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TÚLIO PAIVA CHAVES

FATORES ECOLÓGICOS DETERMINANTES NA ESTRUTURA E NA DIVERSIDADE DE COMUNIDADES DE MACROINVERTEBRADOS AQUÁTICOS: COMUNIDADES BROMELÍCOLAS COMO MODELO

DETERMINANT ECOLOGICAL FACTORS ON THE STRUCTURE AND DIVERSITY OF AQUATIC MACROINVERTEBRATE COMMUNITIES: BROMELIAD COMMUNITIES AS A MODEL

ILHÉUS – BAHIA
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Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutor em Ecologia e Conservação da Biodiversidade.

Área de concentração: Ecologia e Conservação da Biodiversidade.

Orientador: Dra. Maíra Benchimol

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Ilhéus, 03 de julho de 2019

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RESUMO

A estrutura e diversidade das comunidades biológicas podem ser influenciadas tanto por fatores abióticos, como gradientes ambientais e físicos, como bióticos, incluindo as interações entre as espécies coexistentes. Além disto, características espécie-específicas também afetam a estrutura das comunidades ─ a capacidade e a forma de dispersão das espécies, por exemplo, influenciam diretamente na habilidade dos indivíduos em alcançar diferentes localidades, possibilitando a formação de um conjunto de comunidades conectado por eventos de dispersão de ao menos uma das espécies (i.e., metacomunidades). Em sistemas aquáticos, os macroinvertebrados desempenham funções vitais para o funcionamento destes ecossistemas, além de serem excelentes indicadores de qualidade ambiental. Assim, estudos que avaliem a estrutura e os padrões de diversidade destes organismos tornam-se fundamentais para auxiliar na compreensão de quais fatores são responsáveis por moldar estas comunidades e, consequentemente, afetar o seu funcionamento. A partir de uma extensa revisão de literatura e utilizando bromélias como modelos, esta tese tem como objetivo compreender quais são os fatores ecológicos determinantes para explicar a estrutura das comunidades de macroinvertebrados de água doce, assim como avaliar a influência de diferentes variáveis ambientais sobre os padrões de composição e de diversidade taxonômica e funcional de macroinvertebrados presentes em tanques de bromélias terrestres. No primeiro capítulo, apresento uma revisão cienciométrica da produção científica global sobre metacomunidades de macroinvertebrados aquáticos nos mais diversos ambientes de água doce (i.e., rios, lagos, poças e fitotelmatas). Os resultados indicam um crescimento ascendente nos estudos desta temática (especialmente os com foco em rios e riachos), com a “seleção de espécies” atuando como o principal processo explicativo do padrão das metacomunidades. Adicionalmente, fatores como a dinâmica hídrica do corpo d’água e a forma de dispersão das espécies aparentam exercer um importante papel nos padrões registrados. No segundo capítulo, avaliei os efeitos da distância geográfica, de variáveis ambientais e das interações entre as espécies sobre a diversidade beta de macroinvertebrados associados aos tanques de bromélias terrestres em uma restinga no sul da Bahia, Brasil. Ao contrário do esperado, a distância entre as bromélias não foi um fator determinante para explicar a mudança de espécies entre as diferentes bromélias amostradas, enquanto que a matéria orgânica no interior

do tanque e as interações negativas entre as espécies afetaram claramente a diversidade beta. Por fim, no terceiro capítulo, investiguei a influência do tamanho da bromélia e de variáveis físico-químicas de seus tanques sobre os padrões de composição e de diversidade taxonômica e funcional das comunidades de macroinvertebrados aquáticos. Os resultados demonstram que as estruturas taxonômica e funcional respondem de formas distintas aos fatores ambientais, com a intensidade da luz e a entrada de matéria orgânica particulada atuando como os principais determinantes da composição de espécies, da distribuição dos atributos funcionais e da riqueza funcional das comunidades avaliadas. Tendo em vista que perturbações humanas estão aumentando em escala local e global, com consequências diretas sobre as condições abióticas dos sistemas aquáticos, estes resultados sugerem que o funcionamento destes sistemas está severamente comprometido a longo prazo. Assim, esta tese demonstra a necessidade de considerar características físicas, ambientais e biológicas dos sistemas aquáticos em estudos ecológicos sobre a estrutura de comunidades biológicas, e enfatiza a importância de estratégias efetivas de conservação a fim de garantir a manutenção da diversidade de macroinvertebrados nestes sistemas e a provisão dos serviços ecossistêmicos por eles prestados.

Palavras-chave: Bromélias, Diversidade beta, Diversidade funcional, Diversidade taxonômica, Metacomunidades, Perturbações antrópicas, Restinga.

DETERMINANT ECOLOGICAL FACTORS ON THE STRUCTURE AND DIVERSITY OF AQUATIC MACROINVERTEBRATE COMMUNITIES: BROMELIAD COMMUNITIES AS A MODEL

ABSTRACT

Both the structure and diversity of biological communities can be influenced by abiotic factors, such as environmental and physical gradients, and biotic factors, including interactions among coexisting species. In addition, species-specific features also affect the structure of communities ─ the capacity and form of dispersal of the species, for instance, directly influence the individuals' ability to reach different locations, enabling the formation of a set of communities connected by dispersion events of at least one species (i.e., metacommunities). In aquatic systems, macroinvertebrates play vital functions to enable ecosystem functioning, and comprise excellent indicators of environmental quality. Thus, studies assessing the structure and diversity patterns of these organisms become fundamental to enhance our understanding on which factors are likely to modulate these communities and consequently affect their functioning. Based on an extensive literature review and using bromeliads as models, this thesis aims to assess the main ecological predictors to explaining the structure of freshwater macroinvertebrate communities, and evaluate the influence of different environmental variables on the patterns of species composition and taxonomic, and functional diversity of macroinvertebrates inhabiting terrestrial bromeliad tanks. In the first chapter, I present a scientiometric review of global scientific literature on aquatic macroinvertebrate metacommunities in the most diverse freshwater environments (i.e., rivers, lakes, pools and phytotelmats). Results indicate an ascending growth in the studies of this topic (especially those focused on rivers and streams), with "species selection" acting as the main explanatory process explaining the metacommunity pattern. Additionally, factors such as the dynamics of the water body and the species' dispersion form appear to play a fundamental role on the observed patterns. In the second chapter, I evaluated the effects of geographical distance, environmental variables and species interactions on the β-diversity of macroinvertebrates associated with terrestrial bromeliad tanks of a *restinga* in southern Bahia, Brazil. Conversely to expected, the distance between bromeliads was not a determining factor explaining the change of species among the different bromeliads sampled, whereas the organic matter inside the tank and the negative interactions between species clearly affected β-diversity. Finally, in the third chapter, I investigated the effects of bromeliad size and

physicochemical variables related to its tanks on the composition, taxonomic and functional diversity patterns of aquatic macroinvertebrate communities. Results demonstrate that both taxonomic and functional structures respond differently to environmental factors, with light intensity and the input of particulate organic matter acting as the main determinants of species composition, distribution of traits and functional richness of the studied communities. Given that human disturbances have been increasing at local and global scales, with direct consequences on the abiotic conditions of aquatic systems, these results suggest that the functioning of these systems is severely threatened in the long term. Thus, this thesis demonstrates the need to consider physical, environmental and biological characteristics of aquatic systems in ecological studies assessing the structure of biological communities, and emphasizes the importance of effective conservation strategies in order to guarantee the maintenance of macroinvertebrate diversity in these systems and the provision of ecosystem services they provide.

Keywords: Bromeliads, β-diversity, Functional diversity, Taxonomic diversity, Metacommunities, Anthropogenic disturbances, *Restinga*.

SUMÁRIO

INTRODUÇÃO GERAL

I. Fatores determinantes da estrutura de comunidades biológicas

Comunidades biológicas podem ser definidas como um conjunto de populações de diferentes espécies co-ocorrentes no tempo e no espaço, e conectadas por interações ecológicas. Relações harmônicas e desarmônicas interespecíficas, assim como fatores abióticos, são amplamente reconhecidos por influenciar os padrões de composição de uma comunidade (PERONI; HERNÁNDEZ, 2011; RICKLEFS, 2003; TOWNSEND; BEGON; HARPER, 2009). Dentre os fatores abióticos que estruturam as comunidades, a produtividade primária e a heterogeneidade ambiental são amplamente reconhecidas como importantes fatores, principalmente por influenciar a distribuição dos táxons na natureza (RICKLEFS, 2003; TOWNSEND; BEGON; HARPER, 2009). A produtividade primária, descrita pela biomassa produzida pelos produtores primários, é afetada diretamente pela entrada de nutrientes em um sistema ou por mudanças na temperatura, influenciando positivamente ou negativamente a diversidade de espécies local (BARRIOS, 2007; LOREAU et al., 2001; PLISNIER et al., 2003; TILMAN; REICH; ISBELL, 2012). De fato, estudos revelaram uma substancial redução da produtividade primária em lagos na África provocada pelo aumento da temperatura atmosférica global, com consequências negativas na diversidade de peixes (PLISNIER et al., 2003). Adicionalmente, a heterogeneidade ambiental se posiciona como fator determinante na estruturação de comunidades. De acordo com a hipótese proposta MacArthur & MacArthur (1961), habitats exibindo maior complexidade estrutural possibilitam a existência de maior número de sobreposições parciais de nicho, assim como diversificação no uso e exploração dos recursos disponíveis, promovendo consequentemente o aumento da diversidade de espécies (BAZZAZ, 1975; CUMMING; CHILD, 2009; MACARTHUR; WILSON, 1967). Por exemplo, um estudo realizado com poças em área de pastagem, mostrou que o aumento na heterogeneidade (i.e., variações na estrutura física interna e vegetação do entorno) apresentava relação direta com o aumento na riqueza, abundância, composição e diversidade da anurofauna (SILVA; MARTINS; ROSSA-FERES, 2011). Embora, na maioria dos casos, esta diversificação favoreça o aumento na diversidade de alguns grupos, outros estudos têm demonstrado efeitos negativos da complexidade da estrutura do habitat sobre a diversidade de espécies (HILL et al., 1995; SULLIVAN; SULLIVAN, 2001). Assim,

embora amplamente reconhecida como um importante fator explicativo para diversidade de espécies em comunidades naturais, o efeito da heterogeneidade do habitat varia entre diferentes grupos taxonômicos e ambientes, em função da forma como o grupo interage com o habitat, das diferentes medidas estruturais utilizadas, bem como das variações nas escalas espacial e temporal estudadas (TEWS et al., 2004).

Além de fatores abióticos, a estrutura das comunidades pode ainda ser moldada por fatores bióticos, incluindo as interações entre as espécies. Ao se dispersar para outros ambientes, uma espécie deve ser capaz não apenas de sobreviver às novas condições abióticas, mas também obter sucesso nas relações com as espécies ali estabelecidas (CORNELL; LAWTON, 1992). Estas interações podem ser harmônicas, quando não há prejuízo para nenhum dos indivíduos envolvidos, ou desarmônicas, quando pelo menos uma espécie é prejudicada. Um exemplo desta última é a competição ─ isto é, a disputa por um mesmo recurso entre diferentes organismos, que pode ocorrer quando uma nova espécie se estabelece em um determinado ambiente, porém ocupa um determinado espaço de nicho já utilizado por outra espécie (HUTCHINSON, 1957). Neste tipo de interação, espécies podem ser localmente extintas ou ter suas populações substancialmente reduzidas, modificando assim toda a estrutura da comunidade (GIACOMINI, 2007; RICKLEFS, 2003). Estudos demonstraram fortes efeitos da competição entre corais e algas, resultando em um menor crescimento dos corais na presença das algas, e mudança na estrutura das comunidades de organismos marinhos associados (LIRMAN, 2001). Do mesmo modo, a introdução experimental de salamandras em poças temporárias em Michigan (EUA) provocou uma forte competição entre as espécies novas e as já existentes, resultando em bruscas alterações na estrutura trófica e no desenvolvimento das espécies nativas (WILBUR, 1972). Outro importante tipo de interação que afeta a estruturação das comunidades é a predação/herbivoria. Seus efeitos na estrutura das comunidades têm relação direta com o nível de especialização do predador/pastejador sobre uma presa específica (i.e., em caso de predadores especialistas), bem como dos padrões de ocorrências das presas em potencial (i.e., no caso de predadores generalistas) (HOLT, 1977; TOWNSEND; BEGON; HARPER, 2009). Um exemplo clássico deste efeito foi descrito por Huffaker (1957) ao observar mudanças na distribuição de uma espécie de planta (*Hypericum perforatum*) devido à ação da herbivoria por besouros do gênero *Chrysolina*. Além deste efeito direto sobre a presa, a simples presença de um predador

em uma área pode inibir a ocorrência de espécies de presas, e consequentemente alterar a estrutura da comunidade local (DEJEAN et al., 2018; LIMBERGER; WICKHAM, 2011).

Diferentes parâmetros têm sido utilizados por ecólogos para descrever a estrutura de uma comunidade, incluindo a riqueza, abundância, composição e índices de diversidade de espécies (MAGURRAN, 2004). A riqueza se refere ao simples número de espécies presentes em uma comunidade e apresenta uma importante aplicação na definição de locais prioritários para a conservação da biodiversidade; no entanto, este parâmetro não considera tanto o número de indivíduos por espécie como a identificação destas espécies (MAGURRAN, 2004; SCHEFFERS et al., 2012). A abundância relativa representa o total de indivíduos de uma determinada espécie em uma escala espacial definida, sendo uma medida muito útil no entendimento da distribuição dos indivíduos das espécies nas comunidades e possibilita a obtenção de diferentes índices de diversidade (MAGURRAN, 2004; PERONI; HERNÁNDEZ, 2011). As medidas de composição, por sua vez, combinam a riqueza e abundância relativa para entender a relação entre as diferentes espécies em uma comunidade, sendo útil para compreender as relações entre espécies raras e comuns, ou comparar a similaridade entre comunidades distintas (MAGURRAN, 2004; PERONI; HERNÁNDEZ, 2011). Adicionalmente, os índices de diversidade buscam avaliar indiretamente a presença de variações temporais e espaciais das populações existentes em uma comunidade, mas que a depender da sua abordagem matemática, atribuem pesos diferentes para espécies raras e comuns (MAGURRAN, 2004; PERONI; HERNÁNDEZ, 2011). Apesar das vantagens e desvantagens relacionadas aos diferentes parâmetros de comunidade, estas abordagens são importantes para identificar locais prioritários para a conservação (i.e., *hotspots* de biodiversidade, no caso de riqueza), avaliar os efeitos de alterações ambientais em gradiente (composição ou abundância), ou permitir avaliações temporais e espaciais nas populações (composição e índices de diversidade – MAGURRAN, 2004; RIBEIRO et al., 2011; TOWNSEND; BEGON; HARPER, 2009; VELLEND, 2001).

Em termos espaciais, a diversidade biológica pode ser particionada em três componentes ─ diversidade alfa (α), gama (*y*) e beta (β) (WHITTAKER, 1960). A diversidade alfa se caracteriza pela riqueza de espécies de uma comunidade local, enquanto a diversidade gama engloba todas as espécies presentes em uma região

(MAGURRAN, 2004; WHITTAKER, 1960, 1972). Já a diversidade beta considera a diferença entre a composição de espécies que ocorrem em diferentes comunidades em uma mesma região ou escala temporal (DE SOUZA NOGUEIRA et al., 2008; WHITTAKER, 1960, 1972). Este componente da diversidade busca compreender a distribuição e ocorrência das espécies nas diferentes comunidades (ANDERSON et al., 2011; WHITTAKER, 1972), e considera o processo de dispersão como importante fator responsável por moldar a diversidade (ASTORGA et al., 2012; BASELGA, 2010; WANG et al., 2012). Assim, a diversidade beta considera tanto fatores espaciais quanto ambientais e biológicos para melhor compreender os diferentes efeitos sobre a composição de espécies das comunidades locais (CASWELL; COHEN, 1991; SEGRE et al., 2014; SOKOL et al., 2015). Entender os efeitos de mudanças ambientais, sobretudo aquelas resultantes de ações antrópicas, sobre a diversidade beta, é um passo primordial para elaboração de estratégias para a conservação da biodiversidade (SOCOLAR et al., 2016). De fato, aumento da diversidade beta entre habitats remanescentes pode ajudar a manter a diversidade regional em paisagens antropizadas (SOCOLAR et al., 2016).

II. Além das unidades taxonômicas

Parâmetros como riqueza, composição e índices de diversidade descrevem a estrutura das comunidades apenas com base nos seus atributos taxonômicos, desconsiderando aspectos filogenéticos ou funcionais das espécies (CIANCIARUSO; SILVA; BATALHA, 2009; TILMAN, 2001). Embora tenham grande importância para elucidar padrões ecológicos e recomendar medidas de conservação da biodiversidade, a abordagem taxonômica considera que os indivíduos possuem papéis ecológicos equivalentes, o que pode levar a uma compreensão errônea sobre a funcionalidade destas espécies em um determinado ecossistema (CALAÇA; GRELLE, 2017). Neste sentido, surge no final do século XX uma nova abordagem visando melhor caracterizar a estrutura de comunidades, a abordagem funcional (TILMAN et al., 1997; Nicolini et al., 2012; CALAÇA & GRELLE, 2017; SCHMERA et al., 2017). Apresentando como ponto central as características funcionais das espécies e a funcionalidade dos sistemas, esta abordagem deve ser utilizada como forma complementar à taxonômica. Segundo Tilman (2001):

> "A diversidade funcional refere-se aos componentes da biodiversidade que influenciam a forma como um ecossistema opera ou funciona. A diversidade

> biológica, ou biodiversidade, de um habitat é muito mais ampla e inclui todas as espécies que vivem em um local, toda a variação genotípica e fenotípica dentro de cada espécie e toda a variabilidade espacial e temporal nas comunidades e ecossistemas que essas espécies formam. A diversidade funcional, que é um subconjunto disso, é a variação dos valores dos atributos e sua distribuição, para as espécies presentes em um ecossistema, das características orgânicas que influenciam um ou mais aspectos do funcionamento de um ecossistema. A diversidade funcional é de importância ecológica porque, por definição, é o componente da diversidade que influencia a dinâmica do ecossistema, a estabilidade, a produtividade, o balanço de nutrientes e outros aspectos do funcionamento do ecossistema." (Tilman, 2001; p.109)

A partir da sua concepção, os estudos ecológicos abordando aspectos da diversidade funcional têm avançado em um ritmo acelerado, englobando desde índices simples, como a riqueza de características funcionais, à índices mais complexos, os quais buscam avaliar como estas características funcionais se distribuem no espaço funcional das comunidades (MASON et al., 2013; MOUCHET et al., 2010; SCHLEUTER et al., 2010; VILLÉGER; MASON; MOUILLOT, 2008). A abordagem funcional tem permitido que ecólogos e conservacionistas avaliem os efeitos das alterações ambientais, provocados principalmente por atividades antrópicas, sobre o funcionamento e provisão dos serviços ecossistêmicos prestados em ambientes aquáticos e terrestres (BRADTKA et al., 2015; MAYFIELD et al., 2010; MÜLLER et al., 2015; VILLÉGER et al., 2010). Por exemplo, um estudo realizado em uma laguna tropical revelou aumentos na salinidade, turbidez e profundidade provocados por ações antrópicas (pesca, urbanização e desmatamento) que, como consequência, levaram à uma alta redundância funcional da comunidade de peixes ─ i.e., as espécies ali encontradas apresentaram alta sobreposição quanto ao seu desempenho no funcionamento do ecossistema (VILLÉGER et al., 2010). De forma similar, outro estudo mostrou que aumento na intensidade de uso da terra gerou efeitos negativos sobre a diversidade funcional de aves e mamíferos, e nos serviços ecossistêmicos por eles desempenhados, como polinização e controle de pragas (FLYNN et al., 2009). Embora a abordagem funcional tenha grande importância do ponto de vista dos serviços ecossistêmicos, é válido ressaltar a importância de combinar esta forma de abordagem à taxonômica, para assim obtermos uma avaliação mais completa dos efeitos das perturbações sobre a biodiversidade e então propor medidas mais precisas de como amenizar os impactos sobre as comunidades biológicas (CADOTTE; CARSCADDEN; MIROTCHNICK, 2011; PODGAISKI; MENDONÇA; PILLAR, 2011; VILLÉGER et al., 2010).

III. Comunidades locais conectadas em estrutura de metacomunidades

Uma das importantes questões em ecologia visa compreender os papéis dos processos locais (i.e., interações entre espécies, limitação de recursos) e regionais (i.e., tempo de existência do habitat, diferenças nas taxas imigração) sobre a estruturação das comunidades biológicas (RICKLEFS, 1987). A busca por novos locais de forrageio, reprodução e abrigo, são algumas das principais forças que fazem com que indivíduos migrem entre comunidades (BLAUSTEIN et al., 2004; SELLAMI et al., 2011; SODRÉ; ROCHA; MESSIAS, 2010). Por meio destes processos, mudanças nas interações entre as espécies podem ocorrer em uma rede de comunidades locais e gerar padrões em escalas regionais (MOUQUET; LOREAU, 2004). Diante disto, novas abordagens teóricas têm buscado avaliar as comunidades como conectadas (i.e., uma *metacomunidade*), e estruturadas diretamente por processos locais e indiretamente por processos regionais (HEINO et al., 2015; LEIBOLD et al., 2004; SARREMEJANE et al., 2017).

Especificamente, uma metacomunidade é definida como um conjunto de comunidades locais conectadas entre si por dispersão de ao menos uma das espécies (LEIBOLD et al., 2004; WILSON, 1992). Em síntese, os estudos com esta abordagem buscam entender como processos que atuam em escalas espaciais distintas determinam a distribuição e ocorrência local das espécies (BRAGA; DE OLIVEIRA; CERQUEIRA, 2017; LEIBOLD et al., 2004). Proposta originalmente por Hanski & Gilpin (1991), em um estudo conceitual sobre metapopulações, essa teoria tem se desenvolvido rapidamente nos últimos anos, sendo considerada uma das áreas mais promissoras para avaliar as respostas das comunidades às mudanças ecológicas globais (BRAGA; DE OLIVEIRA; CERQUEIRA, 2017; LEIBOLD et al., 2004; LEIBOLD; GEDDES, 2005).

Atualmente, quatro modelos têm sido considerados como os principais descritores dos processos que atuam nas metacomunidades (LEIBOLD et al., 2004). A *dinâmica de manchas*, a qual prediz que mesmo manchas de habitats idênticas são capazes de conter populações de espécies distintas, propõe que a diversidade é limitada pela capacidade de dispersão de cada espécie e pela habilidade competitiva das mesmas (LEIBOLD et al., 2004; LOGUE et al., 2011). Diferentemente, o *efeito de massa* assume que a dispersão é o fator determinante da dinâmica local das comunidades (SHMIDA; WILSON, 1985), enquanto o modelo de *seleção de espécies* propõe que as espécies possuem a mesma capacidade de dispersão, estando sua permanência no ambiente limitada pelas

interações bióticas e variações nos gradientes ambientais (LEIBOLD; GEDDES, 2005; SOININEN, 2014). Por último, o modelo *neutro* assume que a variação na composição de espécies conectadas por dispersão ocorre devido a eventos estocásticos (HUBBELL, 2001). Embora apresentem embasamentos e características distintas, todos os modelos descrevem como os mecanismos de especiação, extinção, dispersão e competição geram e estruturam a diversidade no espaço.

No cerne do seu conceito, os estudos de metacomunidades não assumem os sistemas biológicos analisados como "fechados" (i.e., quando os limites de distribuição ecológica das espécies são iguais aos limites da comunidade), inviabilizando a existência de regras explícitas para a delimitação destes limites (BRAGA; DE OLIVEIRA; CERQUEIRA, 2017). Isto se deve às diferenças na capacidade de dispersão das espécies ─ por exemplo, uma determinada paisagem pode ser uma metacomunidade para um determinado grupo de indivíduos, enquanto para outro grupo, esta mesma paisagem funciona apenas como uma comunidade local (BRAGA; DE OLIVEIRA; CERQUEIRA, 2017). Neste sentido, variações na escala analisada tanto dos ambientes (*microcosmos* – fitotelmata, *mesocosmos* – poças temporárias e *macrocosmos* – lagos e rios), quanto um mesmo tipo de ambiente em diferentes extensões espaciais (local ou regional) podem resultar em metacomunidades distintas (DALLAS; DRAKE, 2014; LECRAW; SRIVASTAVA; ROMERO, 2014; NG; CARR; COTTENIE, 2009; PARADISE et al., 2008). Além disto, dependendo da abordagem, uma metacomunidade pode ser composta por apenas um grupo taxonômico em especial (i.e., como ostracodas em Castillo-Escrivà et al., 2016), por um ou mais grupos funcionais dentro de um mesmo taxón (i.e., como de morcegos em Presley et al., 2009), ou por múltiplos táxons (i.e., como de invertebrados marinhos no golfo da Finlândia em Valanko et al., 2015).

Apesar dos grandes avanços, a teoria de metacomunidades ainda precisa de mais estudos teóricos para ser consolidada (BRAGA; DE OLIVEIRA; CERQUEIRA, 2017). Novos estudos são assim importantes, visto ainda que esta abordagem teórica pode ter papel fundamental na proposição de estratégias de conservação, como observado para um conjunto de comunidade herbáceas florestais no norte da França e de anfíbios no Mediterrâneo (FERREIRA; BEJA, 2013; JAMONEAU et al., 2012). Por exemplo, ao buscar entender como a diversidade de espécies se organiza em diferentes escalas espaciais (i.e., dentro e entre habitats fragmentados) e ao longo do tempo, esta abordagem engloba dois fatores (i.g., variações da diversidade no espaço e no tempo)

essenciais em políticas de conservação a longo prazo (FERREIRA; BEJA, 2013; FISCHER; LINDENMAYER, 2006; JAMONEAU et al., 2012; MOUQUET; LOREAU, 2004). Ademais, revisões e meta-análises que avaliem quais são os padrões usualmente encontrados para diferentes grupos biológicos podem auxiliar no melhor entendimento sobre a estrutura de metacomunidades e consequentemente permitir a elaboração de medidas eficazes para conservar a biodiversidade.

IV. Fatores estruturadores de comunidades de macroinvertebrados aquáticos em sistemas de água doce

Em ecossistemas terrestres e aquáticos, os invertebrados representam um grupo extremamente diverso, que abriga desde organismos de 0,2 mm (como micromoluscos), até 60 cm (como bicho-pau – ordem Phasmatodea), atuando em diferentes grupos tróficos (herbívoros, carnívoros, decompositores) responsáveis por desempenhar uma ampla gama de serviços ecossistêmicos, como polinização, decomposição e ciclagem de nutrientes (PODGAISKI; MENDONÇA; PILLAR, 2011; SCHOWALTER, 2016). Adicionalmente, muitas espécies são altamente sensíveis à alterações ambientais, como insetos das Ordens Ephemeroptera, Plecoptera e Trichoptera, em ecossistemas lóticos. Assim, o grupo é amplamente reconhecido como um excelente indicador de perturbações ambientais, sendo por isso muito utilizado em estudos de impacto ambiental (CZERNIAWSKA-KUSZA, 2005; GONÇALVES; MENEZES, 2011). Considerando apenas os artrópodes, é estimado que existam cerca de 7 milhões espécies descritas no mundo, sendo que mais de 80% ainda não foram descobertas (STORK, 2018). Comparado à outros grupos zoológicos, como vertebrados, existe uma forte lacuna de conhecimento taxonômico das espécies de invertebrados, e consequentemente da ecologia, história de vida e conservação desse grupo (ROSENTHAL et al., 2017; SEDDON; SOORAE; LAUNAY, 2005).

Em ambientes aquáticos, a estrutura da comunidade de invertebrados é influenciada tanto por fatores químicos, quanto físicos e biológicos. Por exemplo, estudos demostraram a importância dos gradientes de elevação (TONKIN et al., 2017), dinâmicas de degelo (CAUVY-FRAUNIÉ et al., 2015) e presença de barragens (VAN LOOY; TORMOS; SOUCHON, 2014) para estruturar as comunidades de macroinvertebrados em sistemas lóticos. Adicionalmente, outros estudos revelaram que fatores físico-químicos como o pH, a incidência de radiação solar, a entrada alóctone de

matéria orgânica e o volume de água são fortes determinantes explicativos para a composição, riqueza taxonômica e funcional de espécies em sistemas lênticos (CARLOS et al., 2001; DOI; CHANG; NAKANO, 2010; PARADISE; SOCIETY, 2000; RANGEL et al., 2017). Por exemplo, em estudos utilizando microhabitats aquáticos de troncos ocos e poças temporárias, pesquisadores observaram alterações positivas na química da água e na entrada de matéria orgânica, provocando um aumento da dissimilaridade, riqueza e diversidade de macroinvertebrados associados (GOSSNER et al., 2016; VANSCHOENWINKEL et al., 2007). Além destes fatores, a distância espacial entre as comunidades e as interações entre as espécies também têm se mostrado determinantes para explicar os padrões de estrutura de comunidades de macroinvertebrados aquáticos (AMUNDRUD; SRIVASTAVA, 2016; ASTORGA et al., 2012; HOWETH; LEIBOLD, 2010; SARREMEJANE et al., 2017). Em microssistemas aquáticos, muitas vezes o efeito da predação sobre a riqueza e diversidade de espécies, por exemplo, pode ser superior à processos físicos como de aquecimento (ANTIQUEIRA; PETCHEY; ROMERO, 2018). Já em outros momentos, as interações podem ter seus efeitos intensificados pelo efeito de outros gradientes ambientais (i.e., baixas nos níveis de precipitação) (DÉZERALD et al., 2017; MELISSA et al., 2018). Sendo assim, interações biológicas podem tanto alterar o efeito de fatores abióticos na estrutura das comunidades, quanto serem moldadas por estes fatores, afetando diretamente a maneira como as comunidades se organizam.

V. Bromélias como modelo para estudos de comunidades

Microcosmos aquáticos artificiais e naturais, definidos como um sistema pequeno e delimitado contendo até 1 L de água (SRIVASTAVA et al., 2004), têm sido considerados excelentes modelos para estudos ecológicos. Além da facilidade de manipulação, constituem habitats para uma ampla gama de espécies, que por sua vez possuem um curto intervalo de tempo entre gerações, facilitando a compreensão das respostas dos organismos frente as mudanças ambientais (MEYER-ROCHOW, 1998; SRIVASTAVA et al., 2004). Neste sentido, o uso de fitotelmatas como bromélias (Bromeliaceae) tem sido amplamente difundido em estudos ecológicos (ANTIQUEIRA; PETCHEY; ROMERO, 2018; SRIVASTAVA et al., 2004; TRZCINSKI et al., 2016). Estas plantas são extremamente abundantes em diferentes ecossistemas tropicais, apresentando distribuição usualmente agrupada, o que possibilita a existência de um

grande número de réplicas naturais (SRIVASTAVA et al., 2004). Somado a isto, a disposição em roseta das folhas desta planta possibilita a criação de microhabitats aquáticos para um grande número de espécies de invertebrados nas mais diversas formas de vida (Fig. 1), as quais as utilizam para reprodução (com ciclos de vida parciais ou totais) e abrigo (LOPEZ et al., 2011; LOUNIBOS; FRANK, 2009; SRIVASTAVA et al., 2004).

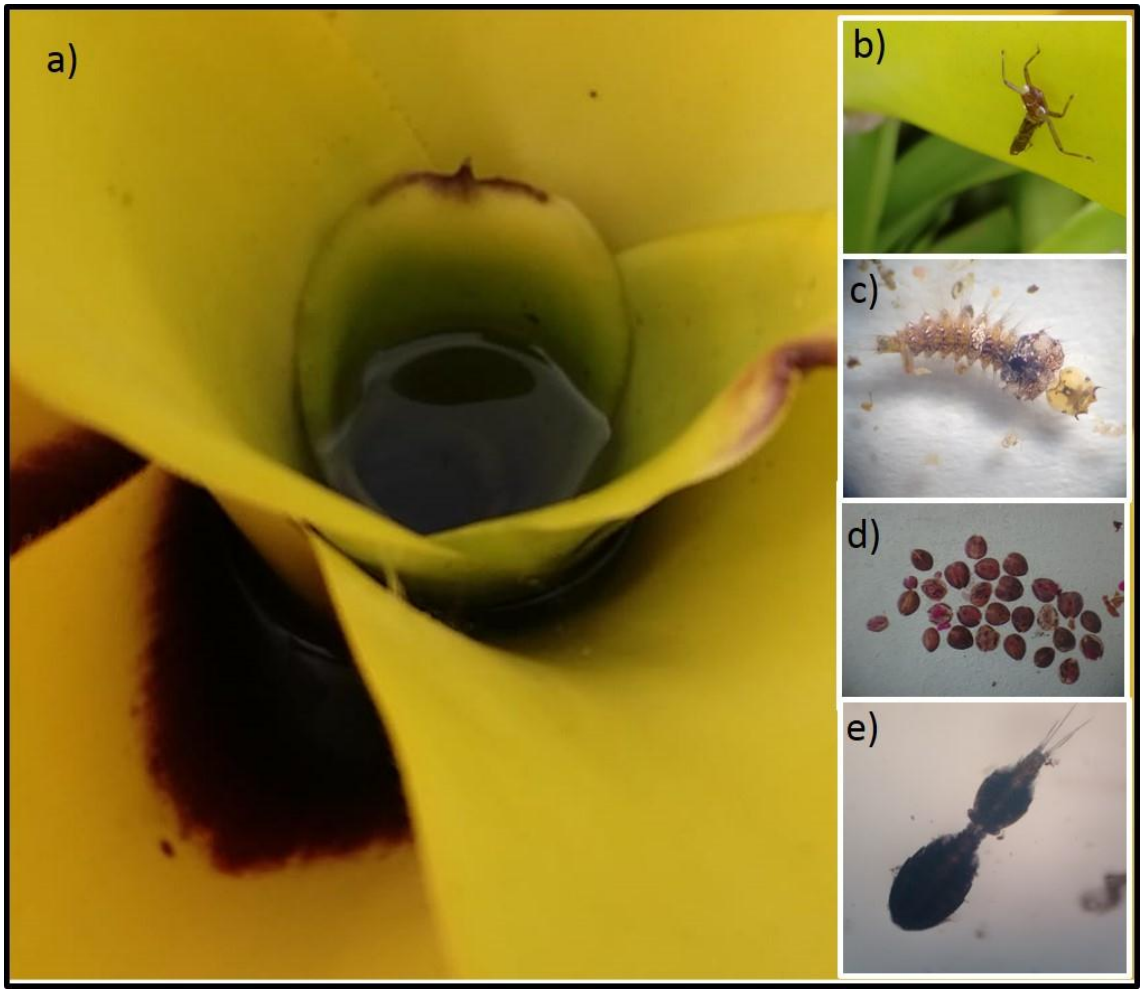

Figura 1. a) Tanque central da bromélia *Vriesea philippocoburgii* Wawra visto de cima; b) exúvia de uma larva de odonata (importante predador componente da fauna de macroinvertebrados aquáticos de bromélias, vive parte do seu ciclo de vida nos tanques desta planta); c) larva do diptera *Toxorhynchites*, outro importante predador em sistemas de bromélias; d-e) adultos de ostracodas (*Elpidium)* e copépodas, respectivamente dois importantes grupos no consumo de detritos finos e microorganismos. Fotos do acervo pessoal.

Em seu contexto histórico, os estudos ecológicos com bromélias têm buscado elucidar desde questões básicas como descrições da sua fauna associada (BALKE et al., 2008; LOUNIBOS; FRANK, 2009; PAULA JÚNIOR et al., 2017), a questões ecológicas mais complexas, como investigar a influência de perturbações antrópicos, incluindo efeitos da cobertura vegetal (BROUARD et al., 2012; CARLOS et al., 2001;

RANGEL et al., 2017), do aquecimento global (ANTIQUEIRA; PETCHEY; ROMERO, 2018; BERNABÉ et al., 2018) e das mudanças nos regimes de precipitação, sobre as comunidades (AMUNDRUD; SRIVASTAVA, 2016; MELISSA et al., 2018). Além disto, tem servido de base para estudos ecológicos envolvendo a relação espécie-área (LECRAW; SRIVASTAVA; ROMERO, 2014; MARINO et al., 2011; SRIVASTAVA et al., 2008) e interações ecológicas (AMUNDRUD; SRIVASTAVA, 2016; CÉRÉGHINO et al., 2011). Entretanto, estudos que abordem, ao mesmo tempo, atributos funcionais e taxonômicos ainda são raros, somado a isto, novos estudos sobre fatores que afetam metacomunidades em bromélias (i.e., tanto bióticos, quanto as abiótico – interações entre as espécies), somam importantes contribuições ao nível de conhecimento atual sobre o tema.

