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PAULA MUNHOZ DE OMENA

EFFECTS OF PREDATORS ON BROMELIAD-AQUATIC ARTHROPOD COMMUNITIES AND ECOSYSTEM FUNCTIONING

EFEITO DE PREDADORES SOBRE COMUNIDADES DE ARTRÓPODES AQUÁTICOS BROMELÍCOLAS E FUNCIONAMENTO ECOSSISTÊMICO

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Supervisor/*Orientador*: Prof. Dr. Gustavo Quevedo Romero

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ABSTRACT

In the face of the increasing transformation of environmental conditions by human activity, understanding the processes that affect communities and ecosystem functioning has become fundamental goals in ecology. The interactions between coexisting species and, their interactions with the abiotic components of environment, affect the patterns of biological diversity and functions of ecosystems. In this study, I sought to understand the relative role of predator-prey interactions and of abiotic factors on the communities' properties and ecosystem functioning. In the first chapter, I investigated the role of habitat size in mediating the effects of terrestrial predators on the structure of communities and the functioning of adjacent ecosystems. Habitat size mediated trophic cascades within ecosystems; therefore, I expected that similar effects of habitat size affect cross-ecosystem trophic cascades. In the second chapter, I explored predictions related to the variation of trophic pyramids of biomass across environmental gradients (i.e., habitat size, detritus concentration and productivity). Furthermore, I investigated the relative contribution of consumptive and non-consumptive effects of predators on the shape of trophic pyramids of biomass. In the third chapter, I sought to investigate the effects of two extremes of an environmental gradient and the effects of predators on the components of detritivores diversity (i.e., functional, phylogenetic and taxonomic). Moreover, I explored the relative role of environment, predators and detritivore diversity components on the functioning of ecosystems (i.e., detritus processing and nitrogen flux). The results from this study demonstrated that abiotic factors are crucial determinants of community properties, predator-prey interactions and ecosystem functioning. The relative role of the predators cascading effects are strongly dependent on the environmental conditions which mediate the interactions between predators and prey.

RESUMO

Com a intensificação das transformações dos sistemas naturais pela atividade humana, o entendimento dos processos que afetam as comunidades e o funcionamento dos ecossistemas tornou-se um tema central para a ecologia contemporânea. As interações entre as espécies, bem como as interações entre as espécies e os componentes abióticos do meio ambiente, afetam tanto os padões de diversidade biológica como funções ecossistêmicas. Neste trabalho, buscou-se compreender o papel relativo das interações predador-presa e dos componentes abióticos sobre as propriedades das comunidades e funcionamento dos ecossistemas. No primeiro capítulo, investiguei o papel do tamanho do habitat sobre os efeitos de predadores terrestres na estrutura de comunidades e funcionamento de ecossistemas adjacentes. O tamanho do habitat modera cascatas tróficas dentro de ecossistemas, deste modo, esperei que efeitos similares do tamanho do habitat poderiam afetar cascatas tróficas que ocorrem através dos limites dos ecossistemas. No segundo capítulo, explorei predições relacionadas a variação no formato de pirâmides tróficas de biomassa ao longo de gradientes ambientais (tamanho do habitat, concentração de detritos e produtividade). Além disso, investiguei a contribuição relativa dos efeitos de consumo direto e do risco de predação nas interações predador-presa como mecanismos estruturadores de pirâmides tróficas de biomassa. No terceiro capítulo, tive como objetivo investigar os efeitos de dois extremos de um gradiente ambiental e os efeitos de predadores sobre os componentes da diversidade de presas detritívoras (i.e., diversidade funcional, filogenética e taxonômica). Além disso, explorei o papel relativo do ambiente, dos predadores e dos componentes da diversidade sobre o funcionamento ecossistêmico (i.e., decomposição e fluxo de nitrogênio). Os resultados encontrados nos três capítulos demonstram que fatores abióticos são cruciais na determinação das propriedades das comunidades, interações predador-presa e, consequentemente, no funcionamento ecossistêmico. O papel relativo dos efeitos cascatas de predadores é altamente dependente das condições ambientais que medeiam as interações entre predadores e presas.

SUMÁRIO

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INTRODUÇÃO GERAL

Com a intensificação das transformações dos sistemas naturais pela atividade humana, o estudo dos processos ecológicos que afetam as comunidades e o funcionamento dos ecossistemas tornou-se um tema central para a ecologia contemporânea (Cardinale et al. 2000, Loreau et al. 2001). As interações bióticas e abióticas influenciam tanto as propriedades das comunidades como funções ecossistêmicas chave (e.g., produtividade, decomposição e fluxo de nutrientes). Neste contexto, as interações entre predadores e presas são de especial importância, pois à medida que regulam as populações de presas, predadores afetam a diversidade biológica nas comunidades (Paine 1966, Leibold 1996, Almany e Webster 2004). Além disso, predadores alteram os padrões de utilização dos recursos pelos organismos e assim, o funcionamento dos ecossistemas (Ives et al. 2005). Apesar de exercerem um papel crucial nos padrões de diversidade e funcionamento dos ecossistemas, predadores são organismos especialmente vulneráveis à ação antrópica e, as taxas de morte destes animais excedem as taxas dos níveis tróficos inferiores (Jackson et al. 2001, Myers e Worm 2003). Assim, determinar a abrangência dos efeitos de predadores sobre suas presas e processos ecossistêmicos é crucial para o entendimento dos possíveis impactos que a exclusão destes animais ocasionaria nas comunidades bióticas e no funcionamento dos ecossistemas (Chapin et al. 1997, Beard et al. 2003, Thébault e Loreau 2003).

Interações tróficas: efeito de predadores e funcionamento ecossistêmico

A estrutura das comunidades e o funcionamento dos ecossistemas dependem da identidade das espécies presentes em uma localidade específica (Estes e Duggins 1995, Power 1995, Hobbie 1996), dos tipos de interações interespecíficas e da relação dessas interações com o ambiente (May 1973, Tilman 1982, 1988, Davis 1986, Lehman e Tilman 2000, Vitousek e Matson 1984, 1985). As interações que modulam a estrutura trófica de comunidades são governadas por características das espécies envolvidas, como história de vida, tamanho corporal e grupo trófico. Predadores de topo podem afetar fortemente as populações de suas presas e, dessa forma, afetar direta ou indiretamente a estrutura trófica de comunidades inteiras. No início da década de 80, Robert Paine (1980) cunhou o termo cascatas tróficas a fim de descrever como os efeitos *top-down* de predadores poderiam influenciar as abundâncias de espécies de níveis tróficos basais. Pace (et al. 1999) definiu cascata trófica como a interação recíproca entre predadores e presas em que abundância, biomassa ou produtividade de uma população, comunidade ou nível trófico são alterados por mais de um ligação em uma dada cadeia alimentar.

A natureza dos efeitos diretos dos predadores sobre suas presas pode influenciar indiretamente comunidades inteiras por meio de cascatas tróficas (Schmitz e Suttle 2001). As interações indiretas podem ser mediadas pela densidade ou pelo comportamento. Interações indiretas mediadas pela densidade, descrevem o efeito de consumo dos predadores na redução das densidades populacionais de presas afetando subsequentemente outros níveis tróficos (Carpenter et al. 1987, Abrams 1995, Werner e Anholt 1996). As interações indiretas mediadas pelo comportamento, descrevem as alterações nos padrões comportamentais das presas frente ao potencial risco de predação (Abrams 1995, Werner e Anholt 1996). Os comportamentos alterados incluem atividade de forrageio, padrões de deslocamento e seleção de habitat (Schmitz 2008, Roberts e Leibgold 2008, Vonesh et al. 2009). Quando as presas diminuem a atividade de forrageamento frente ao risco de predação, o impacto das mesmas sobre os recursos é diminuído (McIntosh e Townsend 1996, Peacor e Werner 1997). Ambos os efeitos (i.e., mediado pela densidade ou pelo comportamento) alteram indiretamente fatores que regulam funções ecossistêmicas-chave, como produtividade, decomposição e ciclagem de nutrientes (Chapin et al. 1997, Beard et al. 2003, Thébault e Loreau 2003).

Estudos de efeitos indiretos de predadores sobre ecossistemas focaram principalmente em teias alimentares com base energética autotrófica (revisão em Brett e Goldman 1996, Schmitz et al. 2000) e na ênfase dos efeitos indiretos dos predadores na diversidade de plantas e na produtividade primária (Paine 2002, Romero e Vasconcellos-Neto 2004, Schmitz 2006). Embora muitos estudos tenham direcionado o entendimento do papel de cascatas tróficas em teias alimentares autotróficas, sabe-se que a maior parte da energia fixada pelas plantas vasculares é transformada em detrito, ao invés de ser consumida por herbívoros (Polis e Strong 1996). Efeitos indiretos de predadores sobre o processamento de matéria orgânica (MO) foram relatados tanto em ecossistemas terrestres (Santos et al. 1981, Beard et al. 2003) quanto em aquáticos (Malmqvist 1993, Konishi et al. 2001, Rosemond et al. 2001). Os predadores podem exercer efeitos negativos no processamento da MO por meio da redução da densidade de presas detritívoras, ou pela diminuição da atividade e/ou eficiência de forrageamento das mesmas (Malmqvist 1993, Konishi et al. 2001). Além dos efeitos negativos, predadores podem influenciar positivamente as taxas de decomposição e ciclagem de nitrogênio (N) (Beard et al. 2003, Ngai e Srivastava 2006), por meio da liberação de nutrientes advindos do consumo de presas (i.e., carcaças e fezes). Beard (et al. 2003) verificaram que a liberação de nitrogênio presente nas excretas de predadores anuros aumentava a disponibilidade de nutrientes para os decompositores de serrapilheira, estimulando assim, maiores taxas de decomposição.

Predadores e seus efeitos além dos limites dos ecossistemas

Estudos recentes têm sugerido que os efeitos mediados por predadores podem ultrapassar as fronteiras dos ecossistemas (Knight et al. 2005, Marckzak et al. 2007, Schmitz et al. 2010). Comumente, os efeitos de predadores ultrapassam os limites dos ecossistemas quando os mesmos e/ou suas presas possuem ciclo de vida complexo. Animais com ciclo de vida complexo mudam de ecossistema entre duas fases ontogenéticas (Werner 1988), como por exemplo, mudança de ambiente aquático nos estágios larvais para ambiente terrestre nos estágios adultos em insetos holometábolos e anfíbios anuros (Wilbur 1980, Werner e Gillian 1984, Polis et al. 1989, Schreiber e Rudolf 2008). Essa mudança de ecossistemas em organismos com ciclo de vida complexo pode exercer fortes efeitos, *top-down* e *bottom-up*, nas teias alimentares dos habitats recipientes. Por exemplo, insetos que emergem de ambientes aquáticos para terrestres podem afetar ecossistemas terrestres por subsidiarem a dieta de consumidores (efeito *bottom-up*) ou até mesmo exercerem efeitos *top-down* em teias alimentares (Knight et al.2005). Predadores terrestres que forrageiam nos limites dos ecossistemas interceptam organismos adultos, os quais emergem dos ecossistemas aquáticos bem como os adultos que utilizam a água como sítio de oviposição. Deste modo, predadores terrestres podem subsidiar ambientes aquáticos por meio da liberação de nutrientes presentes nas carcaças de suas presas (efeito *bottom-up*) ou reduzir a abundância de presas nas comunidades aquáticas adjacentes (efeito *top-down*) (Romero et al. 2010, Romero e Srivastava 2010). A maioria dos trabalhos sobre os efeitos de predadores em ecossistemas subjacentes focaram-se na magnitude e não nas condições que medeiam tais efeitos. Apesar de muitos estudos terem demonstrado que interações predador-presa são amplamente influenciadas por características do habitat, a relação entre ambiente e as interações que ultrapassam os ecossistemas são pouco conhecidas (ver Marczak et al. 2007).

Predação e estrutura do habitat

Como mencionado anteriormente, a estrutura do habitat (i.e., complexidade e tamanho) desempenha um papel fundamental no estabelecimento das comunidades e nas interações entre os organismos de diferentes níveis tróficos (Wardle et al. 1997, Gonzalez e Chaneton 2002, Srivastava 2006). Habitats mais complexos podem afetar as taxas de predação ao disponibilizar refúgios às presas (Langellotto e Denno 2004) ou ao reduzir os encontros entre presas e predadores (Murdoch e Oaten 1975). Em um estudo sobre as relações entre predação, taxa de decomposição e complexidade de habitat observou-se que, na presença de predadores, habitats mais complexos apresentavam taxas de decomposição mais elevadas devido às maiores proporções de presas decompositoras sobreviventes (Srivastava 2006). Além da complexidade, o tamanho do habitat é um fator importante na modificação da intensidade dos efeitos top-down de predadores. Isto ocorre, pois múltiplos componentes da teia alimentar são afetados pelo tamanho do habitat tais como: número de espécies dentro de cada nível trófico (Williams 1943, Hart e Horwitz 1991, Rozenzweig 1995), tamanho das populações (Pimm 1991), taxas de imigração (MacArthur 1972) e comprimento das teias alimentares (Cohen e Newmant 1991). O comprimento e a complexidade das teias alimentares estão diretamente relacionados com a área do habitat; predadores ocorrem com maior frequência e são mais abundantes em áreas maiores (Spencer e Warren 1996, Post 2002, Holt e Hoopes 2005, Srivastava et al. 2008). Apesar da gama de estudos que relacionam efeitos de predadores sobre interações tróficas dentro de ecossistemas, até o momento, nenhum estudo testou como o tamanho do habitat influencia os efeitos de predadores que ultrapassam os limites dos ecossistemas. Neste contexto, busquei compreender o papel do tamanho do habitat sobre os efeitos de predadores terrestres na estrutura de comunidades e funcionamento de ecossistemas aquáticos adjacentes (Fig. 1, Capítulo 1).

Efeitos de predadores e a estrutura trófica de comunidades

A estrutura trófica das comunidades é frequentemente representada por meio de pirâmides de biomassa estratificadas por níveis tróficos. Este tipo de representação transmite informações ricas sobre os mecanismos que moldam a estrutura das comunidades (Trebilco et al. 2013). Pirâmides de biomassa não somente codificam a estrutura das teias alimentares, mas também integram características funcionais, tais como padrões de fluxo de energia, eficiência de transferência trófica e a renovação de diferentes componentes da teia alimentar (Odum 1971, Giorgio et al. 1999, Trebilco et al. 2013). Existe uma variação no formato das pirâmides de biomassa desde (a) pirâmides tradicionais (biomassa de cada nível trófico é menor do que a biomassa do nível trófico anterior), (b) pirâmides em coluna (distribuição homogênea de biomassa dos grupos tróficos) e por fim, (c) pirâmides invertidas (biomassa de predadores de topo é maior do que a biomassa dos níveis tróficos anteriores).

Vários mecanismos hipotéticos explicam a variação no formato das pirâmides tróficas. Atualmente, os mecanismos propostos são todos baseados em relações tróficas de consumo direto entre predadores e presas. Por exemplo, uma das principais hipóteses leva em consideração quanto a razão entre produtividade e biomassa (i.e., renovação) varia entre ecossistemas (Odum 1971, Buck et al. 1996, Gasol et al. 1997, Brown et al. 2004). A inversão da pirâmide ocorre quando a renovação dos níveis tróficos decai com o aumento dos níveis tróficos. Deste modo, predadores de topo apresentariam taxas de morte menores do que suas presas. Em ecossistemas marinhos a base da teia alimentar consiste em fitoplâncton (organismos com ciclo de vida curto e de rápida reprodução), que são consumidos por zooplânctons herbívoros e consumidores maiores. Apesar de diversos estudos terem demonstrado que predadores podem afetar a estrutura trófica das comunidades por meio do potencial risco de predação (Schmitz et al. 1997, 2004, Schmitz 1998, Wener e Peacor 2003), nenhum estudo foi realizado para tentar compreender qual o papel dos efeitos não consumíveis de predadores na estrutura das pirâmides tróficas de biomassa. Deste modo, investiguei a contribuição relativa dos efeitos de consumo direto e do risco de predação nas interações predador-presa como mecanismos estruturadores de pirâmides tróficas de biomassa (Fig. 1, Capítulo 2).

Predadores, componentes de diversidade e funcionamento ecossistêmico

Como abordado nos tópicos anteriores, muitas das funções ecossistêmicas envolvem a interação entre organismos de diferentes níveis tróficos (e.g., interações predador-presa) e os componentes abióticos dos ecossistemas. Além disso, o funcionamento dos ecossistemas tem sido relacionado aos padrões de diversidade dentro das comunidades. Diversos estudos sobre biodiversidade e funcionamento ecossistêmico (BEF) demonstraram uma relação positiva entre os diferentes componentes da diversidade (e.g., diversidade funcional (FD), filogenética (PD) e taxonômica (TD)) e funcionamento dos ecossistemas (Cardinale et al. 2012, Hooper e Vitousek 1998, Tilman et al. 2001). No entanto, existe ainda muita controversa sobre quais componentes da diversidade predizem melhor o funcionamento dos ecossistemas (Hooper et al. 2005). Embora diversos estudos tenham demonstrado que interações tróficas e diversidade afetam processos ecossistêmicos, poucos estudos buscaram compreender, de maneira integrativa, os efeitos das interações tróficas e fatores abióticos sobre os differentes componentes da diversidade e funcionamento ecossistêmico (Srivastava et al. 2012).

Predadores podem afetar a comunidades de presas por meio de alterações dos padrões de colonização (i.e., alterações comportamentais frente ao risco de predação) e das taxas de mortalidade e nascimento das presas, ou por afetarem, indiretamente, as interações entre as espécies e os recursos (Schmitz 2008, Vonesh et al. 2009). O efeito de alguns predadores é tão abrangente sobre as comunidades que eles são considerados espécies-chave, à medida que predadores podem diminuir a abundância de espécies competitivamente dominantes promovendo a manutenção da diversidade em comunidades (Paine 1966, Leibold 1996, Power 1996). Por outro lado, se predadores não limitam a abundância de competidores dominantes, ou se a competição é fraca entre as espécies de presas, predadores podem produzir comunidades menos ricas dominadas pelas espécies resistentes a predação (Almany e Webster 2004). Deste modo, por meio da alteração da diversidade de presas, predadores podem ter um papel chave nas propriedades e funcionamento dos ecossistemas, tais como produtividade, decomposição e fluxo de nitrogênio. Atualmente pouco se sabe a respeito dos efeitos de predadores sobre a diversidade funcional e filogenética de suas presas e as consequências para o funcionamento ecossistêmico.

Estudos recentes têm enfatizado que medidas de diversidade funcional, ou seja, quanto as espécies diferem funcionalmente em uma comunidade (Tilman 2001), poderia predizer melhor o funcionamento dos ecossistemas (Loreau 1998, Chapinet al. 2000, Tilman 2000, Díaz e Cabido 2001, Balvanera et al. 2006). Por outro lado, alguns autores sugerem que a diversidade filogenética pode ser considerada um dos estimadores mais sintéticos das características funcionais das comunidades (Cavender-Bares et al. 2009, Wiens et al. 2010) e, portanto, um bom preditor de funcionamento ecossistêmico. Existem evidências de que um incremento na diversidade filogenética aumenta a complementariedade de nicho e assim o funcionamento dos ecossistemas por meio da maximização da captação de recursos (Maherali e Klironomos 2007, Srivastava et al. 2012).

Sabemos que o funcionamento dos ecossistemas pode ser explicado (i) por meio das interações entre as espécies (e.g., interações predador-presa) e o meio abiótico e, (ii) através dos componentes da diversidade. Neste contexto, buscamos compreender os efeitos de dois extremos de um gradiente ambiental e os efeitos de predadores sobre os componentes da diversidade de presas detritívoras (i.e., diversidade funcional, filogenética e taxonômica) e como tais efeitos podem afetar o funcionamento ecossistêmico (i.e., decomposição e fluxo de nitrogênio) (Fig. 1, Capítulo 3).

Microcosmos naturais como modelos em estudos ecológicos

Apesar da grande importância, estudos de processos em comunidades e ecossistemas são particularmente complexos quanto ao entendimento (Lawton 1999). Por definição, comunidades são assembleias de populações de espécies que ocorrem juntas no tempo e no espaço (Begon et al. 2006). Todavia, a definição das comunidades, muitas vezes, é difícil, pois, na maioria dos casos, não existem limites nítidos para a repartição das comunidades em categorias distintas dentro dos ecossistemas. Além desta dificuldade, o estudo de comunidades biológicas inteiras impõe fortes restrições logísticas. Assim, grande parte dos trabalhos foca-se em grupos taxonômicos únicos (DeVries e Walla 2001) ou em um segmento reduzido da comunidade, incluindo algumas espécies de um mesmo nível trófico (Hooper e Dukes 2004), ou poucas espécies de níveis tróficos distintos (Schmitz 2006, Schmitz 2008).

Trabalhos recentes têm utilizado microcosmos naturais como modelos para teste de questões em ecologia de comunidades, tais como efeitos indiretos, fragmentação, teorias de metacomunidade e efeitos da biodiversidade em processos ecológicos (revisão em Srivastava et al. 2004). Os microcosmos naturais são habitats pequenos, com delimitações físicas bem definidas; além disso, são naturalmente colonizados por pequenos organismos, que compõem comunidades relativamente simples e fáceis de serem descritas (Kitching 2001, Srivastava et al. 2004). O tamanho reduzido dos habitats permite alta replicabilidade, e tanto o tamanho como a simplicidade estrutural e a delimitação desses microecossistemas os tornam sistemas facilmente manipuláveis (Kitching 2001, Srivastava et al. 2004). Como exemplo, temos os fitotelmatas, habitats aquáticos originados em estruturas variadas de plantas com cavidades em troncos de árvore, axilas de plantas, entrenós de bambu, plantas carnívoras em forma de jarros e tanques de bromélias (Kitching 2001).

Neste trabalho utilizamos bromélias e suas faunas como sistema-modelo para a avaliação dos efeitos *top-down* de predadores terrestres na estruturação de comunidades de artrópodes aquáticos e em dois processos ecossistêmicos-chave: decomposição e ciclagem de N (Fig. 2). Utilizamos também a comunidade de artrópodes aquáticos para testar o papel relativo de efeitos do consumo direto de predadores e do risco de predação na estruturação de pirâmides tróficas de biomassa. Além disso, testamos os efeitos relativos de dois extremos de um gradiente ambiental (i.e., restinga aberta e restinga fechada) (Fig. 3) e dos efeitos *top-down* de predadores aquáticos sobre a diversidade de detritívoros (i.e., diversidade funcional, filogenética e taxonômica), bem como a interação desses elementos no funcionamento ecossistêmico. A configuração em roseta das folhas das bromélias possibilita a coleta de água e detritos ricos em nutrientes, que suportam não apenas a comunidade de artrópodes aquáticos, mas também provê uma importante fonte de nutrientes para as bromélias (Armbruster et al. 2002, Ngai e Srivastava 2006). Estas funcionam como microecossistemas bem delimitados, onde os detritos formam a base da cadeia alimentar de uma comunidade rica e diversa composta por decompositores, detritívoros e predadores (Armbruster et al. 2002). Os limites físicos bem definidos e o tamanho reduzido destes ecossistemas possibilitam a coleta e quantificação da comunidade animal inteira; além disso, permitem também o delineamento das interações entre as espécies, bem como o controle das taxas de imigração e emigração (Armbruster et al. 2002, Srivastava et al. 2004). Ainda, os nutrientes originados da decomposição da MO e dos resíduos animais são absorvidos por tricomas especializados presentes na base das folhas que formam o tanque das bromélias (Benzing 1980). Deste modo, a capacidade de absorção de nutrientes pelos tricomas pode ser utilizada como uma ferramenta para estudos de processos ecossistêmicos, tais como ciclagem de N, por meio do uso de traçadores isotópicos (Ngai e Srivastava 2006).

Objetivos Gerais

Capítulo I. No primeiro capítulo, investigamos a importância relativa do tamanho do habitat nos efeitos de predadores terrestres sobre a comunidade de artrópodes aquáticos bromelícolas e em dois processos ecossistêmicos chave, decomposição e fluxo de nitrogênio.

Capítulo II. No segundo capítulo, testamos qual o papel relativo dos efeitos de consumo direto de predadores e do risco de predação sobre as populações de presas na estruturação de pirâmides tróficas de biomassa.

Capítulo III. No terceiro capítulo, tivemos como objetivo investigar os efeitos de dois extremos de um gradiente ambiental e os efeitos de predadores sobre os componentes da diversidade de presas detritívoras (i.e., diversidade funcional, filogenética e taxonômica). Além disso, exploramos o papel relativo do ambiente, dos predadores e dos componentes da diversidade sobre o funcionamento ecossistêmico (i.e., decomposição e fluxo de nitrogênio).

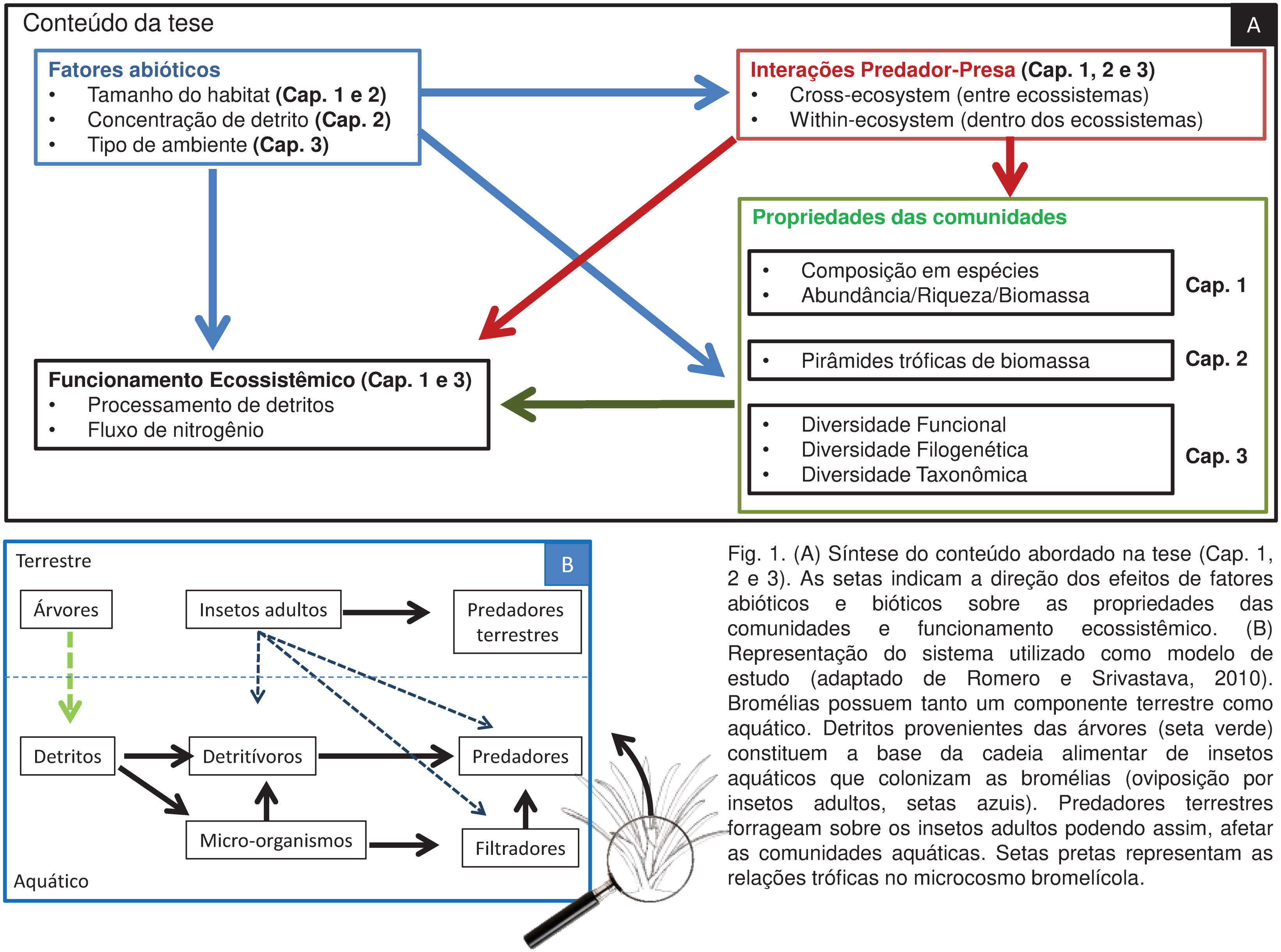

Fig. 1. (A) Síntese do conteúdo abordado na tese (Cap. 1, 2 e 3). As setas indicam a direção dos efeitos de fatores abióticos e bióticos sobre as propriedades das comunidades e funcionamento ecossistêmico. (B) Representação do sistema utilizado como modelo de estudo (adaptado de Romero e Srivastava, 2010). Bromélias possuem tanto um componente terrestre como aquático. Detritos provenientes das árvores (seta verde) constituem a base da cadeia alimentar de insetos aquáticos que colonizam as bromélias (oviposição por insetos adultos, setas azuis). Predadores terrestres forrageam sobre os insetos adultos podendo assim, afetar as comunidades aquáticas. Setas pretas representam as relações tróficas no microcosmo bromelícola.

