# Variação individual de nicho em espécies que coexistem


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Rio Claro, 06 de dezembro de 2018

"Do indivíduo temos que partir, ainda que seja para o abandonar."

— Fernando Pessoa, em *Aforismos e afins*

"In individuals, insanity is rare; but in groups, parties, nations and epochs, it is the rule."

— Friedrich Nietzsche

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# Apresentação

Pela relativa liberdade estilística que esta seção permite, decidi apresentar uma breve coleção de fatos que, na mais parcial das visões sobre esta tese, a minha, foram importantes para que as páginas que seguem tenham o que tenham. Espero que você não se incomode com a pouca formalidade acadêmica das primeiras palavras desta tese, afinal essa é a única que escreverei na vida e não gostaria de perder a oportunidade. Antes, rapidamente, gostaria de explicar ao leitor que meu doutorado gravitou em torno da ideia de que indivíduos em populações naturais são ecologicamente diferentes entre si. Assim como você certamente conhece um cachorro afobado e outro acanhado, indivíduos de uma mesma espécie na natureza também podem ser diferentes. Ao longo dos quatro capítulos se seguem, percorro desde as causas dessa variação individual (*Capítulo 1*), passando pela elucidação de seus padrões entre espécies e comunidades (*Capítulos 2 e 3*), até o estudo das suas consequências (*Capítulo 4*). Espero que a organização dos capítulos como tal faça sentido ao leitor e que seja uma leitura, na medida do possível, leve. Os capítulos estão escritos em Inglês visto que foram formulados visando a publicação em periódicos científicos internacionais. Apesar de, no geral, os capítulos seguirem a estrutura de um manuscrito científico, fiz alguns pequenos ajustes pensando no conforto da leitura, como a inserção de figuras e tabelas no corpo do texto e a adição de algumas fotos. Precedem e sucedem os quatro capítulos, respectivamente, uma *Introdução geral* e uma *Conclusão geral* que, apesar dos títulos, não são tão gerais assim.

∝

A concepção da ideia que permeia esta tese se deu na MS-162, em algum ponto entre Pedro Juan Caballero, Paraguai, e Campo Grande, Mato Grosso do Sul (MS). MS, aliás, estado que considero *terra mater*. Era 2012 e estávamos voltando de um sábado de compras de muambas no Paraguai: minha primeira câmera subaquática e erva paraguaya de tereré. Curiosamente, me lembro do momento em que, já nas cercanias de Sidrolândia, com bloco e caneta na mão, sentado em uma posição pouco ortodoxa no banco de trás, rabisquei a figura que, anos depois, se tornaria o pano de fundo de meu doutorado (*Figura 1*a). Na época eu

estudava uma espécie de lambari no Pantanal e, depois de algum tempo, comecei a me questionar o quanto eu conseguiria entender sobre o papel da variação entre indivíduos num contexto mais amplo olhando apenas para uma única espécie.

Antes mesmo dessa inesperadamente produtiva viagem ao país vizinho, eu tenho que dizer, me desculpe MS, que a primeira fagulha que desta tese estalou em São Lourenço, Minas Gerais, alguns anos antes. Era 2009 e o Centro Acadêmico (CA) da biologia da Universidade Federal de Mato Grosso do Sul (UFMS), onde me graduei em Ciências Biológicas, fretou um ônibus para levar estudantes ao XX Congresso de Ecologia do Brasil. Na época, eu cursava o segundo ano da graduação e lutava para conciliar meu tempo entre entender a formação da blástula e identificar peixes no cavernoso laboratório do saudoso Professor Otávio Froelich. Foi então que, por curiosidade ou sorte, acabei me inscrevendo no minicurso *Especialização individual em populações naturais*, ministrado por quem viria a se tornar o orientador desta tese. Ainda na época em que laptops eram artigos de luxo, eu havia impresso Araújo *et al.* 2007 (*Copeia*) e cheguei a fazer uma breve leitura na cama do hotel arranjado pelo CA, gentilmente batizado de 'cortiço' por meus contemporâneos da UFMS. Apesar de meu nível de Inglês na época não ter permitido que eu entendesse todas as linhas (de fato, poucas delas), aquilo me soava bem. Foi então que conheci o Márcio no minicurso, que na época fazia pós-doutorado em Miami e usava uma longa pulseira de couro no pulso. Sem querer me alongar muito, gostaria apenas de citar que a sala na qual o Márcio ministrou o minicurso tinha uma porta de vidro que dava vista para a piscina do hotel que sediava o congresso. Inevitavelmente, enquanto Márcio explicava como calcular o índice *E* de especialização individual, congressistas-banhistas passavam ao fundo animados, pingando água. Estou certo de que eu estava mais empolgado naquela sala do que os próprios banhistas do lado de lá da porta – afinal, desde então, eu nunca mais deixei de trabalhar com especialização individual.

Outro ponto que considero relevante para entender as raízes desta tese é o motivo pelo qual eu estudei espécies de rãs do gênero *Leptodactylus*. Bom, de acordo com meu modelo visual rodoviário-fronteiriço (*Figura 1*a), eu precisaria encontrar um sistema biológico no qual espécies generalistas coexistissem e que os nichos dessas espécies se sobrepusessem em algum grau, remetendo ao clássico debate do paradoxo da coexistência. Bom, isso não foi tão simples. Durante minha graduação e mestrado, concentrei meus estudos principalmente em peixes e, naturalmente, gostaria de continuar estudando esse grupo. De fato, não é difícil encontrar espécies de peixes parecidas (especialmente para alguém terrível em taxonomia como eu) que

coexistam em riachos ou lagoas (e.g., gênero *Astyanax*). O problema é que, olhando com cuidado, essas espécies se segregam em uso de microhábitat, o que me parece ser acentuado em sistemas aquáticos que têm uma terceira dimensão de partição espacial, a coluna d'água. Pensei então em trabalhar com gambás (*Didelphis albiventris* e *D. aurita*), ventilei estudar indivíduos em bandos mistos de aves, e, finalmente, pensei nas rãs do gênero *Leptodactylus*. Minha amiga Lili Piatti, sob orientação de Franco Souza (que viria a se tornar o co-orientador dessa tese) haviam estudado a dieta dessas espécies em campos de arroz no Pantanal, revelando que essas rãs são altamente generalistas na escala da espécie e que existe alta sobreposição de dieta entre espécies. Melhor ainda, essas rãs são bastantes comuns nas proximidades de corpos de água parada como lagoas e baías e, muitas vezes, mais de uma espécie coexistem localmente, compartilhando recursos alimentares e microhábitats de forrageamento. Na *Introdução Geral* desta tese, forneço mais detalhes sobre a fascinante história natural dessas espécies de rãs.

Um ponto que gostaria de esclarecer aqui é o número de indivíduos que, infelizmente, tive que sacrificar para investigar as ideias desta tese. Primeiro, esse era o único modo de se obter grande parte dos dados necessários para responder as minhas perguntas sobre variação individual de nicho (e.g., valores isotópicos de fígado e músculo, investimento gonadal, carga parasitária). Ainda tentamos utilizar abordagens não-letais para conseguir dados de dieta (lavagem estomacal), as quais não funcionaram bem. Segundo, essas espécies de rãs são bastante comuns e mantêm populações numerosas no Pantanal e entorno, então tenho confiança de que nossas amostragens, que se deram em lagoas pontuais dentro de uma extensa região geográfica, não tiveram impactos negativos substanciais nas populações locais. Finalmente, gostaria de dizer que, de cada indivíduo que coletei em campo, extraí em laboratório o máximo de informações úteis que me pareceram possíveis. Espero que eu as tenha utilizado bem e dignamente nas páginas que se seguem.

Outra passagem que considero importante, mas um tanto frustrante, de meu doutorado foi a tentativa de montar um experimento em campo para quantificar a força da competição intra- *vs.* interespecífica na presença de variação individual. Ter essas informações seria um passo importante para amarrar, empiricamente, a variação individual de nicho ao arcabouço da teoria moderna coexistência. O plano era montar gaiolas na planície de inundação do Rio Miranda, dentro das quais manipularíamos a presença e densidade de competidores de uma mesma e de outra espécie. Não quero me prolongar aqui, mas foram longos meses planejando, preparando e montando o experimento – o qual demandou quase meio quilômetro de tubos

de PVC e 200 m² de telas, além de muito suor e boa vontade dos amigos que me ajudaram. Apesar das valiosas lições aprendidas (e.g., como usar uma estrovenga), o experimento deu errado. Aquele foi um ano excepcionalmente seco no Pantanal e as rãs, acostumadas com a liberdade de uma planície inteira, não se aclimataram bem dentro das gaiolas (*Figura 1*b, *1*c, *1*d). Bem, experimentos são sempre arriscados. Não contar com esses dados, ainda mais depois de tanto esforço, foi sem dúvida frustrante. Por outro lado, isso me estimulou a explorar com mais atenção os dados observacionais que, no final das contas, são usados nos quatro capítulos que compõem esta tese.

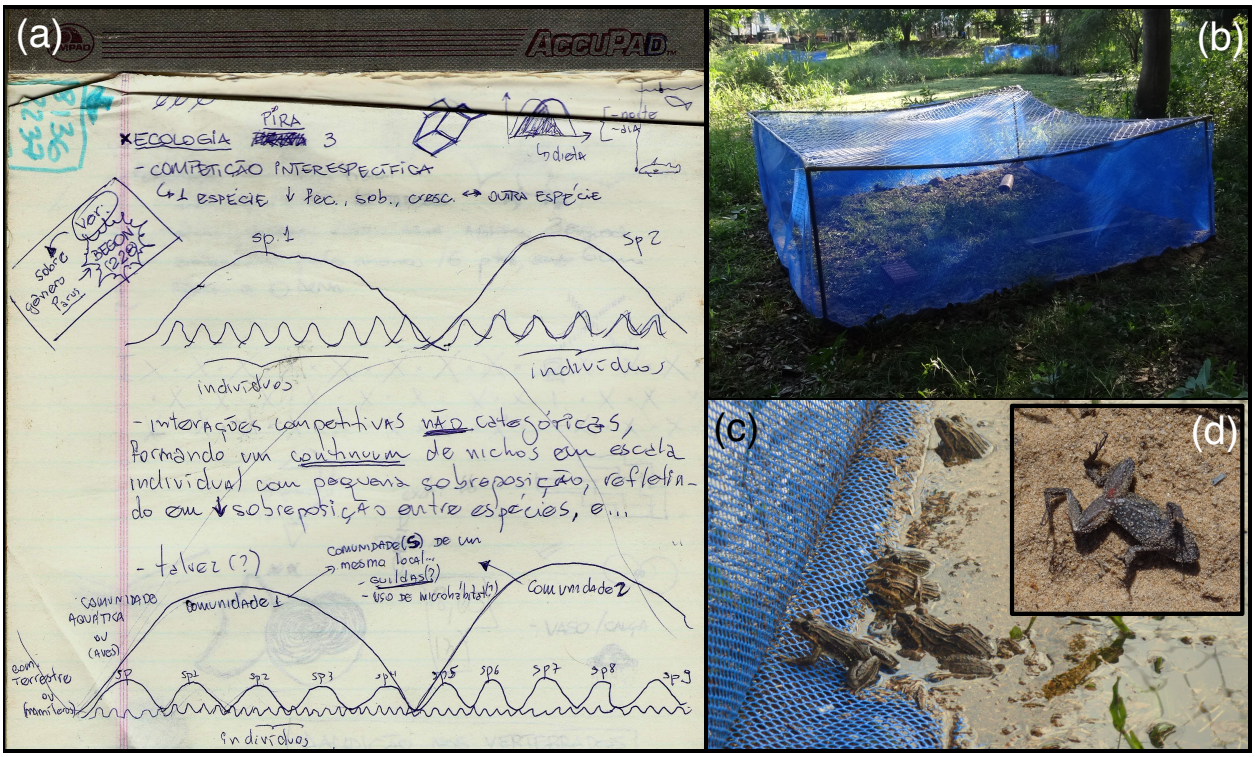



*Figura 1*. (*a*) Rabiscos que deram origem à ideia que permeia esta tese; (*b*) uma das gaiolas montadas na planície de inundação do Rio Miranda como parte de um frustrado experimento de campo para medir competição entre espécies e indivíduos de rãs; (*c*) indivíduos de *Leptodactylus chaquensis* recém colocados em uma das gaiolas; (*d*) indivíduo de *L. podicipinus* que, infelizmente, acabou não resistindo ao tempo surpreendentemente seco e quente durante o experimento.

Gostaria também de mencionar que tive a incrível oportunidade de realizar dois períodos de estágio internacional, graças ao apoio financeiro da FAPESP. Primeiro, trabalhei ~11 meses em Houston, Texas, EUA, onde está o centro espacial da NASA e a antiga sala de controle de missões. Já que dizem que ecologia é mais complexa que *rocket science*, acho que escolhi o lugar certo. Durante esse tempo, trabalhei nos *Capítulos 1* e *2* desta tese no laboratório do competente Volker Rudolf. Depois, tive a sorte de passar pouco mais de dois meses no

outro lado do mundo, em Dunedin, Nova Zelândia, para trabalhar com o também competente Travis Ingram no *Capítulo 3*. Além de desenvolver e apurar minhas habilidades científicas, esses períodos fora do Brasil me proporcionaram experimentar genuinamente como é viver no exterior, sendo, portanto, marcantes não apenas no contexto da presente tese.

Correndo o risco de ser mal interpretado, eu tenho que dizer que ao longo desses 4 anos e meio eu não trabalhei exclusivamente no que tange esta tese de doutorado. Bom, convenhamos que 4 anos e meio é muito tempo. Paralelamente, eu tive a oportunidade de trabalhar academicamente em outros assuntos não necessariamente relacionados ao corpo desta tese e colaborar com um grupo competente de pesquisadores. Essas experiências paralelas me deram confiança e certo lastro para, depois das campanhas de campo e de todo o longo e custoso processamento em laboratório, trabalhar com prazer nos manuscritos que compõe a presente tese. Também fico feliz pelas oportunidades que tive durante meu doutorado de revisar manuscritos para variadas revistas científicas, algumas das quais muito admiro e acompanho, o que, apesar de trabalhoso, é sempre gratificante.

Por fim, eu gostaria de deixar registrado que gostei mesmo de fazer doutorado e me diverti ao longo desses quatro anos e meio. Portanto, o fim é agridoce.

Aos que lerão esta tese, espero que seja uma leitura agradável.

Aos que a folhearão, espero que gostem de algumas das figuras e que tenham sorte de encontrar uma ou outra informação que achem interessante.

# Resumo

Esta tese gravita em torno da ideia de que indivíduos de uma mesma espécie são ecologicamente diferentes. Apesar de esse fato não parecer surpreendente, a teoria ecológica tem historicamente negligenciado a variação intraespecífica em várias de suas frentes. Um exemplo claro é a teoria clássica de nicho, que implicitamente supõe que indivíduos conspecíficos utilizam exatamente os mesmos recursos. De modo similar, a teoria de comunidades considera que espécies são bem representadas em termos ecológicos pela média de atributos de seus indivíduos. Ao longo dos quatro capítulos que compõem esta tese, estudei os padrões, causas e consequências da diversidade ecológica *entre* indivíduos em um contexto de múltiplas espécies que coexistem. Utilizei quatro espécies de rãs do gênero *Leptodactylus* que coexistem em áreas do Pantanal e entorno como sistema de estudo. No *Capítulo 1*, mostro que diferenças de nicho trófico entre indivíduos e espécies são flexíveis e dependentes de contexto, o que pode ter implicações importantes para os padrões locais e regionais de biodiversidade. No *Capítulo 2*, elucido que a tremenda variação na alometria de interações tróficas entre e dentro de comunidades pode ser explicada por gradientes de limitação de presas. No *Capítulo 3*, estudei os nichos tróficos de espécies competidoras em uma perspectiva multidimensional, revelando interessantes mecanismos pelos quais indivíduos e espécies particionam recursos em duas dimensões tróficas. Finalmente, no *Capítulo 4*, ao mostrar que mudanças temporais de dieta podem aumentar o valor adaptativo de indivíduos, avanço na compreensão das ainda pouco estudadas consequências da variação individual de nicho. Em conclusão, esta tese contribui para o entendimento dos mecanismos que geram e mantêm variabilidade ecológica entre indivíduos na natureza, bem como das implicações ecológicas desse fenômeno em escalas de organização biológicas superiores.

*Palavras-chave:* isótopos estáveis, especilização individual, sobreposição de nicho, dieta, variação de nicho, competição, *fitness*

# Abstract

This thesis gravitates around the idea that individuals from the same species are ecologically different. Although this fact does not seem surprising, ecological theory has historically neglected intraspecific variation. A clear instance is the classic niche theory, which implicitly assumes that conspecific individuals utilize the same resources. Accordingly, community theory considers that species are well represented by the mean of individuals' traits. Over the four chapters of this thesis, I studied the patterns, causes, and consequences of the ecological diversity *between* individuals in the context of multiple coexisting species. I studied four frog species from the genus *Leptodactylus* that coexist in the Pantanal wetlands and surrounding areas as model organisms. In *Chapter 1*, I show that trophic niche differences between individuals and species are flexible and context-dependent, which may have important implications to local and regional diversity patterns. In *Chapter 2*, I elucidate that the tremendous variation in the allometric scaling of trophic interactions within and between natural communities is predictable, responding to gradients of prey limitation. In *Chapter 3*, I studied trophic niches of competing species in a multidimensional perspective, revealing interesting mechanisms by which individuals and species partition resources in two trophic dimensions. Finally, *Chapter 4* advances in the understanding of the underexplored consequences of individual niche variation by showing that temporal diet changes may have major fitness implications. Altogether, these results contribute to broadening our understanding of the mechanisms generating and maintaining ecological variability between individuals in nature, as well as of the implications of this phenomenon across scales of biological organization.

*Keywords:* stable isotopes, individual specializiation, niche overlap, diet, niche variation, competition, fitness

# Introdução geral

## 1. Uma ecologia das variações individuais?

Apesar dos esforços hercúleos de gerações de ecólogos, existem raríssimas leis universais em ecologia (Lawton 1999). A estupenda diversidade de formas de vida e suas intrincadas interações é justamente o que torna, ao mesmo tempo, a ecologia uma ciência tão fascinante e tão complexa; *a blessing and a curse*. Tal complexidade faz com que sistemas biológicos sejam quase que invariavelmente contingentes, dependentes de contexto e de escala, e difíceis de prever (MacArthur 1972; Lawton 1999; Chave 2013). Ainda assim, alguns padrões gerais (i.e., regularidades amplamente observadas na natureza) são atualmente bem estabelecidos em ecologia, como por exemplo a relação espécies-área (Storch, Keil & Jetz 2012), a distribuição de frequências de abundâncias (Šizling *et al.* 2009), e as relações de escalonamento alométricas (West, Brown & Enquist 1997).

Frente à inerente complexidade da natureza, ecólogos têm que fazer simplificações para tentar entendê-la. De fato, um paradigma chave da modelagem ecológica é que modelos simples tendem a ser mais gerais e, portanto, preferíveis (Holling 1966; May 2001); *Pluralitas non est ponenda sine necessitate*, i.e., pluralidade não deve ser posta sem necessidade. Provavelmente, a simplificação mais intuitiva e prevalente em modelos ecológicos seja a adoção de espécie como unidade fundamental. Essa abordagem reducionista, muitas vezes esquecida como tal, supõe implicitamente que variações intraespecíficas são inexistentes ou desprezíveis. Tal suposição é inspirada na teoria do campo médio, que considera o comportamento médio de um sistema complexo como uma boa representação do comportamento de seus componentes (Durrett & Levin 1994). De modo análogo, uma vez que indivíduos conspecíficos tendem a ser ecologicamente mais semelhantes entre si do que com indivíduos de outras espécies, ecólogos tradicionalmente se baseiam no sistema taxonômico Lineliano para estudar e medir a natureza (Rudolf *et al.* 2014). Por exemplo, em modelos de teias tróficas, *espécies* são usadas como nós (*Figura 1*a); em ecologia de comunidades, a ocorrência de *espécies* é limitada por filtros ambientais ou bióticos; e em estudos de ecologia de ecossistemas as *espécies* são os agentes do fluxo de energia e matéria. Apesar da conveniência tanto do ponto de vista empírico quanto matemático, é cada vez mais aparente que essa tradicional visão tipológica,

espécie-cêntrica da natureza pode, nem sempre, ser a melhor abordagem para entender sistemas biológicos (Bolnick *et al.* 2003; Violle *et al.* 2012; Evans *et al.* 2013).

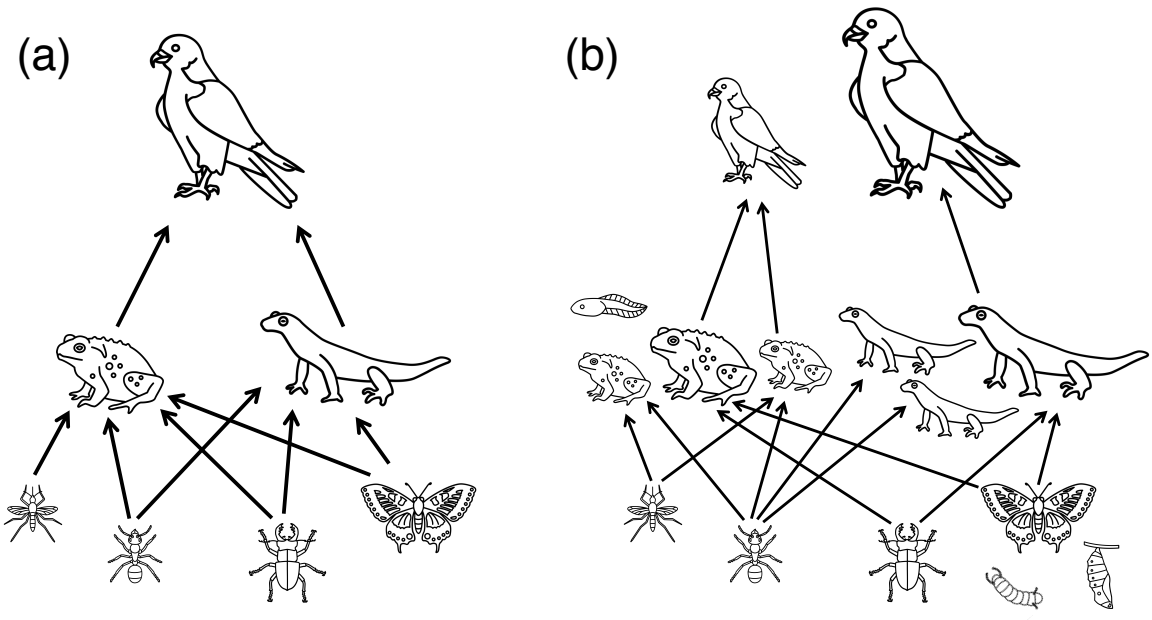



*Figura 1.* Dois exemplos hipotéticos de redes tróficas: (*a*) teia alimentar clássica baseada em interações interespecíficas, na qual espécies são representadas por "caixas" que encapsulam toda a variação ecológica intraespecífica (Miller & Rudolf 2011); (*b*) teia alimentar baseada em interações entre indivíduos, ilustrando como a variação intraespecífica (incluindo a variação ontogenética em espécies com ciclo de vida complexo, e.g., anuro e borboleta) no uso de recursos pode alterar a estrutura e organização das ligações tróficas.

Por definição, indivíduos são únicos. Não é surpreendente, portanto, que indivíduos de uma mesma espécie, sexo e idade possam apresentar consideráveis diferenças de comportamento, morfologia e uso de recursos (Bolnick *et al.* 2003; Dall *et al.* 2012). Aristóteles já havia documentado esse fato há 350 anos antes da Era Comum (Thompson 1907) e, um bom tempo depois, Wallace e Darwin construíram sua revolucionária teoria fundamentada nas diferenças morfológicas entre indivíduos de uma mesma população. Ainda, é razoável supor que um observador atento da natureza encontre diferenças entre qualquer par de indivíduos que exista, mesmo entre clones. Um indivíduo pode ser maior do que outro, mais vistoso, mais tímido, mais faminto, etc. Naturalmente, um questionamento subsequente válido, portanto, é se não deveríamos passar a olhar para a natureza como um emaranhado de inúmeras partículas individuais, independente das espécies a que pertençam, interagindo não-aleatoriamente. De fato, as dinâmicas ecológicas de populações, comunidades e ecossistemas são, na verdade, fruto de processos que operam na escala do indivíduo e emergem para escalas de organização

superiores (Bolnick *et al.* 2011; Chave 2013; de Roos & Persson 2013). Por exemplo, na prática, interações predador-presa se dão entre um indivíduo de predador e um indivíduo presa (*Figura 1*b). Apesar de a lógica por trás dessa abordagem 'individualista' ser um exercício intelectual interessante, ainda existem diversos questionamentos sobre sua real utilidade para nos ajudar a entender e prever sistemas naturais.

Um dos questionamentos frequentemente levantados, como já apresentado acima, é o fato de que incorporar variação individual em modelos ecológicos traz o custo inerente da complexidade (um *many-body problem* em ecologia). De fato, modelos analíticos tendem a intratabilidade conforme a variação intraespecífica é introduzida (de Roos & Persson 2013). Apesar disso, diversos estudos teóricos recentes têm revisitado modelos clássicos incorporando variabilidade ecológica não-aleatória entre indivíduos (Bolnick *et al.* 2011; Barabás & D'Andrea 2016; Hart, Schreiber & Levine 2016; Turcotte & Levine 2016; Snyder & Ellner 2018). Ainda, como vivemos na era dos supercomputadores, a utilização de modelos numéricos baseados-no-indivíduo tem popularizado rapidamente (DeAngelis & Grimm 2014; DeAngelis 2018). No entanto, a complexidade se manifesta mais clara em termos empíricos, uma vez que obter dados sólidos e temporalmente consistentes sobre atributos dos indivíduos (e.g. morfologia funcional, dieta, comportamento) aumenta substancialmente o esforço e tempo necessários em relação a estudos que descrevem atributos das espécies (Clark *et al.* 2007; Clark 2010; Dall *et al.* 2012). Um exemplo de ramo da ecologia que tem rapidamente progredido para incorporar variação no nível do indivíduo é a ecologia funcional ou ecologia de atributos (*trait-based ecology*). Apesar de inicialmente atributos funcionais serem vistos como úteis apenas quando variem mais entre do que dentro das espécies (McGill *et al.* 2006), é cada vez mais evidente que considerar explicitamente variações intraespecíficas pode alterar a nossa percepção de como espécies interagem e como comunidades são montadas (Siefert 2012; Violle *et al.* 2012; Messier *et al.* 2016; Li *et al.* 2017). De fato, aproximadamente 25% da variação total de atributos funcionais dentro de comunidades é encontrada dentro das espécies (Siefert *et al.* 2015).

Que indivíduos conspecíficos variam na natureza, ninguém questiona. Agora, a questão é o quão relevante essa variação é para avançarmos no entendimento de dinâmicas de comunidades. O quanto ganhamos de poder de explicação dos padrões naturais quando reduzimos nossa unidade de interesse para os indivíduos? Ainda estamos distantes de entender ao certo em que circunstâncias e tipos de problemas avançamos o conhecimento ao estudar a natureza sob a perspectiva dos indivíduos que a compõem. É curioso, e quase provocante, ver

que o secular chamado para a "*necessity of first determining empirically our units*" (i.e., 'necessidade de primeiro determinar empiricamente nossas unidades') em ecologia de comunidades (Tansley 1920) continua vívido na ecológica contemporânea. Lamento informar o leitor, mas essa tese não chega nem perto de resolver essa ambiciosa questão, que talvez pertença mais à esfera filosófica do que prática. Nos capítulos que se sucedem, nossa pequena contribuição é tentar aproximar o emergente corpo de teoria de variação individual de nicho (Bolnick *et al.* 2003) a algumas teorias clássicas em ecologia que supõem equivalência individual na natureza.

## 2. A variação individual de nicho

A teoria clássica de nicho é fundamentada nas diferenças ecológicas *entre* espécies para explicar padrões da biodiversidade (Chase & Leibold 2003). Ao eleger as espécies como escala de interesse, esse sólido corpo teórico supõe implicitamente que indivíduos de uma mesma população utilizam os mesmos recursos, nas mesmas proporções (*Figura 2*a) (Hutchinson 1957; Schoener 1989). Por exemplo, a maioria dos modelos de interações predador-presa, estrutura de teias tróficas (*Figura 1*a) e coexistência de espécies supõe que conspecíficos são ecologicamente idênticos. Entretanto, ecólogos têm sido forçados a reconsiderar essa suposição frente ao aumento sem precedentes no número de estudos documentando variação individual de nicho em diversos *taxa* ao longo dos últimos 15 anos. Muito provavelmente o principal gatilho para o despertar do interesse na ecologia trófica de indivíduos seja o trabalho seminal de Daniel I. Bolnick e colegas que cunhou o termo '*especialização individual*' (Bolnick *et al.* 2003). Bolnick *et al.* definem um ' *indivíduo especialista*' como aquele cujo nicho é substancialmente menor do que o nicho de sua população por razões não atribuídas a seu sexo, idade ou grupos morfológicos discretos (e.g., polimorfismos). Em outras palavras, populações generalistas podem ser compostas por indivíduos heterogêneos que usam apenas uma parcela do leque total de recursos consumidos pela população como um todo (*Figura 2*b).

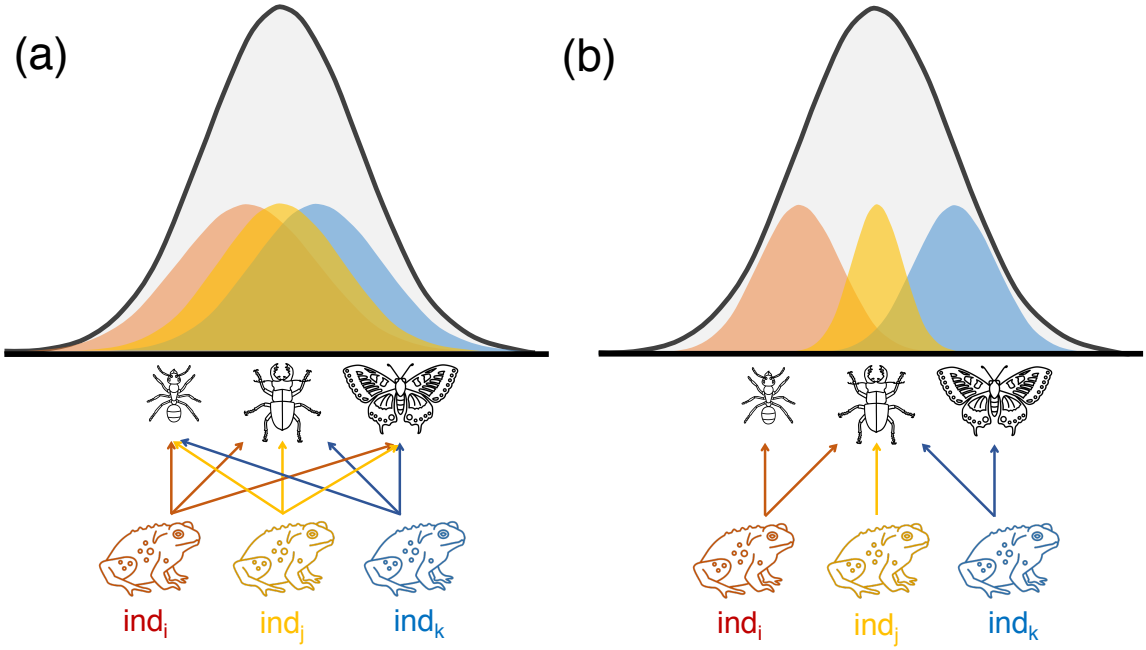



*Figura 3*. Representação conceitual de como os nichos tróficos dos indivíduos (curvas coloridas) podem se distribuir dentro do nicho da população (curva delimitada pela linha preta), que inclui três tipos diferentes de presas. (*a*) cenário suposto pela teoria clássica de nicho, onde as distribuições de uso de recursos dos indivíduos sobrepõem-se amplamente com a distribuição de uso de recursos da população; (*b*) cenário no qual indivíduos são especializados em determinados subconjuntos de recursos alimentares dentro da distribuição de uso de recursos da população.

É importante notar que uma parte substancial dos estudos subsequentes a Bolnick *et al.* (2003) buscou documentar a existência e quantificar o grau de variação interindividual no uso de recursos em populações naturais (Araújo, Bolnick & Layman 2011; Layman, Newsome & Crawford 2015). Sem dúvida, esse foi um passo fundamental para determinar a generalidade e prevalência dessa escala de variação de nicho na natureza, confirmando que virtualmente qualquer população animal, em maior ou menor grau, apresenta indivíduos que variam em sua dieta. Tendo isso estabelecido, naturalmente, o próximo passo é tentar entender as causas ecológicas que levam os nichos dos indivíduos a diferirem dentro de populações. Araújo e colegas (2011) avançaram nesse sentido ao utilizarem o arcabouço teórico de forrageamento ótimo (Stephens & Krebs 1986) para levantar os quatro principais fatores ecológicos moldando o grau de especialização individual, a saber: competição intraespecífica, competição interespecífica, oportunidade ecológica (i.e., diversidade de recursos disponíveis) e predação (Araújo, Bolnick & Layman 2011). Diversos estudos observacionais e experimentais têm testado o efeito específico desses fatores (principalmente competição intraespecífica e

oportunidade ecológica) sobre o grau de especialização individual de populações de uma determinada espécie, os quais, no geral, confirmam as previsões da teoria do forrageamento ótimo (e.g., Bolnick *et al.* 2007; Bolnick *et al.* 2010; Araújo & Costa-Pereira 2013; Evangelista *et al.* 2014; Kernaléguen *et al.* 2015; Newsome *et al.* 2015; Costa-Pereira *et al.* 2017). Apesar desses substanciais avanços na última década, é importante notar que até então os estudos focam primariamente em entender variação no grau de especialização individual entre populações de uma única espécie e no efeito específico de um ou dois dos fatores previstos como potenciais causas dessa variação individual.

Menos exploradas do que as causas ecológicas da especialização individual de nicho são suas consequências, as quais se ramificam num delta de possibilidades que começa com implicações para o próprio indivíduo. Surpreendentemente, poucos estudos empíricos investigaram se diferenças intrapopulacionais de nicho se traduzem em diferenças previsíveis de valor adaptativo (*fitness*) entre indivíduos (Cucherousset *et al.* 2011; Kernaléguen *et al.* 2016), apesar da importância dessa suposição em modelos clássicos de evolução do nicho (Van Valen 1965; Roughgarden 1972; Roughgarden 1979). Além disso, a variação de nicho entre conspecíficos pode diretamente afetar interações ecológicas entre espécies, o que, por sua vez, pode produzir efeitos relevantes em um contexto de comunidades (Bolnick *et al.* 2011; Violle *et al.* 2012). Por exemplo, variações intraespecíficas de nicho influenciam o arranjo de teias tróficas e a magnitude de suas forças de interação (Cantor *et al.* 2012; Melián *et al.* 2014; Svanbäck *et al.* 2015; Uiterwaal, Mares & DeLong 2017), o que tem implicações chave para a estabilidade de ecossistemas e manutenção de mutualismos (Gibert & DeLong 2017; Costa-Pereira *et al.* 2018b).

Um recente e promissor horizonte de implicações ecológicas da variação individual de nicho é seu papel na coexistência de espécies. A teoria moderna de coexistência prevê que a coexistência estável entre espécies competidoras depende de um balanço entre suas diferenças de nicho e habilidades competitivas (Chesson 2000). Entretanto, variações individuais de nicho podem igualar ou até mesmo exceder em termos de magnitude a variação entre espécies (Messier, McGill & Lechowicz 2010), sugerindo que o uso de parâmetros médios das espécies em modelos de coexistência possa não ser apropriado (Clark 2010; Bolnick *et al.* 2011; Violle *et al.* 2012). Especificamente, um corpo recente de teoria propõe que diferenças entre espécies competidoras quanto ao grau de variação intraespecífica de nicho podem ter um papel importante para a coexistência de espécies e manutenção da diversidade biológica (Barabás &

D'Andrea 2016; Hart, Schreiber & Levine 2016; Turcotte & Levine 2016). De modo breve, como diferenças intraespecíficas no uso de recursos tendem a reduzir a competição intraespecífica média experimentada por uma população, a espécie competidora com maior grau de variação intraespecíficas deve ser favorecida (Hart, Schreiber & Levine 2016). Entretanto, as tentativas de traduzir tais predições teóricas sobre o efeito de variações individuais de nicho sobre a coexistência de espécies para o mundo empírico ainda continuam bastante incipientes (Hausch, Vamosi & Fox 2018).

É evidente, portanto, a existência de uma demanda emergente por entender variações individuais de nicho em um contexto de comunidades. O panorama atual da literatura que lida com os padrões, causas e consequências da variação individual de nicho é majoritariamente composto por estudos que investigam esse fenômeno dentro de uma única espécie alvo. Ironicamente, estudar a variação individual de nicho em uma única espécie é, de certo modo, uma abordagem baseada na escala de espécie, assim como a clássica teoria de nicho. De fato, raríssimos estudos quantificaram o grau de variação individual em múltiplas espécies que coexistem no espaço e no tempo (Araújo *et al.* 2007; Araújo *et al.* 2009; Faulks *et al.* 2015; Cloyed & Eason 2016), o que restringe muito a generalização desse prevalente fenômeno para contextos mais amplos, como as teorias de coexistência, teias tróficas e comunidades (Bolnick *et al.* 2011). Essa tese se insere nesse nicho, com o perdão do trocadilho e do clichê que vem logo a seguir. Não existe uma única espécie e, portanto, nenhum indivíduo sequer que não interaja com pelo menos outra espécie ao longo de seu ciclo de vida. Portanto, um entendimento completo da importância dos nichos individuais nas dinâmicas e processos ecológicos necessariamente passa pela elucidação dessas variações entre indivíduos em um contexto de múltiplas espécies que coexistem e interagem diretamente (e.g. dentro de uma guilda). Nesta tese, tento avançar nesse sentido ao estudar variações individuais de nicho em espécies congenéricas de rãs que coexistem em áreas do Pantanal e seu entorno. Na sequência, apresento com mais detalhes esse interessante sistema de estudo.