VI. O papel das bromélias em ambientes tropicais sob pressão antrópica – o exemplo das restingas

A Família Bromeliaceae possuem mais de três mil espécies descritas, e estima-se que 40% delas e 70% dos gêneros ocorram no Brasil (WANDERLEY; MARTINS, 2007). No país, apresentam ampla distribuição na Mata Atlântica, a qual possui atualmente 803 espécies registradas em ambientes florestais, incluindo restingas (MARTINELLI et al., 2018). Áreas de restinga herbácea/arbustiva, que compreendem habitats de dunas de areia costeiras recobertas por vegetação (ROCHA *et al.*, 2007), constituem ambientes naturalmente secos (SCARANO et al., 2001), e por isso os tanques de bromélias representam microhabitats e/ou constituem importantes fontes de água para a fauna local. A grande maioria dos organismos observada nestes microcosmos é composta por formas larvais de dípteras e de outros insetos, os quais possuem importantes papéis na polinização de espécies locais de plantas, na ciclagem de nutrientes, além de representarem fração importante da produção secundária local (DÉZERALD et al., 2018; LAMBRET; BESNARD; MATUSHKINA, 2015; LOUNIBOS; FRANK, 2009; MÜLLER; MARCONDES, 2007).

No entanto, as restingas têm sido severamente afetadas por diferentes atividades antrópicas, como a remoção da vegetação para desenvolvimento imobiliário, o estabelecimento de espécies vegetais exóticas, a alteração do substrato original e a coleta seletiva de bromélias com interesse paisagístico (ROCHA et al., 2007). Neste sentido, as duas primeiras alterações antrópicas podem afetar diretamente o percentual e tipo de cobertura vegetal sobre os tanques de bromélias, modificando a quantidade e

qualidade dos detritos vegetais no interior destes tanques (MIGLIORINI; SRIVASTAVA; ROMERO, 2018). Em sistemas de água doce, de forma geral, a matéria orgânica vegetal alóctone é um das principais fontes de recurso primário para a comunidade de macroinvertebrados (BUSSE et al., 2018; CARLOS et al., 2001; RANGEL et al., 2017). Sendo assim, alterações deste tipo podem afetar a riqueza, a composição e a diversidade de espécies de macroinvertebrados aquáticos em tanques de bromélias (DÉZERALD et al., 2014; GONZÁLEZ; ROMERO; SRIVASTAVA, 2014; LEROY et al., 2017; RANGEL et al., 2017). Especificamente na região sul da Bahia, as restingas têm sofrido grandes impactos gerados pela especulação imobiliária nos últimos anos, sendo poucas as unidades de proteção estabelecidas visando conservar esta fitofisionomia e à biodiversidade associada. De fato, ao visualizar imagens de satélite da zona costeira de Ilhéus ao longo do tempo, é possível identificar a supressão de áreas de restinga (Fig. 2).

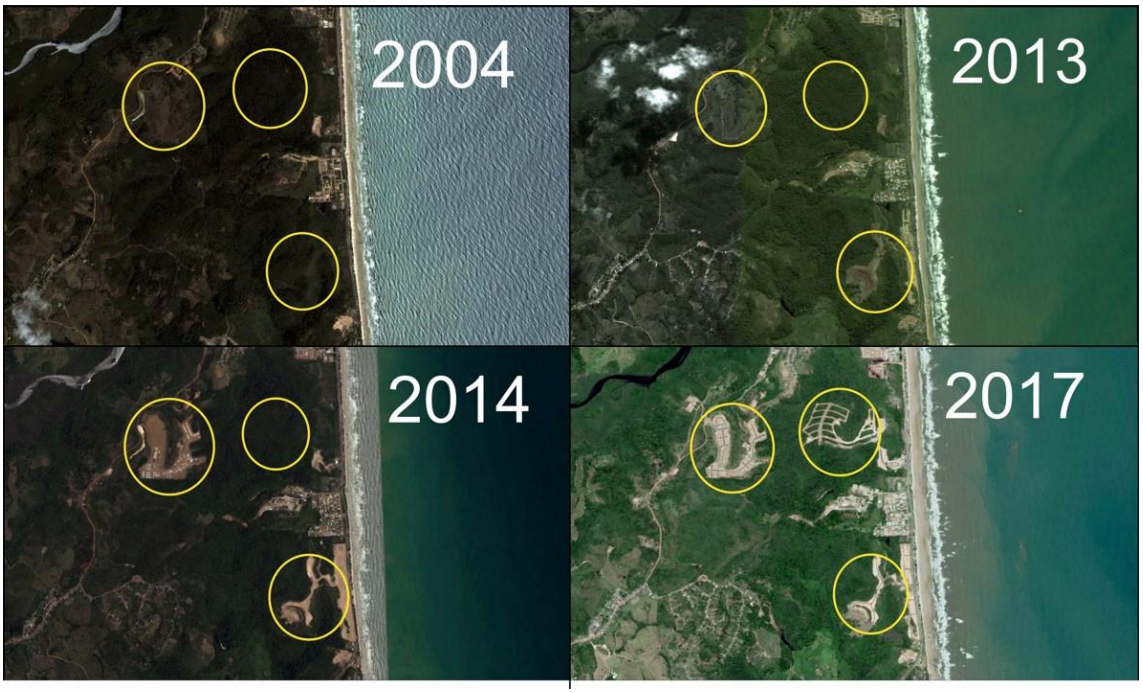

Figura 2. Imagens das áreas de restinga existentes na zona sul do município de Ilhéus - BA, Brasil, suprimidas de 2004 a 2017, por ações do setor imobiliário. Círculos amarelos indicam locais mais atingidos pela supressão da restinga pelo setor imobiliário local. Fotos: Google Earth, 16 de junho de 2019.

Considerando as restingas da região, tanto dentro como fora de Unidades de Conservação, há uma carência de estudos com a fauna local, especialmente de macroinvertebrados. Assim, o presente estudo foi desenvolvido em uma restinga na Área de Preservação Ambiental (APA) da Lagoa Encantada, que abrange parte da

região norte do Município de Ilhéus (além dos municípios de Uruçuca, Itajuípe, Coaraci e Almadina), no Litoral Sul da Bahia, Brasil (14º38’52”S; 39º4’39”O – Fig. 2a-b). Esta área apresenta grandes extensões ocupadas por moitas de bromélias dominadas pela espécie *Vriesea philippocoburgii* Wawra (Fig. 2c).

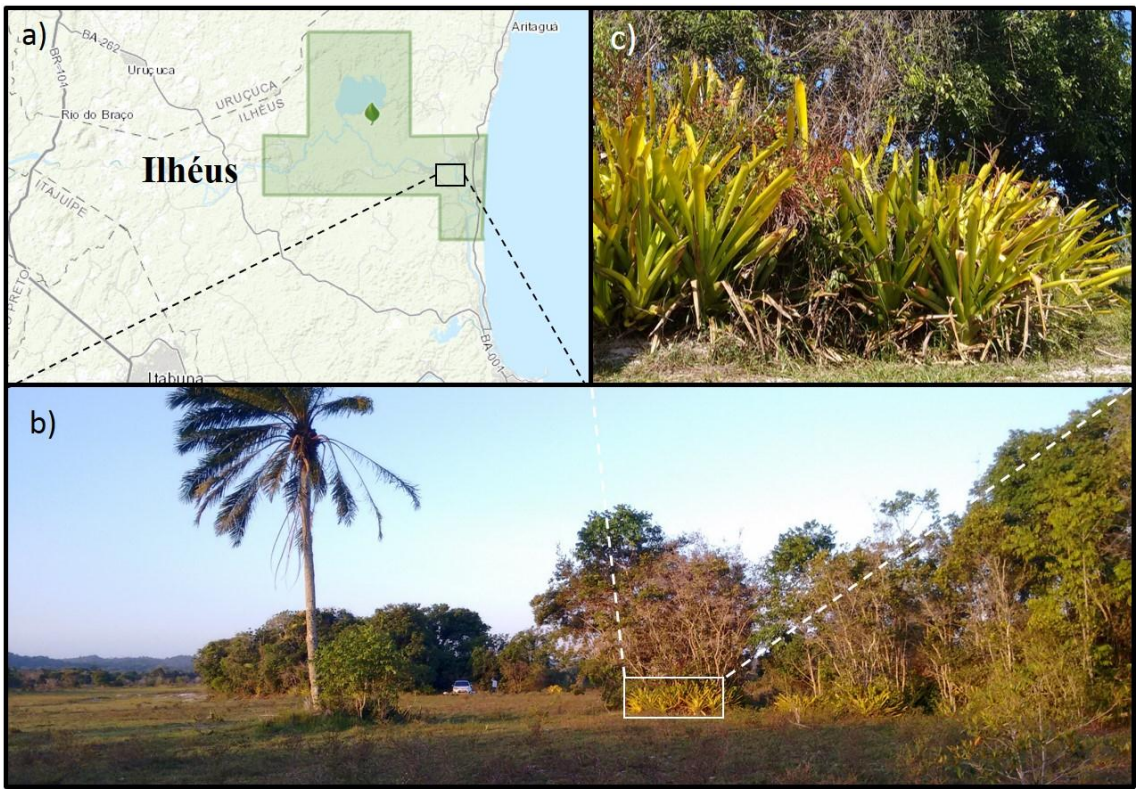

Figura 3. a) Mapa dos limites geográficos da APA da Lagoa Encantada, localizada no município de Ilhéus, Bahia, Brasil. Fonte: (SOCIOAMBIENTAL.ORG, 2019); b) Imagem panorâmica da área de estudo localizada na APA Lagoa Encantada; c) Exemplo de moita de *Vriesea philippocoburgii* Wawra, bromélia utilizada neste estudo.

Criada em 1993 com o intuito de proteger exemplares endêmicos e raros da fauna e flora local e regional, esta Unidade de Conservação possui área total de 157.745 ha, incluindo áreas de florestas, restingas, manguezais, cachoeiras, nascentes, cavernas e uma extensa lagoa (INEMA, 2019; SOCIOAMBIENTAL.ORG, 2019). Apesar de ser uma área protegida, sofre diferentes pressões antrópicas, incluindo o desmatamento de florestas, restingas e manguezais, queimadas, atividades de caça e extração, comercialização ilegal de plantas como bromélias e orquídeas (INEMA, 2019) e invasão por construções irregulares. Além desta condição atual, a construção de uma estrada de ferro para transporte de cargas para o chamado “Porto Sul” em Ilhéus, representa forte ameaça (direta e indireta) para esta APA (DÉCIMO, 2011). Para esta obra, de infraestrutura logística, foram previstos 19 impactos socioeconômicos e outros 29

relacionados ao ambiente físico da região, dentre eles a supressão da vegetação (incluindo moitas de bromélias), e aumento nas quantidades de ferro e outros metais em áreas próximas às ferrovias (DÉCIMO, 2011).

Neste sentido, esta pesquisa possibilita aumentar o conhecimento deste importante grupo ecológico, e poderá servir de base para pesquisas futuras que busquem avaliar eventuais impactos de caráter antrópico ou natural que venham a ocorrer na região.

Objetivo geral:

Esta tese visou (i) identificar os padrões de metacomunidades de macroinvertebrados aquáticos de água doce mais usualmente reportados em estudos científicos, a partir de uma revisão bibliográfica; e (ii) avaliar a influência de diferentes fatores ecológicos sobre padrões de diversidade de comunidades de macroinvertebrados aquáticos de bromélias, situadas em uma restinga no sul da Bahia. Assim, a tese é apresentada em três capítulos, redigidos em formato de artigo científicos (Fig. 4):

- No primeiro capítulo, apresento uma revisão cienciométrica sobre a produção científica de metacomunidades de macroinvertebrados aquáticos de água doce nos mais diversos ambientes (i.e., rios, lagos, poças e fitotelmatas), apresentando quais padrões de metacomunidades são mais comuns em cada ambiente, e como fatores intrínsecos a cada ambiente (por exemplo, a dinâmica hídrica), pode estar relacionado com uma maior ou menor ocorrência de determinado padrão de metacomunidade. Este capítulo será submetido à revista *Acta Oecologica*.

- No segundo capítulo, avalio os efeitos das variáveis espacial, ambientais e das interações entre as espécies sobre a estrutura da diversidade beta de macroinvertebrados associados aos tanques de *Vriesea philippocoburgii* (Bromeliaceae) em uma restinga no sul da Bahia, demonstrando a importância não apenas do ambiente, mas também das interações entre as espécies na determinação da distribuição dos táxons nas comunidade. Este capítulo foi submetido à revista *Freshwater Biology*.

- Por fim, no terceiro capítulo, investigo os efeitos do tamanho da bromélia e de variáveis físico-químicas de seu tanque sobre a estrutura taxonômica e funcional das comunidades de macroinvetebrados aquáticos associados aos tanques de bromélias, e sugiro como alterações antrópicas podem alterar estas estruturas e os serviços ambientais prestados por este grupo de organismos. Este capítulo será submetido e está formatado segundo as normas da revista *Hydrobiologia*.

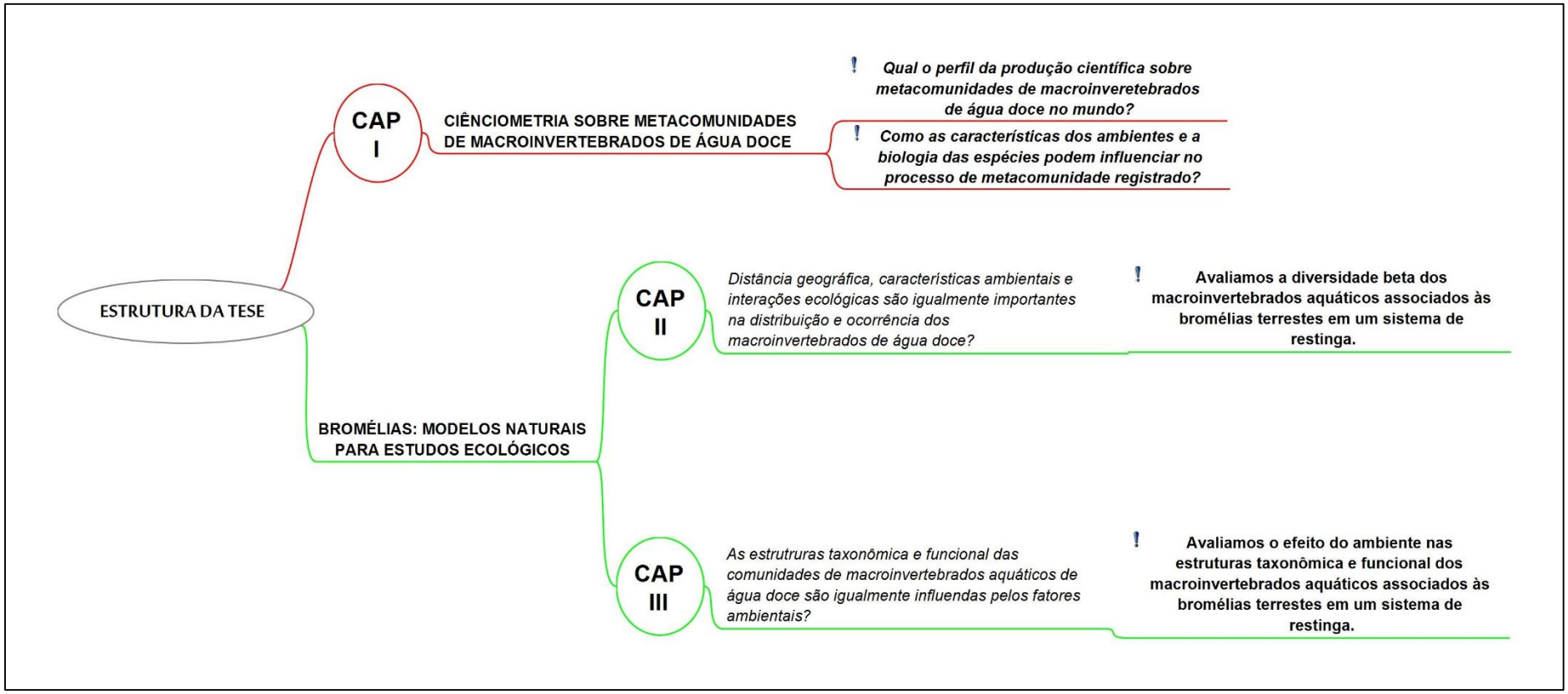

Fig. 4 - Fluxograma da estrutura da tese.

REFERÊNCIAS

AMUNDRUD, S. L.; SRIVASTAVA, D. S. Trophic interactions determine the effects of drought on an aquatic Ecosystem. **Ecology**, v. 97, n. 6, p. 1475–1483, 2016.

ANDERSON, M. J.; CRIST, T. O.; CHASE, J. M.; VELLEND, M.; INOUYE, B. D.; FREESTONE, A. L.; SANDERS, N. J.; CORNELL, H. V.; COMITA, L. S.; DAVIES, K. F.; HARRISON, S. P.; KRAFT, N. J. B.; STEGEN, J. C.; SWENSON, N. G. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. **Ecology Letters**, v. 14, n. 1, p. 19–28, 2011. Disponível em: <http://doi.wiley.com/10.1111/j.1461-0248.2010.01552.x>

ANTIQUEIRA, P. A. P.; PETCHEY, O. L.; ROMERO, G. Q. Warming and top predator loss drive ecosystem multifunctionality. **Ecology Letters**, v. 21, n. 1, p. 72–82, 2018.

ASTORGA, A.; OKSANEN, J.; LUOTO, M.; SOININEN, J.; VIRTANEN, R.; MUOTKA, T. Distance decay of similarity in freshwater communities: Do macro- and microorganisms follow the same rules? **Global Ecology and Biogeography**, v. 21, n. 3, p. 365–375, 2012.

BALKE, M.; GÓMEZ-ZURITA, J.; RIBERA, I.; VILORIA, A.; ZILLIKENS, A.; STEINER, J.; GARCÍA, M.; HENDRICH, L.; VOGLER, A. P. Ancient associations of aquatic beetles and tank bromeliads in the Neotropical forest canopy. **Proceedings of the National Academy of Sciences of the United States of America**, v. 105, n. 17, p. 6356–61, 2008. Disponível em: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2359786&tool=pmcentrez&rendertype=abstract>

BARRIOS, E. Soil biota, ecosystem services and land productivity. **Ecological Economics**, v. 64, n. 2, p. 269–285, 2007.

BASELGA, A. Partitioning the turnover and nestedness components of beta diversity. **Global Ecology and Biogeography**, v. 19, n. 1, p. 134–143, 2010. Disponível em: <https://doi.org/10.1111/j.1466-8238.2009.00490.x>

BAZZAZ, F. A. Plant Species Diversity in Old-Field Successional Ecosystems in Southern Illinois. **Ecology**, v. 56, n. 2, p. 485–488, 1975. Disponível em: <http://www.jstor.org/stable/1934981>

BERNABÉ, T. N.; DE OMENA, P. M.; SANTOS, V. P. Dos; DE SIQUEIRA, V. M.; DE OLIVEIRA, V. M.; ROMERO, G. Q. Warming weakens facilitative interactions between decomposers and detritivores, and modifies freshwater ecosystem functioning. **Global Change Biology**, v. 24, n. 7, p. 3170–3186, 2018.

BLAUSTEIN, L.; KIFLAWI, M.; EITAM, A.; MANGEL, M.; COHEN, J. E. Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. **Oecologia**, v. 138, n. 2, p. 300–305, 2004. Disponível em: <https://doi.org/10.1007/s00442-003-1398-x>

BRADTKA, J. H.; HEIBL, C.; MÜLLER, J.; BÄSSLER, C.; CADOTTE, M. W.; BEUDERT, B.; LANGBEHN, T.; WERTH, S.; BLASCHKE, M. Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. **Ecography**, v. 39, n. 7, p. 689–698, 2015.

BRAGA, C.; DE OLIVEIRA, J. A.; CERQUEIRA, R. Metacomunidades: Uma introdução aos termos e conceitos. **Oecologia Australis**, v. 21, n. 2, p. 108–118, 2017.

BROUARD, O.; CÉRÉGHINO, R.; CORBARA, B.; LEROY, C.; PELOZUELO, L.; DEJEAN, A.; CARRIAS, J. F. Understorey environments influence functional diversity in tank-bromeliad ecosystems. **Freshwater Biology**, v. 57, n. 4, p. 815–823, 2012.

BUSSE, A.; ANTIQUEIRA, P. A. P.; NEUTZLING, A. S.; WOLF, A. M.; ROMERO, G. Q.; PETERMANN, J. S. Different in the dark: The effect of habitat characteristics on community composition and beta diversity in bromeliad microfauna. **PLOS ONE**, v. 13, n. 2, p. e0191426, 2018. Disponível em: <http://dx.plos.org/10.1371/journal.pone.0191426>

CADOTTE, M. W.; CARSCADDEN, K.; MIROTCHNICK, N. Beyond species: Functional diversity and the maintenance of ecological processes and services. **Journal of Applied Ecology**, v. 48, n. 5, p. 1079–1087, 2011.

CALAÇA, A. M.; GRELLE, C. E. V. Diversidade Funcional De Comunidades: Discussões Conceituais E Importantes Avanços Metodológicos. **Oecologia Australis**, v. 20, n. 04, p. 401–416, 2017.

CARLOS, L.; LOPEZ, S.; RIOS, R. I.; LOPEZ, L. C. S.; RIOS, R. I. Phytotelmata Faunal Communities in Sun-Exposed Versus Shaded Terrestrial Bromeliads from Southeastern Brazil. **Selbyana**, v. 22, n. 2, p. 219–224, 2001. Disponível em: <http://www.jstor.org/stable/41760099>

CASTILLO-ESCRIVÀ, A.; VALLS, L.; ROCHERA, C.; CAMACHO, A.; MESQUITA-JOANES, F. Spatial and environmental analysis of an ostracod metacommunity from endorheic lakes. **Aquatic Sciences**, v. 78, n. 4, p. 707–716, 2016.

CASWELL, H.; COHEN, J. E. Disturbance, interspecific interaction and diversity in metapopulations. **Biological Journal of the Linnean Society**, v. 42, n. 1–2, p. 193–218, 1991. Disponível em: <https://academic.oup.com/biolinnean/article-lookup/doi/10.1111/j.1095-8312.1991.tb00560.x>

CAUVY-FRAUNIÉ, S.; ESPINOSA, R.; ANDINO, P.; JACOBSEN, D.; DANGLES, O. Invertebrate metacommunity structure and dynamics in an Andean glacial stream network facing climate change. **PLoS ONE**, v. 10, n. 8, p. 1–19, 2015. Disponível em: <http://dx.doi.org/10.1371/journal.pone.0136793>

CÉRÉGHINO, R.; LEROY, C.; CARRIAS, J. F.; PELOZUELO, L.; SÉGURA, C.; BOSC, C.; DEJEAN, A.; CORBARA, B. Ant-plant mutualisms promote functional diversity in phytotelm communities. **Functional Ecology**, v. 25, n. 5, p. 954–963, 2011.

CIANCIARUSO, M. V.; SILVA, I. A.; BATALHA, M. A. Diversidades filogenética e funcional: novas abordagens para a Ecologia de comunidades. **Biota Neotropica**, v. 9, n. 3, p. 93–103, 2009. Disponível em: <http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1676-06032009000300008&lng=pt&tlng=pt>

CORNELL, A. H. V; LAWTON, J. H. Species Interactions , Local and Regional Processes , and Limits to the Richness of Ecological Communities : A Theoretical Perspective Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/5503 REFERENCES Linked references are. **Journal of**

Animal Ecology, v. 61, n. 1, p. 1–12, 1992.

CUMMING, G. S.; CHILD, M. F. Contrasting spatial patterns of taxonomic and functional richness offer insights into potential loss of ecosystem services. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 364, n. 1524, p. 1683–1692, 2009.

CZERNIAWSKA-KUSZA, I. Comparing modified biological monitoring working party score system and several biological indices based on macroinvertebrates for water-quality assessment. **Limnologica**, v. 35, n. 3, p. 169–176, 2005. Disponível em: <http://www.sciencedirect.com/science/article/pii/S0075951105000411>

DALLAS, T.; DRAKE, J. M. Relative importance of environmental, geographic, and spatial variables on zooplankton metacommunities. **Ecosphere**, v. 5, n. 9, 2014.

DE SOUZA NOGUEIRA, I.; CARLOS NABOUT, J.; EDUARDO OLIVEIRA, J.; DUARTE SILVA, K. Diversidade (alfa, beta e gama) da comunidade fitoplanctônica de quatro lagos artificiais urbanos do município de Goiânia, GO. **Hoehnea**, v. 35, n. 2, p. 219–233, 2008. Disponível em: <http://www.scielo.br/pdf/hoehnea/v35n2/v35n2a05.pdf>

DÉCIMO, T. **Porto na Bahia causará danos ambientais**. 2011. Acessado em: 10 de junho de 2019. <https://uc.socioambiental.org/pt-br/noticia/107126>

DEJEAN, A.; COMPIN, A.; LEPONCE, M.; AZÉMAR, F.; BONHOMME, C.; TALAGA, S.; PELOZUELO, L.; HÉNAUT, Y.; CORBARA, B. Ants impact the composition of the aquatic macroinvertebrate communities of a myrmecophytic tank bromeliad. **Comptes Rendus - Biologies**, v. 341, n. 3, p. 200–207, 2018.

DÉZERALD, O.; LEROY, C.; CORBARA, B.; DEJEAN, A.; TALAGA, S.; CÉRÉGHINO, R. Environmental drivers of invertebrate population dynamics in Neotropical tank bromeliads. **Freshwater Biology**, v. 62, n. 2, p. 229–242, 2017.

DÉZERALD, O.; LEROY, C.; CORBARA, B.; DEJEAN, A.; TALAGA, S.; CÉRÉGHINO, R. Tank bromeliads sustain high secondary production in neotropical forests. **Aquatic Sciences**, v. 80, n. 2, p. 0, 2018. Disponível em: <http://dx.doi.org/10.1007/s00027-018-0566-3>

DÉZERALD, O.; TALAGA, S.; LEROY, C.; CARRIAS, J.-F.; CORBARA, B.; DEJEAN, A.; CÉRÉGHINO, R. Environmental determinants of macroinvertebrate diversity in small water bodies: insights from tank-bromeliads. **Hydrobiologia**, v. 723, n. 1, p. 77–86, 2014. Disponível em: <http://link.springer.com/10.1007/s10750-013-1464-2>

DOI, H.; CHANG, K. H.; NAKANO, S. I. Dispersal, connectivity, and local conditions determine zooplankton community composition in artificially connected ponds. **Aquatic Biology**, v. 10, n. 1, p. 47–55, 2010.

FERREIRA, M.; BEJA, P. Mediterranean amphibians and the loss of temporary ponds: Are there alternative breeding habitats? **Biological Conservation**, v. 165, p. 179–186, 2013.

FISCHER, J.; B. LINDENMAYER, D. Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. **Oikos**, v. 112, n. 2, p. 473–480, 2006. Disponível em: <https://doi.org/10.1111/j.0030-1299.2006.14148.x>

FLYNN, D. F. B.; GOGOL-PROKURAT, M.; NOGEIRE, T.; MOLINARI, N.; RICHERS, B. T.; LIN, B. B.; SIMPSON, N.; MAYFIELD, M. M.; DECLERCK, F. Loss of functional diversity under land use intensification across multiple taxa. **Ecology Letters**, v. 12, n. 1, p. 22–33, 2009. Disponível em: <https://doi.org/10.1111/j.1461-0248.2008.01255.x>

GIACOMINI, H. C. Os mecanismos de coexistência de espécies como vistos pela teoria ecológica. **Oecologia Brasiliensis**, v. 11, n. 04, p. 521–543, 2007. Disponível em: <http://www.ppgecologia.biologia.ufrj.br/oecologia/index.php/oecologiabrasiliensis/article/view/164/130>

GONÇALVES, F. B.; MENEZES, M. S. De. **A comparative analysis of biotic indices that use macroinvertebrates to assess water quality in a coastal river of Paraná state, southern Brazil** , scielo , 2011.

GONZÁLEZ, A. L.; ROMERO, G. Q.; SRIVASTAVA, D. S. Detrital nutrient content determines growth rate and elemental composition of bromeliad-dwelling insects. **Freshwater Biology**, v. 59, n. 4, p. 737–747, 2014. Disponível em: <http://doi.wiley.com/10.1111/fwb.12300>

GOSSNER, M. M.; LADE, P.; ROHLAND, A.; SICHARDT, N.; KAHL, T.; BAUHUS, J.; WEISSER, W. W.; PETERMANN, J. S. Effects of management on aquatic tree-hole communities in temperate forests are mediated by detritus amount and water chemistry. **Journal of Animal Ecology**, v. 85, n. 1, p. 213–226, 2016.

HANSKI, I.; GILPIN, Mi. Metapopulation dynamics: brief history and conceptual domain. **Biological Journal of the Linnean Society**, v. 42, n. 1- 2, p. 3–16, 1991. Disponível em: <https://doi.org/10.1111/j.1095-8312.1991.tb00548.x>

HEINO, J.; MELO, A. S.; SIQUEIRA, T.; SOININEN, J.; VALANKO, S.; BINI, L. M. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. **Freshwater Biology**, v. 60, n. 5, p. 845–869, 2015. Disponível em: <https://onlinelibrary.wiley.com/doi/abs/10.1111/fwb.12533>

HILL, J. K.; HAMER, K. C.; LACE, L. A.; BANHAM, W. M. T. Effects of Selective Logging on Tropical Forest Butterflies on Buru, Indonesia. **Journal of Applied Ecology**, v. 32, n. 4, p. 754–760, 1995. Disponível em: <http://www.jstor.org/stable/2404815>

HOLT, R. D. Predation, apparent competition, and the structure of prey communities. **Theoretical Population Biology**, v. 12, n. 2, p. 197–229, 1977. Disponível em: <https://linkinghub.elsevier.com/retrieve/pii/0040580977900429>

HOWETH, J. G.; LEIBOLD, M. A. Prey dispersal rate affects prey species composition and trait diversity in response to multiple predators in metacommunities. **Journal of Animal Ecology**, v. 79, n. 5, p. 1000–1011, 2010.

HUBBELL, S. P. **The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)**. Princeton University Press, 2001. Disponível em: <http://www.jstor.org/stable/j.ctt7rj8w>

HUFFAKER, C. Fundamentals of biological control of weeds. **Hilgardia**, v. 27, n. 3, p. 101–157, 1957.

HUTCHINSON, G. E. Concluding Remarks. **Cold Spring Harbor Symposia on Quantitative Biology**, v. 22, p. 415–427, 1957. Disponível em:

<http://symposium.cshlp.org/content/22/415.short>

INEMA, I. do M. A. e R. H.-. **APA Lagoa Encantada e Rio Almada**. 2019. Disponível em: <http://www.inema.ba.gov.br/gestao-2/unidades-de-conservacao/apa/apa-lagoa-encantada-e-rio-almada/>. Acesso em: 23 jun. 2019.

JAMONEAU, A.; CHABRERIE, O.; CLOSSET-KOPP, D.; DECOCQ, G. Fragmentation alters beta-diversity patterns of habitat specialists within forest metacommunities. **Ecography**, v. 35, n. 2, p. 124–133, 2012.

LAMBRET, P.; BESNARD, A.; MATUSHKINA, N. Initial preference for plant species and state during oviposition site selection by an odonate. **Entomological Science**, v. 18, n. 3, p. 377–382, 2015. Disponível em: <https://doi.org/10.1111/ens.12130>

LECRAW, R. M.; SRIVASTAVA, D. S.; ROMERO, G. Q. Metacommunity size influences aquatic community composition in a natural mesocosm landscape. **Oikos**, v. 123, n. 8, p. 903–911, 2014.

LEIBOLD, M. A.; GEDDES, P. El concepto de nicho en las metacomunidades. **Ecología austral**, v. 77, p. 181, 2005. Disponível em: <http://papers.uab.cat/article/view/v77-ballester-colom>

LEIBOLD, M. A.; HOLYOAK, M.; MOUQUET, N.; AMARASEKARE, P.; CHASE, J. M.; HOOPES, M. F.; HOLT, R. D.; SHURIN, J. B.; LAW, R.; TILMAN, D.; LOREAU, M.; GONZALEZ, A. The metacommunity concept: A framework for multi-scale community ecology. **Ecology Letters**, v. 7, n. 7, p. 601–613, 2004.

LEROY, C.; CORBARA, B.; DÉZERALD, O.; TRZCINSKI, M. K.; CARRIAS, J. F.; DEJEAN, A.; CÉRÉGHINO, R. What drives detrital decomposition in neotropical tank bromeliads? **Hydrobiologia**, v. 802, n. 1, p. 85–95, 2017.

LIMBERGER, R.; WICKHAM, S. A. Predator Dispersal Determines the Effect of Connectivity on Prey Diversity. **PLoS ONE**, v. 6, n. 12, p. e29071, 2011. Disponível em: <https://dx.plos.org/10.1371/journal.pone.0029071>

LIRMAN, D. Competition between macroalgae and corals: Effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. **Coral Reefs**, v. 19, n. 4, p. 392–399, 2001. Disponível em: <http://link.springer.com/10.1007/s003380000125>

LOGUE, J. B.; MOUQUET, N.; PETER, H.; HILLEBRAND, H. Empirical approaches to metacommunities: a review and comparison with theory. **Trends in Ecology & Evolution**, v. 26, n. 9, p. 482–491, 2011. Disponível em: <http://linkinghub.elsevier.com/retrieve/pii/S0169534711001315>

LOPEZ, L. C. S.; SILVA, E. G. B.; BELTRÃO, M. G.; LEANDRO, R. S.; BARBOSA, J. E. L.; BESERRA, E. B. Effect of tank bromeliad micro-environment on Aedes aegypti larval mortality. **Hydrobiologia**, v. 665, n. 1, p. 257–261, 2011. Disponível em: <http://dx.doi.org/10.1007/s10750-011-0605-8>

LOREAU, M.; NAEEM, S.; INCHAUSTI, P.; BENGTSSON, J.; GRIME, J. P.; HECTOR, A.; HOOPER, D. U.; HUSTON, M. A.; RAFFAELLI, D.; SCHMID, B.; TILMAN, D.; WARDLE, D. A. Ecology: Biodiversity and ecosystem functioning: Current knowledge and future challenges. **Science**, v. 294, n. 5543, p. 804–808, 2001.

LOUNIBOS; FRANK. Insects and allies associated with bromeliads: a review.

Terrestrial Arthropod Reviews, v. 1, n. 2, p. 125–153, 2009. Disponível em: <http://booksandjournals.brillonline.com/content/journals/10.1163/187498308x414742

MACARTHUR, R. H.; MACARTHUR, J. W. On Bird Species Diversity. **Ecology**, v. 42, n. 3, p. 594–598, 1961. Disponível em: <http://www.jstor.org/stable/1932254>

MACARTHUR, R. H.; WILSON, E. O. **The theory of island biogeography**. Princeton university press, 1967. v. 1

MAGURRAN, A. **Measuring Biological Diversity**. 2004. Blackwell Science Ltd. ISBN 0-632-05633-9.

MARINO, N. A. C.; GUARIENTO, R. D.; DIB, V.; AZEVEDO, F. D.; FARJALLA, V. F. Habitat size determine algae biomass in tank-bromeliads. **Hydrobiologia**, v. 678, n. 1, p. 191–199, 2011.

MARTINELLI, G.; VIEIRA, C. M.; GONZALEZ, M.; LEITMAN, P.; PIRATININGA, A.; COSTA, A. F. Da; FORZZA, R. C. Bromeliaceae Da Mata Atlântica Brasileira: Lista De Espécies, Distribuição E Conservação. **Rodriguésia**, v. 59, n. 1, p. 209–258, 2018.

MASON, N. W. H.; DE BELLO, F.; MOUILLOT, D.; PAVOINE, S.; DRAY, S. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. **Journal of Vegetation Science**, v. 24, n. 5, p. 794–806, 2013. Disponível em: <http://doi.wiley.com/10.1111/jvs.12013>

MAYFIELD, M. M.; BONSER, S. P.; MORGAN, J. W.; AUBIN, I.; MCNAMARA, S.; VESK, P. A. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. **Global Ecology and Biogeography**, v. 19, n. 4, p. 423–431, 2010.

MELISSA, L.; ID, G.; VANSCHOENWINKEL, B.; FARJALLA, V. F.; POON, A.; SRIVASTAVA, D. S. A precipitation gradient drives change in macroinvertebrate composition and interactions within bromeliads. **PloS One**, v. 11, n. e0200179, p. 1–14, 2018.

MEYER-ROCHOW, V. B. Natural microcosms. **Trends in ecology & evolution**, v. 13, n. 5, p. 201, 1998.

MIGLIORINI, G. H.; SRIVASTAVA, D. S.; ROMERO, G. Q. Leaf litter traits drive community structure and functioning in a natural aquatic microcosm. **Freshwater Biology**, v. 63, n. 4, p. 341–352, 2018.

MOUCHET, M. A.; VILLÉGER, S.; MASON, N. W. H.; MOUILLOT, D. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. **Functional Ecology**, v. 24, n. 4, p. 867–876, 2010. Disponível em: <http://doi.wiley.com/10.1111/j.1365-2435.2010.01695.x>

MOUQUET, N.; LOREAU, M. Community Patterns in Source- Sink Metacommunities. **The American Naturalist**, v. 162, n. 5, p. 544–557, 2004.

