



UNIVERSIDADE ESTADUAL DE CAMPINAS

INSTITUTO DE BIOLOGIA

FATIMA CAROLINA RECALDE RUIZ

**EFEITOS *TOP-DOWN* E *BOTTOM-UP* EM TEIAS
ALIMENTARES RIPÁRIAS MEDIADOS POR EMERGÊNCIA
ALÓCTONE DE INSETOS AQUÁTICOS**

**TOP-DOWN AND BOTTOM-UP EFFECTS IN RIPARIAN
FOOD WEBS MEDIATED BY ALLOCHTHONOUS
EMERGENCE OF AQUATIC INSECTS**

CAMPINAS

2019

FATIMA CAROLINA RECALDE RUIZ

**EFEITOS *TOP-DOWN* E *BOTTOM-UP* EM TEIAS ALIMENTARES
RIPÁRIAS MEDIADOS POR EMERGÊNCIA ALÓCTONE DE INSETOS
AQUÁTICOS**

**TOP-DOWN AND BOTTOM-UP EFFECTS IN RIPARIAN FOOD WEBS
MEDIATED BY ALLOCHTHONOUS EMERGENCE OF AQUATIC
INSECTS**

*Tese apresentada ao Instituto de
Biologia da Universidade Estadual de
Campinas como parte dos requisitos
exigidos para a obtenção do título de
Doutora em Ecologia*

*Thesis presented to the Institute of
Biology of the University of Campinas
in partial fulfillment on the
requirements for the degree of Doctor
in Ecology*

ESTE ARQUIVO DIGITAL CORRESPONDE À
VERSÃO FINAL DA TESE DEFENDIDA PELA
ALUNA FATIMA CAROLINA RECALDE RUIZ E
ORIENTADA PELO GUSTAVO QUEVEDO
ROMERO.

Orientador: GUSTAVO QUEVEDO ROMERO

CAMPINAS

2019

Ficha catalográfica
Universidade Estadual de Campinas
Biblioteca do Instituto de Biologia
Mara Janaina de Oliveira - CRB 8/6972

R243e Recalde Ruiz, Fátima Carolina, 1987-
Efeitos *top-down* e *bottom-up* em teias alimentares ripárias mediados por emergência alóctone de insetos aquáticos / Fátima Carolina Recalde Ruiz. – Campinas, SP : [s.n.], 2019.

Orientador: Gustavo Quevedo Romero.
Tese (doutorado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Relações tróficas. 2. Animais predadores. 3. Ecossistema. 4. Inseto aquático. I. Romero, Gustavo Quevedo, 1974-. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.

Informações para Biblioteca Digital

Título em outro idioma: Top-down and bottom-up effects in riparian food webs mediated by allochthonous emergence of aquatic insects

Palavras-chave em inglês:

Trophic relationships

Predatory animals

Ecosystem

Aquatic insects

Área de concentração: Ecologia

Titulação: Doutora em Ecologia

Banca examinadora:

Gustavo Quevedo Romero [Orientador]

Fernando Rodrigues da Silva

Ana Zangirolame Gonçalves

Mathias Mistretta Pires

Simone Aparecida Vieira

Data de defesa: 07-08-2019

Programa de Pós-Graduação: Ecologia

Identificação e informações acadêmicas do(a) aluno(a)

- ORCID do autor: <https://orcid.org/0000-0002-0717-1596>

- Currículo Lattes do autor: <http://lattes.cnpq.br/4674678637962351>

Campinas, 7 de Agosto de 2019

COMISSÃO EXAMINADORA

Prof. Dr. Gustavo Quevedo Romero (Orientador)

Prof. Dr. Fernando Rodrigues da Silva

Dra. Ana Zangirolame Gonçalves

Prof. Dr. Mathias Mistretta Pires

Profa. Dra. Simone Aparecida Vieira

Os membros da Comissão Examinadora acima assinaram a Ata de Defesa, que se encontra no processo de vida acadêmica do aluno.

Aos meus pais, Julián e Isabel,

A Miguelito e Jazmincita,

A Nilson

AGRADECIMENTOS

Foram muitas as pessoas que contribuíram no meu caminho até este momento. Vou mencionar aqui as que tiveram um papel fundamental na minha formação tanto acadêmica como pessoal, mas sem esquecer às pessoas que passaram por minha vida e deram uma força, intencional ou não, para eu seguir em frente.

Primeiramente, gostaria de agradecer ao meu orientador Gustavo Quevedo Romero. Graças a seu incentivo, meu conhecimento e motivação científica cresceram de zero até o quanto uma pessoa pode ter para ser chamado de Doutor em Ecologia. Além de apoio acadêmico, o suporte pessoal por parte dele foi importante para lidar com potenciais situações adversas da vida cotidiana.

Aos meus colegas do LIMBio pelas muitas conversas divertidas e discussões teóricas e estatísticas das quais dependeu meu trabalho. Especialmente quero agradecer ao Pablo por tirar minhas dúvidas de estatística de forma desinteressada. À Paula, por me ajudar a entender meu sistema de estudo e discutir os meus resultados obtidos. A Paula sempre esteve ali. À Sandra e a Laura, por me proporcionarem uma linda amizade dentro e fora do laboratório. E ao Crasso, por suas muitas colaborações ao meu trabalho.

Não posso esquecer das pessoas que foram extremamente importantes na realização do árduo trabalho de campo, sempre esperado, mas muito cansativo. Vinícius, por me ajudar eficientemente no meu primeiro campo, Sandra, Rafa, Tiago e Paula, por me ajudarem a montar as primeiras gaiolas do meu experimento. Sandra, Mabel e Marcos por sua disposição de coletar comigo. Ao Crasso, por manejar as redes de neblina e me ajudar nas coletas. E ao Alaercio Marajó dos Reis, técnico de campo do PDBFF, por fazer um ótimo trabalho cozinhando e guiando à gente pela floresta.

Igualmente, agradeço à equipe do PDBFF por proporcionar a oportunidade de coletar na floresta Amazônica. Especialmente ao José Luis Camargo e à Rosely Hipólito, por sempre estar dispostos a tirar minhas dúvidas. Também, agradeço à Fundação Serra do Japi, pela oportunidade de usufruir as dependências da Serra do Japi para o trabalho de campo.

A minha tia Gady, que sempre esteve disposta a me ajudar quando eu precisava. Sou imensamente grata pelos meses que passei com ela nos inícios do doutorado, quando ainda não tinha como me sustentar economicamente. Pelas viagens ao Rio, pelos inúmeros almoços e

ceias, pela ajuda financeira e por todo o apoio emocional que me deu exatamente quando mais precisava. Obrigada tia!

Aos meus pais. A gratidão que sinto eu não conseguiria escrever em poucas palavras. Simplesmente eles me apoiaram em tudo. Apesar de estarmos longe um dos outros, sempre senti o apoio e o orgulho deles, e isso me deixa sem palavras suficientes para agradecer. Grande parte do que fiz durante esse período de formação no Brasil, foi por eles. Todo meu amor e gratidão mami y papi!

Miguelito também foi uma das fortes motivações que tive para me esforçar no caminho da ciência. Agradeço inteiramente a ele por me demonstrar tanto amor e confiança. Assim como agradeço aos seus pais, minha irmã Chabela e meu cunhado Miguel, e a minha irmã Sol, por sempre estar me apoiando não só academicamente, mas principalmente de forma pessoal. Não esqueço de Jazmincita, que com apenas um ano, já conseguiu me inspirar a tranquilidade emocional que precisava para permanecer na vida acadêmica.

Quero fazer um agradecimento especial ao Nilson, por todo seu apoio tanto na minha vida acadêmica como pessoal. Por ser a pessoa a quem eu posso chegar sob qualquer circunstância, pelo resto da vida.

Por último, quero agradecer a Deus, quem embora não precise destas formalidades, esteve e continua estando presente na minha vida.

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) -Código de Financiamento 001. Uma parte deste estudo também foi financiado pela Fundação de Apoio à Pesquisa do Estado de São Paulo/FAPESP (proc. 2017/09052-4) e pelo Conselho Nacional de Desenvolvimento Científico e Tecnológico (400892/2014-6)

RESUMO

As teias alimentares compreendem interações entre os consumidores e seus recursos, sendo que muitas vezes, esses recursos podem vir de ecossistemas adjacentes. Recursos externos que entram nos ecossistemas são conhecidos como recursos alóctones, e podem gerar respostas numéricas e funcionais dos consumidores. Teoricamente, estes recursos alóctones têm um importante papel estabilizador nas teias alimentares receptoras uma vez que mitiga os efeitos negativos da predação ou da competição entre consumidores. Desta forma, quando os recursos alóctones subsidiam os consumidores que sofrem forte pressão de predação ou são competitivamente inferiores, a potencial extinção destes poderia ser evitada. Neste trabalho buscamos entender o papel dos recursos alóctones representados por insetos aquáticos emergentes na heterogeneidade trófica de predadores terrestres e na invariabilidade das interações tróficas. No primeiro capítulo, foi estudado o efeito de insetos aquáticos emergentes sobre a atividade, a dieta e a estrutura trófica (espaço trófico e diversidade trófica) de aves e morcegos predadores. Esta heterogeneidade trófica dos predadores é fortemente influenciada pelos diferentes tipos de presas, sendo que quanto maior a diversidade de presas mais heterogêneo será o nicho trófico dos predadores. No segundo capítulo foi estudado o papel dos insetos aquáticos emergentes na invariabilidade da cadeia alimentar ripária. Uma vez que predadores de topo e mesopredadores estão interconectados por presas em comum, a disponibilidade de presas alternativas, neste caso, insetos aquáticos emergentes, faz com que a pressão de predação sobre os mesopredadores e as presas em comum seja mitigada. Os nossos resultados indicam que a entrada de recursos aquáticos alóctones estrutura a comunidade de predadores de topo, estabilizando as interações entre estes e os níveis tróficos inferiores. Nosso trabalho traz importantes considerações sobre a importância do fluxo entre o ecossistema aquático e a floresta, sendo que ambos são interdependentes e precisam ser manejados de forma conjunta.

ABSTRACT

Food webs depend on interactions between consumers and their resources, and these resources can originate in different ecosystems. The foreign resources are known as allochthonous resources, and can trigger numeric and functional responses of consumers. Theoretically, allochthonous resources are important in stabilizing food webs once they mitigate the negative effects of predation or competition between consumers. Thus, consumers under strong predation pressure or competition can avoid potential extinctions when they are subsidized by allochthonous resources. In this study, we studied the role of allochthonous resources represented by emergent aquatic insects on trophic heterogeneity of terrestrial predators and on the invariability of trophic interactions. In the first part, we studied the effect of emergent aquatic insects on activity, diet and trophic structure (trophic spaces and trophic diversity) of predator bats and birds. The trophic heterogeneity of predators is strongly influenced by their different food items, once the diversity of prey increases the trophic variation of predators. In the second part of this study, we studied the role of emergent aquatic insects in riparian food chain invariability. Top predators and mesopredator are connected by shared prey, so, the input of an alternative prey (emergent aquatic insects) mitigate the predation pressure on mesopredators and shared prey. The results indicate that the input of allochthonous aquatic resources structure the community of top predators, stabilizing the trophic interactions in a food chain. This study brings significant considerations on the importance of cross-ecosystem flux, once both aquatic and terrestrial ecosystems are interdependent and need an integrative management.

SUMÁRIO

Introdução Geral	11
Artigo I. <i>Trophic variation in tropical birds and bats is driven by allochthonous resources</i>	
Abstract	26
Introduction	27
Material and Methods	29
Results	34
Discussion	38
References	42
Artigo II. <i>Allochthonous aquatic subsidies weaken predation pressure in terrestrial ecosystems</i>	
Abstract	48
Introduction	49
Material and Methods	53
Results	56
Discussion	61
References	64
Conclusão Geral	71
Referências	72
Apêndices	83
Anexos	96
Anexo 1. Certificado da Comissão de Ética no uso de animais (CEUA/UNICAMP)	96
Anexo 2. Declaração de Direitos autorais	97

INTRODUÇÃO GERAL

O fluxo de energia e matéria dentro do ecossistema é ubíquo entre o meio abiótico e as comunidades biológicas. Como seres não isolados, os organismos participam das interações mediadas por esse fluxo, o que melhora o crescimento e o desempenho para realizar suas atividades. No entanto, os ecossistemas são abertos e podem receber energia e materiais externos através da migração, vento, marés, precipitação ou pela ação da gravidade. Consequentemente, organismos receptores podem ser total ou parcialmente dependentes desta entrada e, de acordo com o papel desses indivíduos nos ecossistemas, a influência do fluxo alóctone pode ultrapassar o consumidor e governar vários processos ecológicos gerando cascatas tróficas (Henschel et al. 2001, Murakami e Nakano 2002, Leroux e Loreau 2008) (Fig. 1).

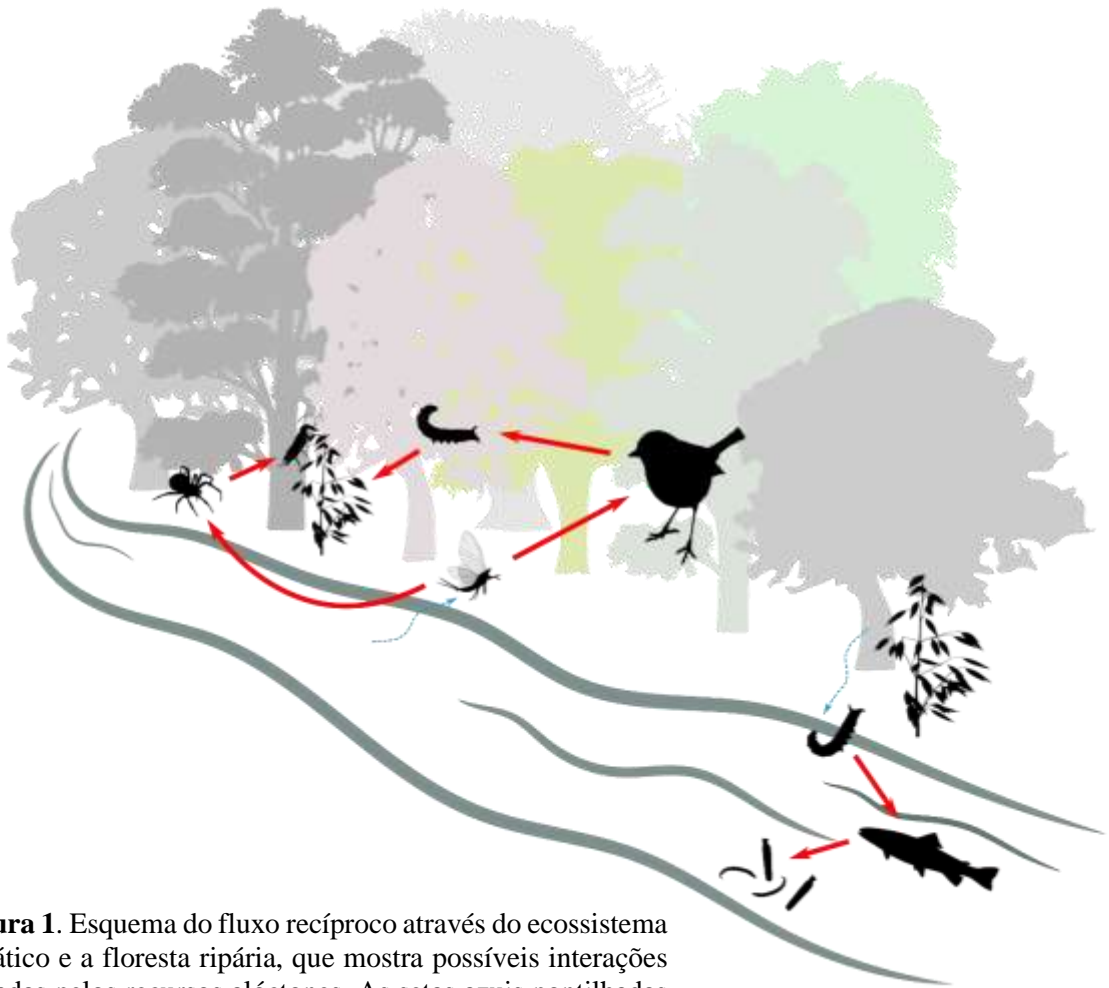


Figura 1. Esquema do fluxo recíproco através do ecossistema aquático e a floresta ripária, que mostra possíveis interações afetadas pelos recursos alóctones. As setas azuis pontilhadas indicam a entrada de recursos alóctones no ecossistema adjacente. As setas vermelhas sólidas indicam os efeitos desencadeados pela entrada de recursos alóctones sobre os níveis tróficos da teia alimentar receptora. As pontas das setas indicam o sentido do efeito.

Fluxo através dos ecossistemas

Os organismos receptores da energia e matéria que entra em um ecossistema abrangem desde produtores, consumidores primários até os predadores de topo. Esses organismos são subsidiados pelo fluxo de energia e matéria, uma vez que recursos autóctones (i.e., próprios do ecossistema) e recursos alóctones (i.e., originados em outros ecossistemas) ficam disponíveis para consumo (Polis et al. 1997). Desta forma, os recursos alóctones são chamados comumente de subsídios. O fluxo de recursos alóctones entre ecossistemas é recíproco, portanto, ecossistemas adjacentes ficam propensos a trocas de subsídios (Nakano e Murakami 2001, Baxter et al. 2005, Richardson et al. 2010). Contudo, a teoria enuncia que a magnitude da entrada alóctone depende da topografia do ecossistema receptor (Leroux e Loreau 2008). Assim, ecossistemas com perfil côncavo como lagos e riachos recebem maior quantidade de recursos alóctones simplesmente por ação da gravidade, atuando como coletores, e experimentando cascatas tróficas mais fortes que aqueles ecossistemas de perfil convexo (e.g., pradarias, florestas, serras) (Leroux e Loreau 2008, Bartels et al. 2012). No entanto, a cascata trófica desencadeada pelos subsídios que entram em florestas ou montanhas, embora mais fraca que nos ecossistemas aquáticos, acarreta importantes consequências para as teias tróficas receptoras (Baxter et al. 2005, Marczak et al. 2007).

Efeitos dos recursos alóctones nos consumidores receptores

O principal fator que desencadeia efeitos indiretos dos recursos alóctones nas teias alimentares receptoras é a resposta do consumidor. Certos consumidores estão adaptados aos recursos do próprio hábitat, consumindo pobremente os recursos alóctones. Portanto, apesar da disponibilidade de recursos alóctones, o efeito *top-down* gerado por esses consumidores na cadeia alimentar apenas será influenciada por fatores próprios do ecossistema (Lam et al. 2013). Por outro lado, muitos consumidores apresentam uma dieta mais generalista e aproveitam os recursos disponíveis de forma oportunista. Neste sentido, recursos alóctones disponíveis aos generalistas serão melhor aproveitados, e potencialmente irão desencadear cascatas tróficas na teia alimentar.

Frequentemente, recursos alóctones geram uma resposta numérica sobre os consumidores subsidiados. Por exemplo, Sabo e Power (2002) realizaram um experimento de exclusão de insetos aquáticos emergentes (recurso alóctone) em uma área ripária habitada por predadores como lagartos e aranhas. Eles encontraram que, devido a essa exclusão, as densidades de lagartos e aranhas decresceram em comparação as áreas controle (i.e., com

entrada natural de recursos alóctones). Similarmente, Kato e colaboradores (2003) evidenciaram que a densidade de aranhas construtoras de teias horizontais (Tetragnathidae) reduziu com a exclusão da entrada de insetos aquáticos emergentes na floresta ripária, principalmente em períodos onde a disponibilidade destes recursos foi alta. Por outro lado, recursos alóctones podem acarretar respostas funcionais dos consumidores receptores, como, por exemplo, mudança na dieta. Consumidores que ocorrem em ambientes sazonais podem mudar o uso de recursos autóctones e alóctones de acordo com a disponibilidade desses (Nakano e Murakami 2001, Mazoni e Rezende 2003, Sánchez-Hernández et al 2016). Por exemplo, em estações chuvosas ou frias, consumidores aquáticos utilizam os recursos mais disponíveis, i.e., recursos autóctones. Por outro lado, em temporadas secas, onde a produção de presas autóctones é menor, ou em temporadas de degelo, quando a entrada de recursos externos é maior, os consumidores aquáticos mudam o uso de recursos, passando a aproveitar mais os recursos alóctones (Mazzoni e Rezende 2003, Sánchez-Hernández et al. 2016).

A dieta dos consumidores receptores, portanto, pode ser estabelecida pela disponibilidade de cada tipo de recurso. Por exemplo, em florestas ripárias da Mata Atlântica foi observado que insetos aquáticos emergentes contribuíram com mais de 85% da dieta de aranhas ripárias (Recalde et al. 2016). Dependendo dos tipos de presas utilizadas, pode se estimar o nicho trófico do consumidor, sendo que a amplitude do nicho é maior quanto mais presas o consumidor utiliza (Newsome et al. 2007). Neste sentido, aranhas capazes de capturar tanto recursos autóctones como recursos alóctones teriam maior nicho trófico comparadas com aranhas que consomem apenas recursos autóctones (Recalde et al. 2016). Esse caso seria análogo a consumidores generalistas e especialistas. Sabe-se que nos trópicos, o grau de especialização é maior que nas áreas temperadas, portanto, é esperado que a amplitude do nicho trófico dos consumidores seja menor (MacArthur 1972). No entanto, a maior disponibilidade de recursos fornecidos nos ecótonos (onde há muito intercâmbio de recursos) tropicais, possibilitaria um maior nicho trófico das populações. Contudo, ainda existem lacunas no conhecimento da influência dos recursos alóctones sobre a amplitude do nicho trófico de consumidores tropicais.

Efeitos dos recursos alóctones nas teias alimentares receptoras: a teoria

O papel dos organismos em um ecossistema acarreta consequências em seu funcionamento, cuja magnitude depende da importância do organismo dentro da rede de interações. Se esse organismo é subsidiado, as consequências poderiam ser ainda mais

significativas. Comunidades que recebem recursos alóctones de forma frequente apresentam teias alimentares interconectadas entre ambos os ecossistemas (Polis e Hurd 1995, Polis et al. 1997). A estabilidade dessas teias alimentares, portanto, pode ser potencialmente mantida pelos recursos alóctones (Huxel e McCann 1998, Huxel et al. 2002).

Huxel e McCann (1998) e Huxel e colaboradores (2002) definiram estabilidade como a persistência da teia alimentar. Eles usaram modelos teóricos de uma cadeia alimentar tri-trófica, formada por predador, consumidor e recurso basal para examinar a influência da entrada alóctone na estabilidade da teia alimentar. Teoricamente, o aproveitamento dos subsídios depende da magnitude da entrada alóctone e da preferência do consumidor, e quanto maior forem esses valores, maior a resposta numérica dos consumidores (Huxel e McCann 1998). Desta forma, um alto nível de entrada alóctone pode incrementar significativamente a capacidade de suporte do ecossistema receptor, dissociando as relações entre os consumidores e seus recursos autóctones e potencialmente levando à extinção de um ou mais níveis tróficos (Rosenzweig 1971, Huxel e McCann 1998, Huxel et al. 2002). Assim, baixos níveis de entrada alóctone mantém a teia alimentar estável.

Complementarmente, a estabilidade das teias alimentares está governada por vários fatores. O primeiro fator está relacionado a qual nível trófico é subsidiado, sendo que a teia alimentar é mais estável (tem menor variação) quando ambos, predadores de topo e consumidores são subsidiados. O subsídio faz com que estes níveis tróficos compitam menos pelos recursos autóctones e, portanto, exista menor pressão entre predadores de topo e consumidores. Além disso, consumidores são controlados pelos predadores de topo e conseqüentemente, o recurso basal não é extinto pela pressão do consumidor. O segundo fator refere-se à preferência alimentar dos níveis tróficos subsidiados. Predadores de topo especializados em recursos alóctones atenuam a pressão de predação sobre os consumidores, no entanto, os generalistas ainda controlam os níveis tróficos inferiores, mantendo a estabilidade devido à partilha dos recursos. O terceiro fator compreende a magnitude da entrada de recursos alóctones. Baixos níveis de entrada alóctone não provocam uma resposta numérica extrema dos níveis tróficos receptores, que poderia levar à desestabilização do sistema. O último fator é a força de interação entre consumidor-recurso; neste sentido, quando o predador é altamente subsidiado e possui uma interação forte com o consumidor, há um incremento na pressão sobre os consumidores podendo conseqüentemente afetar níveis tróficos inferiores (via cascata trófica). No entanto, quando a interação entre predador e consumidor é fraca, a pressão

sobre este é menor possibilitando a persistência dos níveis tróficos inferiores (Huxel et al. 2002).

Ecosistemas aquáticos apresentam cascatas tróficas mais intensas comparados com ambientes terrestres (Shurin et al. 2002, Shurin et al. 2006), e sugere-se que essa intensidade é resultante de uma intensa entrada de subsídios (hipótese dos subsídios, Leroux e Loreau 2008). Neste sentido, os ecossistemas aquáticos recebem maior quantidade de recursos alóctones que os ecossistemas terrestres (Leroux e Loreau 2008, Bartels et al. 2012), experimentando cascatas tróficas mais fortes e potencialmente desestabilizando as teias alimentares (Huxel e McCann 1998).

Mecanismos de entrada dos recursos alóctones

O mecanismo de entrada dos recursos pode ser (1) passivo, quando é gerada por vetores físicos, como vento ou gravidade, sendo arrastados de forma aleatória. Ou (2) ativo, que ocorre quando organismos vivos originados em um ecossistema migram para ecossistemas adjacentes a fim de se alimentar ou reproduzir. A seguir, alguns exemplos de entrada passiva e ativa dos recursos alóctones e o efeito deles sobre a comunidade receptora.