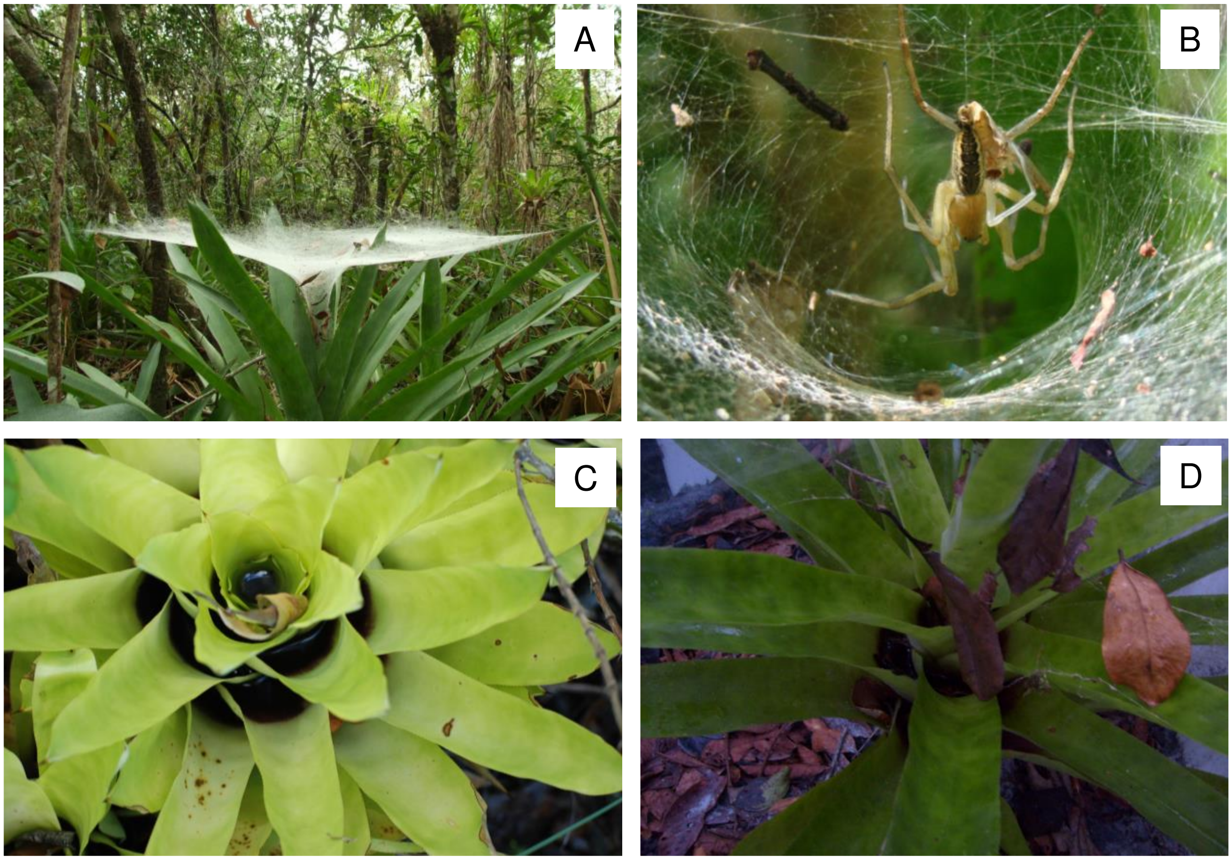

FIG. 2. Bromélia *Quesnelia arvensis* com teia em funil da aranha *Aglaoctenus castaneus* (A), detalhe da aranha *A. castaneus* fazendo muda (B), detalhe de uma bromélia *Q. arvensis* da restinga aberta (C) e bromélia experimental localizada na restinga fechada (D).

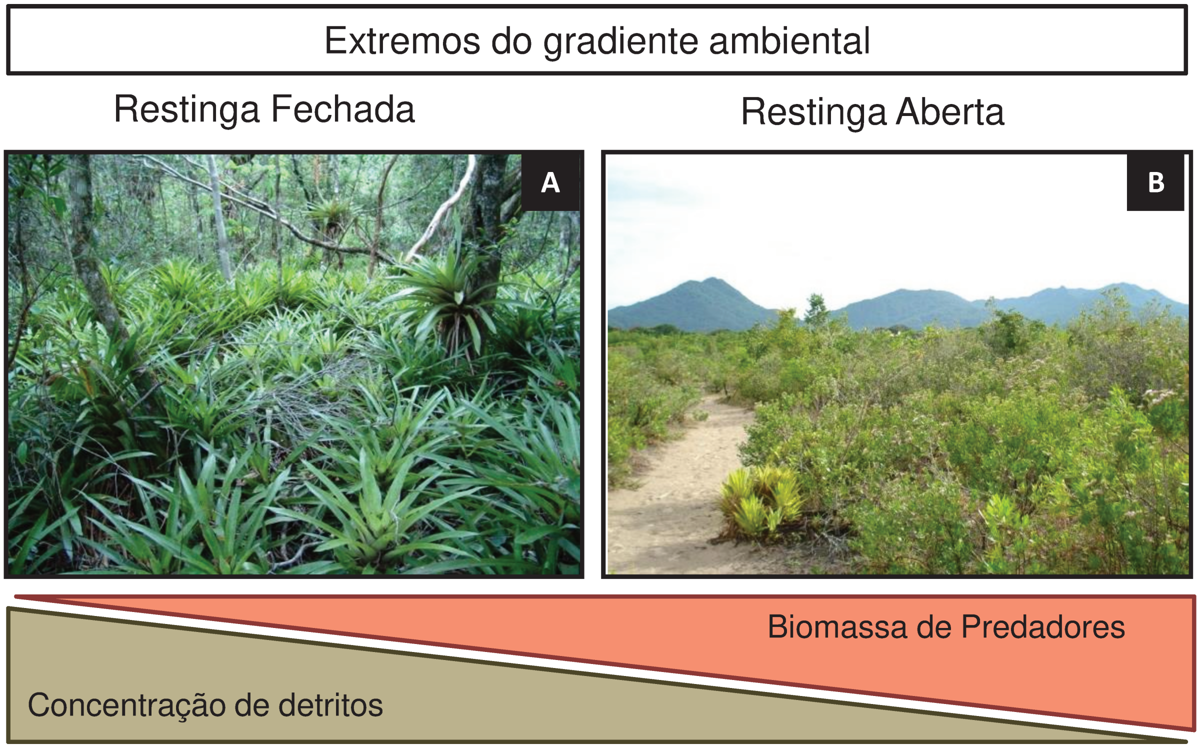

Fig. 3. Representação da variação da concentração de detritos e da biomassa de predadores ao longo de um gradiente ambiental (triângulos marrom e vermelho). Os dois extremos do gradiente são representados pela Floresta de Restinga Fechada e Floresta de Restinga Aberta. Na primeira encontramos maiores densidades de detrito e menor biomassa de predadores aquáticos, enquanto na segunda menores densidades de detrito e maior biomassa de predadores (Capítulo 3).

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CAPÍTULO I

DOES THE STRENGTH OF CROSS-ECOSYSTEM EFFECTS VARY WITH ECOSYSTEM SIZE? A TEST USING A NATURAL MICROCOSM

Does the strength of cross-ecosystem effects vary with ecosystem size? A test using a natural microcosm

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Abstract. The cascading effect of predators on the functioning of adjacent ecosystems typically occur when the life cycles of their prey include two ecosystems, such as insects with both aquatic larval stages and terrestrial adult stages. However, there has been little consideration of which habitat traits can modify the strength of these cross-ecosystem trophic cascades. Habitat size has been shown to mediate within-ecosystem trophic cascades, and we hypothesize that similar effects of habitat size might affect cross-ecosystem trophic cascades. For example, *Aglaoctenus castaneus* (Mello-Leitão 1942) (Lycosidae) spiders, which build a single web over water-filled bromeliads, can capture terrestrial adult insects as they attempt to oviposit in the waters of the bromeliad. Since larger bromeliad have less of their aquatic surface area covered by the spider's web, we predicted that in large bromeliads spiders would have less impact on densities of aquatic insect larvae and the ecosystem functions mediated by these larvae. To test these hypotheses, we manipulated spider presence in bromeliads differing in size, and examined impacts on aquatic invertebrate community and ecosystem functioning (decomposition, detrital nitrogen flux to bromeliad tissue) within the bromeliad. Web-building spiders influenced certain, but not all, components of the bromeliad ecosystem. Contrary to our hypothesis, spiders generally did not have weaker cross-ecosystem effects in larger bromeliads. Adult insects may visually detect the web, and use its presence as a cue to avoid approaching the bromeliad, precluding any effects of web coverage on insect capture rates. However, spiders did initiate strong changes in the trophic structure of aquatic food webs and ecosystem functioning, whereby aquatic predators and detrital biomass both decreased but aquatic detritivores remained the same. This pattern is most parsimoniously explained by a behaviorally mediated trophic cascade, whereby odonate adults avoid bromeliads with spiders, and aquatic detritivores increase detrital processing rates in the absence of odonate larvae. Small bromeliads also had higher decomposition rates, independent of spider presence, consistent with greater densities of detritivores in such habitats.

Keywords: aquatic-terrestrial linkages, habitat size, top-down effect, predation, microcosm experiment, decomposition, ecosystem functioning, trait-mediated effect, *species interaction*s.

INTRODUCTION

Predators can have profound effects on the structure of ecological communities and the flux of energy and nutrients within food webs. There is emerging evidence that such trophically-mediated effects of predators can cross ecosystem boundaries (Knight et al. 2005, Marczak et al. 2007, Schmitz et al. 2010). Typically, such cross-ecosystem effects of predators occur when they or their prey have a life cycle which includes both ecosystems. Animals with complex life cycles (Werner 1988) shift ecosystems between two ontogenetic life stages, such as a shift from aquatic juvenile stages to terrestrial adult stages in many insects and frogs (Wilbur 1980, Werner and Gilliam 1984, Polis et al. 1989, Schreiber and Rudolf 2008). When these organisms shift ecosystems, they may have strong bottom-up or top-down effects on the food-webs of the recipient habitats (Knight et al. 2005, Marczak and Richardson 2007, Romero and Srivastava 2010). For example, insects that emerge from aquatic to terrestrial ecosystems can affect terrestrial ecosystems by subsidizing the diets of terrestrial consumers (a bottom-up effect) (Wesner 2010a) or exerting strong top-down effects in a terrestrial food web (Knight et al. 2005). In such coupled aquatic-terrestrial ecosystems, few studies have considered the impact of predation on the organisms with complex life cycles. Terrestrial predators that forage at the ecosystem boundaries can intercept ovipositing or emerging prey at the point their life cycle crosses between ecosystems, potentially either supplementing the aquatic nutrient pool with carcasses (a bottom-up effect: Romero et al. 2010), or reducing the abundance of prey in the aquatic community (a top-down effect: Romero and Srivastava 2010) and therefore competing with aquatic predators (Marczak et al. 2007).

In addition, most studies of trophically-mediated cross-ecosystem effects have focused on measuring the magnitude of such effects. There has been little consideration of the conditions that mediate the strength of such cross-ecosystem effects, save one study that contrasted the effect of different habitats on suppression of aquatic prey assemblages by water striders (Marczak et al. 2007). By contrast, the effect of predators within ecosystems is well-known to depend on characteristics of both the habitat and organisms (Borer et al. 2005). Habitat size is particularly important in modifying the strength of top-down effects, as it affects multiple components of the food web: the number of species within trophic levels (Williams 1943, Hart and Horwitz 1991, Rosenzweig 1995), population sizes (Pimm 1991), immigration rates (MacArthur 1972) and food-web length (Cohen and Newman 1991). The length and complexity of food-webs generally increase with habitat size, since predators are more likely to be present and abundant in larger areas (Spencer and Warren 1996, Post 2002, Holt and Hoopes 2005, Srivastava et al. 2008). Increases in the incidence or abundance of predators in turn alters patterns of species richness and composition of the prey community. Such habitat-mediated predation effects can cascade through multiple trophic levels, affecting ecosystem functions carried out by lower trophic levels (Terborgh et al. 2001). Despite this wealth of research on how habitat size mediates trophic interactions within an ecosystem, to our knowledge, no study has tested how habitat size mediates the cross-ecosystem effect of predators.

Bromeliad food webs are particularly well-suited to experiments that examine the effects of habitat size on the cross-ecosystem effects of predation. Many bromeliads can impound water between their leaves and so, like other phytotelmata, contain both the aquatic and terrestrial component of ecosystems. Furthermore, bromeliads increase in size with age, so the same species can contain a large range of water volumes, from a few milliliters to many liters (Benzing 2000). Bromeliads are naturally populated by both aquatic invertebrates that live their entire life cycle inside the phytotelmata (e.g. leeches, annelids, ostracods) as well as aquatic insects with complex life cycles that emerge as winged terrestrial adults (Richardson 1999, Armbruster et al. 2002, Romero and Srivastava 2010). This aquatic food web typically relies on allochthonous sources of nutrients derived from dead organic matter (animal and plant), and the bromeliad itself absorbs some of these dissolved nutrient via specialized trichomes on its leaves (Benzing 2000). Many predators, such as spiders, inhabit the terrestrial part of bromeliads (Richardson 1999, Armbruster et al. 2002, Romero 2006). Romero and Srivastava (2010) showed that *Aglaoctenus castaneus* (Lycosidae) web spiders can reduce the richness, abundance and biomass of aquatic insect larvae within bromeliads via reduced oviposition by terrestrial adults. The few other invertebrates that lack terrestrial stages were not reduced by spiders (Romero and Srivastava 2010). We hypothesize that the negative impact of such web spiders on aquatic insects, and the ecosystem processes affected by aquatic insects (see below), will be greatest in small bromeliads (Prediction 1), as in such bromeliads the web of *A. castaneus* occupies the greatest proportion of the surface area of the bromeliad (Fig. 1A, Fig. 2). Note that at most one individual of *A. castaneus* occurs on any given bromeliad, regardless of bromeliad size (Fig. 1B). Aquatic insects in bromeliads are primarily detritivores, and detritivore biomass - especially of the scraper and shredder functional groups – has been shown previously to be a robust predictor of decomposition rates in bromeliads (Srivastava 2006, R. LeCraw, pers. comm.). Thus we would predict that in bromeliad tanks where spiders result in the greatest reduction in aquatic detritivore biomass will also have the greatest reductions in detrital breakdown, and consequently lowest flux of nitrogen from the detritus to the bromeliad (Prediction 2, Fig. 2).

Alternatively, cross-ecosystem effects of spiders may switch from negative to positive as bromeliad size increases (Prediction 3, Fig. 2) because of size-dependent changes in the trophic structure of the aquatic insect community (Srivastava et al. 2008) coupled with greater sensitivity of aquatic predators (as compared to aquatic detritivores) to spiders. Damselflies are top predators from bromeliad food webs (G. Q. Romero, G. C. O. Piccoli, P. M. Omena unpub. data, Srivastava et al. 2008). They are typically more abundant in large bromeliads which likely reflect the drought risk associated with small bromeliads (Srivastava et al. 2008). Spiders may also cause particularly strong reductions in aquatic predators, for example if aquatic predators are not only directly affected by reduced oviposition opportunities but also indirectly affected by reductions in their prey base (Marczak et al. 2007). However, if spiders supress aquatic predators, aquatic detritivores may indirectly benefit: predators such as damselfly larvae are known to have large impacts on the abundance and composition of other aquatic insects in bromeliads (Ngai and Srivastava 2006, Srivastava 2006, Starzomski et al. 2010). The net effect of spiders on detritivores would then combine direct negative effects via reduced oviposition with indirect positive effects via reduced aquatic predation, and could be either neutral or even positive in large bromeliads. Such effects of spiders are expected to cascade to the many bromeliad ecosystem functions known to be affected by aquatic trophic structure, such rates of detrital processing (Srivastava 2006), ecosystem CO_2 flux (Atwood et al. 2013) and nitrogen uptake by bromeliad plants (Ngai and Srivastava 2006). If spiders benefit detritivores by reducing aquatic predatory insects as suggested by Prediction 3, spiders could increase decomposition and detrital nitrogen uptake (Prediction 4, Fig. 2) by either releasing detritivores from consumption by aquatic predators (density-mediated effect) or by increasing detritivore activity, otherwise limited to avoid detection by aquatic predators (trait-mediated effect). A previous study has shown that ovipositing adults alter their behaviour in response to aquatic predators (E. Hammill pers. comm.), and the same may be true of their larvae.

Thus, we have opposing predictions about how bromeliad size could modify the direction of spider impacts on the aquatic invertebrate community and ecosystem processes, depending on whether the trophic structure of the aquatic community is directly affected by bromeliad size and which aquatic invertebrates are most affected by spiders. We now describe a manipulative experiment that is able to distinguish between these hypotheses.

MATERIAL AND METHODS

Study site and organisms

We conducted the experiment in a closed restinga (i.e. coastal sand substrate) forest at the Parque Estadual da Ilha do Cardoso located on the Atlantic island Ilha do Cardoso a few kilometers off the south coast of Sao Paulo State, Brazil (25° 03'S, 48°53'W). The closed restinga consisted of 6 – 8 m high trees with a relatively continuous canopy, high densities of epiphytes and an understory mostly covered by orchids and bromeliads (Appendix 1A). The most abundant bromeliad species is *Quesnelia arvensis* Mez. (Bromeliaceae), a large terrestrial bromeliad which accumulates up to 3 L of rainwater inside tanks formed by its leaves. A diverse aquatic fauna, mainly composed by insect larvae and including several functional groups, live within the tanks formed by *Q. arvensis*, including filter feeders (Culicidae), detrital shredders (Limoniidae, Trichoptera), detrital scrapers (Scirtidae), collectors (e.g. Chironomidae, Psychodidae) and predators (e.g. Coenagrionidae, Corethrellidae, Tanypodinae, Dytiscidae, some Ceratopogonidae). Other non-insect invertebrates like Ostracoda, Oligochaeta (both detritivores) and Hirudinea (predators) also compose the aquatic community (Romero and Srivastava 2010). Several terrestrial organisms such as the bromeliad living spiders *Coryphasia cardoso* (Santos and Romero 2007) (Salticidae), *Psecas* sp. (Salticidae) and *Aglaoctenus castaneus* (Lycosidae) inhabit the non-submerged part of these plants. To run the experiment, we used one of the most common terrestrial spiders, *A. castaneus*. This spider constructs a horizontal funnel-like web, with the funnel attached in the center of the bromeliad rosette, and a horizontal sheet covering the upper part of the bromeliad (Fig. 1B). This spider exhibits a sit-and-wait foraging mode, and it is active both day and night.

Experimental design

To determine whether habitat size mediates the effects of terrestrial predators on the aquatic community and ecosystem functioning (detrital processing and nitrogen flux), we manipulated the presence of spider *A. castaneus* in bromeliads of different sizes (bromeliad capacity: small 100–200 ml; large 800–900 ml) using a randomized block design with 13 blocks. Each block consisted of four treatments representing a 2 x 2 factorial design of spiders and bromeliad size: (1) small bromeliad with an *A. castaneus* spider, (2) small bromeliad without a spider, (3) large bromeliad with an *A. castaneus* spider and (4) large bromeliad without a spider.

To set up the experiment, we collected from the restinga 60 bromeliads (30 small and 30 large) in January 2010. Each bromeliad was inverted and washed thoroughly with spring water to remove detritus and organisms. To capture or kill any residual invertebrates we suspended the bromeliads upside down from a line inside a laboratory for 10 days. We kept bromeliads root moist and inspected the tanks every day using a flashlight to remove remnant insect larvae. After 10 days, we dissected four large and four small bromeliads to test the efficacy of the cleaning procedure; we did not find any insects alive inside bromeliads after dissection. We planted the bromeliads in the sandy substrate of the restinga in 13 blocks of four bromeliads, two large and two small. Each experimental block was 5–20 m from its nearest neighbor, and 0.3–0.5 m separated the plants within each block. We randomly assigned the spider treatments to the large and small bromeliads. To avoid the entry of other non-flying terrestrial arthropods, like ants and spiders, we constructed an open cylinder (60 cm tall, 2 m diameter) made from white PVC (Formica ®) around each block (Appendix 1B). Inside the cylinder, we constructed two cross walls 20 cm high to prevent spiders from moving between plants. We periodically applied solid medical petroleum jelly (Rio Química, São José do Rio Preto, Brazil) to the top of cylinders and cross walls as a further barrier. Finally, we covered the cylinder with a nylon mesh to prevent the colonization of the bromeliads before the spiders had time to construct their webs; we removed the net about two days later, once the webs were built. The experiment lasted three months with daily monitoring of bromeliads to ensure spiders remained on plants (any missing spiders were replaced).

Aquatic community responses to bromeliad size and spider manipulations

To access whether the cross-ecosystem effects of terrestrial predators depend on bromeliad size, we collected the invertebrate community that colonized the bromeliads after three months. We dissected each bromeliad by removing and washing each leaf separately in running water over large buckets, and then filtered this water through 125 and 850 µm soil sieves. We searched each of the two size-fractions of material in white trays. We recorded the morphospecies and abundance of all aquatic invertebrates visible to the naked eye (i.e., body size larger than 0.5 mm). Taxonomists identified some of the morphospecies to the lowest taxonomic level. We then determined the functional group of each taxon through the literature (Merritt and Cummins 1996) and by feeding trials. To estimate invertebrate biomass, we used previously constructed allometric equations between body length and dry mass, or mean of dry mass for very small insects (D. S. S., unpublished data).

Ecosystem responses to bromeliad size and terrestrial predators

We tested the indirect effect of spiders and bromeliad size on the breakdown of detritus and flux of detrital nitrogen into new bromeliad leaves. In order to quantify nitrogen flux from detritus to bromeliad leaves, we added ^{15}N labelled *Eugenia uniflora* L. (Myrtaceae) leaves on the bromeliad tank. To obtain labelled leaves, we watered saplings of *E. uniflora* with solution (2.5 g L^{-1}) of labelled ammonium sulphate $(^{15}NH_4)_2SO_4$ (10 atom % excess, from Cambridge Isotope Laboratories, Andover, MA, USA). We applied 4 ml of labelled solution on the roots of the saplings every other day during two months. The labelled leaves were oven-dried at 60°C for 48 hours. We used a previously established relationship between bromeliad capacity and detrital dry mass (r^2=0.82, n= 25; G. Q. Romero and D. S. S, unpubl. data) to determine that large bromeliads (i.e., maximum tank capacity 850 ml) hold 3.31 times more detritus than the small (i.e., maximum tank capacity 150 ml) ones. Therefore, in order to ensure labelled detritus was added in proportion to bromeliad size, each small bromeliad received a total of 1 g of labelled leaves and larger bromeliads received 3.31 g, with this amount split between additions 20 and 50 days from the beginning of the experiment (approximating the near continuous entry of detritus in natural bromeliads). At the end of the experiment, we removed three new leaves from the innermost node of each experimental bromeliad for isotopic (^{15}N) and nitrogen concentration (µ of total N mn^{-1} of dried plant tissue) analyses. The Stable Isotope Facility laboratory (UC Davis, CA, USA) determined isotope ratios of ^{15}N and % mass-specific N concentration using a continuous flow isotope ratio mass spectrometer (20–20 mass spectrometer; PDZ Europa, Sandbach, England) after sample combustion to N^2 at 1000°C by an on-line elemental analyser (PDZ Europa ANCA-GSL). We also evaluated the mass loss of the labelled leaves added throughout the experiment. At the end of the experiment, we collected and dried (48 hours at 60°C) all leaves of *E. uniflora* retained on the 850 µm sieve.

Statistical analyses

We designed the experiment as a two-way ANOVA with two fixed factors (bromeliad size and presence of spider, two levels each), and one random factor (block). The response variables to test the effect of habitat size and terrestrial predators on aquatic insect community included: richness and total abundance of aquatic insects, abundance and biomass of functional groups (predators, collectors, filter feeders, scrapers and shredders), abundance of the damselfly larva *Leptagrion andromache* (Hagen in Selys, 1876) (Coenagrionidae; top predator), detritivore and predator density. We could not identify the functional group of a few Diptera larvae (percentage of total arthropod abundance: Sciaridae 0.039%, Cyclorrhapha 0.013%, Ephydridae 0.37%, Cecidomyiidae 0.053%), so we did not include these organisms in the functional group analysis. The ecosystem response variables were the detrital mass loss (*E. uniflora* leaves), bromeliad uptake of N^{15} from *E. uniflora* leaves and total nitrogen concentration in bromeliad leaves.