MÜLLER, G. A.; MARCONDES, C. B. Immature mosquitoes (Diptera: Culicidae) on the bromeliad Nidularium innocentii in ombrophilous dense forest of Santa Catarina Island, Florianopolis, Santa Catarina State, southern Brazil. **Biotemas**, v. 20, n. 2, p. 27–31, 2007.

MÜLLER, S. C.; RUI, A. M.; HARTZ, S. M.; BERGMANN, F. B.; SACCO, A. G. Perda de diversidade taxonômica e funcional de aves em área urbana no sul do Brasil. **Iheringia. Série Zoologia**, v. 105, n. 3, p. 276–287, 2015.

NG, I. S. Y.; CARR, C. M.; COTTENIE, K. Hierarchical zooplankton metacommunities: Distinguishing between high and limiting dispersal mechanisms. **Hydrobiologia**, v. 619, n. 1, p. 133–143, 2009.

NICOLINI, E. A.; BARALOTO, C.; BLANC, L.; BONAL, D.; MASSOT, H.; MOLINO, J.-F.; SABATIER, D.; HÉRAULT, B.; PAINE, C. E. T. Contrasting taxonomic and functional responses of a tropical tree community to selective logging. **Journal of Applied Ecology**, v. 49, n. 4, p. 861–870, 2012.

PARADISE, C. J.; BLUE, J. D.; BURKHART, J. Q.; GOLDBERG, J.; HARSHAW, L.; HAWKINS, K. D.; KEGAN, B.; KRENTZ, T.; SMITH, L.; VILLALPANDO, S. Local and regional factors influence the structure of treehole metacommunities. **BMC Ecology**, v. 8, p. 1–16, 2008.

PARADISE, C. J.; SOCIETY, B. E. Effects of pH and resources on a processing chain interaction in simulated treeholes. **Journal of Animal Ecology**, v. 69, n. 4, p. 651–658, 2000. Disponível em: <http://www.jstor.org/stable/2647264>

PAULA JÚNIOR, A. T. De; ROSA, B. F. J. V.; ALVES, R. G.; DIVINO, A. C. Aquatic invertebrates associated with bromeliads in Atlantic Forest fragments. **Biota Neotropica**, v. 17, n. 1, p. 1–7, 2017.

PERONI, N.; HERNÁNDEZ, M. I. M. **Ecologia de Populações e Comunidades**. Florianópolis : CCB/EAD/UFSC, 2011.

PLISNIER, P.D.; O'REILLY, C. M.; ALIN, S. R.; MCKEE, B. A.; COHEN, A. S. Erratum: Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. **Nature**, v. 424, n. 6950, p. 766–768, 2003.

PODGAISKI, L. R.; MENDONÇA, M. de S.; PILLAR, V. D. O uso de atributos funcionais de invertebrados terrestres na ecologia: O que, como e por quê? **Oecologia Australis**, v. 15, n. 4, p. 835–853, 2011.

PRESLEY, S. J.; HIGGINS, C. L.; LÓPEZ-GONZÁLEZ, C.; STEVENS, R. D. Elements of metacommunity structure of Paraguayan bats: Multiple gradients require analysis of multiple ordination axes. **Oecologia**, v. 160, n. 4, p. 781–793, 2009.

RANGEL, J. V.; ARAÚJO, R. E. S.; CASOTTI, C. G.; COSTA, L. C.; KIFFER, W. P.; MORETTI, M. S. Assessing the role of canopy cover on the colonization of phytotelmata by aquatic invertebrates: An experiment with the tank-bromeliad Aechmea lingulata. **Journal of Limnology**, v. 76, n. 2, p. 230–239, 2017.

RIBEIRO, M. C.; MARTENSEN, A. C.; METZGER, J. P.; TABARELLI, M.; SCARANO, F.; FORTIN, M.-J. The Brazilian Atlantic Forest: A Shrinking Biodiversity Hotspot. In: **Biodiversity Hotspots**. Berlin, Heidelberg: Springer Berlin Heidelberg, 2011. v. 13p. 405–434.

RICKLEFS, R. E. Community Diversity: Relative Roles of Local and Regional Processes. **Science**, v. 235, n. 4785, p. 167 LP – 171, 1987. Disponível em: <http://science.sciencemag.org/content/235/4785/167.abstract>

RICKLEFS, R. E. **A economia da natureza**. 2003. 5ªEd. Editora: Guanabara Koogan.

ROCHA, C.; BERGALLO, H.; VAN SLUYS, M.; ALVES, M.; JAMEL, C. The remnants of restinga habitats in the brazilian Atlantic Forest of Rio de Janeiro state, Brazil: habitat loss and risk of disappearance. **Brazilian Journal of Biology**, v. 67, n. 2, p. 263–273, 2007.

ROSENTHAL, M. F.; GERTLER, M.; HAMILTON, A. D.; PRASAD, S.; ANDRADE, M. C. B. Taxonomic bias in animal behaviour publications. **Animal Behaviour**, v. 127, n. August, p. 83–89, 2017. Disponível em: <http://dx.doi.org/10.1016/j.anbehav.2017.02.017>

SARREMEJANE, R.; MYKRÄ, H.; BONADA, N.; AROVIITA, J.; MUOTKA, T. Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. **Freshwater Biology**, v. 62, n. 6, p. 1073–1082, 2017.

SCARANO, F. R.; DUARTE, H. M.; RIBEIRO, K. T.; RODRIGUES, P. J. F. P.; BARCELLOS, E. M. B.; FRANCO, A. C.; BRULFERT, J.; DELEÉNS, E.; LÜTTGE, U. Four sites with contrasting environmental stress in southeastern Brazil: relations of species, life form diversity, and geographic distribution to ecophysiological parameters. **Botanical Journal of the Linnean Society**, v. 136, n. 4, p. 345–364, 2001. Disponível em: <https://academic.oup.com/botlinnean/article-lookup/doi/10.1111/j.1095-8339.2001.tb00579.x>

SCHEFFERS, B. R.; JOPPA, L. N.; PIMM, S. L.; LAURANCE, W. F. What we know and don't know about Earth's missing biodiversity. **Trends in Ecology and Evolution**, v. 27, n. 9, p. 501–510, 2012. Disponível em: <http://dx.doi.org/10.1016/j.tree.2012.05.008>

SCHLEUTER, D.; DAUFRESNE, M.; MASSOL, F.; ARGILLIER, C. A user's guide to functional diversity indices. **Ecological Monographs**, v. 80, n. 3, p. 469–484, 2010. Disponível em: <http://doi.wiley.com/10.1890/08-2225.1>

SCHMERA, D.; HEINO, J.; PODANI, J.; ERŐS, T.; DOLÉDEC, S. Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. **Hydrobiologia**, v. 787, n. 1, p. 27–44, 2017. Disponível em: <http://link.springer.com/10.1007/s10750-016-2974-5>

SCHOWALTER, T. D. **Insect ecology: an ecosystem approach**. Academic Press, 2016.

SEDDON, P. J.; SOORAE, P. S.; LAUNAY, F. Taxonomic bias in reintroduction projects. **Animal Conservation**, v. 8, n. 1, p. 51–58, 2005.

SEGRE, H.; RON, R.; DE MALACH, N.; HENKIN, Z.; MANDEL, M.; KADMON, R. Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. **Ecology Letters**, v. 17, n. 11, p. 1400–1408, 2014.

SELLAMI, I.; ELLOUMI, J.; HAMZA, A.; MHAMDI, M. A.; AYADI, H. Local and regional factors influencing zooplankton communities in the connected kasseb Reservoir, Tunisia. **Water SA**, v. 37, n. 2, p. 201–212, 2011.

SHMIDA, A.; WILSON, M. V. Biological Determinants of Species Diversity. **Journal of Biogeography**, v. 12, n. 1, p. 1, 1985. Disponível em: <https://www.jstor.org/stable/2845026?origin=crossref>

SILVA, R. A.; MARTINS, I. A.; ROSSA-FERES, D. de C. Environmental heterogeneity: Anuran diversity in homogeneous environments. **Zoologia (Curitiba)**, v. 28, n. 5, p. 610–618, 2011.

SOCIOAMBIENTAL.ORG, U. de C. no B. S.-. **Área de Proteção Ambiental da Lagoa Mapa Municípios**. 2019. Disponível em: <https://uc.socioambiental.org/arp/1207>. Acesso em: 10 jun. 2019.

SOCOLAR, J. B.; GILROY, J. J.; KUNIN, W. E.; EDWARDS, D. P. How Should Beta-Diversity Inform Biodiversity Conservation? **Trends in Ecology & Evolution**, v. 31, n. 1, p. 67–80, 2016. Disponível em: <https://linkinghub.elsevier.com/retrieve/pii/S016953471500289X>

SODRÉ, V. M.; ROCHA, O.; MESSIAS, M. C. Chironomid larvae inhabiting bromeliad phytotelmata in a fragment of the Atlantic Rainforest in Rio de Janeiro State. **Brazilian journal of biology = Revista brasleira de biologia**, v. 70, n. 3, p. 587–92, 2010. Disponível em: <http://www.ncbi.nlm.nih.gov/pubmed/20730345>

SOININEN, J. A quantitative analysis of species sorting across organisms and ecosystems. **Ecology**, v. 95, n. 12, p. 3284–3292, 2014. Disponível em: <http://doi.wiley.com/10.1890/13-2228.1>

SOKOL, E. R.; BROWN, B. L.; CAREY, C. C.; TORNWALL, B. M.; SWAN, C. M.; BARRETT, J. E. Linking management to biodiversity in built ponds using metacommunity simulations. **Ecological Modelling**, v. 296, p. 36–45, 2015. Disponível em: <http://dx.doi.org/10.1016/j.ecolmodel.2014.10.022>

SRIVASTAVA, D. S.; KOLASA, J.; BENGTSSON, J.; GONZALEZ, A.; LAWLER, S. P.; MILLER, T. E.; MUNGUIA, P.; ROMANUK, T.; SCHNEIDER, D. C.; TRZCINSKI, M. K. Are natural microcosms useful model systems for ecology? **Trends in Ecology and Evolution**, v. 19, n. 7, p. 379–384, 2004.

SRIVASTAVA, D. S.; TRZCINSKI, M. K.; RICHARDSON, B. A.; GILBERT, B. Why Are Predators More Sensitive to Habitat Size than Their Prey? Insights from Bromeliad Insect Food Webs. **The American Naturalist**, v. 172, n. 6, p. 761–771, 2008. Disponível em: <http://www.journals.uchicago.edu/doi/10.1086/592868>

STORK, N. E. How Many Species of Insects and Other Terrestrial Arthropods Are There on Earth? **Annual Review of Entomology**, v. 63, n. 1, p. 31–45, 2018. Disponível em: <https://doi.org/10.1146/annurev-ento-020117-043348>

SULLIVAN, T. P.; SULLIVAN, D. S. Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. **Journal of Applied Ecology**, v. 38, n. 6, p. 1234–1252, 2001.

TEWS, J.; BROSE, U.; GRIMM, V.; TIELBÖRGER, K.; WICHMANN, M. C.; SCHWAGER, M.; JELTSCH, F. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. **Journal of Biogeography**, v. 31, n. 1, p. 79–92, 2004.

TILMAN, D.; REICH, P. B.; ISBELL, F. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. **Proceedings of the National Academy of Sciences**, v. 109, n. 26, p. 10394–10397, 2012. Disponível em: <http://www.pnas.org/cgi/doi/10.1073/pnas.1208240109>

TONKIN, J. D.; TACHAMO SHAH, R. D.; SHAH, D. N.; HOPPELER, F.; JOHNIG,

S. C.; PAULS, S. U. Metacommunity structuring in Himalayan streams over large elevational gradients: the role of dispersal routes and niche characteristics. **Journal of Biogeography**, v. 44, n. 1, p. 62–74, 2017.

TOWNSEND, C. R.; BEGON, M.; HARPER, J. L. **Fundamentos em ecologia**. Artmed Editora, 2009.

TRZCINSKI, M. K.; SRIVASTAVA, D. S.; CORBARA, B.; DÉZERALD, O.; LEROY, C.; CARRIAS, J. F.; DEJEAN, A.; CÉRÉGHINO, R. The effects of food web structure on ecosystem function exceeds those of precipitation. **The Journal of animal ecology**, v. 85, n. 5, p. 1147–1160, 2016.

VALANKO, S.; HEINO, J.; WESTERBOM, M.; VIITASALO, M.; NORKKO, A. Complex metacommunity structure for benthic invertebrates in a low-diversity coastal system. **Ecology and Evolution**, v. 5, n. 22, p. 5203–5215, 2015.

VAN LOOY, K.; TORMOS, T.; SOUCHON, Y. Disentangling dam impacts in river networks. **Ecological Indicators**, v. 37, n. PART A, p. 10–20, 2014. Disponível em: <http://dx.doi.org/10.1016/j.ecolind.2013.10.006>

VANSCHOENWINKEL, B.; DE VRIES, C.; SEAMAN, M.; BRENDONCK, L. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. **Oikos**, v. 116, n. 8, p. 1255–1266, 2007.

VELLEND, M. Do commonly used indices of β-diversity measure species turnover? **Journal of Vegetation Science**, v. 12, n. 4, p. 545–552, 2001. Disponível em: <http://doi.wiley.com/10.2307/3237006>

VILLÉGER, S.; MASON, N. W. H.; MOUILLOT, D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. **Ecology**, v. 89, n. 8, p. 2290–2301, 2008. Disponível em: <http://doi.wiley.com/10.1890/07-1206.1>

VILLÉGER, S.; MIRANDA, J. R.; HERNÁNDEZ, D. F.; MOUILLOT, D. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. **Ecological Applications**, v. 20, n. 6, p. 1512–1522, 2010. Disponível em: <http://doi.wiley.com/10.1890/09-1310.1>

WANDERLEY, M. G. L.; MARTINS, S. E. Bromeliaceae. In: **Flora fanerogâmica do Estado de São Paulo**. [s.l.] : Instituto de Botânica, 2007. p. 39–161.

WANG, J.; SOININEN, J.; ZHANG, Y.; WANG, B.; YANG, X.; SHEN, J. Patterns of elevational beta diversity in micro- and macroorganisms. **Global Ecology and Biogeography**, v. 21, n. 7, p. 743–750, 2012.

WHITTAKER, R. H. Vegetation of the Siskiyou Mountains, Oregon and California. **Ecological Monographs**, v. 30, n. 3, p. 279–338, 1960. Disponível em: <http://www.jstor.org/stable/1943563>

WHITTAKER, R. H. Evolution and Measurement of Species Diversity. **Taxon**, v. 21, n. 2/3, p. 213, 1972. Disponível em: <http://www.jstor.org/stable/1218190>

WILBUR, H. M. Competition, predation, and the structure of the Ambystoma- Rana sylvatica community. **Ecology**, v. 53, n. 1, p. 3–21, 1972.

WILSON, D. S. **Complex Interactions in Metacommunities, with Implications for Biodiversity and Higher Levels of Selection**. v. 73.

CAPÍTULO I

Metacommunity of freshwater macroinvertebrates: an overall scientiometric analysis

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ABSTRACT

The Theory of Metacommunities preconizes that all communities are interconnect mainly through dispersion processes. It currently includes ecologically consolidated theories, with Patch dynamics (PD), Species sorting (SS), Mass effect (ME) and Neutral model (NM) as its main pillars. We compiled the existing scientific publications about freshwater metacommunities available on-line. Based on this set, we intended to answer some questions about the latest advances in the area, as well as checked for possible links between patterns of metacommunities and different kinds of freshwater environments, their water dynamics, size of the studied area, as well as their mechanisms of dispersion. Most of the researched areas were in North America and Europe. Rivers and streams were the most researched environments in the last 4 years, aside from temporary ponds. The SS model, which lead in number of publications as well as in types of environments, considered passive dispersal to be its main characteristic. This shows the importance of environmental factors, and hydrological dynamics in forming metacommunity patterns for freshwater invertebrates. In addition, we emphasize the importance of using the metacommunities approach in water resources conservation.

Key-words: dispersion, species sorting, mass effect, water resources, conservation, hydrological dynamics.

Introduction

The idea of an isolated community does not mirror the reality found in nature. Communities found in the same region are integrated through species migration and immigration, which translates into inter- and intraspecific interactions peculiar to each environment (Leibold et al., 2004). To define this set of local communities, which can interact because they are potentially connected by dispersion of at least some individuals of part or all present species, the term "metacommunity" was adopted (Leibold & Mikkelson, 2002; Leibold et al., 2004; Holyoak et al., 2005). This term, although with more general concept, had already been used in the 1990s. It was defined as the result of "spatial heterogeneity, which fragments large-scale ecological systems into a mosaic of patches" (Wilson, 1992), currently considered a classic.

Theory of Metacommunities: Concepts and current theoretical approach

Leibold and collaborators (2004) refined the use of the term, applying as base three important ecological theories – The Theory of Niche (Hutchinson, 1957), the Theory of Island Biogeography (MacArthur & Wilson, 1967) and the Neutral Theory (Hubbell, 2001). The first seeks explaining how environmental conditions, at a set location, influence the set of species present and the way they interact. The second and third have as common base, the possibility of species dispersion, between areas. In addition, they assume that these species have no special requirements as to the niche and its fitness, that only physical limitation, within and externally to the habitat, would be important for the composition of the local community.

However, the conceptual base presented by these theories does not consider some ecological processes. Such as the capacity of its members to modify the environment they live in, through intra and interspecific interactions (Leibold & Geddes, 2005); and also the fact that there are more than a single source community and different dispersion capacities of their organisms. Both factors are fundamental for the community structuring and allow a connection between local communities, through migration and immigration (Leibold & Norberg, 2004; Legendre, 2008; Anderson et al., 2011).

Since the connection between habitats is a major factor in the formation of metacommunities (Leibold & Norberg, 2004), it is interesting that related studies of the issue clarify the spatial scale evaluated or the size of sample unit (Wiens, 1989). Research has shown that the richness and diversity of species (Gaston & Blackburn,

2000; Shurin et al., 2000); the composition (Van der Gucht et al., 2007; Alahuhta & Heino, 2013); the variation, whether of species (Mac Nally et al., 2004; Pinel-Alloul et al., 2013), or of functional groups (Alahuhta & Heino, 2013; Dézerald et al., 2013), the species–area relationship (Whittaker, Willis & Field, 2001; Willis, & Whittaker, 2002; Drakare, Lennon & Hillebrand, 2006), species-energy (Evans, Warren & Gaston, 2005), and dispersion processes (Shurin et al., 2000; Heino & Peckarsky, 2014; Heino et al., 2014).

Main patterns of Metacommunity

The mechanisms considered for the formation of a metacommunity are still under discussion (Winegardner et al., 2012; Heino et al., 2014). In general, their main approaches, or formation processes, are called Patch dynamics (PD), Species sorting (SS), Mass effect (ME) and Neutral model (NM) (Leibold et al., 2004), those include as major factors dispersal, selection (niche) and rout (Vellend, 2010).

Patch Dynamics predicts that even identical patches of habitat are capable of holding distinct populations of species, the diversity being hence limited by the dispersion capacity of each species and by the competitive skills of each. Mass Effect assumes that dispersion is a determining factor of the local dynamics of communities, considering the presence of patches with different conditions for migration and immigration and the role of the competitive skills of each species (Leibold et al., 2004). This approach is closely related to spatial distribution factors of patches. Species Sorting proposes that species have identical dispersal capacity, and their presence in environments is limited by how heterogeneous these environments are. Species should be able to survive local conditions as well as establish niche relations (Leibold & Geddes, 2005). Finally, the Neutral Model considers that all species possess similar capacities to compete, disperse and survive, and that variation in the composition is due to stochastic events (Hubbell, 2001; Leibold et al., 2004). So, even if the conditions of the patches eventually occupied are favorable, the local dynamics is due to random losses and gains of species (Leibold et al., 2004; Rosindel, Hubbell & Etienne, 2011) (Tabela 1).

Table 1. Conceptual synthasis, based on Leibold et al. (2004), main patterns of metacomunity identification

PATTERNS OF METACOMUNITIES	HABITAT QUALITY	DISPERSAL CAPACITY	INTERSPECIFI INTERACTIONS (NON HARMONIC)	STOCHASTIC EVENTS
Patch Dynamics	Non limiting	Limiting	Limiting	-
Mass Effect	Limiting	Limiting	Limiting	-
Species Sorting	Limiting	Non limiting	Limiting	-
Neutral Model	Non limiting	Non limiting	Non limiting	Main promoter of "diversity"

More recently, several authors have been discussing the possibility of processes acting together to establish a metacommunity. (Logue et al., 2011; Winegardner et al., 2012). This takes place when different processes acting at different periods, in different regions, or in different periods and regions of the environment under assessment. For example, ME and SS models are equally influenced by differences in niche between species, changing only the amount of specimens, of each species present (Vellend, 2010; Winegardner et al., 2012; Heino et al., 2014). Another possible situation would be the union promoted by interactions between environment dynamics and the life cycle of the local fauna (Vanschoenwinkel, 2009).

Freshwater systems and the influence of their features on the metacommunities

This theory has been also used for freshwater environments, focusing on benthic macroinvertebrate communities. Although the composition and richness of species can vary between environments, the same major macroinvertebrate groups (with emphasis on annelids, insects both adults and larvae, crustaceans and mollusks) have been registered in different lotic or lentic, permanent or temporary, big or small water bodies. The role of these organisms in aquatic systems permeate nutrient cycling (Ngai & Srivastava, 2006), energy flow regulation (Brouard et al., 2012) and structure of the food web. Could involve levels external to the water body (de Bello et al., 2010; Gonçalves et al., 2014; Schmera et al. 2017).

The general research dynamics certainly varies in different environments. For example, nutrients and organic material flow, within lotic and lentic systems, tend to be completely different. Such differences, between environments, take place due to hydrological dynamics, as much as to intra and interspecific interactions (Hall, Wallace & Eggert, 2000), aside from the role these macroinvertebrates play in each system

(Feld, Bello & Dolédec, 2014; Gonçalves et al., 2014). Hence lotic environments, as river and stream networks, besides determining the hydrographic basin, has as main characteristic a continuous flow of water in one direction. Naturally, all material and animals are carried by the unidirectional flow these water bodies (Grant, Lowe & Fagan, 2007), resulting in the increased species richness in this the same direction (Ibañez et al., 2009). Such movement also sets the dispersion dynamics of species, biotic and abiotic interactions, and the diversity of the metacommunities of these systems (Fagan, 2002; Grant *et al*., 2007; Ibañez et al., 2009; Carrara et al., 2012).

Species that disperse by water use the currents in their favor, which allows them to reach greater distances and new environments (Robinson, Tockner & Burgherr, 2002; Jacobsen et al., 2014; Cauvy-Fraunié et al., 2013, 2014, 2015). Generalist species are capable of surviving the heterogeneity brought by the natural flow of organic material, nutrients and potential competitors (Tonkin et al., 2017). Besides the currents, other factors such as the elevation gradient (Jacobsen, 2008), defrost dynamics (Cauvy-Fraunié et al., 2015), presence of dams (Looy, Tormos & Soucho, 2014), and the interactions between rivers as streams of a basin (Wilson & McTammany, 2014), also directly affect macroinvertebrate community dynamics in these systems.

Variations, natural or not, can change the macroinvertebrate biota at different scales of time and space (or space-time). For example, Angeler et al. (2011) observed that groups of organisms, typical of these environments, were affected by regional environmental factors. While organisms whose fluctuation cycle ranges between three and five years, were not influenced by environmental variables, independent of the scale used. Hence, thinking of eco-regions in time and space allows us to better understand the general trends. These in turn, are the results of important minor processes, which should also be investigated (Johnson, 2000; Angeler, Göthe, & Johnson 2013). It is still essential to consider that biological interactions take place in congregations and comunities (local scale); while biogeografic processes depend on larger scales, spatial (regional scale) or temporal (paleologic scale). Following the same, rational, phytogenetic changes reveal themselves slowly in space-time (Kauffman, 1993; Allen et al., 2006).

Lentic environments, as temporary ponds, are extremely unstable environments (Horne, 1971; Brendonck & Riddoch, 2000). The dynamics of communities associated with this kind of habitat have regimes, directly associated with the hydrology (Jeffries, 1994; Williams, 2006) and temperature (Chaves & Couto, 2014) variation. As a result,

each organism's intrinsic ability (such as insects in the larvae or adult phases, micro-crustaceans and annelids) should allow them to survive the quick changes, common to these systems (May, 1987; Benvenuto et al., 2009; Chaves & Couto, 2014). Within this scenario, the ability to produce resistant cysts (strategy to survive drought) becomes an ally to passive dispersion, whether by wind or by other animals (Brendonck & Riddoch, 1997; Gyllstrom & Hansson, 2004; Vandekerckhove et al. 2004; Lopez et al., 2005).

Equally unstable, phytotelemats, represented mainly by hollow trunks and water trapped in bromeliads, usually have a small volume of water and shelter the fauna that accompanies the environmental dimension. There communities are usally made up of metazooans such as insects in both the larvae and adult phases, microcustaceans and annelids, aside from the protists, and bacteria (Srivastava et al., 2004). In these types of microcosms, the ephemerality and the high susceptibility to environmental changes, select short life cycle species (Srivastava et al., 2004; Jocque & Field, 2014).

Scientometric and biological issues

This study aims at presenting quantitatively and conceptually, the state of art research on metacommunities of freshwater benthonic macroinvertebrates. To reach this goal an option was made to investigate the following issues: (1) What profile do journals that mostly publish papers on this issue have? (2) How many are exclusively dedicated to freshwater ecology? (3) What kind of sampling is used in these studies (spatial, temporal or spatio-temporal)? (4) How do studies about patterns of metacommunities of freshwater macroinvertebrates distribute globally? (5) What are the most studied environments? (6) Which patterns are most commonly observed for each type of environment? (7) How are these patterns distributed in different spatial scales (microcosm, mesocosm, metacosm and macroecology)?

Aside from these scientometric issues, we wanted to discuss if there is any relation between the metacommunity patterns: (i) and the various water dynamics (lotic and lentic systems), (ii) ephemerous and permanent environments, (iii) and the form of organism dispersion in the environment, (iv) and the kind of dispersion (active or passive) of organisms.

Methods

Data collection

A "Systematic Revision" following Olsen (1995) and Sampaio & Mancini (2007) protocols was undertaken. The search used "ISI Web of Knowledge data base (Thomson Reuters)" and "Periódicos-CAPES" search engin, covering most of the information available about macroinvertebrate metacommunities in freshwater environments (rivers, streams, lakes, floodplains, temporary ponds, phytotelmates and environments artificially created or modified), so as to answer the questions raised. The review covered articles published between 2004 (publication year of Leibold and collaborators article, a reference for the processes of metacommunity formation discussed in this paper) and December 2017. The following key words were used in the literature reviews: *metacommunit*, macroinvertebrat*, AND river*, OR stream*, OR lake*, OR pool*, OR pond*, OR water body*, OR rock pool*, OR freshwater, OR floodplain*, OR phytotelmata*, OR bromeliad*, OR water-filled*, OR tree holes, OR pitcher plant*.* After reading each article, it was classified within the different categories proposed, and the data tabled for later analysis, by simple counting and percentage. To elaborate the distribution map in the researched areas, we used only unique localizations, so that, even if independent publications used the area, the area counted only one time. Hence, we avoided that distinct publications, with the same set of data, be accounted for twice. When different environments were covered in a single article, of different metacommunity formation process, these were considered independent studies. To assess forms of dispersion (active or passive), the same procedure was adopted. Within this review, some terms designated to define the study scale used adopted meanings based on the size of the sample unit, and not extension of the area in where they were distributed (Wiens, 1989). In addition, some terms and definitions were adopted (see Table 2).

Table 2. Expressions adapted for this study and their definitions.

Terms	Definitions
Type of variation sampled	*Temporal*: study where data collection took place during na established/set period. *Espacial*: study where data collection was dependant on geografic distance spacial scale. *Espace-temporal*: study where the scale covers temporal and spacial variations.
Type of study	*Discriptive (case study)*: study where the samples were taken in natural not intentionally modified environments. *Experimental*: studies where samples were collected in not natural or manipulated environments or in artificial sections located in natural environments.
Environment scale	*Microcosmo*: environments capable of hosting from a few milliliters up to 2L of water (Weins, 1989). Exampel: Phytotelmata environments (Sirivastava et al., 2004) *Mesocosmo*: permanente environments or not, only a few m² extension up to 50cm water depth (Weins, 1989). Exempel: ponds (Howeth & Leibold, 2010b) *Metacosmo*: permanente environments with surfasse covering from tens to thouzand m², and water depth above 1m. Exampel: rivers, streams, lakes, flood planes (Weins, 1989).
Global scale	*Macroecologic*: Represent the general standard registered, considering space (Weins, 1989).

Results and discussion

State of art and scientometrics

Scientific production relative to freshwater benthic macroinvertebrate metacommunities, is ascending, and over 60% were published in the last three years (Fig. 1). The papers based on Leibold and collaborators (2004) proposal, started in 2007, three years after publication of the original paper. This delay before subsequent publications, most probably, was due to ripening of the sampling design and result interpretation, for this new approach within the studies of communities.

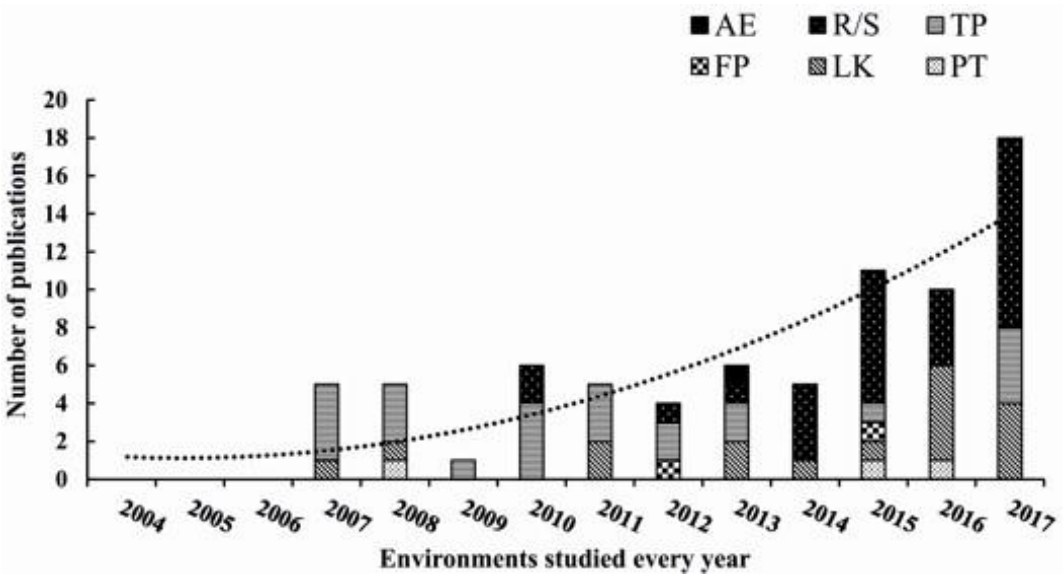

Fig. 1. Number (bars) and growth tendency (dotted line) of publications covering the metacommunity patterns defined by Leibold et al. (2004) for freshwater macroinvertebrates, within the period between 2004 and 2017. Different environments studied in each year: AE= Artificial environments, FP= Flood plains, R/S= Rivers/Streams, LK= Lakes, PT= Phytotelmats, TP= Temporary ponds.

Of the 552 papers during the search, only 62 fit the scope of this review (see Table S1). They were published in 26 journals, only nine of which exclusively dedicated to ecology of aquatic systems. *Hydrobiologia* and *Freshwater Biology*, with respectively nine and four articles each, were our major sources of information. However, journals focusing on general Ecology, such as *Oikos*, with six publications, also stood out as a good source of publications of this issue.

The use of microcosms and controlled experiments

In the current panorama, research on metacommunities usually are based on study cases (92%), while experimental approaches (8%) are quite rare. Although this cannot be considered a fault, covering controlled systems could still strengthen the Metacommunities Theory, as in other areas of ecology (Frases & Keddy, 1997). The use of microcosms as a test model of interfaces between description and experimentation is a good example (Frases & Keddy 1997; Paradise et al., 2008; Jocque & Field, 2014). Although still rare, studies of metacommunities in this kind of environments, certainly present advantages as shown by Frases & Keddy (1997) “ease of replication, precise control over environmental variables, and the power to manipulate the parameters and

treatments under investigation". This kind of approach makes the understanding of the structured processes (environmental and spatial variables) and the stabilizers (imigration and migration, intra- and interspecific interactions, with others) that rule a metacommunity easier. In addition, they may avoid misleading conclusions "sources of confusion" or a "demonic intrusion" (Hurlbert, 1984).

Experimental design could still help improve the understanding of variations in time (approached in only 5% of the studies). As observed, time essays are rare, which renders any time related questions a bit vague. Some studies have shown that metacommunities can change composition when analyzed in distinct time scale (Kneitel & Chase, 2004; Paradise et al., 2008; Ptermann et al., 2015). Similar effects to those of time have been observed in analyses of different spatial scale (72%) and spatio-temporal (23%). Different patterns could rule a metacommunity when evaluated from a local or regional scale (Medleya et al., 2015). Probably, such changes in pattern are directly related to variations of environmental filters. Which in turn, act at different scales (Fahrig & Merriam, 1994; Vanschoenwinkel et al., 2008; Angeler *et al*., 2013; Petsch, Pinha & Takeda, 2016), ripening biotic interactions (temporary niche segregation, for example), and/or abiotic (relations between hydroperiod and lifecycle of the species, for example) (Vanschoenwinkel et al., 2010; Frisch et al., 2012).

Size of the sampling unit studied, water dynamics and dispersion.

Rivers/streams were the most researched (46.8%), followed by temporary ponds (37.5%) and lakes (28.2%). However, ponds were the favorite study object during practically all period, while "lakes" and, mainly, "rivers/streams" triggered more interest only in the last four years (Fig. 1). Phytotelmata (5%) environments can still be considered unexplored.

Although we do not disregard the importance of research that analyzes the influence of geographic distances, the scales used in this review (meta-, meso-, and microcosm) are not related to spatial extension, but rather the size of the sampling unit (Wiens, 1989). We consider this approach more interesting given the intrinsic characteristics of each species which could determine their survive or not in the environment. We assume that prior to the issue of geographic scale; survival is a relationship between environmental boundary and the stability of the sampled system. Thus, we observed that the environments researched mostly fit in the categories of

metacosms (63.3%) and mesocosms (31.5%). The SS pattern is present in all scales, but it is present almost 1.5 times more in the mesocosms scale than in the ME (Fig. 2).

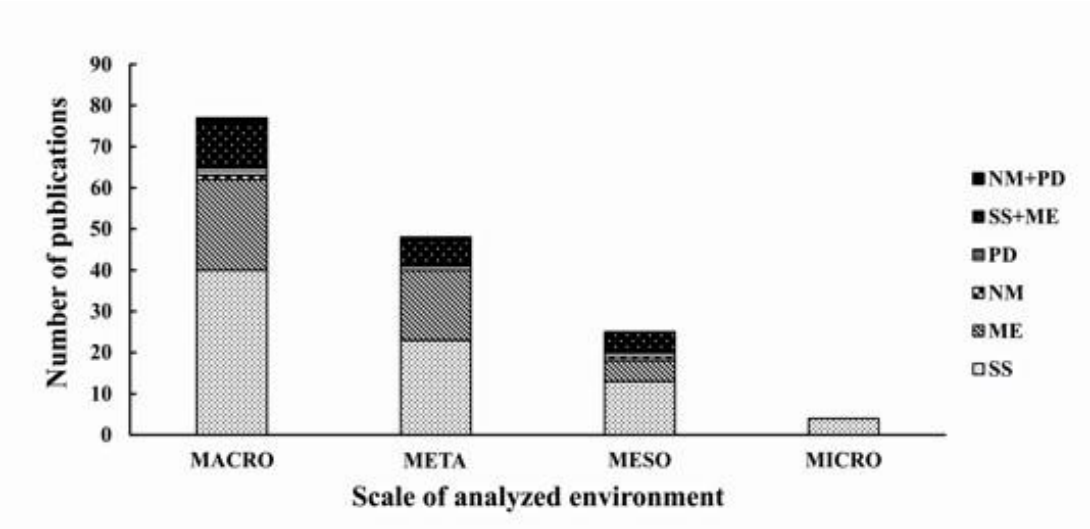

Fig. 2. Distribution of the metacommunity patterns in the different scales analyzed. MACRO = Macroecological Scale, META = Metacosm, MESO = Mesocosm, MICRO = Microcosm, NM = Neutral Model, PD = Dynamic Patch, SS = Species Sorting, ME = Mass Effect.

Lotic metacosms (rivers/streams) and lentic mesocosms (temporary ponds) were the kind of environments that presented the highest number of combinations of metacommunity structuring patterns (Fig. 3). Together they represented all types of patterns, besides combinations of these. For lentic mesocosms PD and NM patterns, were separately registered. Lotic metacosms, on the other hand, exhibited the same patterns working in tandem with (NM+PD) sets.

