ulmeritoides sp.	0	28	0	0	1	0	1	0	0	0
Apobaetis sp.	0	14	0	0	1	0	0	0	0	0
Tricorythodes sp.	0	28	0	0	1	0	0	1	0	0
Anacroneuria sp.1	0	14	1	0	0	0	0	0	1	0
Anacroneuria sp.2	0	14	1	0	0	0	0	0	1	0
Anacroneuria sp.3	0	14	1	0	0	0	0	0	1	0
Anacroneuria sp.4	0	14	1	0	0	0	0	0	1	0
Gripopteryx sp.1	0	50	0	1	0	1	0	0	0	0

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	Gill number					Gill shape				
	dorsal	lateral	ventral	caudal	flat	sharp	fringes	opercular	branched	No gill
Gripopteryx sp.2	0	50	0	1	0	1	0	0	0	0
Tupiperla sp.	0	50	0	1	0	1	0	0	0	0
Kempnya sp.1	0	22	1	0	0	0	0	0	1	0
Kempnya sp.2	0	22	1	0	0	0	0	0	1	0
Contulma sp.	0	0	0	0	0	0	0	0	0	1
Xiphocentron sp.	0	0	0	0	0	0	0	0	0	1
Itauara sp.	0	0	0	0	0	0	0	0	0	1
Atopsyche sp.	0	0	0	0	0	0	0	0	0	1
Leptonema sp.	0	0	44	0	0	0	0	0	1	0
Alisotrichia sp.	0	0	0	0	0	0	0	0	0	1
Blepharopus sp.	12	8	44	4	0	1	0	0	1	0
Cernotina sp.	0	0	0	0	0	0	0	0	0	1
Wormaldia sp.	0	0	0	5	0	0	0	0	0	0
Chimarra sp.1	0	0	0	5	0	0	0	0	0	0
Chimarra sp.2	0	0	0	5	0	0	0	0	0	0
Phylloicus sp.	16	0	26	0	0	0	0	0	1	0
Smicridea sp.1	0	10	40	0	0	0	0	0	1	0
Smicridea sp.2	0	10	40	0	0	0	0	0	1	0
Smicridea sp.3	0	10	40	0	0	0	0	0	1	0
Helicopsyche sp.	0	0	0	0	0	0	0	0	0	0
Polyplectropus sp.1	0	0	0	0	0	0	0	0	0	1
Metricia sp.	0	0	0	0	0	0	0	0	0	1
Neotrichia sp.1	0	0	0	0	0	0	0	0	0	1
Hydroptila sp.	0	0	0	0	0	0	0	0	0	1
Neotrichia sp.2	0	0	0	0	0	0	0	0	0	1
Marilia sp.1	20	6	26	0	0	1	0	0	0	0
Marilia sp.2	0	6	26	0	0	1	0	0	0	0
Marilia sp.3	0	6	26	0	0	1	0	0	0	0
Oecetis sp.	0	0	0	0	0	0	0	0	0	1

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	Gill number					Gill shape				
	dorsal	lateral	ventral	caudal	flat	sharp	fringes	opercular	branched	No gill
Triplectides sp.	12	14	10	0	0	1	0	0	0	0
Austrotinodes sp.	0	0	0	0	0	0	0	0	0	1
Archeogomphus sp.1	0	0	0	0	0	0	0	0	0	1
Brechmorhoga sp.	0	0	0	0	0	0	0	0	0	1
Perithemis sp.	0	0	0	0	0	0	0	0	0	1
Argia sp.1	0	0	0	3	0	0	0	0	0	0
Oxiagrion sp.1	0	0	0	3	0	0	0	0	0	0
Hetaerina sp.	0	0	0	3	0	0	0	0	0	0
Neuraeschna sp.	0	0	0	0	0	0	0	0	0	1
Heteragrion sp.	0	0	0	3	0	0	0	0	0	0

S5. Mayfly traits from Corumbataí River Basin, São Paulo. Body format is fuzzy coded within the levels flat body and cylindrical body. The locomotion trait is separated in swimmer and scrawler and also fuzzy coded. The fore wing size and hind wing are continuous and binary traits, respectively.