Entrada passiva. Um exemplo clássico e bem detalhado do efeito da entrada passiva de recursos alóctones no ecossistema receptor é apresentado no trabalho de Nakano e colaboradores (1999). Os autores manipularam a entrada de artrópodes terrestres e a presença de peixes predadores em um riacho do norte do Japão para testar a influência dos subsídios nas interações aquáticas. Artrópodes terrestres comumente caem de forma acidental pela ação da gravidade e chegam aos riachos ou lagos onde são predados por peixes generalistas. Os autores encontraram efeitos *top-down* mais fortes na ausência de artrópodes terrestres (i.e., recursos alóctones). Neste cenário, os peixes mudaram a dieta passando a consumir majoritariamente herbívoros aquáticos, diminuindo a biomassa destes e, por conseguinte, aumentando a biomassa do perifíton (Nakano et al. 1999). Wallace e colaboradores (1997), por outro lado, encontraram um forte efeito *bottom-up* com a exclusão da entrada de recursos alóctones em um riacho dos Estados Unidos. Especificamente, os autores construíram uma cobertura suspensa de 180 m para excluir a entrada de folhiço no riacho. Após três anos de experimento, houve uma diminuição na abundância de artrópodes predadores aquáticos, evidenciando uma redução na disponibilidade de presas (efeito *bottom-up*). A entrada passiva dos recursos alóctones também pode ocorrer do

ecossistema aquático para o terrestre. Neste caso, recursos como detritos e nutrientes são arrastados pela maré ou por enchentes para o ambiente terrestre. Polis e Hurd (1995) testaram o efeito *bottom-up* da entrada de carcaças e restos de algas arrastados pela maré nas ilhas do Golfo de Califórnia. Aranhas e outros predadores (escorpiões e lagartos) tornaram-se mais abundantes nas áreas costeiras devido ao incremento de detritívoros que consomem os detritos marinhos. Deste modo, a entrada passiva dos recursos alóctones pode ser recíproca (i.e., no sentido terrestre → aquático e aquático → terrestre) causando efeitos indiretos significativos nas teias alimentares receptoras.

Entrada ativa. Dependendo dos hábitos ou do ciclo de vida, os organismos podem chegar aos ecossistemas adjacentes de forma ativa (e.g., migração) alterando a dinâmica destes. Por exemplo, alguns predadores forrageiam nos limites dos ecossistemas e são capazes de consumir presas que se desenvolvem em habitats diferentes (Knight et al. 2005, Marczak et al. 2007). Ao contrário, organismos que se deslocam para ecossistemas adjacentes podem servir de presa para os predadores das comunidades receptoras (Baxter et al. 2005, Richardson e Sato 2015, Recalde et al. 2016). O ciclo de vida complexo permite que insetos aquáticos migrem para ecossistemas adjacentes ao tornarem-se adultos. Assim, nutrientes e energia do ambiente aquático são assimilados pelos insetos imaturos que ao emergirem na fase adulta, acabam fazendo parte do conjunto de recursos disponíveis nos ecossistemas terrestres. Henschel e colaboradores (2001) testaram o efeito da entrada desses insetos na teia alimentar terrestre em um riacho na Alemanha. Eles encontraram que, nas margens do riacho, a abundância de aranhas foi maior e de gafanhotos foi menor. Já em áreas afastadas do riacho (30-60m), com menos recursos alóctones, aranhas foram menos abundantes, enquanto os gafanhotos foram mais abundantes. Consequentemente, plantas da espécie *Urtica dioica* (Urticaceae) sofreram menos herbivoria nas margens em comparação às áreas afastadas (Henschel et al. 2001). Similarmente, Recalde e colaboradores (2016) estudaram o efeito dos insetos emergentes na Mata Atlântica da Serra do Japi (SP). Neste estudo, as aranhas ripárias foram fortemente subsidiadas pela emergência de insetos aquáticos, tendo um aumento em sua abundância e biomassa, diminuindo consequentemente a biomassa de insetos terrestres herbívoros (Recalde et al. 2016). Esses são apenas alguns exemplos representativos do forte efeito da entrada ativa de recursos alóctones nas comunidades receptoras.

Estudos de intercâmbio de recursos entre ecossistemas são comumente abordados na interface aquática-terrestre. Por serem ambientes bem contrastantes (Anderson e Polis 1998, Richardson et al. 2010), o conteúdo nutricional dos recursos aquáticos é facilmente diferenciado dos terrestres (Sitters et al. 2015) e, portanto, a contribuição para os consumidores pode ser estimada (Recalde et al. 2016). As florestas ripárias apresentam características estabelecidas tanto pelo ecossistema terrestre como pelo aquático circundante. Estas áreas possuem uma alta diversidade de recursos disponíveis para os consumidores e, portanto, são sistemas adequados para estudar o efeito da entrada alóctone em um ecossistema.

Florestas ripárias como receptoras do fluxo alóctone

Florestas ripárias são basicamente ecótonos situados entre o ecossistema aquático e a floresta e, portanto, apresentam uma biodiversidade própria que é formada tanto por recursos alóctones como autóctones. A forte influência do ecossistema aquático adjacente faz com que estas áreas apresentem estrutura e funções características (Malanson 1993). A estrutura da zona ripária pode ser caracterizada por espécies vegetais adaptadas às enchentes em que o fluxo de recursos disponíveis é diversificado de acordo com os períodos de alagamento (Bendix 2017). Por outro lado, estas zonas podem ser caracterizadas por apresentarem terrenos firmes, sem enchentes ao longo do ano e, conseqüentemente, com espécies vegetais similares à floresta mais interna. Terrenos firmes são mais comuns em florestas ripárias que margeiam riachos de primeiro ou segundo grau, já que estes apresentam menos fluxo que os grandes cursos d'água. Além disso, a disponibilidade de água, a diversidade de recursos e a estrutura de corredor permitem que as zonas ripárias atuem como refúgios, atraindo organismos para se alimentarem (Malanson 1993, Bendix 2017).

O controle *top-down* gerado pelos recursos alóctones nas florestas ripárias é frequente. A entrada de subsídios nestas florestas é ativa, principalmente na forma de insetos aquáticos adultos, que emergem da superfície d'água para os ambientes terrestres. Nesses lugares, eles são facilmente predados pelos consumidores ripários que por sua vez, exercem maior pressão sobre as presas autóctones (Jackson e Fisher 1986, Bartels et al. 2012).

Insetos aquáticos emergentes como subsídios nas florestas ripárias

Nos trópicos, existe uma diversidade alta de insetos aquáticos com ciclo de vida complexo principalmente das ordens Ephemeroptera, Diptera, Coleoptera e Trichoptera (Jacobsen et al. 2008). Além delas, Odonata e Hemiptera também correspondem a uma porção importante dos insetos aquáticos, assim como Plecoptera, Lepidoptera e Megaloptera, mas em

menor proporção (<1%, Jacobsen et al. 2008). No entanto, alguns grupos das ordens Coleoptera e Hemiptera são completamente aquáticos, e alguns poucos grupos de Coleoptera e Megaloptera possuem estágio larval ou pupal terrestre (Huryn et al. 2008), portanto não são capazes de subsidiar o ambiente ripário.

Numerosos estudos indicam sazonalidade na disponibilidade de insetos aquáticos adultos nos ambientes terrestres (Jackson e Fisher 1986, Nakano e Murakami 2001, Takimoto et al. 2002, Huryn et al. 2008). Entretanto, a sazonalidade nos trópicos não é muito evidente (mas pode acontecer na escala local) devido à grande diversidade de táxons, que possibilita a ocorrência de vários ciclos completos em um ano (gerações multivoltina, Huryn et al. 2008). Sendo assim, os consumidores destes recursos são continuamente subsidiados.

Além de serem recursos disponíveis de forma contínua, os insetos aquáticos emergentes são uma fonte rica de nutrientes e representam presas de alta qualidade para os consumidores, comparado com presas terrestres (Hixson et al. 2015). Ecossistemas aquáticos apresentam produtores primários que sintetizam ácidos graxos poliinsaturados de cadeia longa (PUFAs), que são macromoléculas essenciais para as funções fisiológicas e a saúde em geral de organismos aquáticos e terrestres (Guo et al. 2016, Twining et al. 2016, Fritz et al. 2017). Assim, macroinvertebrados herbívoros assimilam as macromoléculas mediando o transporte de nutrientes de alta qualidade na teia alimentar aquática (Strandberg et al. 2015, Guo et al. 2016). Por outro lado, teias alimentares detritívoras também são beneficiadas pelos ácidos graxos de alta qualidade, uma vez que micélios de fungos que colonizam os detritos sintetizam essas macromoléculas (Chung e Suberkropp 2009, Funk et al. 2015). Ao consumir o perifíton que coloniza os detritos nos riachos, as larvas dos insetos aquáticos assimilam ácidos graxos de alta qualidade, que exportam para os ambientes ripários quando emergem como adultos, aprimorando, desta forma, o funcionamento fisiológico dos consumidores terrestres (Gladyshev et al. 2013, Twining et al. 2016, Martin-Creuzburg et al. 2017).

A alta diversidade local das florestas ripárias, isto é, alta abundância e riqueza de recursos autóctones, permite que os consumidores sejam mantidos por esses recursos. No entanto, embora a entrada de insetos aquáticos emergentes possa ser menor comparado com recursos terrestres, os consumidores podem apresentar preferência por esses recursos (Recalde et al. 2016) devido à maior qualidade destes, resultando em cascatas tróficas entre ecossistemas. Por outro lado, consumidores generalistas subsidiados são mantidos tanto por

recursos autóctones como alóctones, possibilitando que as cascatas tróficas sejam mais fracas e evidenciando, desta forma, o papel estabilizador dos subsídios.

Nas últimas décadas, estudos têm apontado aranhas e vertebrados insetívoros (e.g. aves, lagartos e morcegos) como os consumidores terrestres mais subsidiados pela emergência de insetos aquáticos (Nakano e Murakami 2001, Barrett et al. 2005, Fukui et al. 2006, Marczak e Richardson 2007). Aranhas são dependentes de insetos aquáticos emergentes em florestas temperadas (Kato et al. 2003, Marczak e Richardson 2007), desertos (Sanzone et al. 2003) e florestas tropicais (Chan et al. 2009, Recalde et al. 2016). Além disso, são os predadores com maior importância na transferência dos nutrientes e energia dos ambientes aquáticos para as teias alimentares terrestres (Jackson e Fisher 1986). Embora aves e morcegos insetívoros sejam atraídos para florestas ripárias temperadas, pela grande disponibilidade de presas (Marczak et al. 2007, Fukui et al. 2006), ainda há uma grande lacuna no conhecimento do efeito dos subsídios aquáticos sobre vertebrados insetívoros em ambientes tropicais (Chan et al. 2008). Ecossistemas tropicais como florestas e savanas estão entre os “*hotspots*” de diversidade mais ameaçados do mundo (Myers et al. 2000, Myers 2003), portanto é urgente entender os fatores que governam o funcionamento destes. Florestas ripárias são cosmopolitas nos trópicos, e estão sob pressão das atividades humanas, principalmente pelo uso da terra (Novo Código Florestal Brasileiro, Lei n. 12.651/2012). Portanto, continuar estudando estes ecossistemas como entes abertos capazes de manter o funcionamento e estabilidade dos ecossistemas é de extrema importância para a sustentabilidade das florestas tropicais.

Nesta tese investigamos a importância dos subsídios aquáticos na dinâmica trófica das comunidades terrestres. Primeiramente, testamos se consumidores generalistas, como aves e morcegos insetívoros, são dependentes de subsídios alóctones em florestas ripárias. Essa predição está baseada na premissa bem fundamentada (e.g., Nakano e Murakami 2001, Barrett et al. 2005, Fukui et al. 2006, Marczak e Richardson 2007, Marczak et al. 2007, Muehlbauer et al. 2014, Recalde et al. 2016 e referências citadas) que florestas irrigadas com abundantes riachos são potencialmente mantidas pela entrada ativa de recursos alóctones (i.e., insetos aquáticos emergentes) devido à alta mobilidade destes (Muehlbauer et al. 2014, Recalde et al. 2016). Uma vez que os subsídios aquáticos influenciam predadores ripários, esperamos que as interações tróficas entre predadores de topo (i.e., aves e morcegos) e mesopredadores (i.e., aranhas) mais frequentemente conhecidas como interação intraguilda, e seus efeitos sobre as presas compartilhadas (i.e., insetos terrestres) sejam mitigadas pelo papel estabilizador dos subsídios .

Objetivos Gerais

A tese contém dois capítulos com os seguintes objetivos gerais:

Capítulo I. Determinar o efeito de insetos aquáticos emergentes sobre a atividade de forrageamento e estrutura trófica de aves e morcegos insetívoros.

Capítulo II. Investigar o efeito estabilizador dos recursos alóctones sobre as interações de predação intraguilda entre predadores de topo (i.e., aves e morcegos insetívoros) e mesopredadores (i.e., aranhas ripárias).

Esta tese foi aprovada pela CEUA/UNICAMP (Anexo 1) e não infringe o direito autoral de qualquer editora (Anexo 2).

Referências

- Anderson, W. B. e G. A. Polis. 1998. Marine subsidies of island communities in the Gulf of California: Evidence from stable carbon and nitrogen isotopes. *Oikos* 81:75-80
- Barrett, K., W. B. Anderson, D. A. Wait, L. L. Grismer, G. A. Polis e M. D. Rose. 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations. *Oikos* 109:145-153
- Bartels, P., J. Cucherousset, K. Steger, P. Eklöv, L. J. Tranvik e H. Hillebrand. 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* 93:1173-1182
- Baxter, C. C., K. D. Fausch e C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201-220
- Bendix, J. 2017. Riparian ecosystems. Em: Richardson, D., Castree, N., Goodchild, M. F. et al. (eds). *The International Encyclopedia of Geography*. John Wiley & Sons
- Chan, E. K. W., Y.T. Yu, Y. Zhang and D. Dudgeon. 2008. Distribution patterns of birds and insect prey in a tropical riparian forest. *Biotropica* 40: 623-629
- Chan, E.K.W., Zhang, Y. e Dudgeon, D. 2007. Contribution of adult aquatic insects to riparian prey availability along tropical forest stream. *Marine and Freshwater Research* 58:725-732

- Chung, N. e Suberkropp, K. 2009. Effects of aquatic fungi on feeding preferences and bioenergetics of *Pycnopsyche gentilis* (Trichoptera: Limnephilidae). *Hydrobiologia* 630:257-269
- Fritz, K. A., Kirschman, L. J., McCay, S. D., Trushenski, J. T., Warne, R. W. e Whiles, M. R. 2017. Subsidies of essential nutrients from aquatic environments correlate with immune function in terrestrial consumers. *Freshwater Science* 36:893-900
- Funk, J. A., Bec, A. Perrière, F., Felten, V. e Danger, M. 2015. Aquatic hyphomycetes: a potential source of polyunsaturated fatty acids in detritus-based stream food webs. *Fungal Ecology* 13:205-210
- Fukui, D., M. Murakami, S. Nakano e T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology* 75:1252-1258
- Gladyshev, M. I., Sushchin, N. N. e Makhutova, O. N. 2013. Production of EPA and DHA in aquatic ecosystems and their transfer to the land. Prostaglandins and other lipid mediators. 107:117-126
- Guo, F., Kainz, M. J., Sheldon, F. e Bunn, S. E. 2016. The importance of high-quality algal food sources in stream food webs -current status and future perspectives. *Freshwater Biology*. Doi:10.1111/fwb.12755
- Henschel, J. R., D. Mahsberg e H. Stumpf. 2001. Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. *Oikos* 93:429-438
- Hixson, S. M., Sharma, B., Kainz, M. J., Wacker, A. e Arts, M. T. 2015. Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: a fundamental dichotomy between freshwater and terrestrial ecosystems. *Environmental Reviews* 23:414-424
- Huryn, A. D., Wallace, J. B. e Anderson, N. H. 2008. Habitat, life history, secondary production, and behavioral adaptations of aquatic insects. Em: Merritt, R. W., Cummins, K. W., Berg, M. B. (eds). *An introduction to the aquatic insects of North America*. Fourth Edition. Kendall/Hunt Publishing Company
- Huxel, G. R., and K. McCann. 1998. Food web stability: the influence of trophic flows across habitats. *The American Naturalist* 152:460-469.
- Huxel, G. R., K. McCann, and G. A. Polis. 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. *Ecological Research* 17:419-432.
- Jackson, J. K. e S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran desert stream. *Ecology* 67:629-638

- Jacobsen, D., Cressa, C., Mathooko, J. M. e Dudgeon, D. 2008. Macroinvertebrates: Composition, life histories and production. Em: Dudgeon, D. (ed). *Tropical Stream Ecology*. Elsevier Inc, USA
- Kato, C., T. Iwata, S. Nakano e D. Kishi. 2003. Dynamics of aquatic insect flux affects distribution of riparian web-building spiders. *Oikos* 103:113-120
- Knight, T. M., McCoy, M. W. Chase, J. M., McCoy, K. A. e Holt, R. D. 2005. Trophic cascades across ecosystems. *Nature* 437:880-883
- Lam, M. M-Y, D. Martin-Cewuzburg, K-O. Rothhaupt, K. Safi, E. Yohannes and I. Salvarina. 2013. Tracking diet preferences of bats using stable isotope and fatty acid signatures of faeces. *PLoS ONE* 8: e83452
- Leroux, S. J. e Loreau, M. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* 11:1147-1156
- MacArthur RH (1972) *Geographical Ecology*. Princeton University Press, Princeton, N. J.
- Malanson, G. P. 1993. *Riparian Landscape*. Cambridge University Press. Cambridge. Pages: 12-37
- Marczak, L. B. e J. S. Richardson. 2007. Spiders and subsidies: results from the riparian zone of a coastal temperate rainforest. *Journal of Animal Ecology* 76:687-694
- Marczak. L. B., R. M. Thompson e J. S. Richardson. 2007. Meta-analysis: Trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88:140-148
- Martin-Creuzburg, D., C. Kowarik and D. Straile. 2017. Cross-ecosystem fluxes: Export of polyunsaturated fatty acids from aquatic to terrestrial ecosystems via emerging insects. *Science of the Total Environment* 577: 174-182
- Mazzoni, R. e Rezende, C. F. 2003. Seasonal diet shift in a tetragonopterinae (Osteichthyes, Characidae) from the Ubatiba river, RJ, Brazil. *Braz. J. Biol.* 63:69-74
- Muehlbauer J. D., S. F. Collins, M. W. Doyle e K. Tockner. 2014. How wide is a stream? Spatial extent of the potential “stream signature” in terrestrial food webs using meta-analysis. *Ecology* 95:44-55
- Myers, N. 2003. Biodiversity hotspots revisited. *BioScience* 53:916-917
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. e Kent, J. 2000. Biodiversity hotspot for conservation priorities. *Nature* 403:853-858
- Nakano, S., Miyasaka, H. e Kuhara, N. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* 80:2435-2441

- Nakano, S. e M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences* 98: 166-170
- Newsome, S. D., C. M. del Rio, S. Bearhop, and D. L. Phillippe. 2007. A niche for isotopic ecology. *Front. Ecol. Environ.* 5: 429-436
- Polis, G. A. e S. D. Hurd. 1995. Extraordinarily high spider densities on islands: Flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences* 92:4382-4386
- Polis, G. A., W. B. Anderson e R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289-316
- Recalde, F. C., T. C. Postali, and G. Q. Romero. 2016. Unravelling the role of allochthonous aquatic resources to food web structure in a tropical riparian forest. *Journal of Animal Ecology* 85: 525-536
- Richardson, J. S. e Sato, T. 2015. Resource subsidy flows across freshwater-terrestrial boundaries and influence on processes linking adjacent ecosystems. *Ecohydrology* 8:406-415
- Richardson, J. S., Y. Zhang e L. B. Marczak. 2010. Resource subsidies across the land-freshwater interface and responses in recipient communities. *River research and applications* 26:55-66
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385-387.
- Sabo, J. L. and M. E. Power. 2002. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. *Ecology* 83: 3023-3036
- Sánchez-Hernández, J., Gabler, H. M. e Amundsen, P. A. 2016. From autochthonous to allochthonous resources: seasonal shifts in food use by stream-dwelling YOY arctic charr *Salvelinus alpinus* through the ice-free season. *Journal of Fish Biology* 88:767-773
- Sanzone, D. M., J. L. Meyer, E. Marti, E. P. Gardiner, J. L. Tank e N. B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. *Oecologia* 134:238-250

- Shurin, J. B., Borer, E. T., Seabloom., E. W., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D., e Halpern, B. S. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5:785-791
- Shurin, J. B., Gruner, D. S. e Hillebrand, H. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proc. R. Soc. B.* 273:1-9
- Sitters, J., C. L. Atkinson, N. Guelzow, P. Kelly e L. L. Sullivan. 2015. Spatial stoichiometry: cross-ecosystem material flows and their impact on recipient ecosystems and organisms. *Oikos* doi: [10.1111/oik.02392]
- Strandberg, U., Hiltunen, M., Jelkänen, E., Taipale, S. J., Kainz, M. J., Brett, M. T. e Kankaala, P. 2015. Selective transfer of polyunsaturated fatty acids from phytoplankton to planktivorous fish in large boreal lakes. *Science of the Total Environment* 536:858-865
- Takimoto, G., Iwata, T. e Murakami, M. 2002. Seasonal subsidy stabilizes food web dynamics: balance in a heterogeneous landscape. *Ecological Research* 17:433-439
- Twining, C. W., J. T. Brenna, P. Lawrence, J. R. Shipley, T. N. Tollefson and D. W. Winkler. 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *PNAS* 113: 10920-10925
- Wallace, J. B., Eggert, S. L., Meyer, J. L., e Webster, J. R. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277:102-104

ARTIGO I

Trophic variation in tropical birds and bats is driven by allochthonous resources

FATIMA C. Recalde¹, Crasso P. B. Breviglieri², Mônica F. Kersch-Becker³, and Gustavo Q. Romero²

1. Pos-Graduate Program in Ecology, Institute of Biology, State University of Campinas, Campinas, Brazil.
2. Department of Animal Biology, Institute of Biology, State University of Campinas, Campinas, Brazil.
3. Department of Biological Sciences, University of Alabama, Tuscaloosa, AL, USA

Artigo escrito segundo as normas da revista Oecologia

Abstract

Food webs are spatially connected by cross-ecosystem fluxes of resources, especially in aquatic-terrestrial boundaries. Generalist consumers are often supported by allochthonous resources, which can influence their density, biomass, and distribution. In this study, we investigated the influence of allochthonous aquatic resources on the activity, trophic (isotopic) space and variations, and community structure of tropical insectivorous bats and birds. Activity (ultrasound and birdsongs), isotopic space breadth and community metrics of the vertebrates were measured in riparian (0 m) and upland (200 m) areas of six streams in each Atlantic and Amazon rainforest. Foraging activity of bats and birdsongs of Amazon birds were higher in riparian zones compared to upland areas, while Atlantic birds were more active in upland areas. Bayesian mixing models revealed that insectivorous bats and birds were subsidized by allochthonous resources (i.e., 39% of their diet corresponding to emergent aquatic insects) and spiders (~30%). Nevertheless, the diet of the vertebrates was similar in riparian and upland areas. Although trophic space breadth has been not affected by inputs of aquatic resources, trophic diversity of the community of bats and birds were higher in riparian areas, especially from Amazon rainforest. These results suggest that aquatic allochthonous resources play an important role in community-wide trophic diversity of terrestrial bats and birds. Our results highlight the importance of tropical riparian zones on the maintenance of diversity of biotic interactions triggered by allochthonous subsidies.

Keywords: trophic space, diet preference, insectivorous vertebrates, emergent insects, foraging activity.

Introduction

Food webs are spatially connected through a cross-ecosystem flow of resources (e.g., detritus or prey), and consumers are allowed to intake both local (autochthonous) and foreign (allochthonous) energy (Polis et al. 1997; Sitters et al. 2015; Recalde et al. 2016). The aquatic-terrestrial interface comprises organisms and processes shared between the two ecosystems. However, both ecosystems have distinct abiotic characteristics (e.g., carbon intake, nutrient cycling, oxygen concentration), which influence the nutritional content of aquatic or terrestrial resources exploited by recipient consumers (Sitters et al. 2015). Generalist consumers are known to be efficient transfers of aquatic energy to terrestrial food webs (Ballinger and Lake 2006; Faria and Costa 2010). However, niche partitioning can emerge when different generalist species compete for resources or have distinct food preferences, resulting in differential use of resources (MacArthur 1972, Faria and Costa 2010). Changes in food preferences can trigger contrasting effects on food webs, depending on the importance of subsidized consumers in the community (Huxel and McCann 1998; Power et al. 2004). For instance, a generalist terrestrial predator can respond numerically to the input of aquatic resources, potentially causing negative effects on terrestrial resources through apparent competition (Holt 1977; Henschel et al. 2001; Murakami and Nakano 2002). Therefore, allochthonous resources across ecosystems can subsidy consumers, thus playing a critical role in the dynamics and structure of recipient communities (Polis et al. 1997; Baxter et al. 2005; Ballinger and Lake 2006).

Insectivorous birds and bats are considered top predators in some systems mainly because of their high mobility (Power et al. 2004). They can either capture prey in flight or actively search for prey in trunks, foliage, and leaf litter (Sick 1997; Kunz and Fenton 2003). Riparian forests increase the availability of resources to these predators, mostly through the emergence of aquatic insects (Murakami and Nakano 2002; Sabo and Power 2002; Fukui et al. 2006). Aquatic insects emerge from the water as adults, joining the terrestrial community, and thus establishing a pool of diversified prey items to consumers (Salvarina et al. 2017). Therefore, these predators are frequently found in high numbers in riparian areas, especially when emergent aquatic insects contributed to a large portion of their diet (Hagen and Sabo 2014; Bader et al. 2015; Gomes et al. 2017). Trevelline et al. (2018) used molecular techniques to estimate the type of prey the nestling exploit and found that emergent aquatic insects comprise a large proportion of their diet. Furthermore, emergent aquatic insects provide more polyunsaturated fatty acid than terrestrial insects (Martin-Creuzburg et al. 2017), and this essential lipid is very important to the performance of insectivorous birds (Twining et al. 2016).

Nestlings are likely to grow faster and have better immunocompetence when they feed on aquatic insects due to their fatty acid content (Twining et al. 2016).