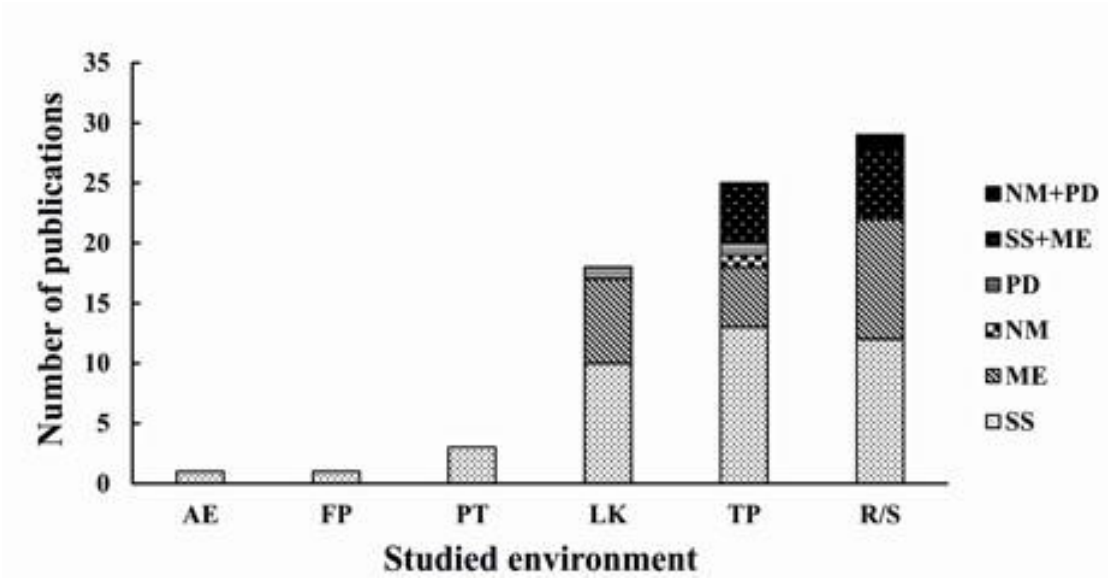

Fig. 3. Occurrence of metacommunity patterns in different freshwater systems. AE= Artificial environments, FP= Flood plains, PT= Phytotelmats, LK= Lakes, TP= Temporary ponds, R/S= Rivers/Streams, NM= Neutral Model, PD= Patch Dynamic, SS= Species Sorting, ME= Mass Effect.

SS was the only process registered in all environments. Although ranking second, ME process was only present in lentic meta- and mesocosms as well as in lotic metacosms. There was a marked difference between these two processes in temporary ponds, which exhibited an SS pattern 1.5 times more frequent than ME processes. Some authors, when researching temporary ponds as well as rivers and streams, considered joint processes as being more adequate. A good example within this context is the hydrographic basin metacommunities. In these systems, environmental configurations and isolation of the headwaters not only mold the community organization – by generally sheltering specialized species – but also through dispersion processes along the basin (Swan & Brown, 2014; De Marco, Batista & Cabette, 2015; Datry et al., 2016). However, in regions close to the river mouth the communities are formed by generalist organisms, which normally, have mass dispersion (ME), presenting distinct needs (Datry et al., 2016; Tonkin et al., 2017). Because of this, authors present SS as being the forming process of metacommunities in headwaters, and ME in estuaries and river mouths (Swan & Brown, 2014; De Marco et al., 2015; Datry et al., 2016; Tonkin et al., 2017).

When environments were grouped according to their water dynamics, we could observe a tendency towards SS patterns (60.5%) dominating lentic environments (Fig. 4). This tendency keeps when lotic and lentic environments are analyzed separately.

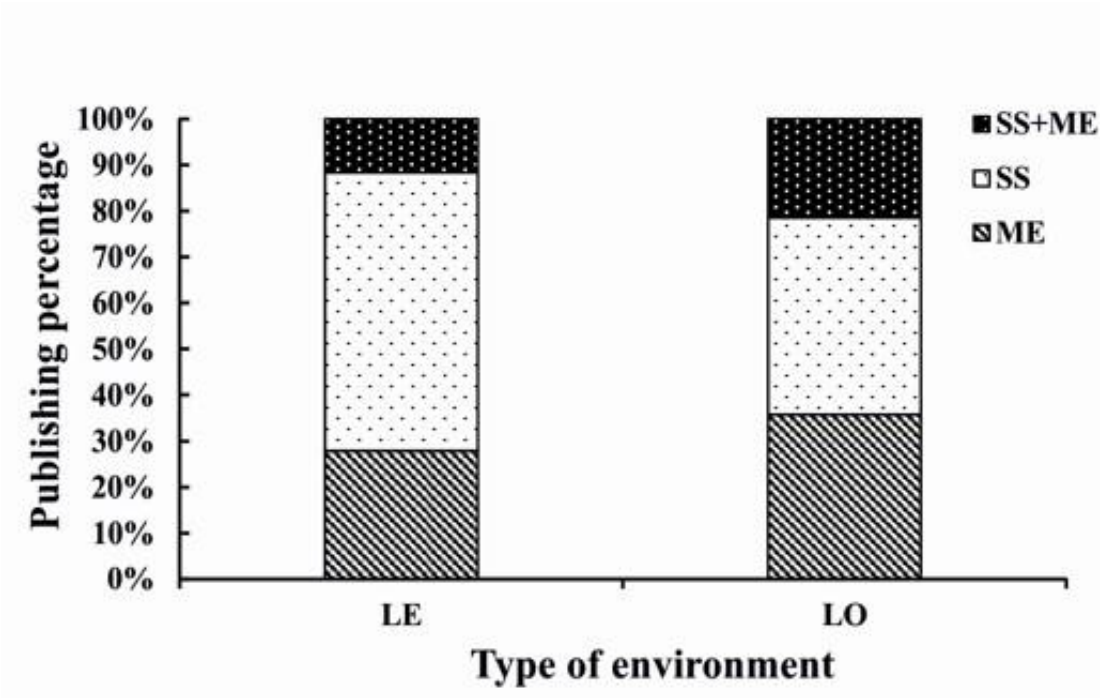

Fig. 4. Distribution of the three main metacommunity patterns found in lotic (LO) and lentic (LE) environments. SS= Species Sorting, ME= Mass Effect.

When we subdivide lentic environments into temporary and permanent, we observe that the differences found in the ME and SS patterns, whether within the same group, or between groups, was small, although only temporary environments had registered joined processes (SS+ME) as a more plausible explanation of local metacommunity dynamics (Fig. 5).

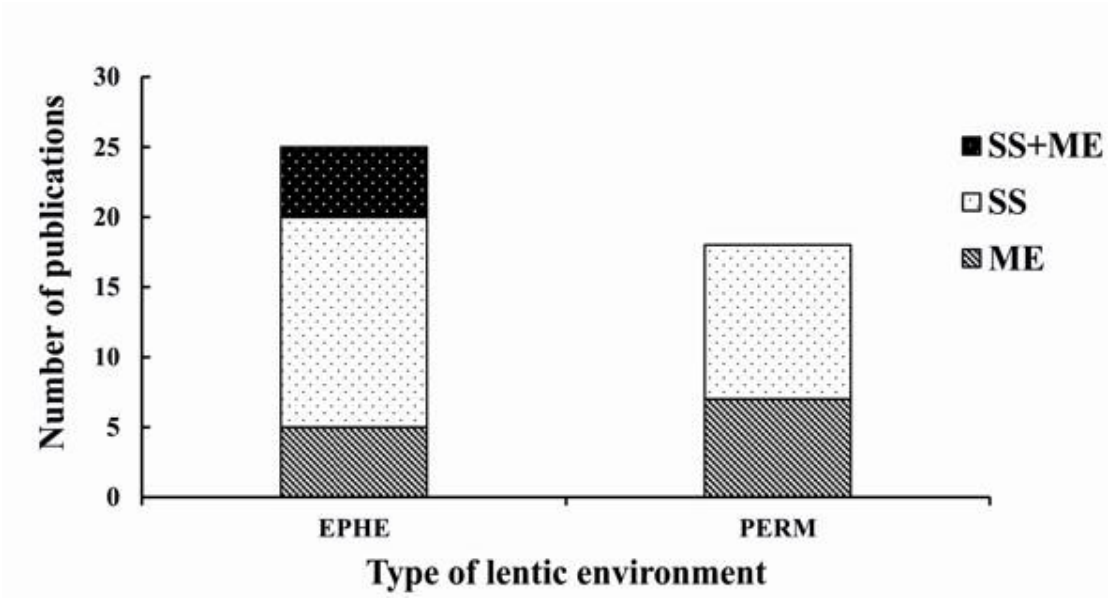

Fig. 5. Distribution of the three main patterns of metacommunities (SS= Species sorting, ME= Mass Effect and the conjunction of those) found in temporary (EPHE) and permanent (PERM) environments.

When the environments were analyzed based on dispersion, we observe that the two exist practically at the same rate. However, phytothelmats environments were the only environments that did not register active dispersal as being effective in the process of local metacommunity formation (Fig. 6).

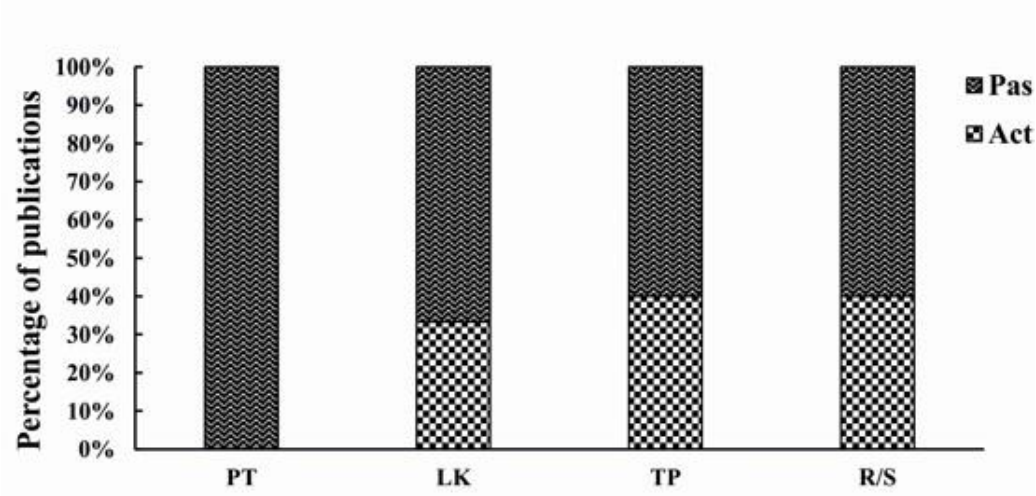

Fig. 6. Distribution of passive (Pas) and active (Act) dispertion in phytothelmata (PT), lakes (LK), temporary ponds (TP), rivers and streams (R/S).

Finally, we analyzed forms of dispersion. ME patterns showed equal passive and active dispersal percentages. However, for SS, and mainly for SS+ME, we observed a tendency toward passive dispersal (Fig. 7).

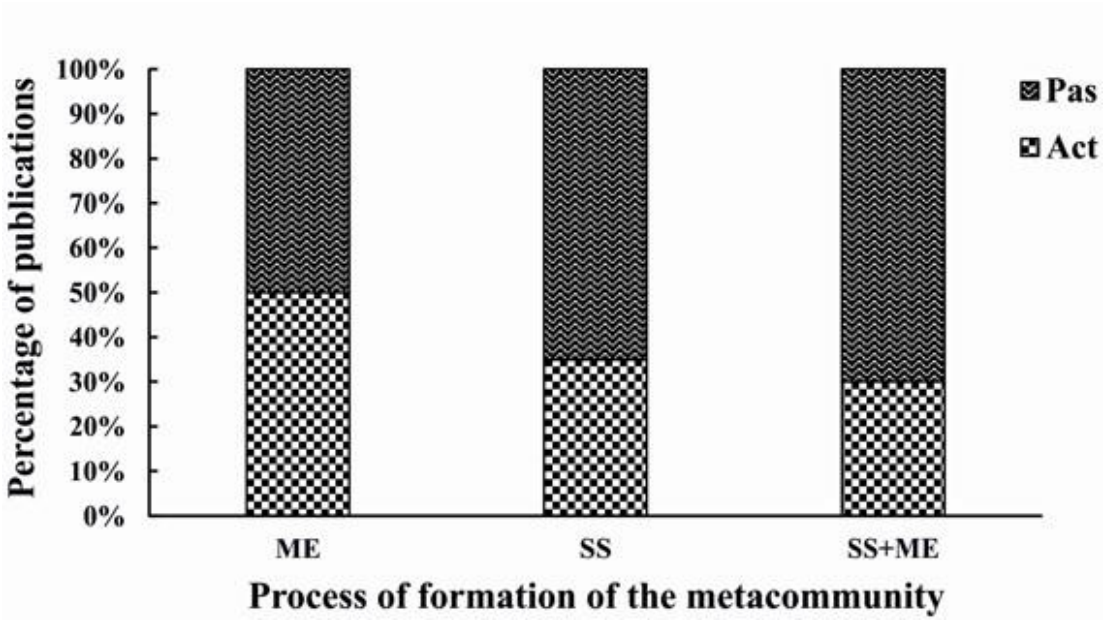

Fig. 7. Distribution of passive (Pas) and active (Act) dispersal in metacommunity processes with the highest number of registers in this review. ME = Mass Effect, SS= Species sorting.

Size of the sampling unit studied, water dynamics and dispersion characteristics of the fauna: integrating concepts and discussing new steps

Analyzing from the size perspective of the sampling unit studied (Wiens, 1989), we observed the predominance of SS structuring the metacommunity at different environmental scales, so it is plausible to suppose that the quality of habitats is more important than their size or the distance between them (Leibold & Geddes, 2005; Vellend, 2010; Winegardner et al., 2012; Swan & Brown, 2014; Datry et al., 2016). So, although distance presents an impact on metacommunities (in ME), they will be molded mainly by the environment and its respective filters. This impression becomes strong when we observe that passive dispersion is more present in SS and SS+ME patterns, than in ME. Therefore, spatial variables have little importance, and the arrival of organisms to new communities is a result of stochastic processes (Thompson & Townsend, 2006; Hájek et al., 2011; Petsch et al., 2016). However, the establishment of organisms in an environment is closely related to the way they disperses whether by water, wind or using other animals), the environmental filters, and the gradient and ecological interactions to be developed in the new location (Fahrig & Merriam, 1994; Vanschoenwinkel et al., 2008; Vanschoenwinkel et al., 2010; Petsch et al., 2016).

The relation between passive dispersal and SS (or SS+ME), also explains the prevalence of this process in ephemeral lentic environments. The environmental characteristics, such as hydrodynamics and level of ephemerality, for example, require the organisms to be capable to survive huge hydric and temperature variations (May, 1987; Benvenuto et al., 2009; Chaves & Couto, 2014). Within this context, organisms that live in temporary ponds produce resistance cists as means to survive the severe conditions (May, 1987; Brendonck & Riddoch, 1997; Gyllstrom & Hansson, 2004; Chaves & Couto, 2014). This kind of reproductive strategy produces propagules or cysts that could be carried by wind or water currents, or even by other animals (Brendonck & Riddoch, 1997; Vandekerckhove et al. 2004; Lopez et al., 2005; Vanschoenwinkel et al., 2008), which would explain passive dispersion and SS as marking characteristics of metacommunities formed in these environments.

Although passive dispersal has already proved to be an important factor in the composition of metacommunities, active dispersal also plays a role in their structuring. An organism that uses this kind or dispersal strategy has, usually, control on the choice of the new environment be colonize or not (Resetarits, 2001). Also, although they do not depend on vectors for dispersal (Vonesh et al., 2009), they have a close relation with the environment and its gradients (Angeler et al., 2013; Petsch et al., 2016). Studies show that Diptera choice of oviposition could vary according to the presence of predators (Angelon, & Petranka, 2002; Blaustein, 2004), potential competitors (Allan, & Kline, 1998) and depth and surface area of the body of water (Reiskind, M. H. & Zarrabi, 2012). These characteristics could help us explain the absence of active dispersion registers in phytothelmats. After all, these are conspicuous water bodies with a small water volume, which should favor competition and capture by predators. In addition, the ephemerality of phytothelmats does not guarantee that Diptera larvae, or any other type of organisms for that purpose, would have time to complete its development (Juliano & Stoffregen, 1994).

Recently, determining the role and importance of dispersion in metacommunity formation has been the goal of more studies (Hill et al., 2017; Rodil et al., 2017; Sarremejane et al., 2017; Valente-Neto et al., 2017). The new information produced could improve the understanding of situations where more than one process is registered (SS+ME), and where differences are registered only in dispersion rates and the mechanisms involved in it (Cottenie, 2005; Vellend, 2010; Winegardner et al., 2012). Studies of temporary ponds have shown that metacommunities in such systems are

sometimes better explained by the conjunction of processes (Vanschoenwinkel, 2007; Doi, Chang & Nakano, 2010), and other times by a single model, associated to a low dispersion rate (Ng, Carr & Cottenie, 2009; Howeth & Leibold 2010a).

Global distribution of studies on metacommunities and the conservation of water resources

On the macroecological perspective (see tab 2) the studies are heterogeneously distributed (Fig. 8). America, (emphasis on the U.S.A., with 11 different study areas) and Europe (emphasis on Finland with six), were the regions covered by most areas researched. Aside from those, only New Zealand, with a total or four environments, stood out.

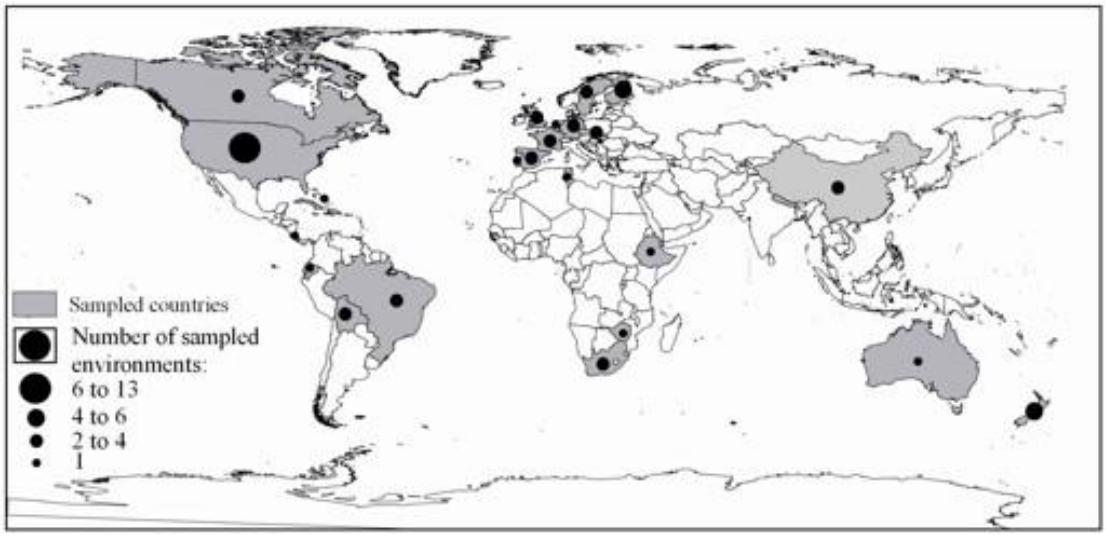

Fig. 8. Map of the countries where freshwater metacommunities of macroinvertebrates were studied.

It is important to highlight two specific points: 1) sites with higher number of studies overlap sites with major chance of future water shortage (see maps in Oki & Kanae, 2006; Vörösmarty et al., 2010); 2) the noteworthy increase in research of lakes and mainly rivers and streams seems to be connected to this scenario, considering the current conservation and management policies of these water bodies.

The importance and the need to better understand the workings of these water bodies becomes evident when we consider that freshwater corresponds to only 0.3% of the water in the world. Only 0.007% of which is distributed in lakes and rivers (Schernikau, 2010). However, these water resources are not always available either due

to difficult access or pollution levels. These conditions further reduce the percentage of water available for human consumption.

Lakes and especially rivers have been receiving special attention from researchers in recent years (Fig. 1). Bearing in mind that these environments are the main sources of drinking water for humans, the information generated by these surveys about biological metacommunities should be used to establish conservation and management strategies (Brown et al., 2011; Nhiwatiwa et al., 2011). According to Vörösmarty et al., (2010) there is a direct relation between water bodies, water shortage and biodiversity. Hence, the strategies that should be designed should go beyond the simple conservation of species, they should also contribute to the maintenance of ecosystem services (Ngai & Srivastava, 2006; de Bello et al., 2010; Brouard et al., 2012; Gonçalves et al., 2014; Schmera et al. 2017) fundamental to environmental health and consequently water quality and life human

Conclusions

Experimental designs at different scales and use of microcosms should be better explored because they can contribute significantly to the understanding of the processes that form a metacommunity.

Although the size of the sample unit has shown to be as good a variable as the geographic scale, in the evaluation and comparison of the patterns of metacommunities, we observe that the quality of habitats is more important than their size or distance that separates them.

The passive dispersion of fauna associated to water dynamics and to stochastic processes, such as the ephemerality of water bodies, are shown as the main conductors of the described patterns for metacommunities of freshwater macroinvertebrates.

The overlap between areas with future water scarcity and those studied from the perspective of metacommunity theory suggests that this approach should be considered during the creation of water management and conservation plans.

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Author contributions

Túlio P. Chaves: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review. **Erminda C. G. Couto:** Conceptualization, Investigation, Methodology, Writing – review.

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References

Alahuhta, J. & Heino, J. (2013). Spatial extent, regional specificity and metacommunity structuring in lake macrophytes. *Journal of Biogeography* **40**, 1572–1582

Allan, S. A. & Kline, D. L. (1998). Larval rearing water and preexisting eggs influence oviposition by *Aedes aegypti* and *Ae.albopictus* (Diptera: Culicidae). *Journal of Medical Entomology* **35**, 943–947.

Allen, C. R., Garmestani, A. S., Havlicek, T. D., Marquet, P. A., Peterson, G. D., Restrepo, C., Stow C. A., & Weeks, B. E. (2006). Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters* **9**, 630–643.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Iinouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N. G. (2011). Navigating the multiple meanings of beta diversity: a road map for the practicing ecologist. *Ecology Letters* **14**, 19–28.

Angeler, D. G., Göthe, E., & Johnson, R. K. (2013). Hierarchical Dynamics of Ecological Communities: Do Scales of Space and Time Match? *PLoS ONE* **8**, e69174.

Angelon, K. A. & Petranka, J. W. (2002). Chemicals of predatory mosquitofish (*Gambusia affinis*) influence selection of oviposition site by *Culex* mosquitoes. *Journal of Chemical Ecology* **28**, 797- 806.

Barquín, J. & Death, R. G. (2006). Spatial patterns of macroinvertebrate diversity in New Zealand springbrooks and rhithral streams. *Journal of the North American Benthological Society* **25**, 768–786.

Benvenuto, C., Calabrese, A., Reed, S. K., & Knott, B. (2009). Multiple hatching events in clam shrimp: Implications for mate guarding behaviour and community ecology. *Current Science* **96**, 130–136.

Biggs J., Williams P., Whitfield P., Nicole, P., & Weatherby, A. (2005). 15 years of pond assessment in Britain: results and lessons learned from the work on pond conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* **15**, 693–714.

Blaustein, L., Kiflawi, M., Eitam, A., Mangel, M., & Cohen, J. E. (2004). Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. *Oecologia* **138**, 300–305.

Brendonck, L. & Riddoch, B. J. (1997). Anostracans (Branchiopoda) of Botswana: morphology, distribution, diversity and endemicity. *Journal of Crustacean Biology* **17**, 111– 134.

Brendonck, L. & Riddoch, B. J. (2000). Egg bank dynamics in anostracan desert rock pool populations (Crustacea: Branchiopoda). *Archiv fuer Hydrobiologie* **148**, 71–84.

Brouard, O., Céréghino, R., Corbara, B., Leroy, C., Pelozuelo, L., Dejean, A., & Carrias, J.F. (2012). Understorey environments influence functional diversity in tank-bromeliad ecosystems. *Freshwater Biology* **57**, 815–823.

Brown B. L., Swan, C. M., Auerbach, D. A., Grant, E. H. C., Hitt, N. P., Maloney, K. O., & Christopher, P. (2011). Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *Journal of the North American Benthological Society* **30**, 310–327.

Cañedo-Argüelles, M., Boersma, K. S., Bogan, M. T., Olden, J. D., Phillipsen, I., Schriever T. A., & Lytle, D. A. (2015). Dispersal strength determines meta-community structure in a dendritic riverine network. *Journal of Biogeography* **42**, 778–790.

Carrara F., Altermatt, F., Rodriguez-Iturbe I., & Rinaldo, A. (2012). Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 5761–5766.

Cauvy-Fraunié, S., Espinosa, R., Andino, P., Jacobsen, D., & Dangles, O. (2015). Invertebrate Metacommunity Structure and Dynamics in an Andean Glacial Stream Network Facing Climate Change. *PLoS ONE* **8**, e0136793.

Cauvy-Fraunié, S., Andino, P., Espinosa, R., Calvez, R., Anthelme, F., Jacobsen, D., & Dangles, O. (2014). Glacial flood pulse effects on benthic fauna in equatorial high-Andean streams. *Hydrological Processes* **28**, 3008–3017.

Cauvy-Fraunié, S., Condom, T., Rabatel, A., Villacis, M., Jacobsen, D., & Dangles, O. (2013). Technical Note: Glacial influence in tropical mountain hydrosystems evidenced by the diurnal cycle in water levels. *Hydrology and Earth System Sciences* **17**, 4803–4816.

Chaves, T. P. & Couto, E. C. G. (2014). Hatching of the eggs of *Eulimnadia colombiensis* (Branchiopoda) at different temperatures and regime of light. *Nauplius* **22**, 145-149.

Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters* **8**, 1175–1182.

Datry, T., Melo, A. S., Moya, N., Zubieta, J., De la Barra, E., & Oberdorff, T. (2016). Metacommunity patterns across three Neotropical catchments with varying environmental harshness. Freshwater Biology **61**, 277–292.

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H., Bardgett, R. D., & da Silva, P. M. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation* **19**, 2873–2893.

De Marco, J. P., Batista, J. D., & Cabette, H.S.R. (2015). Community assembly of adult Odonates in tropical streams: an ecophysiological hypothesis. *PLoS ONE* **10**, e0123023.

Dézerald, O., Leroy, C., Corbara, B., Carrias, J. F., Pelozuelo, L., Dejean, A., & Céréghino, R. (2013). Food-web structure in relation to environmental gradients and predator-prey ratios in tank-bromeliad ecosystems. *PLoS ONE* **8**, 1–8.

Doi, H., Chang, K. H., & Nakano, S. (2010). Dispersal, connectivity, and local conditions determine zooplankton community composition in artificially connected ponds. *Aquatic Biology* **10**, 47–55.

Drakare, S., Lennon, J. J., & Hillebrand, H. (2006). The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology Letters* **9**, 215 – 227.

Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews* **80**, 1–25.

Fagan, W.F. (2002). Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* **83**, 3243–3249.

Fahrig, L. & Merriam, G. (1994). Conservation of Fragmented Populations. *Conservation Biolog*y **8**, 50–59.

Feld, C. K., Bello, F., & Dolédec, S. (2014). Biodiversity of traits and species both show weak responses to hydromorphological alteration in lowland river macroinvertebrates. *Freshwater Biology* **59**, 233–248.

Fraser, L.H. & Keddy, P. (1997). The role of experimental microcosms in ecological research. *Trends in Ecology & Evolution* **12**, 478–481

Frisch, D., Cottenie, K., Badosa, A., & Green, A. J. (2012). Strong Spatial Influence on Colonization Rates in a Pioneer Zooplankton Metacommunity. *PLoS ONE* **7**, e40205

Gaston, K. J. & Blackburn, T. M. (2000). *Pattern and process in macroecology*. Blackwell Science, Oxford.

Gonçalves, J. F. J., Martins, R. T., Ottoni, B. M. P., & Couceiro, S. R. M. (2014). *Uma visão sobre a decomposição foliar em sistemas aquáticos brasileiros. Insetos Aquáticos na Amazônia Brasileira: taxonomia, biologia e ecologia*. Editora do INPA. Manaus, p.89–117.

Grant, E. H. C., Lowe, W. H., & Fagan, W. F. (2007). Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* **10**, 165e175.

Gyllstrom, M. & Hansson, L. A. (2004). Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling. *Aquatic Sciences* **66**, 274–295.

Hájek, M., Rolecek, J., Cottenie, K., Kintrová, K., Horsák, M., Poulícková, A., Hájková, P., Franková, M., & Díte, D. (2011). Environmental and spatial controls of biotic assemblages in a discrete semi-terrestrial habitat: comparison of organisms with different dispersal abilities sampled in the same plots. *Journal of Biogeography* **38**, 1683–1693.

Hall, R. O., Wallace, J. B., & Eggert, S. L. (2000). Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* **81**, 3445–3463.

Heino, J. & Peckarsky, B. L. (2014). Integrating behavioral, population and large-scale approaches for understanding stream insect communities. *Current Opinion in Insect Science* **2**, 7–13.

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., & Bini, L. M. (2014). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* **60**, p. 845–869.

Hill, M. J., Heino, J., Thornhill, I., Ryves, D. B., & Wood, P. J. (2017). Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. *Oikos* **126**, 1575–1585.

Holyoak M., Leibold, M. A., Holt, R. D., & Hoopes, M. F. (2005). A framework for large-scale community ecology. In: *Metacommunities: spatial dynamics and ecological communities.* (eds M. Holyoak, M. A. Leibold & R. D. Holt) pp. 1–31. The University of Chicago Pres.

Horne, F. R. (1971). Some effects of temperature and oxygen concentration on phyllopod ecology. *Ecology* **52**, 343–347.

Howeth, J. G. & Leibold, M. A. (2010a). Prey dispersal rate affects prey species composition and trait diversity in response to multiple predators in metacommunities. *Journal of Animal Ecology* **79**, 1000–1011.

Howeth, J. G. & Leibold, M. A (2010b). Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. *Ecology* **91**, 2727–2741.

Hubbell S. J. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton. Hughes.

Hurlbert, S. H. (1984). Pseudoreplication and the Design of Ecological Field Experiments. *Ecological Monographs* **54**, 187–211.

Hutchinson, G. E. (1957). Concluding remarks. *Cold Springs Harbor Symposia on Quantitative Biology* **22**, 415–427.

Ibañez, C., Belliard, J., Hughes, R. M., Irz, P., Kamdem-Toham, A., Lamouroux, N., Tedesco, P. A., & Oberdorff, T. (2009). Convergence of temperate and tropical stream fish assemblages. *Ecography* **32**, 658–670.

Jacobsen, D., Cauvy-Fraunie, S., Andino, P., Espinosa, R., Cueva, D., & Dangles, O. (2014). Runoff and the longitudinal distribution of macroinvertebrates in a glacier-fed stream: implications for the effects of global warming. *Freshwater Biology* **59**, 2038–2050.

Jacobsen, D. (2008). Low oxygen pressure as a driving fator for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia* **154**, 795–807.

Jeffries, M. J. (1994). Invertebrate communities and turnover in wetland ponds affected by drought. *Freshwater Biology* **32**, 603–612.

Jocque, M. & Field, R. (2014). Aquatic invertebrate communities in tank bromeliads: how well do classic ecological patterns apply? *Hydrobiologia* **730**, 153–166.

Johnson, R. K. (2000). Spatial congruence between ecoregions and litoral macroinvertebrate assemblages. *Journal of the North American Benthological Society* **19**, 475–486.

Juliano, S. A. & Stoffregen, T. L. (1994). Effects of habitat drying on size at and time to metamorphosis in the tree hole mosquito *Aedes triseriatus*. *Oecologia* **97,** 369–376.

Kauffman, S. A. (1993). *Origins of order: self-organization and selection in evolution*. Oxford University Press.

Kevin, L. E. (2008). Wetlands and Global Climate Change: The Role of Wetland Restoration in a Changing World. *Wetlands Ecology and Management* **17,** 71–84.

Kneitel, J. M. & Chase, J. M. (2004). Disturbance, predator, and resource interactions alter container community composition. *Ecology* **85**, 2088-2093.

Legendre, P. (2008). Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *Journal of plant ecology* **1**, 3–8.

Leibold, M. A. & Norberg, J. (2004). Biodiversity in metacommunities: Plankton as complex adaptive systems? *Limnology and Oceanography*, **49(II)**, 1278–1289.

Leibold, M. A. & Geddes, P. (2005). El concepto de nicho en las metacomunidades. *Ecología Austral* **15**, 117–129.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P. J., Chase, M., & Hoopes, M. F. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**, 601–613.

Leibold, M. A. & Mikkelson, G. M. (2002). Coherence, species turnover, and boundary clumping: elements of meta-community structure. *Oikos* **97**, 237–250.

Logue, J. B., Mouquet, N., Peter, H., & Hillebrand, H. (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology & Evolution* **26**, 482–491.

Looy, K.V., Tormos, T., & Soucho, Y. (2014). Disentangling dam impacts in river networks. *Ecological Indicators* **37**, 10– 20

Lopez, L., Filizola, B., Deiss, I., & Rios, R. (2005). Phoretic behaviour of bromeliad annelids (*Dero*) and ostracods (*Elpidium*) using frogs and lizards as dispersal vectors. *Hydrobiologia* **549**, 15–22.

Mac Arthur, R. H. & Wilson, E. O. 1967. *The theory of island biogeography*. Princeton University Press.

Mac Nally, R., Fleishman, E., Bulluck, L. P., & Betrus, C. J. (2004). Coparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. *Journal of Biogeography* **31**, 917– 929.

May, L. (1987). Effect of incubation temperature on the hatching of rotifer resting eggs collected from sediments. *Hydrobiologia* **147**, 335–338.

Medleya, K. A., Boughtonb, E. H., Jenkinsc, D. G., Fauthc, J. E., Bohlenc, P. J., & Quintana-Ascencioc, P.F. (2015). Intense ranchland managementtips the balance of regional and local factors affecting wetland community structure. *Agriculture, Ecosystems and Environment* **212**, 207–244

Ng, I., Carr, C., & Cottenie, K. (2009). Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* **619**, 133–143.

Ngai, J. T. & Srivastava, D. (2006). Predators accelerate nutrient cycling in a bromeliad ecosystem. *Science* **314**, 963.

Nhiwatiwa, T., Brendonck, L., Waterkeyn, A., & Vanschoenwinkel, B. (2011). The importance of landscape and habitat properties in explaining instantaneous and long-term distributions of large branchiopods in subtropical temporary pans. *Freshwater Biology* **56**, 1992–2008.

Oki, T. & Kanae, S. (2006). Global Hydrological Cycles and World Water Resources. *Science* **313**, 1068–1072.

Olsen, J. (1995). Meta-analysis or Collaborative Studies. *Journal of Occupational Environmental Medicine* **37**, 897–902.

Paradise, C. J., Blue, J. D., Burkhart, J. Q., Goldberg, J., Harshaw, L., Hawkins, K. D., Kegan, B., Krentz, T., Smith, L., & Villalpando, S. (2008). Local and regional factors influence the structure of treehole metacommunities. *BMC Ecology* **19**, 8–22.

Petsch, D.K., Pinha, G. D., & Takeda, A. M. (2016). Dispersal mode and flooding regime as drivers of benthic metacommunity structure in a Neotropical floodplain. *Hydrobiologia* **788**, 31–141.

Pinel-Alloul, B., André, A., Legendre, P., Cardille, J. A., Patalas, K., & Salki, A. (2013). Large-scale geographic patterns of diversity and community structure of pelagic crustacean zooplankton in Canadian lakes. *Global Ecology and Biogeography* **22**, 784–795.

Pond, G. J., Passmore, M. E., Borsuk, F. A., Reynolds, L., & Rose, C. J. (2009). Downstream effects of mountaintop coal mining: comparing biological conditions using family-and genus-level macroinvertebrate bioassessment tools. *Journal of the North American Benthological Society* **27**, 717–737.

Ptermann, J. S., Kratina, P., Marino, N. A. C., MacDonald, A. A. M., & Srivastava, D.S. (2015). Resources Alter the Structure and Increase Stochasticity in Bromeliad Microfauna Communities. *PLoS ONE* **10**, e0118952.

Reiskind, M. H. & Zarrabi, A. A. (2012). Water Surface Area and Depth Determine Oviposition Choice in *Aedes albopictus* (Diptera: Culicidae) *Journal of Medical Entomology* **49**, 71–76.

Resetarits, W. J. (2001). Colonization under threat of predation: avoidance of fish by an aquatic beetle, Tropisternus lateralis (Coleoptera: Hydrophilidae). *Oecologia* **129**, 155–160

Robinson C., Tockner, K., & Burgherr, P. (2002). Seasonal patterns in macroinvertebrate drift and seston transport in streams of an alpine glacial flood plain. *Freshwater Biology* **47**, 985–993.

Rodil, I.F., Lucena-Moya, P., Jokinen, H., Ollus, V., Wennhage, H., Villnäs, A., & Norkko, A. (2017). The role of dispersal mode and habitat specialization for metacommunity structure of shallow beach invertebrates. *PLOS ONE* **12**, e0172160.