To understand the mechanism underlying decomposition rates, we tested for the effect of biomass of all predators, or just the top predator *L. andromache,* and detritivores on decomposition rate of *E. uniflora* leaves using linear mixed effect models (LME). We checked for normality and heteroscedasticity of residuals with standard diagnostic plots and metrics. For data with heterogeneous distribution of residuals, we allowed variance of each factor to differ, using the “varident” function within the “nlme” package of R (Zuur et al. 2009). Since we added 3.31 times more labeled leaves inside the tanks of large bromeliads than to small bromeliads (as large were predicted to naturally contain 3.31 times more detritus), we were concerned that effects of bromeliad size in a 2-way ANOVA could be confounded by differences in the amount of detritus used (e.g. if nutrient uptake saturated at high levels of detritus). We therefore conservatively examined small and large bromeliads separately to assess how spiders affected N^{15} uptake by bromeliad leaves and the total nitrogen content of bromeliads. We performed all analyses using the statistical language R (Core Team 2012).

We tested for the effect of habitat size and spider presence on the composition of aquatic insect morphospecies using permutational multivariate analysis of variance (PERMANOVA, Anderson 2001), as coded in the “adonis” function of the vegan package of R (Oksanen et al. 2013), with dissimilarity calculated as Bray-Curtis distances and 9999 permutations. Nonmetric multidimensional analysis (NMDS) was performed to visualize similarities or dissimilarities among our four treatments (Appendix 2). We used the indicator method value (INDVAL) to characterize differences between faunal compositions (Dufrene and Legendre 1997). This method is based on the comparison of relative abundances and relative frequencies of occurrence of taxa in different groups, and it identifies indicator taxa that vary more between groups than would be expected. Indicator values are based only on within-species comparisons, independent of the occurrence of other species. The index varies between 0 and 100, and it attains its maximum value when all individuals of a species occur in a single group of sites, and its minimum value when the species occurs in across sutes of all groups.

RESULTS

Aquatic community responses to habitat size

Bromeliad size strongly affected the community of organisms with complex life cycles (i.e. aquatic insects): larger bromeliads contained insect communities 2.85 times more abundant and 1.85 times richer than small ones (Table 1, Fig. 3A). The occurrence of aquatic non-insects (i.e., leech and ostracods) within bromeliads was extremely low compared with unmanipulated bromeliads; we found four individuals of ostracods and a leech inside a single bromeliad whereas in natural conditions 64% of unmanipulated bromeliads contained ostracods, and 24% contained leeches (survey data from Srivastava D. S. and Romero G. Q. 2008). Leeches and ostracods rely on phoresy to colonize new bromeliads, so colonization rates are probably much slower than those of ovipositing insects. Abundance of Oligochaeta, the only non-insect invertebrate with sufficient numbers for analysis, was not affected by either size or spider presence (Table 1).

We found greater abundance and biomass of aquatic insects from all the functional feeding groups in larger bromeliads, especially predators and filter feeders, but also shredders, collectors, and scrapers (Table 1, Fig. 3A and B). Abundance of predators was on average 80% lower in small bromeliads than in large bromeliads; and the abundance of filter feeders was 97% lower in small bromeliads (Fig. 3A). Contrary to our initial expectation, the abundance of odonates was not higher in larger bromeliads (Fig. 4B). Despite the greater abundance of all insect groups in large bromeliads, the density of detritivores (number of insects per ml water) was 38% higher in small bromeliads (Fig. 4C), whereas the density of predators was not affected by the bromeliad size (Table 1).

Bromeliad size, but not spider presence, affected the composition of aquatic invertebrate morphospecies (PERMANOVA, size: $F_{1,48}$ = 11.701, R^2 = 0.191, P = 0.0001; spider $F_{1,48}$ = 0.805, R^2 = 0.013, P = 0.565; size*spider $F_{1,48}$ = 0.822, R^2 = 0.013, P = 0.563) (Appendix 2). We found indicator species just for larger bromeliads (INDVAL > 25%, $P < 0.05$), from the 57 taxa sampled in the experiment 18 were most associated with this group of bromeliad. The predator *Monopelopia* aff. *caraguata* Mendes, Marcondes and Pinho, 2003 (Chironomidae) presented the higher indicator value (IV = 84.42%, P = 0.001) followed by filter feeding mosquitoes from the genus *Culex* (IV = 78%, P = 0.001).

Aquatic community responses to terrestrial predator

The presence of terrestrial predator *A. castaneus* significantly reduced the richness of aquatic insects (Table 1). Spiders reduced predator biomass, but had no effect on predator abundance (Table 1, Fig. 3B). Spiders also had a negative effect on the occurrence of the predatory damselfly, *Leptagrion andromache* (Table 1, Fig. 4B). The aquatic beetles from the family Dytiscidae occurred only in large bromeliads and the presence of spiders negatively affected the abundance of this predatory beetle (one-way ANOVA, $F_{1,24}$ = 6.81, P = 0.0153).

In general, these responses of the aquatic invertebrate community indicate that bromeliad size influences most aspects of the aquatic insect community, especially predators (except odonates, contrary to our initial prediction) and filter feeders. By contrast, spiders had selective effects on the aquatic insect community, reducing overall species richness but not abundance or composition, and reducing odonate numbers and predator biomass, but not predator abundance. Contrary to Predictions 1 and 3, there were no interactions in the effects of bromeliad size and spiders.

Habitat size and spiders (but not their interaction) affected the mass loss of labelled detritus (Table 1). Small bromeliads and bromeliads with spiders had greater mass loss of *E. uniflora* leaves than the bromeliads from other treatments (Fig. 4A, Table 2), supporting Prediction 4. We explored the potential mechanisms underlying this effect of spiders and bromeliad size on decomposition using linear mixed effect models. When *L. andromache* biomass was added as the first term in the model, the *L. andromache* term became significant and the spider presence term became non-significant, suggesting that changes in *L. andromache* biomass are the underlying driver of spider effects on decomposition (supporting Prediction 4). Similar effects on models were not seen when adding detritivore biomass (contrary to Prediction 3) or total predator biomass, suggesting that these variables do not underlie spider effects on decomposition. Despite spider effects on mass loss of labelled leaves, spiders did not affect the uptake of ^{15}N from labelled leaves by either large or small bromeliads (one-way ANOVA, large bromeliads: $F_{1,12} = 0.791$, $P = 0.383$; small bromeliads: $F_{1,12} = 1.199$, $P = 0.285$, Fig. 4D) nor the total nitrogen content in bromeliad leaves (one-way ANOVA, large bromeliads: $F_{1,12} = 0.64$, $P = 0.437$; small bromeliads: $F_{1,12} = 0.05$, $P = 0.813$, Fig. 4E).

DISCUSSION

This study shows that, although the aquatic invertebrate community within bromeliads was strongly affected by bromeliad size and moderately affected by terrestrial web-building spiders, bromeliad size does not mediate the cross-ecosystem effect of terrestrial predators on either the invertebrate community or ecosystem functions. Specifically, we found no support for the predictions (Prediction 1 and 3) that spiders would have strongest cross-ecosystem effects within small bromeliads, reducing both detritivore abundance and the ecosystem functions carried out by detritivores. Indeed, spiders had no net effect on detritivore abundance and biomass in any size class of bromeliad, unlike a previous study at this site (Romero and Srivastava 2010). Neither did the directionality of the spider effect on detritivores switch from negative to positive as bromeliad size increased (Prediction 2), reflecting increasing indirect positive effects of spiders on detritivores via suppression of aquatic predation. However, the two assumptions underlying this prediction did receive support: increases in bromeliad led to proportionately greater increases in predators than detritivores, and spiders preferentially reduced the biomass of aquatic predators (especially Zygoptera larvae and Dytiscid adults). Spiders increased detrital processing (supporting Prediction 4) in a pattern consistent with trait-mediated effects rather than density-mediated effects but, this change in detrital processing did not translate into changes in nitrogen uptake from the detritus or in the nitrogen content of the bromeliad leaves. We now examine each of these main results in turn.

The strength of bromeliad size effects on the community is perhaps not surprising: the positive relationship between the number of species and area is one of the most established patterns in ecology (Williams 1943, Rosenzweig 1995). In the microecosystem studied here, habitat size is better represented by volume than area, but otherwise the community showed the classic pattern of an increase in both the number and abundance of all insect species with habitat size. Similar patterns have been reported for bromeliads in at least four other countries (Srivastava et al. 2008, Armbruster et al. 2002, Stuntz et al. 2002). Greater bromeliad tank capacity strongly favored the occurrence of some secondary consumers and predators. For example, filter feeders (entirely Culicidae) appeared primarily in larger bromeliads, possibly because these insect larvae are more dependent on the water column to forage. Similarly, aquatic predators occurred disproportionately in large bromeliads, especially Dytiscidae beetles and chironomids from the predatory genus *Monopelopia*. Other studies also highlight the strong effect of habitat size on predator abundance and richness (Spencer and Warren 1996, Post et al. 2000, Holt and Hoopes 2005), including a study of bromeliads in Costa Rica, Dominica, and Puerto Rico (Srivastava et al. 2008). We expected the top-predator *L. andromache* to be negatively affected by the small size of habitat, given that bromeliad-dwelling damselflies in other locations are reported to avoid small bromeliads (Srivastava et al. 2008). However, damselfly were not restricted or more abundant in large bromeliads, possibly because the bromeliads in this study were located in a closed restinga (i.e. shaded substrate) forest where desiccation is rare (A. A. M. MacDonald and D. S. Srivastava, unpubl. data).

Web-building spiders influenced certain, but not all, components of the bromeliad ecosystem. We had predicted that spiders would reduce the abundance and diversity of all aquatic insects (Prediction 1). However, spiders did not reduce insect colonization of all groups of aquatic insects, only the aquatic predators (especially Zygoptera larvae and Dytiscid adults). *Aglaoctenus castaneus* is a sit-and-wait predator that constructs a large, densely-woven, funnel-like web (Fig. 1B) which might be a substantial visual cue of their presence for ovipositing insects. Predator hunting mode determines whether effects of antipredator behavior of prey persist or attenuate at community level (Barbosa and Castellanos 2005). Because sit-and-wait predators like web spiders are relatively sedentary, the presence of their cues should be indicative of predation risk (Schmitz et al. 1997, Preisser et al. 2012). Therefore, it is possible that adult dytiscids and damselflies, both visually guided insects (Sbita et al. 2007, Bybee et al. 2012) detected *A. castaneus* webs and avoided ovipositing in these bromeliads. Previous studies have suggested that adult odonates could be able to detect risk of predation and avoid oviposition in sites with the presence of terrestrial (e.g. spiders and frogs) (Wolf and Waltz 1988, Rehfeldt 1990, 1992) and aquatic predators (e.g. fishes) (McGuffin et al. 2006). In this case, oviposition would be primarily reduced by the mere presence of the web rather than entanglement of adult insects in webs. Thus even though the web constructed by *A. castaneus* covered a smaller proportion of the surface area of large bromeliads, lower entanglement rates in webs on large bromeliads (assumed by Prediction 1) may be of minor importance for oviposition – explaining in part why we found no effects of bromeliad size on cross-ecosystem effects of spiders. We had also predicted that aquatic predators could be indirectly affected by spiders via reduction of aquatic prey (Prediction 3). Although aquatic predator biomass was reduced by spiders, the same did not occur for their prey, contrary to this hypothesis. The only predator species that showed a clear spider *vs* bromeliad size interaction was Dytiscid beetles, and this only because Dytiscids were completely absent from small bromeliads, so that the effect of spiders was restricted to larger bromeliads.

One of the most intriguing results from this experiment was that spiders increased detrital decomposition. We can exclude the possibility that this was due to spiders reducing detritivore oviposition (Prediction 3) because detritivore abundance and biomass were unaffected by spiders, and in any case this mechanism predicts a reduction – not an increase – in decomposition (Fig. 1). Indeed, detritivore biomass is unable to explain any variation in decomposition in our analysis, once spider and bromeliad size effects are considered (Table 2). An alternative explanation is that spiders primarily reduce aquatic predators, and so consequently increase decomposition through either release of detritivore numbers or activity (Prediction 4). Certainly, spiders reduced aquatic predator biomass, but again predator biomass was unable to explain variation in decomposition attributed to spider effects (Table 2). However, biomass of the dominant predatory species, the odonate *L. andromache*, was able to account for most of the variance in decomposition previously attributed to spiders, consistent with the effects of spiders on decomposition being primarily moderated via effects on odonates (Table 2). Spiders had strong negative effects on *L. andromache*, reducing abundances by 80% in small bromeliads and 35% in the larger ones. *L. andromache* does not appear to affect decomposition via changing detritivore biomass, otherwise detritivore biomass could replace spider presence as a predictor of decomposition (Table 2). We suggest that *L. andromache* instead reduces detritivore activity, and so indirectly decreases decomposition rates. Trait-mediated effects of odonates on detritivore behaviour have been shown previously in bromeliads: in bromeliads at both this field site and in Costa Rica, some detritivore adults avoid ovipositing in bromeliads with odonates (E. Hammill unpubl. data, P. M. O., unpubl. data). We suspect that also reducing movement associated with detrital processing would be a useful defense against the very visual cues used by "sit-and-wait" odonate larvae, although we caution that this still remains to be experimentally tested in this system.

Not only spiders, but the size of bromeliads affected detrital processing. We could expect lower decomposition in large bromeliads since the greater biomass and abundance of predators could cause an indirect negative effect of predators on decomposition. However, total predator biomass was unable to explain variation in decomposition. The greater decomposition in small bromeliads could be a result of two factors, the bromeliad tank complexity and detritivore density. Small bromeliads are more complex in terms of tank compartmentalization; the number of leaves for each millilitre of water is higher than for larger bromeliads (Srivastava 2006). The greater tank compartmentalization could reduce predator efficiency and indirectly increase detrital processing rates (Srivastava 2006). Additionally, small bromeliads presented detritivores densities up to 35% greater than large bromeliads, which probably favored decomposition in these microecosystems. It is not clear why the change in detrital decomposition was not reflected in the amount of detrital nitrogen absorbed by the bromeliad, unless the detritivores held most of the detrital nitrogen in their bodies. Previous work has shown that aquatic predation on detritivores is needed to make detrital nitrogen available to the bromeliad (Ngai and Srivastava 2006).

This study demonstrates not only a cross-ecosystem trophic cascade starting with spiders and ending with detrital processing, but potentially also represents a trait-mediated trophic cascade involving behavioural decisions of both ovipositing damselfly adults and of aquatic detritivore larvae (with the caveat that behaviour was inferred in this study, rather than directly examined). Interestingly, the consequence of this inferred behavioural cascade is a dramatic shift in the relative abundances of the aquatic trophic pyramid, whereby spiders cause a reduction of the aquatic predator and detritus levels without a concomitant increase in the detritivore level. Traditional consumptive models of trophic cascades predict an alternation of top-down effects between trophic levels, and thus an increase in the detritivore level. Predation effects on insects with complex life cycles can thus have a large and unexpected effect on food-web structure. Indeed, other studies have shown the reverse pattern, that fish predation on aquatic insects can have unexpected effects on distant components of terrestrial ecosystems, including the biomass of riparian-specialist spiders (Baxter et al. 2004), bee pollination (Knight et al. 2005) and trophic structure of winged insect prey assemblage (Wesner 2010b). We believe that this is the first study to show that terrestrial predators can affect aquatic ecosystem functioning (i.e. decomposition) by reducing the flux of keystone aquatic predators with complex life cycles.

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TABLE 1. Two-way randomized block ANOVAS summarizing the main and interactive effects of bromeliad size (Large and Small) and presence of spiders (*Aglaoctenus castaneus*) on aquatic community and decomposition of *Eugenia uniflora* leaves. One-way randomized blocks ANOVA summarizing the effect of spider presence on δ^{15}N(‰) and N total. Degrees of freedom for all *F* ratios = 1,36, except for the δ^{15}N(‰) and N total *F* ratio = 1,12; significant effects ($P <$ 0.05) are in bold case.

Response variable	Size		Presence of spider		Size*Presence of spider	
	F ratio	*P*-value	*F* ratio	*P*-value	*F* ratio	*P*-value
Richness	82.26	**< 0.0001**	5.00	**0.03**	1.57	0.22
Total abundance	48.36	**< 0.0001**	1.12	0.29	0.52	0.47
Abundance						
Predators (total)	46.25	**<0 .0001**	0.02	0.89	0.04	0.84
Zygoptera	0.89	0.35	5.07	**0.03**	0.67	0.43
Collectors	32.23	**<0.0001**	2.11	0.15	0.89	0.34
Filter feeders	14.05	**0.0006**	3.05	0.08	3.19	0.08
Scrapers	4.86	**0.03**	0.21	0.65	0.30	0.58
Shredders	7.06	**0.01**	0.87	0.35	0.38	0.53
Oligochaeta	0.09	0.76	0.41	0.52	0.79	0.38
Biomass						
Predators	19.79	**0.0001**	5.98	**0.02**	1.57	0.21
Zygoptera	0.01	0.92	8.53	**0.006**	3.36	0.19
Collectors	30.29	**< 0.0001**	0.54	0.46	2.21	0.14
Filter feeders	44.89	**< 0.0001**	1.02	0.31	2.33	0.13
Scrapers	10.32	**0.003**	0.0001	0.99	0.07	0.78
Shredders	17.25	**0.0002**	1.61	0.21	0.02	0.87
Density (insects.ml^{-1})						
Detritivores density	19.43	**0.0001**	1.51	0.22	0.0002	0.98
Predator density	**<0.0001**	0.99	0.003	0.95	0.21	0.64
Ecosystem responses						
Detritus mass loss	36.73	**< 0.0001**	16.29	**0.0002**	2.95	0.09
δ^{15}N(‰) (large bromeliad)	-	-	0.79	0.38	-	-
N total (large bromeliad)	-	-	0.64	0.44	-	-
δ^{15}N(‰) (small bromeliad)	-	-	1.19	0.28	-	-
N total (small bromeliad)	-	-	0.05	0.81	-	-

TABLE 2. Linear mixed effect models (LME) for the effect of the biomass of predators (including: *Leptagrion*, Dytiscidae, *Bezzia* sp. 1 and *Monopelopia*), biomass of *Leptagrion*, biomass of detritivores, bromeliad size and spider presence on detritus mass loss. Significant effects ($P < 0.05$) are in bold case.

Model (decomposition)	Predator	*Leptagrion*	Detritivores	Size	Spider	Size*Spider
~ size*spider	-	-	-	**<0.0001**	**<0.0003**	0.09
~ *Leptagrion* + size*spider	**-**	**0.018**	-	**<0.0001**	0.09	0.19
~ detritivore + size*spider	-	-	0.37	**<0.0001**	0.16	0.07
~ *Leptagrion* + detritivore + size*spider	**-**	**0.02**	0.76	**0.0001**	0.12	0.18
~ predators + detritivore + size*spider	0.64	-	0.40	**< 0.0001**	0.18	0.07

FIGURE LEGENDS

FIG. 1**.** The percentage of bromeliad surface area covered by *Aglaoctenus castaneus* web decreases as bromeliad size (measured as water-holding capacity) increases (A). We measured the largest diameter of the web sheet, as well as its horizontal perpendicular diameter, and them we used the formula for ellipse area to estimate the web sheet area. We used the same principle to estimate the bromeliad rosette area, measuring the largest diameter formed by the bromeliad leaves and its perpendicular diameter. Using these measurements, we could calculate the percentage of *A. castaneus* web cover in bromeliads of different sizes. Bromeliad with a funnel-shaped web constructed by a single *Aglaoctenus castaneus* spider (B). The web was dusted prior to the photograph with flour being taken to improve visibility.

FIG. 2. Cross-ecosystem effects of spiders on the bromeliad ecosystem were predicted to vary with bromeliad size. The magnitude of a trophic level or rate of a process is indicated by the relative size of the font or arrows in the figure below. Arrows show the direction of an impact, and are identified as positive (+), neutral (0), or negative (-) and direct (solid) or net indirect (dashed). Small bromeliads were predicted to have greater top-down effects of spiders on aquatic insects, as more of the surface area is covered by a web (Prediction 1, red arrows). Detritivore biomass was predicted to be the main determinants of decomposition rates and hence detrital N uptake by the bromeliad (prediction 2, green arrows). As bromeliad size increased, we predicted top-down control of detritivores by aquatic predators to increase, and so detritivores to indirectly benefit from spider reductions in the aquatic predators in large bromeliads (prediction 3, gray text). Consequently, we predicted that spiders would have the greatest negative effects on detrital processing and N release in small bromeliads (Prediction 4, black arrows).

FIG. 3. Mean abundance (A) and dry mass (B) of the aquatic insect functional feeding groups. Error bars represent ± SE.

FIG. 4. Percentage of detritus mass loss (A), abundance of *Leptagrion* (B), detritivore density (C), mean δN^{15} (‰) (D) and total N concentration (E) in the experimental bromeliads. Error bars represent ± SE.

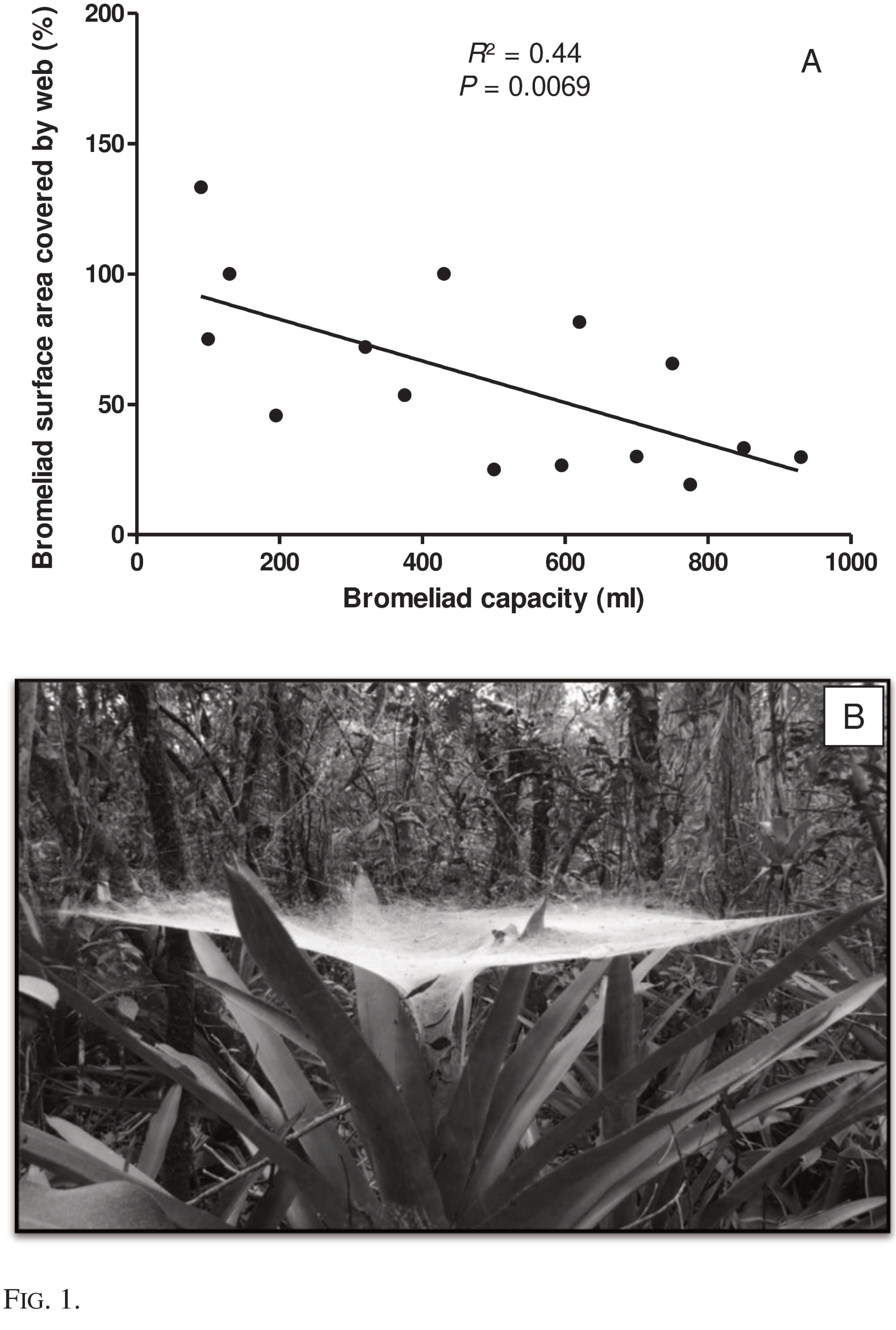

R^2 = 0.44
P = 0.0069
A
Bromeliad surface area covered by web (%)
200
150
100
50
0
0
200
400
600
800
1000
Bromeliad capacity (ml)
B

FIG. 1.