Insectivorous bats seem to be even more dependent on resources from riparian areas than birds because most of them forage on open areas (e.g., corridors structured by streams and rivers), which facilitate echolocation (i.e., use of ultrasonic sounds to detect obstacles and capture prey) (Griffin 2001; Salvarina 2016). Additionally, some bat species capture prey during flight, which is energetically costly, thus they are likely to exploit the availability of prey in riparian habitats to outweigh the costs of the flight (Voigt et al. 2010). Indeed, resource-rich riparian forests maintain a higher foraging activity of insectivorous bats compared to upland areas (Fukui et al. 2006). Through DNA extraction of fecal pellets, Vesterinen et al. (2013) showed that insects of aquatic origin contribute to more than half of the diet of *Myotis daubentonii*, an insectivorous bat. Nevertheless, many insectivorous bats are opportunistic, and the use of aquatic insects is largely due to their great availability in the foraging areas (Bader et al. 2015; Salvarina 2016; Thomas et al. 2012; Shively et al. 2018). Therefore, aquatic resources have important implications to the performance of recipient consumers, but their relative importance is still unclear in tropical regions (but see Chan et al. 2008; Recalde et al. 2016) where the diversity of predators that may rely on these resources is high (Salvarina 2016).

By evaluating the diet of consumers, we can estimate their realized trophic niche (i.e., the total trophic space composed of all food items of a species). Trophic space dimension can change in response to resource use, and identifying the food items utilized by each organism provides insights into the trophic space the consumer occupies (Bearhop et al. 2004; Newsome et al. 2007; Jackson et al. 2011). In this study, we used isotopic analysis of two tracers ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), which is a useful technique to estimate the trophic variation (diet contribution, trophic niche, trophic structure) of vertebrates. We used hair and feather tissues, which have been demonstrated to preserve information on the diet of bat and birds respectively (Bearhop et al. 2004; Newsome et al. 2007). Aquatic and terrestrial invertebrates have unique isotopic signatures, and predators that consume prey originated from both ecosystems may occupy a broader trophic space and more variable trophic structure than those with limited diet (Layman et al. 2007, Voigt et al. 2015; Recalde et al. 2016). Here, we investigated the influence of allochthonous resources (via the emergence of aquatic insects) on performance, diet and trophic structure of bats and birds in Amazonian and Atlantic rainforest. We predicted that (i) the foraging activity of riparian insectivorous bats and birds will be higher compared to their counterparts inhabiting areas far from streams because availability and diversity of prey in

riparian areas are higher. Also, we hypothesized that (ii) isotopic signatures of bats and birds commonly foraging in riparian areas will be different than those foraging in upland areas because of their expected different diet (terrestrial + aquatic vs. more terrestrial, respectively). These particular characteristics of the subsidized vertebrates will allow us to predict that (iii) riparian insectivorous vertebrates may have broader trophic space and (iv) higher trophic diversity compared to their upland counterparts.

Materials and Methods

Study site

We conducted this study in two distinct biomes: the Atlantic and the Amazon forests. In the Atlantic forest we carried out our study at the Reserva Municipal Serra do Japi (23°13' S, 46°56' W), in São Paulo State, Brazil (elevation ~ 1000 m). The climate is seasonal characterized by a warm rainy season (November to April: 18-22 °C, 230 mm/month) and a cool dry season (May – September: 12-15°C, 40 mm/ month). The vegetation is characterized by a semi-deciduous mesophytic forest of altitude (Rolim et al. 2007). In the Amazon forest, we conducted our samplings in permanent plots of the Projeto Dinâmica Biológica de Fragmentos Florestais, from the Instituto Nacional de Pesquisas da Amazônia (PDBFF - INPA). Specifically, we sampled at three permanent plots: km 41 (2°26' S, 59°46' W), Cabo Frio (2°24'S, 59°54' W), and Porto Alegre (2°22' S, 59°58' W). These Amazonian sites are characterized by dense ombrophilous forest with low seasonality. The greater precipitation period is from December to January and the mean annual temperature is ca. 27°C.

Survey Plots

In each biome, we chose six first or second order streams to carry out our surveys. The stream was used as the sampling unity (replicate). Streams were separated from each other for at least 1 km. For each stream, we established two rectangular plots of 12 x 5 m, one at zero meters of stream margin (riparian area) and the other starting at 200 m from the stream margin (upland area). Climatic variables in our study sites did not differ between plots, in the Atlantic (LME, Temperature [°C], $t = -1.445$, $P = 0.243$; Humidity [%], $t = -0.197$, $P = 0.856$), and Amazon forest (LME, Temperature [°C], $t = -2.263$, $P = 0.073$; Humidity [%], $t = 1.061$, $P = 0.337$).

Sampling of aquatic and terrestrial flying insects by using sticky traps

To evaluate whether emergent aquatic insects are more abundant in riparian than upland vegetation, we used one sticky trap per plot in the Atlantic forest; the sticky traps were set up at approximately 1.5 m high. Sticky traps consisted of a transparent plastic square frame of 16 x 16 cm coated with an odorless resin Tanglefoot®. We collected the sticky traps after a week. We quantified the abundance of insects adhered to the traps and we classified them into aquatic or terrestrial according to their aquatic or terrestrial larval stage.

Sampling of insectivorous birds and bats

We sampled the vertebrates in Atlantic and Amazon forest in March and September of 2016, respectively. We used mist nets to collect birds and bats and extracted tissue (feather or hair, respectively) to perform isotopic analysis of carbon and nitrogen (^{13}C and ^{15}N). Isotopic analysis, particularly of ^{13}C and ^{15}N , is a powerful method to estimate diet composition and trophic niche breadth of consumers (Layman et al. 2012) because the stable isotope signature of consumer tissues reflects those present in prey tissues (Bearhop et al. 2004; Newsome et al. 2007). We set up two mist nets of 12 x 5-m in riparian plots, perpendicular to the stream, and another two nets in upland plots. Throughout six days, we exposed the nets from early morning (~0600h) to the night (~2300h), which encompass the periods with the highest activity of birds and bats (Sick 1997; Esbérard & Bergallo 2006; Reis et al. 2007). We inspected the nets every 20 minutes and the vertebrates trapped were carefully manipulated. We collected the young primary feather of each captured bird by cutting the feather at the base. We sampled ~5 mg of hair from the back of the bats using sterilized scissors. As we collected the birds and bats, we recorded their species identity. Immediately afterward, we released them. The tissue samples were separated in individual plastic vials and frozen at -20°C them until processing. Additionally, we recorded birdsongs as a proxy of bird activity rate. Birds vocalize during flight, warning, feeding, and nesting. Birdsongs are important to enhance reproduction and defend the territory (Gill 2007). To record the number of birdsongs of different species, we placed a song recorder (Sony®, ICD-PX240, 4 GB) in each plot for 120 minutes (0600 - 0800 h) and at approximately one meter high. The recorder was able to capture songs within twenty meters of radius. All the recorded birdsongs were identified to species level. To estimate the rate of foraging activity of bats, we recorded the ultrasound emission of food search and predation in each evening (1730 – 1930 h). We used two ultrasound detectors (Pettersson®, model Heterodyne D100) connected to digital sound recorders (Sony®, ICD-PX240, 4 GB), which capture bat ultrasound emissions within 20 meters of radius. We placed one recorder per

plot at one meter high. Because the insectivorous bats often found in our study sites (family Vespertilionidae) emit an ultrasound frequency of 50 kHz, we adjusted the detectors to that frequency level. We called "attack rate" the number of attacks on flying prey, which was determined by a buzz sound followed by a silent interval. The rate of buzz and silent represents the moment a bat attack and chews on its prey (Kunz and Parsons 2009). We used the software Raven Pro 1.4 (The Cornell Lab of Ornithology) to perform a sonogram analysis of sound for both predator taxa.

Sampling the aquatic and terrestrial arthropods, and plants

We sampled aquatic insect larvae in all streams. We collected the larvae with a fine mesh sieve from the detrital bed of streams. Then, we identified each insect larva to order and used only insects with a complex life cycle (aquatic larvae and terrestrial adult), which would represent the potential allochthonous resources to the forest. Additionally, representing potential autochthonous prey, we collected terrestrial arthropods on shrubs (up to 1.5-meter-tall) twice a day: early morning and evening to capture the community of arthropods that would be present during the activity of birds (day/night) and bats (night). Birds display a generalist foraging mode (active search under leaves, on trunks, leaf litter, etc.) (Sick 1997). Therefore, we considered both nocturnal and diurnal arthropods as potential prey. We collected arthropods manually during 40 minutes in each plot and identified them to the family level. Aquatic and terrestrial arthropods were stored in individual vials and frozen (at -20°C) until processing. We also collected flowers and fruits of some abundant families in our study site (e.g., Rubiaceae, Heliconiaceae, Piperaceae, Lecitidaceae, Clusiaceae, Malvaceae, and Solanaceae) because they are potential autochthonous food items for omnivorous birds and frugivorous bats. Most of the bats captured in this study were frugivores that may consume arthropods to supplement their diet, especially in different seasons of the year (i.e., when resources are scarce) or during the reproductive season (i.e., nutritional supplementation for fetal development or breastfeeding) (see details in Kunz and Fenton 2003). Thus, we categorized to them as "omnivorous bats" to simplify.

Isotopic Analyses

We gently washed the feathers with a clean-rinsing, neutral detergent to remove potential contaminants and oil of tissue. Then, we dried the feathers at 60°C in an oven for 48 h. To sterilize hair tissue, we dried it at 70°C for 48 h. This procedure was sufficient to clear the animal tissue from potential infections. We also dried all aquatic and terrestrial arthropods and

plant tissue at 60°C for 48 h. We then grounded the organisms to homogenize the tissue. We added 1 mg (± 0.2 mg) of each sample to tin capsules. The samples were further analyzed in the UC Davis Stable Isotope Facility, California, USA. Values of $\delta^{13}\text{C}$ [$=(^{13}\text{C}:^{12}\text{C}_{\text{sample}}/^{13}\text{C}:^{12}\text{C}_{\text{standard}}) - 1 \times 1000$] and $\delta^{15}\text{N}$ [$=(^{15}\text{N}:^{14}\text{N}_{\text{sample}}/^{15}\text{N}:^{14}\text{N}_{\text{standard}}) - 1 \times 1000$] were determined through elemental analyzer PDZ Europa ANCA-GSL coupled with an Isotope-Ratio Mass Spectrometer (PDZ Europa 20-20, Sercon Ltd., Cheshire, UK). The isotopic ratios (δ) were estimated using standard values of Pee Dee Belamite (PDB) for $\delta^{13}\text{C}$ and of atmospheric air for $\delta^{15}\text{N}$.

Statistical analysis, stable isotope mixing models and trophic space

We performed one-way analysis of variance (ANOVA) to test whether vertebrate activity and abundance of flying arthropods differ in riparian and upland plots. When our model did not reach the parametric assumptions, we performed generalized linear mixed-models with the Poisson distribution. We performed a multivariate analysis of variance (MANOVA) to test whether the isotopic signature is different between the vertebrates in the different plots. Since both birds and bats belong to the insectivorous and omnivorous trophic guild, we performed separated analysis for each guild.

We used Bayesian mixing models of MixSIAR package (Stock et al. 2018) to quantify the relative contribution of each source (spider, aquatic and terrestrial insects, plants) to a mixture (consumers: bats and birds). The package works with *a priori* tracer data of a mixture, different sources and trophic enrichment factor (TEF). We used fixed factor (area: riparian and upland) and random factors (species of vertebrates) for mixture data and a fixed factor of area for source data. We used the multiplicative error formulation of MixSIAR model because it deals better with additional variability of the mixture (absence of important factors affecting consumer population structure or missing a non-negligible source), thus, add biological realism to the mixing model. To estimate the trophic enrichment factor between consumers and resources, we followed the equations of Greer et al. (2015) for feather tissue and adapted their methods for the hair tissue. This method consists in the calculation of the dietary (total food items) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values weighed by elemental (isotope) concentration using mass balance equation (see details in Greer et al. 2015). Stable isotope mixing models (SIMM) were run using a JAGS (Just Another Gibbs Sampler, Plummer 2003) model under Bayesian MCMC tests through 100,000 iterations, with an uninformative/generalist prior with the Dirichlet distribution. Since the output of the diet analyses gives us the mean and standard

deviation values of the proportion of each food item in the diet, we were able to test the difference of diet between riparian and upland vertebrates with unpaired t-test.

We estimated standard ellipses of consumers using the SIBER package (Jackson et al. 2011). We failed to estimate the trophic niche of species because most of them were represented by only one or two individuals, and the SIBER package works with a baseline of at least five individuals in a population. Thus, we adopted the term "trophic space" as a proxy of the total trophic variation of the community of consumers. Standard ellipses measure the dispersion of multivariate data and represent isotopic/trophic variation in δ -space of ^{13}C and ^{15}N bi-plot. The covariance matrix of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ defines the shape and size of the ellipse, and the means of each $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data define its location in bi-plot (Jackson et al. 2011). The SIBER package estimates these values using Bayesian inference with a vague Inverse-Wishart prior. The posterior estimate of the covariance matrix was simulated using Markov Chain Monte Carlo (MCMC). Then, the package used the simulated data to construct an ellipse, in which area (the Standard Ellipse Area, SEA) represents the trophic space breadth of consumers. We estimated the SEA_c , which is a correction of SEA for small sample size and compared the SEA_c between plots in each biome. We calculated data of SEA_c from each stream independently and used the resulting values as replicates (random factor). Then, we measured the differences of these values between plots with LME in package *nlme* (Pinheiro and Bates 2000). Additionally, we used Layman's metrics of community structure (Layman et al. 2007) to estimate the trophic structure of consumers and compare them between riparian and upland areas. We measured trophic diversity by (a) $\delta^{15}\text{N}$ range, and (b) $\delta^{13}\text{C}$ range, that represent the diversity of trophic position occupied and basal resources utilized by consumers, respectively (larger values indicate higher diversity); and by (c) mean distance to centroid (CD), which is the average distance of each species to mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all species, and measure the average degree of trophic diversity within a community. The metric (d) 'total area' (TA) measured the convex hull area encompassed by all consumers in the community. We used TA to estimate the total area occupied by the consumers in the isotopic space ($\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot). In this study, TA did not represent the trophic space breadth of the community because this metric is sensitive to extreme values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Jackson et al. 2011), so, we considered this metric as a complementary measure of trophic diversity. We measured trophic redundancy by (e) the mean nearest neighbor distance (NND) that is the distance of each species' nearest neighbor and measure the density of species packing (smaller values indicate high redundancy), and (f) the standard deviation of NND (SDNND) that measure the evenness

of species within a community. We performed all analyses in the software R (R Core Team 2019).

Results

Abundance of flying insects on sticky traps and of terrestrial prey in vegetation

Adult aquatic insects were 1.5 times more abundant in riparian than upland areas in the Atlantic forest (GLMM, $Z = -4.107$, $P < 0.001$, Online Resource 1). In contrast, the abundance of flying terrestrial insects was similar between areas. All the aquatic insects were dipterans ($N = 376$), from the family Chironomidae (70%) and Ceratopogonidae (30%). Flying terrestrial insects ($N = 1837$) were more diverse and were classified as Diptera (43.5%), Hymenoptera (37.5%) and Coleoptera (7%). On the other hand, a total of 949 and 876 terrestrial arthropods were collected from vegetation in the Atlantic and Amazon forest, respectively. Distribution of spiders and terrestrial insects was similar between plots in the Atlantic (GLMM, abundance of spiders: $z = 0.59$, $P = 0.556$; abundance of insects: $z = 1.33$, $P = 0.185$) and Amazon forest (LME, abundance of spiders: $t = 0.55$, $P = 0.608$; abundance of insects: $t = 0.384$, $P = 0.717$). Similarly, biomass of spiders (LME, Atlantic forest, $t = 1.62$, $P = 0.167$; Amazon forest, $t = -0.45$, $P = 0.674$) and insects (LME, Atlantic forest, $t = -0.795$, $P = 0.463$; Amazon forest, $t = 0.06$, $P = 0.956$) did not differ between plots in both biomes.

Sound and ultrasound records of insectivorous consumers

Activity of birds was 1.8 times higher in upland than riparian areas in the Atlantic forest (ANOVA, $F = 33.75$, $P = 0.002$). Conversely, bird activity was 1.3 times higher in riparian than upland areas in the Amazon forest (ANOVA, $F = 90.25$, $P < 0.001$, Fig. 1A). Bat foraging activity was higher in riparian areas in both the Atlantic (ANOVA, Food search, $F = 171.7$, $P < 0.001$; Attack rate, $F = 68.44$, $P < 0.001$) and Amazon forest (ANOVA, Food search, $F = 7.26$, $P = 0.0431$; Attack rate, $F = 33.01$, $P = 0.002$, Fig. 1B, C).

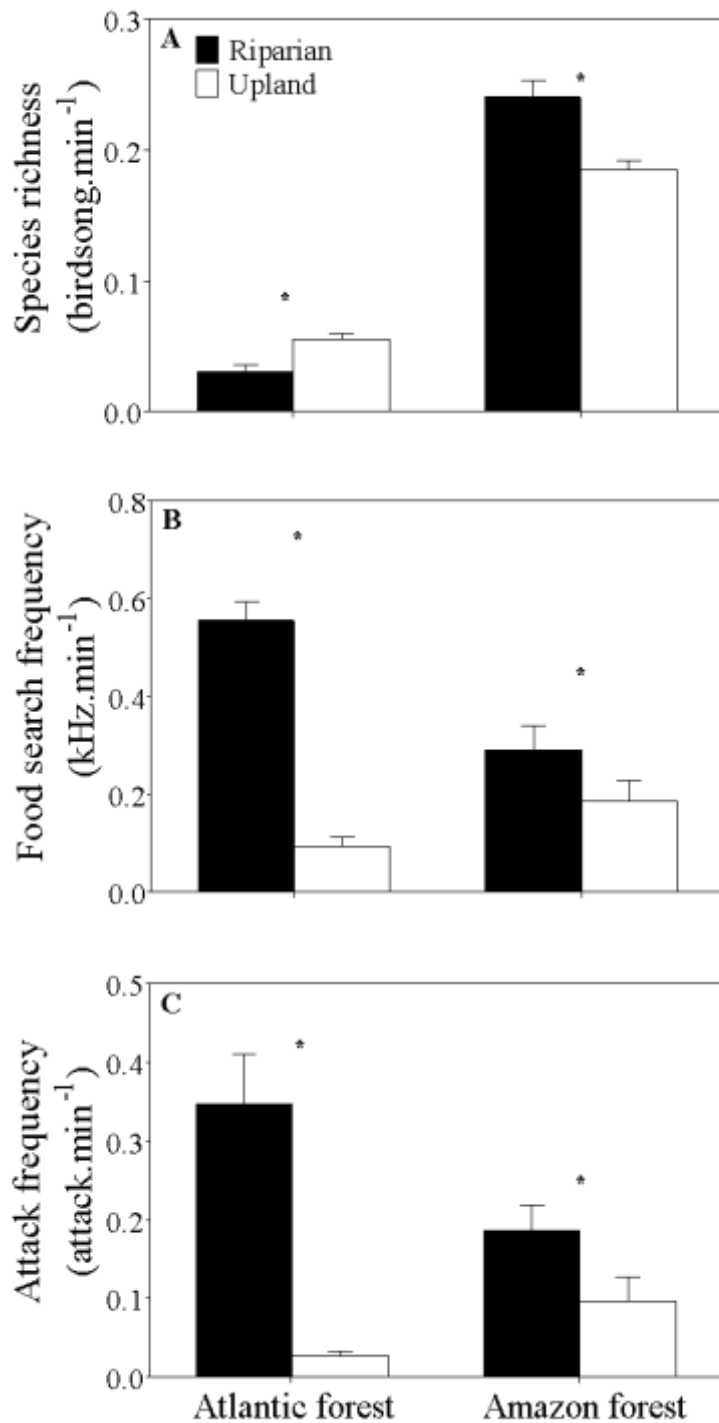


FIGURE 1. Mean activity rate (\pm SE) of insectivorous vertebrates in Atlantic and Amazon forests. **(A)** Richness of birdsongs as a measure of bird activity, **(B)** ultrasound emission as food search and **(C)** attack rate of bats in riparian and upland areas. Asterisk represent significant difference of $\alpha \geq 0.05$.

Isotopic signature and diet composition of birds and bats

Out of 69 bats and 52 birds captured, only 11 and 32 were insectivores, respectively (Online Resource 2). Despite our great sampling effort, only one insectivorous bird and two insectivorous bats were captured respectively in riparian and upland areas in the Atlantic forest, so we were unable to analyze this data. In the Amazon forest, isotopic signatures of C and N of insectivores (MANOVA, *bats*, Pillai's $\lambda = 0.40$, $P = 0.360$; *birds*, Pillai's $\lambda = 0.04$, $P = 0.650$) and omnivores (MANOVA, *bats*, Pillai's $\lambda = 0.05$, $P = 0.410$; *birds*, Pillai's $\lambda = 0.37$, $P = 0.12$) were similar between riparian and upland areas.

The diet of birds and bats of the Atlantic forest are shown in Fig. 2. We were able to compare the contribution of allochthonous resources between riparian and upland areas only for insectivorous bats because it presented sufficient sample size to perform the analysis. The proportion of prey in the diet of vertebrates was similar between riparian and upland areas in the Atlantic and Amazon forest. Proportionally, Atlantic insectivores ate more aquatic prey and spiders than terrestrial insects, both in riparian and upland areas (Fig. 2A, C) We capture only one individual of bird (*Lochmias nematura*) in riparian areas, thus the proportion showed in the figure belong to that individual (Fig. 2C). Atlantic omnivores showed a diet with similar contribution by each food items (Table 1). On the other hand, in the Amazon forest, aquatic prey contributed to about 42 percent on the diet of insectivores, followed by spider contribution (~33%) and terrestrial insects (~25%) (Fig. 2B, D). In the diet of omnivorous bats, the contribution of aquatic insects and spiders was higher. Omnivorous bats had a similar contribution of each prey (Table 1). The results above represent an average proportion of each food item in the whole group of bats and birds. Nevertheless, we found variable contribution of food items between bat and bird individual species (Online resource 3).

TABLE 1. Mean percentage contribution \pm SD of each source on diet of omnivorous bats and birds in Atlantic and Amazon Forest. A. insect and T. insect mean Aquatic and terrestrial insects, respectively.

	Riparian				Upland			
	A. insect	T. insect	Spider	Plant	A. insect	T. insect	Spider	Plant
Atlantic Forest								
Bats	27 \pm 0.19	20 \pm 0.17	34 \pm 0.20	19 \pm .16				
Birds					26 \pm 0.19	21 \pm 0.17	33 \pm 0.20	21 \pm 0.17
Amazon Forest								
Bats	31 \pm 0.19	22 \pm 0.15	36 \pm 0.16	11 \pm 0.11	34 \pm 0.23	27 \pm 0.19	28 \pm 0.16	11 \pm 0.12
Birds	25 \pm 0.19	25 \pm 0.18	30 \pm 0.20	21 \pm 0.18	24 \pm 0.24	28 \pm 0.25	29 \pm 0.25	19 \pm 0.21

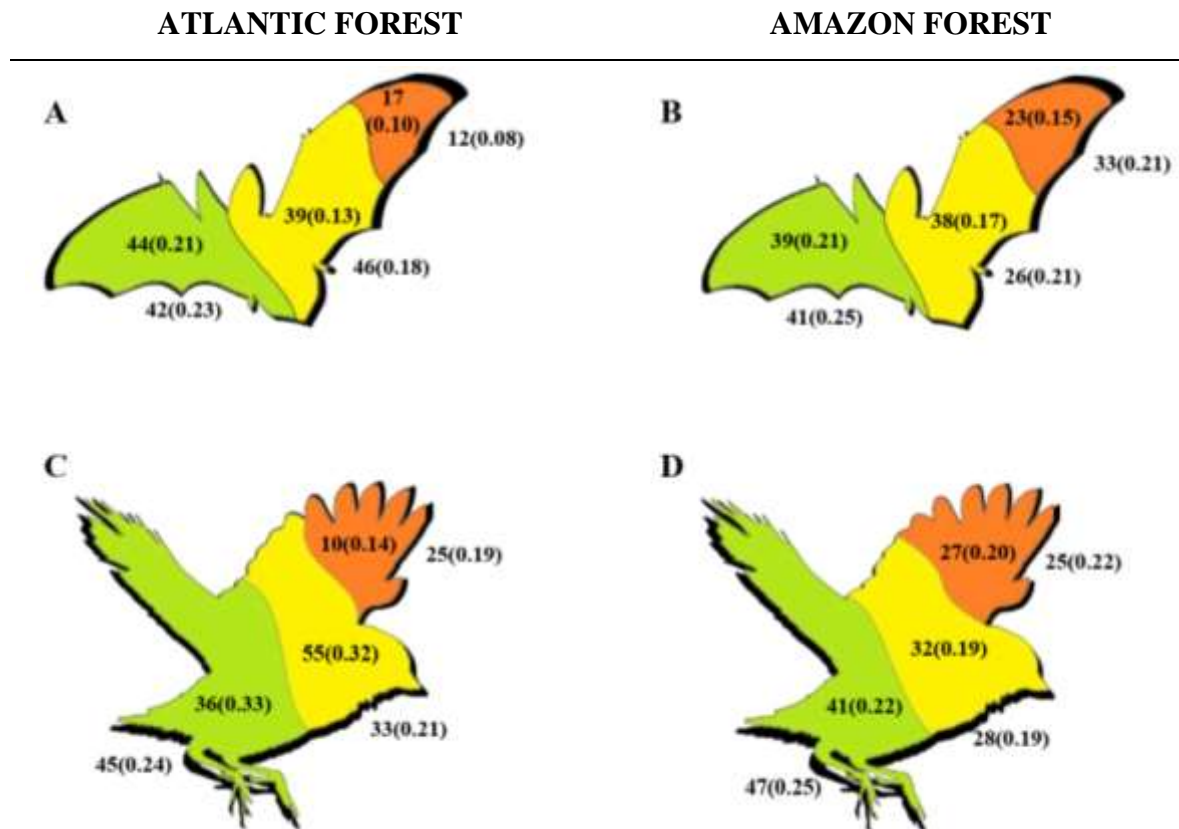


FIGURE 2. Mean percentage contribution (\pm SD) of each source on diet of insectivorous bats (A) and birds (C) in Atlantic forest; and of insectivorous bats (B) and birds (D) in Amazon forest.