Sampaio, R. F. & Mancini, M. C. (2007). Estudos de revisão sistemática: um guia para síntese criteriosa da evidência científica. *Revista Brasileira de Fisioterapia* **11**, 83–89.

Sarremejane, R., Mykrä, H., Bonada, N., Aroviita, J., & Muotka, T. (2017). Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. *Freshwater Biology* **62,** 1073–1082.

Schernikau, L. (2010). *Economics of the International Coal Trade: The Renaissance of Steam Coal*. Springer pp. 301.

Schmera, D., Heino, J., Podani, J., Erös, T., & Dolédec, S. (2017). Functional diversity: A review of methodology and current knowledge in freshwater macroinvertebrate research. *Hydrobiologia* **787**, 27–44.

Shurin, J. B., Havel, J. E., Leibold, M. A., & Pinel-Alloul, B. (2000). Local and regional zooplankton species richness: a scale-independent test for saturation. *Ecology* **81**, 3062–3073.

Soranno, P. A., Webster, K. E., Riera, J. L., Kratz, T. K., Baron, J. S., Bukaveckas, P. A., Kling, G. W., White, D. S., Caine, N., Lathrop, R. C., & Leavitt, P. R. (1999). Spatial Variation among Lakes within Landscapes: Ecological Organization along Lake Chains. *Ecosystems* **2**, 395–410.

Srivastava, D. S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S. P., Miller, T. E., Munguia, P., Romanuk, T., Schneider, D. C., & Trzcinski, M. K. (2004). Are natural microcosms useful model systems for ecology? *Trends in Ecology & Evolution* **19**, 379–384.

Swan, C. M. & Brown, B. L. (2014). Using rarity to infer how dendritic network structure shapes biodiversity in riverine communities. *Ecography* **37**, 993–1001.

Thompson, R. & Townsend, C. R. (2006). A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology* **75**, 476–484.

Tonkin, J. D., Tachamo Shah, R. D., Shah, D.N., Hoppeler, F., Jähnig, S.C. & Pauls, S. U. (2017). Metacommunity structuring in Himalayan streams over large elevational gradients: the role of dispersal routes and niche characteristics. *Journal of Biogeography* **44**, 62–74.

Valente-Neto, F., Durães, L., Siqueira, T., & Roque, F. O. (2017). Metacommunity detectives: Confronting models based on niche and stochastic assembly scenarios with empirical data from a tropical stream network. *Freshwater Biology* **63**, 86–99.

Van der Gucht, K., Cottenie, K., Muylaert, K., Vloemans, N., Cousin, S., Declerck, S., Jeppesen, E., Conde-Porcuna, J., Schwenk, K., Zwart, G., Degans, H., Vyverman, W., & De Meester, L. (2007). The power of species sorting: local factors drive bacterial community composi- tion over a wide range of spatial scales. *Proceedings of the National Academy of Science*, **104**, 20404–20409.

Vandekerckhove, J., Declerck, S., Vanhove, M., Brendonck, L., Jeppesen, E., Conde Porcuna, J. M., & De Meester, L. (2004). Use of ephippial morphology to assess richness of anomopods: potentials and pitfalls. *Journal of Limnology* **63**, 75-84.

Vanschoenwinkel, B., De Vries, C., Seaman, M., & Brendonck, L. (2007). The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* **116**, 1255–1266.

Vanschoenwinkel, B., Gielen, S., Vandewaerde, H., Seaman, M., & Brendonck, L. (2008). Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. *Ecography* **31**, 567–577

Vanschoenwinkel, B., Hulsmans, A., De Roeck, E. R., De Vries, C., Seaman, M., & Brendonck, L. (2009). Community structure in temporary freshwater pools: disentangling eff ects of habitat size and hydroregime. *Freshwater Biology* **54**, 1487–1500.

Vanschoenwinkel, B., Waterkeyn, A., Jocqué, M., Boven, L., Seaman, M., & Brendonck, L. (2010). Species sorting in space and time – the impact of disturbance regime on community assembly in a temporary pool metacommunity. *Journal of the North American Benthological Society* **29**, 1267–1278.

Vellend, M. (2010). Conceptual synthesis in community ecology. *Quarterly Review of Biology* **85**, 183–206.

Verleyen, E., Vyverman, W., Sterken, M., Hodgson, D. A., De Wever, A., Juggins, S., Van de Vijver, B., Jones, V. J., Vanormelingen, P., Roberts, D., Flower, R., Kilroy, C., Souffreau, C., & Sabbe, K. (2009). The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. *Oikos* **118**, 1239–1249.

Vonesh, J. R., Kraus, J. M., Rosenberg, J. S., & Chase, J. M. (2009). Predator effects on aquatic community assembly: disentangling the roles of habitat selection and post-colonization processes. *Oikos* **118**, 1219–1229.

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S. E., Sullivan, C.A., Reidy Liermann, C., & Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature* **467**, 555–561.

Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness: towards a general, hierarchial theory of species diversity. *Journal of Biogeography* **28,** 453–470.

Wiens, J. A. (1989). Spatial Scaling in Ecology. *Functional Ecology* **3**, 385–397.

Williams, D. D. (2006). *The biology of temporary waters*. Oxford University Press, Oxford.

Willis, K. J. & Whittaker, R. J. (2002). Species diversity – scale matters. *Science* **295**, 1245–1248.

Wilson, M. J. & McTammany, M. E. (2014). Tributary and mainstem benthic macroinvertebrate communities linked by direct dispersal and indirect habitat alteration. *Hydrobiologia* **738**, 75–85.

Wilson, D. S. (1992). Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* **73**, 1984–2000.

Winegardner, A. K., Jones, B. K., Ng, I. S.Y., Siqueira, T., & Cottenie, K. (2012). The terminology of metacommunity ecology. *Trends in Ecology and Evolution* **27**, 253–254.

Supplementary material

Metacommunity of freshwater macroinvertebrates: an overall scientiometric analysis

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Table S1 - Articles selected for review according to pre-established criteria.

AUTHORS	YEAR OF PUBLICATION	TITLE
Allen, M. R.	2007	Measuring and modeling dispersal of adult zooplankton
Meutter, F. V., L. Meester & R. Stoks	2007	Metacommunity structure of pond macroinvertebrates: effects of dispersal mode and generation time
Vanschoenwinkel, B., C. De Vries, M. Seaman & L. Brendonck	2007	The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient
McCauley, S. J., C. J. Davis, R. A. Relyea, K. L. Yurewicz, D. K. Skelly & E. E. Werner	2008	Metacommunity patterns in larval odonates
Paradise, C. J, J. D. Blue, J. Q. Burkhart, J. Goldberg, L. Harshaw, K. D. Hawkins, B. Kegan, T. Krentz, L. Smith & S. Villalpando	2008	Local and regional factors influence the structure of treehole metacommunities
Vanschoenwinkel, B., A. Waterkeyn, M. Jocqué, L. Boven, M. Seaman & L. Brendonck	2008	Species sorting in space and time—the impact of disturbance regime on community assembly in a temporary pool metacommunity

Vanschoenwinkel, B., F. Buschke & L. Brendonck	2008	Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity
Ng, I. S. Y., Carr, C. M. & K. Cottenie	2009	Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms
Brown, B. L. & C. M. Swan	2010	Dendritic network structure constrains metacommunity properties in riverine ecosystems
Doi, H., K. H. Chang & S. Nakano	2010	Dispersal, connectivity, and local conditions determine zooplankton community composition in artificially connected ponds
Howeth, J. G. & M. A. Leibold	2010	Species dispersal rates alter diversity and ecosystem stability in pond metacommunities
Howeth, J. G. & M. A. Leibold	2010	Prey dispersal rate affects prey species composition and trait diversity in response to multiple predators in metacommunities
Vanschoenwinkel, B., S. Gielen, M. Seaman & L. Brendonck	2010	Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities
Declerck, S. A. J., J. S. Coronel, P. Legendre & L. Brendonck	2011	Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands
Jeffries, M. J.	2011	The temporal dynamics of temporary pond macroinvertebrate communities over a 10-year period
Lopes, P. M., A. Caliman, L. S. Carneiro, L. M. Bini, F. A. Esteves, V. Farjalla & R. L. Bozelli	2011	Concordance among assemblages of upland Amazonian lakes and the structuring role of spatial and environmental factors
Nhiwatiwa, T., L. Brendonck, A. Waterkeyn & B. Vanschoenwinkel	2011	The importance of landscape and habitat properties in explaining instantaneous and long-term distributions of large branchiopods in subtropical temporary pans
Sellami, I., J. Elloumi, A. Hamza, M. A. Mhamdi & H. Ayadi	2011	Local and regional factors influencing zooplankton communities in the connected Kasseb Reservoir, Tunisia
Buschke, F. T., J. Adendorff, J. Lamprechts, M. Watson & M.T. Seaman	2012	Invertebrates or iron: does large-scale opencast mining impact invertebrate diversity in ephemeral wetlands?
Dejenie, T., S. A. J. Declerck, T. Asmelash, S. Risch, J. Mergeay, T. De Bie & L. De Meester	2012	Cladoceran community composition in tropical semi-arid highland reservoirs in Tigray (Northern Ethiopia): A metacommunity

		perspective applied to young reservoirs
Frisch, D., K. Cottenie, A. Badosa, & J. Green	2012	Strong Spatial Influence on Colonization Rates in a Pioneer Zooplankton Metacommunity
McCreadie, J. W & P. H Adler	2012	The roles of abiotic factors, dispersal, and species interactions in structuring stream assemblages of black flies (Diptera: Simuliidae)
Angeler, D. G., E. Göthe & R. K. Johnson	2013	Hierarchical Dynamics of Ecological Communities: Do Scales of Space and Time Match?
Gossner, M. M., P. Lade, A. Rohland, N. Sichardt, T. Kahl, J. Bauhus, W. W. Weisser & J. S. Petermann	2013	Effects of management on aquatic tree-hole communities in temperate forests are mediated by detritus amount and water chemistry
Howeth, J. G., J. J. Weis, J. Brodersen, E. C. Hatton & D. M. Post	2013	Intraspecific phenotypic variation in a fish predator affects multitrophic lake metacommunity structure
Omelková, M., V. Syrovátka, V. Křoupalová, V. Rádková, J. Bojková, M. Horsák, M. Zhai, & J. Helešic	2013	Dipteran assemblages of spring fens closely follow the gradient of groundwater mineral richness
Pandit, S. N., J. Kolasa & K. Cottenie	2013	Population synchrony decreases with richness and increases with environmental fluctuations in an experimental metacommunity
Vanschoenwinkel, B.,S. Gielen, H. Vandewaerde, M. Seaman & L. Brendonck	2013	Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity
Bini, L. M., V. L. Landeiro, A. A. Padial, T. Siqueira, & J. Heino	2014	Nutrient enrichment is related to two facets of beta diversity for stream invertebrates across the United States
Hall, A. M., S. J. McCauley & M. J. Fortin	2014	Recreational boating, landscape configuration, and local habitat structure as drivers of odonate community composition in an island setting
Looy, K. V., T. Tormos & Y. Souchon	2014	Disentangling dam impacts in river networks
Wilson, M. J. & M. E. McTammany	2014	Tributary and mainstem benthic macroinvertebrate communities linked by direct dispersal and indirect habitat alteration
Brendonck, L., M. Jocqué, K. Tuytens, B. V. Timms & B. Vanschoenwinkel	2015	Hydrological stability drives both local and regional diversity patterns in rock pool metacommunities
Campbell, R. E., M. J. Winterbourn, T. A.	2015	Flow-related disturbance creates a gradient of metacommunity

Cochrane & A. R. McIntosh		types within stream networks
Canedo-Argüelles, M., K. S. Boersma, M. T. Bogan1, J. D. Olden, I. Phillipsen1, T. A. Schriever & D. A. Lytle	2015	Dispersal strength determines metacommunity structure in a dendritic riverine network
Cauvy-Fraunié, S., R. Espinosa, P. Andino, D. Jacobsen & O. Dangles	2015	Invertebrate Metacommunity Structure and Dynamics in an Andean Glacial Stream Network Facing Climate Change
Medley, K. A., E. H. Boughton, D. G. Jenkins, J. E. Fauth, P. J. Bohlen, & P. F. Quintana-Ascencio	2015	Intense ranchland management tips the balance of regional and local factors affecting wetland community structure
Meier, S., M. Luoto & J. Soininen	2015	The effects of local, buffer zone and geographical variables on lake plankton metacommunities
Petermann, J. S., P. Kratina, N. A. C. Marino, A. A. M. MacDonald & D. S. Srivastava	2015	Resources Alter the Structure and Increase Stochasticity in Bromeliad Microfauna Communities
Castillo-Escriva, A., J. Rueda, L. Zamora, R. Hernandez, M. del Moral & F. Mesquita-Joanes	2016	The role of watercourse versus overland dispersal and niche effects on ostracod distribution in Mediterranean streams (eastern Iberian Peninsula)
Castillo-Escriva, A., L. Valls, C. Rochera, A. Camacho & F. Mesquita-Joanes.	2016	Spatial and environmental analysis of an ostracod metacommunity from endorheic lakes
Datry, T., A. S. Melo, N. Moya, J. Zubieta, E. La Barra & T. Oberdorff	2016	Metacommunity patterns across three Neotropical catchments with varying environmental harshness
Dümmer, B., K. Ristau & W. Traunspurger	2016	Varying Patterns on Varying Scales: A Metacommunity Analysis of Nematodes in European Lakes
Gronroos, M., J. Heino, T. Siqueira, V. L. Landeiro, J. Kotanen & L. M. Bini	2016	Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context
Michelson, A. V., L. E. P. Boush & J. J. Pan	2016	Discerning patterns of diversity from biogeographical distributions: testing models of metacommunity dynamics using non-marine ostracodes from San Salvador Island, Bahamas
Petsch, D. K., G. D. Pinha & A. M. Takeda	2016	Dispersal mode and flooding regime as drivers of benthic metacommunity structure in a Neotropical floodplain
Tonkin, J. D., R. D. T. Shah, D. N. Shah, F.	2016	Metacommunity structuring in Himalayan streams over large

Hoppeler, S. C. Jähnig & S. U. Pauls		elevational gradients: the role of dispersal routes and niche characteristics
Árva D., M. Tóth, A. Mozsár & A. Specziár	2017	The roles of environment, site position, and seasonality in taxonomic and functional organization of chironomid assemblages in a heterogeneous wetland, Kis-Balaton (Hungary)
Cai, Y., H. Xu, A. Vilmi, K. T. Tolonen, X. Tang, B. Qin, Z. Gong, J. Heino	2017	Relative roles of spatial processes, natural factors and anthropogenic stressors in structuring a lake macroinvertebrate metacommunity
Heino, J. & K. T. Tolonen	2017	Ecological drivers of multiple facets of beta diversity in a lentic macroinvertebrate metacommunity
Heino, J., L. M. Bini, J. Andersson, J. Bergsten, U. Bjelke & F. Johansson	2017	Unravelling the correlates of species richness and ecological uniqueness in a metacommunity of urban pond insects
Hill, M. J., R. G. Death, K. L. Mathers, D. B. Ryves, J. C. White & P. J. Wood	2017	Macroinvertebrate community composition and diversity in ephemeral and perennial ponds on unregulated floodplain meadows in the UK
Hill, M. J., J. Heino, I. Thornhill, D. B. Ryves & P. J. Wood	2017	Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities
Looy, K. V., J. Piffady & M. Floury	2017	At what scale and extent environmental gradients and climatic changes influence stream invertebrate communities?
Mendoza, G., R. Kaivosoja, M. Gronroos, J. Hjort, J. Ilmonen, O. M. Karna, L. Paasivirta, L. Tokola & J. Heino.	2017	Highly variable species distribution models in a subarctic stream metacommunity: Patterns, mechanisms and implications
Rádková, V., V. Poláŝková, J. Bojková, V. Syrovátka & M. Horsák	2017	Environmental filtering of aquatic insects in spring fens: patterns of species-specific responses related to specialist generalist categorization
Sarremejane, R., H. Mykra, N. Bonada, J. Aroviita & T. Muotka	2017	Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks
Sarremejane, R., M. Cañedo-Argüelles, N. Prat, H. M. T. Muotka, & N. Bonada	2017	Do metacommunities vary through time? Intermittent rivers as model systems
Tolonen, K. T., A. V., S. M. Karjalainen, S.	2017	Ignoring spatial effects results in inadequate models for variation

Hellsten, T. Sutela & J. Heino		in littoral macroinvertebrate diversity
Tonkin, J. D., S. Stoll, S. C. Jähnig & P. Haase	2017	Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system
Tornwall, B. M., C. M. Swan & B. L. Brown	2017	Manipulation of local environment produces different diversity outcomes depending on location within a river network
Zhao, K., K. Song, Y. Pan, L. Wang, L. Da & Q. Wang	2017	Metacommunity structure of zooplankton in river networks: Roles of environmental and spatial factors

CAPÍTULO II

Environmental changes and interspecific interactions affect β-diversity of tropical bromeliad macroinvertebrates

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Summary

1. Environmental characteristics and ecological interactions are key factors affecting species diversity in biological communities, yet few studies have assessed these effects on β-diversity patterns of aquatic macroinvertebrates. We tested the hypothesis that spatial distance, environmental variables internal and external to the bromeliads tank, and interspecific interactions influence β-diversity among phytotelma macroinvertebrates communities.

2. We sampled macroinvertebrates in 60 bromeliads located within a protected area at a *restinga* (i.e., herbaceous/shrubby coastal sand-dune habitats) in southern Bahia, Brazil. First, we estimate the total β-diversity considering richness and abundance separately, and then partitioned into distinct processes (nestedness and/or turnover for richness and abundance-gradient and/or balanced variation for abundance). Subsequently, we evaluated whether β-diversity among bromeliads was related to the location of bromeliads, local environmental characteristics and/or interspecific interactions.

3. We obtained high β-diversity estimates, governed by turnover and balanced variation processes. Contrary to our expectations, the spatial distance did not affect β-diversity, whereas the input of organic matter and negative interspecific interactions increased species dissimilarity among bromeliads.

4. Given that human activities have been altering natural ecosystems and promoting changes in several abiotic factors including the input of organic matter, our results highlight its pervasive effects on the stability of bromeliad macroinvertebrate communities.

Keywords: species turnover, environmental filter, dispersion limitation, competitive exclusion, tropical environment, *restinga*.

Introduction

In general, ecological studies seek to understand how biological communities are structured throughout space and time, and how environmental changes can affect their structure (Whittaker, 1960, 1972; Heino *et al.*, 2015b; Socolar *et al.*, 2016; Anderson & Hayes, 2018). Usually, the smaller the similarity between the characteristics of two or more habitats, the greater is the difference in the structure of species communities (Anderson *et al.*, 2011; Baselga, 2012; Busse *et al.*, 2018). Therefore, several factors such as the geographic distance between the studied sites, the capacity of organisms to disperse, environmental variations, as well as interspecific and intraspecific interactions can directly affect the structure of faunal communities (Baselga, 2010; Talaga *et al.*, 2015; Heino & Tolonen, 2017; Gianuca *et al.*, 2017)

In aquatic environments, both the connectivity between areas and the dispersal ability of organisms have been widely used to explain patterns of species distribution (Viana *et al.*, 2016; Gianuca *et al.*, 2017). Additionally, abiotic changes related to either chemical (e.g., chemical composition, nutrient supply and/or organic matter), temperature, and/or physical aspects (e.g., local habitat structure) have also been recognized as key predictors of changes in the structure of macroinvertebrate communities (Bini *et al.*, 2014; González, Romero & Srivastava, 2014; Gossner *et al.*, 2016; Baumgartner & Robinson, 2017). Furthermore, ecological interactions among species may play an important role in this structuring (Leibold & Geddes, 2005; Segre *et al.*, 2014). For instance, predation events are important modulators of aquatic macroinvertebrate composition associated with bromeliads (Amundrud & Srivastava, 2016; Antiqueira, Petchey & Romero, 2018). Hence, unveiling the major factors affecting the variation of species in aquatic environments can contribute to enhance our understanding of the effects of environmental changes on the structure of biological communities, and thus facilitate the implementation of more adequate conservation measures (Armbruster, Hutchinson & Cotgreave, 2002; Baselga, 2010; Teresa & Casatti, 2012; Gossner *et al.*, 2016; Gianuca *et al.*, 2017).

Specifically in *restinga* environments (i.e., herbaceous/shrubby coastal sand-dune habitats, see Rocha et al., 2007), which is characterized by a prominent water scarcity throughout the year (Scarano *et al.*, 2001), bromeliads act as important resources and refuges for several aquatic invertebrate species (Marino *et al.*, 2011; Rangel *et al.*, 2017). Additionally, the location of the (phytotelma) plays a fundamental

role in the associated faunal composition, since it is likely to influence both the efficiency of species dispersion and local conditions, especially abiotic variables inside the tank (Brouard *et al.*, 2011; Farjalla *et al.*, 2016; Busse *et al.*, 2018). In fact, several studies have shown that chemical water variables (Paradise & Society, 2000; Guzman *et al.*, 2018) and the input of organic matter (Brouard *et al.*, 2011; Rangel *et al.*, 2017; Rodríguez Pérez *et al.*, 2018) are important predictors of bromeliad macroinvertebrate composition. In addition, aspects of the bromeliad structure (e.g., height and central tank surface area) may be critical in the choice of oviposition and foraging sites for different invertebrate species (Angelon & Petranka, 2002; Blaustein *et al.*, 2004; Reiskind & Zarrabi, 2012). Finally, the three-dimensional structure of these plants allows the coexistence of a great number of species (Gyllström & Hansson, 2004; Marino, Srivastava & Farjalla, 2013; Lecraw, Srivastava & Romero, 2014). All these factors can interact positively (i.e., through facilitation, when trophic groups such as shredders detritivores turn gross organic matter into fine particles at basal trophic levels) or negatively (i.e., through competition and predation), affecting patterns of species diversity and composition of local communities (Srivastava *et al.*, 2008; Starzomski, Suen & Srivastava, 2010; Busse *et al.*, 2018).

Measuring β-diversity is among the most reliable way for obtaining information on variation in species composition (Whittaker, 1960, 1972; Anderson *et al.*, 2011). This component of biological diversity seeks to identify the level of change of species composition in a set of communities, and usually considers the environmental variations along the space and time (Whittaker, 1960; Baselga, 2010; Anderson *et al.*, 2011; Jyrkänkallio-Mikkola, Heino & Soininen, 2016). This measurement was firstly created in 1960 by Whittaker, but until to date other ways of estimating and interpreting have been discussed and proposed (Vellend, 2001; Koleff, Gaston & Lennon, 2003; Tuomisto, 2010; Baselga, 2010, 2017). More recently, Baselga (2010, 2017) proposed an approach in which the total beta diversity is partitioned into two distinct processes - nestedness and/or turnover for richness, and abundance-gradient and/or balanced variation for abundance data. In nested systems, smaller communities are subsets of larger communities ─ a non-random loss of species (Baselga, 2010). Differently, turnover is related to species exchange between two localities, due to the action of environmental filters, historical restrictions and ecological interactions (Baselga, 2010). Furthermore, the abundance-gradient describes that individuals of certain taxa are

gradually lost from one site to another, without the substitution of individuals by other taxa (Baselga, 2017). In contrast, balanced variation infers that the total number of individuals of one species is replaced by the same number of individuals of other taxon(s) in different communities (Baselga, 2017).

Despite the different procedures of estimating β-diversity, this measure may be a much more informative tool in understanding the dynamics of biological communities than simply assessing α-diversity patterns, i.e., species richness (Wang *et al.*, 2012; Al-Shami *et al.*, 2013). Here, we measured the β-diversity of aquatic macroinvertebrates associated with *restinga* bromeliads, and evaluated which process ─ i.e., turnover/nestedness and abundance-gradient/balanced variation drives the structure of species composition. In addition, we evaluated whether the geographical distance between bromeliads, environmental changes and interactions among species best predict β-diversity in this system. We expected to detect: (i) pronounced changes in species composition (i.e., high total β-diversity) of the bromeliad associated fauna among different sampling bromeliads, governed by turnover and balanced variation processes, for richness and abundance estimates respectively; and (ii) great variation in species composition, mostly explained by the spatial distance between bromeliads, the action of local environmental filters, and interspecific interactions (especially predation and competition). Specifically, we expect that the marked environmental variation in abiotic conditions, mostly driven by local disturbances, would lead species composition to be extremely variable among sampled bromeliads, therefore explaining a predominance of turnover process (Reiskind & Zarrabi, 2012; González *et al.*, 2014; Gossner *et al.*, 2016; Busse *et al.*, 2018). Additionally, as predicted by the distance decay hypothesis (Astorga et al., 2012; Viana *et al.*, 2016; Baselga, 2017; Gianuca *et al.*, 2017), we presume that the greater is the geographic distance between bromeliad pairs, the greater will be the β-diversity of macroinvertebrates. Finally, we expect that the negative interactions (i.e., predation or competition) established within the tanks will act as strong drivers of species dissimilarity, as the occurrence of certain taxa will tend to exclude or inhibit the establishment of others, resulting in high beta diversity values (Angelon & Petranka, 2002; Howeth & Leibold, 2010; Baselga, 2010; Antiqueira *et al.*, 2018).

Material and methods

Study area and environmental variables

We conducted this study at a *restinga* located in Ilhéus, Bahia, Brazil, protected by the Environmental Preservation Area of Lagoa Encantada (Fig. 1), on December 11, 12, 13, 2016. *Restingas* are sand-dune habitats, covered by herbaceous and arbustive-arboreal vegetation, extensively occurring along the Brazilian coast (Araujo, 1992). Yet this region has been intensively disturbed and exploited since the arrival of Europeans ~500 years ago, leading to the continuous loss of great areas mainly for housing (Rocha *et al.*, 2005). This specific *restinga* presents poor nutrient soil, high salinity and temperature, low water availability, high light radiation and frequency of winds (Scarano *et al.*, 2001). The local climate is characterized as hot and humid, with average annual temperatures varying between 22°C e 25°C (Faria Filho & Araújo, 2003). The pluviometric regime is regular, with abundant rains well distributed during the year, reaching 2,700 mm (Faria Filho & Araújo, 2003). The local environment is composed by a mosaic of dense bush (height (h) > 3 m) and herbaceous (h < 2 m) vegetation and exposed soil. The clumps are composed of small plant species, exhibiting the understory with scandic shrubs, spiny bromeliads, cacti and creepers. Dense populations of ferns and bromeliads that extend beyond the shrub border occupy the herbaceous layer. Small clumps predominantly formed by bromeliads are common. The dominant herbaceous species in both shrubby and herbaceous clumps is the bromeliad *Vriesea philippocoburgii* Wawra. Therefore, we used this species as the sampling site of this study.

We firstly selected a set of 120 bromeliads according to the following characteristics: (*i*) located in the border of clumps; (*ii*) with a minimum distance of 10 m from the next sampling bromeliad; (*iii*) exhibiting tanks of similar diameters (~5 cm) and (*iv*) containing water therein; and (*v*) belonging to different clumps. From this total, we randomly chose 60 individuals for sampling. We thus recorded the distance (GEO) between sampling bromeliads, in order to obtain a spatial map of our sampling sites (Fig. 1).

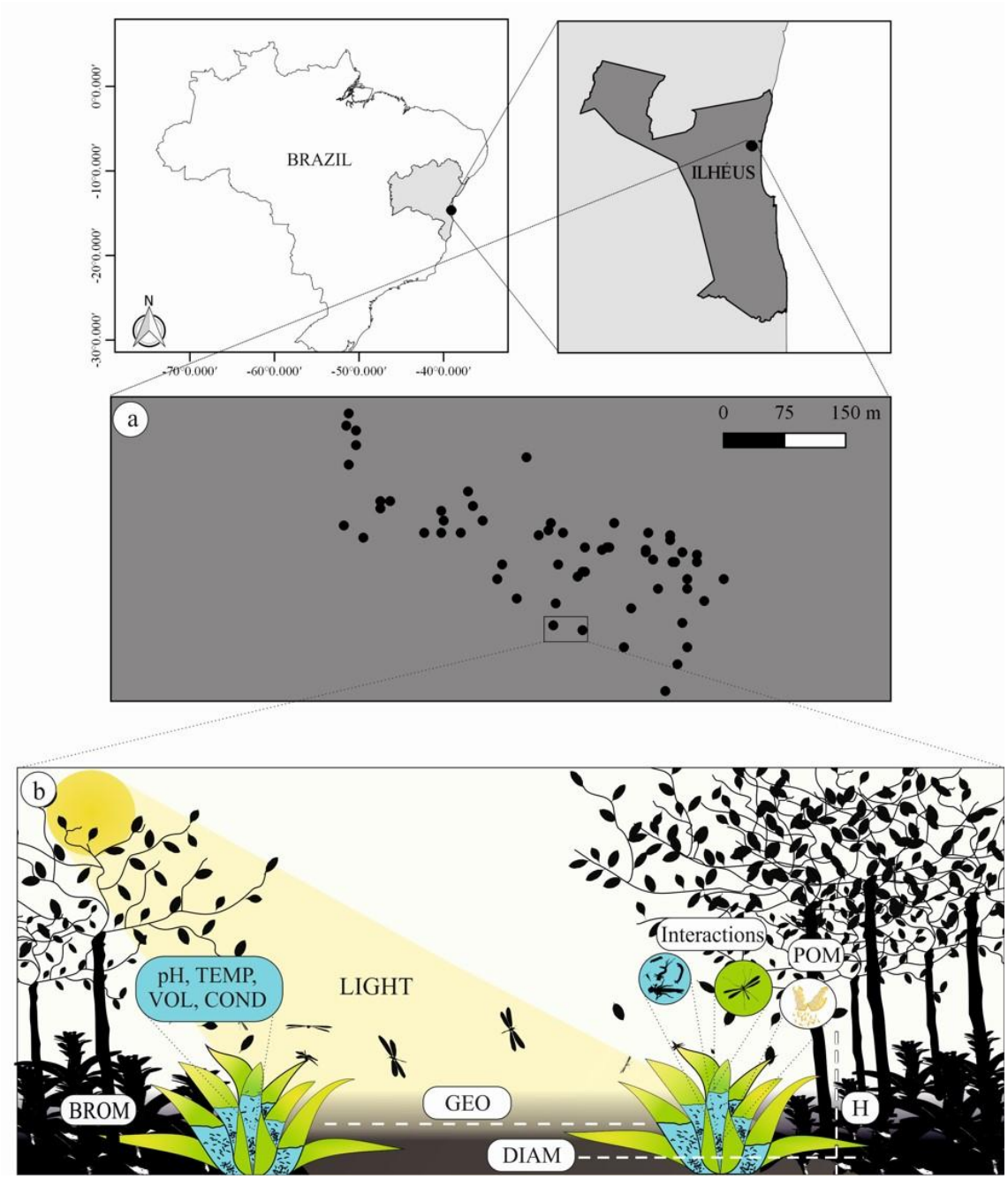

Fig. 1 Location of the study area in the municipality of Ilhéus, Bahia, Brazil, including (a) the spatial distribution of the 60 sampling bromeliads, and (b) illustration of the sampling protocol of environmental variables. GEO - geographical distance between bromeliads, pH - tank water pH, TEMP - temperature, COND - conductivity, VOL - total volume of liquid in the tank, LIGHT - light intensity over the tank, POM – Particulate organic matter, H - height, DIAM - diameter, BROM - total number of bromeliads in the clump.

In the tank water of each individual, we measured six abiotic variables: pH, temperature (TEMP, in ^{o}C), conductivity (COND, in μS), total fluid volume (VOL, in

mL), light intensity (LIGHT, in %), and particulate organic matter (POM, in gPS) (Fig. 1). To obtain the values of the first four variables, we used a multiparameter probe (Instrutemp model ITPH - 3000), whereas the luminous intensity was recorded with a luxmeter (Instrutherm LD - 240). To determine the quantity of POM, we used the protocol proposed by Carmo & Silva (2012), which consists in filtering the fluid sample using paper filters, drying them and removing all the trapped vegetable material. This material is then ground in a processor, and the compound is sieved through a 1 mm mesh. Then, 1.000 g dry weight of the sieved material (analytical balance 0.0001 g) is separated and transported for muffle firing at 550°C for 1 hour, and, after burning, the remaining ashes are weighed. The difference between the initial weight and ash weight refers to the organic matter content in 1000 g, which was extrapolated to obtain the total POM value of each sample. Outside of the tank, we measured the height (H) and the diameter (i.e., the distance between the two outermost leaf tips - DIAM) of each sampled bromeliad. In order to characterize the local habitat structure of each focal bromeliad, we also counted the total number of bromeliads present in each clump (BROM) (Fig. 1).

The sampled bromeliads showed a mean distance of 200 m ± 124 (standard deviation - SD) to each other. The water in the central tank showed a mean pH of 4.28 ± 0.70, a mean TEMP of 26.65 ºC ± 2.03, mean COND of 6.60 µS ± 5.20, mean net VOL of 68.10 mL ± 36.00, mean LIGHT of 30.50 ± 37.06 %, and mean POM of 0.14 gPS ± 0.20. The mean height and the diameter of bromeliads were, respectively, 53.01 cm ± 9.90 and 83.23 cm ± 15.59. On average, we recorded 67 ± 85 bromeliads in each clump.

Macroinvertebrate sampling

We homogenized the liquid inside the tank of each bromeliad by bubbling it, and using a thin metal rod, we released all adhered organisms to the edge of the tanks (adapted from Tun-Lin *et al*., 1995). We subsequently aspirated the liquid (including the local fauna) present in each tank using a transparent hose (diameter 2.5 cm), storing the material in a properly identified plastic container. We thus performed a new tank washing, using distilled water, and a new bubbling to collect the macroinvertebrates leftover (adapted from Pittendrigh, 1950). All organisms larger than 25 µm were fixed in alcohol 70% and identified to the lowest possible taxonomic level, using

stereomicroscope (©Physis) and specific literature (Serra, Coimbra & Graça, 2009; Hamada *et al.*, 2014). In some cases, specimens were sent to specialists for confirming the identification.

Ecological interactions

We also investigated whether positive and/or negative interactions could influence the β-diversity patterns. For this, we constructed a matrix of presence/absence of macroinvertebrates sampled in each bromeliad and created a probabilistic model of species co-occurrence (Veech, 2013) using the *cooccur* package (Griffith, Veech & Marsh, 2016) available in the RStudio (RStudio Team, 2016). This model uses the hypergeometric distribution to estimate the co-occurrence directly based on the number of sites where two species were recorded (see Griffith, Veech & Marsh, 2016). Using a combinatorics, the observed co-occurrence can thus be compared with the expected co-occurrence. When the co-occurrence frequency observed for two species is significantly ($p \leq 0.05$) higher or lower than the expected frequency at random, we classified this co-occurrence as positive or negative, respectively. Finally, if the association does not differ significantly from that expected randomly, it is classified as random (Veech, 2013; Griffith, Veech & Marsh, 2016). After identifying which pairs of species had negative or positive associations, we verified the presence of these associations, and recorded the total number of negative and positive interactions identified in each bromeliad.

Data analyses

We estimated the β-diversity of macroinvertebrates inhabiting the bromeliad tanks following Baselga (2010, 2017), through the *betapart* package in the RStudio (RStudio Team, 2016). This approach uses the Sørensen and the Bray-Curtis dissimilarity indexes, for richness and abundance data, respectively, to calculate total β-diversity. The output varies from 0 to 1, indicating the degree of dissimilarity between two communities ─ i.e., [0] means total similarity and [1] total difference. Then, β-diversity was partitioned to identify which process drives the structure of the studied

communities ─ nestedness or turnover, for richness data (Baselga, 2010), and balanced variation or abundance-gradient, for abundance (Baselga, 2017).

We used Mantel tests to assess whether β-diversity was correlated with GEO (i.e., geographic distance matrix across all bromeliads). We applied these tests also to the matrices pointing to local differences in internal abiotic variables (i.e., pH, Temp, cond, VOL, LIGHT and POM), external characteristic to the tank (DIAM), the local structure (BROM) and the ecological interactions (positive and negative). The matrices were based on Euclidean distances, and the analyses were conducted in the *vegan* package (Oksanen *et al.,* 2018). All analyzes and graphics were performed using the RStudio software (RStudio Team, 2016).

Results

We recorded 8,590 macroinvertebrates, distributed in 60 morphotypes belonging to eight orders considering all sampled bromeliads. Only one bromeliad did not present any individuals. Excluding it, the mean number of morphotypes and individuals per bromeliad was eight (standard deviation - SD ± 3; range 4 to 14) and 72 (± 286; 8 to 1,243), respectively. The larval form predominated in the sampled individuals (83.6%), with the exception of copepods and ostracods. The latter followed by dipterans were the most numerous (respectively 2,292 and 1,421 individuals). Dipterans were more constant, being recorded in 50 bromeliads, followed by ostracods in 27 (Table S1).