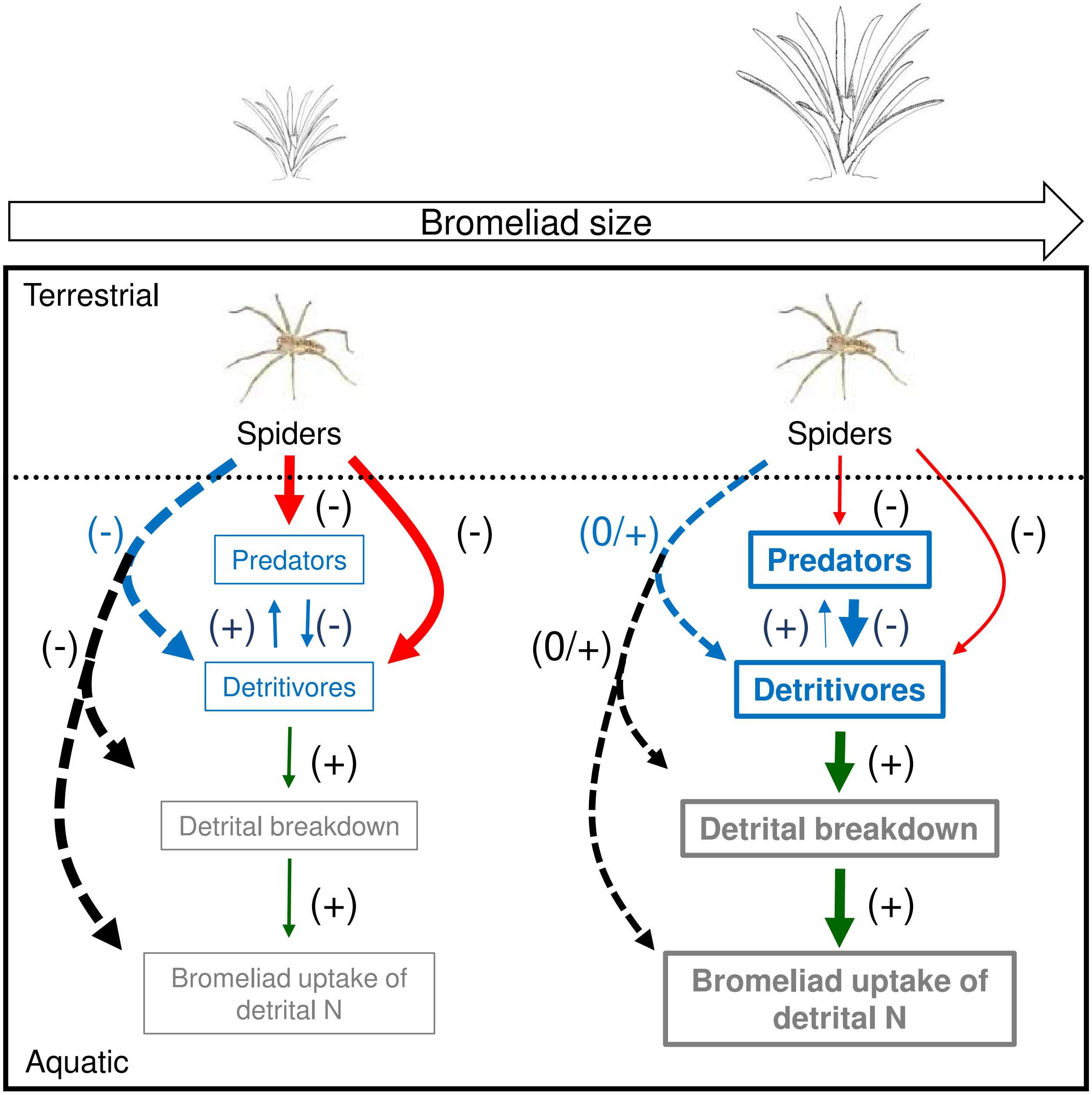
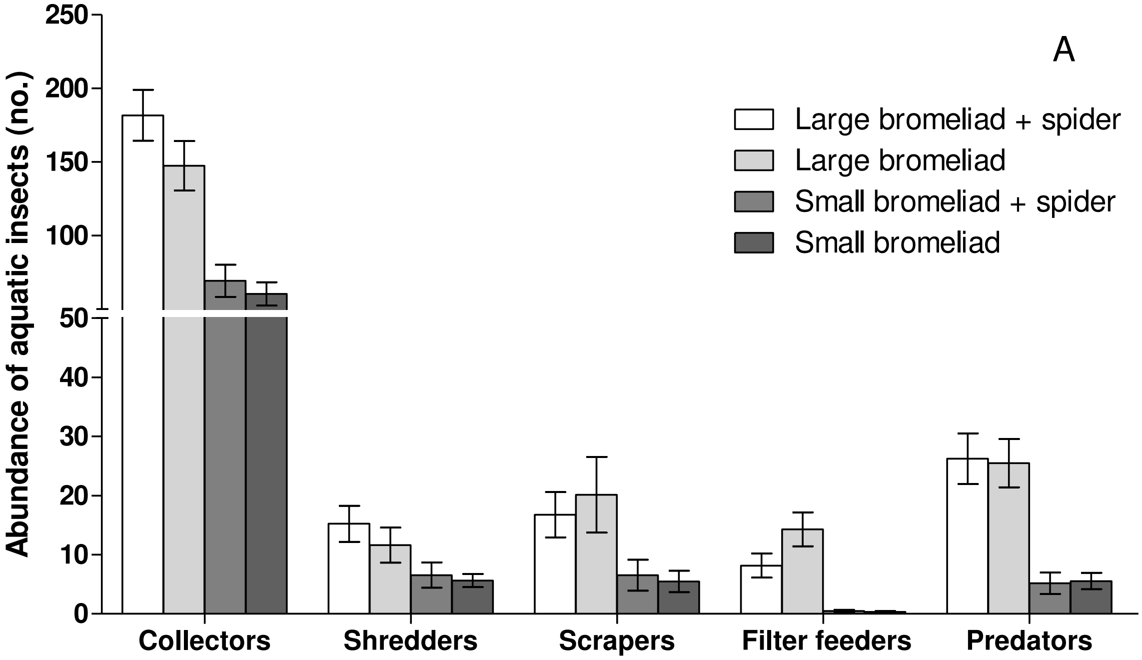

Bromeliad size
Terrestrial
Spiders
Spiders
(-)
(-)
(-)
Predators
(+)
(-)
Detritivores
(-)
(+)
Detrital breakdown
(+)
Bromeliad uptake of detrital N
(0/+)
(-)
(-)
Predators
(+)
(-)
(0/+)
Detritivores
(+)
Detrital breakdown
(+)
Bromeliad uptake of detrital N
Aquatic

FIG. 2.


A
Large bromeliad + spider
Large bromeliad
Small bromeliad + spider
Small bromeliad
Abundance of aquatic insects (no.)
250
200
150
100
50
40
30
20
10
0
Collectors
Shredders
Scrapers
Filter feeders
Predators

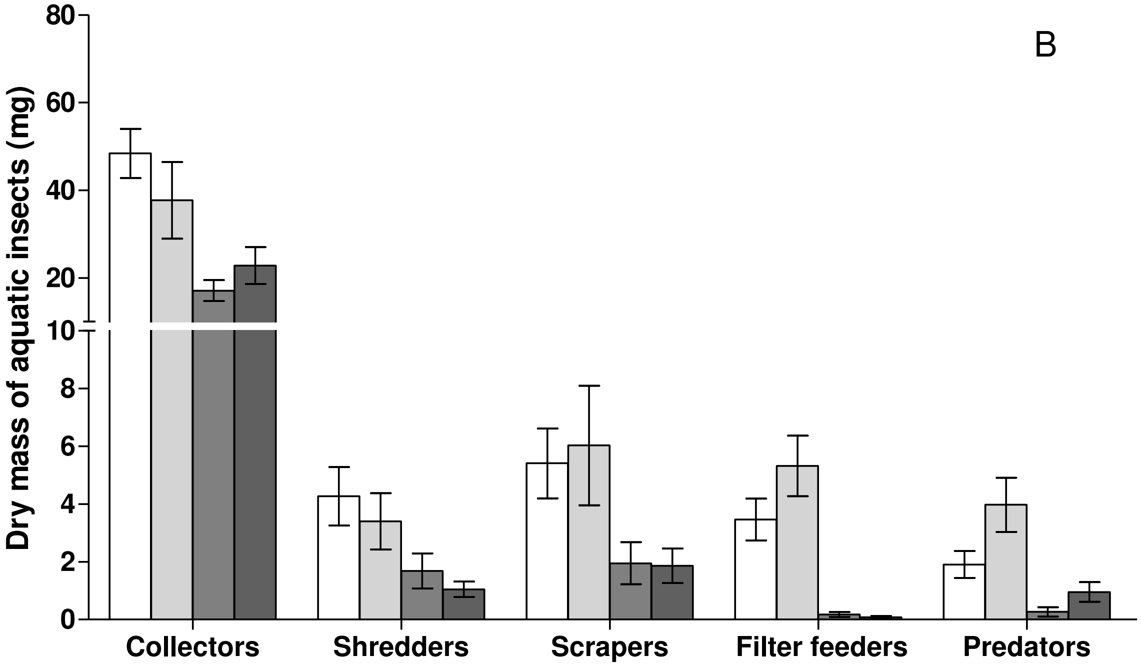

B
Dry mass of aquatic insects (mg)
80
60
40
20
10
8
6
4
2
0
Collectors
Shredders
Scrapers
Filter feeders
Predators

FIG. 3.

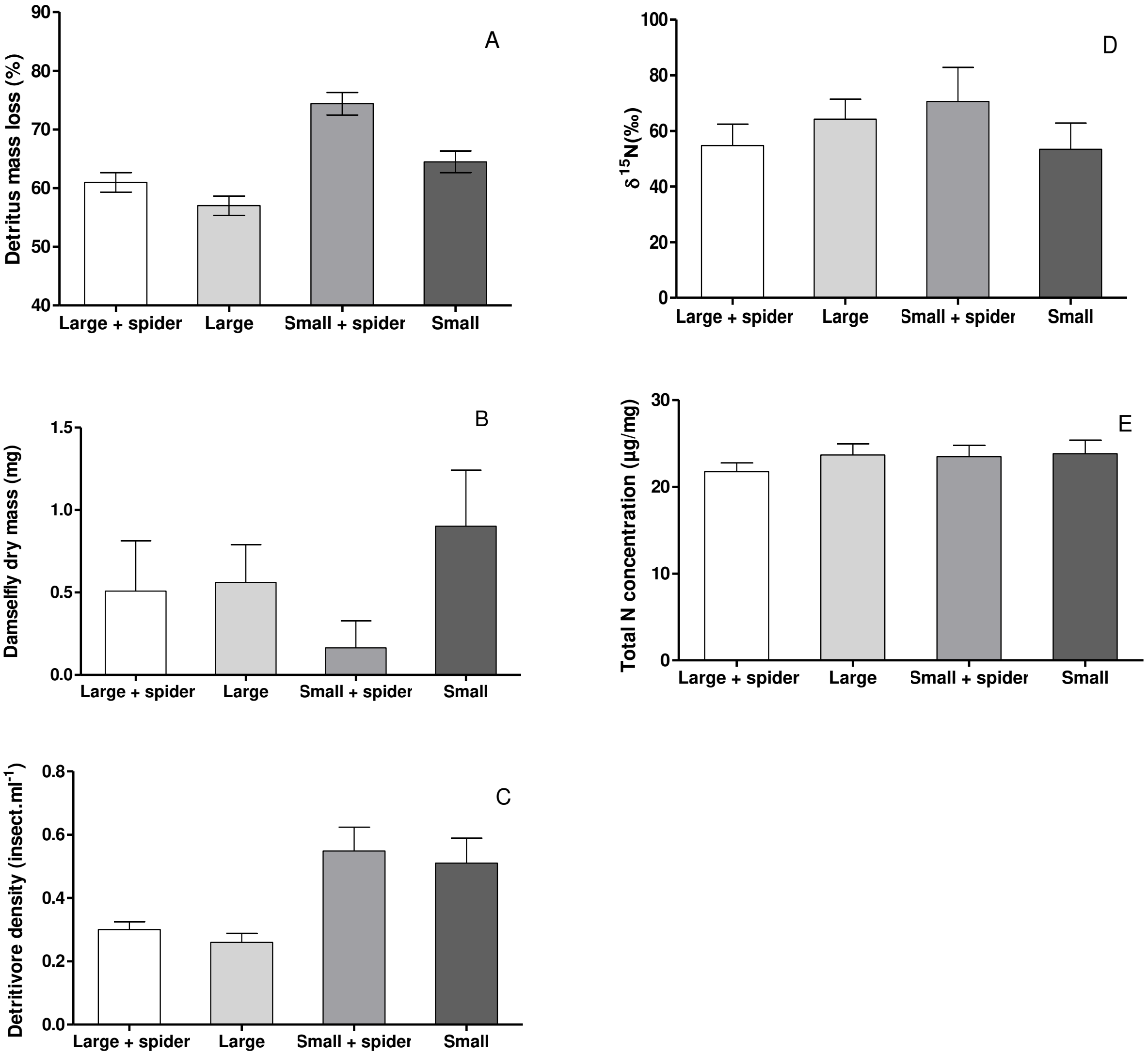
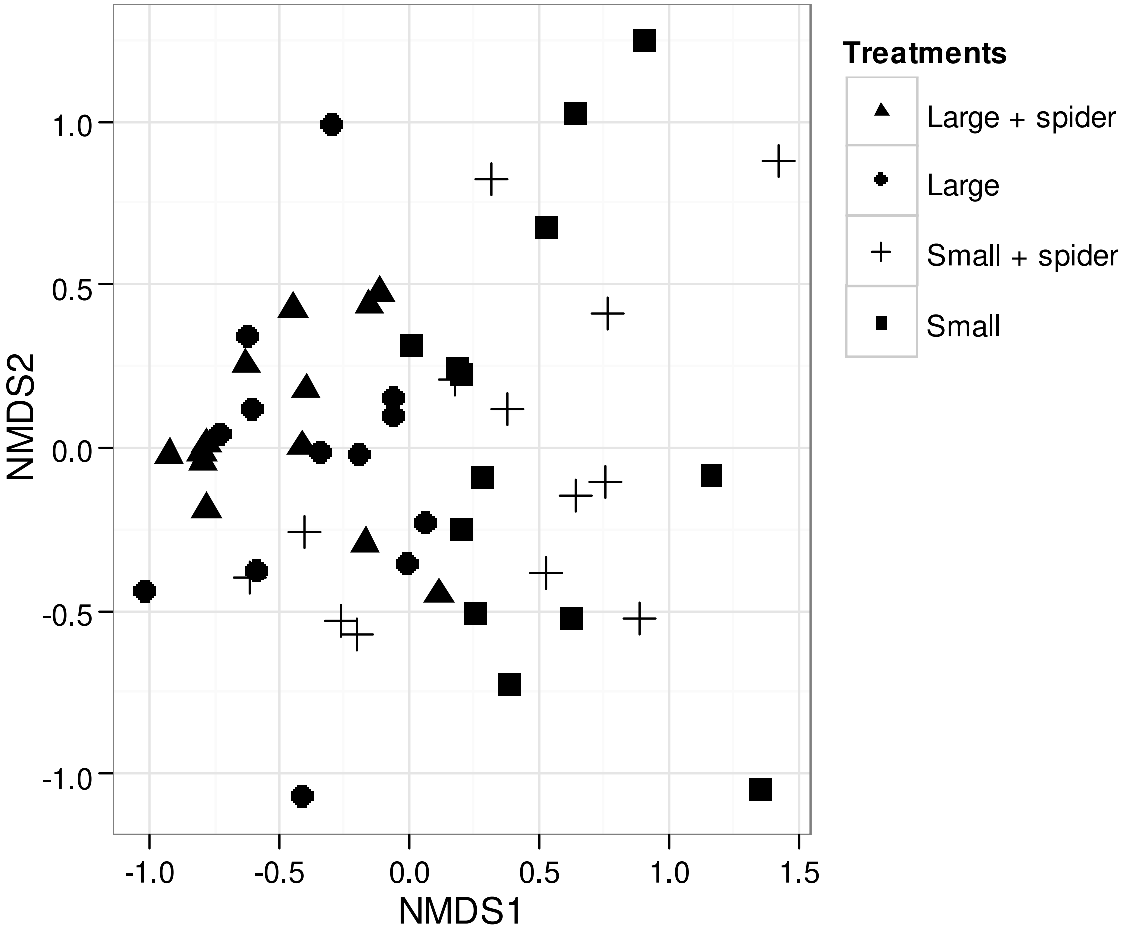

A
Detritus mass loss (%)
90
80
70
60
50
40
Large + spider
Large
Small + spider
Small
D
$\delta^{15}N$(‰)
100
80
60
40
20
0
Large + spider
Large
Small + spider
Small
B
Damselfly dry mass (mg)
1.5
1.0
0.5
0.0
Large + spider
Large
Small + spider
Small
E
Total N concentration (µg/mg)
30
20
10
0
Large + spider
Large
Small + spider
Small
C
Detritivore density (insect.ml^{-1})
0.8
0.6
0.4
0.2
0.0
Large + spider
Large
Small + spider
Small

FIG. 4.

Appendix 1. Understory of the closed restinga forest with an experimental block (white wall) (A) and experimental block containing the four treatments (B). Photo credits: P. M. Omena.



APPENDIX 2. Graphic of nonmetric multidimensional scaling (NMDS) showing variation in species composition among four treatments, large bromeliads - spider absent (Large), large bromeliads – spider present (Large + spider), small bromeliads – spider absent (Small), small bromeliad – spider present (Small + spider).

CAPÍTULO II

CONSUMPTIVE EFFECTS OF TOP PREDATORS DETERMINE INVERTED TROPHIC PYRAMIDS IN BROMELIAD FOOD WEBS

Consumptive effects of top predators determine inverted trophic pyramids in bromeliad food webs

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Abstract. Several mechanisms have been hypothesized to account for the observed variation in shape of biomass pyramids, from bottom to top-heavy pyramids. The "exploitation ecosystems" hypothesis predicts that increases in basal productivity in tri-trophic systems result in increases in biomass of the first and third trophic levels, which would result in a progressive inversion of pyramids across a productivity gradient. Other hypothesis takes into account the extent in which the turnover rate of trophic levels varies among ecosystems. Such hypotheses have been all based on consumptive trophic links between predators and their prey. The relative contribution of non-consumptive effects as a mechanism that shapes ecological pyramids is still unknown. In this study, by using insect communities hosted by tank bromeliads we tested whether the shape of biomass pyramids varies across a gradient of productivity and if the shape of pyramids is affected by consumptive and non-consumptive effects of predators. To determine the shape of biomass pyramids along a gradient of productivity, we surveyed the aquatic community hosted by bromeliads. To test for the effects of predators, we ran a manipulative experiment in a randomized block design including three treatments: (i) bromeliads with the presence of damselfly larvae (uncaged), (ii) bromeliads with predation risk (i.e., cues released by caged damselfly larvae) and (iii) bromeliads in the absence of damselfly. There was a progressive inversion of biomass pyramid over a production gradient (inferred via bromeliad size) as predicted by the "exploitation ecosystems" hypothesis. Direct consumptive effect of predators mediated the inversion of trophic pyramids; biomass pyramids from food webs in the absence of direct consumptive effect of predators became bottom-heavy shaped. The high abundance and biomass of top-predators in natural bromeliads can be explained by the rapid turnover of prey, such as mosquito larvae (Culicidae), which have a very short life cycle. We suggest that the underlying generation length mechanism that produces inverted trophic pyramids in oceans can be extrapolated to other ecosystems, as to the aquatic fauna inhabiting bromeliads.

Keywords: biomass pyramid, top-heavy pyramids, trophic structure, predator prey ratio, experimental microcosm, bromeliad, environmental gradient, macroinvertebrate.

INTRODUCTION

Understanding the processes that govern community structure is one of the fundamental goals in ecology. Communities are frequently represented as a trophically-stratified pyramid of biomass, which conveys rich information about the underlying mechanisms that drive community structure (Elton 1927, Wang et al. 2009, Trebilco et al. 2013). Such biomass pyramids not only encode the structure of food webs, but also integrate functional characteristics of communities, such as the pattern of energy flow, transfer efficiency and turnover rates of different compartments of the food web (Odum 1971, Giorgio et al. 1999). Elton (1927) was the first to suggest that trophic biomass pyramids should be bottom-heavy, meaning that the biomass of each consumer trophic level is less than that of the trophic level immediately below, its resource. Currently it is recognized that there is substantial variation in the shape of ecological pyramids ranging from bottom-heavy, to columns, to top-heavy or inverted pyramids (Holligan et al. 1984, Friedlander and DeMartini 2002, Moustaka-Gouni et al. 2006, Trebilco et al. 2013). It has been proposed that this variation in pyramid shape occurs because of variation in the relative rates by which biomass and energy move between trophic groups (Brown et al. 2004, Sandin et al. 2008). However, there are some controversies regarding the existence of inverted trophic pyramids (Trebilco et al. 2013). Thus, despite decades of quantification of ecological pyramids, there is still no general consensus on the mechanisms that determine their shape.

Several mechanisms have been hypothesized to account for the observed variation in the shape of pyramids. The first hypothesis takes into account the extent in which the relationship between productivity:biomass ratio (i.e., turnover rate) and trophic levels varies among ecosystems (Odum 1971, Buck et al. 1996, Gasol et al. 1997, Brown et al. 2004). When turnover rate is constant amongst trophic levels, a bottom-heavy pyramid results. The inversion of the pyramids occurs when turnover rate declines as trophic rank increases. For example, the base of a plant-miner-parasitoids food web comprise slow growing vascular plants, of little turnover (bottom-heavy pyramid); whereas marine planktonic food webs typically have small, fast growing phytoplankton at the base with high turnover (top-heavy pyramid). The first hypothesis can also be explained by the relationship between quality: edibility of the organisms from different trophic levels (Shurin et al. 2006). Phytoplankton have carbon: nutrient ratios closer to animals than do vascular plants, and so transfer efficiencies are higher in this first plant to animal trophic step (Elser et al. 2000). By contrast, the remaining two hypotheses deny the existence of inverted pyramids, instead arguing that they are sampling artefacts (Trebilco et al. 2013). The second hypothesis assumes that top-heavy pyramids are an artefact of assuming an open system to be closed. The authors suggest that predators may subsidise their diet by consuming items not in the pyramid (faulty identification of pyramid components) or parts of other pyramids (e.g., by foraging over a larger spatial area than used to construct the biomass pyramid). The third hypothesis relates to the spatial distribution of predators. In some habitats, predators spatially aggregate on resources more than their prey do, so that pyramids constructed at too small a spatial scale will overestimate the density of predators (Trebilco et al. 2013).

The published hypotheses that we have just described have been all based on consumptive trophic links between predators and their prey. However, non-consumptive effects of predators are known to be pervasive and surprisingly strong (Schmitz et al. 1997, 2004, Schmitz 1998, Werner and Peacor 2003). These effects can change the trophic structure of communities through a variety of mechanisms including changes in the behavioral traits of feeding, motility and habitat selection of prey (Schmitz 2008, Roberts and Liebgold 2008, Vonesh et al. 2009). Non-consumptive effects of predators, like consumptive effects, reduce the biomass of a lower trophic level in a certain locality. However, the non-consumptive effect of predators reduces the amount of energy flowing to organisms in higher trophic levels, which will tend to make biomass pyramids even more bottom-heavy in shape. We therefore suggest a fourth hypothesis that food webs dominated by non-consumptive effects will tend to have extremely bottom-heavy pyramids.

Biomass pyramids may change shape predictably along environmental gradients. One of the best known hypotheses is the "exploitation ecosystems" hypothesis, whereby increases in basal productivity in tri-trophic systems result in increases in biomass of the first and third trophic levels in the absence of increases in the second trophic level (Oksanen et al. 1981). Although productivity of all trophic levels increases across the productivity gradient, increased productivity in the second trophic level is exactly offset by strong top-down consumption by top predators. For example, as net primary production increases between northern forests, wolf density increases in the absence of a similar increase in their cervid prey base (Ripple and Beschta 2012a), which would result in a progressively greater predator prey mass ratio (PPMR) across this productivity gradient. PPMRs, calculated as the ratio of total predator biomass to total prey biomass, are commonly used to quantify the shape of biomass pyramids, with PPMR<1 signifying a bottom-heavy pyramid, and PPMR > 1 signifying an inverted or top-heavy pyramid.

Many aquatic communities subsidized by allochthonous resources (e.g., detritus), such as stream headwaters and phytotelmata, are ideally suited to studies of trophic pyramids, productivity gradients and non-consumptive effects. These systems often have clear trophic divisions between detritivores and their predators (Thompson et al. 2007), and easily quantifiable gradients of detrital concentration or algal productivity. Furthermore, their food webs are mainly composed of organisms with cross-ecosystem life cycles whereby organisms change ecosystems between two ontogenetic life stages, such as a shift from aquatic juvenile stages to terrestrial adult stages in many insects and frogs (Wilbur 1980, Werner and Gilliam 1984, Schreiber and Rudolf 2008). The communities formed by such organisms may be particularly suitable systems to investigate the consumptive and non-consumptive effects of predators on the trophic structure of communities. The adult females select habitats prior to depositing their gametes, fertilized eggs or offspring, and if females can detect predators prior to such deposition, they may simply avoid locations with predators (Vonesh et al. 2009). Such non-consumptive effects of predators could reduce the density of prey in recipient habitats without increasing energy flow to predators.

Tank bromeliads can impound water, leaf litter and other organic detritus between their leaves and host aquatic macroinvertebrate communities dominated by larval insects (Kitching 2004). The detritus present in the tank constitutes a main source of nutrients for the aquatic food web (Benzing 2000), although bromeliads in full sunlight can also contain substantial algae (Brouard et al. 2011, Marino et al. 2011). Communities inhabiting tank-bromeliads are an excellent system to study the shape of ecological biomass pyramids, as they contain animals of several trophic levels that can be fully sampled. Through the experimental manipulation of bromeliads and their contained fauna, we can easily reduce the five hypotheses regarding the variation in the shape of pyramids to two hypotheses. In bromeliads, we can discard the two sampling artefact hypotheses. The top-predators, damselfly larvae, have no other prey than the aquatic invertebrates within their bromeliad as they are constrained to the water within bromeliads throughout their larval stage. Nor can there be a hidden prey subsidy: not enough terrestrial carcasses fall into bromeliads to be considered a subsidy, and the damselfly does not forage outside bromeliads. Since we have a full census of a contained system, our sampling efficiency or scale cannot be biased between trophic levels. Thus any variation in the shape of biomass pyramids in bromeliads must represent either change in how turnover rates scale with trophic rank or differences in the relative importance of direct consumptive versus non-consumptive effects of predators. Specifically, we asked the following questions: What is the shape of the invertebrate biomass pyramids within bromeliads? How does the shape of biomass pyramids vary across potential gradients in productivity? Does the shape of the biomass pyramids change if we experimentally remove direct consumptive effects of predators?

MATERIAL AND METHODS

Study site and organisms

We conducted this research in open restinga forest (i.e. coastal sand substrate) at the Parque Estadual da Ilha do Cardoso, located in the Atlantic Forest, São Paulo State, Brazil (25° 03’ S, 48° 53’ W). The open restinga forest consists of a sun-exposed area bearing shrub vegetation 1 – 4 m high, with patches of plants containing a mix of shrubs, liana and bromeliads. The bromeliad *Quesnelia arvensis* is the most abundant plant occurring in these patches (Appendix 1). The aquatic fauna inhabiting these bromeliads is mainly composed of insect larvae and includes functional feeding groups from: (a) the apex trophic level, i.e., top-predators (especially *Leptagrion andromache* Hagen in Selys 1876, Odonata: Coenagrionidae) and (b) from more basal trophic levels, all of which are prey of the apex predators, such as small-bodied predators (especially Ceratopogonidae), filter feeders (entirely Diptera; Culicidae), collectors (especially Diptera: Chironomidae), scrapers (entirely Coleoptera: Scirtes) and shredders (especially Diptera: Limonidae).

(i) Shape of biomass pyramids from bromeliad food webs

The aim of this survey was to determine the shape of biomass pyramids in bromeliads, and relate their shape to potential gradients in productivity. To determine the shape of ecological biomass pyramids from bromeliad food webs, we surveyed the aquatic arthropod communities hosted by bromeliads at the opened restinga forest. We collected 37 bromeliads in a range of sizes (bromeliad capacity from 13 ml to 3425 ml). Each bromeliad was removed intact from its attachment point and placed immediately in a bucket. We estimated the maximum tank capacity of each plant, dissected each bromeliad by removing and washing each leaf separately in running water over large buckets, and then filtered this water through 125 and 850 µm soil sieves. We recorded the morphospecies and abundance of all aquatic invertebrates visible to the naked eye (i.e., body size larger than 0.5 mm) present in these two size fractions of the material. We then determined the functional group of each taxon using previous accounts in the literature (Merritt and Cummings 1996) and by feeding trials. To estimate invertebrate biomass, we used previously constructed allometric equations between body length and dry mass, or mean of dry mass for very small insects (D. S. S., P. M. O., unpublished data). Recent analysis of the stable isotope signature of bromeliad invertebrates from this open restinga has revealed that, on average, bromeliad invertebrates obtain ¾ of their carbon from algal sources and ¼ from detrital sources (V. F., A. G., D. S. S. and others, unpublished data). Although we did not measure chlorophyll-a concentrations in our bromeliad, it has been shown in another Brazilian open restinga that bromeliad capacity is the best predictor of chlorophyll-a concentrations (Marino et al. 2011). We therefore approximated the algal productivity gradient as bromeliad capacity. We quantified detrital productivity by detrital concentration (dry g detritus/ml capacity).