Trophic space dimension and community metrics

In the Atlantic forest, the values of SEA_c , a measure of niche breadth of the total community of consumers, were similar in riparian and upland areas (Online resource 4). We failed to compare SEA_c of insectivores between areas because of the lower sample size ($n < 5$). Community metrics were similar in riparian and upland areas in Atlantic forest (Online resource 5). In contrast, in the Amazon forest, $\delta^{15}N$ range, TA and CD were higher in riparian than upland areas (Fig. 3).

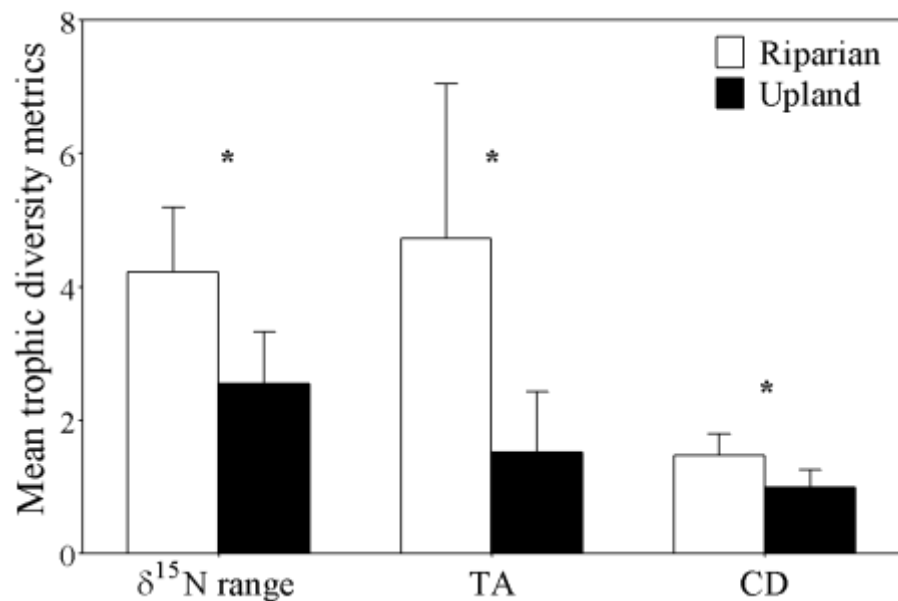


FIGURE 3. Mean values (\pm SD) of $\delta^{15}N$ range, TA and CD of riparian community of bats and birds in Amazon forest. Asterisk represents significance of $\alpha \geq 0.05$.

Discussion

In this study, we showed the role of allochthonous resources in community trophic structure of tropical bats and birds. We found that foraging activity of most of the insectivores (Atlantic bats, Amazonian bats, and birds) was higher in riparian areas where there is greater availability of allochthonous aquatic prey. In contrast, Atlantic insectivorous birds were more active in upland areas despite the great contribution of aquatic prey in their diet. Emergent aquatic insects and spiders were both important contributors to the diet of the insectivores. Nevertheless, this contribution was similar in riparian and upland areas. Additionally, we have shown that there were different responses of terrestrial communities between the studied biomes. In the Atlantic forest, we failed to detect influence of allochthonous resources on

vertebrate consumers. Conversely, the community of Amazonian consumers was more influenced by the input of allochthonous resources. Overall, our expectations that allochthonous resources would benefit riparian bats and birds were partially supported, since foraging activity and isotopic niche diversity, but no diet and trophic spaces, were higher in riparian areas. However, these responses were contingent on the biome studied.

Our results showed that allochthonous aquatic prey contributed greatly to the diet of insectivorous consumers (39–47%), and this is not surprising since the foraging activity and performance of insectivorous Atlantic bats and Amazon bats and birds were higher in riparian habitats (supported our first prediction). Bats relied on riparian habitats likely because those habitats provide high food availability and corridor structure that promotes flying and echolocation (Pereira et al. 2009; Hagen and Sabo 2011; Salvarina 2016). For instance, Grindal et al. (1999) recorded ultrasound emission of commuting and foraging activity in temperate riparian and upland forests. They observed that insectivorous bats showed high foraging activity in riparian areas, and suggested that these areas may offer high availability of emergent aquatic insects as potential prey of bats (Grindal et al. 1999). Nevertheless, contrary to second expectation, the contribution of aquatic prey in the diet was similar between riparian and upland areas. We captured respectively only two and one insectivorous bats in upland areas in Atlantic and Amazon forest during the survey period. Atlantic bats showed a preferred diet of aquatic and spider prey. The abundance of spiders was similar between areas, so, these bats were able to consume the same proportion of spider in the two areas. Also, these individuals could be moving between riparian and upland areas and use resources available in both areas, especially aquatic resources. The unique species of insectivorous bat in Amazon upland was *Lophostoma silvicolum*. This species usually forages within a small ratio (~200 - 500m) from its roost during flight or in perches (Kalko et al. 1999). Probably, the individual captured in our study site roosted within that ratio of the stream and were capable to catch the pool of available prey in both riparian and upland areas.

Amazon birds were more active in riparian areas, likely due to the high variability of prey as demonstrated for other systems by previous studies (Nakano and Murakami 2001, Murakami and Nakano 2002, Chan et al. 2008). Additionally, they consumed a large proportion of aquatic insects, indicating that they were subsidized by these allochthonous resources. Since bats and birds are highly mobile and opportunists, those captured in riparian and upland areas probably belonged to a unique community, and this fact can explain the similar diet. Furthermore, bats and birds in our study might have foraged to other areas besides the ones we sampled, which may have affected their diet. However, we found that diet contribution of food

items was species-specific, and probably the average data of insectivores hides the potential influence of allochthonous resources on each species. We were not able to measure the trophic metrics to each species because of the lower sample size and we consider this issue important to be studied in the future, to then understand the population-level influence of allochthonous resources.

Amazon and Atlantic birds exhibited a different activity distribution, being the first more active in riparian and the last more active in upland areas. This result can explain our difficulty to capture birds in Atlantic riparian areas but contradicts the finding that they are highly subsidized by aquatic prey (~45% of their diet). Numerous factors may have contributed to this result, none of which are mutually exclusive. First, birds are highly mobile and the Atlantic birds may be flying between riparian and upland areas to forage, returning to the upland to mating, reproduction, defense, refuge, etc. Second, the Atlantic and Amazon forest differ in several traits, including species assemblage, environmental variables, and seasonality (Morellato 1992, Junk and Piedade 2010). The isotopic signatures baseline was approximately four times higher in the Amazon forest (Online resource 6), indicating the different concentration of energy and nutrients between forests, and potentially different distribution of preferred resources. Third, predators could have influenced the distribution of birds. Martinez et al. (2018) demonstrated that multispecies-flock of birds that depend on alarm calls modified their realized niche under imminent risk of predation (Martinez et al. 2018). We did not, however, assess the presence of predators or potential risk of predation in our study site because we did not expect this significant, opposing response in the activity of birds. We believe that it will be an important issue to explain the preferential occupation of upland areas by Atlantic birds.

Our third prediction that riparian bats and birds would have broader trophic space than their upland counterparts was not supported. Instead, trophic (isotopic) space of Atlantic and Amazon bats and birds did not vary between areas. In contrast, trophic diversity metrics of the overall community of Amazonian bats and birds were higher in riparian areas than upland (supporting our fourth prediction). This indicates that the riparian community presented more diverse trophic positions (high $\delta^{15}\text{N}$ range, CD), and larger area occupation (TA) by the vertebrates compared with those captured in upland areas. Trophic space relies on the total food items that a consumer can eat (Bearhop et al. 2004; Newsome et al. 2007), and the diet of bats and birds in our study sites were similar in riparian and upland areas. On the other hand, trophic diversity in riparian areas could be influenced by the higher availability of aquatic prey (an important item in the diet) once these preys could have attracted more diverse bats and

birds. Nevertheless, this group of attracted vertebrates was also generalist and opportunistically preyed on not only aquatic resources but also spiders and other available food items, as their upland counterparts. We suggest that input of allochthonous resources affects the community-wide trophic diversity of generalist predators foraging in riparian areas. However, these attracted predators could have preyed on not only aquatic resources but also spiders and other available food items, thus increasing the diversity of trophic niches in riparian zones.

We observed that responses of the community of bats and birds on allochthonous input differed between biomes. Our study site in Atlantic forest corresponds to the sub-tropical formation. Consumers in this biome were more selective in their prey. Both insectivorous bat and bird preferred aquatic and spider over terrestrial insects. On the other hand, tropical Amazon consumers were more generalist since they did not exhibit a preferred feeding (Fig. 2). Apparently, this result contradicts the hypothesis that specialization is higher in more tropical latitudes, so, trophic niches in these places should be smaller (MacArthur 1972, Vázquez and Stevens 2004). Although we did not hypothesize a difference of trophic space between Atlantic and Amazon forest, it is possible to perceive with our results that there is no difference in tropical and sub-tropical trophic space. In this sense, the meta-analysis of Cirtwill et al. 2015 demonstrated that the “latitude-trophic niche width” hypothesis is not a rule in terrestrial environments as it is to aquatic ones. Overall, we recommend conducting replicated empirical studies to better understand the validity of MacArthur’s hypothesis on the role of allochthonous resources across latitudinal scales.

We conclude that allochthonous resources partially influence the trophic variation since the trophic diversity and activity, but no diet and trophic space breadth, were affected by the external input of resources. Additionally, this influence is variable depending on the biome. We propose several non-exclusive mechanisms: first, insectivorous bats and birds are highly mobile and generalist so within our sample range they could have evenly foraged. Bats need a large area for echolocation and attack in flight (Griffin 2001; Salvarina 2016), and riparian areas provide suitable corridors for these purposes. In contrast, the activity of the Atlantic birds was higher in upland areas, which may be linked more likely to potential predation risk and also to the abundance of spider, which was evenly distributed across riparian and upland areas. The activity of the Amazon forest birds, however, correlated with the availability of aquatic resources, because they consumed these resources to a large extent (~41-47%). Second, trophic spaces were similar between riparian and upland areas likely because the vertebrates consumed similar prey in these two areas. Lastly, the Atlantic and Amazon forest have different isotopic baselines that can indicate a different distribution and availability of resources and predators.

Our findings indicate that allochthonous resources play an important role in community-wide trophic diversity of terrestrial bats and birds, but other factors can be interacted to establish the overall trophic space and diet of these consumers. Our results have important implication for the cross-ecosystem processes conservation because the community of bats and birds rely on allochthonous resources, and they act as top predators that can control the terrestrial food webs. Thus, priority areas of conservation have to be reformulated to include both the riparian and upland habitats that rely on these top predators.

Acknowledgment

We thank V. Fernandes Souza and A. Marajó dos Reis for assistance in the field work. We also thank J. L. Camargo for the opportunity to realize fieldwork in the PDBFF areas and RH for the logistic organization fieldwork in the Amazon forest. Fundação Serra do Japi allow us to realize fieldwork in the Atlantic forest. FCR was supported by a postgraduate fellowship from CAPES, finance code 001. CPBB and MKB were supported by a postdoctoral fellowship from CNPq. This study was supported by research grants from FAPESP (proc. 2017/09052-4), coordinated by GQR, and by fellowship Thomas Lovejoy, from the PDBFF-INPA. GQR received a CNPq-Brazil productivity research fellowship.

References

- Bader E, Acácio M, Monadjem A (2015) The importance of water bodies for insectivorous bats in a Malagasy dry deciduous forest: A case example from Kirindy (CNFEREF). *Malagasy Nature* 9: 88-96
- Ballinger A, Lake PS (2006) Energy and nutrient fluxes from rivers and streams into terrestrial food webs. *Mar Freshwater Res* 57:15-28 doi: 10.1071/MF05154
- Baxter CV, Fausch KD, Saunders C (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biol* 50:201-220 doi: [10.1111/j.1365-2427.2004.01328.x](https://doi.org/10.1111/j.1365-2427.2004.01328.x)
- Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73:1007-1012 doi: [10.1111/j.0021-8790.2004.00861.x](https://doi.org/10.1111/j.0021-8790.2004.00861.x)
- Chan EKW, Yu YT, Zhang Y, Dudgeon D (2008) Distribution patterns of birds and insect prey in a tropical riparian forest. *Biotropica* 40:623-629 doi: [10.1111/j.1744-7429.2008.00420.x](https://doi.org/10.1111/j.1744-7429.2008.00420.x)

- Cirtwill AR, Stouffer DB, Romanuk TN (2015) Latitudinal gradients in biotic niche breadth vary across ecosystem types. *Proc. R. Soc. B* 282:20151589 doi: 10.1098/rspb.2015.1589
- Esbérard CEL, Bergallo HG (2005) Coletar morcegos por seis ou doze horas a cada noite? *Rev Bras Zool* 22:1095-1098
- Faria LB, Costa MIS (2010) Omnivorous food web, prey preference, and allochthonous nutrient input. *Ecol Complex* 7:107-114 doi: [10.1016/j.ecocom.2009.08.003](https://doi.org/10.1016/j.ecocom.2009.08.003)
- Fukui D, Murakami M, Nakano S, Aoi T (2006) Effect of emergent aquatic insects on bat foraging in a riparian forest. *J Anim Ecol* 75:1252-1258 doi: [10.1111/j.1365-2656.2006.01146.x](https://doi.org/10.1111/j.1365-2656.2006.01146.x)
- Gill FB (2007) *Ornithology*, 3rd edn. W. H. Freeman and Company, New York
- Gomes M, Rabaça JE, Godinho C, Ramos JA (2017) Seasonal variation in Bird species richness and abundance in riparian galleries in Southern Portugal. *Acta Ornithol* 52:69-79 doi: [10.3161/00016454AO2017.52.1.007](https://doi.org/10.3161/00016454AO2017.52.1.007)
- Greer AL, Horton TW, Nelson XJ (2015) Simple ways to calculate stable isotope discrimination factors and convert between tissue types. *Methods Ecol Evol* 6:1341-1348 doi: 10.1111/2041-210X.12421
- Griffin DR (2001) Return to the magic well: Echolocation behavior of bats and responses of insect prey. *BioScience* 51:555-556 doi: [10.1641/0006-3568\(2001\)051\[0555:RTTMWE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0555:RTTMWE]2.0.CO;2)
- Grindal SD, Morissette JL, Brigham RM (1999) Concentration of bat activity in riparian habitats over an elevational gradient. *Can J Zool* 77:972-977 doi: [10.1139/z99-062](https://doi.org/10.1139/z99-062)
- Hagen EM, Sabo JL (2011) A landscape perspective on bat foraging ecology along rivers: does channel confinement and insect availability influence the response of bats to aquatic resources in riverine landscape? *Oecologia* 166:751-760 doi: 10.1007/s00442-011-1913-4
- Hagen EM, Sabo JL (2014) Temporal variability in insectivorous bat activity along two desert streams with contrasting patterns of prey availability. *J Arid Environ* 102:104-112 doi: [10.1016/j.jaridenv.2013.11.016](https://doi.org/10.1016/j.jaridenv.2013.11.016)
- Henschel JR, Mahsberg D, Stumpf H (2001) Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. *Oikos* 93:429-438 doi: 10.1034/j.1600-0706.2001.930308.x
- Holt RD (1977) Predation, apparent competition, and the structure of prey communities. *Theor Popul Biol* 12:197-229 doi: [10.1016/0040-5809\(77\)90042-9](https://doi.org/10.1016/0040-5809(77)90042-9)

- Huxel GR, McCann K (1998) Food web stability: the influence of trophic flows across habitats. *Am Nat* 152:460-469 doi: [10.1086/286182](https://doi.org/10.1086/286182)
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *J Anim Ecol* 80:595-602 doi: [10.1111/j.1365-2656.2011.01806.x](https://doi.org/10.1111/j.1365-2656.2011.01806.x)
- Junk WJ, Piedade, MTF (2010) An introduction to south american wetland forest: distribution definition and general characterization. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) *Amazonian Floodplain Forest, Ecophysiology, Biodiversity and Sustainable Management*, Springer, pp 3-25
- Kalko EKV, Friemel D, Handley Jr CO, Schnitzler HU (1999) Roosting and foraging behavior of two neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). *Biotropica* 31:344-353 doi: [10.1111/j.1744-7429.1999.tb00146.x](https://doi.org/10.1111/j.1744-7429.1999.tb00146.x)
- Kunz TH, Fenton MB (2003) *Ecology of bats*. The University of Chicago Press. Chicago and London
- Kunz TH, Parsons S (2009) *Ecological and behavioral methods for the study of bats*. Johns Hopkins University Press. Baltimore.
- Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42-48 doi: [10.1890/0012-9658\(2007\)88\[42:CSIRPF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2)
- Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E et al (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol Rev* 87:545-562 doi: [10.1111/j.1469-185X.2011.00208.x](https://doi.org/10.1111/j.1469-185X.2011.00208.x)
- MacArthur RH (1972) *Geographical Ecology*. Princeton University Press, Princeton, N. J.
- Martin-Creuzburg D, Kowarik C, Straile D (2017) Cross-ecosystem fluxes: Export of polyunsaturated fatty acids from aquatic to terrestrial ecosystems via emerging insects. *Sci Total Environ* 577:174-182 doi: [10.1016/j.scitotenv.2016.10.156](https://doi.org/10.1016/j.scitotenv.2016.10.156)
- Martinez AE, Parra E, Muellerklein O, Vredenburg VT (2018) Fear-based niche shifts in neotropical birds. *Ecology* 0:1-8 doi: [10.1002/ecy.2217](https://doi.org/10.1002/ecy.2217)
- Murakami M, Nakano S (2002) Indirect effect of aquatic insect emergence on a terrestrial insect population through by bird predation. *Ecol Lett* 5:333-337 doi: [10.1046/j.1461-0248.2002.00321.x](https://doi.org/10.1046/j.1461-0248.2002.00321.x)
- Nakano S, Murakami M (2001) Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *PNAS* 98:166-170 doi: [10.1073/pnas.98.1.166](https://doi.org/10.1073/pnas.98.1.166)

- Newsome SD, Rio CM, Bearhop S, Phillippe DL (2007) A niche for isotopic ecology. *Front. Ecol. Environ.* 5:429-436 doi: [10.1890/060150.1](https://doi.org/10.1890/060150.1)
- Pereira MJR, Marques JT, Santana J, Santos CD, Valsecchi J et al (2009) Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load. *J Anim Ecol* 78:1163-1171 doi: 10.1111/j.1365-2656.2009.01591.x
- Pineiro JC, Bates DM (2000) *Mixed-Effects Models in S and S-PLUS*. Springer, New York
- Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*. Pages 1-10. URL: <http://www.ci.tuwien.ac.at/Conferences/DSC-2003/Drafts/>
- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28:289-316 doi: [10.1146/annurev.ecolsys.28.1.289](https://doi.org/10.1146/annurev.ecolsys.28.1.289)
- Power ME, Rainey WR, Parker MS, Sabo JL, Smyth A et al (2004) River-to-watershed subsidies in an old-growth conifer forest. In: Polis GA, Power ME, Huxel GR (eds) *Food webs at the landscape level*. University of Chicago Press, Chicago, pp 214-241
- R Core Team (2018) *R: A language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Recalde FC, Postali TC, Romero GQ (2016) Unravelling the role of allochthonous aquatic resources to food web structure in a tropical riparian forest. *J Anim Ecol* 85:525-536 doi: 10.1111/1365-2656.12475
- Reis NR, Peracchi AL, Pedro WA, Lima IP (2007) *Morcegos do Brasil*. Biblioteca Central da Universidade Estadual de Londrina, CDU 599.4, Londrina
- Rolim GS, Camargo MBP, Lania DG, Moraes JFL (2007) Classificação climática de Köppen e de Thornthwaite e sua aplicabilidade na determinação de zonas agroclimáticas para o Estado de São Paulo. *Bragantia* 66:711-720
- Sabo JL, Power ME (2002) Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. *Ecology* 83:3023-3036 doi: [10.1890/0012-9658\(2002\)083\[3023:NROLTA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[3023:NROLTA]2.0.CO;2)
- Salvarina I (2016) Bats and aquatic habitats: a review of habitat use and anthropogenic impacts. *Mammal Rev* doi: 10.1111/mam.12059 doi: [10.1111/mam.12059](https://doi.org/10.1111/mam.12059)
- Salvarina I, Gravier D, Rothhaupt KO (2017) Seasonal insect emergence from three different temperate lakes. *Limnologia* 62:47-56 doi: [10.1016/j.limno.2016.10.004](https://doi.org/10.1016/j.limno.2016.10.004)
- Sick H (1997) *Ornitologia Brasileira*. Editora Nova Fronteira, Rio de Janeiro

- Sitters J, Atkinson CL, Guelzow N, Kelly P, Sullivan LL (2015) Spatial stoichiometry: cross-ecosystem material flows and their impact on recipient ecosystems and organisms. *Oikos* doi: [10.1111/oik.02392](https://doi.org/10.1111/oik.02392)
- Shively R, Barboza P, Doak P, Jung TS (2018) Increased diet breadth of little brown bats (*Myotis lucifugus*) at their northern range limit: a multimethod approach. *Can. J. Zool.* 96:31-38 doi: [10.1139/cjz-2017-0017](https://doi.org/10.1139/cjz-2017-0017)
- Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* 6: e5096; doi [10.7717/peerj.5096](https://doi.org/10.7717/peerj.5096)
- Thomas HH, Moosman Jr. PR, Veilleux JP, Holt J (2012) Foods of bats (Family Vespertilionidae) at five locations in New Hampshire and Massachusetts. *Can Field Nat* 126:117-124 doi: [10.22621/cfn.v126i2.1326](https://doi.org/10.22621/cfn.v126i2.1326)
- Trevelline BK, Nuttle T, Hoenig BD, Brouwer NL, Porter BA, Latta SC (2018) DNA metabarcoding of nestling feces reveals provisioning of aquatic prey and resource partitioning among Neotropical migratory songbirds in a riparian habitat. *Oecologia* 187:85-98 doi: [10.1007/s00442-018-4136-0](https://doi.org/10.1007/s00442-018-4136-0)
- Twining CW, Brenna JT, Lawrence P, Shipley JR, Tollefson TN, Winkler DW (2016) Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *PNAS* 113:10920-10925 doi: [10.1073/pnas.1603998113](https://doi.org/10.1073/pnas.1603998113)
- Vázquez DP, Stevens RD (2004) The latitudinal gradient in niche breadth: concepts and evidence. *The American Naturalist* 164:E1-E19 doi: [10.1086/421445](https://doi.org/10.1086/421445)
- Vesterinen EJ, Lilley T, Laine VN, Wahlberg N (2013) Next generation sequencing of fecal DNA reveals the dietary diversity of the widespread insectivorous predator Daubenton's bat (*Myotis daubentonii*) in Southwestern Finland. *PLoS ONE* 8: e82168 doi: [10.1371/journal.pone.0082168](https://doi.org/10.1371/journal.pone.0082168)
- Voigt CC, Sörgel K, Dechmann DKN (2010) Refueling while flying: foraging bats combust food rapidly and directly to power flight. *Ecology* 91:2908-2917 doi: [10.1890/09-2232.1](https://doi.org/10.1890/09-2232.1)
- Voigt CC, Lehmann D, Greif S (2015) Stable isotope ratios of hydrogen separate mammals of aquatic and terrestrial food webs. *Methods Ecol Evol* 6:1332-1340 doi: [10.1111/2041-210X.12414](https://doi.org/10.1111/2041-210X.12414)

ARTIGO II

Allochthonous aquatic subsidies weaken predation pressure in terrestrial ecosystems

FATIMA C. Recalde¹, Crasso P. B. Breviglieri², and Gustavo Q. Romero²

1. Graduate Program in Ecology, Institute of Biology, State University of Campinas, Campinas, Brazil.
2. Department of Animal Biology, Institute of Biology, State University of Campinas, Campinas, Brazil.

Artigo escrito segundo as normas da revista Ecology

Abstract

The input of external energy and matter in recipient ecosystems can act as a bottom-up force that subsidizes consumers, which can spread their cascading effects throughout the food web. Depending on the amount of the input, preference and the strength of trophic links, allochthonous resources generally play a stabilizing role on food webs since the subsidized consumers alleviate potential extinction by predation pressure or competition. In this study, we investigated the stabilizing role of allochthonous aquatic resources on intraguild predation (IGP) and their consequences on the shared prey in a terrestrial ecosystem. To this end, we manipulated the input of emergent aquatic insects (i.e., the allochthonous resources) to land, and predation pressure by bats and birds, in a multi-trophic food web using an orthogonal exclusion experiment. Using stable isotope metrics, we found that bats and birds (i.e., top predators), and spiders (i.e., mesopredators), were highly subsidized by emergent aquatic insects. Moreover, top predators had a higher preference for feeding on spiders compared with terrestrial insects. As predicted, spiders were strongly affected by the presence of top predators when allochthonous resources were excluded. Consequently, terrestrial insects were two times more abundant in this scenario. Since spiders had a high preference for aquatic resources, we suggest that non-consumptive effects of spiders upon terrestrial insects could be mediating the strong response of those shared prey. We demonstrate that the input of allochthonous aquatic resources can play a fundamental role in stabilizing terrestrial trophic interactions and trophic cascades in riparian zones via decreasing predation pressure.

Key-words: emergent aquatic insects, intraguild interaction, food chain stability, feeding preference, non-consumption effects.

INTRODUCTION

Although terrestrial and aquatic ecosystems have their own physical and biotic characteristics, their functioning depends greatly on the flux of matter and energy between them (Richardson and Sato 2015, Xiang et al. 2016, Schindler and Smits 2017, Ramey and Richardson 2017). The input of allochthonous resources (i.e., resources entering from external sources) can act as a bottom-up force, increasing the productivity of recipient ecosystem and spreading their cascading effects through the food web (Recalde et al. 2016). However, the impact of allochthonous resources on recipient food webs depends on factors including: (i) the amount of subsidies entering the system, (ii) the preference levels of recipient consumers, and (iii) the strength of trophic interactions (Huxel and McCann 1998, Huxel et al. 2002, Faria and Costa 2010). For instance, large input of allochthonous resources may increase the carrying capacity of consumer populations and destabilize trophic interactions (Rosenzweig 1971, Huxel and McCann 1998, Huxel et al. 2002). Therefore, food webs are less variable when there is low to moderate input of allochthonous resources which maintain the growth rate of consumers constant (Huxel and McCann 1998, Huxel et al. 2002).