We detected high total β-diversity among bromeliads, considering both species richness (0.96) and abundance of individuals (0.98). By partitioning the total value of β-diversity based on richness, we found that 98.4% of the observed pattern was a result of a turnover process. Similarly, we observed that the distribution of individuals based on abundance occurred through balanced variation (95.8%). In addition, our results showed that estimates of β-diversity were unaffected by geographic distance and differences in local habitat structure. However, differences in MOP content among bromeliads positively affected β-diversity aquatic macroinvertebrate patterns, considering data from richness and abundance (Table 1, Fig. 2a,b). Finally, we observed that only the negative interactions significantly affected the species turnover in the bromeliads (Table 1, Fig. 2c).

Table 1 Correlation of Mantel (*r*) and significance values (*p*) between β-diversity estimates among macroinvertebrates and inter-site differences (Δ) of the geographic distance among bromeliads (GEO), abiotic (pH, TEMP, COND, VOL, LIGHT, POM, H and DIAM) and local structure (BROM) variables and ecological interactions in 59 *restinga* bromeliads located in the south of Bahia, Brazil (N = 58 pairwise comparisons). Results are presented separately for species richness (i.e., turnover) and abundance (balanced variation), with significant values highlighted in bold.

Variables	**Richness**		**Abundance**	
	r	***P***	***R***	***p***
Δ GEO	-0.047	0.860	-0.017	0.630
Δ pH	0.060	0.096	0.073	0.076
Δ TEMP	0.040	0.202	0.044	0.160
Δ COND	0.075	0.132	0.199	0.050
Δ VOL	0.052	0.206	0.042	0.200
Δ LIGHT	-0.016	0.585	0.050	0.205
Δ POM	**0.230**	**0.001**	**0.270**	**0.001**
Δ H	0.040	0.240	-0.030	0.730
Δ DIAM	3.6^{e-05}	0.504	-0.006	0.550
Δ BROM	0.070	0.15	0.086	0.087
NEG. INT*	**0.301**	**0.001**	-	-
POSI. INT*	-0.038	0.820	-	-

*Variables tested only for richness because co-occurrence analyses were based only on species presence-absence data. GEO - geographical distance between bromeliads, pH - tank water pH, TEMP - temperature, COND - conductivity, VOL - total volume of liquid in the tank, LIGHT - light intensity over the tank, POM – Particulate organic matter, H - height, DIAM - diameter, BROM - total number of bromeliads in the clump, NEG. INT - negative interactions, INT. POSI - positive interactions.

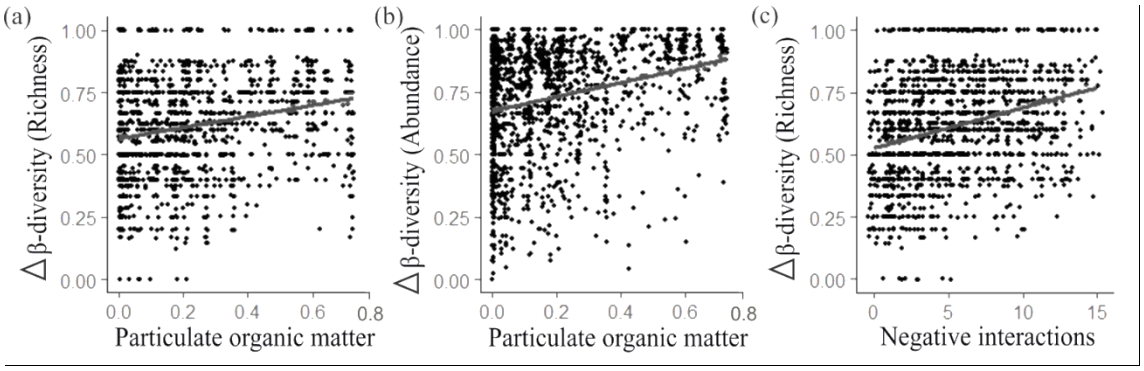

Fig. 2 Correlations between differences (Δ) of β-diversity, considering (a, c) turnover and (b) balanced variation, with the input of particulate organic matter and negative interactions between species recorded in each bromeliad.

Discussion

Our results clearly demonstrate that the composition of (phytotelmic) macroinvertebrate communities in *restinga* bromeliads strongly differ from each other, with β-diversity patterns mostly governed by turnover. Additionally, the observed inter-site differences in species composition were greatly explained by two main factors: the input of particulate organic matter within bromeliad and negative ecological interactions between species. Contrary to our predictions, the spatial distance between the bromeliads did not influence β-diversity patterns of macroinvertebrates, indicating the inexistence of limitation in species' dispersion (Astorga *et al.*, 2012; Cauvy-Fraunié *et al.*, 2015; Heino, Melo & Bini, 2015a). Therefore, our results highlight that both abiotic factors and species interactions are fundamental for structuring the aquatic macroinvertebrate communities inhabiting bromeliads.

The great variation in species composition of macroinvertebrate among bromeliads tanks was also recorded in other aquatic environments, both lentic and lotics (Costa & Melo, 2008; Al-Shami *et al.*, 2013; Viana *et al.*, 2016; Heino & Tolonen, 2017; Rangel *et al.*, 2017; Sarremejane *et al.*, 2017b). Specifically, in our study system, the main process explaining this variation was the turnover, demonstrating that macroinvertebrates inhabiting bromeliad systems experience great rates of replacements among sites and consequently exhibit high variation in its adaptability. In fact, aquatic macroinvertebrates are represented by a wide range of species, exhibiting high differences in morphological and functional terms (Marino *et al.*, 2013; Boersma *et al.*,

2014; Schmera *et al.*, 2017), and consequently present contrasted sensitivities to environmental changes (Burgmer, Hillebrand & Pfenninger, 2007; Sellami *et al.*, 2011; Talaga *et al.*, 2017). Thus, the action of environmental filters ─ particularly abiotic conditions and related species interactions ─ explained the observed high species exchange between bromeliad tanks.

Considering all environmental variables analyzed, we unveiled that particulate organic matter was an important factor driving β-diversity patterns. In freshwater systems, the allochthonous input of organic matter comprises an important energy resource likely to affect secondary production and communities' structure (Parker, 1989; Szkokan-Emilson, Wesolek & Gunn, 2011; Brouard *et al.*, 2011; Farjalla *et al.*, 2016). In lakes, for example, organic matter is the main factor of the trophic chain base, surpassing even the primary production by algae (Pace *et al.*, 2004; Carpenter *et al.*, 2007; Solomon *et al.*, 2011). In bromeliads, differences in the amount of particulate organic matter indeed induced to marked differences in the composition of aquatic macroinvertebrate species (Brouard *et al.*, 2011, 2012; Dézerald *et al.*, 2013; Rangel *et al.*, 2017; Busse *et al.*, 2018), causing therefore an increase in β-diversity. This increment in species turnover is vastly explained by the need of several life stages for processing this organic matter. Thus, different taxa are required to process this resource and enable the available to basal trophic levels (e.g., primary consumers) (Starzomski *et al.*, 2010; Brouard *et al.*, 2012). Hence, it becomes clear that the input of particulate organic matter plays a fundamental role in structuring macroinvertebrates communities in bromeliad systems.

Ecological interactions seem also to be a key factor affecting the structure of communities governed by turnover (Vanschoenwinkel *et al.*, 2010; Baselga, 2010; Segre *et al.*, 2014; Sarremejane *et al.*, 2017a). Negative interactions, such as competition and predation, can act as dominant forces, which can either cause the exclusion of certain species or act as a filter for the establishment of others (Armbruster *et al.*, 2002; Starzomski *et al.*, 2010; Brouard *et al.*, 2011, 2012). For example, studies have shown that competitive exclusion events enhanced β-diversity estimates by extinguishing certain biological groups (see Segre *et al.*, 2014). In addition, both direct predation, which excludes individuals and reduces the population viability against environmental disturbances, and the presence of the predator that can limit the occurrence or behavior of the prey, induce great dissimilarity among macroinvertebrate

communities (Angelon & Petranka, 2002; Blaustein *et al.*, 2004; Howeth & Leibold, 2010; Reiskind & Zarrabi, 2012). Therefore, not only the input of organic matter, but also the negative interactions among organisms played an important role in structuring the community of aquatic macroinvertebrates in bromeliads.

In contrast to several studies that showed the strong importance of geographic distance in structuring assemblages of freshwater macroinvertebrates (Astorga *et al.*, 2012; Heino *et al.*, 2015c; Castillo-Escrivà *et al.*, 2016; Sarremejane *et al.*, 2017b), the distance between the bromeliads was a weak predictor of β-diversity in our studied bromeliads system. It is possible that the distance among bromeliads does not act as a limiting factor of dispersion for our target group (Astorga *et al.*, 2012; Heino *et al.*, 2015c; Sarremejane *et al.*, 2017b; Gianuca *et al.*, 2017), especially because most of the recorded taxa were dipterous. This group presents high dispersion efficiency (i.e. by flight) and its establishment is mostly related to local environmental conditions and/or the risk of predation (Angelon & Petranka, 2002; Blaustein *et al.*, 2004; Reiskind & Zarrabi, 2012). Thus, dissimilarities among communities are basically a result of how organisms react to variations in the environment (Paradise *et al.*, 2008; Doi, Chang & Nakano, 2010), and the ecological relationships established between the species within the tanks (Vanschoenwinkel *et al.*, 2010; Baselga, 2010; Sarremejane *et al.*, 2017a).

Conclusions

This study highlights the importance of considering β-diversity estimates in studies assessing the diversity patterns in aquatic environments, and also enhances our understanding of how and which factors determine the variation among macroinvertebrate communities found in terrestrial bromeliads. Firstly, we revealed the existence of a high turnover considering both occurrence and species abundance data in this system. In addition, we showed that the amount of organic matter available in bromeliad tanks was the strongest predictor explaining the turnover among different bromeliads, according to other studies that assessed its effect on patterns of bromeliad macroinvertebrate composition (Brouard *et al.*, 2011; Dézerald *et al.*, 2013). Finally, we reveal that antagonistic interactions act as additional driving forces to structure these communities, possibly by promoting the exclusion of some species (by predation and/or competition) or acting as a filter and limiting the establishment of others. Considering

the growing expansion of human activities on the planet, which has been severely deteriorating all worldwide ecosystems, especially in the tropics, it is likely that several disturbances will disrupt the structure of macroinvertebrates inhabiting bromeliads in the long term. For example, the global temperature increase due to the high gas emission rates promoted by the various economic activities, and the subsequent effects on rainfall precipitation (Dézerald *et al.*, 2017; Bernabé *et al.*, 2018; Guzman *et al.*, 2018), can induce substantial changes in the input of allochthonous nutrients, thus reducing the productivity rates of aquatic environments, including phytotelmatas. Our results can indicate, therefore, that abrupt changes in the entry of organic matter, such as those induced by human disturbances, can modify the structure of bromeliad macroinvertebrate communities. This represents strong effects on major ecosystem processes performed by macroinvertebrate species, including changes in nutrient cycling and primary productivity in other freshwater systems (Brouard *et al.*, 2011; Cortelezzi *et al.*, 2015; Bernabé *et al.*, 2018; Céréghino *et al.*, 2018).

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References

Al-Shami S.A., Heino J., Che Salmah M.R., Abu Hassan A., Suhaila A.H. & Madrus M.R. (2013). Drivers of beta diversity of macroinvertebrate communities in tropical forest streams. *Freshwater Biology* **58**, 1126–1137. https://doi.org/10.1111/fwb.12113

Amundrud S.L. & Srivastava D.S. (2016). Trophic interactions determine the effects of drought on an aquatic Ecosystem. *Ecology* **97**, 1475–1483. https://doi.org/10.1890/15-1638.1

Anderson K.E. & Hayes S.M. (2018). The effects of dispersal and river spatial structure on asynchrony in consumer-resource metacommunities. *Freshwater Biology* **63**,

100–113. https://doi.org/10.1111/fwb.12998

Anderson M.J., Crist T.O., Chase J.M., Vellend M., Inouye B.D., Freestone A.L., *et al.* (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* **14**, 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Angelon K.A. & Petranka J.W. (2002). Chemicals of Predatory Mosquitofish (Gambusia affinis) Influence Selection of Oviposition Site by Culex Mosquitoes. *Journal of Chemical Ecology* **28**, 797–806. https://doi.org/10.1023/A:1015292827514

Antiqueira P.A.P., Petchey O.L. & Romero G.Q. (2018). Warming and top predator loss drive ecosystem multifunctionality. *Ecology Letters* **21**, 72–82. https://doi.org/10.1111/ele.12873

Araujo D.S.D. (1992). Vegetation Types of Sandy Coastal Plains of Tropical Brazil: A First Approximation. In: *Coastal Plant Communities of Latin America*. pp. 337–347. Elsevier.

Armbruster P., Hutchinson R.A. & Cotgreave P. (2002). Factors influencing community structure in a South American tank bromeliad fauna. **2**, 225–234

Astorga A., Oksanen J., Luoto M., Soininen J., Virtanen R. & Muotka T. (2012). Distance decay of similarity in freshwater communities: Do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography* **21**, 365–375. https://doi.org/10.1111/j.1466-8238.2011.00681.x

Baselga A. (2017). Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution* **8**, 799–808. https://doi.org/10.1111/2041-210X.12693

Baselga A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* **19**, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* **21**, 1223–1232. https://doi.org/10.1111/j.1466-8238.2011.00756.x

Baumgartner S.D. & Robinson C.T. (2017). Changes in macroinvertebrate trophic structure along a land-use gradient within a lowland stream network. *Aquatic Sciences* **79**, 407–418. https://doi.org/10.1007/s00027-016-0506-z

Bernabé T.N., de Omena P.M., Santos V.P. dos, de Siqueira V.M., de Oliveira V.M. & Romero G.Q. (2018). Warming weakens facilitative interactions between decomposers and detritivores, and modifies freshwater ecosystem functioning. *Global Change Biology* **24**, 3170–3186. https://doi.org/10.1111/gcb.14109

Bini L., Landeiro V., Padial A., Siqueira T. & Heino J. (2014). Nutrient enrichment is related to two facets of beta diversity of stream invertebrates across the continental United States. *Ecology* **95**, 1569–1578. https://doi.org/10.1890/13-0656.1

Blaustein L., Kiflawi M., Eitam A., Mangel M. & Cohen J.E. (2004). Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. *Oecologia* **138**, 300–305. https://doi.org/10.1007/s00442-003-1398-x

Boersma K.S., Bogan M.T., Henrichs B.A. & Lytle D.A. (2014). Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. *Freshwater Biology* **59**, 491–501. https://doi.org/10.1111/fwb.12280

Brouard O., Céréghino R., Corbara B., Leroy C., Pelozuelo L., Dejean A., *et al.* (2012). Understorey environments influence functional diversity in tank-bromeliad ecosystems. *Freshwater Biology* **57**, 815–823. https://doi.org/10.1111/j.1365-2427.2012.02749.x

Brouard O., Le Jeune A.-H., Leroy C., Cereghino R., Roux O., Pelozuelo L., *et al.* (2011). Are algae relevant to the detritus-based food web in tank-bromeliads? *PloS one* **6**, e20129. https://doi.org/10.1371/journal.pone.0020129

Burgmer T., Hillebrand H. & Pfenninger M. (2007). Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. *Oecologia* **151**, 93–103. https://doi.org/10.1007/s00442-006-0542-9

Busse A., Antiqueira P.A.P., Neutzling A.S., Wolf A.M., Romero G.Q. & Petermann J.S. (2018). Different in the dark: The effect of habitat characteristics on community composition and beta diversity in bromeliad microfauna. *PLOS ONE*

13, e0191426. https://doi.org/10.1371/journal.pone.0191426

Carpenter S.R., Hodgson J.R., Kritzberg E.S., Cole J.J., Bade D.L., Pace M.L., *et al.* (2007). Ecosystem Subsidies: Terrestrial Support of Aquatic Food Webs From 13 C Addition To Contrasting Lakes . *Ecology* **86**, 2737–2750. https://doi.org/10.1890/04-1282

Castillo-Escrivà A., Valls L., Rochera C., Camacho A. & Mesquita-Joanes F. (2016). Spatial and environmental analysis of an ostracod metacommunity from endorheic lakes. *Aquatic Sciences* **78**, 707–716. https://doi.org/10.1007/s00027-015-0462-z

Cauvy-Fraunié S., Espinosa R., Andino P., Jacobsen D. & Dangles O. (2015). Invertebrate metacommunity structure and dynamics in an Andean glacial stream network facing climate change. *PLoS ONE* **10**, 1–19. https://doi.org/10.1371/journal.pone.0136793

Céréghino R., Pillar V.D., Srivastava D.S., de Omena P.M., MacDonald A.A.M., Barberis I.M., *et al.* (2018). Constraints on the functional trait space of aquatic invertebrates in bromeliads. *Functional Ecology* **32**, 2435–2447. https://doi.org/10.1111/1365-2435.13141

Cortelezzi A., Ocón C., Oosterom M.V.L. van, Cepeda R. & Capítulo A.R. (2015). Nutrient enrichment effect on macroinvertebrates in a lowland stream of Argentina. *Iheringia. Série Zoologia* **105**, 228–234. https://doi.org/10.1590/1678-476620151052228234

Costa S.S. & Melo A.S. (2008). Beta diversity in stream macroinvertebrate assemblages: Among-site and among-microhabitat components. *Hydrobiologia* **598**, 131–138. https://doi.org/10.1007/s10750-007-9145-7

Dézerald O., Leroy C., Corbara B., Carrias J.-F., Pélozuelo L., Dejean A., *et al.* (2013). Food-Web Structure in Relation to Environmental Gradients and Predator-Prey Ratios in Tank-Bromeliad Ecosystems. *PLoS ONE* **8**, e71735. https://doi.org/10.1371/journal.pone.0071735

Dézerald O., Leroy C., Corbara B., Dejean A., Talaga S. & Céréghino R. (2017). Environmental drivers of invertebrate population dynamics in Neotropical tank bromeliads. *Freshwater Biology* **62**, 229–242. https://doi.org/10.1111/fwb.12862

Doi H., Chang K.H. & Nakano S.I. (2010). Dispersal, connectivity, and local conditions determine zooplankton community composition in artificially connected ponds. *Aquatic Biology* **10**, 47–55. https://doi.org/10.3354/ab00262

Faria Filho A.F. & Araújo Q.R. de (2003). Zoneamento do meio físico do município de Ilhéus, Bahia, Brasil, utilizando a técnica de geoprocessamento. *Boletim Técnico* **187**, 1–20

Farjalla V.F., González A.L., Céréghino R., Dézerald O., Marino N.A.C., Piccoli G.C.O., *et al.* (2016). Terrestrial support of aquatic food webs depends on light inputs: a geographically-replicated test using tank bromeliads. *Ecology* **97**, 2147–2156. https://doi.org/10.1002/ecy.1432

Gianuca A.T., Declerck S.A.J., Lemmens P. & De Meester L. (2017). Effects of dispersal and environmental heterogeneity on the replacement and nestedness components of β-diversity. *Ecology* **98**, 525–533. https://doi.org/10.1002/ecy.1666

González A.L., Romero G.Q. & Srivastava D.S. (2014). Detrital nutrient content determines growth rate and elemental composition of bromeliad-dwelling insects. *Freshwater Biology* **59**, 737–747. https://doi.org/10.1111/fwb.12300

Gossner M.M., Lade P., Rohland A., Sichardt N., Kahl T., Bauhus J., *et al.* (2016). Effects of management on aquatic tree-hole communities in temperate forests are mediated by detritus amount and water chemistry. *Journal of Animal Ecology* **85**, 213–226. https://doi.org/10.1111/1365-2656.12437

Griffith D.M., Veech J.A. & Marsh C.J. (2016). cooccur: Probabilistic Species Co-Occurrence Analysis in R. *Journal of Statistical Software* **69**, 1–17. https://doi.org/10.18637/jss.v069.c02

Guzman L.M., Vanschoenwinkel B., Farjalla V.F., Poon A. & Srivastava D.S. (2018). A precipitation gradient drives change in macroinvertebrate composition and interactions within bromeliads. *PLOS ONE* **13**, e0200179

Gyllström M. & Hansson L.-A. (2004). Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling. *Aquatic Sciences* **66**, 274–295. https://doi.org/10.1007/s00027-004-0712-y

Hamada N., Nessimian J.L., Barbosa Querino R. & Querino R.B. (2014). *Insetos*

aquáticos na Amazônia brasileira : taxonomia, biologia e ecologia.

Heino J., Melo A.S. & Bini L.M. (2015a). Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshwater Biology* **60**, 223–235. https://doi.org/10.1111/fwb.12502

Heino J., Nokela T., Soininen J., Tolkkinen M., Virtanen L. & Virtanen R. (2015b). Elements of metacommunity structure and community-environment relationships in stream organisms. *Freshwater Biology* **60**, 973–988. https://doi.org/10.1111/fwb.12556

Heino J., Soininen J., Alahuhta J., Lappalainen J. & Virtanen R. (2015c). A comparative analysis of metacommunity types in the freshwater realm. *Ecology and Evolution* **5**, 1525–1537. https://doi.org/10.1002/ece3.1460

Heino J. & Tolonen K.T. (2017). Ecological drivers of multiple facets of beta diversity in a lentic macroinvertebrate metacommunity. *Limnology and Oceanography* **62**, 2431–2444. https://doi.org/10.1002/lno.10577

Howeth J.G. & Leibold M.A. (2010). Prey dispersal rate affects prey species composition and trait diversity in response to multiple predators in metacommunities. *Journal of Animal Ecology* **79**, 1000–1011. https://doi.org/10.1111/j.1365-2656.2010.01715.x

Jyrkänkallio-Mikkola J., Heino J. & Soininen J. (2016). Beta diversity of stream diatoms at two hierarchical spatial scales: Implications for biomonitoring. *Freshwater Biology* **61**, 239–250. https://doi.org/10.1111/fwb.12697

Koleff P., Gaston K.J. & Lennon J.J. (2003). Measuring beta diversity for presence – absence data. 367–382

Lecraw R.M., Srivastava D.S. & Romero G.Q. (2014). Metacommunity size influences aquatic community composition in a natural mesocosm landscape. *Oikos* **123**, 903–911. https://doi.org/10.1111/oik.01253

Leibold M.A. & Geddes P. (2005). El concepto de nicho en las metacomunidades. *Ecología austral* **77**, 181. https://doi.org/10.5565/rev/papers/v77n0.936

Marino N.A.C., Guariento R.D., Dib V., Azevedo F.D. & Farjalla V.F. (2011). Habitat size determine algae biomass in tank-bromeliads. *Hydrobiologia* **678**, 191–199.

https://doi.org/10.1007/s10750-011-0848-4

Marino N.A.C., Srivastava D.S. & Farjalla V.F. (2013). Aquatic macroinvertebrate community composition in tank-bromeliads is determined by bromeliad species and its constrained characteristics. *Insect Conservation and Diversity* **6**, 372–380. https://doi.org/10.1111/j.1752-4598.2012.00224.x

Pace M.L., Cole J.J., Carpenter S.R., Kitchell J.F., Hodgson J.R., Van de Bogert M.C., *et al.* (2004). Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* **427**, 240

Paradise C.J., Blue J.D., Burkhart J.Q., Goldberg J., Harshaw L., Hawkins K.D., *et al.* (2008). Local and regional factors influence the structure of treehole metacommunities. *BMC Ecology* **8**, 1–16. https://doi.org/10.1186/1472-6785-8-22

Paradise C.J. & Society B.E. (2000). Effects of pH and resources on a processing chain interaction in simulated treeholes. *Journal of Animal Ecology* **69**, 651–658. https://doi.org/10.1046/j.1365-2656.2000.00423.x

Parker M.S. (1989). Effect of Substrate Composition on Detritus Accumulation and Macroinvertebrate Distribution in a Southern Nevada Desert Stream. *The Southwestern Naturalist* **34**, 181–187. https://doi.org/10.2307/3671727

Pittendrigh C.S. (1950). The Ecotopic Specialization of Anopheles homunculus; and Its Relation to Competition with A. bellator. *Evolution* **4**, 64–78. https://doi.org/10.1111/j.1558-5646.1950.tb01383.x

Rangel J. V., Araújo R.E.S., Casotti C.G., Costa L.C., Kiffer W.P. & Moretti M.S. (2017). Assessing the role of canopy cover on the colonization of phytotelmata by aquatic invertebrates: An experiment with the tank-bromeliad Aechmea lingulata. *Journal of Limnology* **76**, 230–239. https://doi.org/10.4081/jlimnol.2016.1526

Reiskind M.H. & Zarrabi A.A. (2012). Water Surface Area and Depth Determine Oviposition Choice in Aedes albopictus (Diptera: Culicidae). *Journal of Medical Entomology* **49**, 71–76

Rocha C.F.D., Van Sluys M., Bergallo H.G. & Alves M.A.S. (2005). Endemic and threatened tetrapods in the restingas of the biodiversity corridors of Serra do Mar and of the central da Mata Atlântica in Eastern Brazil . *Brazilian Journal of*

Biology **65**, 159–168

Rodríguez Pérez H., Borrel G., Leroy C., Carrias J.F., Corbara B., Srivastava D.S., *et al.* (2018). Simulated drought regimes reveal community resilience and hydrological thresholds for altered decomposition. *Oecologia* **187**, 267–279. https://doi.org/10.1007/s00442-018-4123-5

RStudio Team (2016). RStudio: Integrated Development Environment for R

Sarremejane R., Cañedo-Argüelles M., Prat N., Mykrä H., Muotka T. & Bonada N. (2017a). Do metacommunities vary through time? Intermittent rivers as model systems. *Journal of Biogeography* **44**, 2752–2763. https://doi.org/10.1111/jbi.13077

Sarremejane R., Mykrä H., Bonada N., Aroviita J. & Muotka T. (2017b). Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. *Freshwater Biology* **62**, 1073–1082. https://doi.org/10.1111/fwb.12926

Scarano F.R., Duarte H.M., Ribeiro K.T., Rodrigues P.J.F.P., Barcellos E.M.B., Franco A.C., *et al.* (2001). Four sites with contrasting environmental stress in southeastern Brazil: relations of species, life form diversity, and geographic distribution to ecophysiological parameters. *Botanical Journal of the Linnean Society* **136**, 345–364. https://doi.org/10.1111/j.1095-8339.2001.tb00579.x

Schmera D., Heino J., Podani J., Erős T. & Dolédec S. (2017). Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. *Hydrobiologia* **787**, 27–44. https://doi.org/10.1007/s10750-016-2974-5

Segre H., Ron R., De Malach N., Henkin Z., Mandel M. & Kadmon R. (2014). Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. *Ecology Letters* **17**, 1400–1408. https://doi.org/10.1111/ele.12343

Sellami I., Elloumi J., Hamza A., Mhamdi M.A. & Ayadi H. (2011). Local and regional factors influencing zooplankton communities in the connected kasseb Reservoir, Tunisia. *Water SA* **37**, 201–212. https://doi.org/10.4314/wsa.v37i2.65865

Serra S., Coimbra N. & Graça M. (2009). *Invertebrados de água doce: chave de*

identificação das principais famílias. Imprensa da Universidade de Coimbra.

Socolar J.B., Gilroy J.J., Kunin W.E. & Edwards D.P. (2016). How Should Beta-Diversity Inform Biodiversity Conservation? *Trends in Ecology & Evolution* **31**, 67–80. https://doi.org/10.1016/j.tree.2015.11.005

Solomon C.T., Carpenter S.R., Clayton M.K., Cole J.J., Coloso J.J., Pace M.L., *et al.* (2011). Terrestrial, benthic, and pelagic resource use in lakes: Results from a three-isotope Bayesian mixing model. *Ecology* **92**, 1115–1125. https://doi.org/10.1890/10-1185.1

Srivastava D.S., Trzcinski M.K., Richardson B.A. & Gilbert B. (2008). Why Are Predators More Sensitive to Habitat Size than Their Prey? Insights from Bromeliad Insect Food Webs. *The American Naturalist* **172**, 761–771. https://doi.org/10.1086/592868

Starzomski B.M., Suen D. & Srivastava D.S. (2010). Predation and facilitation determine chironomid emergence in a bromeliad-insect food web. *Ecological Entomology* **35**, 53–60. https://doi.org/10.1111/j.1365-2311.2009.01155.x

Szkokan-Emilson E.J., Wesolek B.E. & Gunn J.M. (2011). Terrestrial organic matter as subsidies that aid in the recovery of macroinvertebrates in industrially damaged lakes. *Ecological Applications* **21**, 2082–2093. https://doi.org/10.1890/10-1967.1

Talaga S., Dézerald O., Carteron A., Petitclerc F., Leroy C., Céréghino R., *et al.* (2015). Tank bromeliads as natural microcosms: A facultative association with ants influences the aquatic invertebrate community structure. *Comptes Rendus - Biologies* **338**, 696–700. https://doi.org/10.1016/j.crvi.2015.05.006

Talaga S., Petitclerc F., Carrias J.F., Dézerald O., Leroy C., Céréghino R., *et al.* (2017). Environmental drivers of community diversity in a neotropical urban landscape: a multi-scale analysis. *Landscape Ecology* **32**, 1805–1818. https://doi.org/10.1007/s10980-017-0542-7

Teresa F.B. & Casatti L. (2012). Influence of forest cover and mesohabitat types on functional and taxonomic diversity of fish communities in Neotropical lowland streams. *Ecology of Freshwater Fish* **21**, 433–442. https://doi.org/10.1111/j.1600-0633.2012.00562.x

Tun-Lin W., Kay B.H. & Barnes A. (1995). Understanding productivity, a key to Aedes aegypti surveillance. *The American journal of tropical medicine and hygiene* **53**, 595–601

Tuomisto H. (2010). A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* **33**, 2–22. https://doi.org/10.1111/j.1600-0587.2009.05880.x

Vanschoenwinkel B., Waterkeyn A., Jocqué M., Boven L., Seaman M. & Brendonck L. (2010). Species sorting in space and time—the impact of disturbance regime on community assembly in a temporary pool metacommunity. *Journal of the North American Benthological Society* **29**, 1267–1278. https://doi.org/10.1899/09-114.1

Veech J.A. (2013). A probabilistic model for analysing species co-occurrence. *Global Ecology and Biogeography* **22**, 252–260. https://doi.org/10.1111/j.1466-8238.2012.00789.x

Vellend M. (2001). Do commonly used indices of β-diversity measure species turnover? *Journal of Vegetation Science* **12**, 545–552. https://doi.org/10.2307/3237006

Viana D.S., Figuerola J., Schwenk K., Manca M., Hobæk A., Mjelde M., *et al.* (2016). Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales. *Ecography* **39**, 281–288. https://doi.org/10.1111/ecog.01231

Wang J., Soininen J., Zhang Y., Wang B., Yang X. & Shen J. (2012). Patterns of elevational beta diversity in micro- and macroorganisms. *Global Ecology and Biogeography* **21**, 743–750. https://doi.org/10.1111/j.1466-8238.2011.00718.x

Whittaker R.H. (1972). Evolution and Measurement of Species Diversity. *Taxon* **21**, 213. https://doi.org/10.2307/1218190

Whittaker R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**, 279–338. https://doi.org/10.2307/1943563

Zar J.H. (2007). *Biostatistical Analysis (5th Edition)*. Prentice-Hall, Inc., Upper Saddle River, NJ, USA.

Supplementary material

Environmental changes and interspecific interactions affect β-diversity of tropical bromeliad macroinvertebrates

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Table S1. Richness and abundance considering all individuals (total) and each order of aquatic macroinvertebrates recorded in each sampled bromeliad.

Sample	Richness	Abundance								
		Total	Collembola	Hemiptera	Odonata	Coleoptera	Copepoda	Haplotaxida	Diptera	Ostracoda
1	11	69	0	0	0	0	0	7	62	0
2	8	32	0	0	0	0	0	18	14	0
3	9	18	0	0	0	0	4	6	5	3
4	6	40	0	0	0	0	3	0	37	0
5	5	12	0	0	0	0	4	0	8	0
6	6	32	0	0	0	0	0	0	32	0
7	5	22	0	0	0	0	0	0	22	0
8	8	41	0	0	0	0	2	0	39	0

9	8	28	0	0	0	0	3	1	24	0
10	4	8	0	0	0	0	0	0	8	0
11	4	41	0	0	0	0	0	0	40	1
12	6	40	0	0	0	0	0	3	37	0
13	4	22	0	0	0	1	0	2	19	0
14	8	31	0	0	0	0	1	4	26	0
15	7	45	0	0	0	0	0	0	45	0
16	8	137	0	0	1	0	5	122	9	0
17	11	145	0	0	0	0	3	87	55	0
18	4	25	0	0	0	0	0	0	25	0
19	6	118	0	0	0	0	0	0	65	53
20	8	50	0	0	0	0	0	32	17	1
21	12	100	0	0	0	0	4	2	36	58
22	8	134	0	0	0	0	0	0	33	101
23	7	26	0	0	0	0	2	0	24	0
24	7	51	0	0	0	0	0	1	50	0
25	7	19	0	0	0	0	1	0	11	7
26	6	33	0	0	0	0	2	5	6	20
27	9	57	0	0	0	2	4	36	14	1
28	7	30	0	0	0	0	0	1	29	0

29	5	43	0	0	0	0	4	0	39	0
30	6	25	0	0	0	0	0	0	24	1
31	5	9	0	0	0	0	2	0	7	0
32	0	0	0	0	0	0	0	0	0	0
33	10	93	0	0	0	0	6	0	87	0
34	13	38	0	0	0	0	5	8	25	0
35	5	15	0	0	0	0	0	0	15	0
36	10	194	0	0	0	1	4	11	14	164
37	14	69	0	0	0	0	1	3	53	12
38	8	36	0	0	0	1	1	0	28	6
39	9	25	0	0	0	0	2	0	23	0
40	8	13	0	0	1	0	1	0	11	0
41	8	303	0	0	1	0	5	0	9	288
42	11	97	0	1	0	0	5	0	24	67
43	9	25	0	0	0	1	3	0	21	0
44	5	34	0	0	0	0	2	0	10	22
45	9	16	0	0	0	0	4	0	11	1
46	10	18	0	0	0	0	6	7	5	0
47	9	35	0	0	0	0	3	0	15	17
48	8	23	0	0	0	0	5	0	7	11

49	10	43	0	1	0	0	4	1	22	15
50	14	1243	0	0	0	1	2	6	30	1204
51	11	29	0	0	0	0	2	2	25	0
52	6	40	0	0	0	0	1	2	4	33
53	8	43	0	0	0	0	1	31	11	0
54	7	103	0	0	0	0	0	1	11	91
55	12	34	0	0	0	1	3	2	22	6
56	6	25	0	0	0	0	5	4	2	14
57	14	33	1	0	0	3	2	0	27	0
58	5	122	0	0	0	0	2	25	1	94
59	10	30	0	0	0	2	0	3	24	1
60	13	33	0	0	0	0	4	7	22	0

CAPÍTULO III

Abiotic changes drive taxonomic and functional diversity of macroinvertebrates in tank-bromeliad ecosystems

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Abstract

Anthropogenic activities have led to high rates of species loss worldwide. However, there is still few information on how human disturbances can affect the structure and function of aquatic systems. Using bromeliads as a model, we evaluated the influence of bromeliad size and tank-bromeliad physicochemical variables on the patterns of species composition, and taxonomic and functional diversity of macroinvertebrate communities. For this, we sampled 60 terrestrial bromeliads at a Brazilian *restinga* and captured all macroinvertebrates within each tank, in addition to measure five environmental variables. We performed non-metric ordination analysis to obtain a metric of species composition and calculated traditional indices of taxonomic and functional diversity of communities. We finally used Generalized Linear Models to identify which environmental factors could predict biodiversity components of macroinvertebrate communities. Our results show that the allochthonous input of organic matter was the strongest predictor of community dissimilarity and induced to greater functional evenness. Conversely, increases in light intensity induced to a homogenization of species richness and a decrease in functional richness. We thus demonstrate that abiotic changes, potentially caused by human disturbances, are important drivers of structural and functional changes of bromeliad macroinvertebrate communities, likely affecting the provision of ecosystem services by this faunal group.

KEY-WORDS: Brazilian *restinga*, Ecological traits, Ecosystem functioning, Human disturbance, Species composition, Species diversity

Introduction

Anthropogenic disturbances are promoting a severe crisis for global biodiversity, with species extinction increasing at an unprecedented rate (Ceballos et al., 2015). In fact, one million species are currently threatened due to human activities, including habitat loss and climate change, which have been responsible for dramatically modifying 75% and 66% of all worldwide terrestrial and aquatic environments, respectively (Purvis, 2019). In water systems, the global warming and its consequent changes in rainfall regimes (Rockström et al., 2009; Bernabé et al., 2018; Busse et al., 2018) substantially modify the input of allochthonous nutrients via leaching, and consequently, productivity patterns. These changes may affect species persistence in these environments and/or their functioning (Chessman, 2009; Cauvy-Fraunié et al., 2015; Bernabé et al., 2018; Guzman et al., 2018). For instance, the increase in nutrient supply favors the cyanobacteria growth and accelerates the eutrophication process, affecting therefore the stability of water bodies (Reichwaldt & Ghadouani, 2012; Stewart et al., 2018). However, distinct aquatic systems exhibit divergent sensitivities to environmental changes, with those systems exhibiting high hydric stress more prone to experience longer interval periods between rainfalls, and consequently undergoing to high rates of species loss, biotic homogenization or increase in functional redundancy of the associated fauna (Boersma et al., 2014; Várbíró et al., 2017). In the driest *restinga* environment (i.e., herbaceous/shrubby coastal sand-dune habitats, see Rocha et al. 2007), aquatic invertebrates inhabiting bromeliad tanks or temporary pools exhibit high vulnerability to environmental changes (Antiqueira et al., 2018a). This is mainly due to the ephemeral characteristics and the reduced size of the water bodies typical of this ecosystem (Carlos et al., 2001; Scarano et al., 2001; Carmo et al., 2019).