(ii) Consumptive versus non-consumptive effects of predators

To determine whether the shape of biomass pyramids results from consumptive effect and/or non-consumptive effect of damselfly larvae predators we ran a manipulative experiment in a randomized block design including three treatments: (i) bromeliads with uncaged damselfly larvae, (ii) bromeliads with just the risk of damselfly predation (i.e., cues released by caged damselfly larvae) and (iii) bromeliads without any damselflies, caged or uncaged (Appendix 1). The first treatment permits both consumptive and non-consumptive effects, whereas the second just permits non-consumptive effects. Thus the effect of direct consumption can be isolated by the comparison of (i) from the other two treatments, whereas the effect of non-consumptive effects can be determined by comparing (ii) and (iii).

To set up the experiment, we collected 27 bromeliads (tank capacity 300 – 500 ml) from the restinga in February 2012. There were no significant differences in plant size among treatments and blocks (ANOVA: treatment $F_{2,23} = 0.276$, $P = 0.761$; block $F_{1,23} = 0.459$, $P = 0.505$). Each bromeliad was inverted and washed thoroughly with spring water to remove detritus and organisms. To capture or kill any residual invertebrate we suspended the bromeliads upside down from a line for five days. We kept the roots of bromeliads moist and inspected the tanks every day using a flashlight to remove remnant insect larvae. We planted the bromeliads in the sandy substrate of the restinga in nine blocks of three bromeliads. Each experimental block was 5 – 20 m from its nearest neighbor, and 0.3 – 0.5 m separated the plants within each block.

We randomly assigned the three predator treatments to the bromeliads. For each treatment containing damselflies (i.e., caged or uncaged) we used three late instar damselfly larvae (*L. andromache*, 12 – 15 mm body length). We predicted the number of damselflies to use in each bromeliad by a previously established relationship between bromeliad capacity and damselfly abundance (abundance = 0.0027*capacity in ml + 2.7807, n = 15, $R^2 = 0.26$). The predator cages consisted of a 50 ml centrifuge tube with two 15 mm radius holes drilled in the sides of the tubes and then covered with 80 µm mesh. The mesh allowed water flow from the tubes through the rest of the plant, allowing diffusion of predator chemical cues. Two cages were inserted in wells formed by lateral leaves and one cage was placed in the central well of the bromeliad. For the caged damselfly treatment, we placed one individual damselfly in each tube; the other experimental bromeliads (with uncaged or no damselflies) received three empty tubes each. The experiment lasted three weeks with daily monitoring of bromeliads to ensure that caged damselflies were still alive, with replacement when necessary. During these three weeks, the insect community accumulated through natural colonization. At the end of the experiment, we dissected each bromeliad and sorted the arthropods following the methods described earlier.

Statistical analyses

(i) Shape of biomass pyramids from bromeliad food webs

To determine the shape of biomass pyramids from bromeliads food webs we calculated the average mass of predators at trophic level n divided by the average mass of their prey at trophic level n – 1 for each bromeliad (i.e., Predator Prey Mass Ratio or PPMR). We compared the number of food webs having PPMR > 1 (top-heavy pyramids) and the number of food webs with PPMR < 1 (bottom-heavy pyramids) using a Chi-squared test. We then used general linear models to determine whether bromeliad capacity (ml) and detritus density (g/ml) explained variation in PPMR. We also used multiple regressions to determine how the dry mass of the feeding groups (i.e., top predators, intermediary predators, detritivores and filter feeders) varies along gradients of bromeliad size and detritus concentration. When necessary, variables were log-transformed to fit a normal distribution.

(ii) Consumptive versus non-consumptive effect of predators

Differences in community composition were analysed using permutational multivariate analysis of variance PERMANOVA (Anderson et al. 2008) based on Bray-Curtis dissimilarities performed in PRIMER 6 Version 6.1.13 and PERMANOVA + Version 1.0.3 (PRIMER-E Ltd., Plymouth, UK) (Clarke and Gorley 2006, Anderson et al. 2008). Nonmetric multidimensional analysis (NMDS) was performed to visualize similarities or dissimilarities among our three treatments. To test for differences among the treatments for all remaining parameters (dry mass and abundance of filter feeders, detritivores and predators) we used linear mixed effect model (LME). For data with heterogeneous distribution of residuals, we allowed variance of each factor to differ, using the "varident" function within the "nlme" package of R (Zuur et al. 2009). We performed orthogonal contrasts to demonstrate the consumptive effect of predators (uncaged predator versus caged predator + predator absent treatments). In the second contrast, we tested for the effect of non-consumptive effect (uncaged predator versus predator absent treatments). To perform the contrasts we used the function "glht" (generalized linear hypothesis test) within the "multcomp" package (Hothorn et al. 2008). We also used bootstrap methods to quantify the contribution of trait-mediated effects to total predator effects independently, for the parameters with significant caged predator effect. We randomly sampled, with replacement, the number of replicates within each treatment and calculated a mean. We then calculated the difference between the caged predator mean and the no predator mean (trait-mediated effect), and the difference between the free predator mean and the no predator mean (total predator effect). Dividing the trait-mediated effect by the total predator effect then gave us the percent contribution of the trait-mediated effect. To generate a distribution, this method was repeated 10000 times for each parameter (methods described in Hamill et. al. unpublished data).

RESULTS

(i) Shape of biomass pyramids from bromeliad food webs

The majority of the biomass pyramids from bromeliad food webs had an inverted or top-heavy shape (PPMR > 1; $\chi 2 = 14.29$, $gl = 1$, $P = 0.0001$). The predator prey mass ratio varied positively with the increase in bromeliad capacity (GLM: $Z = 3.45$, $P = 0.0005$) (Fig. 1A). By contrast, there was a negative relationship between the increase in PPMR and the increase in detritus density (GML: $Z = - 2.16$, $P = 0.03$) (Fig. 1B). Detritus density was itself unrelated to changes in bromeliad capacity ($F_{1,35} = 1.88$, $P = 0.17$, $R^2 = 0.17$). These patterns in PPMR can be decomposed into differential responses of different parts of the food web to bromeliad variables. The biomass of the top predator (damselfly larvae) increased positively with bromeliad capacity but had no relationship with detritus density (Table 1, Fig. 2A and 2B). The biomass of the arthropods from all the other feeding groups did not change with variation in bromeliad capacity and detritus density (Table 1, Fig. 2A and 2B).

(ii) Consumptive versus non-consumptive effect of predators

Predators significantly altered the structure of the aquatic invertebrate community in bromeliads (PERMANOVA: $F_{2,26} = 1.91$, $P = 0.003$). Specifically, invertebrate communities in bromeliads with uncaged predators differed from those in bromeliads with no predators (PAIRWISE test uncaged vs control: $t_{2,24} = 1.85$, $P = 0.001$, NMDS plot, Fig. 3). Invertebrate communities in the presence of caged predators were intermediate to – and not different from – those in the presence of uncaged damselflies or without damselflies (uncaged vs caged: $t_{2,24} = 1.14$, $P = 0.26$, caged vs control: $t_{2,24} = 0.99$, $P = 0.45$, Fig. 3). Uncaged damselflies reduced the abundance and biomass of all arthropod groups (Fig. 4). The majority of predator effects were related to the direct consumptive effect of damselfly on prey, especially on the mosquitoes (*Wyeomyia* sp. and *Culex* (Mcx) spp.) and detritivores (including collectors, scrapers and shredders; Table 1, Fig. 3). The biomass of filter feeders (composed entirely of mosquitoes) was 12 times higher in control and in bromeliads with caged damselfly than in bromeliads with uncaged damselfly. The non-consumptive effect of predators on insect colonization was restricted to the group of small body-sized predators (Ceratopogonidae), accounting for 85.18% (95% CI = 50% - 98.66%) of the net predator effect on Ceratopogonidae abundance (Table 2, Fig. 3). Biomass pyramids of food webs from bromeliads in the absence of direct effect of predators (control and caged predator treatments) presented bottom-heavy shape pyramids (Fig. 5).

DISCUSSION

The results from this study support the real existence of inverted pyramids in natural ecosystems. The majority of the aquatic communities within bromeliads showed a pattern whereby the basal trophic group represented less of the community biomass than the apex trophic level. Overall, differences in the shape of biomass pyramid were strongly associated to variation in bromeliad size (a correlate of algal productivity) and negatively related to detrital concentration. Moreover, we experimentally demonstrated that predators have strong consumptive effects on the structure of communities, reducing the abundance and biomass of insects from all feeding groups. We suggest that the consumptive effect of predators, coupled with differences in the turnover rates of different trophic levels, is strong enough to mediate the inversion of biomass pyramid from bromeliad food-webs. Non-consumptive effects were unimportant as a mechanism in shaping trophic pyramid, reducing only the density of intermediary predators. We now discuss each of the main results.

Habitat correlates of biomass pyramid structure

Previous studies of tank bromeliads have shown that both biotic and abiotic factors play an important role in the structure of the contained macroinvertebrate communities (Armbruster et al. 2002, Srivastava 2006, Srivastava et al. 2008, Romero & Srivastava 2010, Dézerald et al. 2013). Aquatic invertebrates in bromeliads are reported to be affected by the availability of detritus resources, differences in understory light environments (energy available for algal production), habitat size and predation (Marino et al. 2011, Dézerald et al. 2013). In this study, biomass pyramids changed in shape from bottom-heavy to top-heavy over a gradient in bromeliad size. Since bromeliad size is a good proxy for algal productivity (Marino et al. 2011) and since insects in this open restinga bromeliad obtain most of their carbon from algae (V. Farjalla, A. Gonzalez, D. Srivastava and others, unpubl. stable isotope results), our data is consistent with a progressive inversion of the biomass pyramid over a productivity gradient as predicted by the "exploitation ecosystems" hypothesis (Fretwell 1977, Oksanen et al. 1981). This shift in pyramid structure reflected an increase in top predator biomass with bromeliad size in the absence of a similar shift in prey functional groups, consistent with strong top-down control of consumers by predators in a tri-trophic food web (Fretwell 1977, Oksanen et al. 1981). Few other studies have attempted to analyse the exploitation ecosystems hypothesis (Crête 1999, Ripple and Beschta 2012b). However, we can not discount the possibility that bromeliad size affected pyramid inversion through other mechanisms. For example, if odonates are more affected by desiccation risk than their prey, and since small bromeliads have greater desiccation risk, an increase in the PPMR with bromeliad size would also be expected if the top trophic level is more limited by disturbance than by energy.

The shape of trophic pyramids was also more top-heavy at low detrital concentrations. At first glance, this result may seem at odds with our earlier result that pyramid inversion increases with algal productivity. However, in sun-exposed bromeliads, unlike forest bromeliads, algae may be a more important energy source than detritus (Dézerald et al. 2013). Detritus may instead be important as a source of environmental heterogeneity (McIntosh et al. 2005). Studies from freshwater environments have shown that less pronounced top-down effects occur in detritus-based food webs when the cover provided by accumulated detritus and leaves makes invertebrates less vulnerable to fish predation (Reice 1991, Rosenfeld 2000). By contrast, strong effects of predatory fish on prey populations have been observed in autotrophic (algal-based) stream food-webs (e.g., Power 1990, Peckarsky et al. 2002). Therefore, we believe that the detrital-based shifts in predator efficiencies observed in stream ecosystems can occur for the highly visual damselfly larvae inhabiting tank bromeliads. Thus, we indirectly assume that detrital concentration can reduce predator detection rate of prey and consequently the transfer efficiency between trophic levels.

Potential causes of pyramid inversion

Our survey showed that the food web in sun-exposed bromeliads is characterized by inverted biomass pyramids. We now use our experimental manipulation to examine reasons why pyramid inversion might occur in this habitat. One explanation is that biomass turnover rates increase with trophic rank. This is possible if there is a large size difference between predators and their prey, so that one predator consumes lots of prey, if prey reproduces or colonizes very quickly or if there is a high rate of emigration. The latter two processes are likely in this system, as other studies have shown that insect prey like mosquitoes colonize and emerge from bromeliads much faster than damselflies (Romero and Srivastava 2010, Srivastava 2006). Our experiment supports the first process, strong consumptive effects of damselflies on their prey. Indeed, the experimental manipulation of predator's presence (consumptive versus non-consumptive effect) showed that the principal prey of damselfly are mosquitoes, organisms with a very short life cycle. The diet of mosquitoes comprises of fine particulate organic matter, microorganisms from the detrital microbial food web as well as algae (Addicott 1974, Cochran-Stafira and Ende 1998, Brouard et al. 2011). Thus, the small densities of coarse particulate organic matter from sun-exposed areas do not restrict the colonization of bromeliads by filter feeders. Damselflies reduced the biomass of filter feeders by 12-fold, when compared to bromeliads in the absence of predators (or caged predators), suggesting a productivity:biomass ratio of 12 over the three weeks of the experiment. By contrast, damselfly productivity during the experiment was entirely due to growth of the damselflies as no new damselflies colonized the bromeliads nor left the bromeliads. Although we did not quantify damselfly growth, it would have been much less than 2-fold, meaning that damselflies have a productivity:biomass ratio substantially lower than their prey. A decline in the productivity:biomass ratio as trophic level increases is one of the most common explanations for inverted pyramids (Odum 1971, Buck et al. 1996, Gasol et al. 1997, Brown et al. 2004).

The shape of biomass pyramids was unaffected by non-consumptive effects of predators. Although recent studies have emphasized the importance of the non-consumptive effects of predators on food webs (Schmitz et al 1997, 2004, Werner and Peacor 2003, Vonesh et al. 2009) our experiment found much that non-consumptive effects changed only the biomass of small-bodied predators, a very minor component of total predator biomass. By contrast, consumptive effects of predators strongly affected prey populations and community structure, reducing the richness, abundance and biomass of organisms from all trophic groups, including detritivores and small intermediary predators. Non-consumptive effects of damselflies on insect colonization were restricted to a single group of small predators (Ceratopogonidae – Diptera). Ceratopogonid larvae are themselves prey for damselflies, so this may be an attempt by ovipositing ceratopogonid females to avoid intraguild predation of their offspring. Alternatively, ovipositing ceratopogonids may avoid bromeliads with damselflies as they have less prey for ceratopogonid larvae.

By the full census of a contained system, we show that the existence of top-heavy pyramids in natural ecosystems is completely plausible. Furthermore, we experimentally demonstrated that the inversion of pyramids can be mediated by direct consumptive effect of dominant predator species. In fact, biomass pyramids from bromeliad food webs in the absence of direct consumptive effect of a dominant predator (i.e., control and caged damselfly treatments) became bottom-heavy in shape. We thus suggest that the inversion of biomass pyramids might be possible in consequence of the high turnover of prey (e.g., mosquitoes) and low turnover of top-predators (i.e., damselfly). Besides the strong top-down effect of predators on detritus-based food webs, our results provide evidences that the inversion of trophic pyramids occurs in a gradient of environmental conditions. First, there was a progressive inversion of biomass pyramid over a productivity gradient (inferred via bromeliad size) consistent with the “exploitation ecosystems” hypothesis. Second, the inversion of pyramids was negatively affected by the increase in detritus concentration, also a good proxy of habitat heterogeneity. We then suggest that further studies should investigate the possible effects of the physical structure of habitats on the structure of ecological pyramids.

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TABLE 1. Multiple regression analysis summarizing the main effects of bromeliad capacity (ml) and detritus density on the biomass of the aquatic arthropods from the functional feeding groups top-predators (damselfly larvae), small predators, detritivores and filter feeders. Degrees of freedom for all *F* ratios = 1,34.

	Volume (ml)		**Detritus density (g/ml)**		
***Biomass* (g/bromeliad)**	***F* ratio**	***P* value**	***F* value**	***P* value**	***Multiple r^2***
Top-predator	32.07	**< 0.0001**	0.0006	0.98	0.45
Small predator	0.11	0.73	1.50	0.22	- 0.01
Detritivore	0.75	0.39	0.72	0.39	- 0.01
Filter feeders	1.05	0.31	0.14	0.71	- 0.02

TABLE 2. Linear mixed effect models (LME) summarizing the main effects of top-predators (damselfly) on aquatic community. Contrasts to demonstrate the differences between: (a) uncaged predator (UP) and no predator (NP) treatments, and (b) caged predator (CP) and no predator (NP) treatments. Degrees of freedom for all *F* ratios = 1,16; significant effects (*P* < 0.05) are in bold case.

Response Variable	**LME**		**Contrasts**			
			UP *vs* NP +CP		**CP *vs* NP**	
	***F* ratio**	***P* value**	***Z* score**	***P* value**	***Z* score**	***P* value**
Abundance	18.27	**0.0001**	- 3.39	**0.004**	- 0.33	0.92
Richness	5.36	**0.016**	- 3.23	**0.002**	- 0.71	0.72
Abundance						
Filter feeders	6.72	**0.007**	- 2.81	**0.008**	0.08	0.99
Detritivores	9.84	**0.005**	- 4.4	**< 0.0001**	- 1.25	0.36
Small predators	4.76	**0.024**	- 2.85	**0.006**	-2.12	**0.04**
Dry Mass						
Filter feeders	10.29	**0.001**	- 4.47	**< 0.0001**	- 0.02	1
Detritivores	10.44	**0.001**	4.26	**< 0.0001**	1.17	0.42
Small predators	4.59	**0.026**	2.86	**0.007**	2.13	**0.04**

FIGURE LEGENDS

FIG. 1. Relationship between bromeliad capacity (volume ml) and biomass of top-predators (i.e., damselfly larvae), small predators, detritivores and filter feeders (A); relationship between detritus density (g/ml) and biomass of top-predators (i.e., damselfly larvae), small predators, detritivores and filter feeders (B).

FIG. 2. Relationship between Predator Prey Mass Ratio and bromeliad capacity (L) (A) and detritus density (g/L) (B). Dashed line cross $y = 1$, data points above the dashed line represent bromeliad food webs with inverted pyramid biomass (PPMR > 1); data points under the dashed line represent bromeliad food webs with bottom-heavy shape (PPMR < 1).

FIG. 3. NMDS plot illustrating similarities and differences among the communities hosted by the experimental bromeliads, treatments: control (gray ●), caged predator (black ▲) and uncaged predator (green ■). Each of the data points represents a single community. Stress value 0.17.

FIG. 4. Mean abundance (A) and dry mass (B) of the aquatic insect functional feeding groups. Error bars represent ± SE.

FIG. 5. Predator Prey Mass Ratio (PPMR) from the experimental bromeliads. Boxes above the dashed line represent bromeliad food webs with inverted pyramid biomass (PPMR > 1). Error bars represent ± SE.

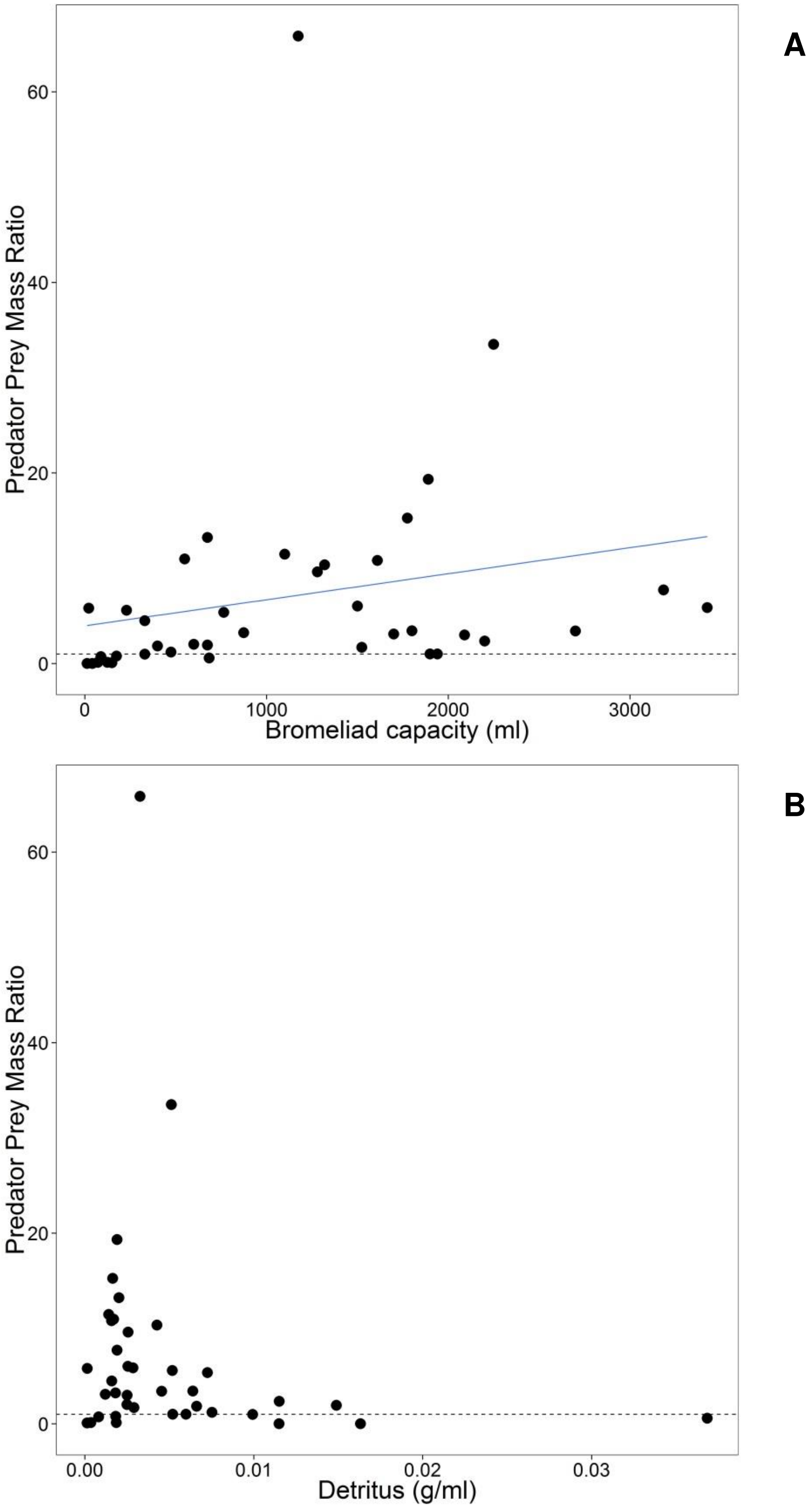
A
Predator Prey Mass Ratio
60
40
20
0
0
1000
2000
3000
Bromeliad capacity (ml)
B
Predator Prey Mass Ratio
60
40
20
0
0.00
0.01
0.02
0.03
Detritus (g/ml)

FIG. 1.

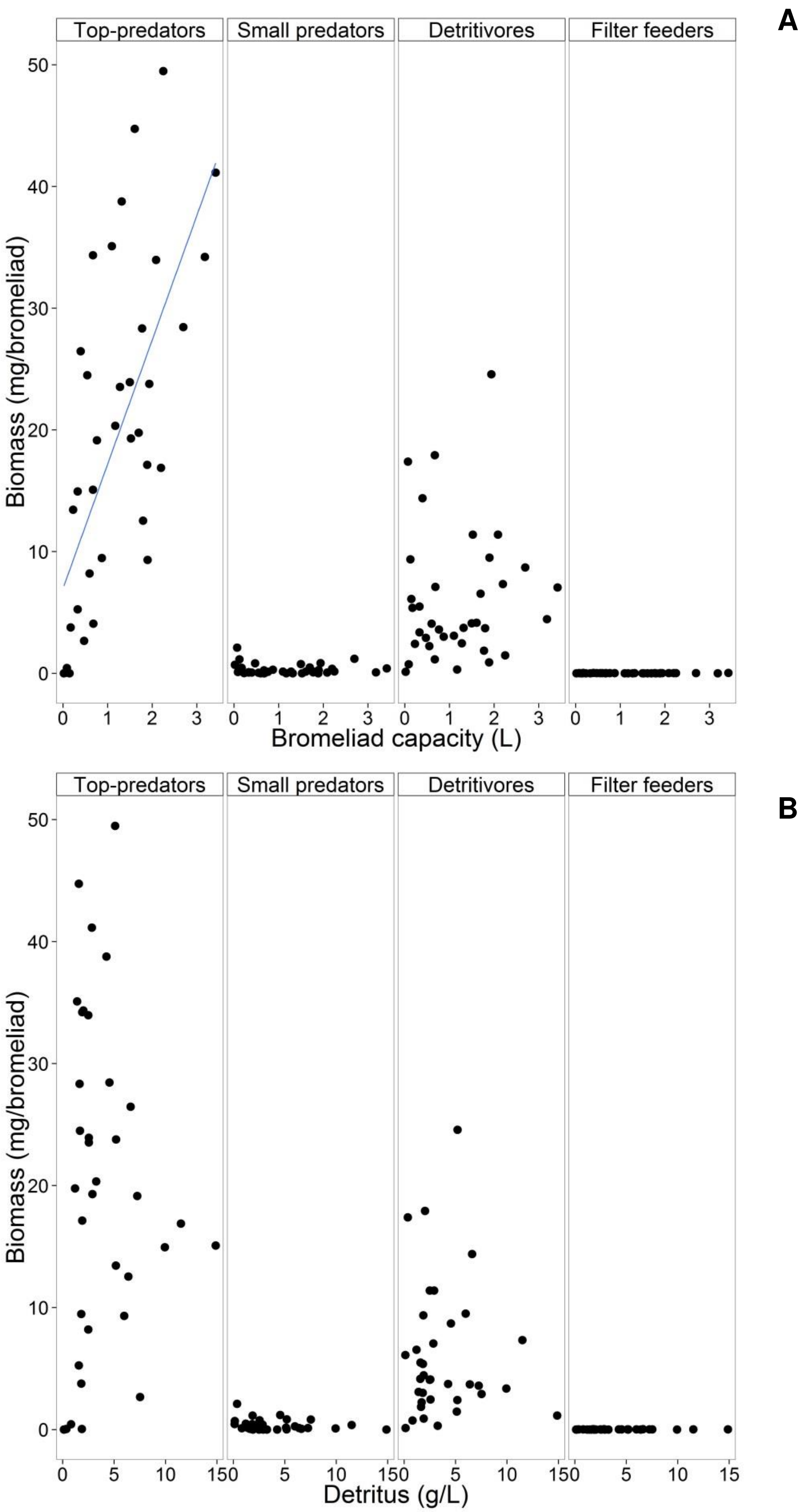
A
Top-predators
Small predators
Detritivores
Filter feeders
Biomass (mg/bromeliad)
0
10
20
30
40
50
0
1
2
3
Bromeliad capacity (L)
B
Top-predators
Small predators
Detritivores
Filter feeders
Biomass (mg/bromeliad)
0
10
20
30
40
50
0
5
10
15
Detritus (g/L)

FIG. 2.