## 3. Rãs do gênero *Leptodactylus* como sistema de estudo

*Leptodactylus* Fitzinger, 1826 é um rico gênero de rãs Neotropicais com 75 espécies atualmente descritas (Sá *et al.* 2014). Curiosamente, essas rãs não tem nome popular em português, mas em inglês são chamadas de *white-liped frogs* ou, mais corretamente, *thin-toed frogs* [do grego *leptos* (fino) e *daktylos* (dedos)] (Caramaschi, de Sá & Heyer 2005). Como 'rãs-de-dedos-finos' me soa um

tanto quanto folclórico, preferi evitar uma tradução literal no texto que segue. Rãs *Leptodactylus* ocorrem em diversos tipos de ambientes ao longo de sua ampla distribuição nos trópicos americanos, ocupando desde áreas florestais úmidas até áreas abertas naturais (Pantanal, Caatinga, Cerrado, Chaco) e alteradas, como pastagens e plantações (Heyer 1969; Piatti & Souza 2011; Sá *et al.* 2014). São anuros de médio a grande porte (em comparação com outras espécies Neotropicais), de hábitos terrestres ou semiaquáticos e de atividade predominantemente noturna (Heyer 1969). Existe uma grande diversidade de modos reprodutivos dentro do gênero *Leptodactylus*, variando dentro de um gradiente com extremos reprodutivos terrestres e aquáticos. Ao longo desse gradiente de dependência de água para reprodução, existem alguns modos reprodutivos curiosos, como a deposição de ovos em ninhos de espuma sobre a água (para proteção a danos físicos e desidratação) (Prado, Uetanabaro & Lopes 2000; Prado *et al.* 2002) ou a construção de câmaras subterrâneas próximas a corpos d'água onde acontece o amplexo e a desova (Heyer 1969; Faggioni *et al.* 2017).

Nesta tese estudamos quatro espécies comuns em áreas do Pantanal e seu entorno: *Leptodactylus bufonius* Boulenger, 1894 (*Figura 3*), *Leptodactylus chaquensis* Cei, 1950 (*Figura 4*), *Leptodactylus fuscus* (Schneider, 1799) (*Figura 5*) e *Leptodactylus podicipinus* (Cope, 1862) (*Figura 6*). De modo geral, essas espécies têm tamanhos corpóreos relativamente parecidos (*Figura 7*), se alimentam dos mesmos tipos de presas, utilizam estratégias de caça similares (geralmente, senta-e-espera), ocupam os mesmos diversos microhábitats para forrageamento (*Figura 8*) e tem períodos de atividade sobrepostos (Prado, Uetanabaro & Haddad 2005; Uetanabaro *et al.* 2008; Piatti & Souza 2011). Tal semelhança ecológica somada ao fato de que, comumente, mais de uma espécie de *Leptodactylus* coexistem sintopicamente em comunidades locais (e.g., margens de lagoas, *Figuras 9* e *10*), evoca uma duradoura questão em ecologia: como espécies similares, que utilizam os mesmos recursos, conseguem coexistir no espaço e no tempo (Hutchinson 1959; Hutchinson 1961). Nesta tese abordamos essa pergunta na perspectiva dos indivíduos, investigando os padrões, causas e consequências das diferenças tróficas entre indivíduos e entre espécies de *Leptodactylus* que coexistem.



*Figura 3*. *Leptodactylus bufonius* Boulenger, 1894. Foto de Paulo R. de Souza.



*Figura 4*. Rã *Leptodactylus chaquensis* Cei, 1950. Foto de Matheus Moroti.



*Figura 5*. Rã *Leptodactylus fuscus*. Foto de Matheus Moroti.



*Figura 6*. Rã *Leptodactylus podicipinus* (Cope, 1862). Foto de Matheus Moroti.

Na literatura, as espécies do gênero *Leptodactylus* são consideradas generalistas tróficas. Diversos estudos que analisaram a dieta de populações dessas rãs encontraram uma grande diversidade de tipos de presas consumidas, na maioria dos casos invertebrados (e.g., diversos

insetos, aracnídeos, diplópodes) mas, por vezes, pequenos vertebrados (e.g., anuros, pequenos mamíferos) (Rodrigues, Uetanabaro & Prado 2004; Piatti & Souza 2011; Sugai, Terra & Ferreira 2012; Costa-Pereira *et al.* 2015; Camurugi *et al.* 2017). Espero que, nas páginas que se sucedem, os leitores se convençam que apesar de as populações dessas rãs serem generalistas tróficas, os indivíduos são, em maior ou menor grau, especializados em determinados tipos de presas.

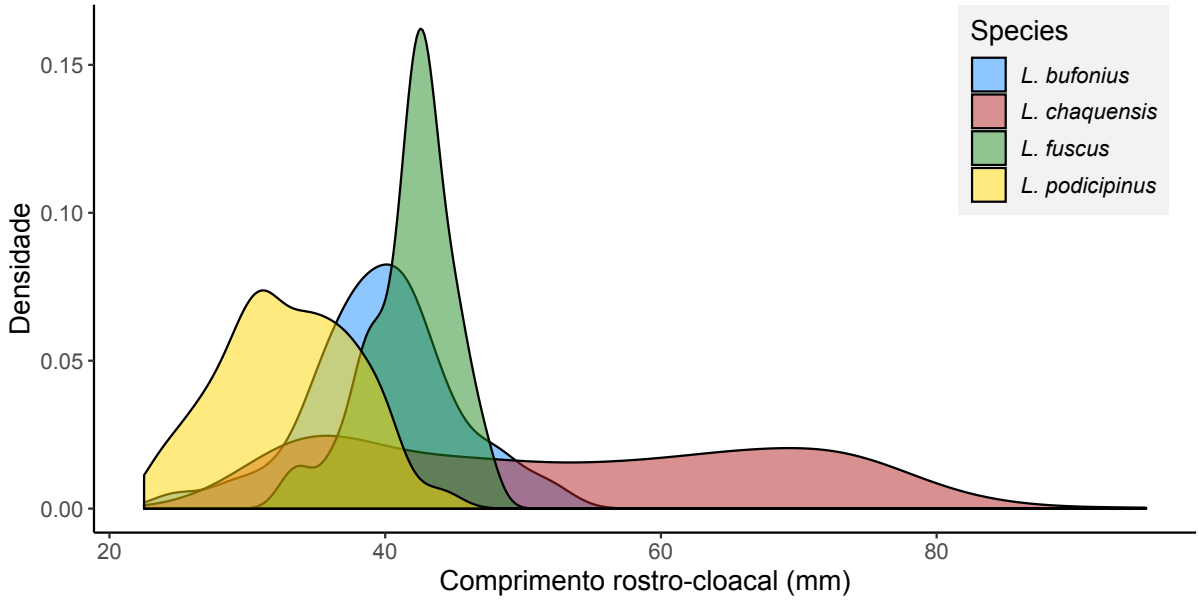



*Figura 7*. Distribuições do comprimento rostro-cloacal (mm) para as quatro espécies de rãs estudadas nessa tese: *Leptodactylus bufonius*, *L. chaquensis*, *L. fuscus* e *L. podicipinus*.

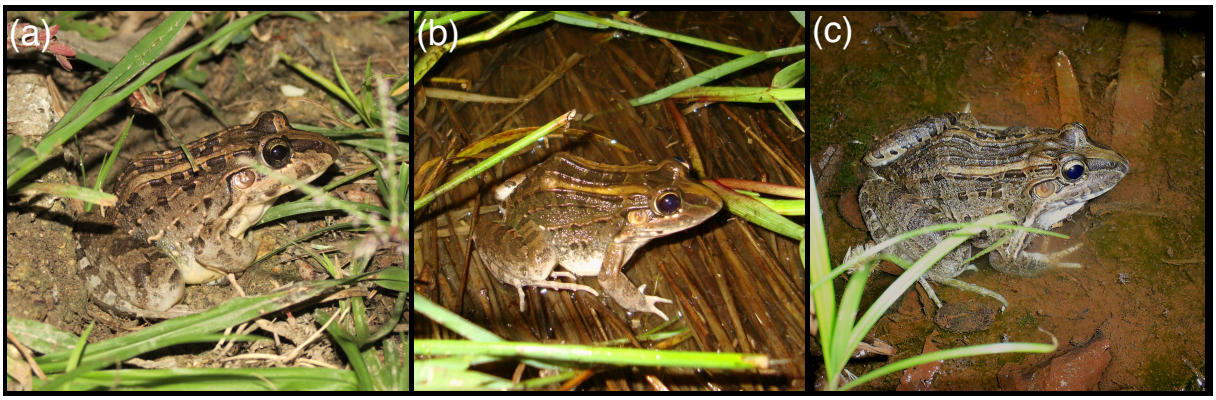



*Figura 8*. Indivíduos de *Leptodactylus chaquensis* em três distintos microhábitats de forrageamento: (*a*) em solo exposto, (*b*) sobre vegetação parcialmente submersa na margem de uma lagoa; (*c*) em água rasa na margem de uma poça. Fotos de Ana Cesquim Campos.

Apesar de o principal foco dessa tese não ser descrever a história natural de *Leptodactylus* no Pantanal e seu entorno, a qual é belamente documentada em diversos trabalhos (e.g., Prado, Uetanabaro & Lopes 2000; Prado *et al.* 2002; Rodrigues, Uetanabaro & Prado 2004; Prado & Haddad 2005; Prado, Uetanabaro & Haddad 2005; Sugai, Terra & Ferreira 2012), nossas

amostragens resultaram em ricas e, por vezes, surpreendentes informações sobre a dieta dessas rãs. Infelizmente, não dedicamos um capítulo desta tese para descrever esses resultados. Para tentar remediar um pouco tal injustiça, apresento a seguir uma breve descrição dos nossos achados quanto a dieta das quatro espécies que estudamos.



*Figura 9.* Uma das lagoas amostradas na região da Serra da Bodoquena, Mato Grosso do Sul, Brasil.



*Figura 10.* Outra das lagoas amostradas, essa localizada na Fazenda Barranco Alto, Pantanal, Mato Grosso do Sul, Brasil.

## 4. O que comem essas rãs?

A resposta rápida é: **muita** coisa. Nas quatro espécies de *Leptodactylus* que estudamos, a largura da boca corresponde a quase totalidade da largura do próprio corpo desses animais (*Figura 11*b), o que significa que eles podem comer presas bastante grandes em relação a seu tamanho corpóreo. Isso se torna particularmente importante pelo fato de essas espécies de rãs não possuírem dentes capazes de despedaçar ou arrancar pedaços de suas presas, as quais tem que ser engolidas por inteiro. Aliás, o Capítulo 3 trata justamente dos determinantes do tamanho relativo de predadores e suas presas. Além de uma boca grande, as rãs que estudamos têm, consequentemente, também um estômago bastante volumoso. Muitas vezes, durante a dissecação desses animais eu me surpreendia com o tamanho das presas que eles conseguem ingerir, como outros anuros (*Figura 11*b), cigarras e até lagartos (*Figura 11*e). Bom, mas não só de banquetes vivem essas rãs. A maior parte das presas encontradas no conteúdo do trato digestivo era, relativamente, pequena. Por esse lado, estômagos grandes permitem que muitas presas sejam capturadas sem que os animais fiquem de barriga cheia (*Figura 11*a). Por exemplo, apenas no estômago de um único indivíduo de *L. chaquensis* cheguei a encontrar 110 presas!

Segue uma sucinta descrição das presas que encontramos na dieta das quatro espécies de *Leptodactylus* que estudei (*Figura 12*). No total, analisei o conteúdo do trato digestivo de 974 indivíduos (somente 3% deles estavam sem conteúdo estomacal), de onde consegui recuperar 6.172 presas (média de ~7 presas/indivíduo), pertencentes a 85 Famílias, e 32 Ordens taxonômicas (*Tabela 1*). As presas mais consumidas foram cupins, formigas e besouros (*Tabela 1*). Rãs comeram presas minúsculas (formigas, mosquitos) e gigantes (lagartos, rãs, cigarras); aquáticas (e.g. larvas de Odonata, besouros aquáticos, caramujos) e terrestres (cupins, formigas e besouros); que voam (vespas, mariposas), saltam (grilos e gafanhotos) e que rastejam (minhocas, diversas larvas); predadoras (louva-a-deus, aranhas) e consumidoras primárias (borboletas, cupins); apetitosas (camarões, caranguejos, peixes) e perigosas (escorpiões, lacraias) (*Figura 12*). Destaco também que essas rãs são, por vezes, canibais (*Figura 11b*) e predadoras intraguilda (*Figura 13*), uma vez que encontramos sete espécies de anuros nos conteúdos estomacais.

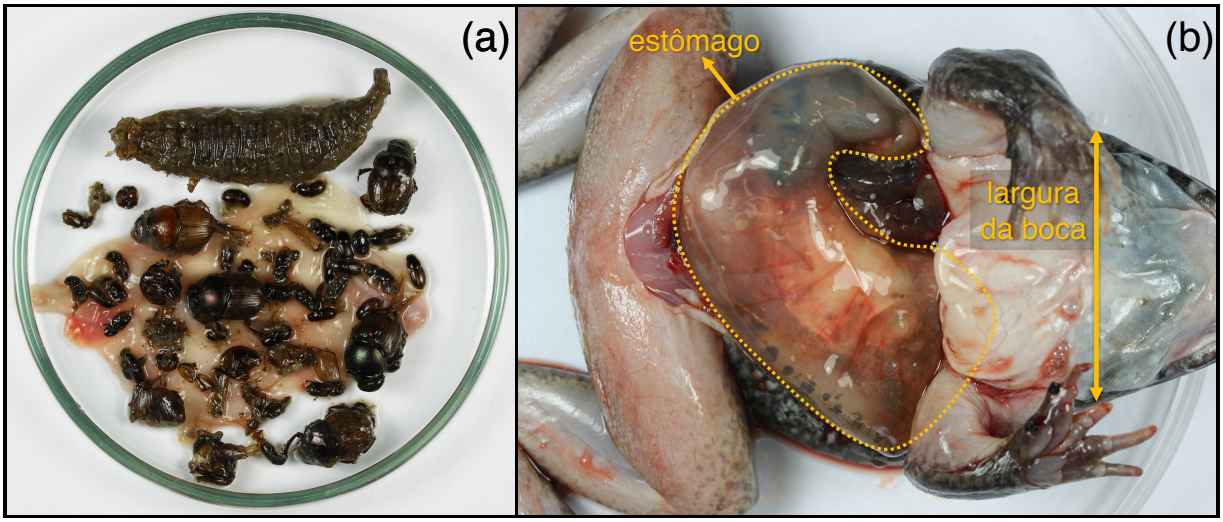



*Figura 11.* (a) Variedade de formas e tamanhos das presas encontradas no conteúdo estomacal de um indivíduo de *Leptodactylus chaquensis*. (b) Macho canibal de *L. chaquensis* com um um conspecífico em seu estômago; detalhe para a largura da boca em relação à largura do corpo e para as volumosas dimensões do estômago (delineado pela linha amarela pontilhada).

*Tabela 1.* Dieta de quatro espécies do gênero *Leptodactylus* em áreas do Pantanal e entorno, representadas como o número de presas consumidas e respectivas porcentagens (entre parênteses) para cada uma das espécies. Apenas tipos de presas com mais de 0,1% de abundância são mostrados na tabela.

| Tipo de presa | *L. chaquensis* | *L. podicipinus* | *L. fuscus* | *L. bufonius* | Total |
|---|---|---|---|---|---|
| Isoptera | 1328 (34,53) | 87 (6,01) | 107 (18,45) | 13 (4.48) | 1535 (24,9) |
| Coleoptera | 764 (19,86) | 426 (29,42) | 91 (15,69) | 65 (22.41) | 1346 (21,8) |
| Formicidae | 686 (17,84) | 231 (15,95) | 247 (42,59) | 64 (22.07) | 1228 (19,9) |
| Homoptera | 251 (6,53) | 116 (8,01) | 30 (5,17) | 20 (6.9) | 417 (6,8) |
| Orthoptera | 129 (3,35) | 141 (9,74) | 10 (1,72) | 37 (12.76) | 317 (5,1) |
| Larva de Coleoptera | 171 (4,45) | 78 (5,39) | 35 (6,03) | 23 (7.93) | 307 (4,98) |
| Lepidoptera | 113 (2,94) | 129 (8,91) | 6 (1,03) | 14 (4.83) | 262 (4,25) |
| Arachnida | 116 (3,02) | 81 (5,59) | 18 (3,1) | 17 (5.86) | 232 (3,76) |
| Heteroptera | 91 (2,37) | 70 (4,83) | 3 (0,52) | 22 (7.59) | 186 (3,02) |
| Diptera | 61 (1,59) | 40 (2,76) | 9 (1,55) | 6 (2.07) | 116 (1,88) |
| Hymenoptera | 47 (1,22) | 13 (0,9) | 14 (2,41) | 2 (0.69) | 76 (1,23) |
| Blattodea | 17 (0,44) | 21 (1,45) | 0 (0) | 4 (1.38) | 42 (0,68) |
| Anura | 21 (0,55) | 2 (0,14) | 0 (0) | 1 (0.34) | 24 (0,39) |
| Gastropoda | 8 (0,21) | 5 (0,34) | 2 (0,34) | 0 (0) | 15 (0,24) |
| Diplopoda | 6 (0,16) | 0 (0) | 1 (0,17) | 0 (0) | 7 (0,11) |
| Chilopoda | 2 (0,05) | 2 (0,14) | 2 (0,34) | 1 (0.34) | 7 (0,11) |
| Trichoptera | 3 (0,08) | 2 (0,14) | 2 (0,34) | 0 (0) | 7 (0,11) |
| Brachyura | 4 (0,1) | 1 (0,07) | 1 (0,17) | 0 (0) | 6 (0,1) |
| Mantodea | 3 (0,08) | 2 (0,14) | 0 (0) | 1 (0.34) | 6 (0,1) |




*Figura 12.* Algumas das presas do variado menu de rãs do gênero *Leptodactylus*; (a) Esperança (Orthoptera, Tettigoniidae) e barata (Blattodea), (b) lacraia (Chilopoda, Scolopendromorpha), (c) Cincidela (Cicindelidae) e barata (Blattodea), (d) peixe, provavelmente *Rivulus* sp., (e) lagarto-de-cauda-azul (infelizmente, sem a cauda azul) *Micrablepharus maximiliani* (Sauria, Gymnophthalmidae), (f) Mollusca, Gastrópoda; (g) escorpião (Arachnida, Scorpiones), (h) camarões (Crustacea, Decapoda), e (i) caranguejos (Crustacea, Brachyura). Marcações maiores e menores na régua representam centímetros e milímetros, respectivamente.

## 5. Objetivos e estrutura da tese

Nesta tese busco entender os padrões, causas e consequências da variação individual de nicho em espécies que coexistem. De modo geral, mensuramos o nicho de indivíduos e populações considerando a identidade taxonômica e o tamanho corpóreo das presas consumidas, bem como isótopos estáveis de carbono e nitrogênio das presas e consumidores. Especificamente, tratamos dos seguintes temas nos capítulos que compõem esta tese:

*Capítulo 1.* Descrevemos os padrões de variação individual de nicho trófico entre espécies e comunidades e investigamos o efeito das quatro principais forças ecológicas apontadas pela teoria como determinantes do grau de variação individual de nicho (Costa-Pereira *et al.* 2018c).

*Capítulo 2*. Nesse capítulo, que talvez seja a ovelha negra da tese, nos afastamos um pouco da teoria de especialização individual *per se* e investigamos como uma importante propriedade de teias tróficas, o tamanho relativo de predadores em relação a suas presas (*predator-prey size ratio*, PPSR), varia entre e dentro de populações ao longo de gradientes ecológicos (Costa-Pereira *et al.* 2018a).

*Capítulo 3*. O principal foco desse capítulo é entender os fatores que moldam o nicho trófico e a sobreposição entre nichos de espécies que coexistem ao longo de gradientes ecológicos. Para isso, usamos um método recentemente proposto para modelar nichos em múltiplas dimensões que explicitamente incorpora variação intra- e interindividual de nicho (Ingram, Costa-Pereira & Araújo 2018).

*Capítulo 4*. O último capítulo é destinado a entender as ainda pouco exploradas consequências ecológicas e evolutivas da variação individual de nicho. Especificamente, investigamos como a consistência trófica individual ao longo dos meses que precedem a reprodução afeta a subsequente aptidão reprodutiva e somática individual.



*Figura 13*. Macho adulto de *Leptodactylus chaquensis* predando um adulto de *Physalaemus centralis* nas margens de uma lagoa em Jardim, Mato Grosso do Sul, Brasil. Foto de Raul Costa Pereira.

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# Capítulo 1

# Drivers of individual niche variation in coexisting species

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## Abstract

*1*. Although neglected by classic niche theory, individual variation is now recognized as a prevalent phenomenon in nature with evolutionary and ecological relevance. Recent theory suggests that differences in individual variation across competitors can affect species coexistence and community patterns. However, the degree of individual variation is flexible across wild populations and we still know little about the ecological drivers of this variation across populations of single species and, especially, across coexisting species.

*2*. Here we aimed to (*i*) elucidate the major drivers of individual niche variation in natural communities and (*ii*) to determine how consistent this variation is across coexisting species and communities.

*3*. We analyzed natural patterns of individual-level niche variation in four species of coexisting generalist frogs across a wide range of tropical communities. Specifically, we used gut contents and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) from frog species and their prey to quantify individual niche specialization. Then we combined data on local community structure, availability of prey, phylogenetic relationships, and predator-prey size models to test how this variation is related to four ecological factors which are predicted to be key drivers of individual specialization: intraspecific competition, interspecific competition, ecological opportunity (i.e., diversity of resources), and predation.

*4*. We found that the degree of individual trophic specialization varied by up to nine-fold across populations within the same species. This sizable variation in trophic specialization across populations was at least partially explained by gradients of density of competitors (both conspecifics and heterospecifics) and intraguild predation. However, the specific relationships between individual specialization and these ecological gradients were strongly species-specific. As consequences, the identity of the species with more individual variation changed among sites and there was typically no spatial correlation in the degree of individual specialization across co-existing species.

*5*. Our results show that individual niche specialization within and across species can be strongly context-dependent and that hierarchies of individual variation among coexisting species are not necessarily consistent across communities. Recent theory suggests that this pattern could lead to concurrent changes in competitive interactions across sites and thereby could play a key role in species coexistence at the landscape level. Our results suggest that individual variation across and within coexisting species has the potential to affect not only species coexistence at local communities, but also regional diversity patterns.


*Keywords*: stable isotopes, species coexistence, intraspecific variation, *Leptodactylus*, competition, ecological opportunity, diet, Thin-toed frogs

## Resumo

*1*. Apesar de negligenciada pela teoria clássica de nicho, a variação entre indivíduos é agora reconhecida como um fenômeno prevalente na natureza com relevância ecológica e evolutiva. Teorias recentes sugerem que diferenças no grau de variação individual entre competidores podem afetar a coexistência de espécies e padrões de comunidades. Entretanto, o grau de variação individual é flexível entre populações naturais e ainda sabemos pouco sobre os mecanismos ecológicos que levam a essa variação entre populações de uma mesma espécie e, especialmente, entre espécies que coexistem.

*2*. Aqui nós buscamos (*i*) elucidar as principais causas de variação individual de nicho em comunidades naturais e (*ii*) determinar o quão consistente é a variação entre espécies que coexistem e entre comunidades.

*3*. Nós analisamos padrões naturais de variação trófica no nível indivíduo em quatro espécies generalistas de rãs que coexistem em comunidades tropicais. Especificamente, nós utilizamos conteúdos estomacais e isótopos estáveis ($\delta^{13}C$ e $\delta^{15}N$) das rãs e suas presas para quantificar a especialização dos nichos individuais. Nós então combinamos dados sobre a estrutura local de comunidades, disponibilidade de presas, relações filogenéticas e modelos de tamanho predador-presa para testar como essa variação está relacionada aos quatro fatores ecológicos previstos como causas importantes de especialização individual: competição intraespecífica, competição interespecífica, oportunidade ecológica (i.e., diversidade de recursos) e predação.

*4*. Nós encontramos que o grau de especialização individual trófico variou até nove vezes entre populações da mesma espécie. Essa grande variação na especialização trófica entre populações foi explicada, em parte, por gradientes de densidade de competidores (tanto coespecíficos quanto heterospecíficos) e predação intraguilda. Entretanto, as relações entre especialização individual e esses gradientes ecológicos foram fortemente espécie-específicas. Como consequências, a identidade da espécie com maior variação individual mudou entre áreas e não houve correlação espacial entre o grau de especialização individual das espécies que coexistem.

*5*. Nossos resultados mostram que a especialização dos nichos individuais dentro e entre espécies pode ser fortemente dependente de contexto e que hierarquias de variação individual entre espécies que coexistem não são necessariamente consistentes entre comunidades. Teorias recentes sugerem que esse padrão poderia levar a mudanças nas interações competitivas entre áreas e, portanto, ter um papel chave na coexistência de espécies na escala da paisagem. Nossos resultados sugerem que a variação individual entre e dentro de espécies que coexistem tem o potencial de afetar não somente a coexistência de espécies em comunidades locais, mas também os padrões regionais de diversidade.


*Palavras-chave:* isótopos estáveis, coexistência de espécies, variação intraespecífica, *Leptodactylus*, competição, oportunidade ecológica, dieta, rãs

## Introduction

Classic niche theory relies on average differences between species to explain diversity patterns in biological communities. Indeed, the assumption of ecological equivalence within species has traditionally underlaid niche theory (Chase & Leibold 2003). However, this long-standing assumption has been challenged in recent years by a boost in the number of studies documenting substantial individual niche variation within populations (Bolnick *et al.* 2003; Araújo, Bolnick & Layman 2011). Furthermore, theory and empirical work indicate that the level of individual variation within populations can have important consequences for population dynamics, species interactions, and long-term coexistence (Bolnick *et al.* 2011; Violle *et al.* 2012; Pruitt & Modlmeier 2015; Barabás & D'Andrea 2016; Forsman & Wennersten 2016; Hart, Schreiber & Levine 2016; Hausch, Vamosi & Fox 2018). Despite these recent advances, it is increasingly apparent that the degree of individual niche variation is spatially and temporally flexible in wild populations, responding to shifts in ecological contexts from local to global scales (Araújo, Bolnick & Layman 2011; Araújo & Costa-Pereira 2013). However, we still know little about the extent and drivers of individual niche variation within and across species in natural communities. Yet, this knowledge is essential to develop biologically realistic models and testable quantitative predictions on how individual variation can affect community dynamics (Bolnick *et al.* 2011; Violle *et al.* 2012; Ingram, Costa-Pereira & Araújo 2018).

Recent theoretical models suggest that the outcome of interspecific competitive interactions (i.e., species coexistence *vs.* competitive exclusion) strongly depends on how the amount of individual variation differs across competitors (Barabás & D'Andrea 2016; Hart, Schreiber & Levine 2016). For example, considering two coexisting species, it is possible that one of them has consistently higher individual niche variation than the other, which would confer a competitive advantage by reducing mean intraspecific competition, regardless of the ecological context where species are interacting (Barabás & D'Andrea 2016; Hart, Schreiber & Levine 2016) (*Figure 1*a). Alternatively, if competitors exhibit no consistency in their differences in individual variation, competitive hierarchies can change across ecological contexts (*Figure 1*b). Thus, it is important to elucidate how coexisting species differ in the degree of individual niche variation across ecological contexts and whether these differences are consistent along environmental gradients. However, the vast majority of previous studies quantified niche specialization within a single target species (Bolnick *et al.* 2003; Araújo, Bolnick & Layman 2011) and little empirical data is available to compare the degree of individual niche variation

in populations of co-occurring species (Araújo *et al.* 2009; Faulks *et al.* 2015; Cloyed & Eason 2016).

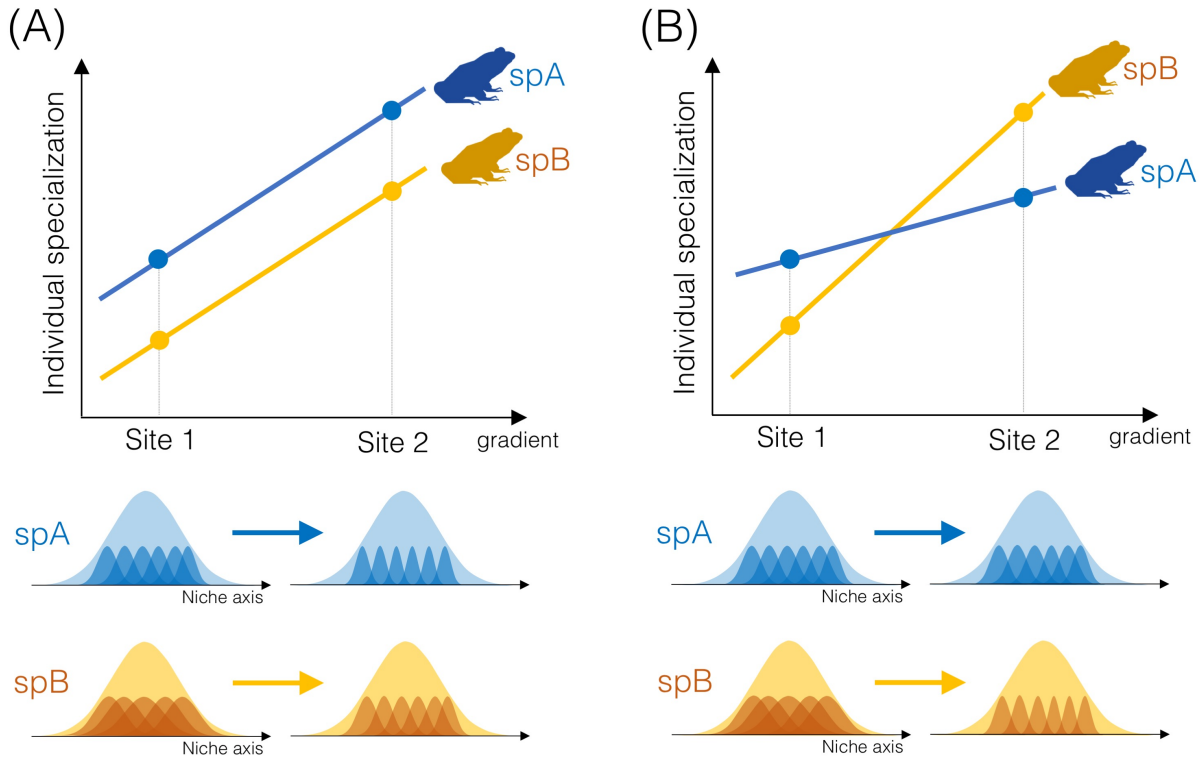



*Figure 1.* Conceptual representation of how the hierarchy of individual specialization across two coexisting species (*spA*, *spB*) may vary along an ecological gradient. (A) *spA* has consistently higher individual niche variation than *spB* (either in Site 1 and Site 2), which would confer a competitive advantage to *spA* by reducing its mean intraspecific competition along the gradient. (B) Competitors exhibit no consistency in their differences in individual variation: in the Site 1, *spA* has higher individual specialization; the scenario is the opposite in Site 2.

Theories on optimal foraging provide guidelines on which ecological factors could drive differences in individual variation. Specifically, these theories posit that four main ecological factors should affect the degree of individual niche variation: intraspecific competition, interspecific competition, ecological opportunity, and predation (Araújo, Bolnick & Layman 2011; but see Toscano *et al.* 2016). Intraspecific competition can increase among-individual niche variation if it constrains the use of a common optimal resource and therefore individuals begin to feed on alternative resources that differ according to individuals' phenotypes (Svanbäck & Bolnick 2005; Svanbäck & Bolnick 2007). Ecological opportunity (i.e., diversity of available resources) is also expected to increase individual niche variation by expanding

individuals' foraging possibilities and then allowing their niches to diverge (Araújo, Bolnick & Layman 2011). In turn, predation may decrease niche variation through density-mediated effects or changes in consumer behavior (Araújo, Bolnick & Layman 2011). Interspecific competition may have positive or negative effects on individual specialization depending on how population and individuals' niches respond to heterospecifics (Van Valen 1965; Bolnick *et al.* 2010).

While some experimental and observational studies confirm these expectations for the role of intraspecific competition and ecological opportunity, effects of predation and interspecific competition remain underexplored (Araújo, Bolnick & Layman 2011). Furthermore, the majority of these studies focused on the specific effect of only one of these four ecological factors (e.g. intraspecific competition, Svanbäck & Persson 2004; Svanbäck & Bolnick 2007; Tinker, Bentall & Estes 2008). Only recently have observational studies started to provide some insights on how two ecological factors can interact to determine the degree of individual niche variation in populations (Evangelista *et al.* 2014; Newsome *et al.* 2015; Costa-Pereira *et al.* 2017). However, under natural conditions, populations are usually facing all four factors simultaneously to varying degrees and the effects of these factors may not be independent. Furthermore, coexisting species that differ in their life-history traits or level of individual specialization may respond differently to gradients of competition, ecological opportunity, and predation. Testing existing theory on ecological drivers of individual variation and its consequences for species interactions, therefore, requires an integrative approach to unravel how these factors drive individual niche specialization in populations of coexisting species (Araújo, Bolnick & Layman 2011; Bolnick *et al.* 2011).

Here, we use a large-scale field survey of natural frog communities to identify key ecological drivers of individual trophic specialization across natural populations and communities of coexisting species. Specifically, we asked: (*a*) how consistent are differences in individual specialization across species and communities? We predict that co-occurring species should present a consistent hierarchy of individual variation across communities (*Figure 1*a), which would favor their local coexistence (Barabás & D'Andrea 2016; Hart, Schreiber & Levine 2016). (*b*) What is the relative importance of intraspecific and interspecific competition, predation and ecological opportunity in explaining the variation of individual specialization across populations? (*c*) Does the relative importance of these ecological factors vary across coexisting species?

## Methods

### *Study system*

Thin-toed frogs (*Leptodactylus* spp.) are a species-rich genus of trophic generalist anurans widely distributed across the Neotropics. Commonly, more than one species of thin-toed frogs can be found co-occurring syntopically (e.g. around ponds) in South American lowlands, exhibiting large diet overlap (De-Carvalho et al. 2008, Piatti & Souza 2011). Thin-toed frogs forage at night on the ground and in low vegetation, consuming a wide taxonomic range of invertebrate prey, but larger individuals can also prey on small vertebrates, including intraguild predation and cannibalism (Costa-Pereira *et al.* 2015; Costa-Pereira *et al.* 2018a). Most of the species within this clade are medium-sized frogs (3 – 11 cm), but some species can reach large body sizes (~20 cm). Individuals within populations of *Leptodactylus* spp. can show substantial diet variation (Araújo *et al.* 2009).

We studied four areas in central Brazil, two of them in the Pantanal wetlands, Fazenda Barranco Alto (central coordinates: 19.559° S, 56.133° W) and Base de Estudos do Pantanal-UFMS (19.494° S, 57.048° W), one in the Bodoquena Plateau (21.384° S, 56.413° W) and one in the Gran Chaco region (21.683° S, 57.72° W), covering a total area of ~ 40,000 km² (*Figure S1*). In general, these regions are characterized by Savannah and grassland habitats, with numerous lagoons or ponds that harbor a high biomass of amphibian anurans during the rainy season. Despite some differences in species composition and community structure between these areas, *Leptodactylus* species frequently represent the most common (> 70% in terms of abundance and biomass) terrestrial anurans around natural or semi-natural lentic water bodies. Here we focus on the four most common species in this geographical region: *Leptodactylus bufonius*, *L. chaquensis*, *L. fuscus*, and *L. podicipinus*. Although these species use similar food resources and microhabitats, they differ in average body size (*Figure S2*) and reproductive mode (Prado, Uetanabaro & Haddad 2005).

### *Data collection*

We sampled 21 frog communities, accounting for 43 populations of four studied species (*L. bufonius*, n = 5 populations; *L. chaquensis*, n = 18; *L. fuscus*, n = 7; and *L. podicipinus*, n = 13) between mid-November 2014 and early January 2015. This period corresponds to the start of the wet season, when *Leptodactylus* spp. are fully active after several months of low activity and

metabolic rates. Importantly, it is a key foraging period to these frogs because it is when they accumulate energy to reproduce (Prado, Uetanabaro & Haddad 2005). Thin-toed frogs have a strong association with lentic water bodies. Thus, we defined a community as all the anurans found around natural or semi-natural lagoons and separated by at least 1.5 km from any other community (*Figure S1*). Around each lagoon, we established six 10 x 10 m plots (sampling area = 600 $m^2$/community). To sample available food resources to frogs we installed 12 pitfall traps (20 cm diameter) and two light traps evenly spaced surrounding the plots. We opened pitfall traps and turned on light traps right after the sunset, and retrieved prey samples after 12h. Two hours after nightfall, we surveyed each plot (standard collection effort of 1h/people/100$m^2$) and hand-captured all frogs and toads found, which were kept in humidified plastic bags. After the anuran survey, collected *Leptodactylus* spp. specimens were euthanized with an overdose of analgesic (lidocaine), kept on ice in the field and then transferred to a -20°C freezer on the same night. Frog and prey samples were kept frozen until lab processing. Individuals from other species were identified and released on the same night of sampling. Collection and euthanasia were carried out in accordance with Universidade Estadual Paulista guidelines for the care of vertebrate animals (UNESP Animal Care and Use Committee 03120501).

The same person (RCP) measured the snout-vent length of each specimen using a digital caliper (0.01 mm) and dissected frogs to obtain gut contents (both stomach and intestine) under stereomicroscope. Individuals were sexed by the examination of gonads. Specimens without developed gonads were considered juveniles. We quantified individual diets by counting and identifying to the lowest taxonomic level possible (family level in most cases) all prey items found in gut contents. To quantify the available resources to frogs, we also counted and identified (family level) all potential prey that we collected using light and pitfall traps (n = 9,470 cumulative prey items over all traps).