Furthermore, preference levels of consumers (i.e., generalist or specialist) on allochthonous resources can weaken trophic cascades through compartmentalization of food web in separate – but not independent – food chains (Huxel et al. 2002, Faria and Costa 2010). For example, when the link between predator and autochthonous resources is weak, some predators can become specialists in consuming allochthonous supplies and release the autochthonous prey (Huxel et al. 2002). However, the presence of generalist predators that have a stronger link with their autochthonous prey still will control their density, but the potential extinction of these prey through predation pressure is avoided by the input of the alternative prey. Thus, this input alleviates the trophic cascade in the whole food web, mainly under a low to moderate input of those resources (Huxel and McCann 1998, Huxel et al. 2002, Faria and Costa 2010). When consumers that suffer some predation pressure by top predators get access to allochthonous resources, it is expected that the effects of predation on them will be weak. This happens because of the input of alternative resources that can compensate the predation pressure suffered by consumers (Holt and Huxel 2007). Overall, the stabilizing role of allochthonous resources is context dependent but very important in systems that depend on those resources.

Cascade effects mediated by allochthonous resources may happen if subsidies trigger a numerical or functional response of recipient consumers, especially when the preference level on these resources is high (Henschel et al. 2001, Murakami and Nakano 2002,

Recalde et al. 2016). For instance, in a tropical rainforest, Recalde and collaborators (2016) have shown that the input of emergent aquatic insects increased riparian spider biomass resulting in a decrease of herbivorous biomass. Nevertheless, the presence of predators that forage on spider, such as birds and bats (Gunnarsson 2008, Foelix 2011, Rogers et al. 2012), may control the direct effect of spiders on herbivores. Thus, intraguild predation should occur between those vertebrates that act as top predators of arthropod communities, and predatory arthropods (i.e., mesopredators), leading to complex interactions in recipient food webs.

Intraguild predation (hereafter IGP) is described as predation between individuals that share the same resources, and hence are potential competitors (Polis et al. 1989, Holt and Polis 1997). Since the term describe the effective competition and predation between members of the same guild (predators), knowing the strength of the competitive and predatory components of IGP, it is possible to predict the direction and magnitude of effects in food webs (Mooney et al. 2010). For example, if top predators prey more on shared prey, mesopredators can be relatively released of predation (i.e., stronger competition). Otherwise, if top predators prey more on mesopredators, shared prey can be benefited through the decreasing pressure of mesopredators (i.e., stronger predation) (Mooney et al. 2010, Karp and Daily 2014). The input of allochthonous resources can potentially weaken the IGP in subsidized food webs through the stabilizing role of resource subsidies (Huxel and McCann 1998, Huxel et al. 2002). For instance, when mesopredators are subsidized by allochthonous resources, they persist despite the stronger predation pressure or higher competition with top predators (Nishijima et al. 2014). Loss of top predators can release subsidized mesopredators and indirectly trigger an eventual extinction of shared prey (Cassano et al. 2016, Wu and Shaner 2016), through apparent competition (Holt and Huxel 2007, Nishijima et al. 2014). In this sense, the influence of allochthonous resources can depend also on the top-down control of top predators on the response of mesopredators and the subsequent cascade effects. On the other hand, if top predators have a higher preference for allochthonous resources, this can trigger a decoupling in the food chain since lower trophic levels (mesopredators and shared prey) will be released from predation and, consequently, extinction of one of these levels may happen (Huxel and McCann 1998). Nevertheless, when top predators prey on both allochthonous and autochthonous prey, the input of the alternative prey will mitigate the predation pressure on lower trophic levels. To the best of our knowledge, only theoretical models have supported these predictions, so it is pivotal that empirical studies test the whole effects of allochthonous resources on IGP in recipient ecosystems.

In this study, we investigated the stabilizing role of allochthonous aquatic resources on intraguild predation (IGP) and their consequences on shared prey in a terrestrial ecosystem. We examine IGP between flying vertebrates (i.e., insectivorous bats and birds) as top predators, spiders as mesopredators and its overall effects on terrestrial insects as shared prey. In our study site, Recalde and collaborators (2016) showed that the diet of riparian spiders comprised mostly of emergent aquatic insects (85%), evidencing that spiders are very efficient in using these aquatic subsidies. Biomass of these riparian spiders was approximately twice as large when allochthonous resources were available. Furthermore, insectivorous birds and bats, frequently observed in our study site, are voracious generalists that potentially consume both aquatic and terrestrial resources (Recalde et al. *unpublished data*). In some cases, it is possible to observe birds (e.g., *Myiothlypis leucoblephara*, *Conopophaga lineata*, *Turdus albicollis*) consuming dipteran, grasshoppers, caterpillars, and spiders on vegetation in the banks of streams (C.P.B. Breviglieri, personal communication). On the other hand, some insectivorous bats (family Vespertilionidae) preferentially forage along river and stream banks, puddles, swamp or on lagoons, especially because these environments present high density of emergent insects (Kunz and Fenton 2003, Fukui et al. 2006).

Here, we predict that input of emergent aquatic insects (i.e., allochthonous resources) weakens IGP in riparian habitats when top predators are generalists (prediction 1, Fig. 1A). Therefore, the exclusion of emergent insects will destabilize food chains through stronger predation pressure on lower trophic levels. However, which level will suffer the pressure of top predators will depend on which predatory or competitive component of IGP predominates, i.e., if top predators consume more mesopredators (spiders) or shared prey (terrestrial insects). We assessed the contribution of each available prey (allochthonous, spiders and terrestrial insects) in the diet of top predators using stable isotope tools. With this we can support one of the two contrasting predictions when allochthonous prey were excluded: top predators will release terrestrial insects through predation on spiders (i.e., predatory component of IGP, prediction 2, Fig. 1B), or top predators will affect negatively terrestrial insects through direct predation, thus competing with spiders (i.e., competitive component of IGP, prediction 3, Fig. 1C). Additionally, if top predators consume more spiders, we predict that top predators will consume more spiders than terrestrial insects because they are larger prey (prediction 4). This prediction is based on the tested observation that subsidized spiders in our system are larger than non-subsidized spiders and insects (Recalde et al 2016), and because larger preys are prone to be detected easier by vertebrate predators (Dial and Rougharden 1995, Mizutani and Hijii 2002).

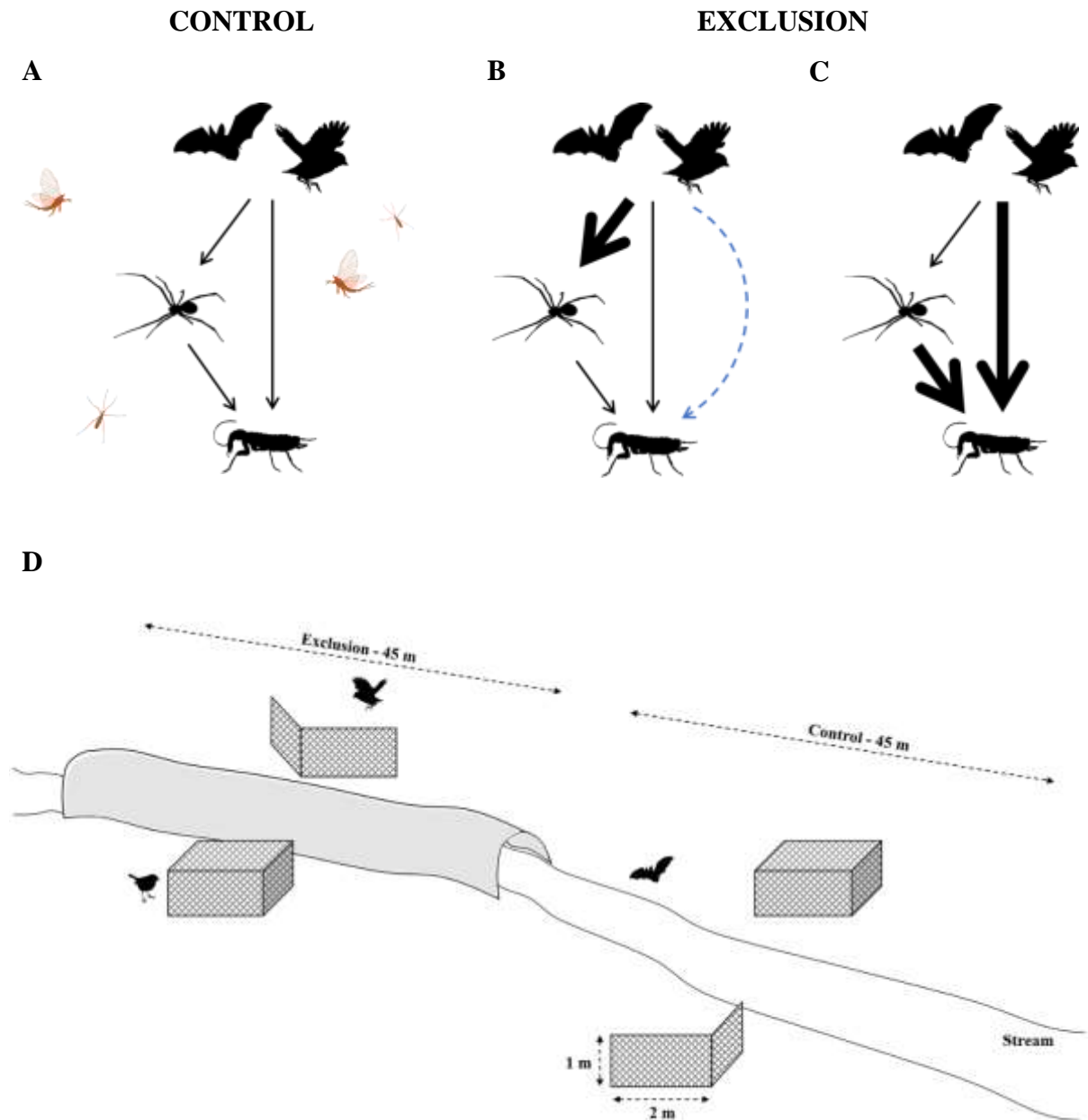


Fig. 1. Predictions about the effect of aquatic subsidies on intraguild predation (IGP) and scheme of an experimental block. Aquatic subsidies influence terrestrial top predator and mesopredator activities, weakening interaction strength in the recipient food web (A). In the absence of aquatic subsidies, top predators can benefit shared prey through mesopredator control (B), or they can release mesopredators through predation on shared prey (C). Solid black arrows represent direct negative interaction. Blue dashed arrow represents indirect positive interaction. The arrows' thickness represents the magnitude of the effect, the wider the arrow, the stronger the expected effect. Emergent aquatic insects are represented by orange color. Lower figure shows an experimental block (D) with 45 m-plastic cover of stream (*Exclusion*) and 45 m of stream as *Control*. Plots are localized in the middle of each treatment. Caged plots are covered with a 20 mm mesh grid, and open cages have only two sides of the grid.

MATERIALS AND METHODS

Study site

From March to April 2016, we performed the experiment at Serra do Japi municipal reserve (23° 13' S, 46° 56' W), São Paulo state, Brazil, at 970 m asl. The vegetation is characterized by semi-deciduous mesophytic altitudinal formation of Atlantic Rainforest (Leitão-Filho 1992). We conducted the experiment in a riparian forest with an understory dominated by herbs, shrubs, young trees and many ferns at stream margins. The studied streams were of first or second order with ca. 0.5 to 1.5 m width and ca. 10 to 40 cm deep (Recalde et al. 2016).

Experimental design

To test the influence of allochthonous resources on intraguild interaction, we designed four randomized blocks along two streams (two blocks on first-order and two blocks in two-order stream). On each block, we randomly established two ‘subsidy’ treatments: an exclusion of emergent aquatic insects and a control. The exclusion treatment consisted in a greenhouse-like cover (i.e., plastic semicircular cover held with PVC tubes, Fig. 1D) along 45-m of the stream that restricts the input of emergent aquatic insects (i.e., subsidies) to land. The control treatment consisted of a 45-m long section of the stream without cover, where aquatic insects emerged naturally. Each block was separated from the other by ca. 100-m to ensure independence.

On the other hand, to estimate the strength of IGP we measured the influence of predation on mesopredators and shared prey through the exclusion of top predators. In each ‘subsidy’ treatments (exclusion and control), we established two ‘predation’ treatments consisted of two plots of 4-m², one in each side of the stream (Fig. 1D). We randomly covered one plot with a 20-mm grid of plastic mesh to form a cage-like plot 1-m tall (caged plot treatment), and the other plot was left uncovered but with two sides of grid (open-cage treatment, Fig. 1D) to control for plastic mesh material in the environment (Romero et al. 2011, Breviglieri and Romero 2017). The 20-mm grid allowed natural movement of arthropods but prevented top predator attacks on arthropods inside the cages. Cages were settled ca. 10-cm above ground to allow the natural movement of ground-dwelling arthropods and small wingless vertebrates.

Sticky-traps surveys

We set one sticky-trap inside each cage at 1-m high to catch and assess the presence of flying aquatic insects in our treatments. Sticky-traps consisted of 256-cm² transparent plastic square set within a wood frame and smeared with Tanglefoot® resin at one side. We left the traps for seven days and thereafter all caught insects were classified into aquatic or terrestrial according to larvae origin.

Terrestrial arthropods surveys

After ten days that cages have been established, we collected shrub-dwelling arthropods in each plot by beating vegetation. This procedure was done for 20 minutes in each cage and repeated weekly along 21 days. All arthropods dropped in beating tray were collected and conserved in 70% ethanol until identification. Individuals that weaved their webs on mesh sides were not considered since they can benefit from these structures. Arthropods were identified into morphospecies and measured to estimate their biomass through allometric equations (Hóðar 1996, Hoffer and Ott 2009). We classified arthropods as mesopredators (i.e., spiders) and shared prey (i.e., terrestrial insects). Additionally, we classified mesopredators into ‘web spiders’ and ‘cursorial spiders’. We separate the effects on each mesopredator guild (web-weaving or cursorial) because the bats captured in our study area were more likely to prey on web spiders than cursorial ones since they catch prey during the flight (Kunz and Fenton 2003). Birds can capture both web and cursorial spiders because of their generalist foraging mode. We analyzed the data including all spiders because guild of many of them was unable to identify (e.g., spiderlings or unidentifiable sample). We also analyzed the individual body size of spiders and terrestrial insects to assess potential prey availability for top predators.

Estimation of the diet of top predators and mesopredators

We analyzed the diet of top predators and spiders to elucidate their feeding preference and thus, disentangle the strength of predatory and competitive components. To this end, we established a mist net of 15x5 m on six streams in the Serra do Japi, separate by more than 1 km. These streams presented similar physical characteristics of those used in the experiment. In this way, we avoided surveys of top predators thus minimizing the possible effects of capture on their activities during our experiment. The mist nets were exposed during ca. 12 hours from early morning (i.e., 06:00h to 12:00h) to evening (i.e., 18:00h to 23:00h), thus comprising the periods of highest activity of insectivorous birds and bats, respectively

(Sick 1997, Kunz and Fenton 2003). The nets were inspected every 20 minutes. After captures, we identified birds and bats until species and collected tissue samples (i.e., feather and hair, respectively) for isotopic analysis (^{13}C and ^{15}N). Since ^{13}C and ^{15}N signatures of consumer tissue is acquired by eating prey (Bearhop et al. 2004, Newsome et al. 2007), the isotopic analysis allowed us to access the percentage contribution of each prey to the diet of top predator vertebrates (Stock et al. 2018). We used data just of insectivorous vertebrates. For birds, we cut a little portion of a young primary feather, and for bats, we cut ca. 5 mg of hair of their back. Immediately after, we released the vertebrates in the same place of capture. The tissue samples were labeled and frozen at -20°C until processing.

Arthropods were also surveyed for isotopic determinations. For this, we established plots of 12 x 5 m, one for every six streams, where we collected manually arthropods in vegetation for 40 minutes. Each arthropod was separated in individual plastic trials, identified until family or order and classified into mesopredators (overall spiders, web and cursorial spiders) and prey (terrestrial insects). Additionally, we collected the aquatic larvae of complex life insects (i.e., insects with aquatic larvae and terrestrial adult) in each stream bed with manual sieves as potential allochthonous prey of the top predators and mesopredators. All materials were frozen as well until processing for isotopic analyses.

Isotopic analysis

To ensure the animal tissue non-infectious and without any contaminants, we washed feather in a clean-rinsing, neutral detergent and the hair tissue was dried at 70°C for 48 h. Cleaned feathers and the arthropod samples were dried then at 60°C for 48 h. Each dried samples and individual were weighed and a little portion of 1 mg (± 0.2) was enclosed in a tin capsule. The capsules were analyzed in the UC Davis Stable Isotope Facility, California, USA. Values of $\delta^{13}\text{C}$ [= $(^{13}\text{C}:^{12}\text{C}_{\text{sample}}/^{13}\text{C}:^{12}\text{C}_{\text{standard}}) - 1 \times 1000$] and $\delta^{15}\text{N}$ [= $(^{15}\text{N}:^{14}\text{N}_{\text{sample}}/^{15}\text{N}:^{14}\text{N}_{\text{standard}}) - 1 \times 1000$] were determined through elemental analyzer PDZ Europa ANCA-GSL coupled with an Isotope-Ratio Mass Spectrometer (PDZ Europa 20-20, Sercon Ltd., Cheshire, UK). The isotopic ratios (δ) were analyzed from standard values of Pee dee Belamite (PDB) for $\delta^{13}\text{C}$ and of atmospheric nitrogen for $\delta^{15}\text{N}$.

Statistical analysis

We used analysis of variance (ANOVA) to test the functionality of plastic cover ('subsidy' treatments) on the abundance of allochthonous resources surveyed in the sticky traps. To test the effect of our fixed effects (i.e., 'subsidy' and 'predation' treatments and their

interaction) on spider abundance and individual body size, we used generalized linear mixed model (GLMMs) with Poisson and Gamma distribution, respectively (package *lme4*, Bates et al. 2015), because our model failed to meet the parametric assumptions. The random factor was the period of survey nested within the block. For other models including fixed effects on spider biomass and richness, and on terrestrial insect abundance, biomass, individual body size, and richness, we performed linear mixed effect models (LME) of the package *nlme* (Pinheiro et al. 2018). The data of the isotopic signature of each sample were analyzed using Bayesian mixing models of MixSIAR package (Stock et al. 2018) that require *a priori* tracer data of mixture (consumers) and sources and a trophic enrichment data of the mixture. We used two isotopes (^{13}C and ^{15}N) and three sources (spider, aquatic and terrestrial insects) for the mixing models. We followed the equations of Greer et al. (2015) to estimate the trophic enrichment factor between consumers (i.e., birds and bats) and sources. This method consists in the calculation of the dietary (total food items) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values weighed by elemental (isotope) concentration using mass balance equation (see details in Greer et al. 2015). To disentangle the trophic links in our multi-trophic interaction tangle, we also assessed the diet preference of mesopredators. We used two sources as potential prey of spiders (aquatic and terrestrial insects) and calculated the trophic enrichment factor following Caut et al. (2009). Analyses were run using a JAGS (Just Another Gibbs Sampler, Plummer 2003) model under Bayesian MCMC tests through 100,000 iterations, with an uninformative/generalist prior with the Dirichlet distribution. All analyses were performed in R (R Core Team 2019). The significance level was $\alpha = 0.05$. We graphically inspected our data for variance heterogeneity, homogeneity, normality, and outliers. Data were log-transformed whenever necessary for analyses, but raw data were used to draw figures.

RESULTS

Sticky Traps

The abundance of adult aquatic insects catching in sticky traps was three times lower at exclusion treatment than control (ANOVA, $F = 6.91$, $P = 0.027$, Appendix S1: Figure S1). On the other hand, the abundance of flying terrestrial insects catching in sticky traps was not affected by the exclusion treatment (ANOVA, $F = 0.89$, $P = 0.371$). Flying terrestrial insects were ten times higher in exclusion treatment and four times higher in control treatment than adult aquatic insects (Appendix S1: Figure S1). Cages presence and the interaction of

'predation' and 'subsidy' treatments did not affect the abundance of adult aquatic and terrestrial insects (Appendix S1: Table S1).

Abundance, biomass, individual body size and richness of terrestrial arthropods on cages

We collected 486 spiders within fourteen families, and 646 terrestrial insects within twelve orders (Appendix S2: Table S1). The effect of predation pressure on spiders was highly dependent on the input of allochthonous aquatic resources (i.e., stronger interaction effect). Interaction between 'predation' and 'subsidies' treatments affected the abundance and richness of the overall groups of spiders (Fig. 2A, E, Table 1).

TABLE 1. Results of generalized linear mixed-effects models (GLMMs) and linear mixed-effects models (LME) testing the influence of allochthonous resources, predation and their interaction on abundance, biomass, and richness of mesopredators and shared prey. Bold numbers represent significant difference $\alpha \leq 0.05$.

	Abundance		Biomass		Body size		Richness	
	z	P	t	P	t	P	t	P
<i>Mesopredators</i>								
Subsidies	2.44	0.015	0.07	0.945	2.57	0.010	1.18	0.246
Predation	1.12	0.264	1.15	0.257	1.59	0.113	1.05	0.303
Predation x Subsidies	-3.15	0.002	-1.41	0.169	-1.32	0.186	-2.41	0.022
<i>Web spiders</i>								
Subsidies	2.32	0.021	0.09	0.927	-0.85	0.402	1.88	0.069
Predation	0.82	0.412	1.12	0.269	0.84	0.407	0.59	0.556
Predation x Subsidies	-2.70	0.007	-1.30	0.202	-0.73	0.469	-2.17	0.037
<i>Cursorial spiders</i>								
Subsidies	1.03	0.304	0.54	0.596	1.00	0.324	0.379	0.705
Predation	2.13	0.034	0.83	0.412	1.00	0.323	1.65	0.099
Predation x Subsidies	-1.96	0.049	-0.96	0.345	-0.78	0.441	-1.14	0.256
<i>Shared prey</i>								
Subsidies	-1.78	0.085	-1.36	0.183	0.09	0.923	-1.80	0.081
Predation	-2.21	0.034	1.05	0.303	2.07	0.047	-0.90	0.376
Predation x Subsidies	3.60	0.001	1.14	0.259	-0.78	0.443	3.07	0.004

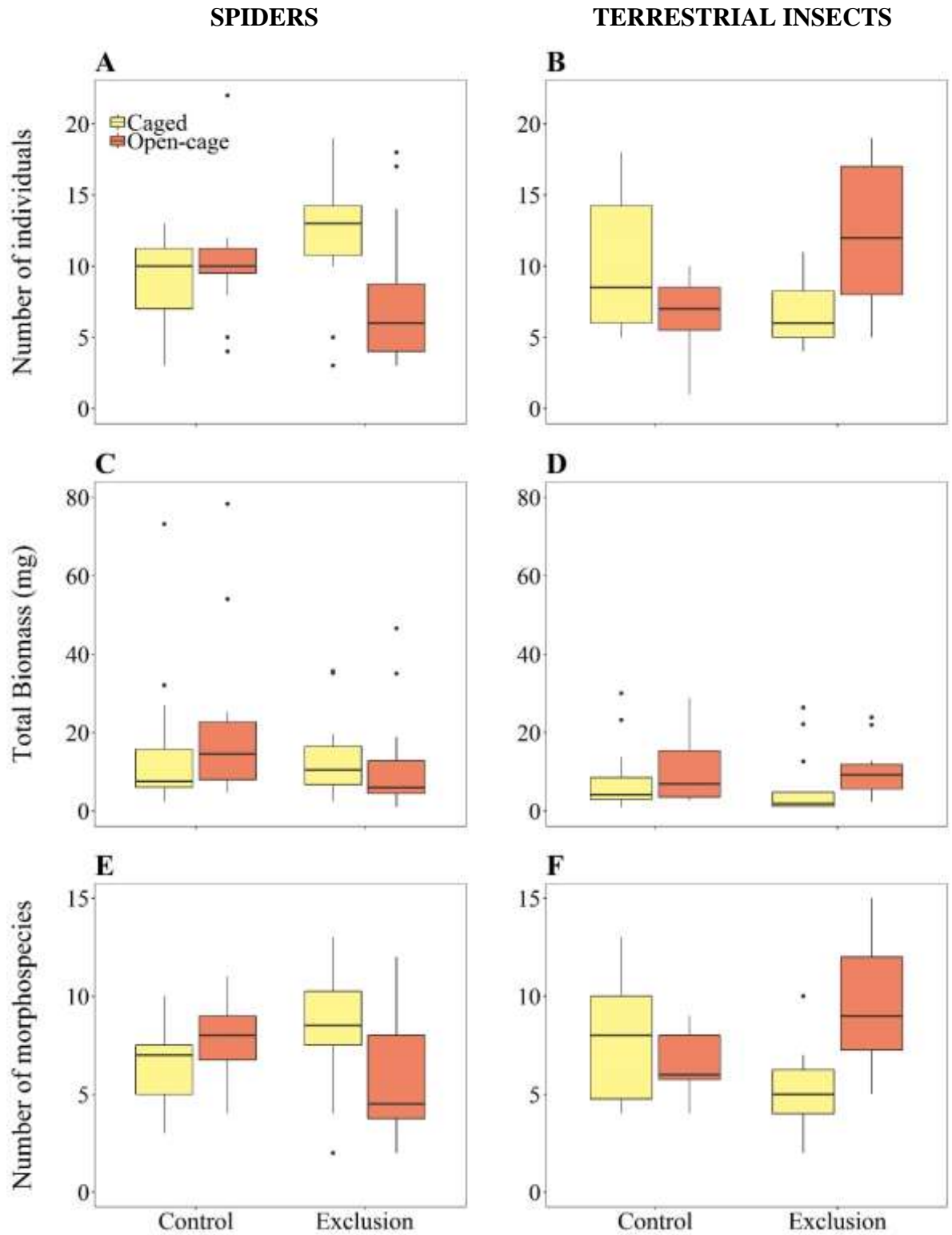


Fig. 2. Abundance (A, B), biomass (C, D), and richness (E, F) of all spiders and terrestrial insects, respectively, collected within caged and uncaged plots, in Control and Exclusion treatments.