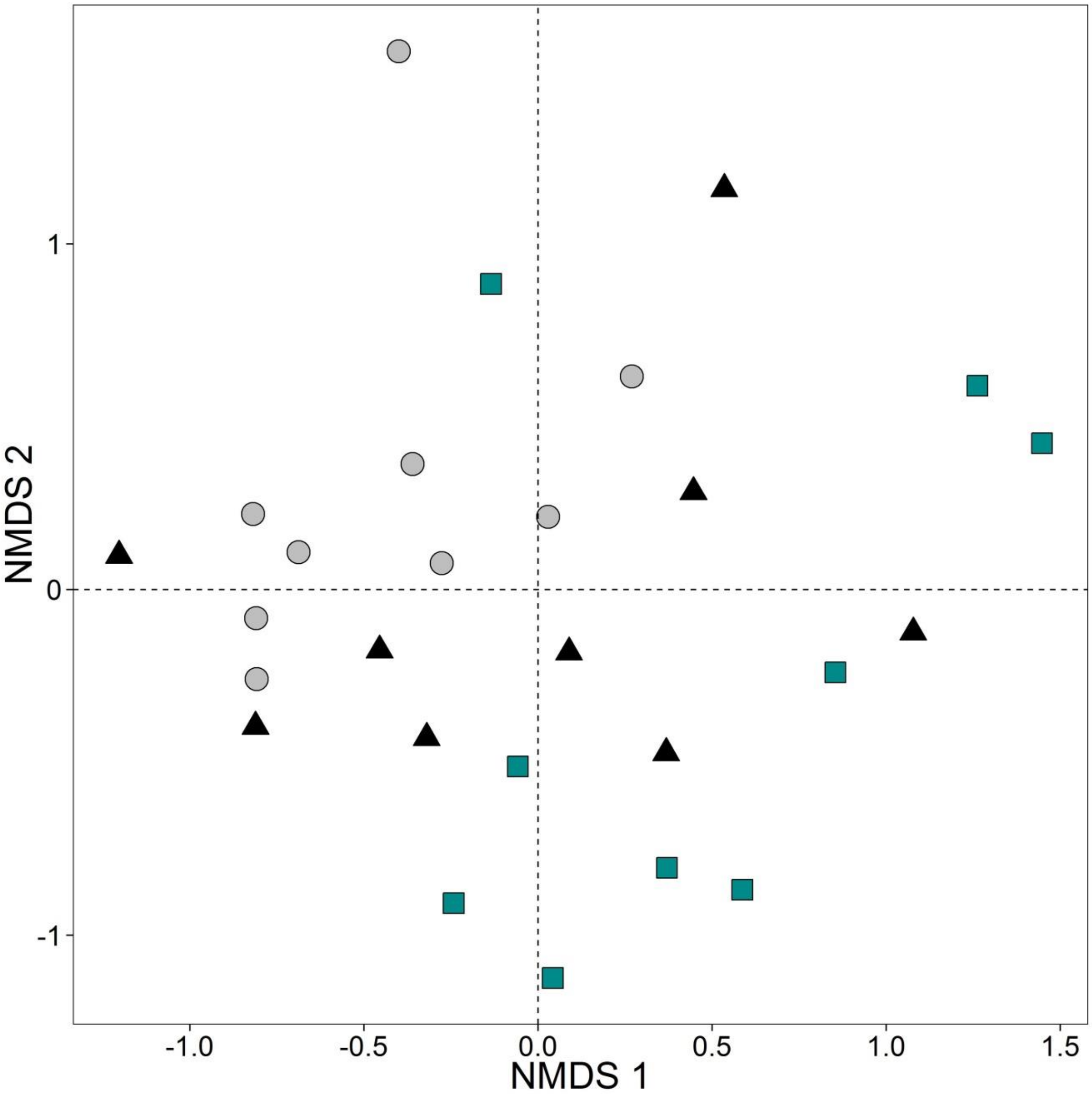

FIG. 3.

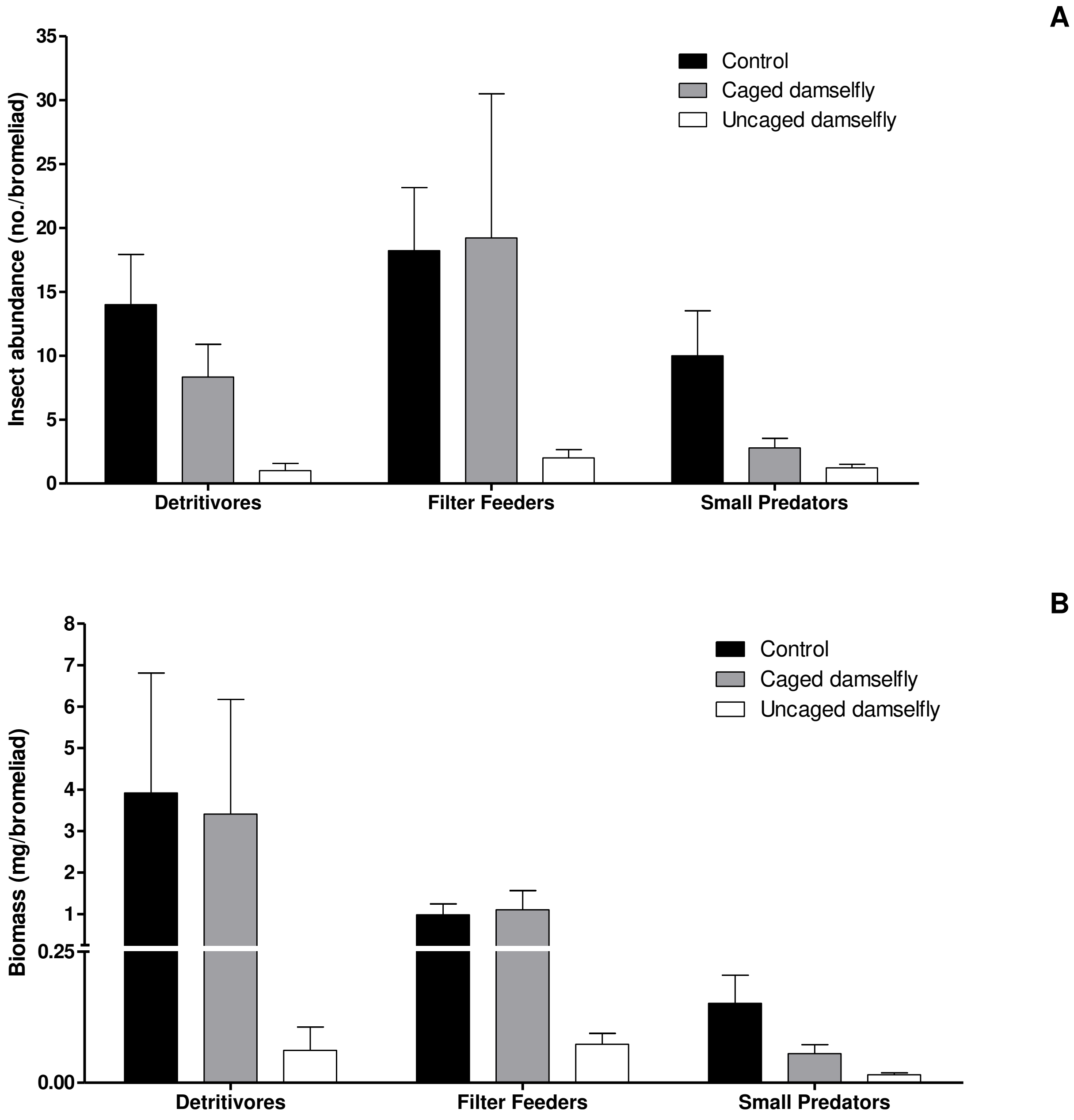
A
Insect abundance (no./bromeliad)
0
5
10
15
20
25
30
35
■ Control
▨ Caged damselfly
☐ Uncaged damselfly
Detritivores
Filter Feeders
Small Predators
B
Biomass (mg/bromeliad)
0.00
0.25
1
2
3
4
5
6
7
8
■ Control
▨ Caged damselfly
☐ Uncaged damselfly
Detritivores
Filter Feeders
Small Predators

FIG. 4.

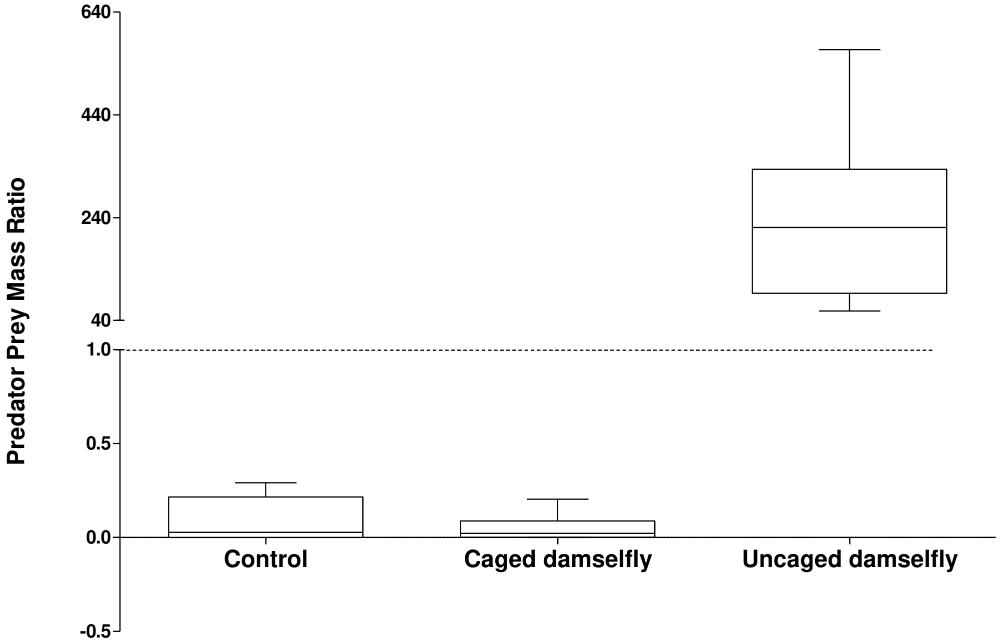
Predator Prey Mass Ratio
640
440
240
40
1.0
0.5
0.0
-0.5
Control
Caged damselfly
Uncaged damselfly

FIG. 5.

APPENDIX 1. Photos from the study system: opened restinga forest with a cluster of bromeliads and shrub vegetation of 1 – 4 m high (A) bromeliads from the experimental block design (B). Photo credits: P. M. Omena.

CAPÍTULO III

DISENTANGLING THE EFFECTS OF ENVIRONMENT AND DIVERSITY COMPONENTS ON ECOSYSTEM FUNCTIONING

Disentangling the role of environment and diversity components on ecosystem functioning

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Abstract. The effects of biodiversity on ecosystem functioning have emerged as a central issue in ecology. Several studies have demonstrated a positive relationship between biodiversity and ecosystem functioning (EF), though there is no general consensus on which component of biodiversity better predicts EF. Moreover, the better understanding on how biodiversity affects ecosystem functioning requires an integrative approach to assess how environment and species interactions (e.g., predator-prey) may affect the patterns of diversity in communities. In this study, by using insect communities hosted by tank bromeliads, we investigated the relative effect of environment and top-down forces on three components of detritivore diversity (i.e., phylogenetic - PD, functional - FD and taxonomic - TD). Furthermore, we tested for the relative effect of environment, predation and diversity on EF. We performed a randomized experiment in two extremes of an environmental gradient (nutrient-rich and nutrient-poor restinga). Bromeliads from the nutrient-rich restinga have high density of detritus and low biomass of predators, whereas bromeliads from nutrient-poor restinga have low density of detritus and high biomass of predators. We found that the effect of environment on detritivore diversity was restricted to FD; meanwhile predators had no effect on diversity. The different components of diversity were not equally good in predicting EF. Specifically, FD negatively affected detritus processing, TD had a positive effect on EF, whereas PD did not explain EF. The negative effect of FD is probably related to the distributions of dominant traits from each restinga. The communities from nutrient-rich restinga had small values of FD and high levels of detritus processing. This counterintuitive result can be explained by the dominant traits present in nutrient-rich restinga, which are related to processing of coarse particulate organic matter. To explain the positive effect of TD, we suggest that for communities with phylogenetic distant groups (e.g., aquatic macroinvertebrates) TD may integrate important evolutionary and functional information. Thus, for such communities, the positive relationship between EF-TD may occur because of the greater scope for mechanisms of complementarity and facilitation to be expressed. Our results also demonstrated that the environment can be a better predictor of ecosystem functioning than measures of biodiversity. These results indicate that abiotic factors can integrate important information related to EF that biotic factors cannot. Thus, we believe that studies that do not consider how environmental gradients affect community assembly (species, traits, lineages) have a limited predictive power for understand how different biodiversity components influence ecosystem functioning. *Keywords: biodiversity-ecosystem functioning, detritus processing, functional diversity, taxonomic diversity, phylogenetic diversity, natural microcosms, bromeliad food web, alpha diversity.*

INTRODUCTION

In the face of the increasing loss of global biodiversity, understanding the importance of biodiversity on ecosystem functioning (EF) has emerged as a central issue in ecological and environmental sciences (Loreau et al. 2001, Cardinale et al. 2012). It has long been hypothesized that diversity influences ecosystem processes, such as productivity, decomposition rate and nutrient cycling (Hooper and Vitousek 1998, Tilman et al. 2001). Although evidences support the positive relationship between biodiversity and ecosystem functioning (BEF) (reviewed in Cardinale et al. 2012), there is no general consensus about the relative importance of different biodiversity components (e.g., functional, phylogenetic and taxonomic) on EF (Hooper et al. 2005). Studies have shown that local species richness positively affects EFs (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006). However, a recent meta-analysis emphasized that the diversity of functional groups has more pronounced effects on EF than species richness (Balvanera et al. 2006). Meanwhile, recent studies have suggested that phylogenetic diversity

(PD) can be considered as one of the most synthetic estimators of community trait diversity and a good predictor of ecological similarity (Cavender-Bares et al. 2009, Wiens et al. 2010). It has been suggested that high PD should enhance niche complementarity and increase ecosystem functioning by maximizing resource uptake (Maherali and Klironomos 2007, Srivastava et al. 2012). To date, most of BEF have studies investigated the effects of diversity on EF within a single trophic level, in spite of many EF be dependent on interactions between different trophic levels. Thus, it is important to merge information about how trophic interactions (e.g., predator-prey interactions) may affect the diversity within trophic levels (e.g., prey diversity) (Duffy et al. 2007), and which factors mediate such interactions (e.g., abiotic factors).

Several studies on a variety of taxa (e.g., yeast, herb-layer plants, birds and bats) have demonstrated that environmental constraints and species interactions affect functional (FD), phylogenetic (PD) and taxonomic diversity (TD), indicating that deterministic ecological processes act in local communities (Pavoine and Bonsall 2011). However, the effects of such interactions on different diversity components (e.g., PD, FD, TD) are numerous and still not completely understood. For instance, environmental heterogeneity and niche complementarity may generate communities with high species diversity and high trait diversity (Mayfield et al. 2005, Grime 2006). Meanwhile, competition on phylogenetically conserved traits may explain communities with high PD and FD (Pavoine and Bolsall 2011). On the other hand, strong negative interactions among similar species may cause low phylogenetic diversity and high functional diversity (irrespective of taxonomic diversity) through, (i) character displacement and divergent evolution of trait-states of coexisting species (past interactions), and/or (ii) replacement of coexisting similar species by less similar ones (present-day interactions) (Prinzing et al. 2008). Therefore, two communities with similar taxonomic diversity may be composed of species with either highly similar or very different evolutionary histories (Webb et al. 2002; Forest et al. 2007). Thus, the relationship between functional, phylogenetic and taxonomic diversity is greatly variable and not easily predictable. Therefore, if ecosystem functioning is better predicted by the diversity of functional traits, niches and ecological interactions (Petchey and Gaston 2006, Diaz et al. 2007; Lavorel et al. 2011; Paquette and Messier 2011), the predictive power of the different dimensions of diversity, especially phylogenetic diversity (PD), will depend on the underlying mechanism generating the observed pattern of diversity in communities.

Nowadays, it is widely known that many functions in ecosystems involve interactions between organisms from different trophic levels (Duffy et al. 2007). However, there is a lack of BEF studies considering the effects of consumptive trophic links (e.g., predator-prey interactions) on the relationship between different biodiversity components, especially considering the effect of PD (but see Helmus et al. 2013) on ecosystem functioning (reviewed in Srivastava et al. 2012). Many studies have shown that predators can have profound effects on the structure of prey communities by altering the colonization (or emigration) patterns of their prey (i.e., through behavioral habitat selection) and their vital rate (e.g., mortality, birth) (Schmitz 2008, Vonesh et al. 2009), or by indirectly influencing interactions among species and their resources (Lima and Dill 1990). Moreover, it is known that keystone predators can enhance diversity of coexisting prey species by feeding selectively on dominant competitors (Paine 1966, Leibold 1996, Power et al. 1996). By contrast, if predators do not limit the abundance of superior competitors, or if competition is weak among prey species, predators can reduce prey diversity and produce communities dominated by the species resistant to predators (Almany and Webster 2004). Thus, by affecting prey diversity patterns, predators can have a key role in ecosystem properties and functioning such as productivity, decomposition, and nitrogen flux. So far, little is known about the relative effect of predators on the functional and phylogenetic diversity of prey and their consequences to EF. To date, one study has demonstrated that high densities of subsidized predators (i.e., fishes) can promote the increase in phylogenetic diversity of macroinvertebrate prey communities by selective feeding on specific taxa (Helmus et al. 2013). Therefore, we can argue that if high PD enhances niche complementarity and increases EF by increasing resource uptake (Maherali and Klironomos 2007, Srivastava et al. 2012) predators have potential to affect EF via changes in prey PD. To date, the majority of studies investigating the effects of predators on diversity of prey were restricted to the taxonomic component of diversity. We thus suggest that predators can play a crucial role in determining the functional and phylogenetic diversity of prey communities.

In this study, we used invertebrates inhabiting natural microcosms (tank bromeliads) to test for the relative effect of environment and top-down forces on the diversity patterns of detritivore communities. In addition, we assessed whether the impacts of environment and predation on taxonomic, functional and phylogenetic diversity of detritivores cascade down to the functioning of ecosystems measured *via* detritus processing and nitrogen flux. The interlocked leaves of tank bromeliads collect rainwater, leaf litter and other organic detritus and host aquatic macroinvertebrates dominated by larval insects (Kitching 2004). This aquatic food web typically relies on allochthonous sources of nutrients derived from dead organic matter, and the bromeliad itself absorbs part of the dissolved nutrients through specialized trichomes present on its leaves (Benzing 2000). Detritus processing is enhanced by complementarity resource use and/or mechanisms of facilitation. For instance, aquatic invertebrates that shred and scrape detritus into fine particles facilitate resource capture by families of organisms that collect or filterer fine particulate organic matter (Paradise and Dunson 1998, Paradise and Kuhn 1999). In this manner, detritus processing and nitrogen flux will be improved in communities with both benefactors (shredders, scrapers) and beneficiaries (collectors, filterers). In addition, detritus not only provides energy, but also is a source of environmental heterogeneity (McIntosh et al. 2005). Studies have shown that less pronounced top-down effects could occur in detritus-based food webs if the cover provided by accumulated detritus and leaves makes invertebrates less vulnerable to predation (Reice 1991, Rosenfeld 2000). Therefore, not surprisingly, the incoming detritus and light incidence strongly affect the aquatic community inhabiting bromeliads (Dézerald et al. 2013).

To understand the effect of environment and top-down forces on the different components of detritivore diversity and the consequences for ecosystem functioning, we performed an experiment in two extremes of an environmental gradient, i.e., the open *restinga* forest (nutrient-poor) and the closed *restinga* forest (nutrient-rich) (Figure 1). Bromeliads that grow in the nutrient-rich *restinga* receive higher litter inputs and lower light incidence than bromeliads in the nutrient-poor *restinga* (sun-exposed areas) [hereafter, nutrient-rich and nutrient-poor refers to the differences in detritus input between the two forests]. Besides clear differences in detritus input, the proportion of predators to prey differs substantially between these two areas (P. M. O., unpublished data). The aquatic insect communities from the nutrient-poor *restinga* suffer strong top-down influence (see Chapter 2) from a keystone predator (damselfly larvae: *Leptagrion andromache* Hagen in Selys 1876). The damselfly larva is a generalist predator, which preys on virtually all invertebrate detritivores. Since the principal predator occurring at the nutrient-poor *restinga* is a generalist, we expected predators to reduce prey diversity (i.e., PD, FD and TD) and produce communities dominated by the species resistant to predators, thus reducing niche complementarity. By contrast, the greater litter input and lowest biomass of predators in bromeliads from nutrient-rich *restinga* might favor the existence of more diverse detritivore communities. The greater availability of resources and environmental heterogeneity provided by detritus may buffers interactions of competition among detritivores and favor the existence of communities dominated by facilitative interactions and niche complementarity. Thus, from the ecosystem functioning perspective, we predict that detritus processing and nitrogen flux will be greater in the more diverse community (nutrient-rich). In fact, there is emerging evidence that distantly related species are more likely to exhibit facilitation (Pausas and Verdú 2010, Srivastava et al. 2012). Thus, if decomposition depends on interactions of facilitation which integrate the diversity of traits, we predict that detrital processing by aquatic insects will be better explained by higher insect PD and FD. We asked the following questions: (i) what is the relative importance of environment on predator biomass, detritivore diversity, and ecosystem processing? (ii) Do predator biomass affect the diversity of detritivores and indirectly ecosystem functioning? (ii) What is the relative importance of the different detritivore diversity components (i.e., PD, FD and TD) on detritus processing and nitrogen flux?

MATERIAL AND METHODS

Study site and organisms

We conducted the experiment in two extremes of an environmental gradient of *restinga* forest, i.e., the open (nutrient-rich) and the closed (nutrient-poor) *restinga* forest, at the Ilha do Cardoso State Park located on the Atlantic island Ilha do Cardoso a few kilometers off the south coast of São Paulo State, Brazil (25° 03'S, 48°53'W). The richness of plants and vegetation height increases from the beach strand (sandy area above the high-tide lines) towards the interior of the island (Barros et al. 1991). After the pioneer vegetation of dunes, there is the nutrient-poor *restinga*. The nutrient-poor *restinga* consists of a sun-exposed area bearing shrub vegetation of 1 – 4 m high, with patches of plants containing a mix of shrubs, liana, and bromeliads. The bromeliad *Quesnelia arvensis* Mez. (Bromeliaceae) is the most abundant plant occurring in these patches; it is a large terrestrial bromeliad, which accumulates up to 3 L of rainwater inside tanks formed by its leaves. The nutrient-rich *restinga* is continuous with the nutrient-poor *restinga* and consists of 6 – 8 m high trees with a relatively closed canopy, high densities of epiphytes and an understory mostly covered by orchids and bromeliads (the most abundant bromeliad species is *Q. arvensis*). The aquatic fauna inhabiting these bromeliads is mainly composed by insect larvae and includes functional feeding groups such as filter feeders (Culicidae), detrital shredders (Limoniidae, Trichoptera), detrital scrapers (Scirtidae), collectors (e.g., Chironomidae, Psychodidae), and predators (e.g., Coenagrionidae, Corethrellidae, Tanypodinae, Dytiscidae, and Ceratopogonidae). Other non-insect invertebrates like Ostracoda, Oligochaeta (both detritivores), and Hirudinea (predators) also compose the aquatic community (Romero and Srivastava 2010).

Experimental design

To test for the relative effects of environment and top-down influence on functional, phylogenetic and taxonomic diversity and their effects on ecosystem functioning, we performed a randomized experiment in nutrient-poor and nutrient-rich *restinga* forest. To set up the experiment, we collected 30 bromeliads from the nutrient-poor *restinga* and 30 bromeliads from the nutrient-rich *restinga*. Each bromeliad was set upside down and washed thoroughly with spring water to remove detritus and organisms. To capture or kill any residual invertebrates we kept bromeliads suspended upside down from a line inside a laboratory for five days. We kept bromeliads root moist and inspected the tanks every day using a flashlight to remove remnant insect larvae. We planted the bromeliads in sandy substrate of the *restinga*, 30 at the nutrient-poor and 30 at the nutrient-rich *restinga* forest. Each bromeliad was planted 5 to 10 m from its nearest neighbor. To avoid the entry of other non-flying terrestrial arthropods, like ants and spiders, we constructed an open cylinder (60 cm tall, 80 diameter) made from white polivinilcloride (Formica ®) around each bromeliad. We periodically applied solid medical petroleum jelly (Rio Química, São José do Rio Preto, Brazil) to the top of cylinders. The experiment lasted three months with daily monitoring of bromeliads to remove terrestrial organisms from the experiment.

The empty bromeliads were colonized naturally during the three months of experiment. After three months of running experiment, we collected the aquatic invertebrate community that colonized the bromeliads. We dissected each bromeliad by removing and washing each leaf separately in running water over large buckets, and then filtered this water through 125 and 850 μm soil sieves (Romero and Srivastava 2010). We searched each of the two size-fractions of material in white trays, and then recorded the morphospecies and abundance of all aquatic invertebrates visible to the naked eye (i.e., body size larger than 0.5 mm). Specialized taxonomists identified some of the morphospecies to the lowest taxonomic level.

In order to quantify detrital processing and loss, and nitrogen flux from detritus to bromeliad leaves (the parameters to estimate ecosystem functioning), we added ^{15}N labelled *Eugenia uniflora* L. (Myrtaceae) leaves on the bromeliad tank. To obtain labelled leaves, we watered saplings of *E. uniflora* with solution (2.5 g L^{-1}) of labelled ammonium sulphate $(^{15}NH_4)_2SO_4$ (10 atom % excess, from Cambridge Isotope Laboratories, Andover, MA, USA). We applied 4 ml of labelled solution on the roots of the saplings every other day during two months. The labelled leaves were oven-dried at 60°C for 48 hours. Each bromeliad received a total of 1 g of labelled detritus, with this amount split between additions 20 and 50 days from the beginning of the experiment (approximating the near continuous entry of detritus in natural bromeliads). At the end of the experiment, we removed three new leaves from the innermost node of each experimental bromeliad for isotopic (^{15}N) and nitrogen concentration (μ of total N mn^{-1} of dried plant tissue) analyses. The Stable Isotope Facility laboratory (UC Davis, CA, USA) determined isotope ratios of ^{15}N and % mass-specific N concentration using a continuous flow isotope ratio mass spectrometer (20–20 mass spectrometer; PDZ Europa, Sandbach, England) after sample combustion to N^{2} at 1000°C by an on-line elemental analyser (PDZ Europa ANCA-GSL). At the end of the experiment, we collected and dried (48 hours at 60°C) all leaves of *E. uniflora* retained on the 850 μm sieve to estimate de mass loss of labeled leaves (detrital processing as a measure of ecosystem functioning).