Complementary to gut-content analysis, we measured stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of the frogs (n = 974 individuals) and their prey. Stable isotopes have been used as a measure of long-term feeding history in trophic studies, allowing inferences on individual temporal consistency in diet (Layman *et al.* 2012). We removed a piece (1 x 1 cm) of liver from each frog individual, which incorporates isotope values of consumers' diets for several weeks (Dalerum & Angerbjörn 2005). Liver and prey samples (retrieved from pitfall and light traps or gut contents) were rinsed in deionized water, oven-dried for 48 hours at constant 60°C, grounded, and weighed (~ 0.5 mg) into tin capsules. Because C:N ratios were

overall low (< 4), we did not extract lipids from our samples or mathematically correct them to account for lipid content (Post *et al.* 2007). The abundances of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were determined at the Washington State University Stable Isotope Core Laboratory using an Elemental Combustion System 4010 elemental analyzer (Costech Analytical, Valencia, CA, USA) and a Delta Plus XP continuous flow isotope ratio mass spectrometer (Thermofinnigan, Bremen, Germany). We report isotope compositions using conventional delta notation, showing differences between the observed concentration and that of Pee Dee Belemnite for carbon and atmospheric $N_2$ for nitrogen. The standard deviation of replicates of the internal reference material (Nylon) was 0.03% for $\delta^{13}C$ and 0.06% for $\delta^{15}N$.

*Proxies to ecological mechanisms*

It was not possible to directly measure the magnitude of the four ecological factors believed to affect individual specialization in wild populations. We therefore followed previous studies (Evangelista *et al.* 2014; Newsome *et al.* 2015; Cloyed & Eason 2016) and used proxies to represent their magnitudes in each population. We measured intraspecific competition and ecological opportunity using the density of conspecifics and the Shannon Index of diversity of available resources as proxies, respectively. The effects of the density of conspecifics (and heterospecifics) on the degree of individual specialization should also depend on the amount of available food resources. Therefore, we also quantified the total biomass of prey in the environment for each community.

We used a metric that combines both the local structure of communities and the phylogenetic relationships between coexisting species to quantify the strength of interspecific competition. Specifically, we calculated a measure of effective density of heterospecifics ($N_z$) experienced by each population in each community based on the quantitative genetic competition model proposed by Doebeli (1996):

$$N_z = \int \rho(z')\alpha(z, z')dz$$

In this model, the effective population density corresponds to the proportion of each alternative phenotype z' (or, in our case, species z'), represented by ϱ(z'), weighted by its competitive effect on the focal phenotype z (species z). The competitive effect, α (z, z'), represents the per capita decrease in the population growth of the species z for each individual

of the species z' added to the community, which can be modeled as:

$$\alpha(z, z') = \exp\left(-\frac{(z - z')^2}{2\sigma_\alpha^2}\right)$$

Here we considered the difference between phenotypes (z, z') as the phylogenetic distance between two given species. Using the R package *picante* (Kembel *et al.* 2010), we calculated the phylogenetic distance between all pairs of coexisting species from a cladogram based on the time-calibrated tree proposed by Pyron and Wiens (2011) (*Figure S2*). The constant $\sigma_\alpha^2$ determines how sharply the competition decays with the increase of the divergence between phenotypes. As an empirical value to this constant is not available in the literature, we determined $\sigma_\alpha^2 = 0.05$, which was the best value to approximate the competitive function based on our data to a Gaussian function (Doebeli 1996). Using smaller or larger values ($\sigma_\alpha^2 = 0.025$ and $\sigma_\alpha^2 = 0.075$) did not qualitatively change the results. In summary, our metric of effective density of heterospecifics for a given population increases when co-occurring species are closely related and abundant. We acknowledge this approach implicitly assumes that closely related species are ecologically more similar and therefore compete more strongly for food resources, which is not always true in biological communities (Godoy, Kraft & Levine 2014; Cadotte, Jonathan Davies & Peres-Neto 2017). However, considering that species diet and reproductive modes are associated with evolutionary proximity in our system (Uetanabaro *et al.* 2008), we believe that phylogenetic relationships can be a good representation of the similarity of trophic niches between frog species.

As a proxy for predation pressure, we quantified the median likelihood of intraguild predation for a given population. During fieldwork and gut content analyses, we observed many events of intraguild predation and cannibalism in our studied system. We acknowledge that intraguild predation is not the only type of predation pressure that thin-toed frogs experience, as predation by birds and snakes have been reported in this system (Costa-Pereira *et al.* 2016). However, numeric and biomass domination of *Leptodactylus* spp. (> 90% of the total biomass of anurans, see Results) in the studied communities suggest that intraguild predation and cannibalism should account for a substantial portion of predation in our system. As predation is strongly size-structured in frogs, we used an approach that combines predator-prey size relationships with the observed local size structure of communities. Specifically, using only the anuran prey consumed by thin-toed frogs (n = 33, gut contents analyses), we regressed the log-transformed predator (y-axis) and prey (x-axis) body sizes (snout-vent length) and

obtained a 95% quantile regression model (intercept = 1.133, $\beta$ = 0.447), which allowed us to establish the upper boundary of the feeding range (Gravel *et al.* 2013). Using this predator-prey body size model, we estimated for each individual the minimum size of a potential intraguild predator. Therefore, we used this critical size value to quantify the number of potential intraguild predators that co-occurred with each individual in the studied communities. Finally, we calculated the median value of the distribution of estimated number of potential intraguild predators to represent the likelihood of intraguild predation pressure for each studied frog population.

*Measures of individual niche specialization*

To quantify the degree of individual specialization, we used two complementary sources of trophic niche information at the individual scale, gut contents and stable isotope data. Stable isotopes allowed us to infer temporal consistency in the diets of individuals because they reflect nutrients assimilated over many feeding events. Gut contents allow us to accurately determine the diet (e.g. high taxonomic resolution) and infer how coexisting species and individuals are partitioning specific resources within a given period of time (Araújo, Bolnick & Layman 2011). Gut contents of thin-toed frogs commonly contain a high number of prey items during the rainy season (mean of 7 prey/individual, max of 110 prey/individual).

For gut contents data, we first calculated the proportional similarity index ($PS_i$) for each individual *i*, which measures the overlap between individual *i*'s niche and the population niche. The average of $PS_i$ values corresponds to the IS individual specialization index, which is the average overlap between individuals' niches and the population niche (Bolnick *et al.* 2002). To obtain a more intuitive measure of individual specialization, we subtracted the observed IS index of each population from 1, resulting in the V index (Bolnick *et al.* 2007). When all individuals' niches overlap totally with the population niche, the V index is 0 and assumes higher values as the amount of individual specialization increases. We tested whether each observed V value could be generated if individuals sample prey stochastically from the population diet distribution (i.e., the significance of V indexes) using Monte Carlo bootstrap simulations (1,000 replicates) (Zaccarelli, Bolnick & Mancinelli 2013). As measures of individual specialization based on gut contents can also be influenced by the degree of taxonomic resolution (Newsome *et al.* 2015), we calculated the V index using both Order and Family level identifications separately. As we found a high correlation between these indexes

($r = 0.84$, $p < 0.001$), we only used family-level data in the analyses.

Gut contents do not necessarily reflect individuals' long-term feeding preferences. Thus, we also obtained a measure of V calculated from stable isotopes of carbon and nitrogen. $\delta^{13}C$ provides information on how individuals' feeding preferences differ in terms of types of foods consumed (e.g., C3 *vs.* C4 food chains), while $\delta^{15}N$ indicates differences in trophic-level of consumed prey over time (Fry 2007). We used empirically observed parameters (population diet distribution, number of individuals sampled, isotope values [$\delta^{13}C$ or $\delta^{15}N$] of all prey and their dry masses) to simulate populations with varying degrees of diet variation and isotopic variance among individuals (see details in Araújo *et al.* 2007). For each sampled frog population, we simulated 5,700 virtual populations and then generated an expected relationship between the V index and isotope variance specific for that population. Finally, we used this relationship to convert empirically observed isotope variances into estimates of $V_{\delta^{13}C}$ and $V_{\delta^{15}N}$ which can be compared to V values calculated from gut-content data. Importantly, as simulations account for local prey's isotopic distributions, V values are comparable among populations even when there are differences in isotopic baselines across sites. We ran simulations in the program VarIso 1.0 (Araújo *et al.* 2007).

### *Statistical analyses*

We performed all statistical analyses in R 3.4.1. To test if differences in the degree of individual specialization between coexisting species are consistent across communities, we first subtracted the calculated V indexes (V, $V_{\delta^{13}C}$ or $V_{\delta^{15}N}$) between each pair of coexisting populations. In this case, if two locally coexisting species have exactly the same degree of individual specialization, the difference between them is zero. To test whether there is a directional trend of difference, i.e. consistently higher or lower individual variation for a given species in relation to other species across communities, we performed a one-sample t-test comparing the values of the difference in individual specialization for each pair of species with zero. Additionally, we correlated (Pearson) the calculated values of individual specialization between each pair of species across communities. If the degree of two given species varies consistently across communities, we would observe a positive correlation, indicating that individual specialization in both species is driven by similar mechanisms. For these and the following analyses, we only used populations with more than seven individuals and with significant V index values (Monte Carlo simulations).

To determine which ecological factors help explain variations in the degree of individual specialization across populations and their relative importance, we constructed linear mixed models in the package *lme4* (Bates *et al.* 2014) with V, $V_{\delta^{13}C}$ or $V_{\delta^{15}N}$ as response variables and density of conspecifics, effective density of heterospecifics, intraguild predation likelihood, resource diversity, and biomass of available prey as additive predictors. These predictors are not correlated (pairwise Pearson correlation, all p-values > 0.13) and we centered and scaled them before the analysis to facilitate comparisons of the resulting coefficients. We included the interaction of species identity with each of these factors (except biomass of prey, which was used only to control the effect of different resource abundances on the densities of conspecifics and heterospecifics) to determine whether effects of predictors vary across species. We also included site (community) nested within the geographical area as random effect. Although prior studies assumed a linear relationship between the degree of individual specialization and ecological gradients, recent studies have found quadratic patterns (Jones & Post 2013; Evangelista *et al.* 2014; Mateus *et al.* 2016). We therefore compared the fit of a linear *vs.* a quadratic model using corrected Akaike's Information Criteria ($AIC_c$). We excluded *L. bufonius* from these analyses because of small sample size (n = 5 populations). Visual inspection of residual plots did not reveal any clear deviations from normality or homoscedasticity. P-values were obtained using Type II Wald Chi-square tests in the package *car* (Fox *et al.* 2016). Data underlying the analyses are deposited in the Dryad Digital Repository: 10.5061/dryad.mq2h237 (Costa-Pereira *et al.* 2018b).

## Results

Across the 21 sites, thin-toed frogs (*Leptodactylus* spp.) were the dominant species accounting for 68.23% of the captured individuals and 93.34% of the total biomass of anurans. In most of the sampled communities we found three thin-toed frog species coexisting, and in four communities only one *Leptodactylus* species was sampled. *Leptodactylus chaquensis* was the most abundant and frequent species (n = 493 individuals, 18 communities), followed by *L. podicipinus* (n = 337, 16), *L. fuscus* (n = 95, 13) and *L. bufonius* (n = 49, 5). These last three species presented similar body size distributions (between 25 and ~ 50 mm), while *L. chaquensis* reached up to 90 mm (see *Introdução Geral*). We identified 6,172 prey items from gut contents. Thin-toed frogs had a broad diet, consuming 85 prey types. Termites (24.8%), ants (19.91%), leafhoppers (4.41%), and micro-moths (4.25%) were the most common prey types,

corresponding to more than half of all food items (see *Introdução Geral*). Thin-toed frogs also exhibited a wide range of isotope values, which can be related to the large spatial extent of our study area. $\delta^{13}C$ ranged from -27.57 to -12.16‰ (mean = -21.14‰, sd = ± 2.85) and $\delta^{15}N$ from -2.88 to 14.14‰ (mean = 7.92‰, sd = ± 1.89).

### *Variation in individual specialization across populations*

Individual diet specialization based on dietary data (V-values) and stable isotopes (either $V_{\delta^{13}C}$ or $V_{\delta^{15}N}$) were positively correlated, and V-values were generally larger than $V_{\delta^{13}C}$ and $V_{\delta^{15}N}$ (*Figures 2*, *S3*). $V_{\delta^{13}C}$ and $V_{\delta^{15}N}$ were not correlated (*Figure S3*), indicating that these two tracers are capturing different aspects of the frogs' trophic ecology. Trophic specialization within populations varied by 2-fold for dietary data, 10-fold for $\delta^{13}C$, and almost 20-fold for $\delta^{15}N$ (Figure 2). For all indexes, species presented relatively high individual specialization (mean values: V = 0.71, $V_{\delta^{13}C}$ = 0.52, $V_{\delta^{15}N}$ = 0.41), indicating that individuals within thin-toed frogs commonly show sizable diet divergence. However, these mean values are not useful to represent the amount of individual specialization in a given species because we found a high variability across populations of each species (*Figure 2*). For example, we observed some populations of *L. chaquensis* composed by generalist individuals (e.g. V = 0.39; $V_{\delta^{13}C}$ = 0.04; $V_{\delta^{15}N}$ = 0.07) and others by individuals with highly specialized diets (V = 0.87; $V_{\delta^{13}C}$ = 0.66; $V_{\delta^{15}N}$ = 0.62).

### *Spatial synchrony of individual specialization across coexisting species*

We found no consistent directional differences in individual specialization across species. The distribution of the magnitudes of difference in individual specialization between pairs of coexisting species was not different from zero for any pair of species and any metric (*Figure 3*, *Table 1*). Overall, we also observed no correlation in the degrees of trophic variation of coexisting species across communities. We only found a significant correlation of individual specialization (gut contents) for *L. chaquensis* and *L. podicipinus* ($r = 0.71$, $p = 0.05$) (*Table S1*).

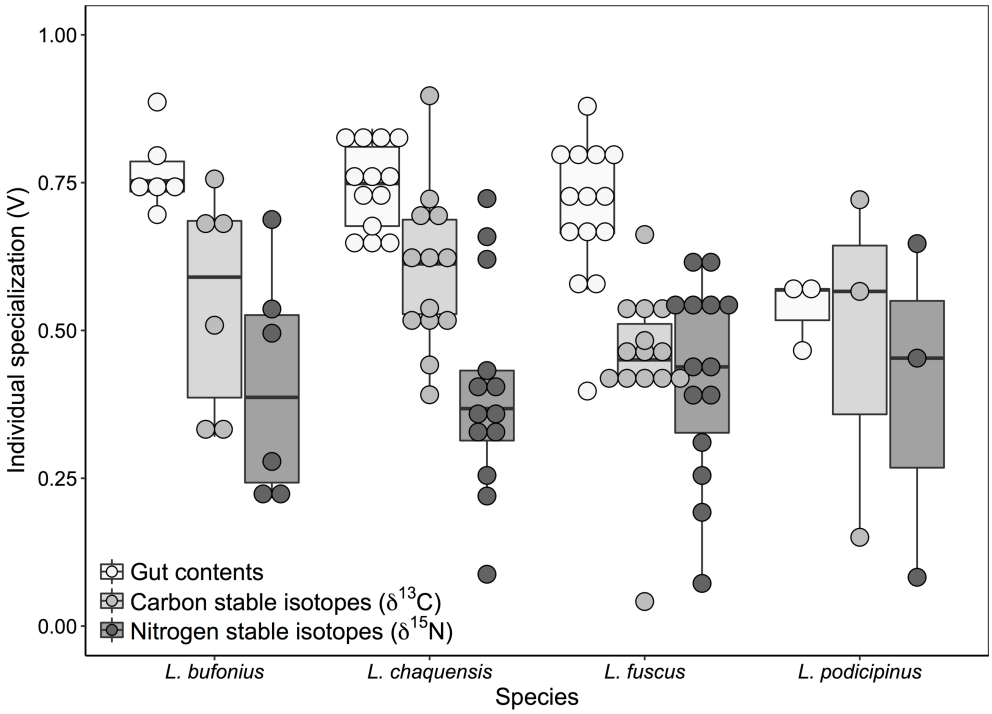



*Figure 2.* Values of individual trophic specialization from populations of four species of thin-toed frogs calculated from gut contents (V) or stable isotopes ($V_{\delta^{13}C}$ and $V_{\delta^{15}N}$). Higher values of V indexes (max = 1) indicate larger trophic divergence among-individuals. Each dot represents a single frog population.

*Table 1.* One-sample t-test results comparing the mean difference in three metrics of individual specialization between pairs of coexisting species with zero (i.e., no difference across species).

| Species pair | V (Gut contents) | | | $V_{\delta^{13}C}$ (Stable isotopes) | | | $V_{\delta^{15}N}$ (stable isotopes) | | |
|---|---|---|---|---|---|---|---|---|---|
| | t | df | p-value | t | df | p-value | t | df | p-value |
| *L. chaquensis* & *L. podicipinus* | -0.34 | 7 | 0.74 | -2.19 | 7 | 0.06 | 1.37 | 7 | 0.21 |
| *L. chaquensis* & *L. fuscus* | -0.35 | 2 | 0.76 | -1.99 | 2 | 0.18 | 0.55 | 2 | 0.64 |
| *L. chaquensis* & *L. bufonius* | -1.98 | 2 | 0.19 | 0.34 | 2 | 0.77 | 0.36 | 2 | 0.75 |
| *L. podicipinus* & *L. fuscus* | -0.72 | 3 | 0.52 | -0.29 | 3 | 0.78 | -1.15 | 3 | 0.33 |

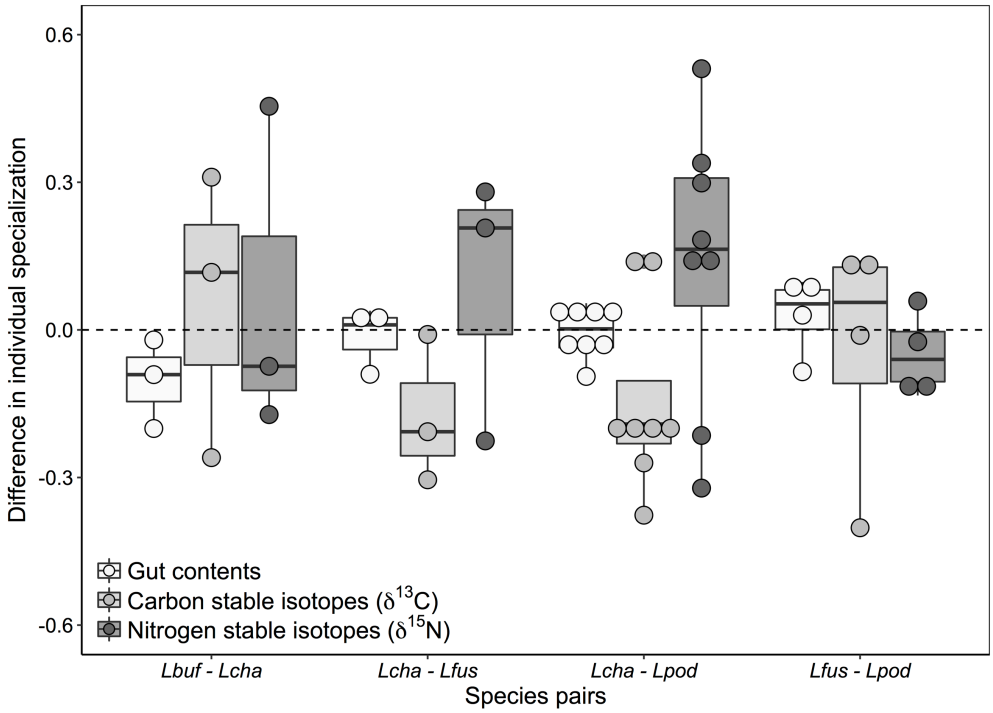



*Figure 3*. Differences in individual trophic specialization across pairs of coexisting thin-toed frog species. Each point corresponds to the magnitude of difference in individual specialization calculated gut contents (V) or stable isotopes ($V_{\delta^{13}C}$ and $V_{\delta^{15}N}$) across two populations of different species that co-occur in a given community. Each dot represents the magnitude of the difference in individual specialization across two coexisting frog populations (not all potential pairwise species combinations occurred). The dashed line represents a scenario where coexisting species have exactly the same degree of individual specialization (i.e., difference in the strength of individual specialization equal to zero).

## *Ecological drivers of individual trophic variation*

For dietary and stable isotope-based metrics of individual specialization, models including fixed effects as quadratic terms presented substantially lower $AIC_c$ values when compared to models with linear terms (V = -58.52 vs. -336.74; $V_{\delta^{13}C}$ = -21.67 vs. -267.49; $V_{\delta^{15}N}$ = -8.42 vs. -47.95), so our inferences are based on quadratic models. Density of conspecifics was a major factor explaining the trophic variation across populations (*Table 2*). Consistent with theory, intraguild predation and effective density of heterospecifics also significantly contributed to explain variation in individual specialization, but diversity of resources had no significant explanatory power (*Table 2*, *Table S2*). Importantly, we observed significant interaction terms of our predictors with species identity, indicating that the effects of these ecological drivers on the degree of individual specialization differ across species (*Table 2*, *Figures*

*4*, *S4*). Generally, responses of individual specialization to the four gradients were similar across metrics for each species (*Figure 4*, *S4*). Overall, results were robust and did not change when we removed extreme points or one species to make sure all species had similar ranges of values for the predictors (*Table S3*).

*Table 2*. Results of mixed-effects linear models investigating how ecological drivers of niche variation (effective density of heterospecifics, density of conspecifics, intraguild predation likelihood, prey diversity, and prey biomass) affect individual specialization (V indexes) in thin-toed frogs (*Leptodactylus* spp.).

| Ecological factor | V (gut contents) | | | $V_{\delta^{13}C}$ (stable isotopes) | | | $V_{\delta^{15}N}$ (stable isotopes) | | |
|---|---|---|---|---|---|---|---|---|---|
| Polynomial models [*poly(x,2)*] | $\chi^2$ | df | p | $\chi^2$ | df | p | $\chi^2$ | df | p |
| Effective density of heterospecifics | 27.18 | 2 | <0.01 | 20.99 | 2 | <0.01 | 7.46 | 2 | 0.02 |
| Density of conspecifics | 4191 | 2 | <0.01 | 6507 | 2 | <0.01 | 300.2 | 2 | <0.01 |
| Intra-guild predation likelihood | 25.57 | 2 | <0.01 | 239.5 | 2 | <0.01 | 68.84 | 2 | <0.01 |
| Prey diversity | 5.15 | 2 | 0.07 | 0.566 | 2 | 0.75 | 4.30 | 2 | 0.12 |
| Prey biomass | 9.08 | 2 | 0.01 | 6.353 | 2 | 0.04 | 1.74 | 2 | 0.42 |
| Species | 62245 | 2 | <0.01 | 3011 | 2 | <0.01 | 2539 | 2 | <0.01 |
| *Interactions* | | | | | | | | | |
| Effective density of heterospecifics*spp | 39.82 | 3 | <0.01 | 37.36 | 3 | <0.01 | 1.48 | 3 | 0.25 |
| Density of conspecifics*spp | 45.97 | 4 | <0.01 | 7.133 | 4 | 0.13 | 4.62 | 4 | 0.33 |
| Intra-guild predation likelihood*spp | 22.35 | 4 | <0.01 | 14.18 | 4 | <0.01 | 5.58 | 4 | 0.23 |
| Prey diversity*spp | 170.3 | 2 | <0.01 | 94.76 | 2 | <0.01 | 63.62 | 2 | <0.01 |

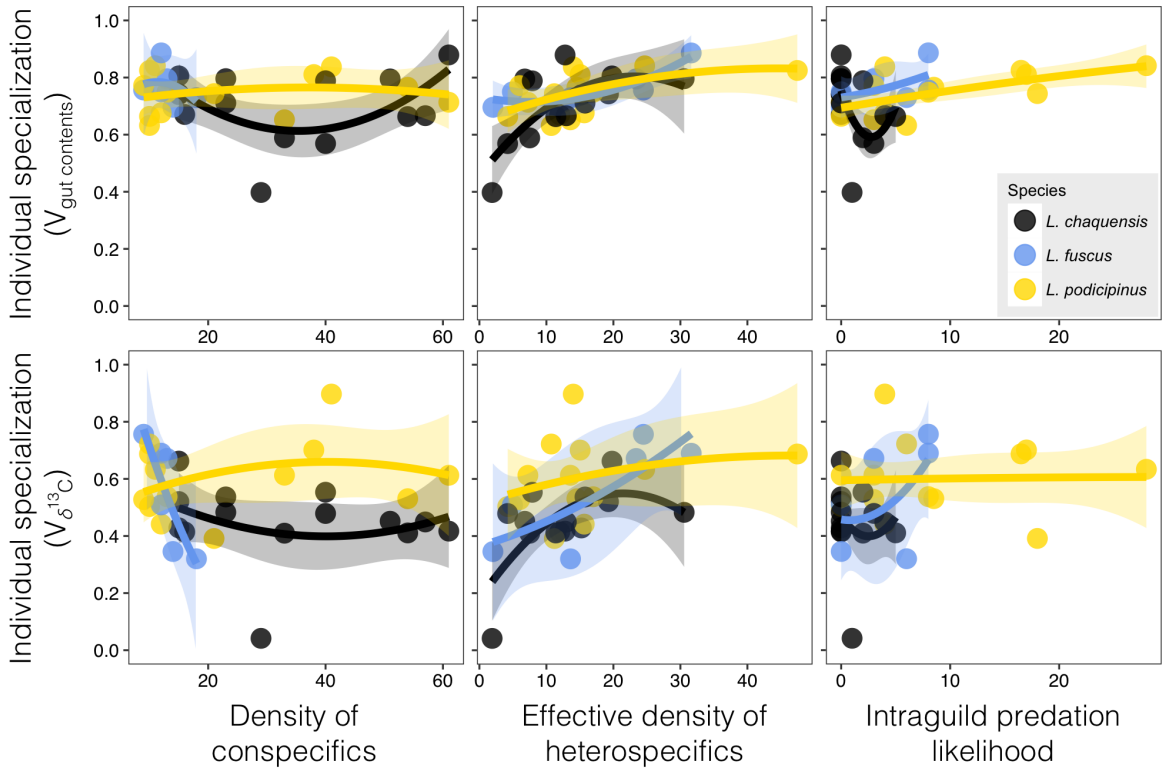



*Figure 4.* Relationships between three significant drivers of individual niche variation and the observed strength of individual diet specialization calculated from dietary data ($V_{gut\ contents}$) and carbon stable isotopes data ($V_{\delta^{13}C}$) across populations and species (represented by different colors) of thin-toed frog species.

## Discussion

One of the tenets of ecological theory is that niche variation in ecological systems is primarily associated with differences between species. Recent studies have challenged this principle by demonstrating substantial variation within species (Bolnick *et al.* 2003; Rudolf *et al.* 2014; Siefert *et al.* 2015), but the primary sources of this variation and its ecological consequences are still unclear. Here we show that individual specialization varied up to nine-fold across populations within the same species. This sizable variation in trophic specialization across populations was at least partially explained by density gradients of competitors (both conspecifics and heterospecifics) and intraguild predation. However, these responses to ecological gradients were highly species-specific. As a consequence, there was typically no correlation in the degree of individual specialization (either calculated from gut contents or stable isotopes) across co-existing species. Our results indicate that individual niche specialization is strongly context-dependent (i.e., flexible along ecological gradients) and that there is no consistent hierarchy of individual variation across species in our system. These results emphasize the need to account

for differences in individual variation across competing species along ecological contexts to understand how this phenomenon affects species coexistence.

### *Ecological drivers of individual trophic variation*

Theory suggests that the magnitude of individual trophic variation should depend on the level of intra- and interspecific competition, ecological opportunity and predation (Araújo, Bolnick & Layman 2011). Our study system allowed us to measure proxies of all these ecological factors and test their simultaneous effects on the degree of individual specialization in coexisting frog species. We found that these factors, particularly intraspecific competition, helped to explain differences in the degree of individual diet specialization across populations in the short (gut contents) and longer terms (stable isotopes). However, our results show that the responses of individual specialization to competition and predation is not the same across coexisting species, the sign of which (positive or negative) depending on species identity. Despite these idiosyncrasies, the observed effects of the four ecological factors on the degree of diet variation partially matched theoretical predictions and previous experimental evidence.

Intraspecific competition has been indicated as a major driver of inter-individual niche differences (Araújo, Bolnick & Layman 2011). Consistent with this prediction we found that density of conspecifics was a significant and the most important predictor of short- and long-term individual specialization. However, in contrast to previous evidence suggesting that intraspecific competition generally favors individual niche variation (Svanbäck & Persson 2004; Svanbäck & Bolnick 2007), we found that it may either increase or decrease individual specialization. These distinct responses can arise from species-specific mechanisms that govern how prey rank preferences differ among individuals (Svanbäck & Bolnick 2005). For example, if individuals within a population differ in their top-ranked prey (e.g., because of foraging trade-offs) low population density results in stronger individual specialization ('distinct preferences model'; Svanbäck & Bolnick 2005), such as the pattern observed for *L. fuscus* (Figs. 4, 5). Alternatively, if consumers share their top-ranked prey, but rank less preferred resources differently, diet variation should increase with intraspecific competition ('refuge model'; Svanbäck & Bolnick 2005). Overall, our results suggest that the nature of the effect of intraspecific competition on the degree of individual specialization in natural populations may be less obvious than commonly assumed (Araújo, Bolnick & Layman 2011).

Surprisingly, the diversity of available resources did not explain variations in the degree

of individual specialization. This contrasts with previous studies revealing an overall positive effect of ecological opportunity on diet variation because higher prey diversity creates more opportunity for individual diet variation by expanding individuals' foraging options (Evangelista *et al.* 2014; Newsome *et al.* 2015; Costa-Pereira *et al.* 2017). This discrepancy may simply arise because thin-toed frogs are generalists which consume a wide variety of species. Since communities always harbored a large richness of prey types in our system (> 14 invertebrate families), it is very likely that ecological opportunity was never constrained enough to refrain individual diets from diverging. Systems where consumers experience a clearer gradient of prey diversity may still show a positive relationship with prey diversity, but our results suggest that ecological opportunity may not be biologically important in generalist species in diverse communities. However, because our proxy for ecological opportunity is a "snapshot" of the diversity of available prey for frogs, we acknowledge that the lack of a relationship between individual variation and diversity of resources might also be driven by fluctuations in diversity of available resources over time that were not captured by our sampling method.

The observed species-specific effects of intraguild predation on the strength of individual specialization might be explained by its complex effects on population and individual niches. Predation can affect diet specialization indirectly via density-mediated effects and/or directly by altering prey foraging activity. A number of studies show that predators can drastically reduce foraging activity and habitat use on prey populations (Werner *et al.* 1983; Lima 1998). Importantly, these non-lethal predation effects can differ across coexisting species (Walls, Taylor & Wilson 2002; Pearl *et al.* 2003). Thus, predation might constrain, to a higher or lower degree, individuals to forage in restricted areas, affecting the strength of individual specialization if resources are patchy on the landscape (Araújo, Bolnick & Layman 2011). For example, conspecific individuals vary in their boldness (i.e. propensity to forage in the presence of risk) in a diverse range of taxa (Toscano *et al.* 2016). Similar behavioral variation could promote individual diet variation in the presence of predation in our system. In this case, shy individuals should forage in safer refuges while bold individuals in more risky areas, potentially increasing diet divergence (Araújo, Bolnick & Layman 2011). The relation between individual-level variations in animal personality and diet is a promising subject to future studies aiming to understand the causes and consequences of individual niche variation within wild populations and across coexisting species (Pruitt & Modlmeier 2015; Toscano *et al.* 2016).

The effect of interspecific competition on individual specialization remains controversial both in the theoretical and empirical literature (Bolnick *et al.* 2010; Araújo, Bolnick & Layman 2011; Cloyed & Eason 2016). In general, we found that increases in the effective population sizes of heterospecifics led to an increase in the degree of individual trophic differences, but to varying degrees across frog species (Figs. 4). This pattern is opposite to predictions of the long-standing niche variation hypothesis (Van Valen 1965). According to this hypothesis, higher interspecific competition tends to deprive populations of certain resources, constraining individual variation (Bolnick *et al.* 2007). In this case, release from interspecific competition increases population (but not individual) niche widths via increased among-individual variation. We tested a posteriori this hypothesis by modeling the population total niche width (TNW, Roughgarden 1972) as a function of the effective density of heterospecifics and species identity (fixed effects, site included as a random effect), but we found no significant relationship (GLMM, $\chi^2 = 0.08$, $p = 0.76$). However, we did detect a significant reduction in the within-individual niche component (WIC) as the effective density of conspecifics increased (GLMM, $\chi^2 = 3.74$, $p = 0.05$) (parallel release, Bolnick *et al.* 2010). Altogether, these results suggest that interspecific competition does not necessarily lead to population niche packing as assumed by classic niche theory (Van Valen 1965; Taper & Case 1985), but can actually result in individual niche contraction. This mismatch between population and individual niche responses indicates that release from interspecific competition might not lead to the inclusion of novel prey in a population's diet, but can cause individuals to become more specialized in their diets, decreasing niche overlap with other conspecifics (Bolnick *et al.* 2010).

### *Magnitude of individual variation in coexisting species*

Theory indicates that differences in the amount of individual variation across coexisting species can determine the outcome of competitive interactions. Specifically, it predicts that individual variation makes species coexistence less feasible in most cases because it usually reinforces competitive hierarchies. However, under the specific case of higher variation within the weak competitor, coexistence can be favored (Barabás & D'Andrea 2016; Hart, Schreiber & Levine 2016). Thus, differences in individual specialization between coexisting species should play a key role in determining the outcome of species interactions and long-term coexistence. Our results show that individual trophic specialization inferred from different temporal scales

(hours for gut contents; weeks for liver stable isotopes) and functional dimensions (prey types for dietary and $\delta^{13}C$ data; trophic level for $\delta^{15}N$) can differ considerably even between closely related and ecologically similar co-occurring species in natural communities. However, we also found that the degree of trophic specialization was highly variable across wild populations of the same species (for both gut content and stable isotopes-based metrics), and this variation was typically not correlated across species across sites. As a consequence, differences in individual specialization between coexisting species were context dependent and varied across communities. As a consequence, the identity of the species with more individual variation changed among sites for various species pairs. For example, in some communities, *L. chaquensis* presented a substantially higher degree of diet variation than *L. podicipinus*, but in other communities the scenario was the opposite.

This pattern could at least partially be explained by the observed species-specific responses to how intraspecific variation scales with different ecological gradients. For instance, our results suggest that long term individual specialization in *L. fuscus* has a strong negative response to density of conspecifics across populations, while the strength of individual variation in *L. chaquensis* is more driven by the density of heterospecifics (Figure 4). Thus, different combinations of these ecological drivers across communities could lead to shifts in relative individual specialization between coexisting species. These idiosyncratic responses might affect, ultimately, how species interact across communities. For example, if individual niche variation increases more sharply in weaker than in stronger competitors along an ecological gradient, the chance of coexistence might increase as well along this gradient. Thus, the high context-dependency of individual variation across populations and species has the potential to impact stabilizing niche differences and competitive asymmetries.

Regardless of the specific underlying mechanisms, our results indicate that species differ in their degree of individual specialization across different ecological contexts. This pattern has several important implications. First, it indicates that we cannot assume a constant amount of individual variation within competing species in natural communities. Second, it suggests that this pattern might play an important role in species coexistence at the landscape level because it creates a mosaic of diverse competitive interactions across sites, in which species might be superior competitors in some areas but inferior competitors in others. This mechanism is not considered in current metacommunity models but could potentially provide a novel and unexplored mechanism that favors or inhibits species coexistence. New empirical and

theoretical models that measure and implement this variation could provide insight into how variation within populations is linked to regional community patterns.

### *Conclusions*

Resolving the causes and consequences of individual niche variation in natural communities is of key importance for understanding the structure and dynamics of populations and communities and ultimately the maintenance of biological diversity (Bolnick *et al.* 2011; Barabás & D'Andrea 2016; Hart, Schreiber & Levine 2016). Our study elucidates important aspects of individual variation in similar coexisting species that can contribute to more realistic models. While our results support some predictions of current theory, they also provide novel insights into how individual variation differs across and within coexisting species. Our findings indicate that individual variation in natural communities could play an important role not only in species coexistence at local communities, as assumed by current theory, but also in the organization of regional diversity patterns.

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## Supplementary Information

*Simulations to quantify individual specialization from stable isotopes*

We used VarIso 1.0 to generate an expected relationship between V and the variance of isotopic signatures among individuals of each population (Araújo *et al.* 2007). The parameters used by the program are the population niche (proportions of the different resources in the population diet), number of individuals sampled, and the isotopic composition of each prey type and average dry mass of the resources consumed. Briefly, for a population composed of $N$ individuals, each individual was given $s$ random draws (with replacement) from a multinomial probability distribution formed by the proportions of different resources in the empirical population niche, $q$. Vectors $p_i$ representing the niches of each individual were then calculated, after which V was calculated. For a set of $n$ replicate populations (we used 5,700), $s$ changed from 1 to 1,000 in successive increments. When $s$ is 1 (individuals are given one single draw), individuals specialize on one single resource, e.g. $p_i$ = (1.0, 0, 0, …, 0). Since different individuals will eventually draw different resources from the population niche $q$, $s$ = 1 yields maximum variation among individuals. As $s$ increases, individuals' vectors $p_i$ converges towards $q$ (Law of Large Numbers) and within-population niche variation declines. This procedure was aimed at creating a relationship between V and the isotopic variance that spanned the whole range of within-population niche variation.