In exclusion treatment, their abundance and richness were 1.5 and 1.4 times higher, respectively, when top predators were absent. The interaction effect was detected on terrestrial insects as well, but inverse to the response on spiders, i.e., their abundance and richness decreased 1.7 times when predators were absent. (Fig. 2B, F, Table 1). Biomass of spiders and terrestrial insects were not affected by the ‘predation’ and ‘subsidy’ treatments, nor their interaction terms (Fig. 2C, D, Table 1). However, the individual body size of spiders was affected only by ‘subsidy’ treatment, being three times higher in control than exclusion treatment (Table 1). Individual body size of terrestrial insects was affected only by ‘predation’ treatment and was 1.7 times higher in open-cage than caged plots (Table 1). Additionally, spiders were on average two times larger than terrestrial insects in both ‘subsidy’ and ‘predation’ treatments (mean dry mass (mg) \pm SD spider: 3.43 ± 6.15 , insect: 1.11 ± 0.97 , t-test, $t = 1.815$, $p = 0.038$).

We collected 375 web spiders corresponding to 267 morphospecies, and 78 cursorial spiders corresponding to 66 morphospecies. Under exclusion treatment, the abundance of web spiders decreased 65% in open-cage compared with caged plots, and their richness was 1.4 times lower in open-cage than caged plots (Table 1, Fig. 3). Similarly, cursorial spiders were significantly 1.3 times less abundant in open-cage than caged plots, but their richness was similar between cages (Table 1, Fig. 3). In control treatment, there was no difference in abundance and richness between ‘predation’ treatments for web spiders and cursorial spiders (Table 1, Fig. 3). Biomass and individual body size were not affected by the treatments (Table 1).

TABLE 2. Mean (\pm SD) of proportions of three sources in the diet of top predators and two sources of the diet of mesopredators. Letters represent significant difference between contribution of the sources calculated through *t* tests.

Consumers	Sources		
	Aquatic insects	Terrestrial insects	Spiders
Bats	0.44 \pm 0.21 a	0.17 \pm 0.10 b	0.39 \pm 0.13 a
Birds	0.45 \pm 0.24a	0.25 \pm 0.19b	0.33 \pm 0.21a, b
Spiders	0.64 \pm 0.11a	0.36 \pm 0.11b	-

Food preference of top predators and mesopredators

We captured nine and eight individuals of insectivorous birds and bats, respectively (Appendix S3: Table S1). Mixing models of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ showed that these vertebrates consumed more spiders and emergent aquatic insects than terrestrial insects (Table 2). On the other hand, spiders showed a stronger preference for aquatic resources than terrestrial ones (Table 2).

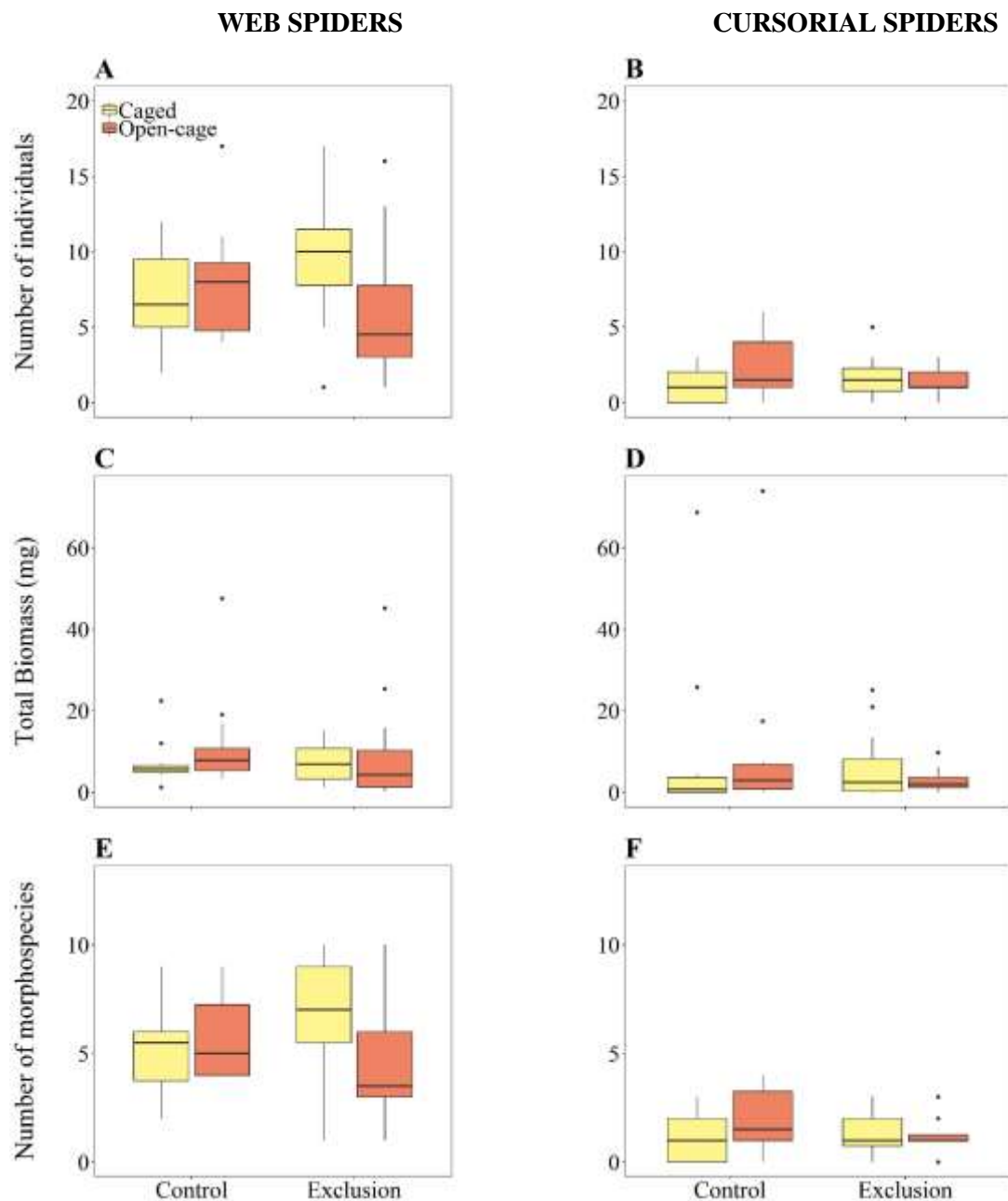


Fig. 3. Abundance (A, B), biomass (C, D), and richness (E, F) of web spiders (first column) and cursorial spiders (second column) collected within caged and open-cage plots, in Control and Exclusion treatments.

DISCUSSION

Our study evidenced empirically that the input of allochthonous resources weakens the interaction between top predators and mesopredators, with cascading effects to shared prey. Whereas mesopredators suffered strong predation pressure under exclusion of aquatic resources, the abundance, richness and body size of shared prey were particularly high in the presence of top predators. When aquatic resources were available, spiders and shared prey were not affected by top predators. Insectivorous bats and birds showed a food preference on spiders and aquatic resources, but terrestrial insects were scarcely used by these top predators. Likewise, the mesopredators greatly preferred aquatic prey over the terrestrial one. Thus, the strong and positive responses of terrestrial insects to the reduction of spiders were probably via non-consumptive effects. Overall, these results demonstrated a strong interaction between top-down (predation by bats and birds) and bottom-up forces (input of aquatic prey) driving abundance and diversity of mesopredators and shared prey.

According to our first prediction, we found that the input of allochthonous resources weakens intraguild predation in our system. Top predators showed a generalist foraging mode, in the sense that they consumed both allochthonous and autochthonous (spiders) prey. Thus, they were highly subsidized by allochthonous resources and had strong control over the food chain. Theory states that low to moderate input of allochthonous resources and preference of them stabilizes trophic interactions in recipient food webs (Huxel and McCann 1998). Thus, under allochthonous input, the strength of links between members of the food chain becomes weak due to the availability of alternative resources (Huxel and McCann 1998). These weak to moderate links stabilize food chains because of the resultant weak trophic cascade (Huxel and McCann 1998, Huxel et al. 2002). In our system, predation pressure on spiders was mitigated by the input of emergent aquatic insects. Since top predators consumed both spiders and aquatic prey, predation pressure on spiders probably avoid the increment of their density and, at the same time, mitigate their extinction through the input of aquatic prey. Moreover, spiders showed a higher preference on aquatic prey over terrestrial one, and this high subsidy to spider could have supported their populations. On the other hand, when emergent aquatic insects were excluded, the predation pressure on spiders was strong, decreasing their density and richness and benefiting indirectly the terrestrial insects. Accordingly, we suggest that the potential mechanism by which input of allochthonous insects stabilized the food chain was the higher subsidy to spiders, that avoid their extinction by top

predators. Thus, top-down (i.e., predation) and bottom-up (i.e., aquatic prey) forces interacted to stabilize food chain dynamics in our system.

Spiders were more affected by top predators than terrestrial insects. This result indicates that predation component of IGP was stronger than the competition component (corroborating our second prediction over our third prediction). It is widely known that spiders are common prey of birds and bats (Pereira et al. 2002, Burles et al. 2008, Gunnarsson 2008, Goiti et al. 2011, Rogers et al. 2012, Recalde et al. *unpublished data*), as also demonstrated in this study. We observed spiders' body size to be larger than of terrestrial insects which potentially facilitate their capture or selection by top-predators. In this sense, Dial and Roughgarden (1995) studied lizard predation on canopy arthropods and showed that larger arthropods were more preyed by the lizards, and smaller arthropods did not suffer any effects. Accordingly, some birds have been reported to select larger prey according to their species-specific preference (Mizutani and Hijii 2002). On the other hand, the preference of aquatic resources by spiders and top predators can be explained by the high quality of these resources. In this fashion, it was widely evidenced that aquatic primary producers are of better quality than terrestrial one according to the fatty acid composition (Ahlgren et al. 1992, Arce Funk et al. 2015, Twining et al. 2016). Essential ω -3 polyunsaturated fatty acids (ω -3 PUFA) are characteristic of aquatic food webs where primary consumers (e.g., larvae of emergent insects) assimilate them from basal resources and become high-quality prey of secondary consumers (Gladyshev et al. 2013, Martin-Creuzburg et al. 2017). Riparian spiders, birds, and bats are highly subsidized by emergent aquatic insects (Nakano and Murakami 2001, Fukui et al. 2006, Recalde et al. 2016) and several studies have demonstrated that high quality of these subsidies enhance immunocompetence, growth and torpor duration (Munro and Thomas 2004, Twining et al. 2016, Fritz et al. 2017) of the predators. Spiders were also an important food item for bats and birds. As predators, these vertebrates have high nitrogen demand that is not commonly supplied by their non-predatory insect prey (Fagan and Denno 2004). Consequently, they need to adapt their foraging strategy to optimize nutrient-rich prey intake (Denno and Fagan 2003, Tsahar et al. 2006). For instance, omnivory and intra-guild predation arise since predators eaten by other predators sustain better the N demand than other nutrient-deficient prey (Denno and Fagan 2003, Matsumura et al. 2004). Greenwood and collaborators (2010) evidenced that cannibalism (i.e., a type of IGP) between spiders increase their N content. In our system, we found strong intra-guild predation where bats and birds preyed on spiders. Besides spiders are higher N content than insect prey, they can assimilate the high-quality PUFA from aquatic

subsidies in their tissues (Uscian and Stanley-Samuelson 1994). Thus, we suggest that top predators selected more spiders than terrestrial insects because these mesopredators become very suitable prey in our study site.

We found that top predators affected shared prey through the direct consumption on mesopredators, in a scenario of exclusion of allochthonous resources (Fig. 1B). Nevertheless, spiders consumed mainly aquatic prey, and consequently, the direct consumption on terrestrial prey may have been weak. We suggest that non-consumptive effects could have mediated the strong response of terrestrial insects. Non-consumptive signals leaving by spiders are stronger factors that influence many traits of potential prey (Romero et al. 2011, Hawlena et al. 2012, Rypstra and Buddle 2013). It has been seen in a previous study that the presence of spider silk emits a warning signal to herbivorous beetles, which forage less and consequently reduce plant damage (Rypstra and Buddle 2013). We registered five times more web spiders than cursorial spiders, which potentially emit risk signals to terrestrial insects. Additionally, risk signals of web spiders are fixed and constant because of their sit-and-wait foraging mode that allows the prey to identify the risk easier (Preisser et al. 2007, Schmitz 2008). Thus, these signals represent an imminent predation risk for terrestrial insects (Preisser et al. 2007). On the other hand, the few cursorial spiders that we found emit confounding cues since they are more active (i.e., more mobile) foragers and the prey cannot necessarily realize the possible risk (Preisser et al. 2007, Schmitz 2008). Our results thus can indicate that a higher abundance of web spiders triggered a change in insect behavior, for example, minimizing courtship or stimulating escape (Wing 1988, Losey and Denno 1998, Cooper 2006). Overall, although spiders did not preferentially consume terrestrial insects, we propose that as potential enemies, high abundance of these mesopredators determined behavioral responses of terrestrial insects.

In summary, in this study, we have supported our hypothesis that input of allochthonous aquatic resources in riparian ecosystems plays a fundamental role in stabilizing terrestrial trophic interactions and consequently, trophic cascades in a food chain. When aquatic resources were negligible, top predators exerted a strong predation pressure on mesopredators, and consequently, shared prey was benefited through cascading effects. Nevertheless, mesopredators had not a feeding preference on terrestrial insects. We propose that the indirect effects of top predators on shared prey were mainly through non-consumptive effects of mesopredators, possibly affecting the presence of shared prey in the study plots. When aquatic resources were available, the predation pressure of top predators was mitigated and did not influence the spiders because the allochthonous resources supported the community

persistence of these mesopredators. The role of allochthonous resources in recipient habitats involves the stability of the food web since this depends greatly on the input of those resources. In this way, potential extinction of some trophic levels (e.g., mesopredator in the case of this study) which can trigger trophic cascades, can be avoided by alternative resources that support those levels. These results have an important implication on riparian forest management since these areas hold great stability and hence can improve the sustainability of ecosystem functions. We contribute with the knowledge of cross-ecosystem interactions hoping for more powerful conservation efforts and awareness.

Acknowledgment

We thank V. Fernandes Souza and S. Benavides Gordillo for the help in field work, and P. Munhoz de Omena and M. Kersch-Becker for their valuable comments and suggestions on the general development of the study and on the discussion of results. FCR was supported by a postgraduate fellowship from CAPES, finance code 001. CPBB was supported by a postdoctoral fellowship from CNPq. This study was supported by research grants from FAPESP (proc. 2017/09052-4), coordinated by GQR. GQR received a CNPq-Brazil productivity research fellowship.

LITERATURE CITED

- Ahlgren, G., I. B. Gustafsson, and M. Boberg. 1992. Fatty acid content and chemical composition of freshwater microalgae. *Journal of Phycology* 28:37-50.
- Arce Funk, J., A. Bec, F. Perrière, V. Felten, and M. Danger. 2015. Aquatic hyphomycetes: a potential source of polyunsaturated fatty acids in detritus-based stream food webs. *Fungal Ecology* 13:205-210.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48.
- Bearhop, S., C. E. Adams, S. Waldrons, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* 73: 1007-1012.

- Breviglieri, C. P. B., and G. Q. Romero. 2017. Terrestrial vertebrate predators drive the structure and functioning of aquatic food webs. *Ecology* 98:2069-2080.
- Burles, D. W., R. M. Brigham, R. A. Ring, and T. E. Reimchen. 2008. Diet of two insectivorous bats, *Myotis lucifugus* and *Myotis keenii*, in relation to arthropod abundance in a temperate Pacific northwest rainforest environment. *Canadian Journal of Zoology* 86:1367-1375.
- Cassano, C. R., R. M. Silva, A. Mariano-Neto, G. Schroth, and D. Faria. 2016. Bat and bird exclusion but not shade cover influence arthropod abundance and cocoa leaf consumption in agroforestry landscape in northeast Brazil. *Agriculture, Ecosystems and Environment* 232:247-253.
- Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology* 46:443-453.
- Cooper, Jr. W. E. 2006. Risk factors and escape strategy in the grasshopper *Dissosteira Carolina*. *Behaviour* 143:1201-1218.
- Denno, R. F., and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* 84:2522-2531.
- Dial, R., and J. Roughgarden. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology* 76:1821-1834.
- Fagan, W. F., and R. F. Denno. 2004. Stoichiometry of actual vs. Potential predator-prey interactions: insights into nitrogen limitation for arthropod predators. *Ecology Letters* 7:876-883.
- Faria, L. B., and M. I. S. Costa. 2010. Omnivorous food web, prey preference, and allochthonous nutrient input. *Ecological Complexity* 7:107-114.
- Foelix, R. F. 2011. *Biology of spiders*. Oxford University Press. New York.
- Fritz, K. A., Kirschman, L. J., McCay, S. D., Trushenski, J. T., Warne, R. W. e Whiles, M. R. 2017. Subsidies of essential nutrients from aquatic environments correlate with immune function in terrestrial consumers. *Freshwater Science* 36:893-900
- Fukui, D., M. Murakami, S. Nakano e T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology* 75:1252-1258.

- Gladyshev, M. I., Sushchin, N. N. e Makhutova, O. N. 2013. Production of EPA and DHA in aquatic ecosystems and their transfer to the land. Prostaglandins and other lipid mediators. 107:117-126
- Greenwood, M. J., A. R. McIntosh, and J. S. Harding. 2010. Disturbance across an ecosystem boundary drives cannibalism propensity in a riparian consumer. Behavioral Ecology 21:1227-1235.
- Greer, A. L., T. W. Horton, and X. J. Nelson. 2015. Simple ways to calculate stable isotope discrimination factors and convert between tissue types. Methods in Ecology and Evolution 6: 1341-1348.
- Goiti, U., J. Aihartza, M. Guiu, E. Salsamendi, D. Almenar, M. Napal, and I. Garin. 2011. Geoffroy`s bat, *Myotis emarginatus*, preys preferentially on spiders in multistratified dense habitats: a study of foraging bats in the Mediterranean. Folia Zoologica 60:17-24.
- Gunnarsson, B. 2008. Bird predation on spiders: Ecological mechanisms and evolutionary consequences. Journal of Arachnology 35:509-529.
- Hawlena, D., M. S. Strickland, M. A. Bradford, and O. J. Schmitz. 2012. Fear of predation slows plant-litter decomposition. Science 336:1434-1438.
- Henschel, J. R., D. Mahsberg, and H. Stumpf. 2001. Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. Oikos 93:429-438.
- Hóðar. J. A. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Oecologica 17:421-433.
- Höfer, H., and R. Ott. 2009. Estimating biomass of neotropical spiders and other arachnids (Araneae, Opiliones, Pseudoscorpiones, Ricinulei) by mass-length regressions. The Journal of Arachnology 37:160-169.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. The American Naturalist 149:745-764.
- Holt, R. D., and G. R. Huxel. 2007. Alternative prey and the dynamics of intraguild predation: theoretical perspectives. Ecology 88:2706-2712.
- Huxel, G. R., and K. McCann. 1998. Food web stability: the influence of trophic flows across habitats. The American Naturalist 152:460-469.

- Huxel, G. R., K. McCann, and G. A. Polis. 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. *Ecological Research* 17:419-432.
- Karp, D. S., and G. C. Daily. 2014. Cascading effects of insectivorous birds and bats in tropical coffee plantations. *Ecology* 95:1065-1074.
- Kunz TH, Fenton MB (2003) *Ecology of bats*. The University of Chicago Press. Chicago and London.
- Leitão-Filho, H. L. 1992. A flora arbórea da Serra do Japi. Pages: 40-62 *in* Morellato, L. P. C., ed. *História Natural da Serra do Japi*. Editora UNICAMP, Campinas.
- Losey, J. E., and R. F. Denno. 1998. Interspecific variation in the escape responses of aphids: effect of risk of predation from foliar-foraging and ground-foraging predators. *Oecologia* 115:245-252.
- Martin-Creuzburg, D., C. Kowarik and D. Straile. 2017. Cross-ecosystem fluxes: Export of polyunsaturated fatty acids from aquatic to terrestrial ecosystems via emerging insects. *Science of the Total Environment* 577: 174-182
- Matsumura, M., G. M. Traftlet-Smith, C. Gratton, D. L. Finke, W. F. Fagan, and R. F. Denno. 2004. Does intraguild predation enhance predator performance? A stoichiometric perspective. *Ecology* 85:2601-2615.
- Mizutani, M., and N. Hijii. 2002. The effects of arthropod abundance and size on the nestling diet of two *Parus* species. *Ornithological Science* 1:71-80.
- Mooney, K. A., D. S. Gruner, N. A. Barber, S. A. Van Bael, S. M. Philpott, and R. Greenberg. 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *PNAS* 107: 7335-7340
- Munro, D., and D. W. Thomas. 2004. The role of polyunsaturated fatty acids in the expression of torpor by mammals: a review. *Zoology* 107:29-48.
- Murakami, M., and S. Nakano. 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through by bird predation. *Ecology Letters* 5:333-337.
- Nakano, S. e M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences* 98: 166-170

- Newsome, S. D., C. M. del Rio, S. Bearhop, and D. L. Phillippe. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment* 5: 429-436.
- Nishijima, S., G. Takimoto, and T. Miyashita. 2014. Roles of alternative prey for mesopredators on trophic cascades in intraguild predation systems: a theoretical perspective. *The American Naturalist* 183:625-637.
- Pereira, M. J. R., H. Rebelo, A. Rainho, and J. M. Palmeirim. 2002. Prey selection by *Myotis myotis* (Vespertilionidae) in a Mediterranean region. *Acta Chiropterologica* 4:183-193.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2018. nlme: linear and nonlinear mixed effects models. R package version 3.1-137. URL: <https://CRAN.R-project.org/package=nlme>.
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Pages 1-10 *in* Proceedings of the 3rd International Workshop on Distributed Statistical Computing. URL: <http://www.ci.tuwien.ac.at/Conferences/DSC-2003/Drafts/>.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297-330.
- Preisser, E. L., J. L. Orrock, e O. J. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology* 88:2744-2751
- R Core Team. 2019. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.
- Ramey, T. L., and J. S. Richardson. 2017. Terrestrial invertebrates in the riparian zone: mechanisms underlying their unique diversity. *Bioscience* 67:808-819.
- Recalde, F. C., T. C. Postali, and G. Q. Romero. 2016. Unraveling the role of allochthonous aquatic resources to food web structure in a tropical riparian forest. *Journal of Animal Ecology* 85: 525-536.
- Richardson, J. S., and T. Sato. 2015. Resource subsidy flows across freshwater-terrestrial boundaries and influence on processes linking adjacent ecosystems. *Ecohydrology* 8:406-415.

- Robbins, L. W., K. L. Murray, and P. M. McKenzie. 2008. Evaluating the effectiveness of the standard mist-netting protocol for the endangered Indiana bat (*Myotis sodalis*). *Northeastern Naturalist* 15:275-282.
- Rogers, H., J. Hille Ris Lambers, R. Miller, and J. J. Tewksbury. 2012. 'Natural experiment' demonstrates top-down control of spiders by birds on a landscape level. *PLoS ONE* 7:e43446
- Romero, G. Q., P. A. P. Antikeira e J. Koricheva. 2011. A meta-analysis of predation risk effects on pollinator behaviour. *PLoS ONE* 6:e20689
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385-387.
- Rypstra, A. L., and C. M. Buddle. 2013. Spider silk reduces insect herbivory. *Biology Letters* 9:20120948.
- Schindler, D. E., and A. P. Smits. 2017. Subsidies of aquatic resources in terrestrial ecosystems. *Ecosystems* 20:78-93.
- Sick, H. 1997. *Ornitologia Brasileira*. Editora Nova Fronteira, Rio de Janeiro.
- Spotswood, E. N., K. R. Goodman, J. Carlisle, R. L. Cormier, D. L. Humple, J. Rousseau, S. L. Guers, and G. G. Barton. 2012. How safe is mist netting? Evaluating the risk of injury and mortality to birds. *Methods in Ecology and Evolution* 3:29-38.
- Stock, B. C., A. L. Jackson, E. J. Ward, A. C. Parnell, D. L. Phillips, and B. X. Semmens. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* 6: e5096; DOI 10.7717/peerj.5096.
- Tsahar, E., Z. Arad, I. Izhaki, and C. Martínez del Rio. 2006. Do néctar- and fruit-eating birds have lower nitrogen requirements than omnivores? An allometric test. *The Auk* 123:1004-1012.
- Twining, C. W., J. T. Brenna, P. Lawrence, J. R. Shipley, T. N. Tollefson and D. W. Winkler. 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *PNAS* 113: 10920-10925.
- Uscian, J. M., and D. W. Stanley-Samuelson. 1994. Fatty acid compositions of phospholipids and triacylglycerols from selected terrestrial arthropods. *Comparative Biochemistry and Physiology* 107B:371-379.

- Wing, S. R. 1988. Cost of mating for female insects: risk of predation in *Photinus collustrans* (Coleoptera: Lampyridae). *The American Naturalist* 131:139-142.
- Wu, P. C., and P. J. L. Shaner. 2016. Trophic cascade effects of avian predation on a willow in an urban wetland. *Oecologia* 180:293-303.
- Xiang, H., Y. Zhang, and J. S. Richardson. 2016. Importance of riparian zone: effects of resource availability at land-water interface. *Riparian Ecology and Conservation* 3:1-17.