	Flat body	Cylindrical body	Swimmer	Scrawler	Fore wing size	Hind wing
A. longetron	0	2	3	2	5.8	0
A. alphus	0	2	3	2	4.9	0
Baetodes sp.1	1	2	3	2	4.0	0
Baetodes sp.2	1	2	3	2	3.0	0
Caenis chamie	1	2	1	3	3.8	0
Caenis pflugfelderi	1	2	1	3	2.5	0
Callibaetis sellacki	0	2	2	3	7.0	1
Cloeodes maracatu	0	2	2	3	4.0	0
Farrodes sp.	2	0	1	2	5.7	1
Paracloeodes sp.	0	2	3	2	4.2	1
Traverhyphes edmundisi	1	2	0	3	3.9	1
Tricorythopsis sp.	1	2	0	3	2.0	0
Zelusia sp.	0	2	3	2	4.0	0
Thraulodes sp.	3	0	1	3	9.0	0
Hylister sp.	2	0	1	3	10.4	1
Leptohyphes sp.	1	2	0	3	4.5	0
Hagenulopsis sp.	2	0	1	3	5.6	0
Waltzoyphius sp.	0	2	3	2	4.0	0
Miroculis sp.	2	0	1	2	5.6	0
Ulmeritoides sp.	2	0	0	3	8.0	0
Apobaetis sp.	0	2	3	1	6.0	0
Tricorythodes sp.	1	2	0	3	4.4	0
Anacroneuria sp.1	3	0	1	3	13.5	1
Anacroneuria sp.2	3	0	1	3	13.5	1
Anacroneuria sp.3	3	0	1	3	13.5	1
Anacroneuria sp.4	3	0	1	3	13.5	1
Gripopteryx sp.1	2	0	1	3	16.8	1
Gripopteryx sp.2	2	0	1	3	16.8	1
Tupiperla sp.	2	0	1	3	9.0	1
Kempnya sp.1	3	0	1	3	28.3	1
Kempnya sp.2	3	0	1	3	28.3	1
Contulma sp.	0	3	1	2	4.2	1
Xiphocentron sp.	0	3	1	2	4.4	1
Itauara sp.	0	3	1	3	2.5	1
Atopsyche sp.	0	3	2	3	6.3	1
Leptonema sp.	0	3	1	2	17.4	1
Alisotrichia sp.	1	2	0	3	1.9	1
Blepharopus sp.	0	3	1	2	5.6	1
Cernotina sp.	0	3	0	3	4.8	1

continua

	Flat body	Cylindrical body	Swimmer	Scrawler	Fore wing size	Hind wing
Wormaldia sp.	0	3	1	3	5.0	1
Chimarra sp.1	0	3	0	3	5.6	1
Chimarra sp.2	0	3	0	3	5.6	1
Phylloicus sp.	2	3	1	2	10.5	1
Smicridea sp.1	0	3	1	2	6.0	1
Smicridea sp.2	0	3	1	2	6.0	1
Smicridea sp.3	0	3	1	2	6.0	1
Helicopsyche sp.	0	3	0	3	4.5	1
Polyplectropus sp.1	0	3	1	2	5.5	1
Metricia sp.	0	3	0	3	3.0	1
Neotrichia sp.1	0	3	0	3	1.8	1
Hydroptila sp.	2	3	0	3	3.0	1
Neotrichia sp.2	1	3	0	3	1.8	1
Marilia sp.1	0	3	0	3	10.0	1
Marilia sp.2	0	3	0	3	10.0	1
Marilia sp.3	0	3	0	3	10.0	1
Oecetis sp.	0	3	0	3	8.0	1
Triplectides sp.	0	3	0	3	14.0	1
Austrotinodes sp.	0	3	0	3	5.2	1
Archeogomphus sp.1	0	2	0	2	19.8	1
Brechmorhoga sp.	2	3	0	2	39.1	1
Perithemis sp.	2	3	0	2	17.5	1
Argia sp.1	1	3	1	3	23.8	1
Oxiagrion sp.1	1	3	1	3	19.7	1
Hetaerina sp.	1	3	1	3	30.0	1
Neuraeschna sp.	2	3	0	2	64.0	1
Heteragrion sp.	2	3	0	2	26.0	1