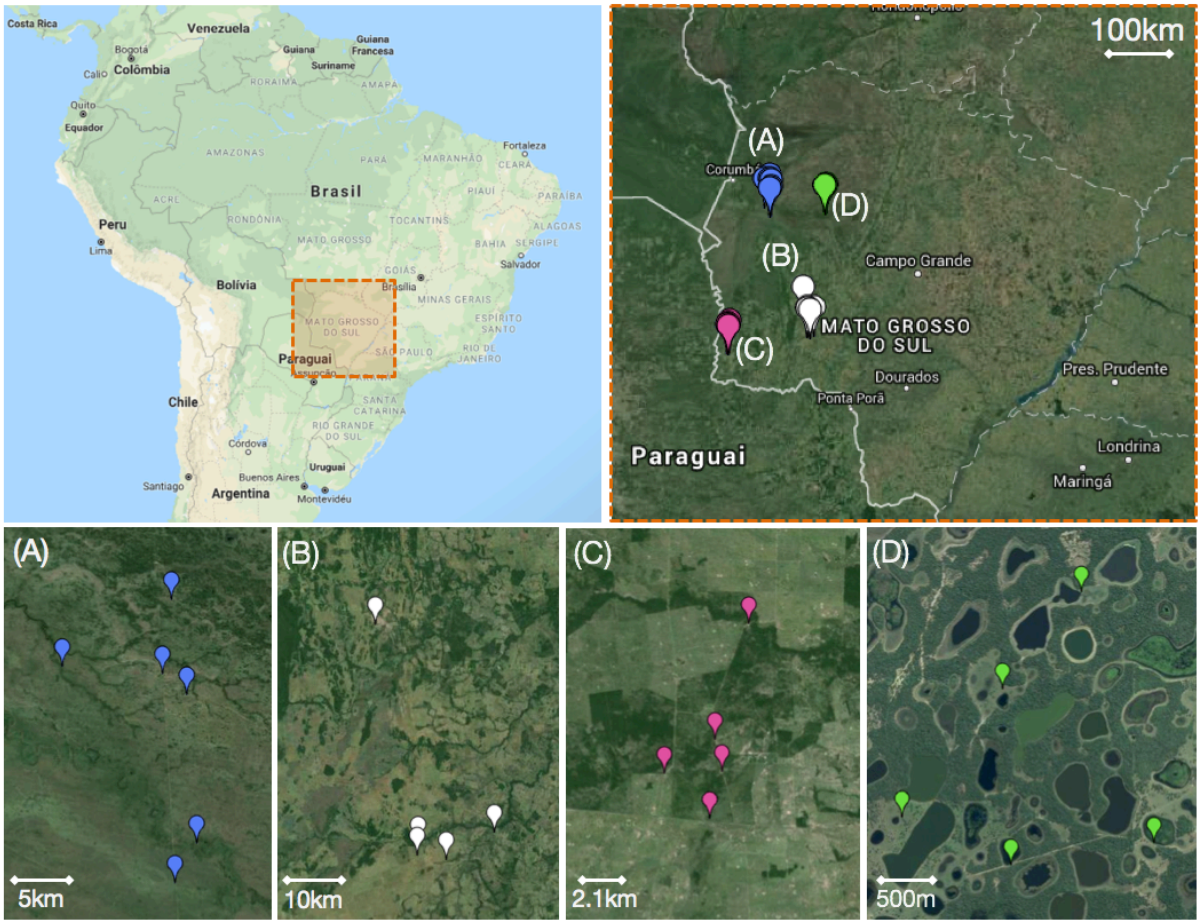



*Figure S1.* Location of the four studied geographic areas in central Brazil and the respective sampled lagoons in each area: Base de Estudos do Pantanal (A), Bodoquena Plateau (B), Gran Chaco (C), and Fazenda Barranco Alto (D). Images from Google Earth.

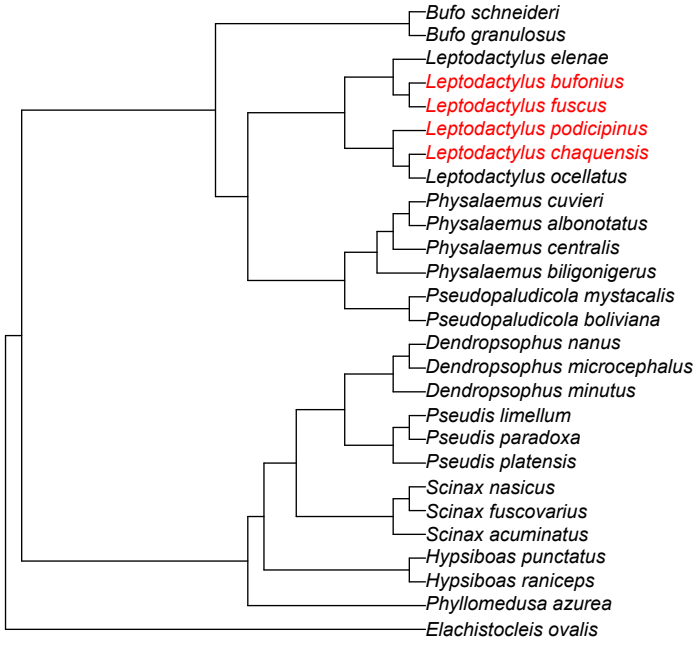



*Figure S2.* Cladogram of the anuran species found in the 21 sampled communities based on the time-calibrated tree proposed by Pyron and Wiens (2011).

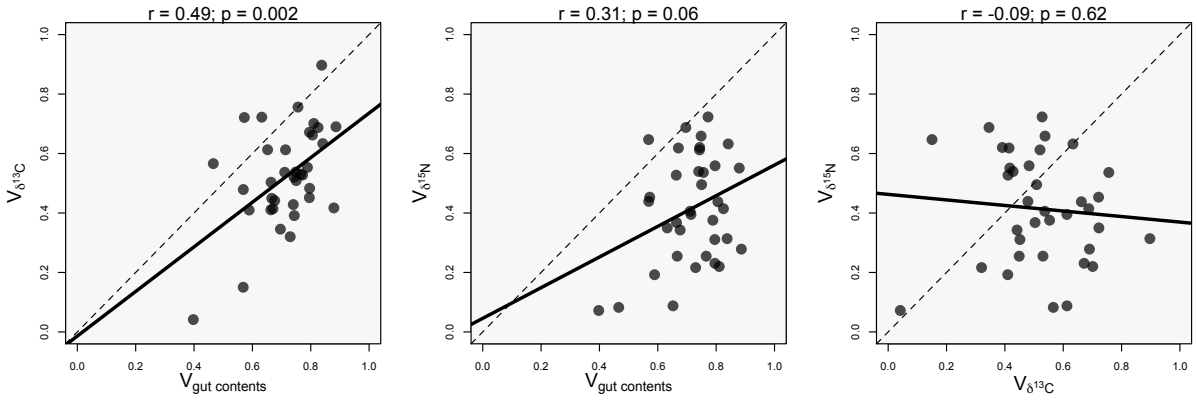



*Figure S3*. Correlation between gut contents ($V_{gut\ contents}$) *vs.* stable isotopes-based ($V_{\delta^{13}C}$ and $V_{\delta^{15}N}$) metrics of individual specialization for populations of thin-toed frogs. V indexes may vary between 0 (individuals extremely generalist) and 1 (individuals extremely specialists). Dashed line corresponds to the 1:1 relationship; solid black line represents the linear relationship between these two metrics.

*Table S1.* Correlations between indexes of individual specialization for each pair of coexisting *Leptodactylus* species across communities. Lower-diagonal values indicate r-values (Pearson correlation) and upper-diagonal indicate p-values for each pair of species.

| V (gut contents) | *L. chaquensis* | *L. fuscus* | *L. podicipinus* | *L. bufonius* |
|---|---|---|---|---|
| *L. chaquensis* | | 0.91 | 0.05 | 0.66 |
| *L. fuscus* | -0.15 | | 0.48 | - |
| *L. podicipinus* | 0.71 | 0.52 | | - |
| *L. bufonius* | -0.5 | - | - | |

| $V_{\delta^{13}C}$ | *L. chaquensis* | *L. fuscus* | *L. podicipinus* | *L. bufonius* |
|---|---|---|---|---|
| *L. chaquensis* | | 0.45 | 0.52 | 0.82 |
| *L. fuscus* | -0.76 | | 0.47 | - |
| *L. podicipinus* | -0.27 | 0.52 | | - |
| *L. bufonius* | 0.27 | - | - | |

| $V_{\delta^{15}N}$ | *L. chaquensis* | *L. fuscus* | *L. podicipinus* | *L. bufonius* |
|---|---|---|---|---|
| *L. chaquensis* | | 0.42 | 0.12 | 0.98 |
| *L. fuscus* | -0.79 | | 0.28 | - |
| *L. podicipinus* | -0.59 | 0.72 | | - |
| *L. bufonius* | 0.01 | - | - | |

*Figure S4.* Relationships between three drivers of individual niche variation and the observed strength of individual diet specialization calculated from nitrogen stable isotopes ($V_{\delta^{15}N}$) across populations and species (represented by different colors) of thin-toed frog species.

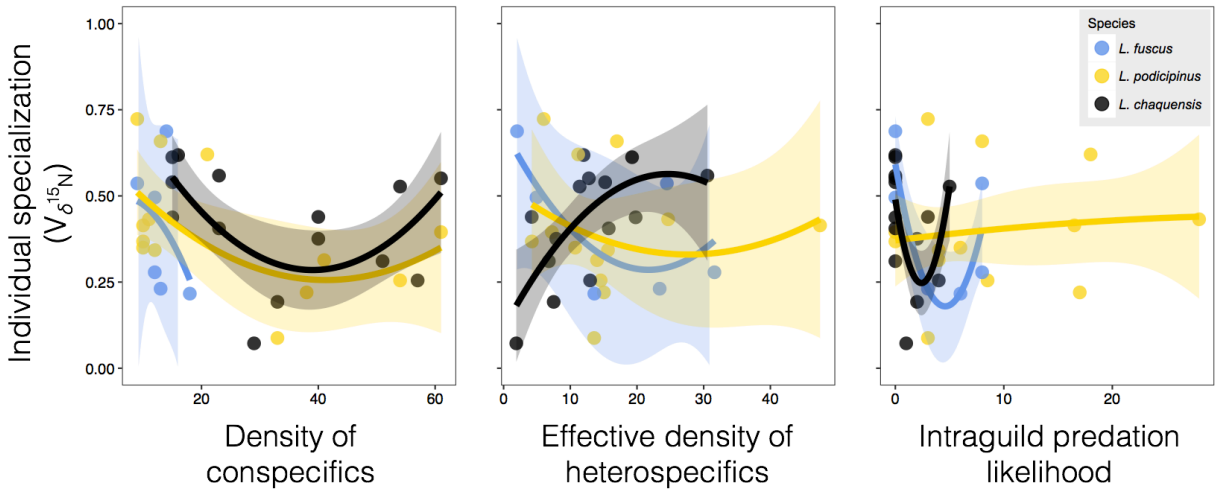



*Table S2.* Output of mixed models investigating the effect of ecological factors on different metrics of individual specialization in populations of thin-toed frog species.

| Ecological factor | V index (Gut contents) | | $V_{\delta^{13}C}$ (Stable isotopes) | | $V_{\delta^{15}N}$ (Stable isotopes) | |
|---|---|---|---|---|---|---|
| | Estimate | SE | Estimate | SE | Estimate | SE |
| Intra-guild predation likelihood | -14.9739 | 5.4907 | -22.909 | 12.4955 | -14.827 | 13.53 |
| Density of conspecifics | 0.41971 | 0.28677 | 0.7687 | 0.6526 | 1.0051 | 0.7067 |
| Effective density of heterospecifics | -1.03302 | 0.25481 | -1.7838 | 0.5799 | -0.2975 | 0.6279 |
| Prey diversity | 0.53131 | 0.18292 | 1.1264 | 0.4163 | 0.7419 | 0.4512 |
| Prey biomass | 0.34409 | 0.12667 | 0.4888 | 0.2883 | 0.3259 | 0.3122 |
| Random effect | | | | | | |
| Site | -1.56318 | 1.74 | -2.67 | 1.7476 | 0.0199 | 0.1412 |

*Table S3.* As differences in the range of predictors can influence the result of interaction term with species identity, we fit additional models removing specific point(s) or species in order to make all species have a similar range of a giving predictor. Below are the issues related to differences in range across species, the proposed solution and the updated result.

| Predictor | Range issue | Solution | Updated result | | | Qualitative change the results? |
|---|---|---|---|---|---|---|
| | | | Term | $\chi^2$ | p | |
| Density of conspecifics | *L. fuscus* has a clearly shorter range of values. This suggests that this species occurs naturally in lower densities. | Remove *L. fuscus* | Density of conspecifics | 428.29 | <0.01 | No |
| | | | Density of conspecifics * spp | 12.32 | <0.01 | No |
| Effective density of heterospecifics | *L. podicipinus* has one population with a higher value (out of the range of *L. fuscus* and L. *chaquensis*) | Remove this population | Effective density of heterospecifics | 27.59 | <0.01 | No |
| | | | Effective density of heterospecifics * spp | 2.18 | 0.53 | Yes |
| Intraguild Predation likelihood | *L. podicipinus* have four populations with values higher than the observed for the other species | Remove these populations | Predation likelihood | 13.16 | <0.01 | No |
| | | | Predation likelihood * spp | 25.77 | <0.01 | No |

# Capítulo 2

# Prey limitation drives variation in allometric scaling of predator-prey interactions

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## Abstract

Ecologists have long searched for a universal size-scaling constant that governs trophic interactions. Although this is an appealing theoretical concept, Predator-Prey Size Ratios (PPSR) vary strikingly across and within natural food webs, meaning that predators deviate from their optimal prey size by consuming relatively larger or smaller prey. Here, we suggest that this unexpected variation in allometric scaling of trophic interactions can be predicted by gradients of prey limitation consistent with predictions from Optimal Foraging Theory. We analyzed >6,000 trophic interactions of 52 populations from four tropical frog species along a gradient of prey limitation. The mean of PPSR and its variance differed up to two orders of magnitude across and within food webs. Importantly, as prey availability decreased across food webs, PPSR and its variance became more size-dependent. Thus, trophic interactions did not follow a fixed allometric scaling but changed predictably with the strength of prey limitation. Our results emphasize the importance of ecological contexts in arranging food webs and the need to incorporate ecological drivers of PPSR and its variance in food web and community models.

*Keywords*: food web, predator-prey size ratio, predator-prey mass ratio, trophic interactions, prey availability, size scaling.

## Resumo

Ecólogos têm buscado há muito tempo uma constante alométrica universal que governe relações tróficas. Embora esse seja um conceito teórico atraente, razões de tamanho predador-presa (PPSR) variam amplamente entre e dentro de teias tróficas naturais, o que indica que predadores desviam de seus tamanhos ótimos de presa consumindo recursos relativamente maiores ou menores. Aqui, nós sugerimos que essa inesperada variação alométrica em interações tróficas pode ser predita por gradientes de limitação de presas, o que seria consistente com a Teoria do Forrageamento Ótimo. Nós analisamos >6.000 interações tróficas em 52 populações de quatro espécies de rãs tropicais ao longo de um gradiente de limitação de presas. A PPSR média e sua variância diferiram até duas ordens de magnitude entre e dentro das teias tróficas. Particularmente, conforme a disponibilidade de presas diminuiu nas teias tróficas, a PPSR e sua variância se tornaram mais dependentes do tamanho corpóreo dos predadores. Desse modo, interações tróficas não seguem uma constante alométrica fixa, mas variam previsivelmente de acordo com a magnitude da limitação de presas. Nossos resultados enfatizam a importância de diferentes contextos ecológicos no arranjo de teias tróficas e a necessidade de incorporar os mecanismos ecológicos que afetam a PPSR e sua variância em modelos de teias tróficas e comunidades.

*Palavras-chave*: food web, predator-prey size ratio, predator-prey mass ratio, trophic interactions, prey availability, size scaling.

## Introduction

The structure and functioning of biological communities strongly depends on the distribution and characteristics of trophic links connecting predators and their prey in complex ecological networks (Paine 1966; Estes *et al.* 2011). One of the most striking patterns of predator-prey interactions is that they are inherently size-structured (Emerson, Greene & Charnov 1994). Indeed, the allometric scaling of predator-prey size relationships is one of the pillars of food web and metabolic theories (Brose, Williams & Martinez 2006; Petchey & Dunne 2012; Kalinkat *et al.* 2013), and plays a key role in determining the stability and dynamics of natural food webs (Emmerson & Raffaelli 2004; Otto, Rall & Brose 2007). However, identifying the general laws which govern the size-scaling of predator-prey interactions has troubled ecologists for decades (Hatton *et al.* 2015).

An important concept to predict predator-prey interactions is the predator-prey size ratio (PPSR) which describes the relative size-differences between predators and their prey. Theory predicts a preferred, intermediate optimal predator-prey size ratio that maximizes energetic intake and interaction strength (Wootton & Emmerson 2005; Petchey *et al.* 2008; Brose 2010; Kalinkat *et al.* 2013). While the concept of a preferred predator prey mass ratio is appealing, its application to food web theory is still problematic. For instance, current size-structured food web models and size-spectra community models assume a universal constant predator-prey size ratio that can be applied to all predators (*Figure 1*a, right). (Andersen & Beyer 2006; Petchey *et al.* 2008; Blanchard *et al.* 2009; Hartvig, Andersen & Beyer 2011). This contrasts with empirical studies demonstrating that predator-prey size ratios are (*i*) highly variable across food webs (Brose *et al.* 2006; Barnes *et al.* 2010) and (*ii*) can change with predator body size within food webs (i.e. size-dependent predator-prey size ratios) (Brose *et al.* 2006; Barnes *et al.* 2010; Nakazawa, Ushio & Kondoh 2011; Nakazawa 2017). Specifically, in natural food webs predator-prey size ratios tend to increase towards large-bodied predators, i.e. large predators consume proportionally smaller prey (*Figure 1*a, left) (Barnes *et al.* 2010; Nakazawa, Ushio & Kondoh 2011; Nakazawa, Ohba & Ushio 2013). This discrepancy between the theoretical concept of a universal size-scaling constant *vs.* the natural variation in empirical systems suggests that we are likely missing key mechanisms that also play an important role in shaping predator-prey allometries (Tsai, Hsieh & Nakazawa 2016; Nakazawa 2017).

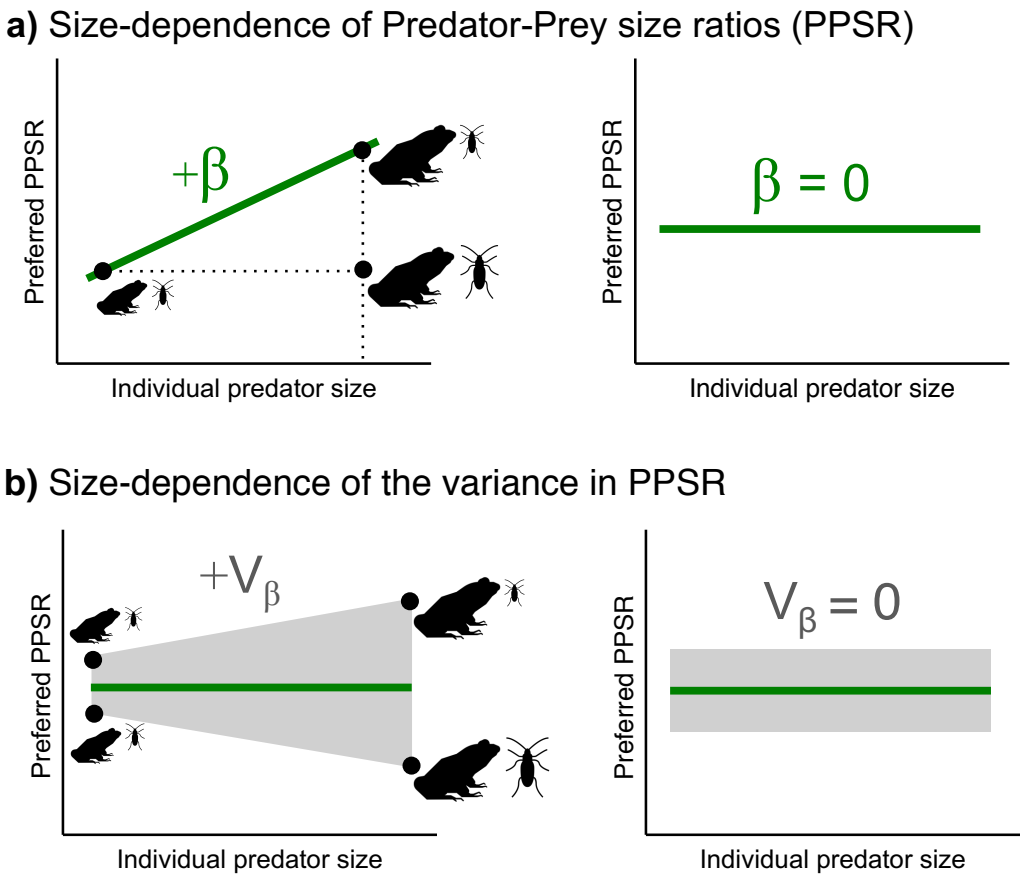



*Figure 1.* Schematic view of how preferred Predator-Prey Size Ratios (PPSR) and its variance can change within a given food web. As commonly assumed by food web theory, predator-prey size ratios are invariant (*a*, right panel). Alternatively, empirical studies have found that commonly large predators tend to consume on average proportionally smaller prey, leading to a size-dependent PPSR (*a*, left panel). Regarding the variance in PPSR (*b*), food web theory implicitly assumes that the variance in PPSR is negligible and constant across large and small predators (*b*, right panel). If the variance around the but the average PPSR may scale with predator body size (*b*, left panel) if large and small-sized predators differ in their degree of variation in foraging decisions regarding prey size.

Here we suggest that the much of the variation in predator-prey size ratios likely stems from ecological factors restricting optimal foraging via prey availability. Theory predicting a single size-ratio typically makes the implicit assumption that prey availability is unrestricted and constant across ecological scenarios (Nakazawa 2017). However, differences in environmental conditions across food webs, e.g. variation in productivity, food web configuration, or density of competitors, can limit the abundance of ideal prey size forcing predators to deviate from their optimal prey size ratio. Thus, the natural variation in size-ratios might simply reflect the difference between optimal *vs.* realized prey preference under sub-optimal availability (Tsai,

Hsieh & Nakazawa 2016; Nakazawa 2017). Specifically, factors that increase prey limitation should force predators to include relatively smaller less-profitable prey in the diet (Griffiths 1980; Barnard & Brown 1981; Nakazawa, Ushio & Kondoh 2011). Overall, this suggests that predator-prey size ratios should vary predictably across communities with ecological factors that drive prey availability, but this hypothesis remains untested.

Furthermore, environmental availability of prey is not homogeneous to all consumers within food webs or even within a consumer species. Larger predators have inherently a broader size range of potential prey (Wilson 1975; Wheelwright 1985; Karpouzi & Stergiou 2003). Thus, the actual availability of prey for a given predator tends to increase with its body and gape sizes and this difference could lead to size-dependent predator-prey ratios. Importantly, as the availability of potential resources depends on predator's body size (due to gape limitation, *Figure 2*), prey size selection by small- and large-sized predators could respond differently across ecological contexts, which may constitute an underlying driver of the variation of size-dependence of predator-prey size ratios commonly observed in natural food webs (Barnes *et al.* 2010; Nakazawa, Ushio & Kondoh 2011).



*Figure 2.* Gape constrained predators, such as thin-toed frogs, only can eat what fits in their mouth. Thus, the availability of potential resources depends on predator's gape size.

The same mechanisms altering the average scaling of predator-prey interactions should also change their variance around that average. Importantly, the variance in predator-prey size ratios provides an indication of the consistency of foraging decisions by predators within food webs, which has the potential to affect the stability of biological communities (Kalinkat *et al.* 2013). Therefore, ecological factors limiting prey availability might constrain the access to optimal prey size, leading to increased variance in size selection patterns. This effect should be stronger for large-sized predators within food webs because of their larger scope for diet variation (i.e. wider range of potential prey sizes), suggesting that the variance in size ratio might also scale predictably with consumer body size in natural food webs (*Figure 1*b, left). However, this hypothesis remains untested because previous studies focused solely on the average predator-prey size ratios of whole food webs, species or size classes, implicitly assuming that variations in scaling patterns are negligible and size-invariant (*Figure 1*a). Yet identifying whether and how variation in predator prey size ratios changes across predator sizes and ecological contexts is essential to develop more realistic and accurate food web models.

Here, we analyzed predator-prey size patterns across tropical food webs to understand how prey limitation affects the allometric scaling of trophic interactions. Specifically, we quantified prey availability and predator diets of all size classes of four congeneric amphibian predators across 52 populations to test the hypotheses that (*a*) average predator-prey size ratios and (*b*) variation around that mean should differ predictably across food webs and predator size. We predicted that food webs under low prey availability (i.e. low biomass of prey and high densities of conspecifics and heterospecifics) should present stronger size-dependence of average predator-prey size ratios (positive relationship between predator body size and average PPSR). Accordingly, we also expect that resource limitation leads to a positive scale of the variance in size ratios with predator body size.

## Methods

### *Study system*

To examine the ecological drivers of predator-prey size scaling relationships we analyzed trophic interactions in four congeneric Thin toed frog species (*Leptodactylus bufonius*, *L. chaquensis*, *L. fuscus*, and *L. podicipinus*) in tropical lowland ponds. This is a suitable system for studying predator-prey interactions because Thin toed frogs vary largely in size within species

and are trophic generalists, consuming a wide range of prey sizes (from tiny invertebrates to vertebrates) (Piatti & Souza 2011; Costa-Pereira *et al.* 2015). Moreover, these species are highly abundant in tropical communities and forage intensively at night during the summer, allowing us to recover a relatively large number of consumed prey (i.e., foraging events) from gut contents. Finally, frogs swallow their prey whole, enabling us to obtain direct and thus accurate measures of prey size from gut content data.

*Data collection*

In the summer of 2014 we sampled 52 populations of Thin toed frogs in an area covering ~ 400 km$^2$ of the Pantanal wetlands, central Brazil. Anurans were hand-collected in six 10 x 10 m plots (standard collection effort of 1h/people/100m$^2$). After the anuran survey, *Leptodactylus* spp. individuals were euthanized with an overdose of analgesic (lidocaine) and then kept in a -20°C freezer. Individuals from other species were identified and released in the same night of sampling. We collected locally available prey to each frog population using pitfall and light traps (see Supporting Information for details on data collection).

We quantified predator body-size by measuring the snout-vent length (SVL) and body mass of each individual predator using a digital caliper (0.01 mm) and a precision scale (0.001 g) respectively. Predator length and mass ranged between 22.51 - 95.11 mm and 0.97 - 69.95 g, respectively. We obtained prey size measurements for each predator by dissecting frogs to retrieve gut and analyze its contents (both stomach and intestine) under a stereomicroscope. We identified, counted and measured body size of all prey items found in gut contents. As frogs swallow their prey whole, most prey were found intact in the guts. For partly digested prey or body parts, we estimated body size using a reference collection from our environment samples. Highly digested prey were not considered in our analyses (1.73% of prey). To quantify resource availability in the environment, we counted, identified and measured all prey collected from the field. We estimated the mass of each prey from length measurements using length-mass relationships generated from our environmental samples or literature (Sabo, Bastow & Power 2002; Wardhaugh 2013). Overall, our individual-level data set includes 974 predator individuals, 6,172 observed trophic interactions, and 9,470 prey individuals available in the environment.

### *A novel approach to calculate Predator-Prey Size Ratios (PPSR)*

The vast majority of previous studies calculates Predator-Prey Size Ratios (hereafter, PPSR) from gut contents or foraging observations (i.e. dietary data). However, using only observed trophic interactions to obtain PPSR implicitly assumes that prey size composition in the environment does not affect prey selectivity by predators, which is an unreasonable assumption in natural food webs (Tsai, Hsieh & Nakazawa 2016; Nakazawa 2017). For example, if relatively large prey types are absent in a given site, realized PPSR tends to be large not because predators are actively selecting smaller prey, but because the local food availability constrains their foraging options.

To work around this problem, Tsai, Hsieh and Nakazawa (2016) proposed a method for quantifying Preferred PPSR that accounts for how changes in environmental prey size distributions can affect relative prey size in predator diets. By comparing the magnitudes of realized PPSR (from gut contents) *vs.* environmental PPSR (prey availability), it is possible to assess preferred PPSR. Deviations between realized and environmental PPSRs would indicate variation in relative prey size preference not associated with differences in environmental prey availability across food webs (Tsai, Hsieh & Nakazawa 2016). While this approach provides a more realistic measure of PPSR, it still assumes that the environmental availability of prey is equal to all predators. However, this is unlikely to hold true if there is enough body size variation across predators (e.g. ontogenetic variation, interspecific size differences) and across prey types. For example, small predators may not be physically able to consume the largest prey of a larger predator (*Figure 2*). Thus, even though the prey is technically "available" for both, it would be unreasonable to assume that the set of prey choices (i.e., environmental prey availability) is identical for the small- and a large-sized predator.

Our method aims to overcome this shortcoming by incorporating gape limitation at the individual level in the calculation of preferred PPSR. As measures of body size we considered length (mm) or mass (mg). However, because results for length- and mass-based metrics of PPSR were qualitatively the same, we describe only the results for the length-based metric because we directly measured length in predator and prey. The first step was to determine the relationship between predator body size and maximum prey size. Thus, we obtained the upper boundary of the feeding range by fitting the 95% quantile regression between log10 (Predator body size) and log10 (Prey size) across all species (results per species were quantitatively similar) (Gravel *et al.* 2013). Using this allometric scaling model (intercept = 1.127, $\beta = 0.641$, length

data, *Figure 3*), we estimated the respective maximum size of a potential prey for each individual predator. We used this critical maximum prey size to restrict the size distribution of total local prey available, obtaining for each individual predator an actual size distribution of available prey (*Figure 3*). Then, we calculated the Environmental PPSR$_i$ (Tsai, Hsieh & Nakazawa 2016) for each individual predator $i$ by dividing $S_i$ (body size of individual predator $i$) by $m_i$ (median of the truncated size distribution of locally available prey). In turn, Realized PPSR$_i$ was calculated by dividing $S_i$ by $s_j$ (body size of individual prey $j$). As proposed by Tsai, Hsieh and Nakazawa (2016), Preferred PPSR$_i$ is then obtained by subtracting $\log_{10}$(Realized PPSR$_i$) from $\log_{10}$(Environmental PPSR$_i$) (see details in Supporting Information). Our metric of preferred PPSR$_i$ that incorporates gape limitation was well correlated with Tsai, Hsieh and Nakazawa (2016)'s metric ($r = 0.85$, $p < 0.001$), but for many individuals, particularly small-bodied predators, our metric resulted in remarkably lower estimated values of PPSR$_i$ (*Figure S3*).

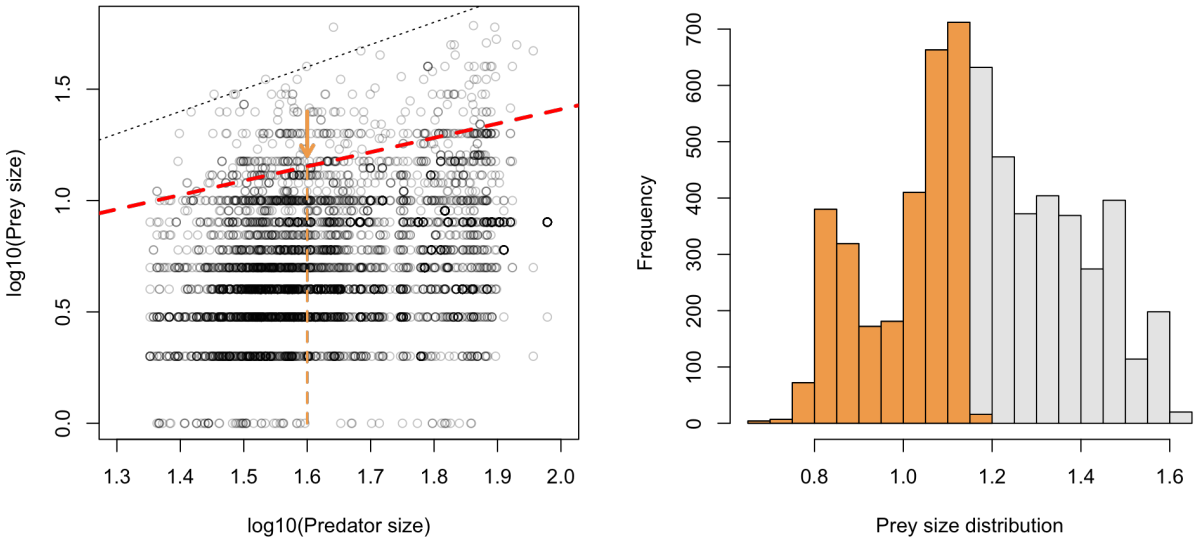



*Figure 3*. How to incorporate gape limitation in estimates of Predator Prey Size Ratios (PPSR)? The first step is to determine the maximum prey size for a predator given its body size. The model describing the upper boundary of the feeding range (95% quantile regression) for Thin toed (*Leptodactylus* spp.) frogs is represented by the red dashed line (left panel). Each point represents one realized trophic interaction and the back dotted line represents the 1:1 relationship between predator and prey body sizes. Then, for a given predator body size (e.g., log10[predator size] = 1.6, *orange dashed line*) it is possible to estimate its respective maximum prey size (*orange arrow*, left panel). Using this critical maximum prey size, it is possible to obtain an actual size distribution of available prey (orange bars, right panel) by restricting the total size distribution of local prey available. Black dotted line (left panel) indicates the 1:1 relationship.

### *Size-dependence of Predator-Prey Size Ratio*

For each studied population, we tested when and how PPSR varies with predator size using linear mixed models (normal error distribution), with Preferred $PPSR_i$ as response variable, the size of a predator individual as fixed effect, and the individual identity as random effect (package 'lme4', Bates *et al.* 2014). We used the resulting fixed coefficient (and respective standard error) as a metric of size-dependence for each frog population. When $\beta = 0$, $PPSR_i$ is size independent, while $\beta > 0$ or $\beta < 0$ would indicate that $PPSR_i$ is size dependent, with larger individuals including proportionally smaller or larger prey in their diets respectively (*Figure 1*a). For this and the following analyses, we only considered populations with more than 10 individuals and with a range of predator body size higher than 12 mm (total size range: 22.51 - 95.11 mm), which is sufficient to result in differences in gape size and prey consumption across predators (RC-P personal observation).

### *Variance in the size-dependence of Predator-Prey Size ratio*

To elucidate how the variance in $PPSR_i$ scales with predator body sizes (*Figure 1*b), we calculated a metric based on successive quantile regressions that quantifies how differences in foraging decisions vary within a given predator size. Quantile regressions allow one to estimate multiple rates of change (slopes) between variables for all portions of a distribution of the response variable (Cade & Noon 2003). We can use this technique to fit regression curves to different parts of the distribution of observed $PPSR_i$. If all individual predators exhibit exactly the same $PPSR_i$, successive quantile regressions (e.g. 5%, 50% and 100%) result in models with very similar slopes (β). However, as individual predators begin to deviate from average $PPSR_i$, quantile regressions assume different slopes (*Figure S1*). The difference of estimated $PPSR_i$ values by these successive quantile models thus estimate the variance in $PPSR_i$ within predators with the same body-size. Specifically, for each population we fitted 21 successive quantile regressions (0.1% to 100%, increments of 5%) with $PPSR_i$ as response variable and predator body size as predictor in the package *quantreg* (Koenker *et al.* 2017). Then, to obtain estimates of variance in $PPSR_i$ along all the range of predator body sizes, we obtained 11 equidistant values of predator body-size values (quantile values of the body-size distribution) and then used the estimated quantile models to estimate values of $PPSR_i$ for each of these predator body-size values (*Figure S2*). Next, we calculated the variance between estimated values $PPSR_i$ for the quantile regressions within a given predator size (for each of the 11 quantile body-size

values). Finally, our metric of size-dependence of the variance in $PPSR_i$ is the slope of a linear regression model with the variance in $PPSR_i$ as response variable and predator size as predictor. A positive slope ($V_\beta$) indicates a positive size-dependence of the variance in $PPSR_i$ (*Figure 1*b).

## *Quantifying prey limitation*

We quantified three complementary ecological factors to represent variation in the intensity of competition and prey limitation across food webs. Following previous studies (e.g. Ward, Webster & Hart 2006; Evangelista *et al.* 2014; Newsome *et al.* 2015), we considered the density of conspecific predators as a proxy for intraspecific competition. To represent the magnitude of interspecific competition we calculated a metric of effective density of heterospecifics combining data on the local structure of frog communities and their phylogenetic relationships into the quantitative genetic competition model of Doebeli (1996) (see Supporting Information for details). This metric increases for a given population when locally co-occurring species are closely related and abundant. Finally, we quantified the total biomass of available prey at each food web.

## *Hypotheses testing*

We first tested which predator (species identity and body size) and prey (prey taxonomic identity) traits explain variation in predator-prey size ratios at the individual scale ($PPSR_i$) using linear mixed models in the package *lme4* (Bates *et al.* 2014). We constructed five categories of statistical candidate models following Nakazawa, Ushio and Kondoh (2011): (*i*) Null model, (*ii*) Allometric model (predator size as fixed effect), (*iii*) Taxonomic models (predator species identity or prey taxonomic group as fixed effect), (*iv*) Combined models, and (*v*) Full model (*Table 1*). All these models included the population and individual identities as random factors. We compared candidate models using $\Delta AIC_c$, which represents the difference in the corrected Akaike information criterion ($AIC_c$) relative to the model with the lowest score, i.e. most parsimonious model.

To evaluate how differences in prey limitation across food webs affect the size dependence of predator-prey size ratios, we built Mixed-Effects Meta-Regression models in the package *metafor* (Viechtbauer 2010). This type of model has the advantage that it allowed us to incorporate standard errors in the estimate of our response variables ($\beta$ and $V_\beta$, *Figure 1*).