CONCLUSÃO GERAL

No primeiro capítulo foi encontrado que a disponibilidade de insetos aquáticos emergentes como subsídios para predadores terrestres afeta a atividade e a diversidade trófica das comunidades destes. No entanto, contrário às expectativas, a dieta dos predadores não foi influenciada pelos recursos alóctones, e, conseqüentemente, o espaço trófico ocupado por esses predadores foi similar entre comunidades próximas e distantes da fonte desses recursos. Adicionalmente, e não menos importante, foi encontrado que a resposta dos predadores à entrada de recursos alóctones variou entre os biomas estudados (i.e., Mata Atlântica e Amazonas). Foi proposto vários mecanismos para explicar esses resultados: Primeiro, as aves e morcegos estudados aqui tem alta capacidade de deslocamento e possuem uma alimentação generalista, portanto, os indivíduos registrados nas áreas próximas e distantes dos riachos puderam se deslocar entre as duas áreas forrageando oportunisticamente as presas mais nutritivas. Segundo, a dieta similar de estes predadores explica que o espaço trófico (como proxy de nicho trófico) foi o mesmo para toda a comunidade de aves e morcegos nas áreas de estudo. Por último, organismos da Mata Atlântica e do Amazonas mostraram uma assinatura isotópica básica diferente, que pode indicar uma diferente distribuição e disponibilidade de recursos para os predadores. Os resultados deste capítulo indicam que os recursos alóctones jogam um importante papel na diversidade trófica de aves e morcegos tropicais, no entanto, as características próprias de cada espécie de ave e morcego deve-se levar em consideração ao estudar a dieta e os espaços tróficos que estes organismos ocupam. Estas descobertas contribuem ao conhecimento dos processos interdependentes de ambos os ecossistemas e suportam os esforços de conservação de estas áreas de transição.

No segundo capítulo foi evidenciado que os recursos alóctones estabilizam as interações tróficas nos ecossistemas terrestres uma vez que evitam grandes flutuações nas populações dos consumidores. Especificamente, aves e morcegos, como predadores de topo, e aranhas, como mesopredadores, foram subsidiados pelos insetos aquáticos emergentes. Desta forma, a pressão de predação gerada pelos predadores de topo sobre as aranhas foi amenizada pelo subsídio alóctone. Assim, embora sendo predadas, as aranhas mantiveram uma abundancia e riqueza estáveis que foi suportada pela disponibilidade dos recursos alóctones. Estes resultados tem uma implicância importante no manejo de florestas ripárias já que estas são áreas de grande estabilidade e podem favorecer a sustentabilidade das funções dos ecossistemas.

REFERÊNCIAS

- Ahlgren, G., I. B. Gustafsson, e M. Boberg. 1992. Fatty acid content and chemical composition of freshwater microalgae. *Journal of Phycology* 28:37-50.
- Anderson, W. B. e G. A. Polis. 1998. Marine subsidies of island communities in the Gulf of California: Evidence from stable carbon and nitrogen isotopes. *Oikos* 81:75-80
- Arce Funk, J., A. Bec, F. Perrière, V. Felten, e M. Danger. 2015. Aquatic hyphomycetes: a potential source of polyunsaturated fatty acids in detritus-based stream food webs. *Fungal Ecology* 13:205-210.
- Bader, E., Acácio, M., e Monadjem, A. 2015. The importance of water bodies for insectivorous bats in a Malagasy dry deciduous forest: A case example from Kirindy (CNFEREF). *Malagasy Nature* 9: 88-96
- Ballinger, A., e Lake, P. S. 2006. Energy and nutrient fluxes from rivers and streams into terrestrial food webs. *Mar Freshwater Res* 57:15-28
- Barrett, K., W. B. Anderson, D. A. Wait, L. L. Grismer, G. A. Polis e M. D. Rose. 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations. *Oikos* 109:145-153
- Bartels, P., J. Cucherousset, K. Steger, P. Eklöv, L. J. Tranvik e H. Hillebrand. 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* 93:1173-1182
- Bates, D., M. Maechler, B. Bolker, e S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48.
- Baxter, C. C., K. D. Fausch e C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201-220
- Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A., Macleod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73:1007-1012
- Bendix, J. 2017. Riparian ecosystems. Em: Richardson, D., Castree, N., Goodchild, M. F. et al. (eds). *The International Encyclopedia of Geography*. John Wiley & Sons
- Breviglieri, C. P. B., e G. Q. Romero. 2017. Terrestrial vertebrate predators drive the structure and functioning of aquatic food webs. *Ecology* 98:2069-2080.
- Burles, D. W., R. M. Brigham, R. A. Ring, e T. E. Reimchen. 2008. Diet of two insectivorous bats, *Myotis lucifugus* and *Myotis keenii*, in relation to arthropod abundance in a

- temperate Pacific northwest rainforest environment. *Canadian Journal of Zoology* 86:1367-1375.
- Cassano, C. R., R. M. Silva, A. Mariano-Neto, G. Schroth, e D. Faria. 2016. Bat and bird exclusion but not shade cover influence arthropod abundance and cocoa leaf consumption in agroforestry landscape in northeast Brazil. *Agriculture, Ecosystems and Environment* 232:247-253.
- Caut, S., E. Angulo, e F. Courchamp. 2009. Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology* 46:443-453.
- Chan, E. K. W., Y.T. Yu, Y. Zhang e D. Dudgeon. 2008. Distribution patterns of birds and insect prey in a tropical riparian forest. *Biotropica* 40: 623-629
- Chan, E.K.W., Zhang, Y. e Dudgeon, D. 2007. Contribution of adult aquatic insects to riparian prey availability along tropical forest stream. *Marine and Freshwater Research* 58:725-732
- Chung, N. e Suberkropp, K. 2009. Effects of aquatic fungi on feeding preferences and bioenergetics of *Pycnopsyche gentilis* (Trichoptera: Limnephilidae). *Hydrobiologia* 630:257-269
- Cirtwill, A. R., Stouffer, D. B., e Romanuk, T. N. 2015. Latitudinal gradients in biotic niche breadth vary across ecosystem types. *Proc. R. Soc. B* 282:20151589
- Cooper, Jr. W. E. 2006. Risk factors and escape strategy in the grasshopper *Dissosteira Carolina*. *Behaviour* 143:1201-1218.
- Denno, R. F., e W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* 84:2522-2531.
- Dial, R., e J. Roughgarden. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology* 76:1821-1834.
- Esbérard, C. E. L., Bergallo, H. G. 2005. Coletar morcegos por seis ou doze horas a cada noite? *Rev Bras Zool* 22:1095-1098
- Fagan, W. F., e R. F. Denno. 2004. Stoichiometry of actual vs. Potential predator-prey interactions: insights into nitrogen limitation for arthropod predators. *Ecology Letters* 7:876-883.

- Faria, L. B., Costa, e M. I. S. 2010. Omnivorous food web, prey preference, and allochthonous nutrient input. *Ecol Complex* 7:107-114
- Foelix, R. F. 2011. *Biology of spiders*. Oxford University Press. New York.
- Fritz, K. A., Kirschman, L. J., McCay, S. D., Trushenski, J. T., Warne, R. W. e Whiles, M. R. 2017. Subsidies of essential nutrients from aquatic environments correlate with immune function in terrestrial consumers. *Freshwater Science* 36:893-900
- Funk, J. A., Bec, A. Perrière, F., Felten, V. e Danger, M. 2015. Aquatic hyphomycetes: a potential source of polyunsaturated fatty acids in detritus-based stream food webs. *Fungal Ecology* 13:205-210
- Fukui, D., M. Murakami, S. Nakano e T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology* 75:1252-1258
- Gill, F. B. 2007. *Ornithology*, 3rd edn. W. H. Freeman and Company, New York
- Gladyshev, M. I., Sushchin, N. N. e Makhutova, O. N. 2013. Production of EPA and DHA in aquatic ecosystems and their transfer to the land. Prostaglandins and other lipid mediators. 107:117-126
- Goiti, U., J. Aihartza, M. Guiu, E. Salsamendi, D. Almenar, M. Napal, e I. Garin. 2011. Geoffroy's bat, *Myotis emarginatus*, preys preferentially on spiders in multistratified dense habitats: a study of foraging bats in the Mediterranean. *Folia Zoologica* 60:17-24.
- Gomes, M., Rabaça, J. E., Godinho, C., e Ramos, J. A. 2017. Seasonal variation in Bird species richness and abundance in riparian galleries in Southern Portugal. *Acta Ornithol* 52:69-79
- Greenwood, M. J., A. R. McIntosh, e J. S. Harding. 2010. Disturbance across an ecosystem boundary drives cannibalism propensity in a riparian consumer. *Behavioral Ecology* 21:1227-1235.
- Greer, A. L., Horton, T. W., e Nelson, X. J. 2015. Simple ways to calculate stable isotope discrimination factors and convert between tissue types. *Methods Ecol Evol* 6:1341-1348
- Griffin, D. R. 2001. Return to the magic well: Echolocation behavior of bats and responses of insect prey. *BioScience* 51:555-556
- Grindal, S. D., Morissette, J. L., Brigham, R. M. 1999. Concentration of bat activity in riparian habitats over an elevational gradient. *Can J Zool* 77:972-977
- Gunnarsson, B. 2008. Bird predation on spiders: Ecological mechanisms and evolutionary consequences. *Journal of Arachnology* 35:509-529.

- Guo, F., Kainz, M. J., Sheldon, F. e Bunn, S. E. 2016. The importance of high-quality algal food sources in stream food webs -current status and future perspectives. *Freshwater Biology*.
- Hagen, E. M., Sabo, J. L. 2011. A landscape perspective on bat foraging ecology along rivers: does channel confinement and insect availability influence the response of bats to aquatic resources in riverine landscape? *Oecologia* 166:751-760
- Hagen, E. M., Sabo, J. L. 2014 Temporal variability in insectivorous bat activity along two desert streams with contrasting patterns of prey availability. *J Arid Environ* 102:104-112
- Hawlena, D., M. S. Strickland, M. A. Bradford, e O. J. Schmitz. 2012. Fear of predation slows plant-litter decomposition. *Science* 336:1434-1438.
- Henschel, J. R., D. Mahsberg e H. Stumpf. 2001. Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. *Oikos* 93:429-438
- Hixson, S. M., Sharma, B., Kainz, M. J., Wacker, A. e Arts, M. T. 2015. Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: a fundamental dichotomy between freshwater and terrestrial ecosystems. *Environmental Reviews* 23:414-424
- Hódar. J. A. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica* 17:421-433.
- Höfer, H., e R. Ott. 2009. Estimating biomass of neotropical spiders and other arachnids (Araneae, Opiliones, Pseudoscorpiones, Ricinulei) by mass-length regressions. *The Journal of Arachnology* 37:160-169.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theor Popul Biol* 12:197-229
- Holt, R. D., e G. A. Polis. 1997. A theoretical framework for intraguild predation. *The American Naturalist* 149:745-764.
- Holt, R. D., e G. R. Huxel. 2007. Alternative prey and the dynamics of intraguild predation: theoretical perspectives. *Ecology* 88:2706-2712.
- Huryn, A. D., Wallace, J. B. e Anderson, N. H. 2008. Habitat, life history, secondary production, and behavioral adaptations of aquatic insects. Em: Merritt, R. W., Cummins, K. W., Berg, M. B. (eds). *An introduction to the aquatic insects of North America*. Fourth Edition. Kendall/Hunt Publishing Company

- Huxel, G. R., e K. McCann. 1998. Food web stability: the influence of trophic flows across habitats. *The American Naturalist* 152:460-469.
- Huxel, G. R., K. McCann, e G. A. Polis. 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. *Ecological Research* 17:419-432.
- Jackson, A. L., Inger, R., Parnell, A. C., e Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *J Anim Ecol* 80:595-602 doi:
- Jackson, J. K. e S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran desert stream. *Ecology* 67:629-638
- Jacobsen, D., Cressa, C., Mathooko, J. M. e Dudgeon, D. 2008. Macroinvertebrates: Composition, life histories and production. Em: Dudgeon, D. (ed). *Tropical Stream Ecology*. Elsevier Inc, USA
- Junk, W. J., e Piedade, M. T. F. 2010. An introduction to south american wetland forest: distribution definition and general characterization. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) *Amazonian Floodplain Forest, Ecophysiology, Biodiversity and Sustainable Management*, Springer, pp 3-25
- Kalko, E. K. V., Friemel, D., Handley, Jr C. O., e Schnitzler, H. U. 1999. Roosting and foraging behavior of two neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). *Biotropica* 31:344-353
- Kato, C., T. Iwata, S. Nakano e D. Kishi. 2003. Dynamics of aquatic insect flux affects distribution of riparian web-building spiders. *Oikos* 103:113-120
- Karp, D. S., e G. C. Daily. 2014. Cascading effects of insectivorous birds and bats in tropical coffee plantations. *Ecology* 95:1065-1074.
- Knight, T. M., McCoy, M. W. Chase, J. M., McCoy, K. A. e Holt, R. D. 2005. Trophic cascades across ecosystems. *Nature* 437:880-883
- Kunz, T. H., e Fenton, M. B. 2003. *Ecology of bats*. The University of Chicago Press. Chicago and London
- Kunz, T. H., e Parsons, S. 2009. *Ecological and behavioral methods for the study of bats*. Johns Hopkins University Press. Baltimore.
- Lam, M. M-Y, D. Martin-Cewuzburg, K-O. Rothhaupt, K. Safi, E. Yohannes e I. Salvarina. 2013. Tracking diet preferences of bats using stable isotope and fatty acid signatures of faeces. *PLoS ONE* 8: e83452

- Layman, C. A., Arrington, D. A., Montaña, C. G., Post, D. M. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42-48
- Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E. et al. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol Rev* 87:545-562
- Leitão-Filho, H. L. 1992. A flora arbórea da Serra do Japi. Pages: 40-62 *in* Morellato, L. P. C., ed. *História Natural da Serra do Japi*. Editora UNICAMP, Campinas.
- Leroux, S. J. e Loreau, M. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* 11:1147-1156
- Losey, J. E., e R. F. Denno. 1998. Interspecific variation in the escape responses of aphids: effect of risk of predation from foliar-foraging and ground-foraging predators. *Oecologia* 115:245-252.
- MacArthur, R. H. 1972 *Geographical Ecology*. Princeton University Press, Princeton, N. J.
- Malanson, G. P. 1993. *Riparian Landscape*. Cambridge University Press. Cambridge. Pages: 12-37
- Marczak, L. B. e J. S. Richardson. 2007. Spiders and subsidies: results from the riparian zone of a coastal temperate rainforest. *Journal of Animal Ecology* 76:687-694
- Marczak, L. B., R. M. Thompson e J. S. Richardson. 2007. Meta-analysis: Trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88:140-148
- Martin-Creuzburg, D., C. Kowarik e D. Straile. 2017. Cross-ecosystem fluxes: Export of polyunsaturated fatty acids from aquatic to terrestrial ecosystems via emerging insects. *Science of the Total Environment* 577: 174-182
- Martinez, A. E., Parra, E., Muellerklein, O., Vredenburg, V. T. 2018. Fear-based niche shifts in neotropical birds. *Ecology* 0:1-8
- Matsumura, M., G. M. Trafelet-Smith, C. Gratton, D. L. Finke, W. F. Fagan, e R. F. Denno. 2004. Does intraguild predation enhance predator performance? A stoichiometric perspective. *Ecology* 85:2601-2615.
- Mazzoni, R. e Rezende, C. F. 2003. Seasonal diet shift in a tetragonopterinae (Osteichthyes, Characidae) from the Ubatiba river, RJ, Brazil. *Braz. J. Biol.* 63:69-74
- Mizutani, M., e N. Hijii. 2002. The effects of arthropod abundance and size on the nestling diet of two *Parus* species. *Ornithological Science* 1:71-80.

- Mooney, K. A., D. S. Gruner, N. A. Barber, S. A. Van Bael, S. M. Philpott, e R. Greenberg. 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *PNAS* 107: 7335-7340
- Muehlbauer J. D., S. F. Collins, M. W. Doyle e K. Tockner. 2014. How wide is a stream? Spatial extent of the potencial “stream signature” in terrestrial food webs using meta-analysis. *Ecology* 95:44-55
- Munro, D., e D. W. Thomas. 2004. The role of polyunsaturated fatty acids in the expression of torpor by mammals: a review. *Zoology* 107:29-48.
- Murakami, M., e Nakano, S. 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through by bird predation. *Ecol Lett* 5:333-337
- Myers, N. 2003. Biodiversity hotspots revisited. *BioScience* 53:916-917
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. e Kent, J. 2000. Biodiversity hotspot for conservation priorities. *Nature* 403:853-858
- Nakano, S., Miyasaka, H. e Kuhara, N. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* 80:2435-2441
- Nakano, S. e M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences* 98: 166-170
- Newsome, S. D., C. M. del Rio, S. Bearhop, e D. L. Phillipe. 2007. A niche for isotopic ecology. *Front. Ecol. Environ.* 5: 429-436
- Nishijima, S., G. Takimoto, e T. Miyashita. 2014. Roles of alternative prey for mesopredators on trophic cascades in intraguild predation systems: a theoretical perspective. *The American Naturalist* 183:625-637.
- Pereira, M. J. R., Marques, J. T., Santana, J., Santos, C. D., Valsecchi, J. et al. 2009. Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load. *J Anim Ecol* 78:1163-1171
- Pinheiro, J. C., e Bates, D. M. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer, New York
- Pinheiro, J., D. Bates, S. DebRoy, e D. Sarkar. 2018. nlme: linear and nonlinear mixed effects models. R package version 3.1-137. URL: <https://CRAN.R-project.org/package=nlme>.
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd International Workshop on Distributed Statistical*

Computing. Pages 1-10. URL: <http://www.ci.tuwien.ac.at/Conferences/DSC-2003/Drafts/>

- Polis, G. A., C. A. Myers, e R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297-330.
- Polis, G. A. e S. D. Hurd. 1995. Extraordinarily high spider densities on islands: Flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences* 92:4382-4386
- Polis, G. A., W. B. Anderson e R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289-316
- Power, M. E., Rainey, W. R., Parker, M. S., Sabo, J. L., Smyth, A. et al. 2004. River-to-watershed subsidies in an old-growth conifer forest. In: Polis GA, Power ME, Huxel GR (eds) *Food webs at the landscape level*. University of Chicago Press, Chicago, pp 214-241
- Preisser, E. L., J. L. Orrock, e O. J. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology* 88:2744-2751
- R Core Team 2018. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Ramey, T. L., e J. S. Richardson. 2017. Terrestrial invertebrates in the riparian zone: mechanisms underlying their unique diversity. *Bioscience* 67:808-819.
- Recalde, F. C., T. C. Postali, e G. Q. Romero. 2016. Unravelling the role of allochthonous aquatic resources to food web structure in a tropical riparian forest. *Journal of Animal Ecology* 85: 525-536
- Reis, N. R., Peracchi, A. L., Pedro, W. A., e Lima, I. P. 2007. *Morcegos do Brasil*. Biblioteca Central da Universidade Estadual de Londrina, CDU 599.4, Londrina
- Richardson, J. S. e Sato, T. 2015. Resource subsidy flows across freshwater-terrestrial boundaries and influence on processes linking adjacent ecosystems. *Ecohydrology* 8:406-415
- Richardson, J. S., Y. Zhang e L. B. Marczak. 2010. Resource subsidies across the land-freshwater interface and responses in recipient communities. *River research and applications* 26:55-66

- Robbins, L. W., K. L. Murray, e P. M. McKenzie. 2008. Evaluating the effectiveness of the standard mist-netting protocol for the endangered Indiana bat (*Myotis sodalis*). *Northeastern Naturalist* 15:275-282.
- Rogers, H., J. Hille Ris Lambers, R. Miller, e J. J. Tewksbury. 2012. 'Natural experiment' demonstrates top-down control of spiders by birds on a landscape level. *PLoS ONE* 7:e43446
- Rolim, G. S., Camargo, M. B. P., Lania, D. G., e Moraes, J. F. L. 2007. Classificação climática de Köppen e de Thornthwaite e sua aplicabilidade na determinação de zonas agroclimáticas para o Estado de São Paulo. *Bragantia* 66:711-720
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385-387.
- Rypstra, A. L., e C. M. Buddle. 2013. Spider silk reduces insect herbivory. *Biology Letters* 9:20120948.
- Sabo, J. L. e M. E. Power. 2002. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. *Ecology* 83: 3023-3036
- Salvarina, I. 2016. Bats and aquatic habitats: a review of habitat use and anthropogenic impacts. *Mammal Rev* doi: 10.1111/mam.12059
- Salvarina, I., Gravier, D., e Rothhauopt, K. O. 2017. Seasonal insect emergence from three different temperate lakes. *Limnologica* 62:47-56
- Sánchez-Hernández, J., Gabler, H. M. e Amundsen, P. A. 2016. From autochthonous to allochthonous resources: seasonal shifts in food use by stream-dwelling YOY arctic charr *Salvelinus alpinus* through the ice-free season. *Journal of Fish Biology* 88:767-773
- Sanzone, D. M., J. L. Meyer, E. Marti, E. P. Gardiner, J. L. Tank e N. B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. *Oecologia* 134:238-250
- Schindler, D. E., e A. P. Smits. 2017. Subsidies of aquatic resources in terrestrial ecosystems. *Ecosystems* 20:78-93.
- Shively, R., Barboza, P., Doak, P., e Jung, T. S. 2018. Increased diet breadth of little brown bats (*Myotis lucifugus*) at their northern range limit: a multimethod approach. *Can. J. Zool.* 96:31-38

- Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D., e Halpern, B. S. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5:785-791
- Shurin, J. B., Gruner, D. S. e Hillebrand, H. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proc. R. Soc. B.* 273:1-9
- Sick, H. 1997. *Ornitologia Brasileira*. Editora Nova Fronteira, Rio de Janeiro
- Sitters, J., C. L. Atkinson, N. Guelzow, P. Kelly e L. L. Sullivan. 2015. Spatial stoichiometry: cross-ecosystem material flows and their impact on recipient ecosystems and organisms. *Oikos* doi: [10.1111/oik.02392]
- Spotswood, E. N., K. R. Goodman, J. Carlisle, R. L. Cormier, D. L. Humple, J. Rousseau, S. L. Guers, e G. G. Barton. 2012. How safe is mist netting? Evaluating the risk of injury and mortality to birds. *Methods in Ecology and Evolution* 3:29-38.
- Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., e Semmens, B. X. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* 6: e5096
- Strandberg, U., Hiltunen, M., Jelkänen, E., Taipale, S. J., Kainz, M. J., Brett, M. T. e Kankaala, P. 2015. Selective transfer of polyunsaturated fatty acids from phytoplankton to planktivorous fish in large boreal lakes. *Science of the Total Environment* 536:858-865
- Takimoto, G., Iwata, T. e Murakami, M. 2002. Seasonal subsidy stabilizes food web dynamics: balance in a heterogeneous landscape. *Ecological Research* 17:433-439
- Thomas, H. H., Moosman, Jr. P. R., Veilleux, J. P., Holt, J. 2012. Foods of bats (Family Vespertilionidae) at five locations in New Hampshire and Massachusetts. *Can Field Nat* 126:117-124
- Trevelline, B. K., Nuttle, T., Hoenig, B. D., Brouwer, N. L., Porter, B. A., e Latta, S. C. 2018. DNA metabarcoding of nestling feces reveals provisioning of aquatic prey and resource partitioning among Neotropical migratory songbirds in a riparian habitat. *Oecologia* 187:85-98
- Tsahar, E., Z. Arad, I. Izhaki, e C. Martínez del Rio. 2006. Do néctar- and fruit-eating birds have lower nitrogen requirements than omnivores? An allometric test. *The Auk* 123:1004-1012.
- Twining, C. W., J. T. Brenna, P. Lawrence, J. R. Shipley, T. N. Tollefson e D. W. Winkler. 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *PNAS* 113: 10920-10925

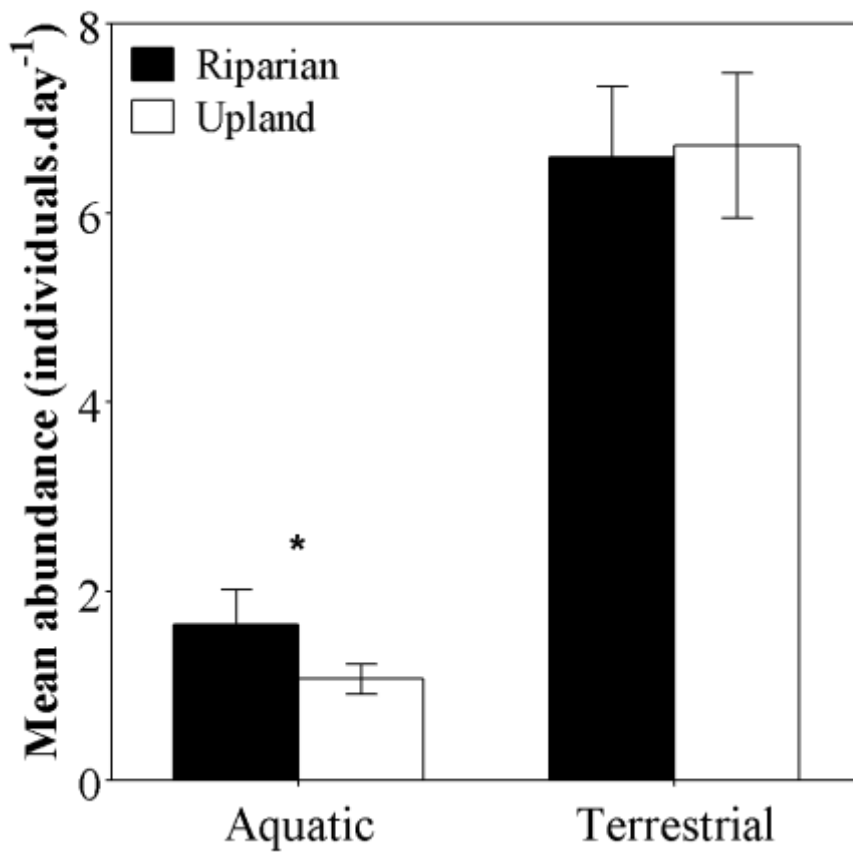
- Uscian, J. M., e D. W. Stanley-Samuelson. 1994. Fatty acid compositions of phospholipids and triacylglycerols from selected terrestrial arthropods. *Comparative Biochemistry and Physiology* 107B:371-379.
- Vázquez, D. P., e Stevens, R. D. 2004. The latitudinal gradient in niche breadth: concepts and evidence. *The American Naturalist* 164:E1-E19
- Vesterinen, E. J., Lilley, T., Laine, V. N., Wahlberg, N. 2013. Next generation sequencing of fecal DNA reveals the dietary diversity of the widespread insectivorous predator Daubenton's bat (*Myotis daubentonii*) in Southwestern Finland. *PLoS ONE* 8: e82168
- Voigt, C. C., Sörgel, K., Dechmann, D. K. N. 2010. Refueling while flying: foraging bats combust food rapidly and directly to power flight. *Ecology* 91:2908-2917
- Voigt, C. C., Lehmann, D., Greif, S. 2015. Stable isotope ratios of hydrogen separate mammals of aquatic and terrestrial food webs. *Methods Ecol Evol* 6:1332-1340
- Wallace, J. B., Eggert, S. L., Meyer, J. L., e Webster, J. R. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277:102-104
- Wing, S. R. 1988. Cost of mating for female insects: risk of predation in *Photinus collustrans* (Coleoptera: Lampyridae). *The American Naturalist* 131:139-142.
- Wu, P. C., e P. J. L. Shaner. 2016. Trophic cascade effects of avian predation on a willow in an urban wetland. *Oecologia* 180:293-303.
- Xiang, H., Y. Zhang, e J. S. Richardson. 2016. Importance of riparian zone: effects of resource availability at land-water interface. *Riparian Ecology and Conservation* 3:1-17.