In aquatic environments, microcosms (i.e., small-sized environments exhibiting a complex, but organized and harmonic structure) have been considered excellent theoretical models for testing ecological issues (Meyer-Rochow, 1998; Srivastava et al., 2004), mostly explained due to its reduced size, handling facility, and fast response of the associated fauna to environmental conditions. Additionally, microcosms can be interesting models to evaluate the effects of disturbances on ecosystem functioning (Srivastava et al., 2004; Shurin et al., 2012; Rangel et al., 2017; Bernabé et al., 2018). In this context, bromeliads are seen as excellent microcosms ─ these plants naturally store water inside their tanks and harbor different organisms in their tanks, and given the ease

of sampling and the existence of a large number of replicas in nature, ecological patterns can be detected through these studies (Srisvastava *et al.*, 2004). In addition, the type and intensity of disturbance induce to abiotic oscillations easily measurable in their tanks (Marino et al., 2013; Busse et al., 2018). For example, studies have shown that changes in both water volume and temperature in the phytotelmats tanks led to the loss of decomposers, as well as the shrinkage of detritivore abundance through the indirect effect caused by the intensification of predation (Trzcinski et al., 2016; Bernabé et al., 2018; Busse et al., 2018). Conversely, the input of organic matter may increase the richness and abundance of those decomposers inhabiting bromeliads, among other functional groups of aquatic invertebrates, by increasing the quantity and diversification of resources in the system (Brouard et al., 2011, 2012; Busse et al., 2018).

Macroinvertebrates pose as fundamental organisms in most diverse freshwater environments worldwide (Covich et al., 1999; Mermillod-Blondin, 2011; Statzner, 2012). In bromeliads, these organisms play an important role in the nutrient cycling, in addition to acting as key components in the secondary productivity (Ngai & Srivastava, 2006; Dézerald et al., 2018). This group encompasses a wide variety of species, exhibiting substantial differences in body size (from microscopic organisms to micro and macroinvertebrates of 0.5 mm to 1.5 cm), food (i.e., based on debris, living tissue and/or live preys), and ecological function (i.e., collectors, such as filterers and gatherers, shredders, scrapers, predators). For instance, several studies revealed that Odonata larvae are voracious predators in bromeliads, which can lead detritivore species to local extinction and therefore substantially affect nutrient cycling (Trzcinski et al., 2016). Furthermore, macroinvertebrates act as important indicators of environmental quality, due to the high sensitivity of several species to abiotic changes. Indeed, changes in temperature, light and organic matter affect patterns of species occurrence and might disrupt the functionality of these systems (Brouard et al., 2012; Antiqueira et al., 2018; Busse et al., 2018).

Several studies have evaluated the anthropogenic impacts on aquatic macroinvertebrates, yet the main focus has been on taxonomic attributes ─ i.e., on the species richness and relative abundance of each species (Gossner et al., 2016; Cai et al., 2017; Schmera et al., 2017). However, disturbances tend to affect species in a non-random way (Heino et al., 2008; Gossner et al., 2016; Baumgartner & Robinson, 2017), with the loss or arrival of a new species leading to different consequences for the

ecosystem functioning. It has been documented that changes in the input of organic matter and water chemistry caused by management intensity have led to the rapid decay of species richness and abundance of macroinvertebrates, particularly of groups as scavengers, filterers and predators (Gossner et al., 2016). In addition, experiments using the bromeliad fauna and simulating the increase in temperature, showed drastic changes on macroinvertebrate composition as well as in vital ecological processes such as decomposition and nutrient cycling (Antiqueira et al., 2018; Bernabé et al., 2018). Although the assessment of taxonomic diversity of macroinvertebrates in water bodies is essential, this approach alone impedes an adequate understanding of the functionality and health status of these sites (Villéger et al., 2010; Schmera et al., 2017). Therefore, studies focusing on functional diversity (i.e., which analyses the variation of ecological traits within organisms; see Tilman, 2001; Petchey & Gaston, 2002) become extremely useful to understand the effects of human disturbances on ecosystem functioning (Cadotte et al., 2011).

The effects of environmental disturbances on aquatic systems can act as homogenizing filters, selecting only species with adapted functional characteristics (Keddy, 1992; Southwood & Society, 1977; Grime, 2006; Weiher et al., 2011; Heino et al., 2013; Boersma et al., 2014). In this context, it is likely that those remaining species in disturbed habitats exhibit the same functional attributes, which would lead to high functional redundancy (Mayfield et al., 2010; Mouchet et al., 2010). These results were observed with macroinvertebrate fauna in streams in the USA and Europe, due to the severe action of environmental filters (Statzner et al., 2004; Bêche & Statzner, 2009), and in pools in the USA, due to prolonged drought events (Boersma et al., 2014). Thus, it is possible that aquatic communities exhibiting high taxonomic diversity of macroinvertebrates may present low functional diversity (Göthe et al., 2017; Schmera et al., 2017; Céréghino et al., 2018), demonstrating that a high number of species does not necessarily indicates high variation of ecological roles played by these species in disturbed environments. Therefore, studies evaluating different components of bromeliad species diversity, including functional attributes, can enhance our understanding on how environmental changes can modify community structure and thus the functionality of these systems.

In this study, we sampled 60 terrestrial bromeliads at a Brazilian coastal *restinga* in order to examine the influence of bromeliad size and physicochemical variables

related to their tanks on the patterns of species composition, taxonomic diversity (TD) and functional diversity (FD) of macroinvertebrate communities. Given that anthropogenic disturbances, such as habitat loss, acid rain and urbanization, tend to modify the abiotic conditions of bromeliad tanks, we expected that patterns of both species composition (species similarity) and diversity (TD and FD) of macroinvertebrates would be strongly affected by changes in local conditions ─ i.e., area of bromeliad, light exposure, pH, input of organic matter and water volume inside the tank – which we understand as a proxy for the effects of the anthropogenic actions. However, we expected that similar local environmental conditions favor similar functional species, resulting in different species compositions, similar TD, but divergent FD indexes (Keddy, 1992; Mayfield et al., 2010; Mouchet et al., 2010; Boersma et al., 2014). Specifically, we predict that: *(i)* a high similarity in species composition will be detected in bromeliads presenting lower organic matter content, under higher exposure to light, at alkaline pH, and lower volumes of water inside the tank, since these factors act as primary source of food resource and play an important role in the of environment harshness (Lopez & Rios, 2001; Marino et al., 2013; Talaga et al., 2017; Busse et al., 2018); *(ii)* both TD metrics (i.e., number of species and Shannon index) will be strongly and positively influenced by the bromeliad area and the volume of liquid inside the tank, due to the widely recognized species-area relationship (MacArthur & Wilson, 1967; Marino et al., 2011; Omena et al., 2017); and (*iii*) the functional diversity metrics as richness, evenness and dispersion will be positively affected by the input of organic matter in the system and volume of water in the tank, since sites containing high concentrations of organic matter and great water volumes potentially favor the co-existence of different functional groups, exhibiting different strategies survival (Szkokan-Emilson et al., 2011; Dézerald et al., 2017; Busse et al., 2018; Guzman et al., 2018). Conversely, the environmental filters generated by increases in light intensity and low pH would negatively affect richness and functional divergence, given that only species exhibiting specific traits to these conditions will be favored (Courtney & Clements, 1998; Lopez & Rios, 2001; Boersma et al., 2014).

Methods

Study area

This study was conducted at the *restinga* situated within the Environmental Preservation Area of Lagoa Encantada, in the north of the municipality of Ilhéus, Bahia, Brazil (14º38’52”S; 39º4’39”O; Fig. 1a). *Restingas* comprise sand deposits parallel to the sea, formed by strings of beaches and sand-dunes covered by herbaceous-shrubby and arbustive-arboreal vegetation (Araujo, 1992; Rocha et al., 2007), constituting one component habitat of the Brazilian Atlantic Forest ─ a global biodiversity hotspot (Myers et al., 2000). The *restingas* once covered a great extension of the Brazilian coast, but due to the intense degradation process induced by human activities, these habitats have been dramatically deforested and converted to urban or degraded areas (Rocha et al., 2007; Fundação SOS Mata Atlântica & INPE, 2018). The environment of *restingas* presents low availability of water, with soil poor in nutrients and exhibiting high salinity (Scarano et al., 2001). In this APA, the climate is characterized as hot and humid, with average annual temperatures ranging between 22°C and 25°C (Faria Filho & Araújo, 2003). The pluviometric regime is regular, with abundant and well distributed rains during the year, reaching up to 2,700 mm in localities near the coast (Faria Filho & Araújo, 2003). The local vegetation is spatially arranged in a mosaic interspersing shrub clumps (height (h) <3 m) and dense herbaceous (h <2 m), including tree species, thorny bromeliads, cacti and creepers. The herbaceous layer is largely occupied by ferns and dense clumps of bromeliads of *Vriesea philippocoburgii* Wawra, which was therefore selected for sampling in this study.

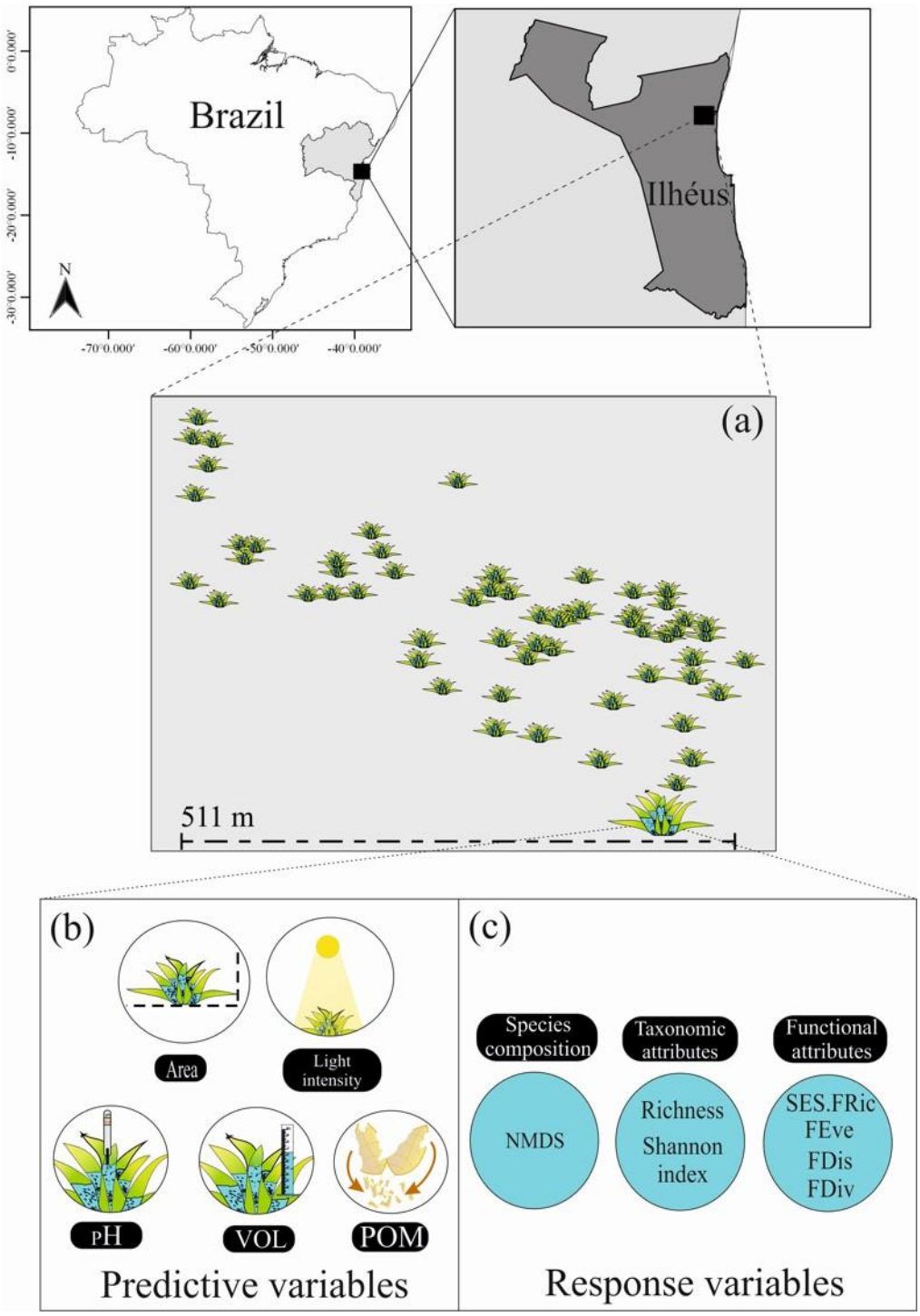

Figure 1. Location of the study area in the municipality of Ilhéus, Bahia, Brazil, including (a) the distribution of the 60 bromeliads sampled, (b) environmental predictors and (c) the response variables analyzed. AREA = Bromeliad size sampled in cm²; VOL = Total volume of liquid in the central tank; POM = input of particulate organic matter, in grams of dry weight; NMDS = Non-metric multidimensional scaling considering the species abundance data; Richness = Total number of species; Shannon index = Shannon diversity index; SES.FRic = standardized effect size for the functional

richness; FEve = Functional Evenness; FDis = Functional dispersion; FDiv = Functional Divergence.

Sampling of macroinvertebrates and environmental variables

In December 2016, we performed three consecutive days of sampling surveys in the study site. We initially selected 120 bromeliads in distinct clumps, keeping a minimum distance of 10 m from the next sample bromeliad. All the bromeliads chosen were located on the edge of clumps and contained water inside their tanks. Then, we randomly selected 60 individuals to sample aquatic macroinvertebrates inside the central tank and to measure environmental variables.

First, we measured five different environmental variables likely to affect the occurrence of macroinvertebrate species. Outside of the tank, we measured the bromeliad area by multiplying the height of individual per its diameter - distance between the two tips of the outermost leaves (AREA; Fig. 1b), and the percentage of light intensity (LIGHT) using a luxmeter (Instrutherm LD-240). Within the water tank of each bromeliad, we measured three physicochemical variables widely recognized for influencing the associated macrofauna (Sodré et al., 2010; Brouard et al., 2012; Talaga et al., 2017; Guzman et al., 2018). We used a multiparameter probe (model Instrutemp ITPH - 3000) to obtain pH values and a graduated cylinder (in mL) to obtain the total volume of liquid (VOL), measured at the time of collection of macroinvertebrates. We also used the protocol proposed by Carmo & Silva (2012) to obtain the particulate organic matter (POM gDW - grams dry weight) content, which consists in filtering the collected liquid sample in paper filters, drying them and removing all the plant material retained. This material is then ground in a processor, and the compound is sieved through a 1 mm mesh. Then, 1.000 g dry weight of the sieved material (analytical balance 0.0001 g precision) are separated and transported for muffle firing at 550°C for 1 hour. After this step, the remaining ashes are weighed. The difference between the initial weight and the ash weight refers to the organic matter content in 1.000 g. On average, bromeliads presented an AREA of 47.0 cm^3 ± 1.33 (SD, standard deviation), LIGHT of 38.24 ± 30.60, pH of 4.29 ± 0.68, VOL of 68.22 mL ± 36.28 and POM of 0.14 gDW ± 0.20.

Concomitantly, we homogenized the liquid inside the tank of each bromeliad by bubbling and, using a thin metal rod, released all organisms adhered to the edge of the tanks (adapted from Tun-Lin et al., 1995). We thus aspirated the liquid (including the fauna) present in each tank using a transparent hose (diameter 2.5 cm), storing it in a properly identified plastic container. We performed a new tank washing, using distilled water, and a new bubbling to collect the remaining macroinvertebrates (adapted from Pittendrigh, 1950). All organisms larger than 25 μm were fixed in 70% alcohol and identified to the lowest possible taxonomic level, using stereomicroscope (Physis) and bibliographical (charts). In some cases, specimens were sent to specialists for identification.

Functional traits

We used four functional traits largely related to aquatic organisms, including the maximum body size (i.e., energy demand), food (i.e., food niche), form of resistance (i.e., ability to survive in unfavorable environmental conditions, such as drought periods), and morphology (i.e., the presence of physical structures responsible for self-defense and consequently increasing survival probability) (Schmera et al., 2015, 2017; Céréghino et al., 2018; Table 1). To obtain maximum body size, we measured the length (mm) of all collected individuals using a magnifying glass with a milimetric eyepiece, obtaining a mean per morphotype. Other traits were categorically classified (see Table 1), in which each trait was firstly subdivided into categories based on the literature (Céréghino et al., 2011, 2018), and subsequently assessed its affinity with each taxon ─ scoring from 0 (no affinity) to 3 (high affinity). This technique, known as diffuse coding (see Chevene et al., 1994), has been widely used as an efficient way to evaluate the functionality of a system where groups present at least one trait with more than one category (Céréghino et al., 2011, 2018; Schmera et al., 2015, 2017; Dézerald et al., 2017). The traits evaluated were obtained at the lowest possible taxonomic level ─ i.e., genus (when available) or family. Indeed, previous studies have shown that these taxonomic levels enable to capture the variety of functional characteristics of freshwater macroinvertebrate communities (Dolédec et al., 1998; Schmera et al., 2017; Céréghino et al., 2018).

Table 1. Description of each functional trait used in this study to calculate all functional diversity indexes for bromeliad macroinvertebrate communities.

Traits	Functional interpretation	Continuous or category of traits
Maximum body size	Energetic demands increase with body size (Céréghino et al., 2018)	0.03-1.5 (cm)
Food	Use and partition of food resource (Céréghino et al., 2018)	Microorganisms Detritus (<1 mm) Dead plant (litter) Living microphytes Living leaf tissue Dead animals (>1 mm) Living microinvertebrates Living macroinvertebrates
Resistance form	Stages of resistance allow organisms to survive in unfavorable environmental conditions (Céréghino et al., 2018)	Eggs, statoblasts Cocoons Diapause or dormancy None
Morphological defense	Defense structures reduce the risk of predation and increase survival (Céréghino et al., 2018)	None Elongated tubers Hairs Sclerotized spines Back plates Sclerotic exoskeleton Shell Case or protective tube

Species composition and taxonomic and functional components of communities

We performed a Non-Metric Multidimensional Scaling ordination (NMDS) based on the dissimilarity among species, using the Bray-Curtis index for quantitative

(abundance) data. The stress was 0.2, therefore demonstrating a good representation of the dataset (Clarke et al, 1993). After this, we used the first axis of the NMDS as a metric of species composition. This step was done using the *vegan* package (Oksanen et al., 2018) in the RStudio software (RStudio Team, 2016).

The taxonomic diversity (TD) of macroinvertebrates recorded in each bromeliad was measured considering *(i)* the number of species ($\hat{S}$) (i.e., taxonomic richness) and *(ii)* the Shannon diversity index (H') –which accounts for both abundance and evenness of the species present (Magurran, 2004). Species richness has been the most widely used biodiversity metric in ecological studies due to its easy obtainment and application (Araújo et al., 2007; Lecraw et al., 2014; Rangel et al., 2017), whereas the Shannon index is important when communities contain a large number of rare species (Magurran, 2004), which is the case of our study. All TD analyzes were performed in the RStudio software (RStudio Team, 2016), using the *vegan* package (Oksanen et al., 2018).

Additionally, we measured four functional diversity (FD) indexes widely used in ecological studies (Petchey & Gaston, 2002; Villéger et al., 2008; Schmera et al., 2009, 2017; Esler & Rebelo, 2014). All are based on a multidimensional trait space occupied by the species of a community (Villéger et al., 2008) – *(i)* Functional Richness (FRic), which considers the amount of niche space occupied by species within a community (Mason et al., 2005); *(ii)* Functional Evenness (FEve), characterized by how species are distributed in the functional space by considering the distribution of abundances of the total set of traces in the niche space (Mason et al., 2005); *(iii)* Functional Dispersion (FDis), which measures the mean distance of species to the centroid of the functional space, weighted by their abundance (Laliberté & Legendre, 2010; Esler & Rebelo, 2014); and (*iv*) Functional Divergence (FDiv), which considers the variation in the attribute values of the species present at a site, weighted by the abundance of each taxon (Mason et al., 2003; Esler & Rebelo, 2014). For this, we used a similarity matrix considering the modified Gower distance (Pavoine et al., 2009), since continuous and categorical data were combined. To minimize the influence of species richness on functional richness, we calculated and used the Standardized Effect Size Functional Richness (SES.FRic) instead of using simply FRic. This metric is calculated as: Observed FRic value - Mean of randomized FRic values / SD of randomized FRic values; where positive and negative values indicate greater and lower functional diversities than expected by chance, respectively. Out of the 60 sampled communities,

four were unable to have their SES.FRic values calculated due to the low number of recorded species, which turns impracticable the obtainment of functional richness data through the standardized process. All FD analyzes were conducted using RStudio software (RStudio Team, 2016), using the packages *FD* (Laliberté et al., 2014) and *ade4* (Dray & Dufour, 2007).

Data analysis

We firstly used a Mantel test to assess potential spatial dependence between the geographic distance of sampling sites and the matrices of the TD and FD indexes. The results indicated no spatial dependence ($r < 0.1$; $P > 0.05$) in all tests (see Table S1). We thus used Generalized Linear Models (GLMs) with Gaussian distribution (for NMDS, *H'* and SES.FRic), poisson *($\hat{S}$)* and beta (FEve, FDis and FDiv) to evaluate the influence of all environmental variables on our response variables. Prior of this, we calculated the variance inflation factor (VIF) to test the multicollinearity between all variables for each GLM (Dormann et al., 2013). As none of the variables showed high or moderate collinearity (i.e., $VIF \leq 6$), all five variables were maintained in the global model for all response variables. We thus ran all possible combinations of subsets using the *"dredeg"* function of the *MuMIn* package, in addition to the null model. We used the Akaike Information Criterion (AIC) and Akaike information weights corrected for small samples (AICc) for ranking models (Burnham & Anderson, 2002). As parsimonious models, we selected those presenting $\Delta AIC \leq 2$, and selected the best model as the first one if it presented a low tendency in the residues in relation to the others. Then, we calculated the relative importance of each variable included in the best model, based on the sum of the Akaike weights in all models in which each this variable appears (Barton, 2017). In all cases, more than one model has been considered parsimonious (see Table S2), and in case that the null model appeared amongst parsimonious models, we assume that no other model has explained the specific pattern better than chance. All analyzes were performed using the *ade4* (Dray & Dufour, 2007), *glmmTBM* (Brooks et al., 2017), *lme4* (Bates et al., 2015) and *MuMIn* (Barton, 2017) packages, in the RStudio software (RStudio Team, 2016).

Results

We recorded 8,590 organisms, distributed in 60 morphotypes belonging to eight orders. A single bromeliad did not present any individuals. From the others, the number of morphotypes and individuals captured ranged from four to 14 (mean ± standard deviation = 8 ± 3) and from 8 to 1,243 (72 ± 286), respectively. Most individuals were found in larval form (83.6%), except for copepods and ostracods. The latter order, was the most abundant (N= 2,292), followed by Diptera (N=1,421). Ostracods were recorded in 27 bromeliads, whereas Diptera was recorded in 59 bromeliads (see Table S3).

The NMDS ordination showed that macroinvertebrate communities inhabiting bromeliads containing high input of organic matter were more dissimilar to each other (Fig. 2a). In fact, we verified that POM, in addition to LIGHT, PH and AREA were included in the best explanatory model for species composition (Table 2). However, only POM and LIGHT significantly affected patterns of species dissimilarity (Fig. 2b,c; Table 2).

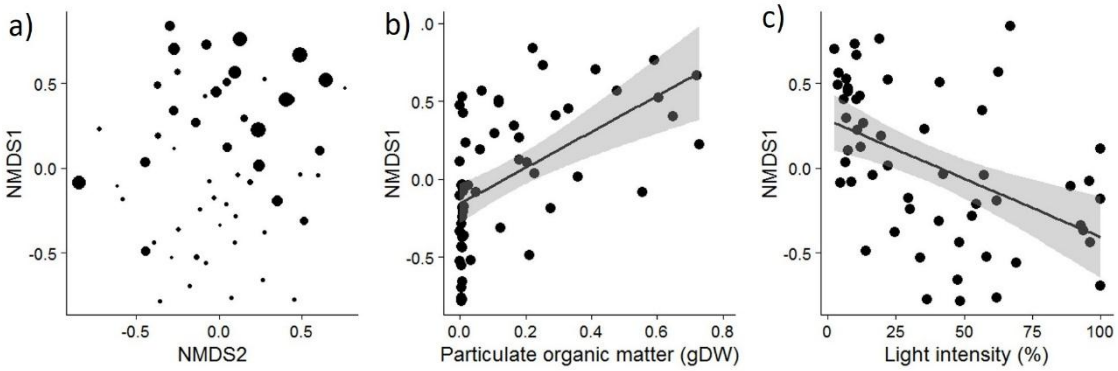

Figure 2. Non-metric multidimensional scaling (NMDS) ordination plot based on the (a) Bray-Curtis dissimilarity matrix of macroinvertebrate species composition recorded in 59 surveyed bromeliads; and the relationship between the first NMDS axis and (b) the input of organic matter (POM) and (c) light intensity. In (a), circles are sized proportionally to POM. Shaded area represents the 95% confidence region.

Table 2. Statistical summary of the best explanatory model for species composition (axis 1 of the NMDS), the taxonomic ($\hat{S}$ and *H'*) and functional (SES.FRic, FEve, FDis and FDiv) diversity indexes of aquatic macroinvertebrates recorded in 59 bromeliads surveyed in this study. Coefficients estimates (β), their respective standard error values (SE) and the relative importance (RIV) of each variable are shown. In all cases where the null model appeared among the parsimonious models, we assume that no other model explains the specific pattern better than chance. Significant variables are indicated as: *** P ≤ 0.001, ** P ≤ 0.01 and * P ≤ 0.05. NMDS – first axis values for abundance data; ($\hat{S}$) = Number of species; (*H'*) = Shannon diversity index; SES.FRic = Standardized Effect Size Functional Richness; FEve = Functional Evenness; FDis - Functional Dispersion; FDiv = Functional Divergence; AREA = Bromeliad area (in cm²); LIGHT = Intensity of light incident in the central tank (in %); VOL = Total volume of liquid in the central tank (in mL); POM = Input of particulate organic matter (in gDW).

Index	**Best Model**	**β (±SE)**	**RIV**
NMDS	Intercept***	0.02137 (±0.047)	
	AREA	0.084 (±0.049)	0.65
	LIGHT *	-0.117 (±0.053)	0.82
	pH	0.076 (±0.04833)	0.56
	POM **	0.18216 (±0.053)	0.99
$\hat{S}$	Intercept***	2.106 (±0.047)	
	AREA	0.089 (±0.047)	0.67
	POM	0.083 (±0.045)	0.65
H'	NULL	1.511(±0.064)	
SES.FRic	Intercept***	0.588 (±0.106)	
	LIGHT *	-0.290 (±0.118)	0.92
	POM	0.179 (±0.118)	0.53
FEve	Intercept***	0.167 (±0.066)	
	AREA	0.125 (±0.068)	0.60
	POM**	0.209 (±0.070)	0.90
FDis	NULL	-0.803 (±0.080)	
FDiv	NULL	1.651 (±0111)	

Indeed, we observed that the increase in POM leading to more dissimilar communities, while the increase in LIGHT driving to more similar communities. Additionally, we verified that AREA and POM were the only variables included in the best model explaining FEve patterns. However, only POM was significant and presented high relative importance for FEve (Fig. 3a; Table 2), indicating that lower values of functional evenness are recorded in bromeliads with lower organic matter in their tank (Table 2). Differently, POM and LIGHT were present in the best model explaining the patterns of SES.FRic. However, LIGHT was the only variable that presented significance and had a high relative importance for this model (Fig. 3b; Table 2). Thus, bromeliads with lower light exposure showed greater functional richness (Fig. 3c). For the other metrics of DT (*H'*) and DF (FDis and FDiv), the null model appeared among the parsimonious models (Table 2).

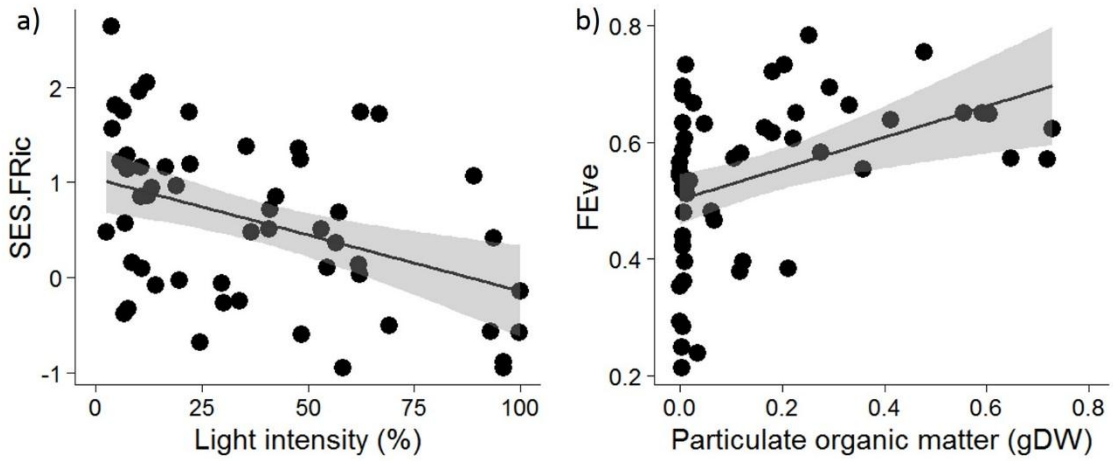

Figure 3. Relationship between (a) light intensity and (b) input of organic matter, with their respective significant functional diversity metrics (SES.Fric and FEve) considering 59 surveyed bromeliads.

Discussion

Our results clearly demonstrate that the input of particulate organic matter and light intensity are the main predictors of species composition and functional diversity of macroinvertebrate communities inhabiting terrestrial bromeliads. Thus, anthropogenic disturbances altering abiotic components are likely to directly affect the species distribution and their abundance, as well as minimize the efficiency in using the available resources in the system (Bêche & Statzner, 2009; Mayfield et al., 2010;

Mouchet et al., 2010; Boersma et al., 2014). The emergent loss of vegetation cover in tropical regions, in addition to the drastic increase in greenhouse emissions leading to global warming, are human disturbances prone to reduce the input of plant debris and increase the incidence of light in aquatic communities (Sivasakthivel & Reddy, 2011; Dézerald et al., 2014; Rangel et al., 2017; Busse et al., 2018). Thus, our results suggest that macroinvertebrate communities tend to become more dissimilar and exhibit lower functionality in highly disturbed bromeliad-tank systems.

Among the different environmental variables considered in this study, we found that the input of organic matter was the most important predictor for explaining patterns of species composition of macroinvertebrate among bromeliads, as well as for leading to a more homogeneous distribution of traits in the communities (FEve). In this context, we detected that the greater is the contribution of nutrients within the bromeliads, the more dissimilar are macroinvertebrate communities and more uniformly are the occupation of available niche spaces. This result can indicate greater efficiency in resource use and in the nutrient processing (Ngai & Srivastava, 2006; Villéger et al., 2008; Mouchet et al., 2010; Jiang et al., 2019). The amount of organic matter that reaches the environment is a key source of primary supply available through different food processing stages carried out by species of different trophic levels (Szkokan-Emilson et al., 2011; Brouard et al., 2012; Rangel et al., 2017). These various stages of processing promoted by macroinvertebrates are extremely important in nutrient cycling, in bromeliad tanks and other aquatic systems (Covich et al., 1999; Ngai & Srivastava, 2006; Bernabé et al., 2018). For example, Gossner et al. (2016) found that increases in management intensity in temperate forests led to a reduction in the organic material input to phytotelmatas and a subsequent loss in the number of aquatic macroinvertebrate species, potentially affecting the entire nutrient cycling process In addition, changes in the quality of plant debris entering in aquatic systems have directly affected the structure and functioning of freshwater ecosystems (Migliorini et al., 2018).

The incident light arriving in the bromeliad tanks was a key variable for explaining patterns of species composition and functional richness (SES.FRic) of macroinvertebrates, bromeliads subjected to greater concentration of light showed higher species similarity among communities, and lower functional richness. In aquatic systems, light entrance comprises an important factor for promoting primary production by algae and favor the dormancy breakage and consequent the development of some

macroinvertebrates groups (Dupuis & Hann, 2009; Brouard et al., 2011; Chaves & Couto, 2014). However, the substantial increase in light intensity turns aquatic systems extremely stressful due to the increase in temperature, reduction in dissolved oxygen levels, and greater predisposition to drought; factors that may limit the occurrence of some taxa (Lopez & Rios, 2001; Boersma et al., 2014; Rangel et al., 2017; Busse et al., 2018). This abiotic change may result in the homogenization of macroinvertebrate community, as well as reduce or even eliminate certain functional groups (Rangel et al., 2017; Scrine et al., 2017; Bernabé et al., 2018; Guzman et al., 2018). The increase of luminosity and consequent reduction in the pool of functions performed by the studied taxa indicate that these bromeliads present communities with high functional redundancy. In addition, it is possible that some ecological traits are being selected, including species that present specific resistance form, food and morphological defense. In fact, organisms in which the form of resistance is based on strategies such as diapause or dormancy, exhibit greater tolerance to high temperatures (Gyllström & Hansson, 2004; Díaz et al., 2008; Chaves & Couto, 2014). For example, studies revealed the great ability of certain decomposer groups (including Ceratopogonidae and ostracods of genus *Elpidium*) in resist to dry seasons and high temperatures, becoming more abundant in bromeliads more exposed to sunlight (Lopez & Rios, 2001). In addition, environments exposed to high light incidence are prone to harbor communities more structurally simplified, given the stronger action of environmental filters (Brouard et al., 2011, 2012; Amundrud & Srivastava, 2016; Guzman et al., 2018). Considering that several anthropogenic activities, such as the changes of natural forest cover percentage (Rangel et al., 2017; Busse et al., 2018) may exacerbate the light incident in the bromeliad tanks, our results suggest that the increasing of human pressure is likely to provoke substantial losses of ecosystem functions performed by macroinvertebrates, mostly driven by a process of homogenization of functional attributes (Bêche & Statzner, 2009; Mayfield et al., 2010; Boersma et al., 2014).

Conversely, other physicochemical variables herein evaluated were unimportant predictors of composition, taxonomic diversity and functional diversity. Despite area has been vastly known to exhibit a positive relationship with species richness (MacArthur & Wilson, 1967; Cumming & Child, 2009; Marino et al., 2011), neither bromeliad size nor tank volume affected biodiversity patterns of macroinvertebrates. Furthermore, pH inside of the bromeliad tank also unaffected the investigated patterns,

despite its high importance for the occurrence and reproduction of certain macroinvertebrate taxa in aquatic systems (Haines, 1981; Courtney & Clements, 1998; Paradise & Dunson, 1998; Díaz et al., 2008). In combination, these factors confer environmental heterogeneity for the system, potentially favoring the co-existence of a wide variety of macroinvertebrates but not leading to greater diversity. Therefore, the conceptual idea that bigger bromeliads house higher diversity of macroinvertebrates is failed for terrestrial bromeliads of our study site, indicating that physicochemical variables (with exception of pH) play a stronger role in explaining compositional, taxonomic and functional diversity of macroinvertebrates.

Conservation Implications

Our study highlights the importance of combining descriptors of composition, taxonomical and functional diversity in ecological studies, in order to unveil the main drivers for structuring biological communities in natural environments (Podgaiski et al., 2011; Gerisch et al., 2012). Supporting our hypotheses, we find that in terrestrial bromeliads, the contribution of organic matter and light incidence are the strongest factors explaining species composition of macroinvertebrate, as well as the distribution of the functional traits of species inhabiting their central tanks. Considering the rapid advance of environmental degradation induced by human activities in tropical ecosystems and their drastic effects on local biodiversity, our results indicate that anthropogenic actions (such as habitat loss, urbanization and global warming) that have an effect on this environmental parameters can directly affect the ecosystem services provided by macroinvertebrates inhabiting bromeliads and other aquatic environments. More specifically, the increasing suppression of Atlantic Forest (WWF, 2017; Martinelli et al., 2018), and especially the *restingas*, may result in structural changes of macroinvertebrate communities, including a homogenization and thus a reduction of functional roles played by these organisms. Therefore, we emphasize the importance of preventing the occurrence of invasive anthropogenic activities in *restinga* ecosystems at the local scale (i.e., prohibiting the removal of forest cover for conversion to urban areas). In addition, public policies should be encouraged to reduce the habitat loss, acid rain, urbanization and global warming at global scale, in order to ensure a high functional diversity of macroinvertebrates and consequently, the maintenance of environmental services.