We included density of conspecifics, effective density of heterospecifics, and biomass of available prey as additive predictors, and individual identity and site as random effects. We performed all data analyses in R 3.4.1. Data underlying the analysis are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.011v40v (Costa-Pereira et al. 2018).

## Results

### *Variation in predator-prey size ratios*

In general, predators were 9.27 times longer and 266.56 times heavier than their prey (median values, see Supporting Information for details), but there was a sizable variation in $PPSR_i$ across individual predators (*Figure 3*, log10-transformed). For example, in some cases, predators were actually shorter than their respective prey (minimum realized $PPSR_i$ = 0.73), while in other cases predators were > 70 times longer than their prey (maximum realized $PPSR_i$ = 72.76). This tremendous variation in preferred $PPSR_i$ was best explained by the model including individual predator body size and prey taxonomic identity (*Table 1*). Although the full model including predator species identity performed equally well, only 1.3% of the total variance in $PPSR_i$ was attributed to predator identity (df = 3, F = 27.84).

*Table 1*. Candidate models to explain variation in predator-prey size ratios at the individual scale ($PPSR_i$) in thin toed frogs (*Leptodactylus* spp.) using predator (species identity and body size) and prey (prey taxonomic identity) traits. $\Delta AIC_c$ represents the difference in $AIC_c$ (corrected Akaike information criterion) score relative to the model with the lowest value (most parsimonious model).

| Model | Formulation | $\Delta AIC_c$ |
|---|---|---|
| Combined model | $PPSR_i$ ~ Predator Size + Prey group | 0 |
| Full model | $PPSR_i$ ~ Predator Size + Predator spp + Prey group | 0.36 |
| Taxonomic model | $PPSR_i$ ~ Predator spp + Prey group | 88.68 |
| Taxonomic model | $PPSR_i$ ~ Prey group | 236.63 |
| Allometric model | $PPSR_i$ ~ Predator size | 2457.38 |
| Combined model | $PPSR_i$ ~ Predator Size + Predator spp | 2455.94 |
| Taxonomic model | $PPSR_i$ ~ Predator spp | 2549.62 |
| Null model | $PPSR_i$ ~ 1 | 2664.76 |

### *PPSR - predator size relationship across communities*

While preferred $PPSR_i$ varied with predator body-size overall (i.e. size-dependent PPSR), we found a striking shift in the degree of size-dependence of $PPSR_i$ across food webs. Observed patterns ranged from strong negative relationships between $PPSR_i$ and predator body-size in some sites (i.e. large predators consuming proportionally larger prey, $\beta < 0$) to a weakly positive relationship (i.e. large predators consuming proportionally smaller prey, $\beta > 0$) (*Figure 4*). This variation in size-dependency ($\beta$) was significantly related to biomass of available prey, but not to density of conspecifics and heterospecifics (*Table 2*, *Figure 5*). As the biomass of food resources increased across food webs, $PPSR_i$ was less size-dependent ($\beta$ values approached 0), meaning that small and large-bodied individual predators tended to consume prey with proportionally similar sizes in high-resource biomass food webs. Overall these results indicate that body size ratios are not constant but instead change predictably with ecological context and predator size.

*Table 2.* Effects of density of conspecifics, effective density of heterospecifics, and total prey biomass on the degree of size-dependence of Predator-Prey Size Ratios and its variance across populations of Thin toed frogs (*Leptodactylus* spp.).

| Predictors | Size-dependence of PPSR | | | Variance in size-dependence | | |
|---|---|---|---|---|---|---|
| | Estimate (SE) | z | p | Estimate (SE) | z | p |
| Intercept | -0.659 (0.41) | -1.6 | 0.11 | -0.029 (0.05) | 0.56 | 0.57 |
| Density of conspecifics | -0.001 (0.01) | -0.1 | 0.92 | 0.002 (0.01) | 1.93 | 0.05 |
| Effective density of heterospecifcs | -0.005 (0.01) | -0.26 | 0.79 | -0.002 (0.01) | -0.69 | 0.48 |
| Prey biomass | -0.164 (0.08) | 2.06 | 0.04 | -0.047 (0.01) | -3.13 | 0.001 |

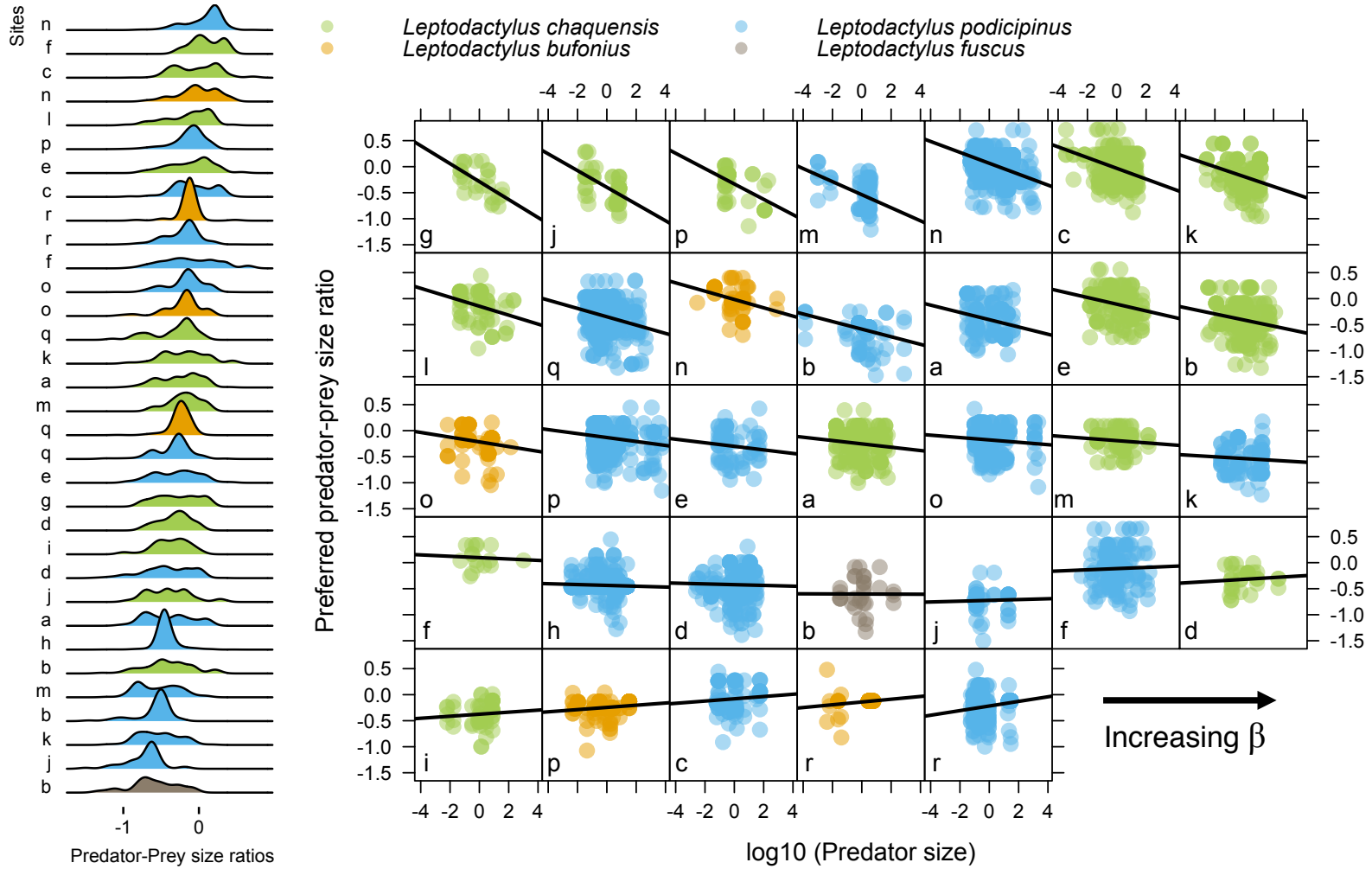



*Figure 4*. Distribution of preferred Predator-Prey Size Ratios ($PPSR_i$) for populations of four species of thin toed frogs (*right panel*) and the large variation in how PPSR respond to predator body-size across studied sites (*left*). We quantified this size-dependence of PPSR*i* as the slope (β) of a linear mixed model with preferred PPSR*i* as response variable and predator size as predictor. When β = 0 PPSR*i* is size independent. Positive (β > 0) and negative slopes (β < 0) indicate that PPSR*i* is size dependent, with larger individuals including proportionally smaller or larger prey in their diets respectively. Plots are arranged in order of increasing β.

## *Variance in PPSR*

Variance in $PPSR_i$ around the mean was not constant but instead changed with predator body size within food webs and this relationship was strikingly different across food webs. (*Figure S5*). In some cases, large-bodied predators exhibited much more variation in their foraging choices than small predators ($V_\beta > 0$), but in other food webs there was no relationship or even the opposite trend ($V_\beta < 0$) (*Figure S5*). At least part of these differences in size-specific variation in $PPSR_i$ was explained by density of conspecifics and total biomass of available prey (*Table 2*, *Figure 6*). As the density of conspecifics increased and food biomass decreased across food webs (i.e., competition increased), large-bodied predators tended to exhibit proportionally larger variance in their consumed prey sizes when compared to small-sized predators. Overall this indicates that variance in PPSR is not fixed within food webs as commonly assumed by food web models, and can respond predictably to predator body size along prey limitation and productivity gradients.

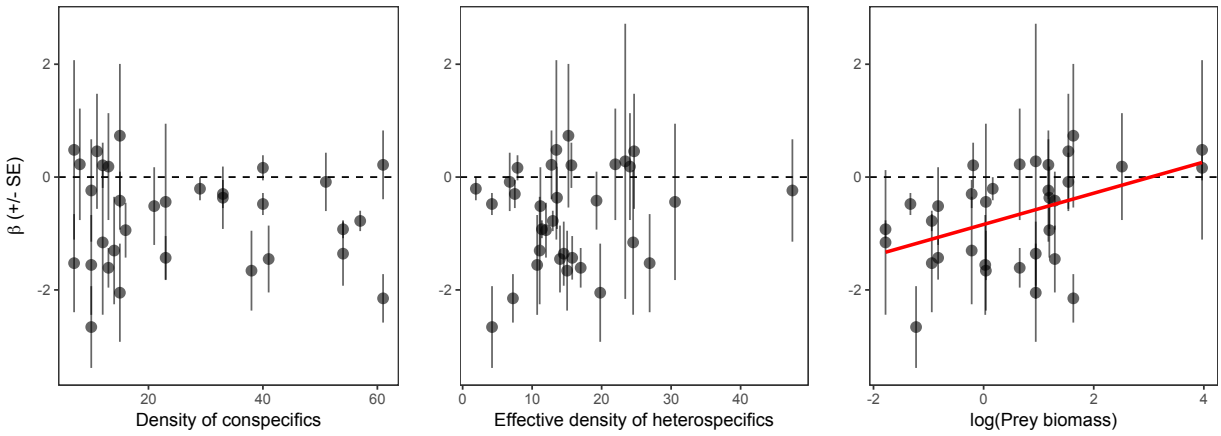



*Figure 5.* Effect of prey biomass, but not density of conspecifics and effective density of heterospecifics, on the degree of size-dependence of average Predator-Prey Size Ratios in thin toed frogs (*Leptodactylus* spp.).

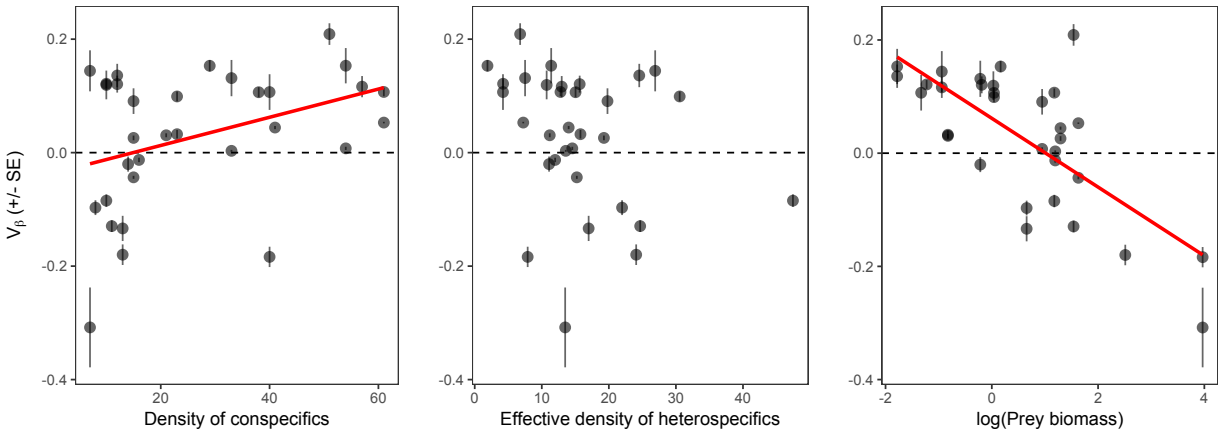



*Figure 6.* Effect of density of conspecifics and prey biomass, but not effective density of heterospecifics, on the degree of size-dependence of the variance in Predator-Prey Size Ratios in thin toed frogs (*Leptodactylus* spp.).

## Discussion

Predator-prey size ratios are key drivers of population and community dynamics and food web structure. Food web theory has traditionally assumed a single universal scaling of predator-prey size ratios based on metabolic principles (Brose, Williams & Martinez 2006; Kalinkat *et al.* 2013). This tenet is inconsistent with variation in predator-prey size ratios with predator body size and across natural systems (Nakazawa, Ushio & Kondoh 2011), but it remains unclear what factors are driving this variation. Using a new method to quantify Predator Prey Size Ratios (PPSR) that incorporates gape limitation of predators, we show that mean predator-prey size ratios (both in terms of length and mass) and variance around that mean change substantially across food webs and across predator body size within food webs. Both patterns in mean and variance of PPSR were partially explained by a gradient of biomass of available resources, with populations subject to lower prey biomass (and thus stronger food limitation) exhibiting greater size-dependence of PPSR. Together, these results demonstrate that there is no universal constant predator-prey size-scaling pattern in natural food webs, but rather that it varies predictably with ecological contexts, such as competition for food resources. Moreover, our results show that variance in PPSR is neither as negligible nor as constant as commonly assumed, but instead it depends on predator body-size and the strength of competition within a given ecosystem. Overall, our results emphasize the need to incorporate both ecological drivers of PPSR and its variance in food web and community models.

## *Variation in Predator-Prey Size Ratios*

Inspired by metabolic theory, predator-prey studies often predict and search for universal power-laws that can help explain and predict predator-prey interactions. In contrast, we found that predator-prey size ratios varied significantly across and within food webs by up to two orders of magnitude, emphasizing that trophic links do not follow one universal allometric relationship across this range of predator sizes. Consistent with previous studies (Barnes *et al.* 2010; Naisbit *et al.* 2011; Nakazawa, Ushio & Kondoh 2011), we found that part of this variation was linked to prey (taxonomic) identity and predator body size. This is not surprising given that traits of both predators and prey play an important role in determining the likelihood of trophic interactions, including encounter rates, handling time, and the ability to consume a prey of a certain size (Sherry & McDade 1982; Chang *et al.* 2017; Uiterwaal, Mares & DeLong 2017).

Predators in our system encountered a large taxonomic and functional diversity of prey types (> 14 invertebrate families), and it is reasonable to expect that prey types exhibit differential vulnerability to predators (Woodward & Hildrew 2002; Boukal 2014; Uiterwaal, Mares & DeLong 2017). Unfortunately our data did not allow us to identify which specific traits (e.g. offensive or defensive structures) confer lower or higher vulnerability to predation. Identifying these traits is an important next step to help explain and predict the importance of taxonomic identity in driving variation in PPSR (Klecka & Boukal 2013). Taxonomic identity of predators did not explain variation in PPSR, likely due to the ecological and morphological similarity among studied congeneric predator species (e.g. similar hunting behavior, morphology, trophic level). Predator identity should be a relevant driver of PPSR when it encompasses a wider taxonomic and functional range of organisms though (e.g. large spatial scales, Barnes *et al.* 2010; Nakazawa, Ushio & Kondoh 2011).

PPSR varied largely with predator body size for most of the food webs in our studied system. This size-dependent pattern is consistent with previous empirical studies (Barnes *et al.* 2010; Naisbit *et al.* 2011; Nakazawa, Ushio & Kondoh 2011) and likely arises because small- and large-sized predators experience environmental prey availability differently, resulting in the commonly observed size-dependence of PPSR in natural communities. Importantly, our results indicate that the direction and strength of this size-dependence is flexible and in part predictable across ecological contexts.

A key environmental factor contributing to the large variation observed in PPSR (both across and within food webs) is prey availability. While prey availability is commonly equated to total prey abundance, it is important to keep in mind that actual prey availability is also dependent on individuals' gape limitation, i.e. the gape of a predator determines the largest prey it can consume imposing a biomechanical limit on available prey. As a consequence, studies relying on species-averaged predator and prey body size values are likely to misrepresent actual feeding relationships and underestimate the real variance in PPSRs in natural food webs given that the vast majority of natural populations and ecological interactions are size-structured (Woodward & Warren 2007; Nakazawa, Ushio & Kondoh 2011). Here we used a novel approach that specifically incorporates changes in prey availability with predator body sizes and identifies interactions which are morphologically unlikely (Jordano 2016). This approach demonstrates that traditional estimates that do not account for this gape limitation tend to overestimate preferred predator-prey size ratios for small-sized predators. Therefore, this biased overestimation of PPSR towards smaller predators may be an underlying reason for the negative relationship between predator body size and PPSR (i.e. size-dependence of PPSR) commonly observed in natural food webs (Barnes *et al.* 2010; Nakazawa, Ushio & Kondoh 2011; Nakazawa, Ohba & Ushio 2013) (see below *Ecological drivers of size dependent predator-prey size ratios*). Overall, these findings suggest that at least part of the current discussion on the variation and size-dependence of PPSR in natural systems may have underlying methodological sources, which can be amended by incorporating prey availability (Tsai, Hsieh & Nakazawa 2016) and gape limitation in PPSR estimates.

### *Ecological drivers of size dependent predator-prey size ratios*

Intriguingly, two major bodies of theory in ecology diverge in a fundamental point; while food web and metabolic theories assume a universal scaling of predator-prey size ratios (Petchey *et al.* 2008; Petchey & Dunne 2012; Kalinkat *et al.* 2013), optimal foraging theory postulates that predators adjust their feeding decisions with changes in abundance of resources to maximize net energetic income across contexts (Stephens & Krebs 1986). Our results matched the theoretical expectation from the latter. As predators commonly select prey primarily by size (Werner & Hall 1974; Turner 1982), competition should deplete optimal-sized resources, shifting predator selectivity towards sub-optimal resources (e.g. proportionally larger or smaller prey) (Stephens & Krebs 1986). Accordingly, we found that the slope of the relationship

between average PPSR and predator body size became flatter as available prey biomass increased (*Figure 5*). This pattern implies that, on average, foraging decisions are more divergent between small- and large-sized predators under prey limitation; large-bodied predators foraged on relatively larger prey than small-sized predators. This relationship could decrease niche overlap between conspecific individuals with different body sizes (e.g. ontogenetic niche shift), which can affect population and community persistence and dynamics (Miller & Rudolf 2011; Nakazawa 2015). Moreover, it suggests that regardless of body size, prey limitation forces predators to deviate from their optimal predator-prey size ratio, emphasizing the context-dependency of predator-prey size allometric scaling in natural food webs.

Our findings reveal that resource limitation may not only affect the average prey size selectivity of predators within natural food webs (i.e. size-dependence of PPSR), but also its variance. Sites with high densities of conspecifics and low biomass of available prey exhibited a greater size dependence of the variance in PPSR, with large-sized predators exhibiting more variation in their foraging decisions than small ones. This pattern may be associated with the intrinsically higher scope for variation in prey size for large-sized predators because of their larger gapes. Therefore, if optimal-sized resources are depleted in high competition sites, large-sized predators have more alternative foraging options (i.e. proportionally smaller or larger prey) than small-sized predators, which could result in a stronger variance in predator-prey size ratio towards larger individuals. This predictable density dependence of the scaling of the variance with body size is not yet included in food web models, but it can have important eco-evolutionary consequences and affect food web stability and functioning.

### *Implications*

For the first time, we demonstrate that not only average predator-prey size ratios scales with predator size, but also its variance. Because diverse animal taxa are unable to mechanically reduce their prey before ingestion - including fish, amphibians, caecilians, and many reptiles and birds (Schwenk 2000) - our findings can have broad implications beyond the studied system. In fact, all predators (except group hunters, which represents a small proportion of predators in nature) are constrained to capture prey larger than a critical body size, which not necessarily reflects gape limitation, but also, for example, the ability to overcome and subdue prey. Further, as prey size influences fitness components in consumers, such as survival, lifetime and fecundity (Griffiths 1980; Travis, Keen & Juilianna 1985; Arsovski *et al.* 2014;

Dodrill *et al.* 2016), our results suggest that prey limitation may affect predators' fitness landscapes by increasing the variation in foraging decisions among individuals. Importantly, prey size is a potential driver of rapid evolution in gape-constrained predators (Eloy de Amorim *et al.* 2017). Thus, understanding the drivers and magnitude of variation around the average PPSR in food web studies may bring new eco-evolutionary perspectives on food web theory. Furthermore, as food availability and density of competitors vary temporally and spatially in virtually all biological systems, our results emphasize that it is unreasonable to assume a single predator-prey scaling law for different ecological contexts. Food web models should therefore incorporate this context-dependency of PPSR along gradients that affect prey limitation in natural systems (e.g. productivity, deforestation).

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# Supplementary Information

## *Data collection*

We sampled 21 frog communities, accounting for 52 populations of four studied species (*Leptodactylus bufonius*, n = 5 populations; *L. chaquensis*, n = 18; *L. fuscus*, n = 7; and *L. podicipinus*, n = 13) between mid-November 2014 and early January 2015. As thin toed frogs have a strong association with lentic water bodies, we defined a community as all the frogs found around lagoons separated by at least 1.5 km from any other community. Around each lagoon, we set up six 10 x 10 m plots to sample anurans. We installed 12 pitfall traps (20 cm diameter) and two light traps evenly spaced surrounding the plots to sample available food resources to frogs. We opened pitfall traps and turned on light traps right after the sunset, and retrieved prey samples after 12h. Two hours after nightfall, we surveyed each plot (standard collection effort of 1h/people/100m$^2$) and hand-captured all frogs and toads found, which were euthanized (in the case of *Leptodactylus* spp. specimens) or released in the same lagoon (all other species).

## *Proxies to prey limitation*

We estimated intraspecific competition and prey biomass using the density of conspecifics and the total biomass of available resources (captured in pitfall and light traps) as proxies, respectively. As a proxy of interspecific competition, we calculated a metric that combines both the local structure of communities and the phylogenetic relationships between coexisting species. Specifically, we calculated a measure of effective density of heterospecifics ($N_z$) experienced by each frog population based on the quantitative genetic competition model proposed by Doebeli (1996):

$$N_z = \int \rho(z')\alpha(z, z')dz$$

In this model, the effective population density corresponds to the density of each alternative phenotype z' (or, in our case, species z'), represented by ϱ(z'), weighted by its competitive effect on the focal phenotype z (species z). The competitive effect, α (z, z'), represents the *per capita* decrease in the population growth of the species z for each individual of the species z' added to the community, which can be modeled as:

$$\alpha(z, z') = \exp\left(-\frac{(z - z')^2}{2\sigma_\alpha^2}\right)$$

Here we considered the difference between phenotypes (z, z') as the phylogenetic distance between two given species. Using the package *picante* (Kembel *et al.* 2010), we calculated the

phylogenetic distance between all pairs of coexisting species from a cladogram based on the time-calibrated tree proposed by Pyron and Wiens (2011). The constant $\sigma_\alpha^2$ determines how sharply the competition decays with the increase of the divergence between phenotypes. As an empirical-based value to this constant is not available in the literature, we determined $\sigma_\alpha^2 = 0.05$, which was the best value to approximate the competitive function based on our data to a Gaussian function proposed by Doebeli (1996). Using smaller or larger values ($\sigma_\alpha^2 = 0.025$ and $\sigma_\alpha^2 = 0.075$) did not qualitatively change the results. In summary, our metric of effective density of heterospecifics for a given population increases when co-occurring species are closely related and abundant.

### *Metrics of Predator Prey Size Ratios (PPSR)*

Tsai, Hsieh and Nakazawa (2016) propose that accurate estimates of Predator-Prey Size Ratios (i.e., preferred PPSR) should consider not only realized PPSR, but also environmental PPSR. These authors suggest that environmental PPSR is obtained as follows:

$$Environmental\ PPSR_i = \sum_{j\ \epsilon\ prey\ category} \frac{S_i}{s_j} \times q_j$$

where, $S_i$ is the body size of predator individual $i$, $s_j$ is the average (or median) body size of prey type $j$, and $q_j$ is the relative abundance of prey type $j$ in the local environment. We propose an adaptation to this metric by incorporating a flexible prey availability component ($q_{ij}$) that varies according to individual predator body size. As the size of a predator limits its foraging options due to gape limitation, we first estimated for each individual predator its upper boundary of the feeding range and then subset the total available prey size (*Figure 2*). Thus, environmental prey availability is not homogeneous anymore to all predators and $q_j$ has to be replaced by $q_{ij}$:

$$Environmental\ PPSR_i = \sum_{j\ \epsilon\ prey\ category} \frac{S_i}{s_j} \times q_{ij}$$

To calculate Realized PPSR, the $q_{ij}$ should be replaced by $p_{ij}$ that is the relative abundance of prey type $j$ in the gut of predator individual $i$ and $s_j$ is the individual size of the individual prey $j$:

$$Realized\ PPSR_i = \sum_{j\ \epsilon\ prey\ category} \frac{S_i}{s_j} \times p_{ij}$$

Finally, preferred PPSR is simply obtained by subtracting log10(Realized PPSR) from log10(Environmental PPSR) (Tsai, Hsieh & Nakazawa 2016).

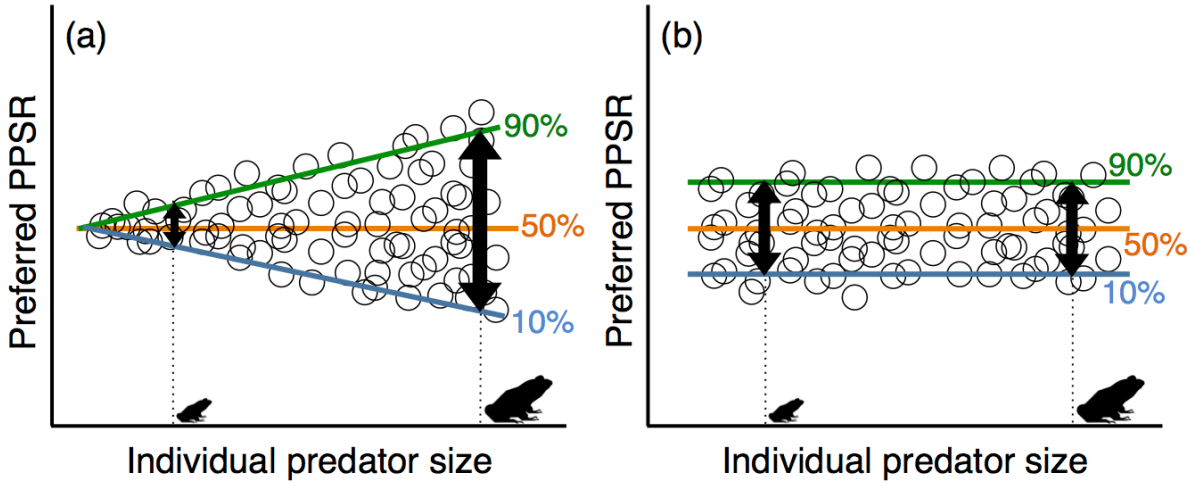



*Figure S1.* Schematic representation of how successive quantile regressions (5%, 50% and 100%) can be used to quantify variance in $PPSR_i$ along predator body size. If all individual predators exhibit similar $PPSR_i$, successive quantile regressions result in models with very similar slopes (*right panel*). Slopes begin to deviate when the amount of variation in $PPSR_i$ scales with predator body size (*left panel*).

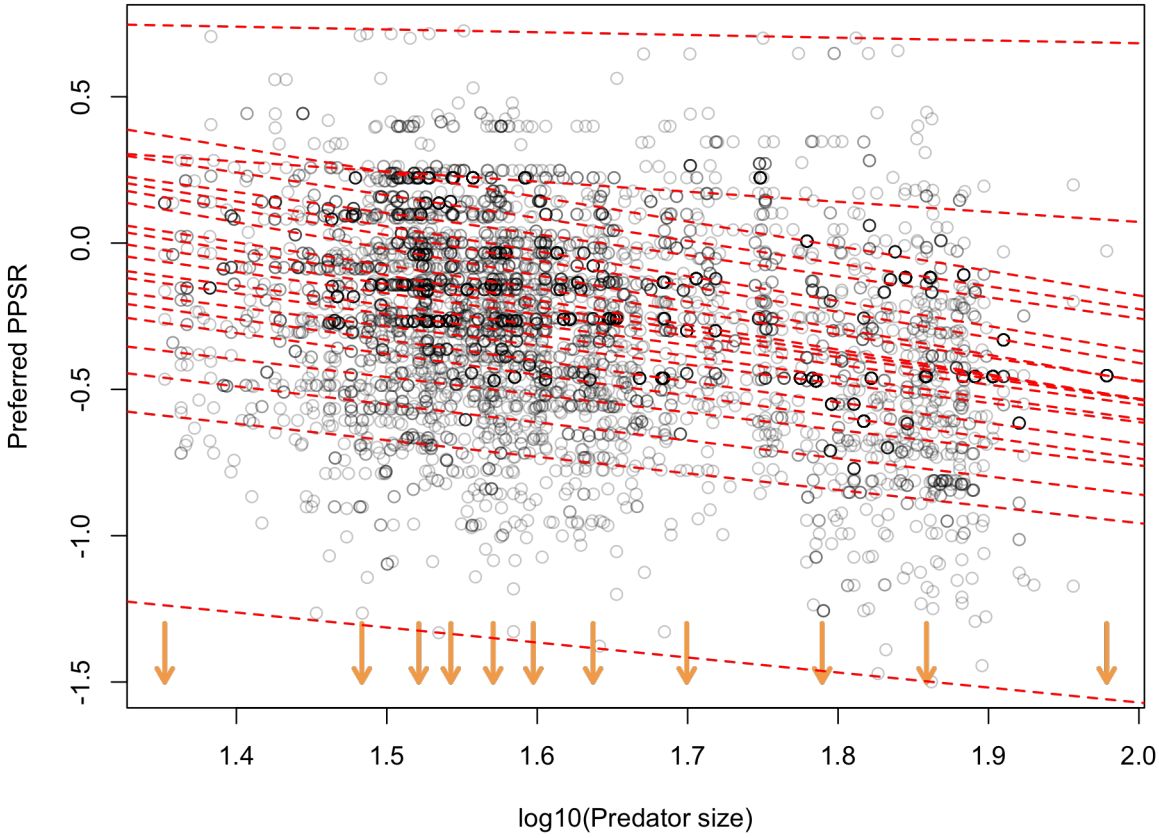



*Figure S2.* Successive quantile regressions (red dashed lines, from 0.1% to 100%, increments of 5%) with $PPSR_i$ as response variable and predator body size as predictor for all the observed trophic interactions (n = 6,172) between Thin toed frogs and their prey. Orange arrows represent 11 equidistant values of predator body-size values (quantile values of the body-size distribution).

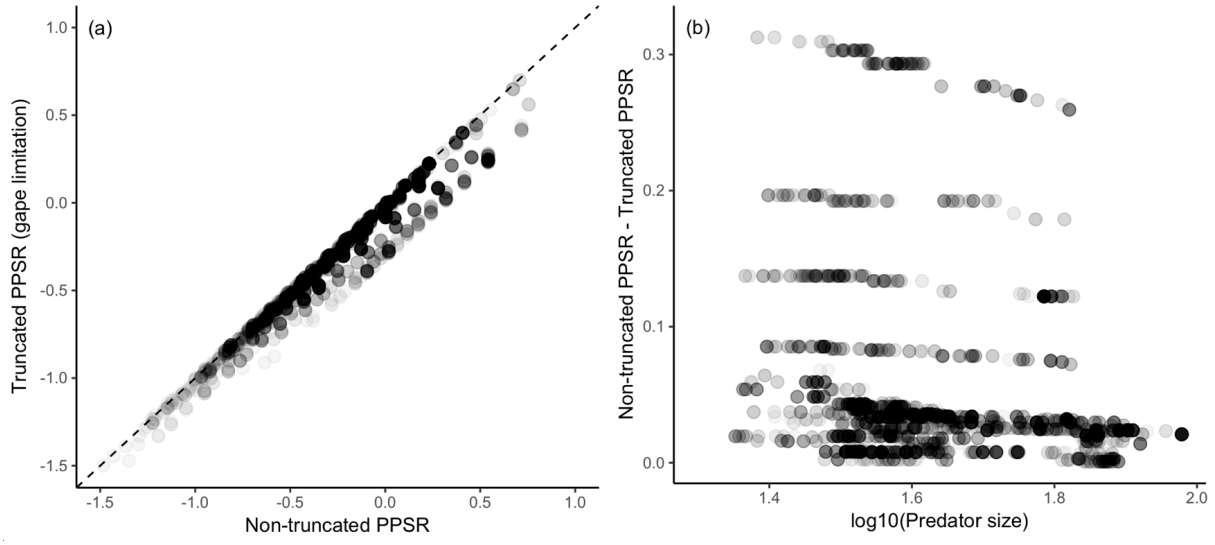



*Figure S3*. (*a*) Correlation between preferred $PPSR_i$ incorporating gape limitation (Truncated PPSR) and Tsai et al. (2016)'s metric of PPSR (Non-truncated PPSR). Dashed line corresponds to the 1:1 relationship. (*b*) Relationship between predator body size (log10-transformed) and the magnitude of the difference between truncated PPSR and non-truncated PPSR.

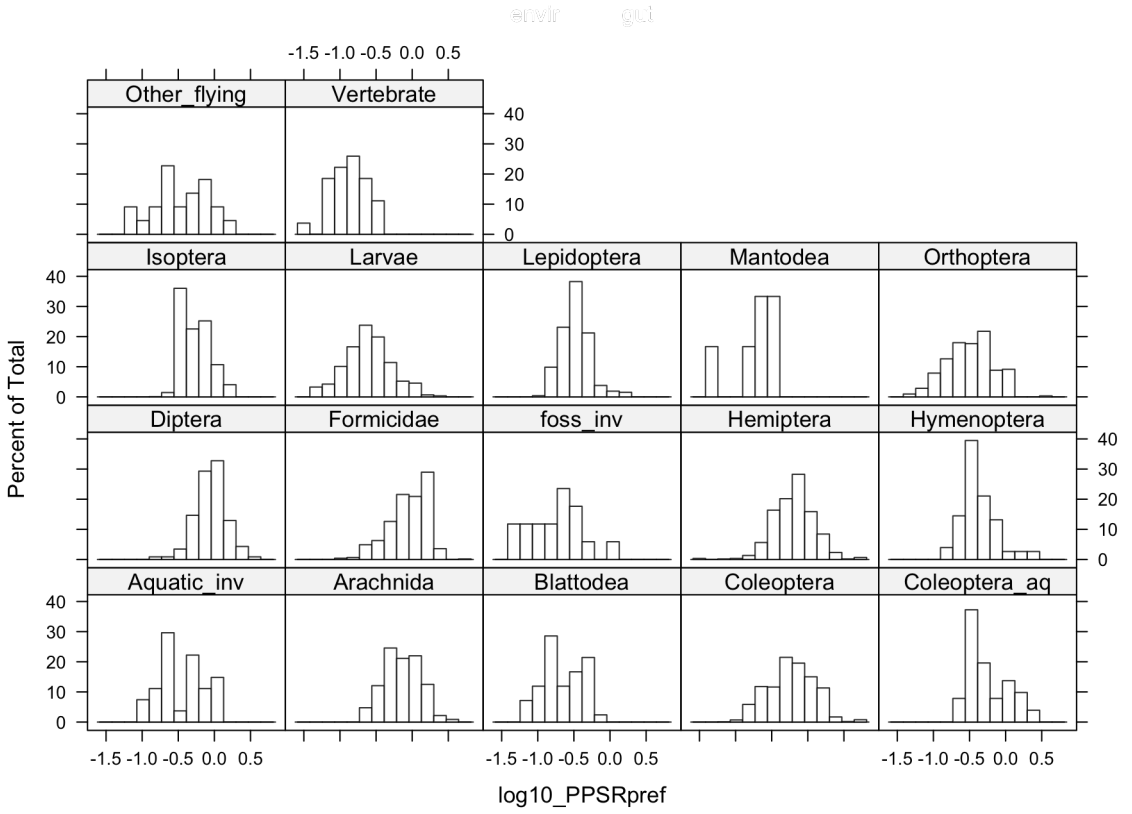



*Figure S4*. Differential distribution of preferred Predator Prey Size Ratios ($PPSR_i$) for 17 prey taxonomic groups consumed by Thin toed frogs.