a)

	v1	v2	v3	v4	v5	v6	v7	v8	v9	v10	v11	v12	v13	v14
v2	0.66													
v3	0.71	0.75												
v4	0.06	0.48	0.17											
v5	0.16	0.58	0.48	-0.06										
v6	0.49	0.22	0.01	0.22	0.78									
v7	0.05	0.01	0.36	0.01	0.45	0.57								
v8	0.26	0.36	-0.08	0.05	0.08	-0.38	-0.12							
v9	0.48	0.05	-0.03	0.03	0.01	0.02	0.53							
v10	-0.11	0.3	0.02	0.53	1	1	1	1						
v11	0.02	0.53	1	1	1	1	1	1	1					
v12	1	1	1	1	1	1	1	1	1	1				
v13	1	1	1	1	1	1	1	1	1	1	1			
v14	1	1	1	1	1	1	1	1	1	1	1	1		

b)

	v12	v13	v14	v15	v16	v17	v18	v19	v20	v21	v22	v23	v24	v25	v26
v13	0.01														
v14	0.53	0.09													
v15	0.09	0.32	0.51												
v16	0.02	0.74	0.84	0.26											
v17	0.09	0.00	0.37	0.36	0.66										
v18	0.12	0.03	0.43	0.38	0.28	0.14									
v19	-0.01	0.47	0.1	0.20	0.23	0.21	0.06								
v20	0.07	0.11	0.19	0.14	0.16	0.05	0.15	0.11							
v21	0.26	0.1	-0.29	-0.05	-0.09	-0.01	0.20	-0.04							
v22	1	1	1	1	1	1	1	1	1						
v23	1	1	1	1	1	1	1	1	1	1					
v24	1	1	1	1	1	1	1	1	1	1	1				
v25	1	1	1	1	1	1	1	1	1	1	1	1			
v26	1	1	1	1	1	1	1	1	1	1	1	1	1		
v27	1	1	1	1	1	1	1	1	1	1	1	1	1	1	

S6- Covariance between the variables of the connectivity path model (a) and instream habitat path model (b). v1=overland dispersal costs in 1962; v2=overland dispersal costs in 1978; v3=overland dispersal costs in 2003; v4=overland dispersal costs in 2011; v5= riparian land use in 1962; v6= riparian land use in 1978; v7= riparian land use in 2011; v8= uncover stream length in 1962; v9= uncover stream length in 1978; v10= uncover stream length in 2011; v11=drainage length upstream; v12=local abundance; v13=rarefied richness; v14= functional dispersion; v15= catchment forest in 1962; v16= catchment forest in 1972; v17= catchment forest in 1978; v18= catchment forest in 2003; v19= catchment forest in 2011;v20= coefficient of variation of altitude; v21= forest cover canopy; v22=leaf litter; v23=temperature; v24= pebble proportion; v25= Dissolved oxygen; v26= phosphorus total; v27= site depth.

CONCLUSÃO

Os achados desta tese corroboraram a necessidade de se investigar influências de características passadas das paisagens para compreender padrões atuais de biodiversidade. Nós mostramos que a observação de legados e sua interpretação depende de como o histórico da paisagem é caracterizado e varia entre descritores da comunidade. Nós também avançamos no entendimento das múltiplas relações que ocorrem simultaneamente nos sistemas fluviais tomando os insetos aquáticos como modelo de estudo. Neste caso, demonstramos que a cobertura florestal e usos do solo têm efeitos indiretos na estrutura das comunidades os quais são mediados pelas condições ambientais dos riachos e pela conectividade espacial. Os achados que sustentam tais avanços foram alcançados com a elaboração de dois manuscritos.