Traits of the detritivore macroinvertebrate communities

We listed traits from detritivore macroinvertebrates that we considered important for ecosystem functioning (i.e., decomposition, nitrogen flux from detritus to bromeliad leaves, and total nitrogen content of bromeliad leaves). We classified the traits in four main categories: (1) **main components of diet** (i.e., FPOM – fine particulate organic matter, CPOM – coarse particulate organic matter, plant fibers, leaf, saprophagous - decaying organic matter in general), (2**)** **foraging group** (i.e., collector-gatherer, collector-filterers, conveyor belt deposit feeder, filter feeders, scraper, shredder,, surface filter feeders, column filter feeders), (3) **main foraging substrate** (e.g., surface swimmer, full water swimmer, crawler, burrower, interstitial, tube builder), and (4) **biomass** (dry mass (mg)/ bromeliad) (Table 1). The reasons why we choose the four main categories are (1) the main component of diet indicate the contribution of detritivores to EF (i.e., detritus mass loss and nitrogen flux), (2) the foraging group is important since it integrate differences in morphology related to the use of resource, (3) the main foraging substrate integrates information regarding the uptake of resources in relation to the use of environment and (4) biomass indicates the amount of resource that organisms can assimilate. We compiled the categorical trait data from several sources (Wallace and Merritt 1980, Armitage et al. 1995, Merritt and Cummings 1996, Henriques-Oliveira et al. 2003, Bouchard 2004, Sanseverino and Nessimian 2008, Silva et al. 2008, Ceneviva-Bastos et al. 2012). The biomass of each organism was estimated using constructed allometric equations between body length and body dry mass, or by the use of mean dry mass for very small insects (D.S.S., unpublished data).

Phylogeny of the detritivore bromeliad community

To construct a community phylogeny, we built a topological tree in Mesquite 2.75 (Maddison and Maddison 2011) using the phylogeny of Koenemann et al. (2010) as a reference, following the methods outlined by Hortal et al. (2011). Then we used phylogenies for families of macroinvertebrates present in our community (Bertone et al. 2008, Cranston et al. 2012, Harbach et al. 2012) to set the relationships among genera and species. The composite tree was based on 37 detritivore macroinvertebrate species/morphospecies observed in this study occurring in either bromeliads from nutrient-poor and nutrient-rich *restingas*. Branch lengths of the phylogeny were re-scaled so that distances from tips to root varied between 0 and 1 (Grafen 1989).

Testing for phylogenetic signal in detritivores' traits

We used two different methods for testing phylogenetic signals. For the continuous trait, biomass, we used Pagel's λ that assume a Brownian motion model of trait evolution. The Pagel's λ measures phylogenetic dependence of trait data and its value varies from 0 (absence of phylogenetic signal, which indicates that the trait has evolved independently of phylogeny) to 1 (high phylogenetic signal, which indicates that the trait has evolved accordingly to the Brownian motion model of evolution) (Pagel 1999, Münkemüller et al. 2012). For binary traits, we used Fritz & Purvis' *D* that is based on the sum of sister-clade differences in a given phylogeny (Fritz and Purvis 2010). We did 1000 permutations to randomize traits throughout the phylogeny. The random values are compared with the observed phylogenetic pattern. To obtain the value of *D* we used the observed sum of sister-clade differences minus the Brownian motion model expectation divided by the difference between the random expectation and the Brownian expectation. The more clumped are the traits in the phylogeny, the lower will be the sum of sister-clade differences. Values of $D = 1$ indicate a random mode of evolution (absence of phylogenetic signal), and values of $D < 0$ indicate that trais are clumped (i.e., presence of phylogenetic signal). The null hypothesis (H_0) in the permutation is that *D* is equal to 1 (random mode of evolution) (Fritz and Purvis 2010).

Statistical analysis

Estimating functional, phylogenetic and taxonomic diversity of detritivores

Functional diversity (FD) requires calculating the multivariate distance between each pair of species based on their functional traits. We used the mixed-variable Gower's coefficient of distance, which accommodates both continuous and binary data, to calculate functional distance among species (Pavoine et al. 2009). We used our community phylogeny to estimate the phylogenetic (patristic) distance between species. The phylogenetic and functional distances were used to calculate alpha phylogenetic (hereafter PD) and functional diversities (hereafter FD) of detritivores using the Rao's diversity coefficient (also called Quadratic Entropy). The alpha diversity is calculated by using phylogenetic or functional distances and relative abundances (de Bello et al. 2010, Meynard et al. 2011):

$$\alpha_{Rao} = \sum d_{ij} \, p_i p_j$$

where d_{ij} is the phylogenetic distance between species i and j, and p_i e p_j are species relative abundances (Meynard et al. 2011). For taxonomic diversity (TD) we used the same formula and considered the distance between different species as 1, and the distance between individuals of the same species as 0. The Rao index of diversity is equivalent to the Simpson diversity index in the case of taxonomic diversity (Meynard et al. 2011). Rao's diversity measures the differences of two randomly selected individuals based on their relative abundances (de Bello et al. 2010). Importantly, Rao's diversity is one estimator of diversity that formally combines different measures of species dissimilarities (e.g., phylogenetic or functional) with relative species abundances, providing a standardized methodology applicable to compare taxonomic, phylogenetic, and functional diversity (de Bello et al 2010).

Effect of environment and top-down control on detritivore diversity and their effects on ecosystem functioning

We analysed the relative magnitude of the environment (nutrient-rich and nutrient-poor *restinga* forest; binary variable), predators (biomass, continuous variable), and detritivore diversity (TD, PD and FD) on ecosystem functioning (i.e., detritus mass loss, total nitrogen content in bromeliad leaves and nitrogen flux estimated via δ^{15}N) through structural equation modeling (SEM, Grace 2006). In order to reduce the number of endogenous variables in the SEM, we performed a series of linear regressions using the Akaike Information Criterion corrected for small samples (AICc). We performed a linear regressions in two steps: first, we tested for the effects of environment and predators (fixed variables) on the phylogenetic, functional, and taxonomic diversity of detritivores (response variables); second, we tested for the effects of environment, predators, phylogenetic, functional, and taxonomic diversity of detritivores (fixed variables) on detritus mass loss, nitrogen content, and $\delta^{15}N$ (response variables). To construct the SEM, we chose the predictor variables from the linear models in which the delta AICc was lower than two (Table 2). We analysed adjustments of the SEM model with chi-square; all the SEM showed a good fit to the data ($P > 0.825$ chi-squared test). We evaluated the normality of each structural equation model with the Mardia test and inspected outliers using Mahalanobis distance. We verified the normality of the residuals of each variable by evaluating their kurtosis and asymmetries. The linear models, AICc, and estimation of functional, phylogenetic, and taxonomic diversity of detritivores were performed in R (R Development Core Team) using the packages MuMIn (Bartón 2012), FD (Laliberté and Legendre 2010), vegan (Oksanen et al. 2013), and the self-written function provided by de Bello et al. (2010) to calculate Rao's diversity. We constructed and analysed all structural equations with AMOS 21 (Arbuckle 2012).

We also performed linear regressions to test for the relationship between PD, TD and FD. Moreover, we tested for the effect of the two extreme of environmental gradient (nutrient-rich and nutrient-poor *restinga*) (fixed term) on the diversity components (i.e., FD, PD and TD) and on the measures of ecosystem functioning (i.e., detritus mass loss, $\delta^{15}N$ and total nitrogen content) (response variables).

Dominant traits in each extreme of the environmental gradient

To determine the dominant trait distribution within each type of *restinga*, we used a method from Pillar and Duarte (2010). We multiplied the matrix containing species traits (matrix **B**) by the matrix of species abundance in each bromeliad (matrix **W**), which resulted in the matrix **T** that is the community-weighted mean traits (Appendix 1; Pillar and Duarte 2010). To visualize the distribution of the dominant traits of each *restinga*, we calculated the Gower's distance of the matrix **T** (Dt), and then performed a Principal Coordinates Analysis (PCoA) to extract the eigenvectors of Dt. We labeled the eigenvectors by *restinga* type (i.e., nutrient-poor or nutrient-rich).

RESULTS

Phylogenetic signal in detritivores' traits

The test for phylogenetic signal, including the Pagel's λ and Fritz & Purvis' *D,* indicated that most of the traits that we used had phylogenetic signal (see Table 1). The only two traits that did not present phylogenetic signal were FPOM (fine particulate organic matter) and saprophagous (consumption of decaying organic matter) (Table 1).

Selection of variables for the SEM

In order to simplify the initial hypothetical SEM, we used linear regressions implemented by stepwise model selection. Phylogenetic diversity (PD) of detritivores was not explained by any predictor variables (i.e., predators' biomass and environment) (Table 2). Moreover, PD did not explain any of the three ecosystem functioning variables (i.e., detritus mass loss, $\delta^{15}N$, and total N concentration). Furthermore, predators' biomass was not selected as a predictor of phylogenetic, taxonomic, or functional diversity of detritivores. However, the model including predator biomass was selected ($\Delta AICc < 2$) as a good model to explain nitrogen flux ($\delta^{15}N$). The environment was the most important predictor variable, since it was included in all linear models (Table 2). Functional diversity and taxonomic diversity were selected as predictors' variables for detritus mass loss (Table 2). In order to keep the comparability among the SEM, we used the same predictor variables in all the three SEM (Fig. 1).

Environment, predators, diversity components, and ecosystem functioning

The SEM analysis explained 62% of the variation of the functional diversity in bromeliads; both environment and taxonomic diversity had positive and significant effects on FD (Fig. 1). The environment also affected positively the biomass of predators; however, it had no effect on taxonomic diversity (Fig. 1). The SEM explained 53% of the variation in detritus mass loss among bromeliads (Fig. 1A). Among the four variables used to explain detritus processing, TD, FD, and environment had a significant effect (Fig. 1A). Functional diversity and environment negatively affected the processing of detritus (Fig. 1A). Meanwhile, taxonomic diversity had a positive, direct effect on detritus mass loss, and a negative, indirect effect via FD (Table 3). However, the total net effect of TD on detritus mass loss was positive (Fig. 1A). The environment affected detritus mass loss, with higher percentage of detritus processing in bromeliads from nutrient-rich *restinga* (ANOVA: $F_{1,58} = 41.31$, $P < 0.0001$, Fig. 2A) than in bromeliads from nutrient-poor *restinga*. The SEM explained 28% of the variation in nitrogen flux, estimated via labelled detritus. The environment affected negatively the nitrogen uptake by bromeliads (Fig. 2B). Leaves of bromeliads from the nutrient-rich *restinga* presented higher values of δ^{15}N (ANOVA: $F_{1,58} = 20.08$, $P < 0.0001$, Fig. 2B), than bromeliads from the nutrient-poor area. The same pattern occurred for the total nitrogen content in bromeliad leaves. SEM explained only 15% of the variation of N content in the leaves of bromeliads, and only the environment had a negative significant effect on total N (ANOVA: $F_{1,58} = 9.54$, $P = 0.003$, Fig. 1C). Bromeliads occurring in the nutrient-rich *restinga* presented higher values of total N concentration (Fig. 2C) than bromeliads from the nutrient-poor *restinga*. In addition, communities inhabiting bromeliads from the nutrient-rich *restinga* presented lower values of FD ($F_{1,58} = 8.33$, $P = 0.005$, Appendix 3). Environment did not affected TD and PD (TD: $F_{1,58} =$

3.301, $P = 0.074$, PD: $F_{1,58} = 1.50$, $P = 0.22$, Appendix 3). Moreover, all the components of diversity were strongly related with each other (FD vs TD: $F_{1,58} = 81.05$, $P < 0.0001$, PD vs TD: $F_{1,58} = 35.33$, $P < 0.0001$, PD vs FD: $F_{1,58} = 174.59$, $P < 0.0001$) (see Appendix 4).

The first two PCoA eigenvectors explained 25.9% and 18.6%, respectively, of the total variation in trait distribution within each type of *restinga* (i.e., nutrient-poor and nutrient-rich *restinga*; Fig. 3). CPOM, the interstitial habit, plant fiber (components of diet), and crawler as the main traits related to foraging substrate were the dominant traits negatively correlated to PC1 in the nutrient-rich *restinga* (Fig. 3, Appendix 2). The dominant traits of detritivores from the nutrient-poor *restinga* were traits related to foraging substrate, i.e., column filter feeders and full water swimmers (Fig. 3, Appendix 2).

DISCUSSION

Several experimental studies have demonstrated a positive relationship between biodiversity and ecosystem functioning (Tilman et al. 1997, Cardinale et al. 2002, Loreau et al. 2001, Cardinale et al. 2012). However, there is still much debate regarding the importance of the different components of diversity (i.e., FD, PD and TD) in maintaining the functioning of ecosystems (Cadotte et al. 2010). Our results demonstrated that the positive relationship between diversity and ecosystem functioning is not always a rule. Furthermore, we found that the different components of biodiversity are not equally good in predicting ecosystem functioning. Specifically, functional diversity negatively affected detritus processing, and the effect of taxonomic diversity in predicting ecosystem functioning was higher than FD. Contrary to our initial expectation, phylogenetic diversity of detritivores did not explain detrital decomposition. Moreover, we found that the effect of environment on the different components of diversity was restricted to the functional diversity of detritivores. Additionally, the environment was a powerful predictor in all models evaluating detrital processing and nitrogen flux.

Our results demonstrated that the effects of abiotic factors on the different components of diversity were not homogeneous. The two extremes of the environmental gradient played a modest role in predicting detritivore diversity. Indeed, the extremes of the environmental gradient only explained the variation in functional diversity of detritivores. We expected that the greatest litter input and lower biomass of aquatic predators in bromeliads from nutrient-rich *restinga* should favor the existence of a more diverse detritivore community. However, taxonomic diversity and phylogenetic diversity were similar between these two areas while the functional diversity was smaller in bromeliads from the nutrient-rich *restinga* than in bromeliads from the nutrient-poor *restinga*. Interestingly, the three components of diversity (PD, TD, and FD) were strongly and positively correlated with each other (Appendix 4); however, their responses to environment were contrasting. The patterns of phylogenetic diversity at large spatial scale are thought to be primarily determined by species richness (Pavoine and Bonsall 2011). Thus, the lack of differences between TD and PD in the two *restingas* indicates that all detritivore species from the regional pool are able to colonize the bromeliads irrespective of environmental abiotic factors. Therefore, it is possible that the different clades of detritivore species evolved in a range of abiotic conditions, which allows them to colonize bromeliads independent of the abiotic factors. However, we found that the nutrient-rich *restinga* presented lower FD than nutrient-poor *restinga*. We believe that environmental effects on FD reflect the differences of bottom-up forces acting through the availability of resources in different concentrations and states (size of particle) in the two areas. The bromeliads from nutrient-rich *restinga* present high quantity of large particulate detritus (CPOM), since this *restinga* has a relative closed and continuous canopy. Thus, the lower FD can be explained by dominance of organisms specialized in the use of CPOM.

The rates of ecosystem processes are influenced by both biotic and abiotic factors (Lavorel and Garnier 2002). However, the relative contribution of each of these factors can be greatly variable. Our results demonstrated that abiotic conditions could play a major role in determining the functioning of ecosystems. The experimental bromeliads in nutrient-rich sites presented greatest detrital processing and highest nitrogen flux (i.e., N from detritus to bromeliad leaves) than bromeliads in nutrient-poor sites. The differences in nitrogen uptake by bromeliad leaves were only explained by the environment. Therefore, we believe that the differences in nitrogen flux between the two *restingas* may involve differences in the bacterial community between the two areas. Possibly greater concentrations of detritus and lower concentrations of algae in bromeliads from nutrient-rich *restingas* may favor the proliferation of bacterial communities, which might favor the uptake of N by bromeliads (Gonçalves et al. 2013).

By contrast, the processing of detritus (i.e., detritus mass loss) was affected by both environment and diversity components. Despite the greatest performance on detritus processing, detritivore macroinvertebrate communities from nutrient-rich *restinga* presented lower functional diversity in relation to communities from nutrient-poor *restinga*. Therefore, we found a negative relationship between functional diversity and detritus processing. This somewhat counterintuitive result could be attributed to the relevance of traits that dominate each community. The process of decomposition comprises the gradual breaking of coarse organic matter (CPOM) into particulate/dissolved detritus, to simpler constituents and eventually, to nutrient mineralization (Tenore et al. 1982, Schlesinger 1997, Cebrian 1999). In this context, we found that the dominant traits present in nutrient-rich *restinga* were related to the processingof leaf litter into small particle. For instance, the main components of the diet of detritivores from the nutrient-rich *restinga* comprise the coarse particulate organic matter, which also includes plant fibers and leaf litter (Appendix 2). Moreover, two other main traits were interstitial habit and tube builder (i.e., larvae that make tubes by incorporating detritus with their sticky saliva) both of these traits are present in organisms that feed mainly on CPOM. Conversely, the dominant traits from the nutrient-poor *restinga* were related to the organisms that feed primarily on fine particulate (i.e., column filter feeders, full water swimmers and collector gatherer). The differences regarding the distribution of traits between the two *restingas* are possibly related to the differences in detritus availability between the *restingas*. The great concentration of coarse particulate organic matter in nutrient-rich *restinga* may favor the existence of species with traits that allow them to feed on larger detritus size (e.g., Trichoptera). By contrast, nutrient-poor *restinga* have higher concentrations of fine particulate detritus as well as algae (Chapter 2), thus favoring species with filter feeding habits.

Previous studies have also attempted to evaluate the predictive power of the different components of diversity on the functioning of ecosystems. So far, the literature has shown very contrasting results and, most of the research has investigated the effect of plant diversity on ecosystem functioning (Cardinale et al. 2011). For instance, Flynn et al. (2011) have found that measures of FD and PD have similar abilities to predict biodiversity effects on aboveground biomass production. On the other hand, Petchey et al. (2004) demonstrate that FD was a powerful predictor of aboveground production than richness and functional group richness. By contrast, our results demonstrated that the power of taxonomic diversity in predicting ecosystem functioning was higher than FD. Meanwhile, PD had no relationship with ecosystem functioning, despite we have found evidences for phylogenetic signal for almost all functional traits. Thus, it is possible that individual traits important to detrital processing are not conserved in the phylogeny within each *restinga*, since we did not find differences of PD between the two *restingas*. An alternative explanation is that those traits that affect detritus processing have different evolutionary histories in the two environments (see Venail et al. 2008, Gravel et al. 2011). By contrast, taxonomic diversity affected positively the processing of detritus at bot *restinga* forest. In contrast with most of studies that study one taxonomic group (e.g., plants), we investigated the predictive power of the diversity components in groups that included many phylogenetically distant groups (e.g., Insecta, Crustacea, Oligochaeta). In addition, due to the phylogenetic resolution (Swenson 2006) and the absence of actual branch lengths, our phylogenetic tree could not properly represent the evolutionary history of those groups. In this context, we believe that TD of communities with phylogenetic distant groups may integrate strong evolutionary and functional information. Therefore, the positive relationship between TD and detrital processing may encapsulate patterns of complementarity of resource use and/or the inclusion of combination of traits that most contribute to ecosystem functioning.

Moreover, our results demonstrated that top-down forces might not be a good predictor of diversity and ecosystem functioning. Despite of the greater biomass of predators (most part composed by damselfly larvae) in the nutrient-poor *restinga* we did not find any effect of predators on the diversity of detritivores (AIC-based model selection did not select predators' biomass) and EF. We expected predators to affect negatively the diversity of detritivores via production of communities dominated by species resistant to predation. The lack of predator effect on FD and PD suggest that there is no species more resistant to predator's effect. Moreover, it seems that damselfly predators do not consume prey bearing particular functional traits (e.g., body size of prey) or prey from a specific clade. It has been shown that damselflies can prey on virtually all invertebrates within bromeliads (except leech; A. S. Neutzling., pers. comm.). Therefore, as generalist predators, their effects on detritivore community might be restricted to negative effects on the abundance of aquatic insects (see Chapter 2). We, thus, could expect predators to affect negatively decomposition in bromeliads from nutrient-poor *restinga* (via density mediated effect). However, we found no relationship between biomass of predators and detrital processing. As we described previously, the main component of detritivore community in the nutrient-poor *restinga* are organisms that feed on fine particulate organic matter. Therefore, even if predators are able to feed on prey almost to its depletion (Chapter 2), their consumptive effects are not expected to affect the processing of detritus.

In this study we demonstrated that the positive relationship between the different components of diversity and ecosystem functioning is not always a rule. We argue that recent studies considering the positive relationship between functional diversity and EF should only be true in cases where the dominant traits affect EF, which means that increasing in FD do not necessarily reflect an increasing in relevant traits for EF. Moreover, we suggest that, for communities with phylogenetic distant groups, TD may integrate evolutionary and functional information. Thus, for such communities, the positive relationship between EF-TD may occur because of the greater scope for mechanisms of complementarity and facilitation to be expressed. Our results also demonstrated that the environment can be a better predictor of ecosystem functioning than measures of biodiversity. These results indicate that abiotic factors can integrate important information related to EF that biotic factors cannot. Thus, we believe that studies that do not consider how environmental gradients affect community assembly (species, traits, lineages) have a limited predictive power in understanding how different biodiversity components influence ecosystem functioning. Consequently, future studies should integrate the context-dependent effect of abiotic factors on biodiversity to disentangle the relationship between diversity and ecosystem functioning.

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TABLE 1. Phylogenetic signal of aquatic invertebrate traits related to ecosystem functioning in bromeliad phytotelmata. Fritz & Purvis's (D) and Pagel's (λ) methods were used to test phylogenetic signal in binary and continuous data, respectively. See text for additional details.

Trait type		**Categories**	**D**	***P* for H_0: D=1**	**λ**
Foraging group					
	Collector-gatherer	Binary	-0.195	<0.001	-
	Collector-filterers	Binary	-0.569	<0.001	-
	Conveyor belt deposit feeders	Binary	-2.142	<0.001	-
	Filter feeder	Binary	0.006	<0.001	-
	Scraper	Binary	0.004	0.001	-
	Shredder	Binary	-0.167	<0.001	-
	Surface filter feeders	Binary	-2.815	<0.001	-
	Column filter feeders	Binary	-1.035	<0.001	-
Main components of diet					
	FPOM	Binary	1.009	0.426	-
	CPOM	Binary	0.149	0.013	-
	Plant fibers	Binary	-1.071	<0.001	-
	Leaf	Binary	-0.539	<0.001	-
	Saprophagous (decaying organic matter)	Binary	0.086	0.264	-
Main foraging substrate					
	Surface swimmer	Binary	-0.176	0.011	-
	Full water swimmer	Binary	-1.059	<0.001	-
	Crawler	Binary	-0.450	<0.001	-
	Burrower	Binary	-0.388	<0.001	-
	Sprawler	Binary	-1.243	<0.001	-
	Interstitial	Binary	-0.555	<0.001	-
	Tube Builder	Binary	-0.609	<0.001	-
	Biomass	Continuous	-	-	1.024*

* $P < 0.001$

TABLE 2. Comparison of candidate models with fixed effects for (1) taxonomic, functional, and phylogenetic diversity, and (2) ecosystem functioning variables. The following abbreviations were used: phylogenetic diversity (PD), functional diversity (FD), taxonomic diversity (TD), total nitrogen content (Nt), percentage of detritus mass loss (DML), environmental gradient (Env), and predators (P).

Complete model	**Selected fixed terms**	**AICc**	**ΔAICc**	**Weight**
Diversity components				
PD ~ Env + P	No fixed term selected	-	-	-
FD ~ Env + P	Env	- 92.61	0.00	0.53
TD ~ Env + P	Env	193.38	0.00	0.35
Ecosystem functioning				
Nt ~ Env + P + FD + TD + PD	Env	- 146.10	0.00	0.25
	Env + P	- 144.17	1.93	0.14
Δ^{15}N (‰) ~ Env + P + FD + TD + PD	Env	605.78	0.00	0.28
	Env + FD	606.96	1.18	0.18
	Env + Predators	606.33	1.55	0.15
DML ~ Env + P + FD + TD + PD	Env + FD + TD	451.02	0.00	0.33

TABLE 3. Explanatory variables for variation in detritus mass loss, total nitrogen content and nitrogen flux in bromeliads according to the casual models presented in the Figure 2.

Response variable	**Explanatory variable**	**Direct effect *(d)***	**Indirect effect *(i)***	**Total effect *(e = d + i)***
Detritus mass loss	Environment	-0.36	-0.01	-0.37
	Functional diversity	-0.302	0	-0.302
	Taxonomic diversity	0.497	-0.217	0.28
	Predators	0	0	0
Total nitrogen content	Environment	-0.42	0.045	-0.375
	Functional diversity	-0.015	0	-0.015
	Taxonomic diversity	0.008	-0.011	-0.003
	Predators	0.087	0	0.087
Nitrogen flux ($\delta^{15}N$)	Environment	-0.524	0.017	-0.507
	Functional diversity	-0.127	0	-0.127
	Taxonomic diversity	0.009	-0.092	-0.083
	Predators	0.108	0	0.108

FIGURE LEGENDS

FIG. 1. Results from the structural equation models showing the relative effects of the environmental gradient (environment), predators, taxonomic diversity, and functional diversity on the percentage of detritus mass loss (A), total nitrogen content (B) and $\delta^{15}N$ (C). Dashed arrows represent non-significant effect. The thickness of the arrows represents the magnitude of the standardized path coefficient. The values associated with arrows between variables represent standardized values of the path coefficients. *$P < 0.05$; ** $P < 0.01$; $P < 0.001$.

FIG. 2. Box plots showing the relationship between environment and (A) detritus mass loss (%), (B) $\delta^{15}N$ and (C) total nitrogen content.

FIG. 3. Ordination plot resulting from a Principal Coordinate Analysis (PCoA) of 60 communities of aquatic insects inhabiting bromeliads and 21 biological traits according to Gower's similarity coefficient. The arrows outside the plot represent the dominant trait contributions (eigenvector loading values for each trait inside brackets) to the principal coordinate analysis.