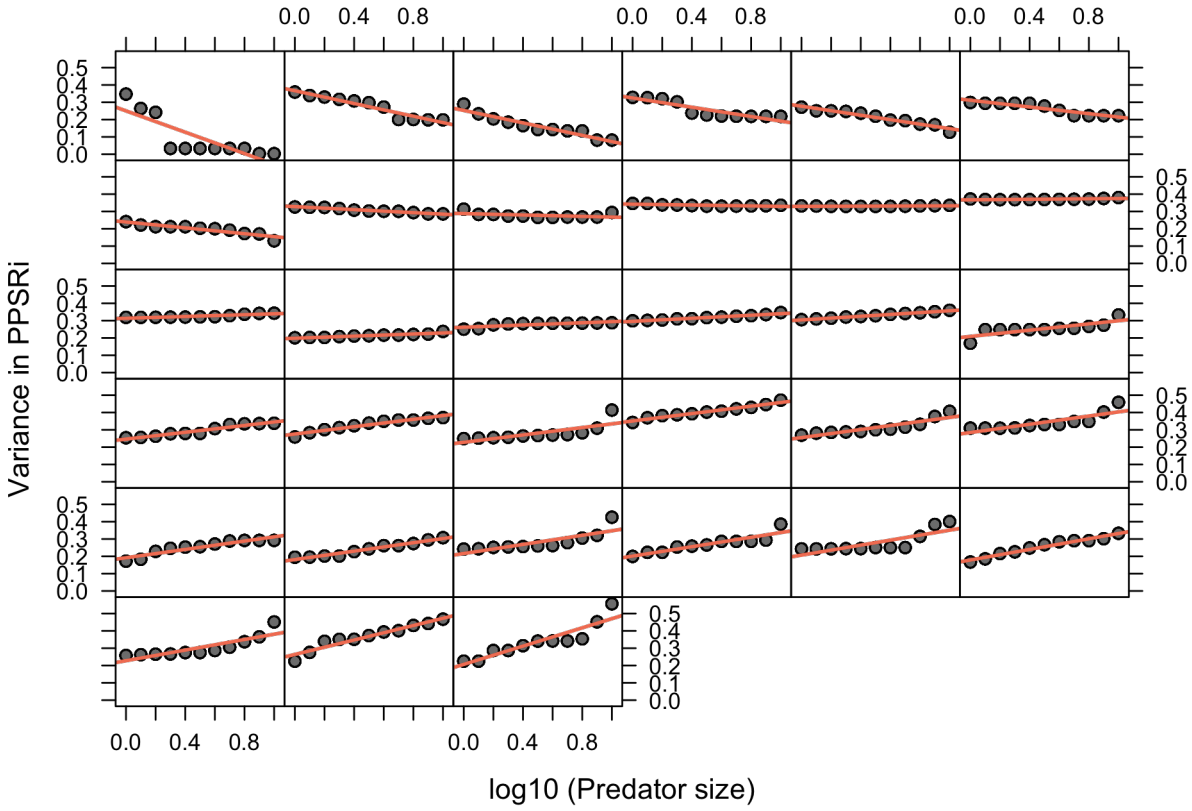



*Figure S5*. Plots showing the differences on how the variance in PPSR responds to predator body-size across food webs. We quantified the size-dependence of the variance in $PPSR_i$ as the slope of a linear regression model with the variance in $PPSR_i$ as response variable and predator size as predictor. A positive slope ($V_\beta$) indicates a positive size-dependence of the variance in $PPSR_i$ (Figure 1 b). Plots are ordered based on the magnitude of $V_\beta$.

# Capítulo 3

# Competition and resource breadth shape niche variation and overlap in multiple dimensions

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Costa-Pereira, R. *et al.* (2018a) Prey Limitation Drives Variation in Allometric Scaling of Predator-Prey Interactions. *Proceedings of the Royal Society of London B: Biological Sciences*, **in revision**.

## Abstract

Competition plays a central role in the maintenance of biodiversity. A backbone of classic niche theory is that local coexistence of competitors is favoured by the contraction or divergence of species' niches. However, this segregating effect should depend on the diversity of resources available in the local environment, particularly when resources vary in multiple ecological dimensions. Here, we investigated how available resource breadth and competition together shape multidimensional niche variation (between and within individuals) and interspecific niche overlap in 42 populations of congeneric tropical frog species. We modelled realised niches in two key trophic dimensions (prey size and carbon stable isotopes) and sampled available food resources to quantify two-dimensional resource breadth. We found 14-fold variation in multidimensional population niche width across populations, most of which was accounted for by within-individual diet variation. This striking variation was predicted by an interaction between available resource diversity and the number of coexisting competitors. These gradients also influenced the degree of niche overlap across species, providing novel insights on how similar species can coexist in local community. Together, our results emphasise that patterns of exploitation of resources in multiple dimensions are driven by both competitive interactions and extrinsic factors such as local resource breadth.

*Key-words*: individual specialisation, niche partitioning, multidimensional, *Leptodactylus*, niche shift, stable isotopes

## Resumo

A competição entre espécies desempenha um papel central para a manutenção da biodiversidade. A ideia de que a coexistência local de competidores é favorecida pela contração e divergência dos nichos das espécies é a espinha dorsal da teoria clássica de nicho. Entretanto, tal efeito particionador deve depender da diversidade de recursos disponíveis no ambiente local, particularmente quando os recursos variam em múltiplas dimensões ecológicas. Aqui nós investigamos como a amplitude de recursos disponíveis e o número de espécies que coexistem localmente afetam os padrões de variação de nicho (entre populações e indivíduos) e o grau de sobreposição de nicho interespecífico em 42 populações de rãs tropicais. Nós modelamos nichos realizados em duas dimensões tróficas chave (tamanho de presa e isótopos estáveis de carbono) e amostramos recursos alimentares disponíveis para quantificar a amplitude de recursos no ambiente nas mesmas duas dimensões. Encontramos que o tamanho de nicho variou quatorze vezes entre populações, o que, em grande parte, foi associado a indivíduos se tornarem mais generalistas em suas dietas. Essa variação expressiva de nicho entre populações foi explicada pela interação entre a diversidade de recursos disponíveis e o número de competidores que coexistem. Esses gradientes também influenciaram o grau de sobreposição de nicho entre espécies, fornecendo novas perspectivas sobre como espécies similares podem coexistir em comunidades. No geral, nossos resultados destacam que padrões de exploração de recursos em múltiplas dimensões são moldados tanto por interações competitivas quanto por fatores extrínsecos como a amplitude local de recursos.


*Palavras-chave*: especialização individual, partição de nicho, multidimensional, *Leptodactylus*, variação de nicho, isótopos estáveis

## Introduction

The niche is a foundational concept in ecology that permeates most theories aiming to explain biodiversity patterns. In particular, niche differences between co-occurring species have long been recognised as a fundamental aspect of the assembly of natural communities. Throughout the evolution of niche-based theories of diversity maintenance, from the principle of limiting similarity (MacArthur & Levins 1967) to the modern coexistence framework (Chesson 2000), the magnitude of overlap in the exploitation of limiting resources between co-occurring species has been key to predicting their stable coexistence or local exclusion (Chase & Leibold 2003; Letten, Ke & Fukami 2017). Specifically, stabilizing mechanisms associated with niche differences between species should promote negative frequency dependence within species and therefore favour long-term coexistence (Chesson 2000).

Natural communities vary along ecological gradients, which creates a mosaic of competitive interactions and shapes patterns of niche variation. Specifically, classic niche theory predicts that the co-occurrence of competing species leads to niche segregation and/or contraction onto a narrower variety of resources (Van Valen 1965; Diamond 1970). This long-standing hypothesis, though, implicitly assumes that the diversity of available resources is necessarily constrained by the competitors, i.e. competitive interactions are mediated by strong top-down effects on limiting local resources (Terborgh 2015). However, resource availability (e.g., diversity of prey and microhabitat types) may change strikingly in space and time due not to the direct effects of competitors, but instead to the presence of ecological gradients such as productivity, seasonality, and human impacts (Winemiller 1989; Rutz & Bijlsma 2006; Araújo & Costa-Pereira 2013; Jha & Kremen 2013), which may have a marked influence on species' niches and competitive interactions (Layman *et al.* 2007; Tinker, Bentall & Estes 2008; Sánchez-Hernández, Gabler & Amundsen 2017). Accordingly, the 'resource diversity hypothesis' predicts that the local variety of available resources favours niche expansion and divergence among species of consumers (MacArthur 1969; Lawton 1983). Therefore, the expected segregating effect of interspecific competition on species' niches should be stronger when there is a greater diversity of available resources, or when resources vary in more ecological dimensions, because there should be more scope for niche partitioning (Pianka 1973; Case 1981). Although this is an intuitive idea, explicit empirical support for the simultaneous and interactive effects of competition and resource diversity on niche breadth and overlap in multiple dimensions is lacking.

A central assumption underlying most of the large body of theoretical and empirical research on niche variation is that niches are properties of populations or species (Hutchinson 1957; Chase & Leibold 2003). This typological view assumes that conspecific individuals are ecologically equivalent, and overlooks the pervasiveness of intraspecific resource use variation within natural populations (Bolnick *et al.* 2003; Araújo, Bolnick & Layman 2011; Bolnick *et al.* 2011). As a consequence, the pathways by which variation in individuals' foraging decisions translate into changes in population niche width remain largely unexplored (Tinker, Bentall & Estes 2008). Specifically, population niche expansion can occur via individuals becoming more generalist (increased within-individual niche variation) and/or individuals diverging in their diets (increased between-individual variation). Importantly, these two non-mutually exclusive paths have distinct ecological and evolutionary implications, including the degree of individual specialisation in the population and the potential for disruptive selection (Roughgarden 1972; Bolnick *et al.* 2010). Understanding how both within- and between-individual niche variation respond to environmental factors will therefore be necessary if we are to predict how niche width and niche overlap influence community-level processes.

Another enduring issue when studying competitive interactions is whether and how to account for the multidimensional nature of niches. Hutchinson's niche concept describes species' niches as multivariate constructs because resources used by organisms inherently vary in multiple dimensions (Hutchinson 1959; Pianka 1976). From an empirical perspective, however, ecologists have traditionally investigated variation along niche axes (e.g. food type, prey size, microhabitat use) by analysing each axis separately (Bolnick *et al.* 2003; Kamath & Losos 2017). Importantly, recent studies indicate that considering multiple dimensions of niche variation may affect estimates of interspecific niche overlap (Friedemann *et al.* 2016; Pulla *et al.* 2017; Ingram, Costa-Pereira & Araújo 2018). Specifically, multidimensional approaches capture the orientation and shape of species' niches, providing a more complete representation of their resource use and partitioning (*Figure 1*). Because of this disconnect between a conceptual multivariate niche *vs.* empirically estimated univariate niche axes, meaningful quantification of niche overlap remains a challenge in ecology and evolution (Hurlbert 1978; Abrams 1980; Hart *et al.* 2018).

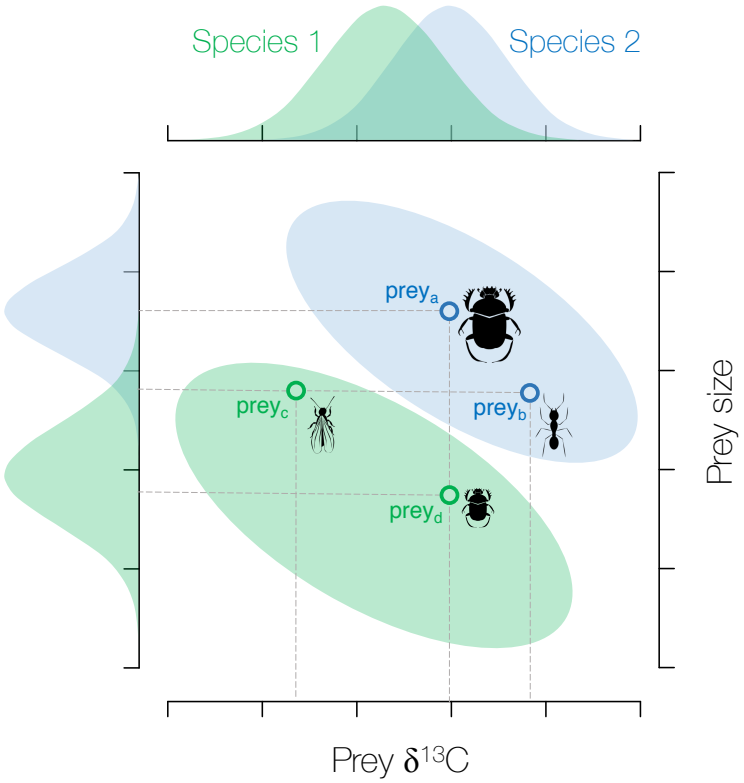



*Figure 1.* A schematic diagram of how the dimensionality of niche variation may affect the perceived niche overlap between coexisting populations. When only one niche axis is taken into consideration at a time, populations seem to overlap substantially in prey $\delta^{13}$C and partially in prey size (Gaussian distributions in the upper and left sides, respectively). However, when niches are represented as standard ellipses (Ingram, Costa-Pereira & Araújo 2018) and, therefore, both niche axes are considered simultaneously (see *Figure 2* for more details), there is no overlap between populations' diets. This clear disparity between uni- and multidimensional estimates of multidimensional estimates of niche overlap arise due to a combination of multidimensionality per se and the specific orientation and shape of the niches.

Here, we studied the spatial variation of multidimensional individual- and population-level niche variation in congeneric tropical thin-toed frog species (*Leptodactylus* spp.) across ecological gradients. The focal species overlap in activity period, foraging microhabitat and prey types and may sometimes but not always co-occur in local communities, (Piatti & Souza 2011; Costa-Pereira *et al.* 2018b). Specifically, we investigated how the presence of congeneric competitors and local resource breadth, defined as the diversity of resources available to consumers, interact to determine (*i*) population niche width, (*ii*) intraspecific niche variation,

and (*iii*) interspecific niche overlap. We used a recently proposed analytical framework to model species' niches by simultaneously incorporating multiple niche dimensions and individual-level niche variation (Ingram, Costa-Pereira & Araújo 2018), which allowed us to elucidate whether multidimensional population niche width expands via individuals becoming more generalist (increase in within-individual variation) or diverging in their diets (increase in between-individual variation). We predicted that population niche width would increase with the breadth of available resources (resource diversity hypothesis) and decrease with the number of interspecific competitors. We also predicted that increased resource breath would reduce interspecific niche overlap by providing more scope for species to diverge in their diets. Finally, we predicted that the absence of congeneric competitors and increased resource breadth would cause individuals either to diverge in their diets (increased between-individual variation) (Van Valen 1965), or to become more generalist (increased within-individual variation) (Bolnick *et al.* 2010).

## Methods

### *Study system*

Thin-toed frog species (genus *Leptodactylus*) are a suitable system for studying how competition and resource breadth shape niche variation for several reasons. First, thin toed frogs have broad but patchy distributions across Neotropical lowlands, and several ecologically similar congeneric species may co-occur syntopically in local communities. Second, they are trophic generalist and exhibit a similar diet (Piatti & Souza 2011). Adult thin toed frogs forage at night on the ground and in low vegetation, consuming a broad variety of invertebrates (e.g. ants, termites, leafhoppers, and micromoths) and, occasionally, small vertebrates (Costa-Pereira *et al.* 2015; Costa-Pereira *et al.* 2018b). Finally, recent evidence suggests that the diet of these congeneric species is flexible and context-dependent, responding to natural gradients of competition and prey limitation (Costa-Pereira *et al.* 2018a; Costa-Pereira *et al.* 2018b). For more details about our study region, see the Electronic Supplementary Information.

### *Field sampling and lab processing*

In the rainy season, between November 2014 and January 2015, we sampled frog communities around the margins of 21 ponds in a grassland area of ~40,000 km$^2$ in the Brazilian Pantanal,

one of the largest and most pristine tropical wetlands. The rainy season in the Pantanal is an important period to native frogs during which they are fully active and forage extensively to accumulate energy for reproduction (Prado, Uetanabaro & Haddad 2005). In each sampled site, we surveyed an area of 600 $m^2$ (six 10 × 10 m plots, < 15% of the area surrounding the target lagoon; sampling effort of 1h/person/100$m^2$), hand-capturing all frogs and toads that were found.

Thin-toed frogs accounted for 93.3% of the total biomass of anurans captured, therefore we opted to focus on interspecific competition only among these congeneric species. Communities consisted of one, two, or three coexisting *Leptodactylus* species (seven communities in each scenario), with a total of 42 populations represented across sites. All *Leptodactylus* spp. (*L. bufonius*, *L. chaquensis*, *L. fuscus*, and *L. podicipinus*) specimens ($n_{total}$ = 904, average of ~22 individuals/population, *Table S1*) were euthanised with an overdose of lidocaine and then transferred to a -20°C freezer. In order to sample food resources available to frogs we used 12 pitfall traps (20 cm diameter, 2 traps/plot) and two light traps evenly spaced in each local community. We opened pitfall traps and turned on light traps right after sunset, and retrieved prey samples after 12h. Collection and euthanasia procedures were carried out in accordance with Universidade Estadual Paulista guidelines for the care of vertebrate animals (UNESP Animal Care and Use Committee 03120501).

We analysed individuals' and species' niches in two key continuous trophic dimensions: prey size and prey carbon stable isotopes ($\delta^{13}C$). Prey size is strongly associated with energetic return, interaction strengths, and attack rates across diverse taxa and ultimately can affect individual fitness (Werner & Hall 1974; Griffiths 1980; Emmerson & Raffaelli 2004). In turn, $\delta^{13}C$ varies among primary producers (e.g., C3 *vs.* C4 photosynthetic pathways in plants) and provides temporally integrated information on prey species' food chains (Dalerum & Angerbjörn 2005; Fry 2007). We counted, identified (to family level in most cases, *Table S1, S2*), and measured body size (length) of all prey items found in frogs' gut contents (n = 6,172 cumulative prey items). To quantify the available resources to frogs, we carried out the same procedures for all individuals of potential prey species collected in the light and pitfall traps (n = 9,470 cumulative available prey). We measured carbon stable isotopes ($\delta^{13}C$) of organisms from each prey category in each community. Samples were rinsed in deionised water, oven-dried for 48 hours at 60°C, ground, and weighed (~0.5 mg) into tin capsules. The abundance of $^{13}C/^{12}C$ was determined at the Washington State University Stable Isotope Core Laboratory

using an Elemental Combustion System 4010 elemental analyser (Costech Analytical, Valencia, CA, USA) and a Delta Plus XP continuous flow isotope ratio mass spectrometer (Thermofinnigan, Bremen, Germany), then converted to conventional delta units, referenced against the international reference Pee Dee beleminite (PDB). The standard deviation of replicates of the internal reference material (Nylon) was 0.03‰.

*Modelling multidimensional niches and interspecific overlap*

To represent species' niche width in a multidimensional space, we used a recently proposed framework for modeling the between- and within-individual components (BIC and WIC, respectively) of the population niche as a set of variance-covariance matrices (Ingram, Costa-Pereira & Araújo 2018). WIC represents the variation in prey size and $\delta^{13}C$ of the resources used by each individual in the population; while BIC the variation among individuals in average resource use (Roughgarden 1972). These niche components were inferred using multiple response generalised linear mixed models (MGLMM) employing Bayesian Markov Chain Monte Carlo analysis in the R package *MCMCglmm* (Hadfield 2010).

We first standardised the data to ensure that the niche component matrices would be readily interpretable (Ingram, Costa-Pereira & Araújo 2018). Because prey size and $\delta^{13}C$ values are measured on different scales (prey size ranged from 1 to 64 mm; prey $\delta^{13}C$ from -34.09 to -10.91 ‰) (*Table S1*, *Figure S1*), estimates of bi-dimensional niche components would be skewed toward the dominant axis (Ingram, Costa-Pereira & Araújo 2018). Therefore, within each sampling site we scale available prey size and $\delta^{13}C$ to vary between 0 (minimum prey size or $\delta^{13}C$ observed in the environment) and 1 (maximum values) and then calculate the correspondent scores for the consumed prey (see details in Electronic Supplementary Information). Importantly, this rescaling procedure did not affect the relative position of prey in the bivariate niche space (*Figure S2*). Then, for each population, individual identity was modelled as a random effect to obtain the variances and covariances between individuals in the prey size (log-transformed) and prey carbon stable isotope dimensions (G-structure, BIC). The residual variances and covariances (R-structure) corresponded to the average within-individual variation (WIC). The multivariate matrices BIC and WIC were estimated using the posterior means of each variance and covariance, then summed to estimate the total niche width (TNW) (see details in Ingram, Costa-Pereira & Araújo 2018). Each MCMC ran for 43,000 iterations (thinning interval = 50, burn-in = 3,000), and convergence was assessed using the Gelman-

Rubin diagnostic based on multiple independent runs. A similar model without the random effect of individual identity was fit using samples from the pitfall and light traps to estimate the two-dimensional breadth of available resources in each community.

Our study framework is illustrated in *Figure 2*. For each species in a community, the variance-covariance matrices representing between- and within-individual niche components and total niche width are represented as standard ellipses expected to contain ~40% of the data regardless of sample size (Batschelet 1981). Standard ellipses are often used in ecological studies because their projection on either niche axis corresponds to a standard interval, $\bar{X}_1 \pm 1s_{X1}$ and $\bar{X}_2 \pm 1s_{X2}$ (Friendly, Monette & Fox 2013), therefore representing "core" niche areas that should be relevant for competitive interactions. Different panels in *Figure 2* show the gradients of species richness (one, two, or three) and of resource breadth (white filled area representing standard ellipses occupied by available food resources). The area of resource breadth ellipses quantifies the degree to which available prey are spread in this two-dimensional niche space. Importantly, the number of coexisting *Leptodactylus* spp. was not correlated with resource breadth across sites ($r = -0.17$, $df = 19$, $p = 0.44$), suggesting that these gradients are independent in our study system.

To quantify the amount of multidimensional niche overlap between each pair of coexisting species we computed the overlapping area between TNW standard ellipses in each community in the R package *spatstat* (Baddeley, Turner & Rubak 2013). As a more intuitive relative measure of niche overlap experienced by each population, we calculated the proportion of its TNW standard ellipse that overlapped with at least one heterospecific population TNW's standard ellipse. Finally, we calculated the degree of individual specialisation as the size (i.e. sum of the eigenvalues) of the WIC matrix divided by the size of the TNW matrix (see details in Ingram, Costa-Pereira & Araújo 2018). This ratio assumes lower values as individual specialisation increases, because BIC is a larger proportion of TNW (Bolnick *et al.* 2002). To explore the relationship between uni- *vs.* multidimensional niche overlap, we calculated analogous unidimensional overlap based on the intersection between species' standard intervals for prey size or $\delta^{13}C$ (see details in the Electronic Supplementary Information).

## *Statistical analyses*

To investigate the drivers of variation in the size of each multidimensional niche component (TNW, WIC, and BIC) across populations we constructed linear mixed models in the package *lme4* (Bates *et al.* 2014). We modelled each of these niche components as a function of resource breadth, the number of coexisting *Leptodactylus* spp. (one-, two-, or three-species sites), and their interaction, with species identity nested within site (community) as a random effect. Each sampled population used in the analyses consisted of more than ten individuals and an average of more than three prey items per individual.

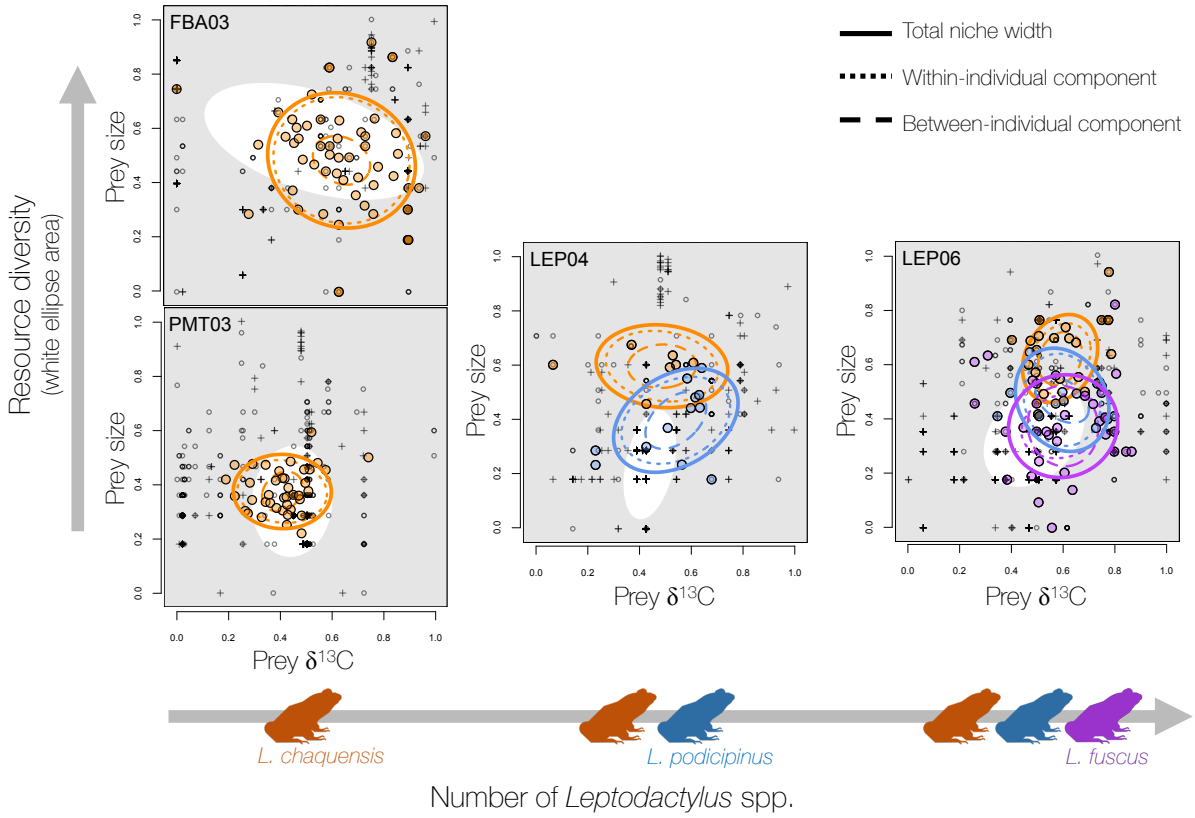



*Figure 2.* Representation of available and realised individual-level trophic interactions for tropical frog species (*Leptodactylus* spp.) in four sites (FBA03, PMT03, LEP04, LEP06) across gradients of resource breadth and number of congeneric competitors. Available prey items at each sampling site along body size and $\delta^{13}C$ niche axes are represented with "+" and local prey breadth is represented by the white-filled ellipse. Realised trophic interactions (i.e., each prey item found in gut contents) are shown as unfilled grey circles and individual frogs' means of prey size and $\delta^{13}C$ are the same plot indicated by filled circles. Niche axes were scaled to vary between 0 (min prey size or $\delta^{13}C$ observed in the environment) and 1 (max value observed in the environment). Finally, the variance-covariance matrices corresponding to between- and within-individual niche components (WIC and BIC) and the corresponding total niche width (TNW) for each frog population are represented by dashed, dotted, and continuous coloured lines, respectively. We present this graphical representation for all 21 studied sites in the Supporting Information (*Figure S3*).

We also constructed two separate generalised linear mixed models with beta distributions in the package *glmmTMB* (Magnusson *et al.* 2017) to elucidate the ecological drivers of variation in niche overlap and individual specialisation across populations. We included resource breadth, number of coexisting *Leptodactylus* spp., their interaction, and TNW as additive predictors, and species identity nested within site (community) as a random effect. P-values were obtained using likelihood ratio tests. All data analyses were performed in R 3.4.1 (R Development Core Team 2017).

## Results

### *Variation of population and individual niches*

The size of the multidimensional total niche width (TNW) on the prey size and $\delta^{13}C$ axes varied 14-fold across populations (*Figure S3*). This variation was explained by differences in the number of coexisting *Leptodactylus* species and available niche area in the environment, which varied 10-fold across sites (*Table 1*, *Figures 2* and *3*). Frog populations in sites with greater resource breadth had larger TNW, but the presence of competitors seemed to prevent TNW from reaching the largest values observed in one-species sites (*Figure 3*, left). Interestingly, we found a significant interaction between these two predictors (Table 1), indicating that the rate of increase of TNW as a function of the available niche was steeper in sites with one or two *Leptodactylus* species when compared to communities with three congeneric coexisting species (*Figure 3*, right).

In general, the within-individual component of niche variation (WIC, variation in prey size and $\delta^{13}C$ of the resources used by each individual in the population) contributed more to the total population niche than the between-individual component of niche variation (BIC, variation among individuals in average resource use), resulting in a relatively low average degree of individual specialisation (median WIC/TNW = 0.72). WIC and BIC responded differently to the studied gradients. As the area of the available niche increased across communities, individuals became more generalist (increase in WIC), particularly in one- and two-*Leptodactylus* species sites. On the other hand, niche divergence among individuals (BIC) did not respond to gradients of niche availability and competition (*Table 1*, *Figure 4*). As a result, the degree of individual niche variation tended to decrease as population niche expanded, meaning that more generalist populations (large TNW) had relatively lower diet specialisation among individuals (i.e. larger WIC/TNW) because individual niche width expanded faster than population niche width.

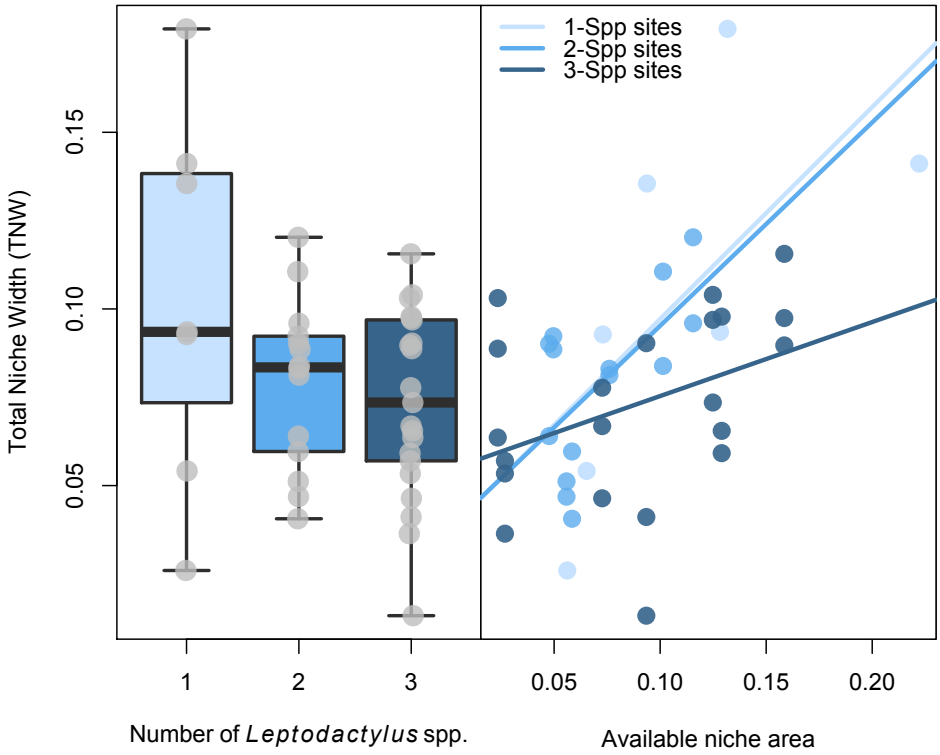



*Figure 3*. Effect of the number of coexisting congeneric species and breadth of available resources on the total niche width (TNW) of populations of tropical frog species (*Leptodactylus* spp.) in the Pantanal wetlands, Brazil.

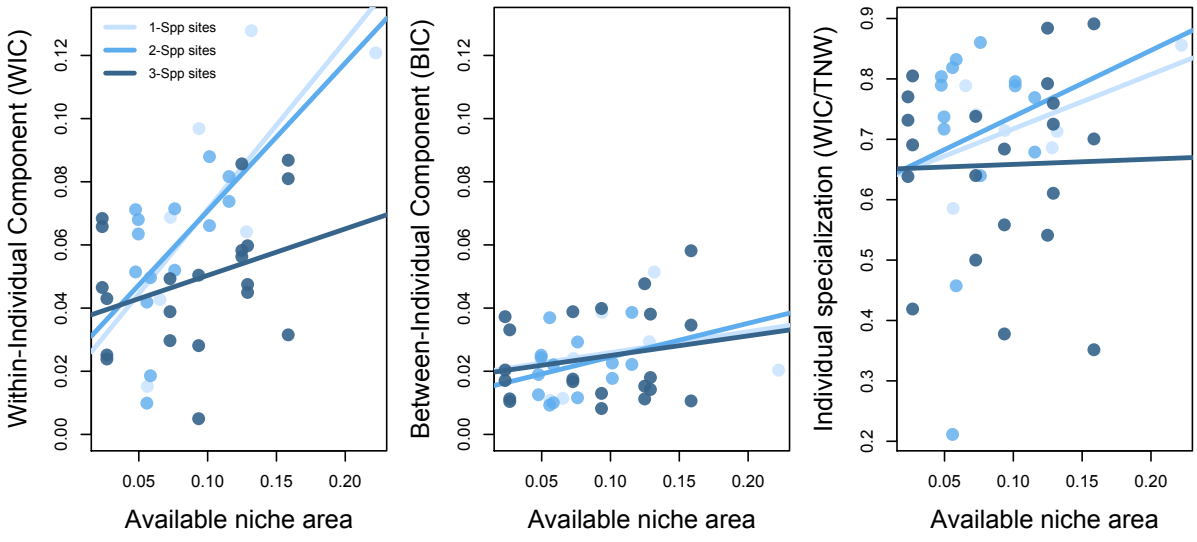



*Figure 4*. Effect of the number of coexisting congeneric species and breadth of available resources on the three niche components of populations of tropical frog species (*Leptodactylus* spp.): within-individual variation (WIC), between-individual variation (BIC), and total niche width (TNW).

*Table 1.* Effects of the presence of congeneric competitors and local resource breadth on multidimensional niche components (total niche width, within- and between individual components (Roughgarden 1972)), individual niche specialisation, and interspecific niche overlap in Thin-toed frogs (*Leptodactylus* spp.).

| Response variable | Intercept | Resource breadth | | | Number of *Leptodactylus* spp. | | | Interaction | | | Total niche width (TNW) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Estimate | $\chi^2$ | p | Estimate | $\chi^2$ | p | Estimate | $\chi^2$ | p | Estimate | $\chi^2$ | p |
| Total niche width (TNW) | 0.034 | 0.78 | 13.88 | <0.001 | 0.007 | 6.71 | 0.03 | -0.19 | 3.64 | 0.05 | | | |
| Within-individual component (WIC) | 0.016 | 0.69 | 14.62 | <0.001 | 0.007 | 8.49 | 0.01 | -0.18 | 4.13 | 0.04 | | | |
| Between-individual component (BIC) | 0.017 | 0.08 | 2.66 | 0.26 | 0.0006 | 0.04 | 0.98 | -0.009 | 0.04 | 0.85 | | | |
| | Intercept | Estimate | z | p | Estimate | z | p | Estimate | z | p | Estimate | z | p |
| Proportion of overlapping niche | -6.547 | 94.17 | 3.27 | 0.001 | 3.18 | 4.05 | <0.001 | -30.49 | -3.09 | 0.002 | -26.51 | -3.93 | <0.001 |
| Individual specialisation (WIC/TNW) | 0.045 | -1.33 | -0.18 | 0.86 | -0.003 | -0.007 | 0.99 | 0.06 | 0.008 | 0.99 | 11.09 | 1.845 | 0.06 |

*Variation in trophic overlap across coexisting species*

The proportion of niche overlap across coexisting *Leptodactylus* populations was highly variable. As expected, unidimensional niche overlap was usually higher than multidimensional overlap (*Figure 5*), ranging from 21% to 100% for prey size and from 46% to 100% for prey $\delta^{13}C$. Considering the overlap calculated from our multidimensional approach, in two-species sites populations showed between 11% and 76% niche overlap with the other species, while in 3-species sites this percentage varied from 40% to 100% (*Figure 6*, left). This observed decrease in overlap is due to a combination of multidimensionality per se and the specific orientation and shape of the niches (*Figure 5*).

The striking variation of nine-fold in multidimensional niche overlap was significantly explained by the focal population's total niche width (TNW), the number of coexisting congeneric species, and the available resource breadth (*Table 1*). As expected, the proportion of overlapping niche decreased with the available resource breadth. However, intriguingly, populations with larger niche area (larger TNW) experienced relatively lower niche overlap (*Figure 6*), suggesting that a decrease in niche breadth does not necessarily reduce overlap across species as predicted by niche theory.

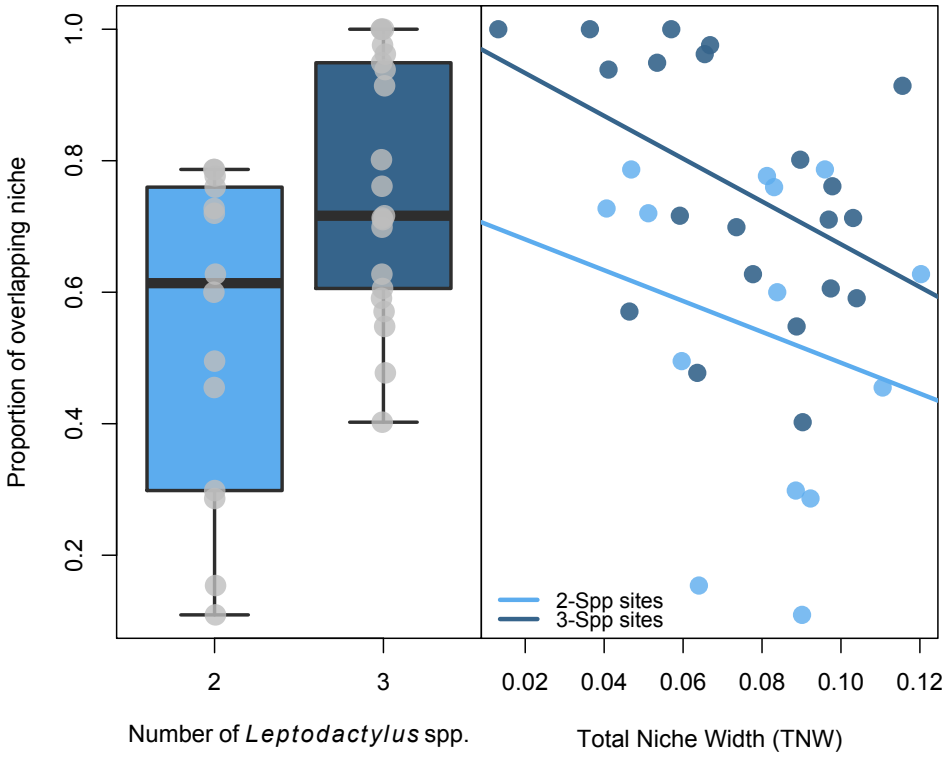



*Figure 6*. Effect of the number of coexisting congeneric species and total niche width (TNW) on the proportion of overlapping niche in populations of tropical frog species (*Leptodactylus* spp.) in the Pantanal wetlands, Brazil.