APÊNDICES

ARTIGO I

ONLINE RESOURCES

Online Resource 1. Mean abundance (\pm SE) of flying aquatic and terrestrial insects captured in sticky traps in Atlantic Forest. Asterisk represents statistical difference ($\alpha < 0.05$) between riparian and upland areas.



Online Resource 2. Abundance of bird and bat species captured in Atlantic and Amazon forest. Bolded names indicate insectivorous guild. Non-bolded names are omnivores.

	Atlantic forest	Amazon forest
<u>Birds</u>		
<i>Attila phoenicurus</i>	2	-
<i>Automolus infuscatus</i>	-	1
<i>Basileuterus leucoblepharus</i>	2	-
<i>Chiroxiphia caudata</i>	3	-
<i>Conopophaga lineata</i>	1	-
<i>Dixiphia pipra</i>	-	2
<i>Galbula albirostris</i>	-	1
<i>Glyphorhynchus spirurus</i>	-	5
<i>Lochmias nematura</i>	1	-
<i>Malacoptila striata</i>	1	-
<i>Mionectes macconnelli</i>	-	8
<i>Myrmeciza ferruginea</i>	-	1
<i>Myrmotherula axillaris</i>	-	1
<i>Myrmotherula longipennis</i>	-	2
<i>Phaethornis bourcieri</i>	-	1
<i>Philydor atricapillus</i>	1	-
<i>Pithys albifrons</i>	-	3
<i>Pyriglena leucoptera</i>	1	-
<i>Thamnomanes ardesiacus</i>	-	4
<i>Thamnomanes caesius</i>	-	1
<i>Trichothraupis melanops</i>	1	-
<i>Turdus albicollis</i>	2	1
<i>Xiphorhynchus fuscus</i>	2	-
<i>Xiphorhynchus pardalotus</i>	-	4
<u>Bats</u>		
<i>Carollia perspicillata</i>	9	-
<i>Carollia brevicauda</i>	-	17
<i>Carollia castanea</i>	-	1

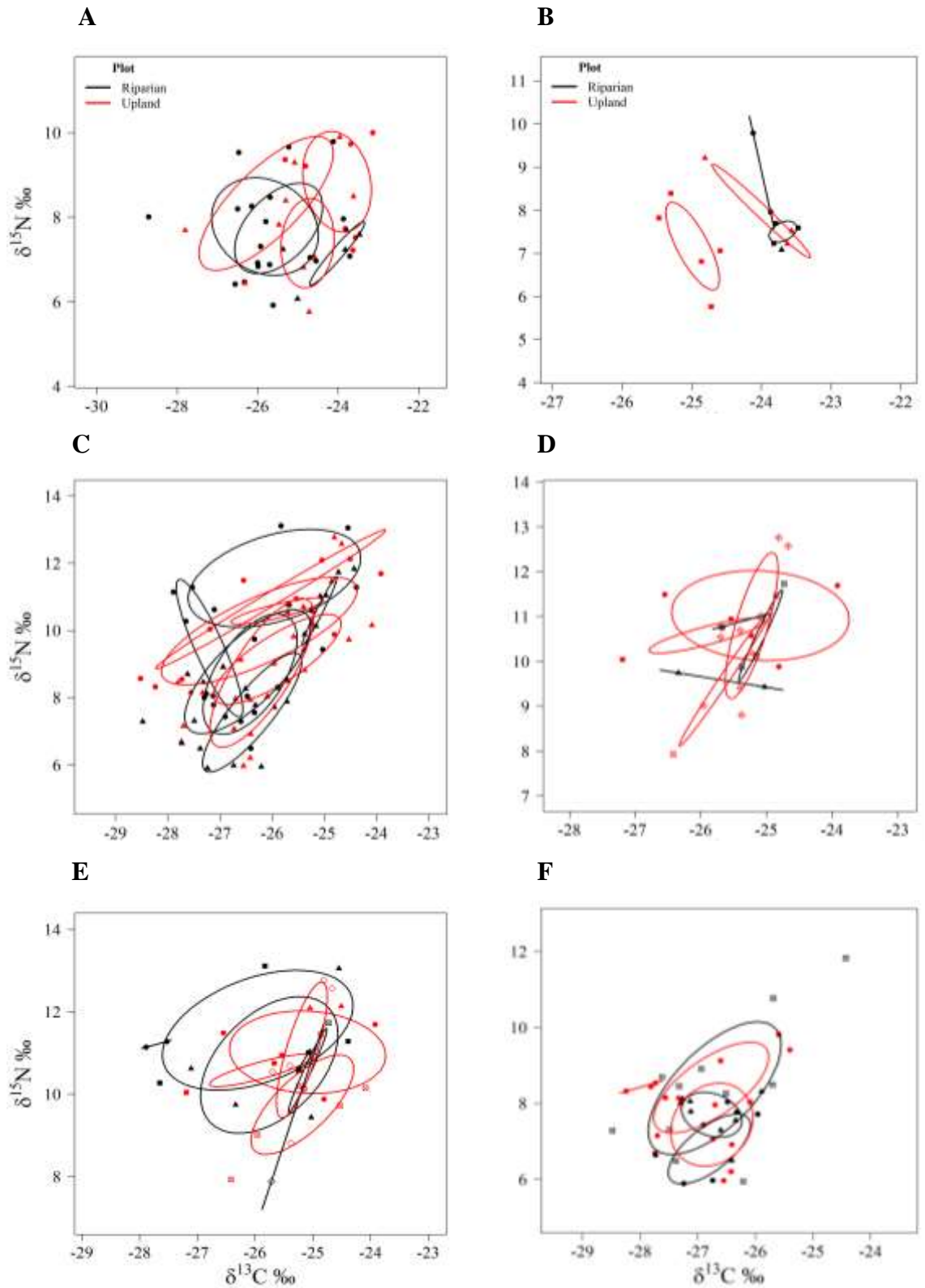
<i>Lonchophylla thomasi</i>	-	5
<i>Myotis albensis</i>	1	-
<i>Myotis nigricans</i>	7	2
<i>Rhinophylla pumilio</i>	-	15
<i>Sturnira lilium</i>	8	-
<i>Lophostoma silvicolum</i>	-	1
<i>Trachops cirrhosus</i>	-	1

Online Resource 3. Mean proportion contribution (\pm SD) of sources on diet of each bat and bird species in riparian and upland areas. AI, TI, S and V represent aquatic insects, terrestrial insect, spider and vegetation, respectively. R and U represent riparian and upland areas.

Species	Sources							
	AI		TI		S		V	
	R	U	R	U	R	U	R	U
<u>Atlantic birds</u>								
B. leucoblepharus		0.69 (0.32)		0.15 (0.19)		0.16 (0.19)		
C. lineata		0.52 (0.37)		0.33 (0.32)		0.15 (0.19)		
L. nematura	0.36 (0.33)		0.10 (0.14)		0.55 (0.32)			
M. striata		0.45 (0.37)		0.42 (0.35)		0.13 (0.17)		
P. atricapillus		0.28 (0.31)		0.09 (0.14)		0.63 (0.33)		
P. leucoptera		0.30 (0.34)		0.10 (0.16)		0.60 (0.35)		
X. fuscus		0.62 (0.36)		0.21 (0.24)		0.18 (0.20)		
A. phoenicurus		0.20 (0.34)		0.04 (0.11)		0.73 (0.36)		0.03 (0.08)
C. caudata		0.18 (0.24)		0.51 (0.40)		0.08 (0.12)		0.22 (0.27)
T. melanops		0.22 (0.35)		0.05 (0.15)		0.70 (0.38)		0.04 (0.09)
T. albicollis		0.51 (0.41)		0.04 (0.10)		0.38 (0.36)		0.06 (0.11)
<u>Atlantic bats</u>								
C. perspicillata	0.54 (0.35)		0.09 (0.10)		0.22 (0.19)		0.14 (0.15)	
S. lilium	0.20 (0.25)		0.09 (0.10)		0.68 (0.21)		0.04 (0.06)	

<u>Amazonian birds</u>								
X.pardalotus	0.52 (0.36)	0.56 (0.34)	0.38 (0.32)	0.36 (0.32)	0.10 (0.11)	0.09 (0.10)		
T. ardesiacus	0.62 (0.27)	0.68 (0.24)	0.19 (0.21)	0.17 (0.18)	0.19 (0.17)	0.15 (0.12)		
T. caesius		0.28 (0.27)		0.12 (0.19)		0.61 (0.29)		
P. albifrons	0.31 (0.20)	0.37 (0.22)	0.12 (0.13)	0.12 (0.15)	0.58 (0.17)	0.51 (0.18)		
G. spirurus	0.41 (0.41)	0.43 (0.42)	0.54 (0.41)	0.52 (0.41)	0.06 (0.08)	0.05 (0.07)		
G. albirostris		0.12 (0.18)		0.11 (0.19)		0.77 (0.26)		
A. infuscatus		0.65 (0.33)		0.25 (0.28)		0.13 (0.15)		
M. longipennis		0.44 (0.41)		0.52 (0.40)		0.04 (0.06)		
M. axillaris		0.33 (0.30)		0.13 (0.21)		0.54 (0.31)		
M. ferruginea		0.61 (0.33)		0.23 (0.29)		0.16 (0.17)		
M. macconnelli	0.43 (0.41)	0.41 (0.41)	0.42 (0.35)	0.46 (0.36)	0.11 (0.14)	0.11 (0.16)	0.04 (0.10)	0.03 (0.08)
D. pipra	0.34 (0.37)		0.36 (0.38)		0.05 (0.09)		0.26 (0.29)	
T. albicolis	0.10 (0.23)		0.06 (0.16)		0.82 (0.29)		0.03 (0.07)	
P. bourcierii	0.21 (0.35)		0.08 (0.20)		0.67 (0.38)		0.04 (0.09)	
<u>Amazon omnivorous bats</u>								
C. perspicillata	0.39 (0.30)		0.17 (0.17)		0.36 (0.20)		0.08 (0.11)	
C. brevicauda	0.40 (0.29)	0.43 (0.30)	0.21 (0.15)	0.26 (0.19)	0.35 (0.15)	0.27 (0.13)	0.05 (0.07)	0.05 (0.06)
C. castanea		0.32 (0.31)		0.41 (0.31)		0.19 (0.17)		0.08 (0.16)
L. thomasi	0.16 (0.16)	0.20 (0.18)	0.12 (0.10)	0.16 (0.12)	0.69 (0.15)	0.60 (0.12)	0.04 (0.05)	0.04 (0.05)
R. pumilio	0.50 (0.31)	0.52 (0.29)	0.15 (0.16)	0.16 (0.16)	0.16 (0.13)	0.14 (0.12)	0.19 (0.17)	0.19 (0.14)

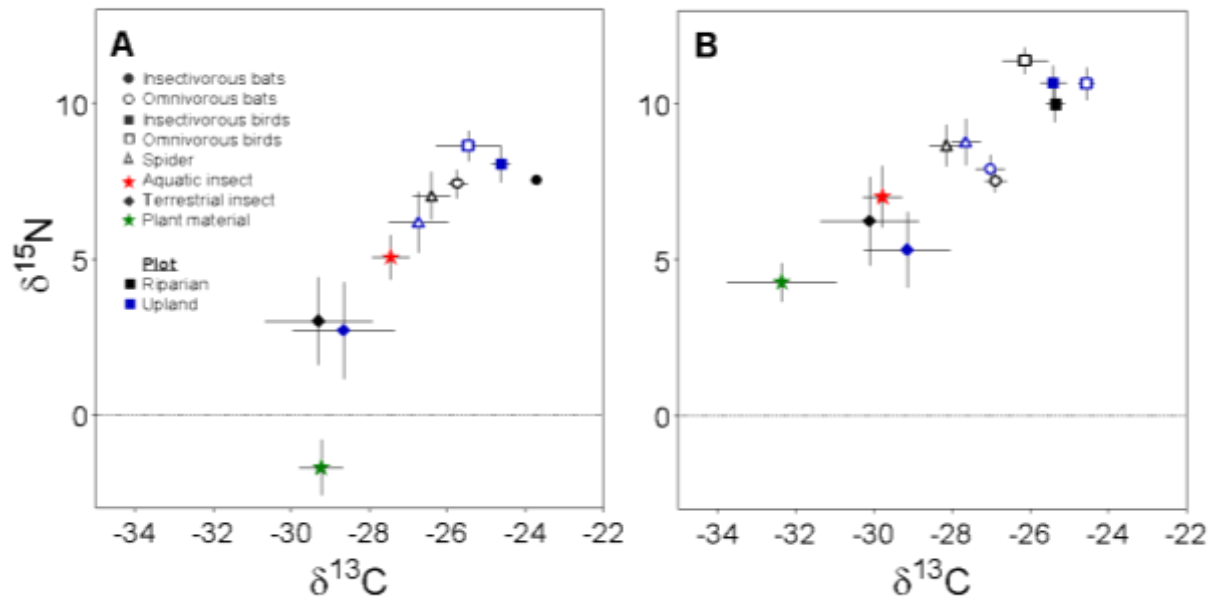
Online resources 4. Stable isotope biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ showing the trophic space breadth of total vertebrates (**A**) and insectivores (**B**) in Atlantic forest, and of total vertebrates (**C**), insectivores (**D**), birds (**E**) and bats (**F**) in Amazon forest. The ellipse areas (SEA_c) represent 40% of the data of bats and birds in each riparian and upland areas.



Online Resource 5. Mean (\pm SD) of SEA_c and community-wide metrics of total community of vertebrates in Atlantic and Amazon forest. Metrics were compared between riparian and upland areas. P-values were calculated by unpaired t-test.

	Areas		<i>t</i>	<i>P</i>
	Riparian	Upland		
<u>Atlantic forest</u>				
SEA_c	3.10 (1.00)	4.00 (1.50)	0.86	0.436
dNr	0.88 (0.49)	1.66 (0.63)	1.69	0.166
dCr	1.94 (0.63)	1.73 (0.68)	0.39	0.715
TA	0.42 (0.36)	1.10 (0.67)	1.55	0.196
CD	0.89 (0.22)	1.03 (0.26)	0.71	0.516
MNND	1.03 (0.29)	1.45 (0.41)	1.45	0.221
SDNND	0.59 (0.36)	0.33 (0.28)	0.99	0.379
<u>Amazon forest</u>				
<u>SEA_c</u>	4.90 (4.50)	4.10 (2.70)	0.35	0.737
dNr	4.22 (0.97)	2.55 (0.77)	3.11	0.013
dCr	2.48 (1.01)	1.36 (0.75)	2.05	0.071
TA	4.73 (2.32)	1.52 (0.91)	2.89	0.018
CD	1.47 (0.32)	0.99 (0.26)	2.69	0.025
MNND	1.08 (0.27)	0.75 (0.27)	2.02	0.074
SDNND	0.70 (0.37)	0.40 (0.31)	1.44	0.184

Online Resource 6. Stable isotope bi-plot (abundance \pm SE of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of bats, birds, and resource types in both riparian and upland areas from (A) Atlantic and (B) Amazon forests.



ARTIGO II**APPENDIX S1**

Figure S1. Boxplot of the abundance of flying aquatic and terrestrial insects captured in sticky traps within plots from Control and Exclusion treatments. Letters between the bars and whiskers represent significance of $\alpha \leq 0.05$ (factorial ANOVA)

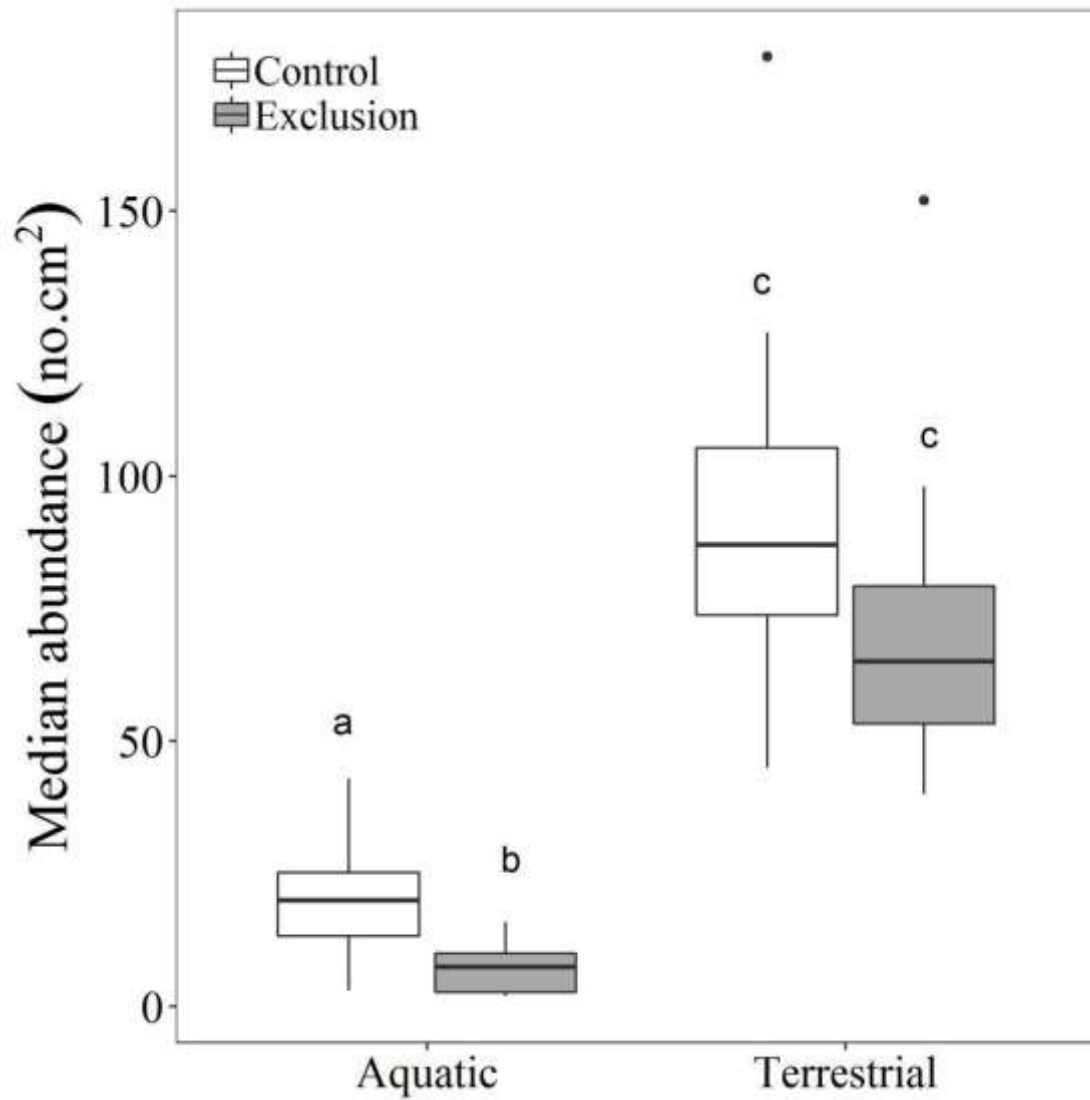


Table S1. Results of analysis of variance testing the abundance of emergent aquatic and terrestrial insects in our study plots. Bold numbers indicate statistical difference.

<u>Treatment</u>	<i>Aquatic</i>		<i>Terrestrial</i>	
	F	P	F	P
Subsidy	6.91	0.027	0.88	0.371
Predation	1.53	0.257	0.31	0.589
Subsidy*Predation	0.00	0.992	0.11	0.149

APPENDIX S2

Table S1. List of arthropod taxa collected in each survey period and ‘subsidy’ treatment. Asterisk represents presence of the taxon in the corresponding period and treatment.

Order	Family	Survey I		Survey II		Survey III	
		Control	Exclusion	Control	Exclusion	Control	Exclusion
Araneae	Anyphaenidae	*	*	*	*	*	*
	Araneidae	*	*	*	*	*	*
	Corinnidae			*			
	Deinopidae			*			
	Linyphiidae	*	*	*	*	*	*
	Mimetidae		*		*		*
	Palpimanidae	*					
	Pisauridae	*	*	*		*	
	Salticidae	*	*	*	*	*	*
	Sparassidae			*		*	
	Tetragnathidae		*				
	Theridiidae	*	*	*	*	*	*
	Thomisidae	*	*	*	*	*	*
	Uloboridae		*				
Unidentified	*	*	*	*		*	
Blattodea		*	*	*	*		
Coleoptera	Cerambycidae						
	Chrysomelidae		*	*	*	*	*
	Curculionidae	*	*	*	*	*	*
	Eucnemidae						*
	Lycidae		*				
	Staphyliniidae	*	*	*	*	*	*
	Unidentified	*	*	*	*	*	*
Collembola		*	*	*	*	*	*
Diptera	Cecidomyiidae		*		*		
	Ceratopogonidae	*	*				
	Chironomiidae	*		*	*		
	Heleomyzidae	*	*		*		*
	Limoniidae		*				
	Phoridae	*				*	
	Psychodidae						
	Sciaridae		*	*	*	*	*
	Stratiomyidae						

	Tipulidae			*		*	
	Unidentified	*	*	*		*	*
Hemiptera	Cercopidae				*		
	Cicadellidae		*	*			
	Kinnaridae		*				*
	Membracidae						
	Miridae		*	*	*	*	
	Pentatomidae						
	Thyreocoridae		*				
	Tingidae	*		*	*	*	*
	Unidentified	*	*	*	*	*	*
Hymenoptera	Braconidae		*				*
	Diapriidae	*	*	*	*	*	*
	Formicidae	*	*	*	*	*	*
	Ichneumonidae				*		
	Unidentified	*	*	*	*	*	*
Lepidoptera		*	*	*	*	*	*
Mantodea							*
Orthoptera	Gryllidae			*		*	
	Tettigonidae			*		*	
Phasmatodea							
Psocoptera		*	*	*	*	*	*
Thysanoptera			*	*	*	*	*

APPENDIX S3

Table S1. List of bat and bird species captured in our study site and their respective abundance. Tissues (hair for bats and feather for birds) of these vertebrates were used for diet (isotopic) analysis.

Bird species	Number of individuals
<i>Basileuterus leucoblepharus</i>	2
<i>Conopophaga lineata</i>	1
<i>Lochmias nematura</i>	1
<i>Malacoptila striata</i>	1
<i>Philydor atricapillus</i>	1
<i>Pyriglena leucoptera</i>	1
<i>Xiphorhynchus fuscus</i>	2
Bat species	
<i>Myotis albensis</i>	1
<i>Myotis nigricans</i>	7

ANEXOS**Anexo 1. Certificado da Comissão de Ética no uso de animais (CEUA/UNICAMP)****CERTIFICADO**

Certificamos que o projeto intitulado "**Efeitos top-down e bottom-up em teias alimentares ripárias mediados por emergência alóctone de insetos aquáticos**", protocolo nº **4052-1**, sob a responsabilidade de **Prof. Dr. Gustavo Quevedo Romero / Fátima Carolina Recalde Ruiz**, que envolve a produção, manutenção e/ou utilização de animais pertencentes ao filo *Chordata*, subfilo *Vertebrata* (exceto o homem) para fins de pesquisa científica ou ensino, encontra-se de acordo com os preceitos da **LEI Nº 11.794, DE 8 DE OUTUBRO DE 2008**, que estabelece procedimentos para o uso científico de animais e do **DECRETO Nº 6.899, DE 15 DE JULHO DE 2009**, e com as normas editadas pelo Conselho Nacional de Controle da Experimentação Animal - CONCEA, e foi aprovado pela Comissão de Ética no Uso de Animais da Universidade Estadual de Campinas - CEUA/UNICAMP, em reunião de **19 de outubro de 2015**.

Vigência do projeto: **02/2016-09/2016**

Espécie/Linhagem: **aves e morcegos (não há eutanásia)**

Origem: **Reserva Municipal - Serra do Japi, SP**

A aprovação pela CEUA/UNICAMP não dispensa autorização prévia junto ao IBAMA, SISBIO ou CIBio.

Campinas, 19 de outubro de 2015.

Profa. Dra. Liana Maria Cardoso Verinaud
Presidente

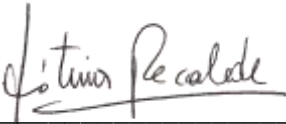
Fátima Alonso
Secretária Executiva

Anexo 2. Declaração de Direitos autorais

Declaração

As copias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada **Efeitos top-down e bottom-up em teias alimentares ripárias mediados por emergência alóctone de insetos aquáticos**, não infringem os dispositivos da Lei n.º 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 13/09/2019

Assinatura: 
Nome do(a) autor(a): **FATIMA CAROLINA RECALDE RUIZ**
RG n.º V810505-U

Assinatura: 
Nome do(a) orientador(a): **GUSTAVO QUEVEDO ROMERO**
RG n.º 23.985.512-7