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References

Amundrud, S. L., & D. S. Srivastava, 2016. Trophic interactions determine the effects of drought on an aquatic Ecosystem. Ecology 97: 1475–1483.

Antiqueira, P. A. P., O. L. Petchey, & G. Q. Romero, 2018. Warming and top predator loss drive ecosystem multifunctionality. Ecology Letters 21: 72–82.

Araujo, D. S. D., 1992. Vegetation Types of Sandy Coastal Plains of Tropical Brazil: A First Approximation Coastal Plant Communities of Latin America. Elsevier: 337–347, http://dx.doi.org/10.1016/B978-0-08-092567-7.50027-1.

Araújo, V. a, S. K. Melo, a P. a Araújo, M. L. M. Gomes, & M. a a Carneiro, 2007. Relationship between invertebrate fauna and bromeliad size. Brazilian journal of biology = Revista brasleira de biologia 67: 611–617, http://www.ncbi.nlm.nih.gov/pubmed/18278311.

Barton, K., 2017. MuMIn: Multi-model inference. R package version 1.40.0 1–74, https://cran.r-project.org/package=MuMIn.

Bates, D., M. Mächler, B. Bolker, & S. Walker, 2015. Fitting Linear Mixed-Effects Models Using {lme4}. Journal of Statistical Software 67: 1–48.

Baumgartner, S. D., & C. T. Robinson, 2017. Changes in macroinvertebrate trophic structure along a land-use gradient within a lowland stream network. Aquatic Sciences 79: 407–418, https://doi.org/10.1007/s00027-016-0506-z.

Bêche, L. A., & B. Statzner, 2009. Richness gradients of stream invertebrates across the USA: Taxonomy- and trait-based approaches. Biodiversity and Conservation 18: 3909–

3930.

Bernabé, T. N., P. M. de Omena, V. P. dos Santos, V. M. de Siqueira, V. M. de Oliveira, & G. Q. Romero, 2018. Warming weakens facilitative interactions between decomposers and detritivores, and modifies freshwater ecosystem functioning. Global Change Biology 24: 3170–3186.

Boersma, K. S., M. T. Bogan, B. A. Henrichs, & D. A. Lytle, 2014. Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. Freshwater Biology 59: 491–501.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, & B. M. Bolker, 2017. {glmmTMB} Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9: 378–400, https://journal.r-project.org/archive/2017/RJ-2017-066/index.html.

Brouard, O., R. Céréghino, B. Corbara, C. Leroy, L. Pelozuelo, A. Dejean, & J. F. Carrias, 2012. Understorey environments influence functional diversity in tank-bromeliad ecosystems. Freshwater Biology 57: 815–823.

Brouard, O., A.-H. Le Jeune, C. Leroy, R. Cereghino, O. Roux, L. Pelozuelo, A. Dejean, B. Corbara, & J.-F. Carrias, 2011. Are algae relevant to the detritus-based food web in tank-bromeliads?. PloS one Public Library of Science 6: e20129, http://dx.doi.org/10.1371/journal.pone.0020129.

Burnham, K. P., & D. R. Anderson, 2002. Model Selection and Multimodel Inference 2nd ed. Berlin: Springe. .

Busse, A., P. A. P. Antiqueira, A. S. Neutzling, A. M. Wolf, G. Q. Romero, & J. S. Petermann, 2018. Different in the dark: The effect of habitat characteristics on community composition and beta diversity in bromeliad microfauna. PLOS ONE 13: e0191426, http://dx.plos.org/10.1371/journal.pone.0191426.

Cadotte, M. W., K. Carscadden, & N. Mirotchnick, 2011. Beyond species: Functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48: 1079–1087.

Cai, Y., H. Xu, A. Vilmi, K. T. Tolonen, X. Tang, B. Qin, Z. Gong, & J. Heino, 2017.

Relative roles of spatial processes, natural factors and anthropogenic stressors in structuring a lake macroinvertebrate metacommunity. Science of the Total Environment Elsevier B.V. 601–602: 1702–1711, http://dx.doi.org/10.1016/j.scitotenv.2017.05.264.

Carlos, L., S. Lopez, & R. I. Rios, 2001. Phytotelmata Faunal Communities in Sun-Exposed Versus Shaded Terrestrial Bromeliads from Southeastern Brazil Phytotelmata Community Distribution in Tanks of Shaded and Sun Exposed Terrestrial Bromeliads from Restinga Vegetation . L UIZ C ARLOS S ERRAMO L. .

Carmo, D. L. do, & C. A. Silva, 2012. Métodos de quantificação de carbono e matéria orgânica em resíduos orgânicos . Revista Brasileira de Ciência do Solo . scielo , 1211–1220.

Carmo, L. F., I. R. Miguel, P. H. Pinna, D. S. Fernandes, & M. Woitovicz-Cardoso, 2019. Amphibians of the Parque Nacional da Restinga de Jurubatiba, a sandy coastal environment in southeastern Brazil. Biota Neotropica 19:, http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1676-06032019000200304&lng=en&tlng=en.

Cauvy-Fraunié, S., R. Espinosa, P. Andino, D. Jacobsen, & O. Dangles, 2015. Invertebrate metacommunity structure and dynamics in an Andean glacial stream network facing climate change. PLoS ONE 10: 1–19, http://dx.doi.org/10.1371/journal.pone.0136793.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, & T. M. Palmer, 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. Science Advances 1: 1–6.

Céréghino, R., C. Leroy, J.-F. Carrias, L. Pelozuelo, C. Ségura, C. Bosc, A. Dejean, & B. Corbara, 2011. Ant-plant mutualisms promote functional diversity in phytotelm communities. Functional Ecology 25: 954–963, http://doi.wiley.com/10.1111/j.1365-2435.2011.01863.x.

Céréghino, R., V. D. Pillar, D. S. Srivastava, P. M. de Omena, A. A. M. MacDonald, I. M. Barberis, B. Corbara, L. M. Guzman, C. Leroy, F. Ospina Bautista, G. Q. Romero, M. K. Trzcinski, P. Kratina, V. J. Debastiani, A. Z. Gonçalves, N. A. C. Marino, V. F. Farjalla, B. A. Richardson, M. J. Richardson, O. Dézerald, B. Gilbert, J. Petermann, S. Talaga, G. C. O. Piccoli, M. Jocqué, & G. Montero, 2018. Constraints on the functional

trait space of aquatic invertebrates in bromeliads. Functional Ecology 32: 2435–2447.

Chaves, T. P., & E. da C. G. Couto, 2014. Hatching of the eggs of Eulimnadia colombiensis (Branchiopoda) at different temperatures and regime of light. Nauplius 22: 145–149.

Chessman, B. C., 2009. Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. Global Change Biology 15: 2791–2802, http://doi.wiley.com/10.1111/j.1365-2486.2008.01840.x.

Chevene, F., S. Doleadec, & D. Chessel, 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshwater Biology 31: 295–309, http://doi.wiley.com/10.1111/j.1365-2427.1994.tb01742.x.

Clarke et al, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian journal of ecology 18: 117–143, http://onlinelibrary.wiley.com/doi/10.1111/j.1442-9993.1993.tb00438.x/full.

Courtney, L. A., & W. H. Clements, 1998. Effects of acidic pH on benthic macroinvertebrate communities in stream microcosms. Hydrobiologia 379: 135–145, https://doi.org/10.1023/A:1003442013650.

Covich, A. P., M. a. Palmer, & T. a. Crowl, 1999. The Role of Benthic Invertebrate Zoobenthic species influence energy flows and nutrient cycling. BioScience 49: 119–127.

Cumming, G. S., & M. F. Child, 2009. Contrasting spatial patterns of taxonomic and functional richness offer insights into potential loss of ecosystem services. Philosophical Transactions of the Royal Society B: Biological Sciences 364: 1683–1692.

Dézerald, O., C. Leroy, B. Corbara, A. Dejean, S. Talaga, & R. Céréghino, 2017. Environmental drivers of invertebrate population dynamics in Neotropical tank bromeliads. Freshwater Biology 62: 229–242.

Dézerald, O., C. Leroy, B. Corbara, A. Dejean, S. Talaga, & R. Céréghino, 2018. Tank bromeliads sustain high secondary production in neotropical forests. Aquatic Sciences Springer International Publishing 80: 0, http://dx.doi.org/10.1007/s00027-018-0566-3.

Dézerald, O., S. Talaga, C. Leroy, J.-F. Carrias, B. Corbara, A. Dejean, & R. Céréghino, 2014. Environmental determinants of macroinvertebrate diversity in small water bodies:

insights from tank-bromeliads. Hydrobiologia 723: 77–86, http://link.springer.com/10.1007/s10750-013-1464-2.

Díaz, A. M., M. L. S. Alonso, & M. R. V.-A. Gutiérrez, 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. Freshwater Biology 53: 1–21, https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2427.2007.01854.x.

Dolédec, S., B. Statzner, & V. Frainay, 1998. Accurate description of functional community structure: Identifying stream invertebrates to species- level?. Bulletin of the North American Benthological Society 15: 154–155.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. Mcclean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, & S. Lautenbach, 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36: 027–046.

Dray, S., & A.--B. Dufour, 2007. The {ade4} Package: Implementing the Duality Diagram for Ecologists. Journal of Statistical Software 22: 1–20.

Dupuis, A. P., & B. J. Hann, 2009. Climate change, diapause termination and zooplankton population dynamics: An experimental and modelling approach. Freshwater Biology 54: 221–235.

Esler, K., & A. Rebelo, 2014. Quantifying Functional Biodiversity. African Journal of Range & Forage Science 31: 235–236.

Faria Filho, A. F., & Q. R. de Araújo, 2003. Zoneamento do meio físico do município de Ilhéus, Bahia, Brasil, utilizando a técnica de geoprocessamento. Boletim Técnico 187: 1–20.

Fundação SOS Mata Atlântica, & INPE, 2018. Atlas dos Remanescentes Florestais da Mata Atlântica, 2017-2018. Relatório Técnico http://mapas.sosma.org.br/.

Gerisch, M., V. Agostinelli, K. Henle, & F. Dziock, 2012. More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. Oikos John Wiley & Sons, Ltd (10.1111) 121: 508–515, https://doi.org/10.1111/j.1600-0706.2011.19749.x.

Gossner, M. M., P. Lade, A. Rohland, N. Sichardt, T. Kahl, J. Bauhus, W. W. Weisser, & J. S. Petermann, 2016. Effects of management on aquatic tree-hole communities in temperate forests are mediated by detritus amount and water chemistry. Journal of Animal Ecology 85: 213–226.

Göthe, E., A. Baattrup-Pedersen, P. Wiberg-Larsen, D. Graeber, E. A. Kristensen, & N. Friberg, 2017. Environmental and spatial controls of taxonomic versus trait composition of stream biota. Freshwater Biology .

Grime, J. P., 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. Journal of Vegetation Science 17: 255–260, http://doi.wiley.com/10.1111/j.1654-1103.2006.tb02444.x.

Guzman, L. M., B. Vanschoenwinkel, V. F. Farjalla, A. Poon, & D. S. Srivastava, 2018. A precipitation gradient drives change in macroinvertebrate composition and interactions within bromeliads. PLOS ONE Public Library of Science 13: e0200179, https://doi.org/10.1371/journal.pone.0200179.

Gyllström, M., & L.-A. Hansson, 2004. Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling. Aquatic Sciences 66: 274–295.

Haines, T. A., 1981. Acidic Precipitation and Its Consequences for Aquatic Ecosystems: A Review. Transactions of The American Fisheries Society. .

Heino, J., H. Mykrä, & J. Kotanen, 2008. Weak relationships between landscape characteristics and multiple facets of stream macroinvertebrate biodiversity in a boreal drainage basin. Landscape Ecology 23: 417–426.

Jiang, X., J. Wang, Z. Li, X. Meng, Z. Xie, & J. Heino, 2019. Multiple facets of stream macroinvertebrate alpha diversity are driven by different ecological factors across an extensive altitudinal gradient. Ecology and Evolution 1306–1322.

Keddy, P. A., 1992. International Association of Vegetation Science. Journal of Vegetation Science 3: 157–164.

Laliberté, E., & P. Legendre, 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91: 299–305.

Laliberté, E., P. Legendre, & B. Shipley, 2014. FD: measuring functional diversity from

multiple traits, and other tools for functional ecology. R package version. 1. 0-12.

Lecraw, R. M., D. S. Srivastava, & G. Q. Romero, 2014. Metacommunity size influences aquatic community composition in a natural mesocosm landscape. Oikos 123: 903–911.

Lopez, L. C. S., & R. I. Rios, 2001. Phytotelmata Faunal Communities in Sun-Exposed Versus Shaded Terrestrial Bromeliads from Southeastern Brazil. Selbyana Marie Selby Botanical Gardens, Inc 22: 219–224, http://www.jstor.org/stable/41760099.

MacArthur, R. H., & E. O. Wilson, 1967. The theory of island biogeography. Princeton university press.

Magurran, A., 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford. .

Marino, N. A. C., R. D. Guariento, V. Dib, F. D. Azevedo, & V. F. Farjalla, 2011. Habitat size determine algae biomass in tank-bromeliads. Hydrobiologia 678: 191–199.

Marino, N. A. C., D. S. Srivastava, & V. F. Farjalla, 2013. Aquatic macroinvertebrate community composition in tank-bromeliads is determined by bromeliad species and its constrained characteristics. Insect Conservation and Diversity 6: 372–380.

Martinelli, G., C. M. Vieira, M. Gonzalez, P. Leitman, A. Piratininga, A. F. da Costa, & R. C. Forzza, 2018. Bromeliaceae Da Mata Atlântica Brasileira: Lista De Espécies, Distribuição E Conservação. Rodriguésia 59: 209–258.

Mason, N. W. H., K. MacGillivray, J. B. Steel, & J. B. Wilson, 2003. An index of functional diversity. Journal of Vegetation Science 14: 571–578, http://doi.wiley.com/10.1111/j.1654-1103.2003.tb02184.x.

Mason, N. W. H., D. Mouillot, W. G. Lee, & J. B. Wilson, 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111: 112–118, http://www.blackwell-synergy.com/doi/abs/10.1111/j.0030-1299.2005.13886.x.

Mayfield, M. M., S. P. Bonser, J. W. Morgan, I. Aubin, S. McNamara, & P. A. Vesk, 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. Global Ecology and Biogeography 19: 423–431.

Mermillod-Blondin, F., 2011. The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems. Journal of the North American Benthological Society 30: 770–778, https://doi.org/10.1899/10-121.1.

Meyer-Rochow, V. B., 1998. Natural microcosms. Trends in ecology & evolution 13: 201.

Migliorini, G. H., D. S. Srivastava, & G. Q. Romero, 2018. Leaf litter traits drive community structure and functioning in a natural aquatic microcosm. Freshwater Biology 63: 341–352.

Mouchet, M. A., S. Villéger, N. W. H. Mason, & D. Mouillot, 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology 24: 867–876, http://doi.wiley.com/10.1111/j.1365-2435.2010.01695.x.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, & J. Kent, 2000. Biodiversity hotspots for conservation priorities. Nature Springer Berlin Heidelberg, Berlin, Heidelberg 403: 853–858, https://doi.org/10.1038/35002501.

Ngai, J. T., & D. S. Srivastava, 2006. Predators Accelerate Nutrient Cycling in a Bromeliad Ecosystem. Science 314: 963–963, http://www.sciencemag.org/cgi/doi/10.1126/science.1132598.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, & H. Wagner, 2018. vegan: Community Ecology Package. , https://cran.r-project.org/package=vegan.

Omena, P. M., D. S. Srivastava, & G. Q. Romero, 2017. Does the strength of cross-ecosystem trophic cascades vary with ecosystem size? A test using a natural microcosm. Freshwater Biology 62: 724–736.

Paradise, C. J., & W. A. Dunson, 1998. Relationship of atmospheric deposition to the water chemistry and biota of treehole habitats. Environmental Toxicology and Chemistry 17: 362–368, https://setac.onlinelibrary.wiley.com/doi/abs/10.1002/etc.5620170303.

Pavoine, S., J. Vallet, A.-B. Dufour, S. Gachet, & H. Daniel, 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos 118: 391–402, http://doi.wiley.com/10.1111/j.1600-0706.2008.16668.x.

Petchey, O. L., & K. J. Gaston, 2002. Functional diversity (FD), species richness and community composition. Ecology Letters 5: 402–411, http://doi.wiley.com/10.1046/j.1461-0248.2002.00339.x.

Pittendrigh, C. S., 1950. The Ecotopic Specialization of Anopheles homunculus; and Its Relation to Competition with A. bellator. Evolution John Wiley & Sons, Ltd (10.1111) 4: 64–78, https://doi.org/10.1111/j.1558-5646.1950.tb01383.x.

Podgaiski, L. R., M. de S. Mendonça, & V. D. Pillar, 2011. O uso de atributos funcionais de invertebrados terrestres na ecologia: O que, como e por quê?. Oecologia Australis 15: 835–853.

Purvis, A., 2019. A million threatened species? Thirteen questions and answers. Science and policy for people and nature. , https://www.ipbes.net/news/million-threatened-species-thirteen-questions-answers.

Rangel, J. V., R. E. S. Araújo, C. G. Casotti, L. C. Costa, W. P. Kiffer, & M. S. Moretti, 2017. Assessing the role of canopy cover on the colonization of phytotelmata by aquatic invertebrates: An experiment with the tank-bromeliad Aechmea lingulata. Journal of Limnology 76: 230–239.

Reichwaldt, E. S., & A. Ghadouani, 2012. Effects of rainfall patterns on toxic cyanobacterial blooms in a changing climate: Between simplistic scenarios and complex dynamics. Water Research 46: 1372–1393, http://www.sciencedirect.com/science/article/pii/S0043135411007445.

Rocha, C., H. Bergallo, M. Van Sluys, M. Alves, & C. Jamel, 2007. The remnants of restinga habitats in the brazilian Atlantic Forest of Rio de Janeiro state, Brazil: habitat loss and risk of disappearance. Brazilian Journal of Biology 67: 263–273.

Rockström, J., W. Steffen, K. Noone, Å. Persson, F. S. I. Chapin, E. Lambin, T. M. Lenton, M. Scheffer, C. Folke, H. J. Schellnhuber, B. Nykvist, C. A. de Wit, T. Hughes, S. van der Leeuw, H. Rodhe, S. Sörlin, P. K. Snyder, R. Costanza, U. Svedin, M. Falkenmark, L. Karlberg, R. W. Corell, V. J. Fabry, J. Hansen, B. Walker, D. Liverman,

K. Richardson, P. Crutzen, & J. Foley, 2009. Planetary Boundaries: Exploring the Safe Operating Space for Humanity. Ecology and Society 14: 32.

RStudio Team, 2016. RStudio: Integrated Development Environment for R. Boston, MA, http://www.rstudio.com/.

Scarano, F. R., H. M. Duarte, K. T. Ribeiro, P. J. F. P. Rodrigues, E. M. B. Barcellos, A. C. Franco, J. Brulfert, E. Deleéns, & U. Lüttge, 2001. Four sites with contrasting environmental stress in southeastern Brazil: relations of species, life form diversity, and geographic distribution to ecophysiological parameters. Botanical Journal of the Linnean Society 136: 345–364, https://academic.oup.com/botlinnean/article-lookup/doi/10.1111/j.1095-8339.2001.tb00579.x.

Schmera, D., J. Heino, J. Podani, T. Erős, & S. Dolédec, 2017. Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. Hydrobiologia 787: 27–44, http://link.springer.com/10.1007/s10750-016-2974-5.

Schmera, D., J. Podani, & T. Erős, 2009. Measuring the contribution of community members to functional diversity. Oikos 118: 961–971, http://doi.wiley.com/10.1111/j.1600-0706.2009.17076.x.

Schmera, D., J. Podani, J. Heino, T. Erős, & N. L. Poff, 2015. A proposed unified terminology of species traits in stream ecology. Freshwater Science 34: 823–830, http://www.journals.uchicago.edu/doi/10.1086/681623.

Scrine, J., M. Jochum, J. S. Ólafsson, & E. J. O'Gorman, 2017. Interactive effects of temperature and habitat complexity on freshwater communities. Ecology and Evolution 7: 9333–9346, http://doi.wiley.com/10.1002/ece3.3412.

Shurin, J. B., J. L. Clasen, H. S. Greig, P. Kratina, & P. L. Thompson, 2012. Warming shifts top-down and bottom-up control of pond food web structure and function. Philosophical Transactions of the Royal Society B: Biological Sciences 367: 3008–3017.

Sivasakthivel, T., & K. K. S. K. Reddy, 2011. Ozone Layer Depletion and Its Effects: A Review. International Journal of Environmental Science and Development 30–37, http://www.ijesd.org/show-29-343-1.html.

Sodré, V. M., O. Rocha, & M. C. Messias, 2010. Chironomid larvae inhabiting bromeliad phytotelmata in a fragment of the Atlantic Rainforest in Rio de Janeiro State. Brazilian journal of biology = Revista brasleira de biologia 70: 587–592, http://www.ncbi.nlm.nih.gov/pubmed/20730345.

Srivastava, D. S., J. Kolasa, J. Bengtsson, A. Gonzalez, S. P. Lawler, T. E. Miller, P. Munguia, T. Romanuk, D. C. Schneider, & M. K. Trzcinski, 2004. Are natural microcosms useful model systems for ecology?. Trends in Ecology and Evolution 19: 379–384.

Statzner, B., 2012. Geomorphological implications of engineering bed sediments by lotic animals. Geomorphology 157–158: 49–65, http://www.sciencedirect.com/science/article/pii/S0169555X11003060.

Statzner, B., S. Dolédec, & B. Hugueny, 2004. Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. Ecography 27: 470–488, http://doi.wiley.com/10.1111/j.0906-7590.2004.03836.x.

Stewart, S. D., D. P. Hamilton, W. T. Baisden, P. Verburg, & I. C. Duggan, 2018. The role of mobile consumers in lake nutrient cycles: a brief review. Hydrobiologia Springer International Publishing 818: 11–29, https://doi.org/10.1007/s10750-018-3603-2.

Szkokan-Emilson, E. J., B. E. Wesolek, & J. M. Gunn, 2011. Terrestrial organic matter as subsidies that aid in the recovery of macroinvertebrates in industrially damaged lakes. Ecological Applications 21: 2082–2093.

Talaga, S., F. Petitclerc, J. F. Carrias, O. Dézerald, C. Leroy, R. Céréghino, & A. Dejean, 2017. Environmental drivers of community diversity in a neotropical urban landscape: a multi-scale analysis. Landscape Ecology 32: 1805–1818.

Tilman, D., 2001. Functional Diversity_tillman.pdf. Encyclopedia of Biodiversity. .

Trzcinski, M. K., D. S. Srivastava, B. Corbara, O. Dézerald, C. Leroy, J. F. Carrias, A. Dejean, & R. Céréghino, 2016. The effects of food web structure on ecosystem function exceeds those of precipitation. The Journal of animal ecology 85: 1147–1160.

Tun-Lin, W., B. H. Kay, & A. Barnes, 1995. Understanding productivity, a key to Aedes aegypti surveillance. The American journal of tropical medicine and hygiene United States 53: 595–601.

Várbíró, G., J. Görgényi, B. Tóthmérész, J. Padisák, É. Hajnal, & G. Borics, 2017. Functional redundancy modifies species–area relationship for freshwater phytoplankton. Ecology and Evolution 7: 9905–9913.

Villéger, S., N. W. H. Mason, & D. Mouillot, 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89: 2290–2301, http://doi.wiley.com/10.1890/07-1206.1.

Villéger, S., J. R. Miranda, D. F. Hernández, & D. Mouillot, 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecological Applications 20: 1512–1522, http://doi.wiley.com/10.1890/09-1310.1.

Weiher, E., D. Freund, T. Bunton, A. Stefanski, T. Lee, & S. Bentivenga, 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philosophical Transactions of the Royal Society B: Biological Sciences 366: 2403–2413.

WWF, 2017. State of the Atlantic Forest: Three Countries, 148 Million People, One of the Richest Forests on Earth. Fundación Vida Silvestre Argentina, Puerto Iguazú, Argentina.

Supplementary material

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Abiotic changes drive taxonomic and functional diversity of macroinvertebrates in tank-bromeliad ecosystems

Table S1. Results of the Mantel test (*r*) with the significance (P) used to test the existence of spatial dependence between the geographic distance of sampling points and the matrices of the different metrics of taxonomic and functional diversity. ($\hat{S}$) = Number of species; (*H'*) = Shannon diversity index; SES.FRic = Standardized Functional Richness; FEve = Functional Evenness; FDis = Functional Dispersion; FDiv = Functional Divergence.

Index	***r***	**P**
$\hat{S}$	0.022	0.295
H'	0.079	0.128
SES.FRic	0.047	0.054
FEve	0.029	0.283
FDis	0.036	0.250
FDiv	0.033	0.268

Table S2. Ranking of model selection based on a candidate set of 'best models' (ΔAIC ≤ 2.00) predicting species composition (NMDS), taxonomic diversity ($\hat{S}$ and *H'*) and functional diversity (SES.FRic, FEve, FDis and FDiv) of aquatic macroinvertebrates recorded in 59 bromeliads surveyed in this study. In all cases where the null model appeared among the parsimonious models, we assume that no other model explains the specific pattern better than chance. NMDS = first axis values of the quantitative ordination; Richness ($\hat{S}$) = Number of species; Shannon (*H'*) = Shannon diversity index; SES.FRic = Standardized functional richness; FEve = Functional Evenness; FDis = Functional Dispersion; FDiv = Functional Divergence; AREA = area of bromeliad sampled (in cm²); LIGHT = Intensity of light incident in the central tank; VOL = Total volume of liquid in the central tank (in mL); POM = input of particulate organic matter (in gDW). The difference from the best model (ΔAIC), Akaike weight (ωi) and the AIC score (AICc) are shown.

INDEX	**PARSIMONIOUS MODEL**	**Intercept**	**ΔAIC**	**ω_i**	**AICc**
NMDS	AREA+LIGHT+pH+POM	0.213	0.00	0.291	48.5
	AREA+LIGHT+POM	0.213	0.11	0.275	48.6
	LIGHT+pH+POM	0.213	0.68	0.207	49.2
	LIGHT+POM	0.213	1.81	0.117	50.3
	AREA+LIGHT+VOL+POM	0.213	1.94	0.110	50.4
$\hat{S}$	AREA+ POM	2.107	0.00	0.475	256.5
	AREA	2.110	1.04	0.282	257.6
	POM	2.111	1.34	0.243	257.9
H'	NULL	1.511	0.00	0.298	77.3
	LIGHT	1.511	0.83	0.197	78.1
	pH	1.511	1.55	0.137	78.9
	POM+LIGHT	1.511	1.58	0.135	78.9
	VOL	1.511	1.88	0.116	79.2
	POM	1.511	1.88	0.116	79.2
SES.FRic	LIGHT+POM	0.588	0.00	0.345	135.1
	LIGHT	0.588	0.04	0.337	135.2
	LIGHT+VOL	0.588	1.47	0.166	136.6
	LIGHT+VOL+POM	0.588	1.63	0.152	136.7
FEve	AREA+POM	0.167	0.00	0.390	-68.4
	POM	0.167	0.97	0.241	-67.5
	AREA+LIGHT+POM	0.167	1.25	0.209	-67.2
	LIGHT+POM	0.167	1.79	0.159	-66.6
FDis	NULL	-0.803	0.00	0.361	-69.9
	AREA	-0.804	1.37	0.182	-68.5

	POM	-0.804	1.49	0.171	-68.4
	pH	-0.803	1.77	0.149	-68.1
	LIGHT	-0.803	1.95	0.136	-67.9
FDiv	AREA	1.662	0.00	0.234	-99.1
	AREA+LIGHT	1.667	0.54	0.179	-98.6
	LIGHT	1.661	0.88	0.150	-98.2
	AREA+pH	1.666	1.03	0.140	-98.1
	NULL	1.651	1.50	0.110	-97.6
	AREA+LIGHT+pH	1.669	1.72	0.099	-97.4
	AREA+VOL	1.663	1.94	0.089	-97.2

Table S3. Total number of species ($\hat{S}$) and individuals recorded considering each order of aquatic macroinvertebrates within each sampled bromeliad.

Sample	Number of individuals								
	$\hat{S}$	Collembola	Hemiptera	Odonata	Coleoptera	Copepoda	Haplotaxida	Diptera	Ostracoda
1	69	0	0	0	0	0	7	62	0
2	32	0	0	0	0	0	18	14	0
3	18	0	0	0	0	4	6	5	3
4	40	0	0	0	0	3	0	37	0
5	12	0	0	0	0	4	0	8	0
6	32	0	0	0	0	0	0	32	0
7	22	0	0	0	0	0	0	22	0
8	41	0	0	0	0	2	0	39	0
9	28	0	0	0	0	3	1	24	0
10	8	0	0	0	0	0	0	8	0
11	41	0	0	0	0	0	0	40	1
12	40	0	0	0	0	0	3	37	0
13	22	0	0	0	1	0	2	19	0
14	31	0	0	0	0	1	4	26	0
15	45	0	0	0	0	0	0	45	0
16	137	0	0	1	0	5	122	9	0
17	145	0	0	0	0	3	87	55	0
18	25	0	0	0	0	0	0	25	0

19	118	0	0	0	0	0	0	65	53
20	50	0	0	0	0	0	32	17	1
21	100	0	0	0	0	4	2	36	58
22	134	0	0	0	0	0	0	33	101
23	26	0	0	0	0	2	0	24	0
24	51	0	0	0	0	0	1	50	0
25	19	0	0	0	0	1	0	11	7
26	33	0	0	0	0	2	5	6	20
27	57	0	0	0	2	4	36	14	1
28	30	0	0	0	0	0	1	29	0
29	43	0	0	0	0	4	0	39	0
30	25	0	0	0	0	0	0	24	1
31	9	0	0	0	0	2	0	7	0
32	0	0	0	0	0	0	0	0	0
33	93	0	0	0	0	6	0	87	0
34	38	0	0	0	0	5	8	25	0
35	15	0	0	0	0	0	0	15	0
36	194	0	0	0	1	4	11	14	164
37	69	0	0	0	0	1	3	53	12
38	36	0	0	0	1	1	0	28	6
39	25	0	0	0	0	2	0	23	0
40	13	0	0	1	0	1	0	11	0

41	303	0	0	1	0	5	0	9	288
42	97	0	1	0	0	5	0	24	67
43	25	0	0	0	1	3	0	21	0
44	34	0	0	0	0	2	0	10	22
45	16	0	0	0	0	4	0	11	1
46	18	0	0	0	0	6	7	5	0
47	35	0	0	0	0	3	0	15	17
48	23	0	0	0	0	5	0	7	11
49	43	0	1	0	0	4	1	22	15
50	1243	0	0	0	1	2	6	30	1204
51	29	0	0	0	0	2	2	25	0
52	40	0	0	0	0	1	2	4	33
53	43	0	0	0	0	1	31	11	0
54	103	0	0	0	0	0	1	11	91
55	34	0	0	0	1	3	2	22	6
56	25	0	0	0	0	5	4	2	14
57	33	1	0	0	3	2	0	27	0
58	122	0	0	0	0	2	25	1	94
59	30	0	0	0	2	0	3	24	1
60	33	0	0	0	0	4	7	22	0
Total abundance		1	2	3	13	123	440	1421	2292

CONSIDERAÇÕES FINAIS

Os resultados aqui obtidos ampliam o conhecimento sobre os fatores que estruturam as comunidades e metacomunidades de macroinvertebrados aquáticos de água doce. A partir de uma robusta revisão sobre metacomunidades de macroinvertebrados de água doce, verificamos um gradual aumento de estudos nos últimos anos, provavelmente impulsionada pela atual preocupação com a possibilidade de uma crise hídrica global (Vörösmarty *et al.*, 2010). Constatamos que áreas importantes globalmente, como a bacia amazônica, ainda permanecem inexploradas, possivelmente devido à menor concentração de institutos de pesquisa na região quando comparado a E.U.A e Europa. Em sistemas de bacias, principalmente, constatamos que as características ambientais (i.g. físicas e químicas da água) tem importante papel na distribuição das espécies, muitas vezes suprimindo características biológicas como baixo poder de dispersão.

Adicionalmente, evidenciamos a importância dos fatores ambientais e das interações ecológicas na distribuição e ocorrência de macroinvertebrados existentes em bromélias, bem como na manutenção da riqueza e equitabilidade funcional. No caso especial das restingas, as interações negativas e fatores ambientais como a luz e a disponibilidade de matéria orgânica foram os fatores determinantes para explicar padrões de composição e diversidade de macroinvertebrados aquáticos associados às bromélias. Sendo assim, o crescente efeito das perturbações antrópicas que alterem estes fatores (i.e., perda de habitat e emissão de gases que afetam o clima) podem comprometer não só a estrutura taxonômica das comunidades de macroinvertebrados de água doce, como também a eficiência dos serviços ecossistêmicos desempenhados por eles. Além disto, a partir destes resultados fica evidente que é prudente investir em estratégias de conservação que visem reduzir às pressões antrópicas em ecossistemas de restinga a fim de garantir uma alta diversidade funcional dos macroinvertebrados e, consequentemente, a manutenção dos serviços ambientais; em escala local, a remoção da cobertura florestal para conversão em áreas urbanas deve ser impedida, enquanto incentivos para redução da emissão de gases de efeito estufa para a atmosfera devem ser estimulados pelos governantes em escala global.

Por fim, ressaltamos que a pesquisa presente nesta tese serve como subsídio para traçar estratégias mais completas de conservação e biomonitoramento, principalmente de sistemas hídricos. A sua abordagem apresenta ainda o uso de microcosmos de bromélias como modelos para estudos e deixa claro que pesquisas sobre a estrutura de comunidades biológicas devem avaliar tanto aspectos taxonômicos quanto funcionais, permitindo a obtenção de resultados mais robustos para o entendimento de como os fatores ambientais afetam diferentes estruturas de comunidades.

APÊNDICE I

Table 1. List of taxonomic groups found in the 60 bromeliads analyzed in this study, including their overall abundance and –the total number of bromeliads in which the taxon was recorded (NBT).

Order	Family	Morphospecies	Abundance	NBT
DIPTERA	Chironominae	*Polypedilum sp1*	86	17
		Polypedilum sp2	5	2
		Polypedilum sp3	21	4
		Polypedilum sp4	5	1
		Endotribelos sp1	2	1
		Tanytarsus sp1	100	12
		Chironomini n.ID	2	2
	Tanypodinae	*Monopelopia sp1*	41	16
		Monopelopia sp2	6	4
		Monopelopia sp3	4	1
		Larsia sp1	2	1
		Larsia sp2	16	8
		Larsia sp3	1	1
		Coelotanypus sp1	1	1
	Ortocladinae	*Limnophyes sp1*	4	2
		Corynoneura sp1	2	2
		Thienemannia sp1	2	1
	Ceratopogonidae	*Forcipomyia sp1*	119	32
		Forcipomyia sp2	44	12
		Atrichopogon sp1	8	5
		Atrichopogon sp2	1	1
		Atrichopogon sp3	1	1
		Alluaudomyia sp1	6	4
		Ceratopogoniinae sp1	48	5
	Tipulidae	*Trentepholia sp1*	6	3
		Tipulidae sp1	3	2
	Sciomyzidae	*Sepedon sp1*	0	0
	Psycodidae	*Clogmia sp1*	9	4
	Calliphoridae	*Calliphoridae sp1*	2	2
	Culicidae	*Culex sp1*	270	34
		Culex sp2	261	32
		Culex sp3	49	20
		Culex sp4	3	1
		Culex sp5	91	13
		Culex sp6	48	11
		Toxorhynchites sp1	18	18
		Anopheles sp1	12	9
		Wyeomyia sp1	55	16
		Aedes sp1	23	6
		Culiseta	1	1
	Corethrellidae	*Corethrella sp1*	43	22
COLEOPTERA	Scirtidae	*Prionocyphon sp1*	7	5
	Mecoptera	*Panorpa sp1*	1	1

	Hydrochidae	*Hydrochus sp1*	1	1
	Lampyridae	*Luciola sp1*	2	2
	Curculionidae	*Curculionidae sp1*	1	1
	Helmidae	*Elmidae sp1*	1	1
HEMIPTERA	Hebridae	*Hebrus sp1*	2	2
ODONATA	Coenagrionidae	*Bromeliagrion sp1*	1	1
	Coenagrionidae	*Ischnura sp1*	2	2
COLLEMBOLA		*Collembola sp1*	1	1
HAPLOTAXIDA	Naididae	*Pristina sp1*	121	7
		Pristina sp2	138	19
	Tubificidae	*Tubifex sp1*	181	18
COPEPODA		*Cyclopoida*	100	39
		Harpacticoida	23	19
OSTRACODA		*Elpidium sp1*	2167	20
		Elpidium sp2	2	1
		Elpidium sp3	91	1
		Elpidium sp4	32	6