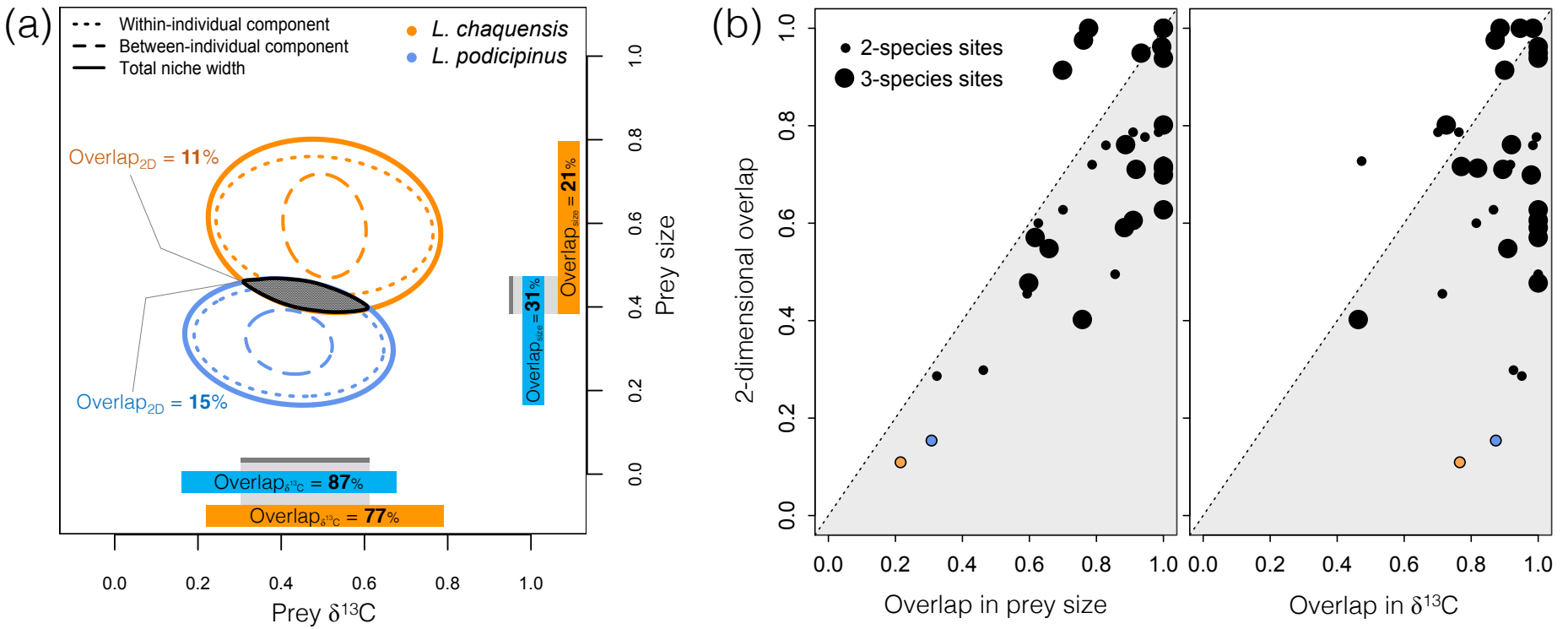



*Figure 5*. (*a*) An example (site LEP08) of how perceived niche overlap between coexisting populations of thin-toed frogs (*Leptodactylus chaquensis* and *L. podicipinus*) may be considerably distinct when one or two trophic dimensions are considered at a time. When niche axes are analysed separately (blue and orange bars), frog populations appear to overlap substantially in prey $\delta^{13}C$ (77 and 87% of overlapping area) and moderately in prey size (21 and 31%). However, given the specific orientationand shape of the bi-dimensional niches ellipses, the amount of perceived overlap is lower than the observed for individual dimensions; (*b*) Relationship between multidimensional (y-axis) vs. unidimensional (x-axes; left panel: prey size, right panel: prey $\delta^{13}C$) estimates of the percentage of overlapping population niche. Dashed line corresponds to the 1:1 relationship. Populations in the grey area had higher unidimensional niche overlap than multidimensional. Orange and blue points indicate the populations of *Leptodatylus chaquensis* and *L. podicipinus* showed in the (*a*).

## Discussion

Ecologists have long been fascinated by patterns of variation in resource use between and within coexisting species. The multidimensionality of niches has been acknowledged for some time, while heterogeneity among individuals within populations has become increasingly apparent in recent years. However, few if any studies have considered both niche dimensionality and individual-level niche variation simultaneously to address the drivers of niche width and niche overlap in coexisting species. By modelling the trophic niches of congeneric tropical frogs in two key dietary dimensions, we showed that the spatial variation in population niche width was mostly accounted for by within-individual diet variation. In line with predictions from classic niche theory, this multidimensional niche variation can be predicted by gradients of resource breadth and species richness across natural communities. These gradients affected not only single species' niches, but also the degree of trophic niche overlap across ecologically similar species. Together, these results emphasise that patterns of multidimensional resource use and differentiation among consumers are highly flexible across ecological contexts, depending strongly on local resource breadth.

### *Population and individual niche variation*

We found the influence of putative interspecific interactions on multidimensional niche breadth to be largely dependent on locally available resources. This context-dependent effect of competition on niche breadth arises because diversity in available prey sizes and $\delta^{13}C$ may enhance the scope for consumer niche expansion (Duffy *et al.* 2007; Sánchez-Hernández, Gabler & Amundsen 2017). Indeed, our results indicate that the diversifying effects of available prey diversity (available niches) on dietary niche width are stronger than the constraining effects of the number of coexisting competitors. Historically, competition has been invoked as the major driver of niche variation in nature, but our findings support the idea that available resource diversity is an important yet neglected force structuring the exploitation of resources in multiple dimensions.

As expected by the Optimal Foraging Theory (Van Valen 1965; Roughgarden 1972), we found that multidimensional population niche width (TNW) expansion occurs predominantly via increased within-individual niche diversity (WIC). In other words, the absence of competitors and increased resource breadth lead individuals to increase their own niche width by adding new resources to the diet (e.g. larger or smaller prey), becoming more generalist. Bolnick *et al.* (2010) refer to this scenario as 'parallel release' because individual and

population niche widths expand accordingly. Although this finding agrees with the optimal foraging theory, which predict that WIC should evolve to approach TNW (Taper & Case 1985; Stephens & Krebs 1986), it contradicts the long-standing niche variation hypothesis (Van Valen 1965), which posits that competitive release leads to an expansion in TNW via greater between-individual variation (BIC) while individual niche widths remain constant. This prediction has received recent empirical support (Bolnick *et al.* 2007; Costa *et al.* 2008; Araújo *et al.* 2009) and is expected when functional trade-offs constrain individuals' ability to incorporate additional prey types, limiting WIC expansion (Wainwright 1996). Therefore, our results suggest that the trophic niches of *Leptodactylus* species are not strongly limited by functional trade-offs (e.g. morphological, physiological, or cognitive constraints) but instead that individuals possess substantial behavioural plasticity to explore alternative resources (but see Araújo *et al.* 2007). Therefore, an interesting research topic for future studies is to elucidate the links between behavioural (e.g. propensity to forage in the presence of risk) and trophic niche variation in natural communities (Toscano *et al.* 2016).

*Context-dependence of niche overlap*

Although the concept of limiting similarity among coexisting species is the backbone of classic niche theory (MacArthur & Levins 1967), we found that the studied syntopic, congeneric frog species exhibit variable and often high (or even complete) trophic niche overlap. As expected, niche overlap was overall higher when calculated from single axis in isolation (i.e., prey size or carbon stable isotopes) than when obtained from two axes simultaneously, corroborating the enduring idea that niche multidimensionality provides more scope for partition between competitors (Hutchinson 1961; Pianka 1976; Pacala & Roughgarden 1982). Unidimensional niche overlap was particularly high when only $\delta^{13}C$ was considered, suggesting that thin-toed frogs tend to partition the trophic niche based mainly on prey size, which may be associated with differences in body size and gape limitation across species (Costa-Pereira *et al.* 2018a).

Even in a multidimensional perspective, thin-toed frogs varied substantially in their degree of niche overlap across communities. This surprising variation was only partially explained by the number of coexisting congeneric species (two or three). The magnitude of resource distribution along prey size and $\delta^{13}C$ dimensions had a strong negative effect on the proportional overlap of the population niche, indicating that diversity of potential resources in these two important dietary dimensions permits niche partitioning among consumers, as has been discussed in theoretical and empirical research considering one trophic niche dimension

(Pianka 1976; Duffy *et al.* 2007; Sánchez-Hernández, Gabler & Amundsen 2017). Importantly, the effects of competition and resource breadth were interactive, meaning that the number of coexisting *Leptodactylus* species limits the increase in population niche width as resource area increases. Together, these findings indicate the need to consider the trophic environment in which species are interacting to understand their niche complementarity across gradients.

The total population niche breadth also affected proportional niche overlap, but the direction of this effect was opposite to what was predicted by niche theory. Niche packing (i.e. narrower niche widths) is traditionally proposed as a key process to decrease interspecific trophic overlap in species-rich communities (Klopfer & MacArthur 1961; MacArthur 1969; Case 1981). In this view, reductions in niche breath tend to decrease interspecific overlap and therefore favor coexistence. However, our results show that populations with large-sized niches exhibit relatively smaller niche overlap with coexisting species. This counterintuitive result suggests that trophic generalism may constitute a strategy to decrease relative overlap within trophic guilds if niche expansion occurs toward regions of unoccupied multidimensional niche space, increasing TNW and niche segregation in trophic space simultaneously. This hypothesis deserves further investigation, likely in experimental systems, and may contribute to the enduring debate on how numerous generalist species can coexist within a trophic guild, particularly in hyperdiverse tropical ecosystems (Polis 1991; Scheffer & van Nes 2006; Orlando & Hall 2015).

*Implications*

Our findings bring new insights to the long-standing debate on how similar species can coexist in a local community. First, our data set including multiple foraging observations per individual allowed us to infer that within-individual variation plays an important role in the dynamics of niche expansion, as is suggested by niche models (Taper & Case 1985; Ackermann, Doebeli & Gomulkiewicz 2004) but rarely empirically evaluated. Further, instead of treating niche area and interspecific overlap as unidimensional properties, we modelled niches in a two-dimensional trophic space, revealing that niche multidimensionality reduces interspecific overlap. Simultaneous consideration of multiple niche dimensions can directly impact the perceived functional role of species in ecosystems (Wojdak & Mittelbach 2007) and the estimation of stabilizing forces in empirical studies (Hart *et al.* 2018). Finally, our results emphasise how strongly species interactions can depend on extrinsic variables such as local resource breadth, which links classic niche theory with recent attempts to understand how

environmental change, such as climate change and habitat conversion, affects species interactions.

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## Supplementary Information

### *Study area*

Our study took place in the Brazilian Pantanal, the largest and most pristine tropical wetland. This highly seasonal system is a mosaic of seasonally flooded grasslands and savannas that experiences a drastic change between the dry and wet seasons. Specifically, we studied four areas (comprising ~ 40,000 km$^2$) in the Pantanal wetlands and surroundings: Base de Estudos do Pantanal-UFMS (central coordinates: 19.494° S, 57.048° W), Bodoquena Plateau (21.384° S, 56.413° W), Gran Chaco (21.683° S, 57.72° W), and Fazenda Barranco Alto (19.559° S, 56.133° W). These geographical regions harbour numerous permanent lagoons and seasonal ponds, which constitute important habitats for anurans (Prado, Uetanabaro & Haddad 2005; Uetanabaro *et al.* 2008).

Despite subtle differences in species composition across these four regions, in all of them local anuran communities around ponds are dominated by thin-toed frogs (genus *Leptodactylus*) both in terms of abundance and biomass (Costa-Pereira *et al.* 2018b). Here, we have focused on the four most common and abundant thin-toed frog species in this geographical region: *Leptodactylus bufonius*, *L. chaquensis*, *L. fuscus*, and *L. podicipinus*. Although differing in reproductive mode and body size (Prado, Uetanabaro & Haddad 2005), frequently more than one of these congeneric species coexist syntopically in local communities, exploring overlapping food resources and microhabitats.

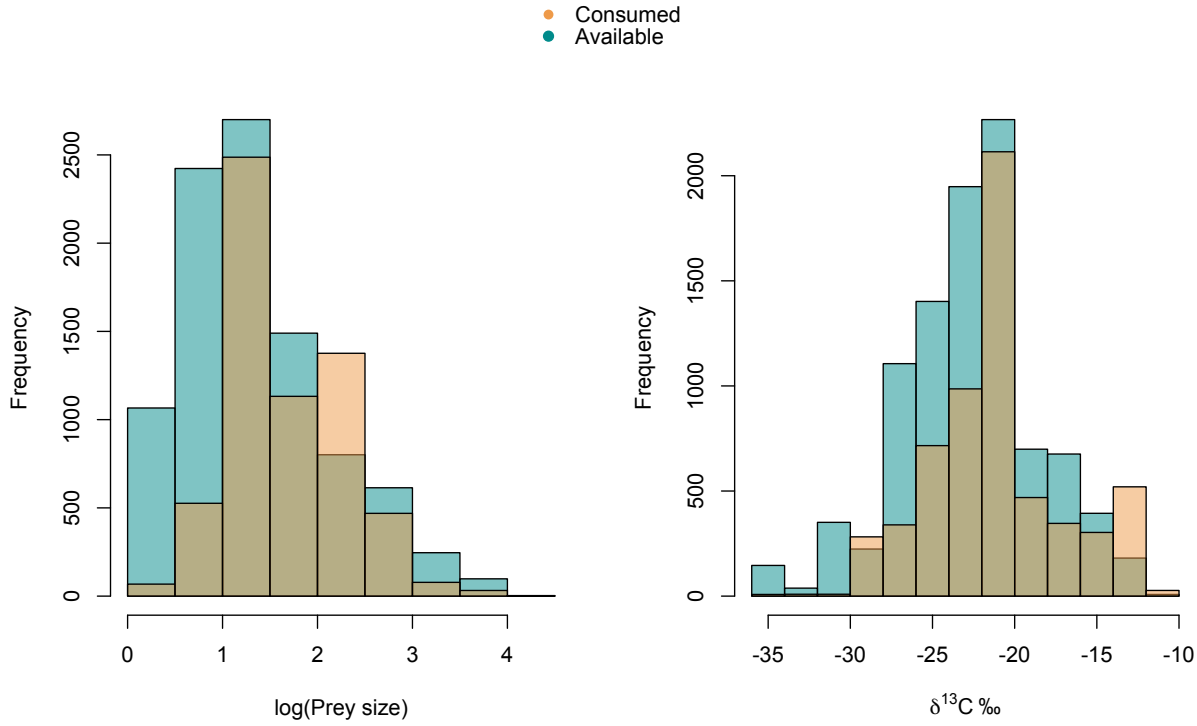



*Figure S1.* Distribution of consumed (orange) *vs.* available (green) prey in two niche dimensions: body size (log-transformed, left panel) and carbon stable isotopes ($\delta^{13}C$).

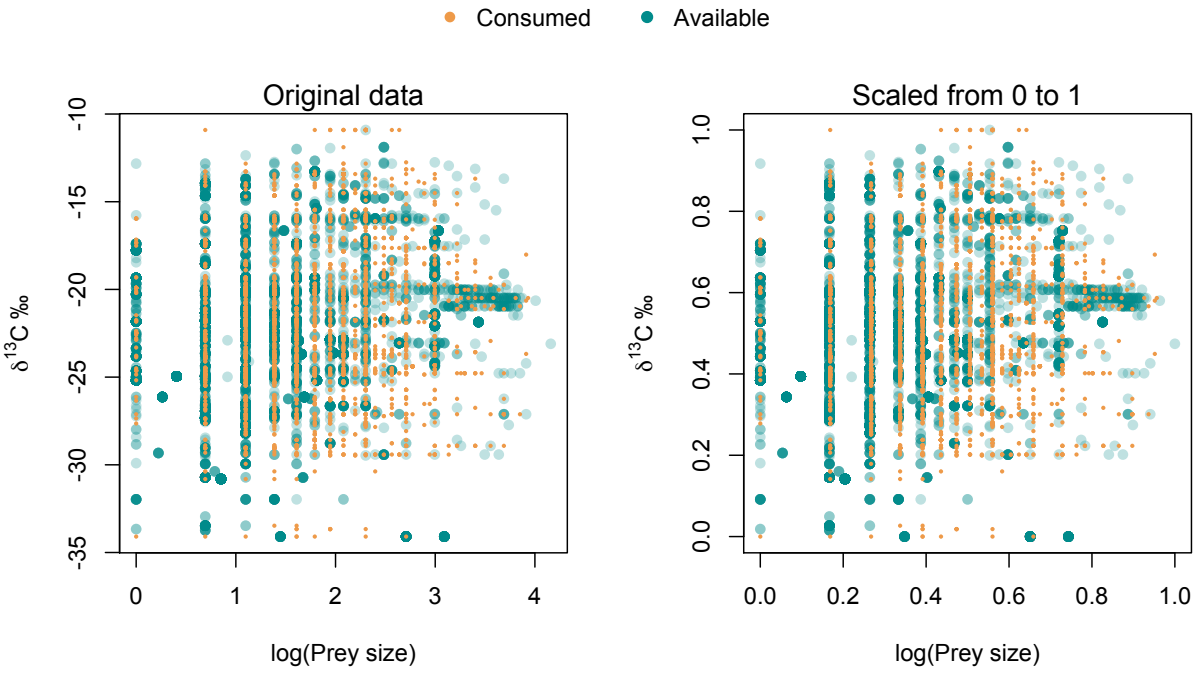



*Figure S2.* Biplot showing the distribution of available and consumed prey in original data (left panel) *vs* rescaled data to vary between 0 and 1 (right panel). For the sake of interpretability, this transformation is necessary because prey size and carbon stable isotopes vary in different scales.

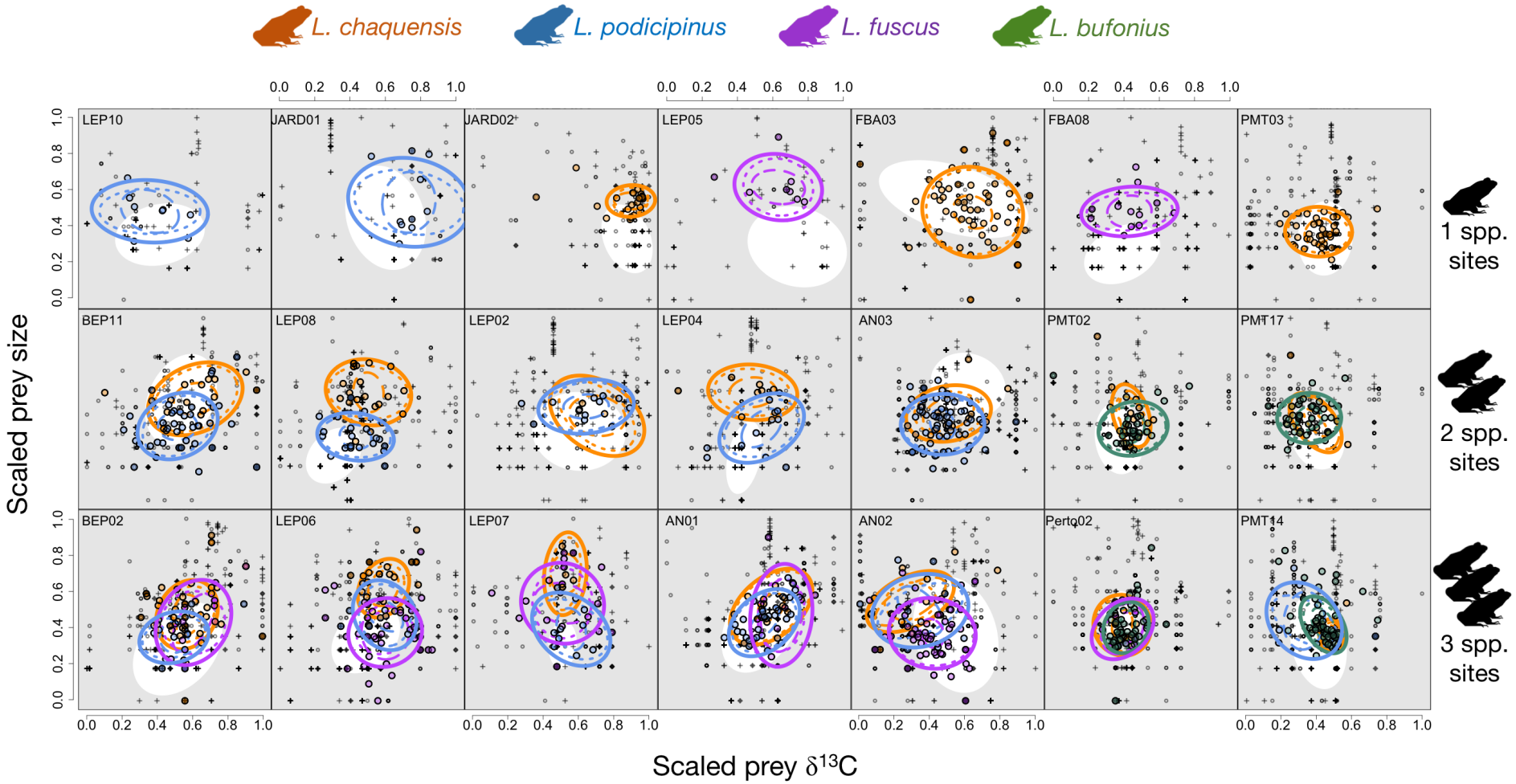



*Figure S3*. Representation of available and realised individual-level trophic interactions for tropical frog species (*Leptodactylus* spp.) in the 21 studied sites. Available prey items at each sampling site along body size and $\delta^{13}C$ niche axes are represented with "+" and local prey breadth is represented by the white-filled ellipse. Realised trophic interactions (i.e., each prey item found in gut contents) are shown as unfilled grey circles and individual frogs' means of prey size and $\delta^{13}C$ are the same plot indicated by filled circles. Finally, the variance-covariance matrices corresponding to between- and within-individual niche components (WIC and BIC) and the corresponding total niche width (TNW) for each frog population are represented by dashed, dotted, and continuous coloured lines, respectively.

*Table S1.* Summary table presenting number of individuals, mean (and standard deviation) prey size (mm) and $\delta^{13}C$, and top-consumed prey for 42 populations of four species of tropical frog species (*Leptodactylus* spp.) in the 21 studied sites in the Pantanal wetlands, Brazil.

| Pop | Site | Species | Number of individuals | Mean prey size | SD prey size | Mean prey $\delta^{13}C$ | SD prey $\delta^{13}C$ | Top-consumed prey type |
|---|---|---|---|---|---|---|---|---|
| 1 | AN01 | *L. chaquensis* | 16 | 8.16 | 5.54 | -19.96 | 3.39 | Microlepidoptera |
| 2 | AN01 | *L. fuscus* | 10 | 6.33 | 5.71 | -19.17 | 1.89 | Formicidae |
| 3 | AN01 | *L. podicipinus* | 33 | 5.53 | 3.99 | -20.51 | 2.96 | Formicidae |
| 4 | AN02 | *L. chaquensis* | 14 | 7.69 | 6.36 | -25.79 | 2.92 | Isoptera |
| 5 | AN02 | *L. fuscus* | 12 | 8.61 | 7.32 | -23.64 | 3.75 | Formicidae |
| 6 | AN02 | *L. podicipinus* | 54 | 5.57 | 4.91 | -22.77 | 3.59 | Formicidae |
| 7 | AN03 | *L. chaquensis* | 11 | 7.74 | 4.63 | -22.08 | 3.13 | Microlepidoptera |
| 8 | AN03 | *L. podicipinus* | 60 | 7.06 | 4.88 | -22.15 | 3.31 | Microlepidoptera |
| 9 | BEP02 | *L. chaquensis* | 46 | 7.35 | 7.18 | -23.70 | 2.99 | Formicidae |
| 10 | BEP02 | *L. fuscus* | 10 | 6.45 | 5.45 | -23.38 | 3.25 | Formicidae |
| 11 | BEP02 | *L. podicipinus* | 11 | 4.45 | 2.22 | -25.02 | 3.22 | Formicidae |
| 12 | BEP11 | *L. chaquensis* | 15 | 10.13 | 7.62 | -21.04 | 3.72 | Acrididae |
| 13 | BEP11 | *L. podicipinus* | 41 | 5.82 | 4.32 | -22.72 | 3.25 | Formicidae |
| 14 | FBA03 | *L. chaquensis* | 46 | 8.06 | 6.76 | -22.21 | 5.08 | Formicidae |
| 15 | FBA08 | *L. fuscus* | 12 | 7.02 | 3.66 | -24.45 | 3.57 | Pentatomidae |
| 16 | JAR01 | *L. podicipinus* | 10 | 6.04 | 3.94 | -16.23 | 4.47 | Arachnida |
| 17 | JAR02 | *L. chaquensis* | 28 | 7.86 | 2.34 | -13.85 | 1.73 | Isoptera |
| 18 | LEP02 | *L. chaquensis* | 10 | 7.79 | 9.40 | -16.74 | 3.28 | Isoptera |
| 19 | LEP02 | *L. podicipinus* | 11 | 7.96 | 4.86 | -18.08 | 3.75 | Coleoptera |
| 20 | LEP04 | *L. chaquensis* | 10 | 11.17 | 6.34 | -20.22 | 3.48 | Isoptera |
| 21 | LEP04 | *L. podicipinus* | 12 | 5.84 | 3.60 | -19.80 | 3.41 | Isoptera |
| 22 | LEP05 | *L. fuscus* | 10 | 11.71 | 6.75 | -18.36 | 3.59 | Grylidae |
| 23 | LEP06 | *L. chaquensis* | 23 | 12.19 | 7.76 | -23.21 | 2.31 | Formicidae |
| 24 | LEP06 | *L. fuscus* | 11 | 7.48 | 6.05 | -22.30 | 2.84 | Isoptera |
| 25 | LEP06 | *L. podicipinus* | 35 | 5.53 | 4.31 | -22.43 | 3.49 | Formicidae |
| 26 | LEP07 | *L. chaquensis* | 10 | 15.60 | 8.95 | -20.48 | 1.30 | Cicindelidae |
| 27 | LEP07 | *L. fuscus* | 17 | 8.95 | 6.77 | -20.88 | 3.86 | Formicidae |
| 28 | LEP07 | *L. podicipinus* | 10 | 5.02 | 4.39 | -19.85 | 3.54 | Cicadellidae |
| 29 | LEP08 | *L. chaquensis* | 22 | 10.33 | 6.37 | -22.95 | 3.52 | Cicindelidae |
| 30 | LEP08 | *L. podicipinus* | 21 | 4.17 | 2.12 | -24.16 | 3.09 | Coleoptera |
| 31 | LEP10 | *L. podicipinus* | 10 | 8.76 | 5.42 | -25.20 | 4.50 | Diptera larvae |
| 32 | Per02 | *L. bufonius* | 11 | 6.38 | 4.68 | -22.11 | 2.80 | Formicidae |
| 33 | Per02 | *L. chaquensis* | 52 | 5.10 | 3.90 | -21.90 | 2.38 | Formicidae |
| 34 | Per02 | *L. fuscus* | 10 | 4.68 | 2.14 | -21.75 | 2.35 | Formicidae |
| 35 | PMT02 | *L. bufonius* | 12 | 5.37 | 4.78 | -21.15 | 1.64 | Isoptera |
| 36 | PMT02 | *L. chaquensis* | 33 | 5.04 | 3.57 | -21.05 | 3.50 | Formicidae |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 37 | PMT03 | *L. chaquensis* | 40 | 4.38 | 3.47 | -21.83 | 3.35 | Isoptera |
| 38 | PMT14 | *L. bufonius* | 13 | 4.09 | 2.03 | -20.51 | 1.07 | Isoptera |
| 39 | PMT14 | *L. chaquensis* | 57 | 5.89 | 5.23 | -21.47 | 2.41 | Isoptera |
| 40 | PMT14 | *L. podicipinus* | 10 | 6.00 | 5.53 | -24.25 | 3.77 | Formicidae |
| 41 | PMY17 | *L. bufonius* | 10 | 4.47 | 2.37 | -21.18 | 1.63 | Isoptera |
| 42 | PMT17 | *L. chaquensis* | 40 | 5.69 | 3.55 | -22.37 | 3.31 | Isoptera |

# Capítulo 4

# Fitness consequences of individual variation in niche trajectories

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## Abstract

Fitness variation across individuals is central to population growth, species coexistence and eco-evolutionary dynamics, yet the drivers of variation in reproductive and somatic allocation within natural populations remain underexplored. Particularly, as cumulative foraging decisions strongly influences fitness, the temporal dimension of individual diet change potentially have major fitness implications. We used multi-tissue stable isotopes to determine isotopic niche trajectories within species, populations and sexes of thin-toed frogs and then explored how this temporal dimension of diet change affects individual reproductive investment, body condition and parasite load. Null model comparisons revealed that individual frogs shifted their diets less than expected by chance, likely due to functional tradeoffs that limit the incorporation of new prey types over time. Yet, within this universal constraint, individuals which modified their diet to a greater degree exhibited higher fitness, though this effect was species and sex-dependent. We suggest that these different relationships between isotopic niche trajectory length and fitness within thin-toed frogs are driven by variability in the resource environment, negative density-dependence and allometric constraints. These strong fitness effects suggest that the temporal dimension of diet change is a potential target of natural selection and, therefore, drive correlated evolution in phenotypic and behavioral traits underlying diet flexibility. Finally, our results have important implications to community theory by providing a mechanistic understanding on how variability in per capita contribution to population growth emerge via temporal niche variation.

*Key-words:* stable isotopes, reproductive investment, body condition, *Leptodactylus*, trophic niche, parasites, individual specialization.

## Resumo

A variação de valor adaptativo entre indivíduos desempenha um papel chave para o crescimento populacional, coexistência de espécies e dinâmicas ecoevolutivas. Apesar de tal importância, os fatores que geram e mantem a variabilidade na alocação reprodutiva e somática dentro de populações naturais continuem pouco explorados. Como sucessivas decisões de forrageio influenciam o valor adaptativo, a dimensão de mudança temporal da dieta de indivíduos pode ter importantes implicações para o valor adaptativo. Nós usamos isótopos estáveis de dois tecidos com diferentes taxas de incorporação para determinar trajetórias isotópicas de nicho em espécies, populações e sexos em rãs e, então, explorar como essa dimensão temporal de mudança na dieta afeta o investimento reprodutivo, a condição corpórea, e a carga parasitaria de indivíduos. Modelos nulos revelaram que a indivíduos de rãs mudaram suas dietas menos do que seria esperado ao acaso, provavelmente devido a demandas conflitantes que limitam a inclusão de novos tipos de presa à dieta. Mesmo com essa limitação, os indivíduos que modificaram mais sua dieta apresentaram maiores valores adaptativos, embora esse efeito seja dependente da espécie e do sexo em questão. Nós sugerimos que as diferentes relações observadas entre a magnitude das trajetórias isotópicas de nicho e o valor adaptativo de indivíduos sejam relacionadas a variabilidade temporal de recursos no ambiente, dependência de frequência negativa e limitações alométricas. Os efeitos observados sugerem que a dimensão temporal de variação de nicho pode ser um potencial alvo para a seleção natural e, portanto, levaram à evolução de atributos fenotípicos e morfológicos associados a tal flexibilidade. Finalmente, nossos resultados têm implicações importantes para a teoria de comunidades por fornecerem uma base mecanística para o entendimento de como a variabilidade na contribuição per capita para o crescimento de populações emerge através de da variação temporal de nicho.

*Palavras-chave:* isótopos estáveis, investimento reprodutivo, condição corpórea, *Leptodactylus*, nicho trófico, parasitas, especialização individual.

## Introduction

Fitness and niche variation are key to ecological and evolutionary dynamics across biological scales. Particularly, community theory explores how species-level fitness and niche differences between competitors affect diversity and stability (Chesson 2000; Vellend 2010). This *mean field* approach assumes subtly that individuals are ecologically and demographically equivalent, an analytically tractable approximation (Clark *et al.* 2007; Bolnick *et al.* 2011). However, ecologists have recently reconsidered this simplification because of the increasingly recognized relevance of intraspecific variation. First, individual variation in fitness underpins selection and adaptation (Hallgrímsson & Hall 2005), which are central processes driving eco-evolutionary dynamics (Hendry 2016). Moreover, mounting evidence across diverse taxa suggests that individuals *within* populations often differ in their resource use (Bolnick *et al.* 2003; Araújo, Bolnick & Layman 2011), which have important community-structuring effects (Bolnick *et al.* 2011; Violle *et al.* 2012; Hart, Schreiber & Levine 2016).

Although niche theory has long supposed that individual niche variation leads to intrapopulational fitness differences (Van Valen 1965; Schoener 1971), we still know little about how these facets of individual variability are associated in natural populations (Grémillet *et al.* 2008; Cucherousset *et al.* 2011; Kernaléguen *et al.* 2016). Because resource uptake and the consequent allocation of energy and nutrients for reproduction and growth strongly influence fitness (Schoener 1971), variation in foraging strategies may constitute an important phenomenon shaping variation in per capita contribution to population growth (Bolnick *et al.* 2011; Bolnick & Araújo 2011).

Classic foraging theory compares the energetic and nutritional benefits of diet generalist *vs.* diet specialist strategies (Van Valen 1965; Schoener 1971). Indeed, natural populations of diverse taxa are often a mixture of both individual trophic specialists and generalists (Werner, Mittelbach & Hall 1981; Golet *et al.* 2000; Estes *et al.* 2003; Powell & Taylor 2017). However, individuals do not necessarily have temporally-fixed foraging strategies. For example, certain individuals within populations may shift their diets over time, while others may have relatively constant diets (Bearhop *et al.* 2004; Martínez del Rio *et al.* 2009). Although this temporal dimension of individual foraging strategies is rarely considered in trophic studies (Warburton, Retif & Hume 1998; Novak & Tinker 2015; Szigeti *et al.* 2018), it may be particularly relevant in the context of individual fitness variation because reproductive and somatic allocation depends on multiple cumulative foraging events (Metcalfe & Monaghan 2001).

Theory suggest that the fitness consequences of temporally-invariant vs. temporally-flexible diets depend on environmental context (Bolnick *et al.* 2003; Estes *et al.* 2003; Patrick & Weimerskirch 2014). Because each prey type presents specific costs and benefits, consumer individuals with a consistent diet may optimize their intake by repeatedly consuming persistent and profitable resources; e.g., prey types with decreased handling time, higher digestibility, lower pathogen loads (Stephens & Krebs 1986). In turn, temporally flexible diets come at the cost of the '*Jack of all trades-master of none*' principle, which states that individuals with high performance on one resource will necessarily perform poorly on other resources (MacArthur 1972). Yet, these predictions only hold when resource availability is high and stable. Other ecological contexts, such as temporal fluctuations in prey availability and competition for highly profitable resources, may reduce the benefits of temporal diet consistency (Svanbäck & Bolnick 2005; Svanbäck & Bolnick 2007; Costa-Pereira *et al.* 2017), instead favoring generalist foraging strategies due to an access to wider range of resources (Van Valen 1965; Roughgarden 1972).

In organisms with seasonal reproduction, patterns of resource intake prior to reproductive bouts are crucial in determining individual fecundity and growth. In wetland thin-toed frogs (*Leptodactylus* spp), the beginning of the rainy season triggers an intense foraging period (after months of low activity and metabolic rates during the dry season) during which frogs accumulate fat and energy to subsequent reproduction a few months later (Prado, Uetanabaro & Haddad 2005; Uetanabaro *et al.* 2008). During this window, environmental resource availability shifts gradually (Junk *et al.* 2011; Wantzen *et al.* 2011) and thin-toed frogs consume a wide spectrum of prey types (~70 invertebrate families, fish, anurans), though not without considerable individual specialization (Costa-Pereira *et al.* 2018b). Here we used multi-tissue stable isotopes to evaluate whether the consistency of individuals' trophic niches over this key foraging period leads to different fitness payoffs.

Stable isotopes are powerful tools to characterize trophic niches because, among other reasons, they allow understanding resource use by organisms over distinct temporal scales (Dalerum & Angerbjörn 2005; Newsome *et al.* 2007). This application is particularly useful when stable isotopes from the same organism are measured in body tissues that differ in the rate at which they incorporate new materials, i.e., turnover rate (Schmidt *et al.* 2007; Martínez del Rio *et al.* 2009). By comparing isotope values of body tissues with distinct turnover rates, it is possible to quantify the temporal consistency of individual diet through isotopic niche trajectories (*Figure 1*), because individuals with temporally consistent diets have more similar

isotope values across tissues than individuals with temporally variable diets (Martínez del Rio *et al.* 2009).