No primeiro manuscrito, nós modelamos a riqueza de espécies, a abundância local e o índice de diversidade de Tsallis em função das proporções de cobertura florestal em 1962, 1972, 1978, 2003 e 2011. Também modelamos o histórico da cobertura florestal caracterizando-o com as trajetórias de perda e ganho de floresta – considerando as diferenças de cobertura entre os anos final e inicial – as quais foram combinadas com valores médios e variação da proporção de floresta observada nos diferentes anos e, posteriormente, relativizadas pelo intervalo de tempo entre estes. Pela primeira vez na literatura, nós confirmamos que insetos aquáticos em região tropical apresentam respostas atrasadas a mudanças na cobertura florestal. Observamos um maior lapso temporal na abundância local do que na riqueza rarefeita e nenhum para o índice de diversidade quando consideradas as florestas nos anos individuais. Mostramos que os padrões de diversidade ao longo dos riachos desmatados são explicados não só pela proporção média de floresta naquele período, mas também pela trajetória. Por exemplo, nas microbacias com uma menor média de cobertura florestal, encontramos maior riqueza rarefeita nas microbacias que foram desmatadas do que naquelas onde a cobertura florestal foi mais consistente ao longo do tempo. Estes resultados sugerem um padrão típico de débito de extinção, isto é, espécies que estão excedentes e que podem ser perdidas futuramente. Também mostramos que os descritores de comunidade aumentavam com o ganho florestal nas microbacias que, tomando a média do período, eram as mais florestadas. Com isso sinalizamos que a preservação de grandes quantidades de floresta remanescente sustenta os efeitos positivos de reflorestamento nas comunidades.

No segundo manuscrito, nós construímos um modelo de caminho teórico a partir de relações previamente descritas para analisar os efeitos diretos e indiretos da história do uso e cobertura da terra observados sob diferentes escalas espaciais e da heterogeneidade topográfica nas comunidades

ribeirinhas. Demonstramos que o histórico de cobertura florestal afeta indiretamente as comunidades ribeirinhas aumentando a quantidade de serapilheira e fósforo nos riachos, principalmente na escala de captação. Também apresentamos evidências de que alterações na conectividade espacial relacionadas à zona ribeirinha, devido a usos do solo passados e recentes, afetam fortemente comunidades de insetos aquáticos. Neste caso, nós inovamos ao mensurar tal conectividade usando o comprimento de córregos descobertos pelas florestas. Estes resultados mostram que estudos que investigam impactos da mudança da paisagem, como os de bioavaliação, focando apenas na seleção de espécies pelas condições locais (filtros ambientais) alcançam apenas uma parte dos fatores estruturadores das comunidades de insetos aquáticos. Também mostram que além da proporção de floresta nas microbacias, considerar o arranjo espacial de fragmentos florestais é essencial para a bioavaliação de água doce.

Futuros estudos poderiam complementar tais achados investigando a redução do lapso temporal e do crédito de espécies quando realizada a recuperação de corredores ecológicos para a dispersão de insetos aquáticos, ou mesmo considerando outros grupos taxonômicos. Infelizmente, a compreensão das respostas tardias em virtude de mudanças *positivas* na paisagem tem persistido como uma das maiores lacunas desta área de estudo – conforme consta na mais recente revisão sobre ela (LIRA; LEITE; METZGER, 2019). Paralelamente, uma avaliação mais rápida e consistente dos efeitos das mudanças da paisagem também aguarda que futuras investigações identifiquem características que sejam comuns entre as comunidades que apresentam respostas atrasadas (ou seja, indicadores de *delay* ao nível da comunidade). Até o momento, a grande maioria dos estudos tem focado em atributos que são observados ao nível de espécies e não de comunidades. Uma recente e pioneira iniciativa nesta direção foi tomada por Kitzes e Harte (2015) – os quais buscaram por uma sinalização de resposta tardia em comunidades observando padrões de distribuição das abundâncias nas espécies. Por fim, ainda necessitamos esclarecer como as assincronias entre as mudanças da paisagem e respostas das comunidades contribui para a variação espacial da composição de comunidades locais (i.e., diversidade beta) e como ela se relaciona com outros mecanismos que suportam tal variação. De todo modo, as dinâmicas que explicam a persistência das metacomunidades em paisagens modificadas precisam ser revisitadas sob a perspectiva de tais assincronias, como tem sido feito com outros temas, tais como os serviços ecossistêmicos e as interações ecológicas.

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