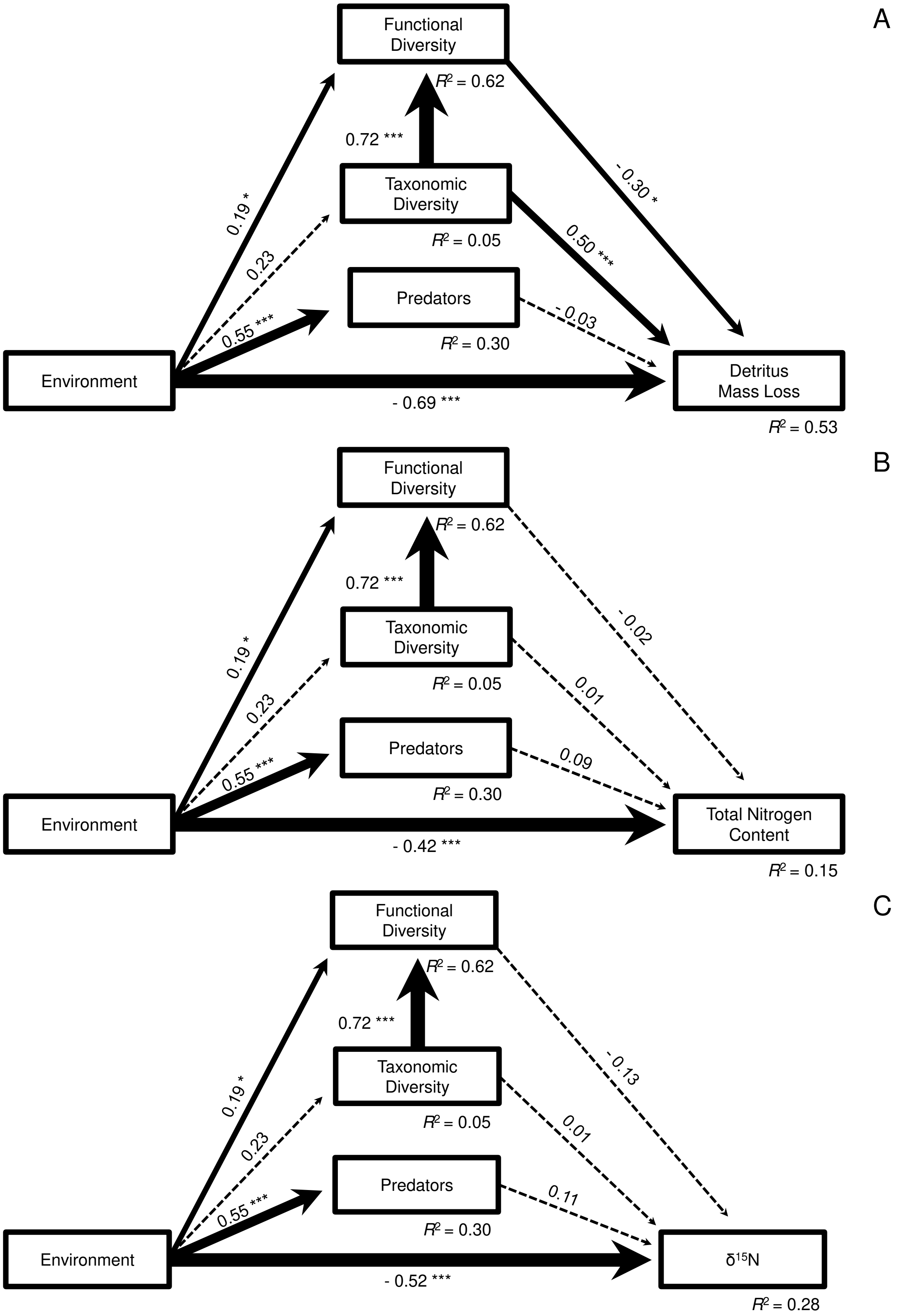

A
Functional Diversity
R^2 = 0.62
0.72 ***
Taxonomic Diversity
R^2 = 0.05
Predators
R^2 = 0.30
Environment
Detritus Mass Loss
R^2 = 0.53
0.19 *
0.23
0.55 ***
- 0.69 ***
- 0.30 *
0.50 ***
- 0.03
B
Functional Diversity
R^2 = 0.62
0.72 ***
Taxonomic Diversity
R^2 = 0.05
Predators
R^2 = 0.30
Environment
Total Nitrogen Content
R^2 = 0.15
0.19 *
0.23
0.55 ***
- 0.42 ***
- 0.02
0.01
0.09
C
Functional Diversity
R^2 = 0.62
0.72 ***
Taxonomic Diversity
R^2 = 0.05
Predators
R^2 = 0.30
Environment
$\delta^{15}N$
R^2 = 0.28
0.19 *
0.23
0.55 ***
- 0.52 ***
- 0.13
0.01
0.11

FIG. 1.

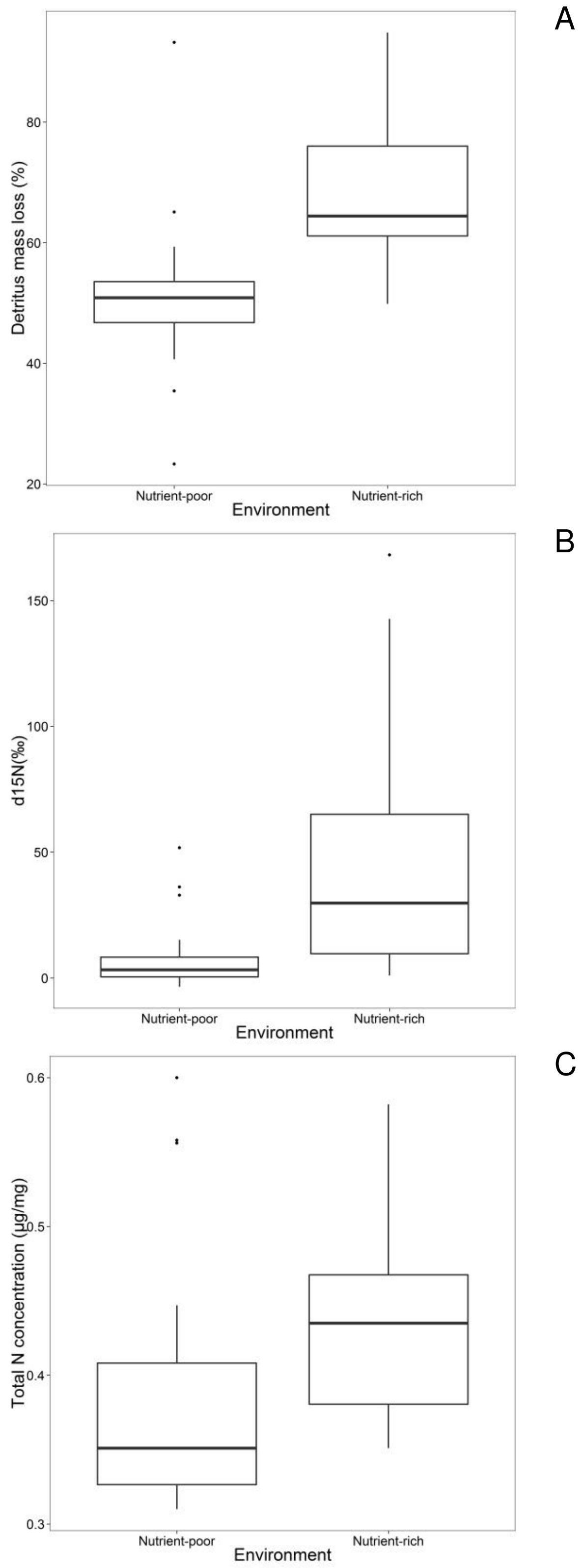

A
Detritus mass loss (%)
80
60
40
20
Nutrient-poor
Nutrient-rich
Environment
B
d15N(‰)
150
100
50
0
Nutrient-poor
Nutrient-rich
Environment
C
Total N concentration (µg/mg)
0.6
0.5
0.4
0.3
Nutrient-poor
Nutrient-rich
Environment

FIG. 2.

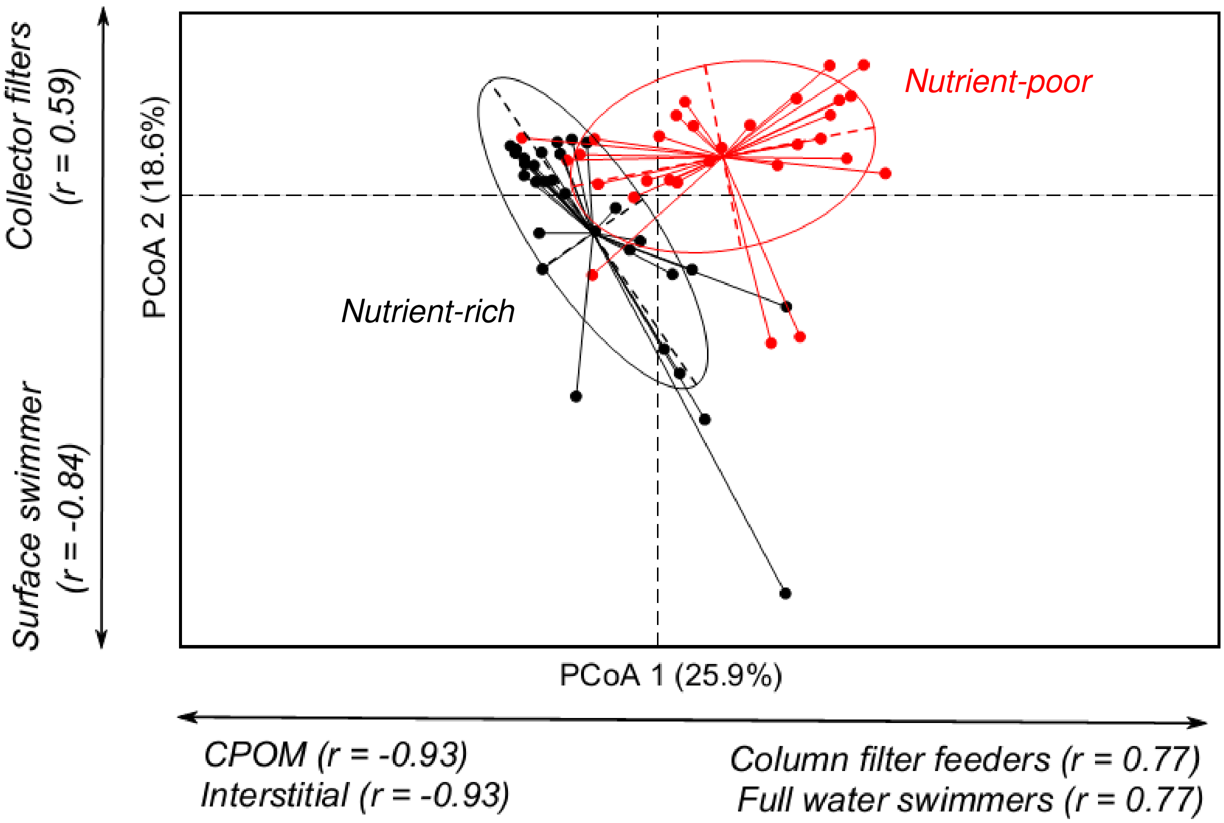
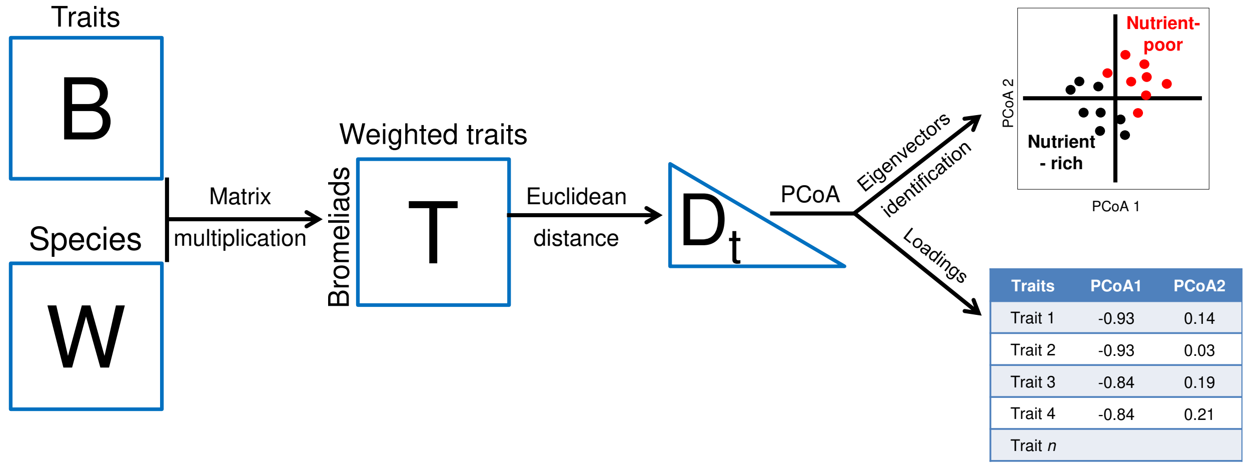

Nutrient-poor
Nutrient-rich
PCoA 2 (18.6%)
PCoA 1 (25.9%)
Collector filters (r = 0.59)
Surface swimmer (r = -0.84)
CPOM (r = -0.93)
Interstitial (r = -0.93)
Column filter feeders (r = 0.77)
Full water swimmers (r = 0.77)

FIG. 3.

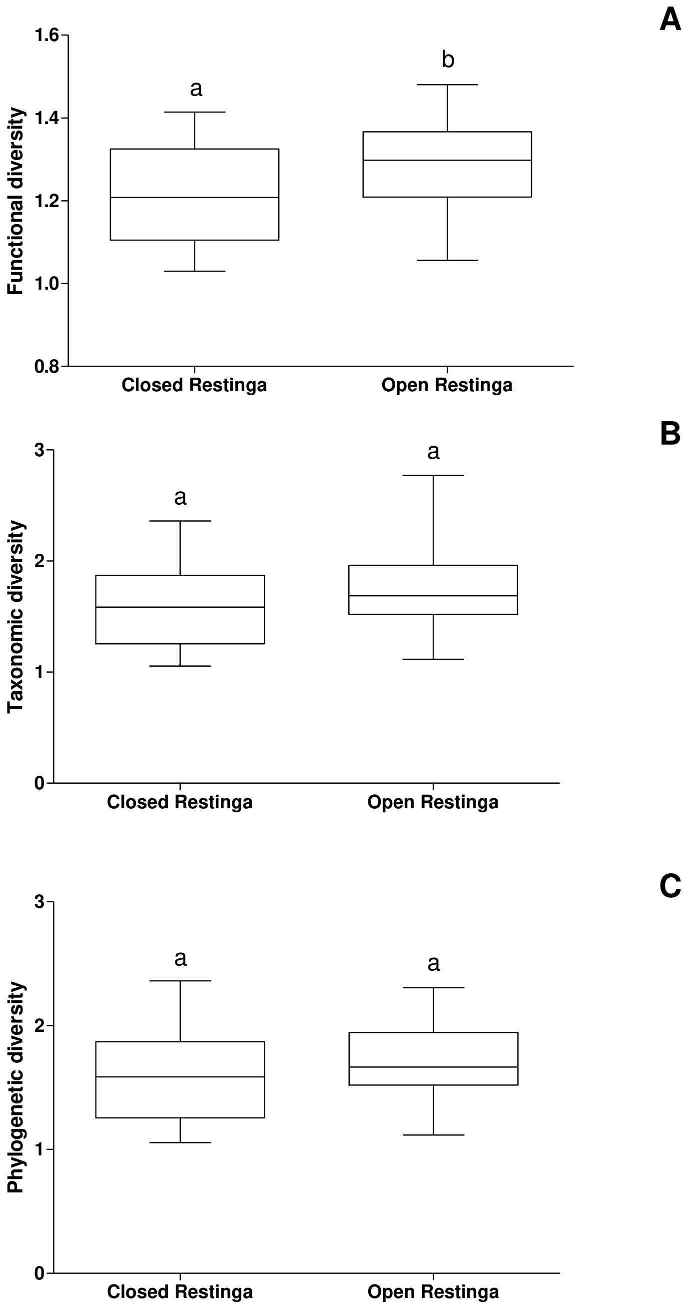


Traits	PCoA1	PCoA2
Trait 1	-0.93	0.14
Trait 2	-0.93	0.03
Trait 3	-0.84	0.19
Trait 4	-0.84	0.21
Trait *n*		

APPENDIX 1. Schematic representation of matrix multiplication of species traits (matrix B) *versus* the species abundance in each bromeliad (matrix W), which results in the matrix T that is the community weighted mean traits (Pillar and Duarte 2010). To visualize the distribution of the dominant traits of each *restinga* we calculated the Gower's distance of the matrix T (Dt) and then, performed the Principal Coordinates Analysis (PCoA) to extract the eigenvectors of Dt to draw a biplot figure. We identified the eigenvectors by the identity of the *Restinga* Forest (i.e., nutrient-rich or nutrient-poor).

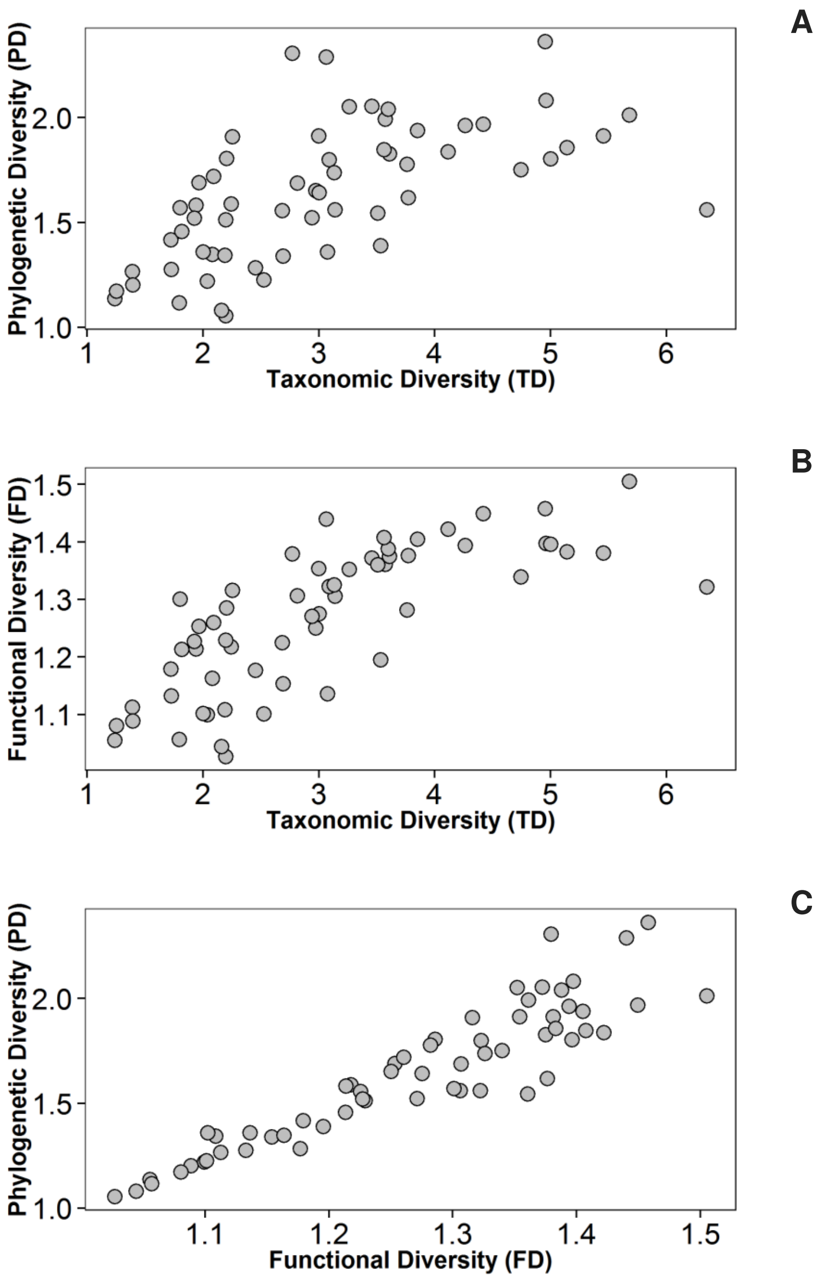
APPENDIX 2. The extent to each trait contributed to the Principal Coordinate Analysis. Traits that most contributed for axis one and two from the PCoA are in bold-face (eigenvector loading > 0.50). FPOM: fine particulate organic matter; CPOM: coarse particulate organic matter.

Trait type	**Trait**	**Loadings PCoA1**	**Loadings PCoA2**
Main components of diet	1. FPOM	-0.24	-0.17
	2. CPOM	**-0.93**	0.14
	3. Plant fibers	**-0.84**	0.19
	4. Leaf	**-0.74**	-0.31
	10. Saprophagous (decaying organic matter)	0.13	-0.55
Foraging group	5. Collector-gatherer	**0.61**	-0.44
	6. Collector-filters	-0.49	**0.59**
	7. Conveyor belt deposit feeder	-0.21	**-0.52**
	8. Filter feeders	0.43	-0.08
	9. Scraper	0.42	-0.01
	11. Shredder	**-0.77**	-0.24
Main foraging substrate	12. Surface filter feeders	-0.04	-0.19
	13. Column filter feeders	**0.77**	0.43
	14. Surface swimmers	0.19	**-0.84**
	15. Full water swimmer	**0.77**	0.43
	16. Crawler	**-0.84**	0.21
	17. Burrower	**-0.71**	-0.25
	18. Interstitial	**-0.93**	0.03
	19. Tube builder	**-0.84**	0.19
Body size	20. Body dry mass	0.44	-0.48



APPENDIX 3. Box plot showing the relationship between (i) functional diversity and environment (A), (ii) taxonomic diversity and environment (B), and (iii) phylogenetic diversity and environment. Different letters above each bar indicate significant differences in the detritivore diversity components within bromeliads from nutrient-poor and nutrient-rich *restinga* (linear

model: functional diversity $F_{1,58} = 8.339$, $P = 0.0054$; taxonomic diversity: $F_{1,58} = 3.301$, $P = 0.074$; phylogenetic diversity $F_{1,58} = 1.501$, $P = 0.225$).



APPENDIX 4. Relationship between (A) taxonomic diversity and phylogenetic diversity, (B) functional diversity and taxonomic diversity and (C) phylogenetic diversity and functional diversity. All the linear relationship are positive and significant (FD vs TD: $F_{1,58} = 81.05$, $P < 0.0001$, PD vs TD: $F_{1,58} = 35.33$, $P < 0.0001$, PD vs FD: $F_{1,58} = 174.59$, $P < 0.0001$).

SÍNTESE

No primeiro capítulo, mostramos que o tamanho da bromélia afeta as comunidades de organismos com ciclo de vida complexo. Abundância e biomassa de insetos foram maiores em bromélias grandes, especialmente a biomassa dos insetos predadores e filtradores, mas também dos fragmentadores, coletores e raspadores. Ao contrário das nossas predições iniciais, a abundância de odonatas não aumentou com o tamanho das bromélias. O tamanho do habitat, assim como a presença de aranhas, afetou o processamento dos detritos. Bromélias pequenas e bromélias com presença de aranhas possuíram maiores perdas de massa de detritos. Neste trabalho, demonstramos que cascatas tróficas iniciadas por predadores terrestres podem ultrapassar os limites dos ecossistemas e afetar o processamento da matéria orgânica (i.e., detritos). Encontramos evidências que suportam a existência de uma cascata trófica mediada pelo comportamento, a qual envolve a escolha do sítio de oviposição por odonatas bem como a atividade de forrageamento dos detritívoros. Aranhas reduziram a biomassa do nivel trófico superior (predadores de topo) e a da base da teia alimentar (detritos), sem alterar, no entanto, o nível intermediário (detritívoros). Nossos resultados indicam que o mecanismo subjacente aos efeitos das aranhas no processamento de detritos consiste na redução da biomassa de odonatas.

No segundo capítulo, por meio da amostragem de comunidades de organismos aquáticos presentes em bromélias, nós mostramos que a existência de pirâmides tróficas invertidas em ecossistemas naturais é completamente plausível. A inversão das pirâmides ocorreu ao longo de um gradiente de produtividade, i.e., produção de algas inferida por meio do tamanho da bromélia. As mudanças na estrutura das pirâmides refletem um aumento na biomassa de predadores com o aumento do tamanho da bromélias e ausência de uma mudança similar na biomassa de presas, resultado este consistente com fortes efeitos top-down de predadores em teias alimentares tri-tróficas. Demonstramos experimentalmente que a inversão das pirâmides tróficas pode ser mediada pelo consumo direto de predadores sobre suas presas. De fato, na ausência de consumo direto, as pirâmides tróficas tornaram-se tradicionais em formato. Nossos resultados reforçam a hipótese de que o formato das pirâmides tróficas depende de quanto a relação entre produtividade: biomassa (renovação ou *turnover*) e os níveis tróficos variam entre ecossistemas. Neste contexto, a inversão da pirâmide é possível como consequência da grande renovação de presas (e.g., mosquitos, ciclo de vida curto) e da baixa renovação de predadores de topo (i.e., larvas de odonata, ciclo de vida longo).

No último e terceiro capítulo, buscamos compreender o papel relativo do ambiente e dos effeitos *top-down* sobre os componentes da diversidade de presas detritívoras (i.e., diversidade funcional - FD, filogenética - PD e taxonômica - TD). Além disso, exploramos o papel relativo do ambiente (dois extremos de um gradiente ambiental), predadores e componentes da diversidade sobre o funcionamento ecossistêmico (EF) (i.e., decomposição e fluxo de nitrogênio). Os dois extremos do gradiente ambiental analisado diferem em relação a vários componentes, mas em especial, na quantidade de detritos presentes nas bromélias e quantidade/biomassa de predadores. A restinga aberta (a qual denominamos pobre em nutrientes) possui baixas densidades de detritos e grandes quantidades/biomassa de predadores. Já a restinga fechada (rica em nutriente), possui um padão oposto ao encontrado na restinga aberta, i.e., muito detrito e pouco predador. Nossos resultados mostraram que fatores ambientais não influenciam os diferentes componentes da diversidade de forma homogênea, de fato, ambiente explicou apenas a FD dos detritívoros. Predadores não explicaram qualquer variação na diversidade dos detritívos e/ou EF. Apesar de muitos estudos terem demonstrado uma relação positiva entre biodiversidade e EF, nossos resultados mostraram que uma relação positiva entre diversidade e

EF não pode ser considerada uma regra. Por exemplo, FD afetou negativamente o processamento da matéria orgânica, enquanto TD afetou positivamente. A restinga rica em nutriente apresentou menores valores de FD, no entanto, o processamento da matéria orgânica foi maior nesta restinga. No nosso artigo, sugerimos que o maior processamento da matéria orgânica se deve, em partes, aos caracteres funcionais que dominam cada restinga. Os caracteres dominantes na restinga rica em nutrientes são aqueles relacionados à quebra do particulado vegetal grosso, enquanto os da restinga pobre em nutrientes os caracteres relacionados a filtragem do particulado fino. Deste modo, mesmo com menores valores de FD, restingas ricas em nutrientes apresentam maior processamento de detritos, pois os organismos alí presentes possuem os caracteres impotantes ao início da quebra da matéria (fragmentação e raspagem). Deste modo, nós sugerimos que a relação positiva entre FD e EF é apenas verdadeira quando os caracteres dominantes são os melhores preditores de EF. Não somente, vimos que a TD foi um bom preditor de EF (afetou positivamente o processamento da matéria). Neste trabalho, sugerimos que TD de comunidades composta por grupos filogeneticamente distantes integram informações funcionais e evolutivass. Deste modo, a relação positiva entre TD e processamento de detrito pode encapsular padrões de complementariedade do uso de recursos. Acreditamos que o melhor entendimento da relação entre biodiversidade e EF em ecossistemas complexos será melhor compreendida um aumento no número de estudos que integrem a relação entre diversidade e fatores abiótios (que podem explicar muito do EF).