Here, we quantified the extent and direction of trophic niche trajectories across individuals, sexes, and species in two species of thin-toed frogs. Specifically, we asked (*i*) whether individual niche trajectories are smaller (i.e. more consistent diets) or larger (i.e. more flexible diets) than expected by chance. Then, to understand temporal diet shift congruence across individuals, we asked (*ii*) whether niche trajectories show trends in directionality towards specific prey. Finally, we investigated (*iii*) how variation in the magnitude of niche trajectories affects three components of individual fitness: reproductive investment, body condition, and parasite load. Because thin-toed frogs inhabit dynamic environments, we expected that individuals with larger niche trajectories (more flexible diets) should exhibit less parasites, be richer in body condition, and have increased reproductive investment. Accordingly, individuals should exhibit niche trajectories larger than expected by chance. Regarding the directionality, we expected that individuals should converge their diets towards optimal resources along the foraging season, resulting in directional niche trajectories in the isotopic space.

## Material and methods

### *Study system*

We studied thin-toed frog populations in the Pantanal wetlands, the largest and most pristine continental wetland (Junk *et al.* 2011). The Pantanal is a seasonal system with a peculiar annual flood regime that influences the life history of native anurans. During the dry season (usually from April to late September in southern Pantanal) many frog species reduce their activity and metabolism to avoid hot and low-humidity conditions (Uetanabaro *et al.* 2008). By the end of the summer, however, the runoff of rainfall waters from surrounding highlands floods ~80% of the Pantanal's area (Junk *et al.* 2011). Because predatory fish and water bugs (mainly Belostomatidae, Hemiptera, Odonata larvae) are highly abundant in these floodplains, most local frog species breed in ponds and lagoons before the beginning of flooding season to avoid predation on their eggs and larvae (Prado & Haddad 2005). Therefore, the annual alternation of dry and flooded seasons, both adverse to reproduction, forces anuran species to temporally concentrate their reproductive activities between the peaks of these contrasting periods (Prado,

Uetanabaro & Haddad 2005; Uetanabaro *et al.* 2008). Here, we aim to understand how foraging consistency within this temporal window affects subsequent reproduction.

We investigated niche and fitness variation in two congeneric species of thin-toed frogs, *Leptodactylus chaquensis* and *L. podicipinus*. Within the Pantanal, these syntopic species are particularly abundant and exhibit considerable diet overlap (Piatti & Souza 2011; Costa-Pereira *et al.* 2018b). Both species forage on the ground and in low vegetation at night, feeding on a large variety of invertebrate and small vertebrate prey (Costa-Pereira *et al.* 2015; Costa-Pereira *et al.* 2018b). However, because *L. podicipinus* is smaller (max size: ~50 mm), this species tends to consume smaller-sized and less diverse prey types when compared to *L. chaquensis* (max size: ~100 mm) (Costa-Pereira *et al.* 2018a). Despite some differences in their reproductive activities, both species deposit eggs in foam nests in water-filled depressions at the edges of water bodies in which exotrophic tadpoles develop (Prado, Uetanabaro & Haddad 2005). As males and females assume different reproductive roles in *Leptodactylus* spp. (Prado, Uetanabaro & Haddad 2005), we tested whether putative fitness payoffs are sex-specific.

### *Field and lab data collection*

We sampled 15 populations of *Leptodactylus chaquensis* and 12 of *L. podicipinus* around 21 grassland lagoons in an extensive Pantanal area (encompassing four different regions) between mid-November 2014 and early January 2015. In each sampled site, we established six 10 x 10 m plots and hand-captured all individuals of *L. chaquensis* and *L. podicipinus*. Frogs were euthanized with an overdose of lidocaine and then stored in a -20°C freezer until laboratory processing. Collection and euthanasia procedures were carried out in accordance with Universidade Estadual Paulista guidelines for the care of vertebrate animals (UNESP Animal Care and Use Committee 03120501).

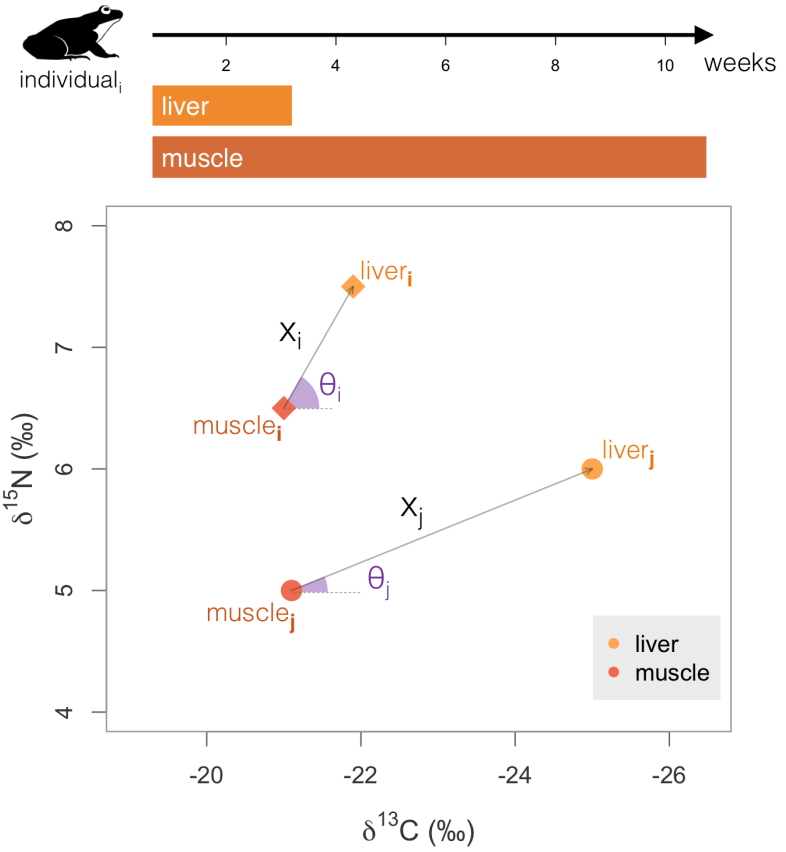



*Figure 1.* Schematic representation of niche trajectory length and angle of change for two individuals *i* and *j* in the isotopic δ-niche space. A niche trajectory is defined as the vector between stable isotope values ($\delta^{15}N$ and $\delta^{13}C$) from muscle and liver, respectively, from a given individual. Because muscle isotope values reflect dietary carbon and nitrogen intake over several months and liver reflects intake along the last few weeks, niche trajectories (represented by arrows in the plot) measure temporal consistency of individuals' diets. We used vector arithmetic to calculate two properties of niche trajectories: length (i.e., magnitude of change) and direction (i.e., angle of change). Trajectory length ($X_i$) increases as the diet of an individual is less consistent over time. In turn, variation in angle of change ($\theta_i$) indicates the direction in which individuals' diets temporally shift regarding prey trophic level (δ15N, vertical shift) and prey position in food webs ($\delta^{13}C$, horizontal shift; e.g., C4 vs. C4 food chains). In this hypothetical example, both individuals feed on prey at increasingly higher trophic (vertical change) and towards higher $\delta^{13}C$ values (i.e., C4 food chain, horizontal change) positions over time.

In the laboratory, we measured snout-vent length (0.01 mm) and body mass (0.001 g) of each adult specimen of *L. chaquensis* (n = 296) and *L. podicipinus* (n = 267). We then dissected adult frogs to obtain gonads and weighed testes (*Figure 2*c) or mature ovaries and eggs (only mature females with fully developed eggs were analyzed) using a precision scale (0.00001 g). During dissection, we inspected each frog's body cavity, digestive tract, kidneys, liver, urinary bladder, lungs and musculature for helminth parasites (*Figures 2*a and *2*b). Due to challenges in identifying Neotropical anuran parasites to precise taxonomic scales (Campião *et al.* 2014), we counted the total abundance of helminth parasites found in each individual frog as a measure of parasite load. Aggregate helminth abundance is a strong predictor of the negative effects of parasites on anuran hosts growth and survival (Goater & Ward 1992).

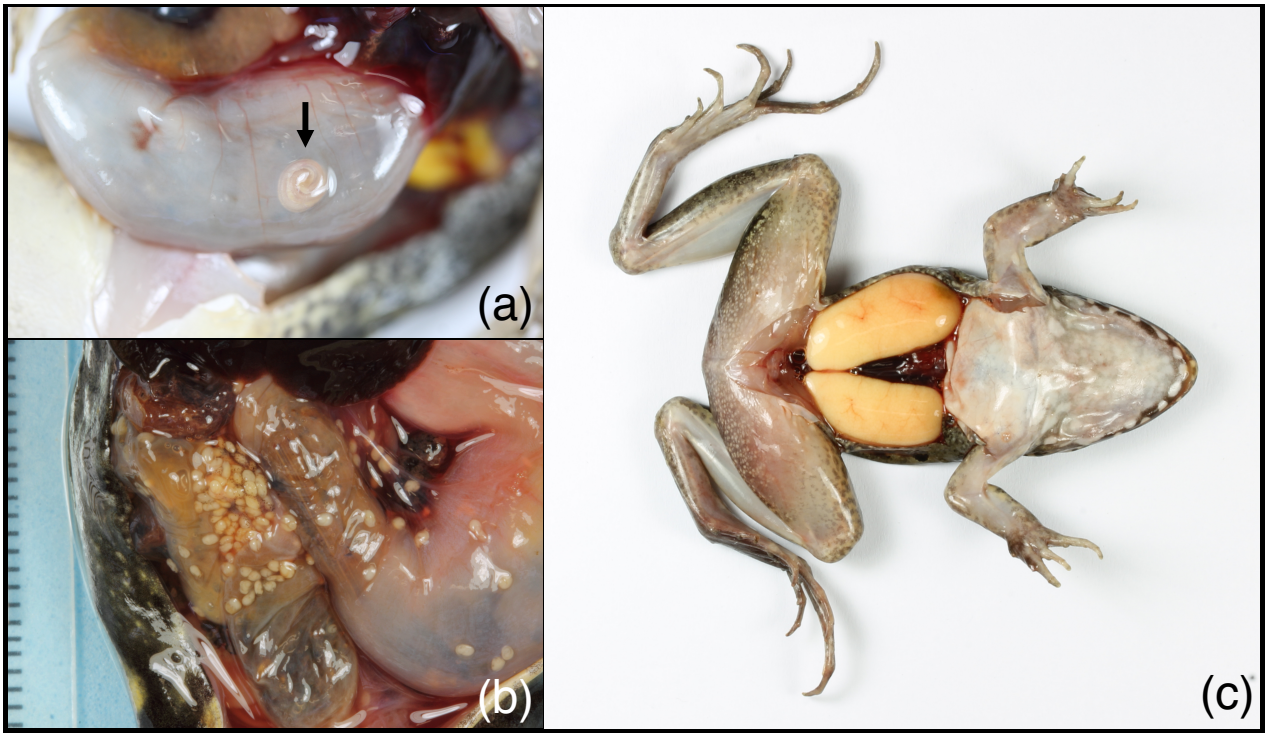



*Figure 2.* (*a*) and (*b*), examples of helminth parasites found in thin-toed frogs' body cavity; (*c*) testes of a *Leptodactylus chaquensis* specimen.

To quantify stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) we removed pieces (~ 1 $cm^3$) of muscle and liver from each individual and rinsed them in deionized water. We then oven-dried samples for 48 h at 60°C and placed ground and weighed samples (~0.5 mg) into tin capsules. Because C:N ratios were generally low (<4), we did not extract lipids from our samples or mathematically correct for lipid content (Post *et al.* 2007). The abundances of

$^{13}C/^{12}C$ and $^{15}N/^{14}N$ were quantified at the Washington State University Stable Isotope Core Laboratory using an Elemental Combustion System 4010 elemental analyzer (Costech Analytical, Valencia, CA, USA) and a Delta Plus XP continuous flow isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany). We report isotope compositions using conventional delta notation, showing differences between the observed concentration and that of Pee Dee Belemnite for carbon and atmospheric $N_2$ for nitrogen. The standard deviation of replicates of the internal reference material (Nylon) was 0.03‰ for $\delta^{13}C$ and 0.06‰ for $\delta^{15}N$.

*Using stable isotopes to quantify niche trajectories*

Multi-tissue stable isotopes analyses are particularly useful to investigate temporal changes in individual trophic niches. By comparing the isotopic values of body tissues deposited at different times, it is possible to identify individuals that shift diets over time and individuals with relatively constant diets (i.e., feed on the same resources over time) (Martínez del Rio *et al.* 2009). We used liver and muscle to represent different trophic temporal scales: liver has a higher turnover rate and its isotopic values represent integration of dietary inputs along the last few weeks, while muscle has a relatively low turnover rate and its isotope values reflects dietary carbon and nitrogen intake over several months (Tieszen *et al.* 1983; Dalerum & Angerbjörn 2005).

We compared isotope values of liver and muscle to quantify the temporal consistency of individual diet, i.e., isotopic niche trajectories. Vector arithmetic is used to calculate two key properties of niche trajectories in the bivariate isotopic δ-space: length (i.e., magnitude of change) and direction (i.e., angle of change, $\theta_i$) (Schmidt *et al.* 2007; Martínez del Rio *et al.* 2009) (*Figure 1*). The utility of these properties to quantify niche variation hinges on the idea that individuals with temporally consistent diets have more similar liver and muscle isotope values than individuals with temporally variable diets (Martínez del Rio *et al.* 2009).

First, we determined the vector representing the niche trajectory between muscle $\delta^{13}C$ and $\delta^{15}N$ (starting point) and liver $\delta^{13}C$ and $\delta^{15}N$ (endpoint) for each individual (*Figure 1*). Then, we quantified the length of each individual niche trajectory ($X_i$) as the Euclidean distance between muscle and liver $\delta^{13}C$ and $\delta^{15}N$ values:

$$X_i = \sqrt{(muscle_i\ \delta^{13}C - liver_i\delta^{13}C)^2 + (muscle_i\delta^{15}N - liver_i\delta^{15}N)^2}$$

To quantify the angle of change $\theta_i$ (*Figure 1*), we measured the counter clockwise angle between the positive x-axis and the vector representing niche trajectories, which may result in values from a circular distribution ranging from 0 to 360° (or 0 to 2π). In biological terms, differences in the angle of change indicate that individuals' isotopic values temporally shift regarding trophic level ($\delta^{15}N$, vertical shift) and ultimate carbon sources ($\delta^{13}C$, horizontal shift; e.g., C3 vs. C4 food chains, aquatic vs. terrestrial primary production) (Dalerum & Angerbjörn 2005; Newsome *et al.* 2007).

*Are niche trajectories random walks in the trophic space?*

We constructed null models to test whether (*i*) the length of observed niche trajectories is shorter than expected by chance; and (*ii*) observed turning angles show signs of directionality or assume a uniform circular distribution. First, for each subset of individual trajectories from a given sex from a given species (i.e. *L. chaquensis* females, *L. chaquencis* males, *L. podicipinus* females, *L. podicipinus* males), we computed the observed mean niche trajectory length ($\bar{X}_i$) and the Rao's spacing statistic (*U*). Rao's spacing test aims to measure the uniformity of circular data by aggregating the deviations between consecutive angular observations, resulting in larger *U* values as directionality increases (i.e. less deviation in angles of change between individuals' trajectories) (Jammalamadaka & Sengupta 2001). We calculated all circular statistics in the R package *circular* (Agostinelli & Lund 2013).

Then, we performed a randomization process to produce stochastic individual niche trajectories in the isotopic space. For each individual, we held constant the observed isotopic starting point (muscle $\delta^{13}C$ and $\delta^{15}N$ values) and then assigned the isotopic endpoint by drawing randomly a pair of liver $\delta^{13}C$ and $\delta^{15}N$ values from the distribution of observed liver isotope values within the group of the focal individual, i.e., trajectories' endpoint can assume isotope values observed in the conspecific individuals, from the same sex, and that were captured in the same local site. We then generated the random distributions of mean niche trajectory length and Rao's spacing statistic observed for species and sex. We used 10,000 replicates in Monte Carlo bootstrap simulations to obtain P-values for these metrics.

### *Fitness-related metrics*

Lifetime fecundity and survivorship are very difficult to measure in most of natural populations of vertebrates. Therefore, we quantified three widely used proxies for these fitness components: reproductive investment, body condition, and parasite load. Reproductive investment was quantified as the percentage of mass of mature ovaries and eggs (for females) or testis (for males) relative to total body mass (Prado & Haddad 2005). We calculated a metric for parasite load by dividing the total number of parasites found in each individual by its somatic body mass. Finally, to quantify individual body condition we used the scaled mass index (Peig & Green 2009), which is body size independent and can readily be used to compare different populations (Peig & Green 2010):

$$\widehat{M_i} = M_i \left(\frac{L_0}{L_i}\right)^e$$

where $\widehat{M_i}$ is the scaled body condition index, $M_i$ and $L_i$ are respectively body mass and snout-vent length of the individual $i$, $e$ is the scaling exponent estimated by the standardized major axis linear regression of *ln*(body mass) on *ln*(snout vent length), and $L_0$ is the arithmetic mean value of $L$ for the study population.

To account for multicollinearity among fitness components and summarize their main patterns of variation, we used a principal component analysis (PCA) on the correlation matrix. Then we used the resulting principal component in subsequent analyses.

### *Statistical Analyses*

We performed all statistical analyses in R 3.5.1. For each sex, we tested how individual-level fitness components respond to variation in niche trajectories using linear mixed-effects models in the package *lme4* (Bates *et al.* 2014). We included principal component 1 or 2 from PCA (see details below in *Effects of niche trajectories on individual fitness*) as the response variable, site identity as the random effect, and three predictors interacting with species identity: *1*) niche trajectory length $X_i$ and the *2*) sine and *3*) cosine of the trajectory angle of change $\theta_i$. Because $\theta_i$ is a circular variable (i.e. the beginning of the scale is the same as the end, 0° = 360°) it is problematic to directly use it as a predictor of a linear model. Therefore, we decomposed $\theta_i$ into its sine and cosine and used these as predictors in our model (Cox 2006) representing, respectively, vertical ($\delta^{15}N$) and horizontal ($\delta^{13}C$) components of niche direction.

## Results

### *Variation in individual niche trajectories*

Thin-toed frogs were widely dispersed in isotopic niche space (*Figure 3*). The length of isotopic niche trajectories varied across individuals up to 100-fold for *L. podicipinus* and 55-fold for *L. chaquensis* (*Figures 3*, *S1*). Even when we consider only variation within a given population, niche trajectory length varied up to 83-fold. In biological terms, this means that individuals vary strikingly in the consistency of their feeding strategies along the foraging period that precedes reproduction. While some individuals presented very similar isotope values in their liver and muscle, indicating a temporally consistent diet (a small isotopic niche trajectory), others presented remarkably distinct isotopic variation across tissues, revealing sizable temporal diet change (a large isotopic niche trajectory) (*Figures 3*, *S1*). Despite the high degree of niche variation observed for some individuals, null models revealed that observed mean niche trajectory length was smaller than expected by chance for both sexes in *L. podicipinus* ($p_{females}$ = 0.006, $p_{males}$ = 0.002) and for females in *L. chaquensis* ($p_{females}$ = 0.002, $p_{males}$ = 0.26) (*Figure 4*, left panels).

Individual frogs also varied substantially in the direction of their niche trajectories in isotopic niche space, although turning angles overall showed a significant directionality towards larger $\delta^{15}N$ values (U = 179.95, P = 0.03), meaning that they are shifting to relatively higher trophic levels (*Figure 3*). Interestingly, species differed in the degree of directionally in their niche trajectories. While for *L. chaquensis* both males ($p < 0.001$) and females ($p < 0.001$) exhibited turning angles significantly more directional than expected by chance, for *L. podicipinus* females had turning angles more uniform than expected by chance ($p < 0.001$) and males' turning angles indicated a random scatter ($p = 0.82$) (*Figure 4*, right panels).

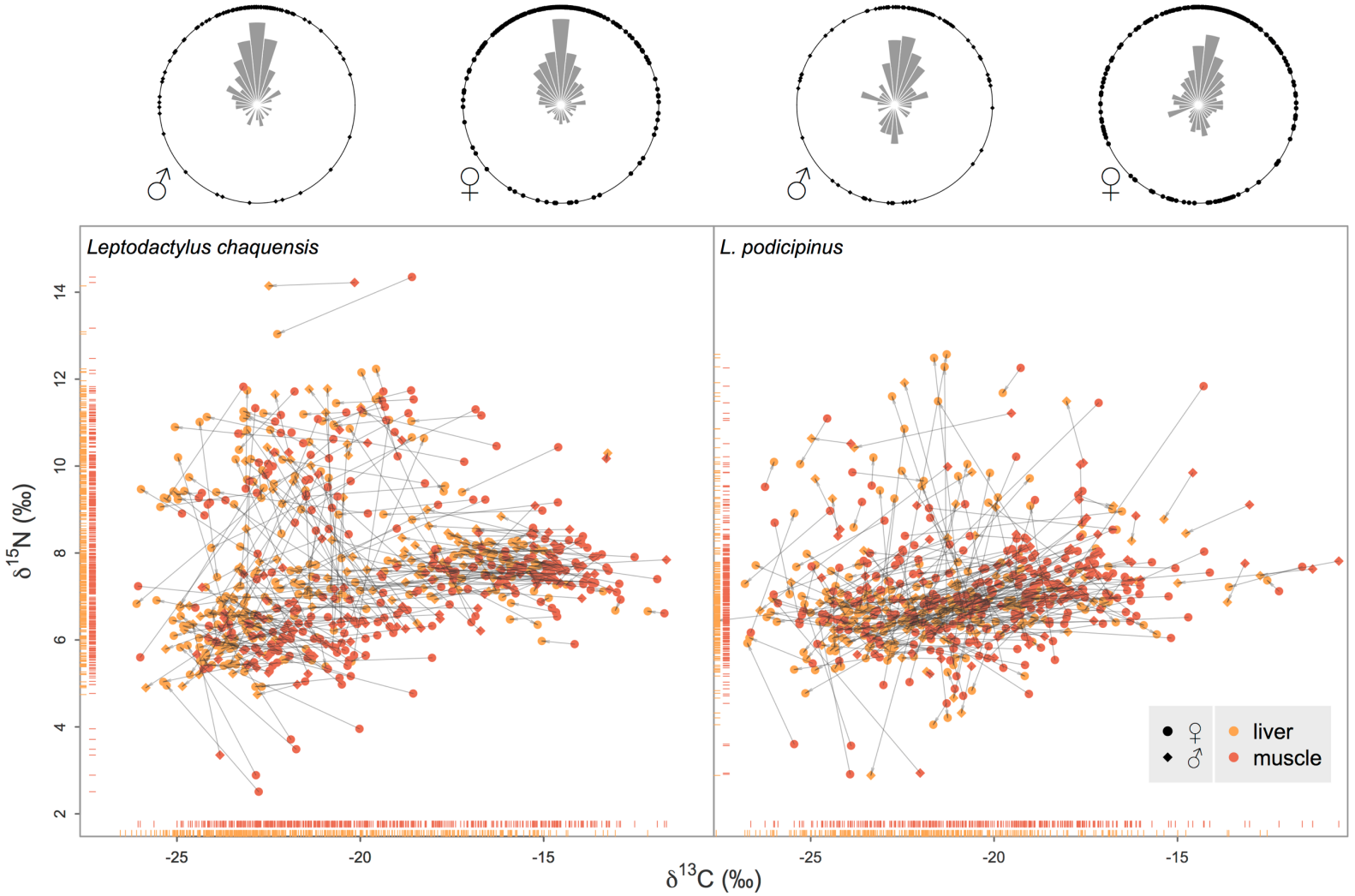



*Figure 3.* Niche trajectories, i.e. vector between muscle (red symbols) and liver (orange) isotope values, respectively, for all individuals *Leptodactylus chaquensis* (left) and *L. podicipinus* (right). Upper circles represent the observed circular frequency of angles of change in niche trajectories for each sex.

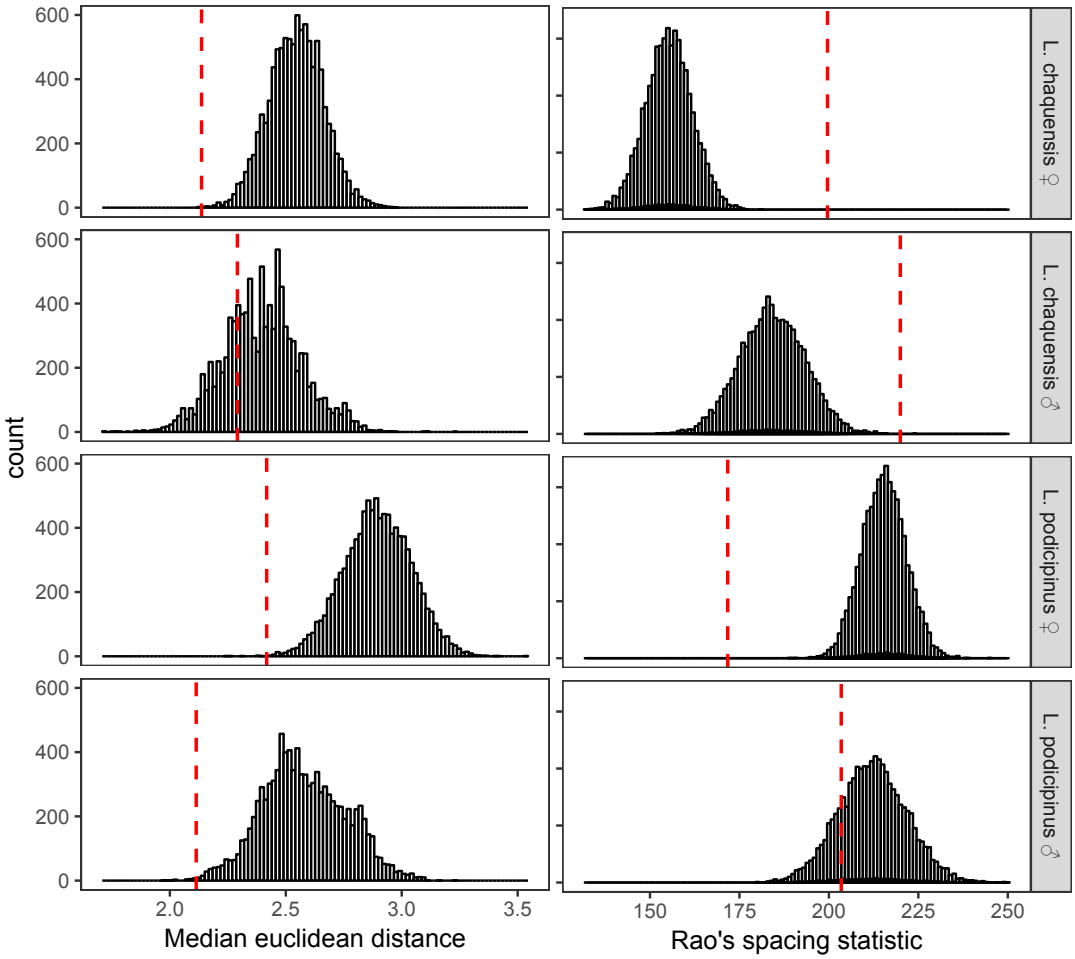



*Figure 4.* Null distributions of niche trajectory length (left panels), quantified as the mean Euclidean distance between muscle and liver stable isotope values from a given individual), and Rao's spacing statistic (right panels), which quantifies the degree of directionality in niche trajectories angle of change. Null distributions were obtained from null models simulating random niche trajectories in the niche space (see details in the Methods). Red vertical line indicates the observed values.

## *Effects of niche trajectories on individual fitness*

Individual fitness components varied largely between and within sexes and species (*Figure S1*). For instance, some *L. chaquensis* females invested very little in reproduction, while others had more than 30% of their body mass allocated in reproductive tissues. Similarly, most frogs had between zero and 20 helminth parasites, but we observed individuals hosting more than 300 parasites. Body condition also varied considerably, particularly within males of *L. chaquensis* (*Figure S1*). Interestingly, some individual fitness components were correlated: individuals with better body condition had higher reproductive investment ($r = 0.21$, $p<0.001$) and relatively less parasites ($r = -0.28$, $p<0.001$). Reproductive investment and parasite load were not

correlated (r = 0.03, p = 0.39). The first two principal components explained 79.9% of this total variation in individual fitness. The first principal component (PC1, 44.4%) was positively correlated with parasite load and negatively correlated with body condition, while the second principal component (PC2, 35.5%) was positively correlated with reproductive investment and parasite load (*Table 1*, *Figure 5*).

The magnitude of niche trajectories was a major predictor of fitness variation across individuals. Overall, in both frog species, individuals with larger niche trajectories had better body condition and less parasites (PC1; *Table 1*, *Figure 5*). Curiosly, females of *L. chaquensis* with larger niche trajectories invested more in reproduction, but had more parasites (PC2; *Table 1*, marginally nonsignificant). The direction of niche change, represented in our models by the sine and cosine of the angular change, had no significant explanatory power on fitness variation across individuals. Although sine significantly interacted with species identity in females (PC2, *Table 1*), species-specific models revealed no-significant effect of this predictor on PC2.

*Table 1*. PCA loadings for the first two components (cumulative variance explained = 79.9%) summarizing variation in three fitness components (reproductive investment, body condition, and parasite load) (Upper part) and results of linear mixed-effects models testing the effects of niche trajectories parameters on PC1 and PC2.

| Fitness component | | PC 1 (44.4%) | | | PC 2 (35.5%) | | |
|---|---|---|---|---|---|---|---|
| Reproductive Investment | | -0.40 | | | 0.80 | | |
| Body Condition | | -0.72 | | | 0.03 | | |
| Parasite load | | 0.56 | | | 0.60 | | |
| Predictors | | β | $\chi^2$ | p | β | $\chi^2$ | p |
| ♀ | Niche trajectory length | -0.09 | 5.87 | 0.01 | 0.136 | 3.17 | 0.06 |
| | Spp | 1.702 | 349.58 | <0.001 | 0.401 | 0.04 | 0.85 |
| | Sine (turning angle) | -0.01 | 1.66 | 0.19 | 0.06 | 1.39 | 0.24 |
| | Cosine (turning angle) | -0.1 | 0.07 | 0.79 | -0.164 | 1.08 | 0.31 |
| | Trajectory length * Spp | 0.049 | 1.17 | 0.29 | -0.128 | 3.96 | 0.05 |
| | Sine * Spp | -0.12 | 1.51 | 0.22 | -0.304 | 4.89 | 0.03 |
| | Cosine * Spp | 0.169 | 2.92 | 0.09 | 0.178 | 1.57 | 0.21 |
| ♂ | Niche trajectory length | -0.15 | 9.07 | <0.001 | -0.005 | 1.43 | 0.23 |
| | Spp | 1.73 | 367.36 | <0.001 | 0.233 | 0.55 | 0.46 |
| | Sine (turning angle) | -0.02 | 0.01 | 0.91 | 0.039 | 0.22 | 0.67 |
| | Cosine (turning angle) | -0.02 | 0.57 | 0.45 | 0.036 | 1.89 | 0.17 |
| | Trajectory length * Spp | 0.09 | 2.05 | 0.15 | -0.066 | 1.32 | 0.25 |
| | Sine * Spp | 0.08 | 0.44 | 0.51 | -0.026 | 0.04 | 0.84 |
| | Cosine * Spp | 0.15 | 1.79 | 0.18 | 0.1 | 0.73 | 0.39 |

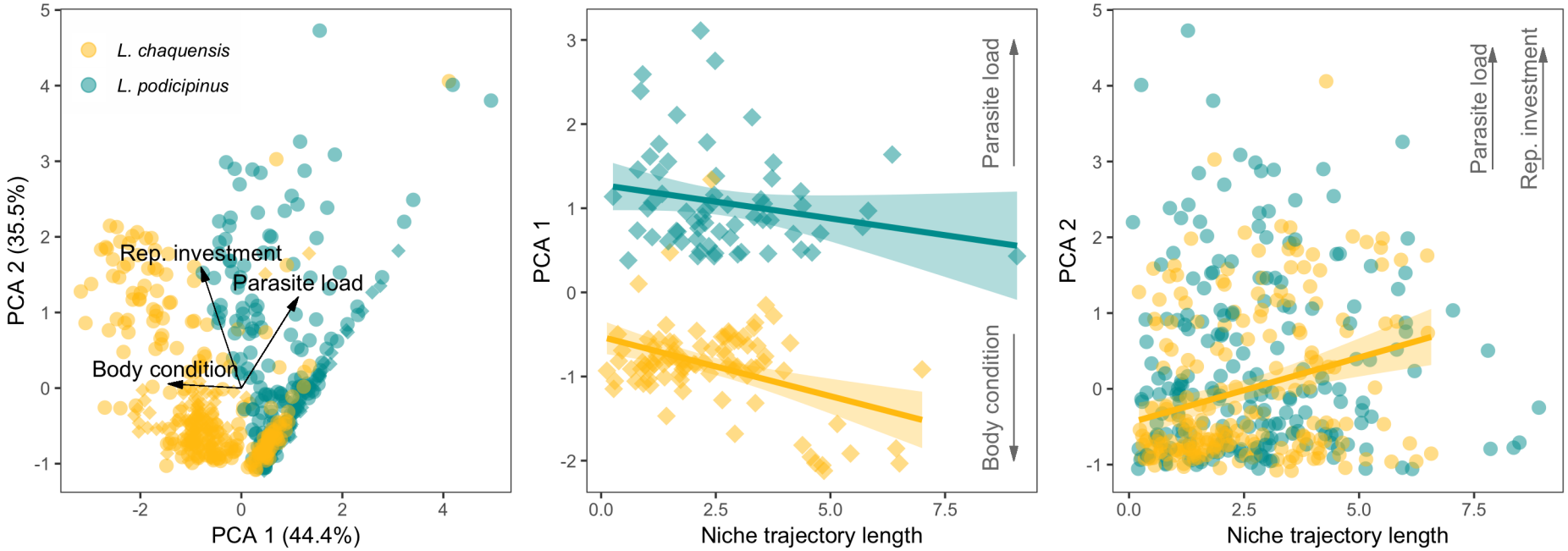



*Figure 5*. PCA biplot showing the variation of individual's fitness components along the two first principal components (left panel). Each dot represents one frog individual. Species (*Leptodactylus chaquensis* or *L. podicipinus*) are represented by different colors. The first principal component (PCA 1) accounted for 44.4% of the total variation in fitness components and was positively correlated with body condition and negatively correlated with parasite load. In turn, the second principal component (PCA2) accounted for 35.5% of the total variation is positively correlated with reproductive investment and parasite load. Then we tested the effect of niche trajectory length on PCA 1 and PCA2 (only significant for *L. chaquensis*) across individuals (central and right panels, respectively).

## Discussion

Although recent work has revealed the causes of individual niche variation in natural populations (Araújo, Bolnick & Layman 2011; Costa-Pereira *et al.* 2018b), the ecological and evolutionary consequences of this variation remain unclear. One hypothetical consequence is that intraspecific diet variation may diversify per capita contribution to population growth increment by leading to different fitness payoffs across conspecifics (Bolnick & Araújo 2011). To evaluate this idea, we explored relationships between individual trophic consistency over the foraging period preceding reproduction (represented as isotopic niche trajectories) and three key fitness components in tropical thin-toed frogs. Interestingly, we found that thin-toed frog individuals adopting a more flexible feeding strategy (i.e., larger niche trajectories) had higher fitness due to larger reproductive investment, improved body condition, and, overall, lower parasite load. Yet despite this fitness advantage of generalists, null models indicate that individual frogs shifted their diets less than expected by chance. Together, these findings emphasize the fitness advantages of trophic flexibility within populations, which may bring new insight into the role of niche variation in shaping life history strategies in dynamic environments.

### *Variation in individual niche trajectories*

The tremendous inter-individual variation in the magnitude and direction of isotopic niche trajectories in thin-toed frogs adds to fast growing body of evidence that natural populations are often composed of ecologically diverse individuals (Bolnick *et al.* 2003; Araújo, Bolnick & Layman 2011; Dall *et al.* 2012). Particularly, our results emphasize a little explored facet of individual-level niche variation: individuals vary in their trophic trajectories over time. Thin-toed frog individuals may therefore be placed along a continuum from individuals that keep a temporally consistent diet (small niche trajectories) to trophically-plastic individuals that have a flexible diet. Recent evidence based on gut contents and single-tissue (liver) isotope analysis suggests that while thin-toed frogs are considered trophic generalists as a species, individuals actually function as specialists within relatively short periods of time (Costa-Pereira *et al.* 2018b). However, by analyzing diet consistency along the foraging window that anticipates reproduction, our findings suggest that foraging strategies observed at a given time in thin-toed frogs may not be consistent over months. As recent theory indicates that the degree of individual niche variation impacts how species interact in local communities (Bolnick *et al.*

2011; Hart, Schreiber & Levine 2016; Costa-Pereira *et al.* 2018b), our results emphasize the importance of considering the temporal dimension of individual niche variation.

Despite some individuals changing their diets much more than others, we found that, on average, thin-toed frogs exhibit smaller niche trajectories than expected by chance (except for males of *L. chaquensis*). This finding suggests that, despite the fitness benefits of relatively larger niche trajectories (see below *Effects of niche trajectories on fitness*), there should be an opposing force that constrains individuals to shift their diets substantially over time. Allometric constraints provide one general. Because thin-toed frogs swallow their prey whole, gape size constrains the potential size spectrum of prey to any individual (Costa-Pereira *et al.* 2018a). Thus small-sized and, therefore, more gape-limited individuals, would have access to a narrower range of prey types with less scope for temporal diet change. These allometric constraints could explain why only males in *L. chaquensis* (mean snout-vent length: 64.04 ± 9.83), which are often larger than conspecific females (SVL: 58.19 ± 13.58) and *L. podicipinus* (mean SVL: 33.7 mm ± 4.48), did not exhibit niche trajectories smaller than expected by chance. We tested *a posteriori* this hypothesis by correlating individual snout-vent length with niche trajectory length, but we found no significant relationship ($r = -0.03$, $p = 0.39$). An alternative explanation with wide theoretical and empirical support is that other types of functional trade-offs prevent individuals from changing their diets over time. For example, adding a novel resource might require cognitive skills and/or biomechanical and physiological features that are not possible for a given individual (Robinson, Wilson & Shea 1996; Bolnick *et al.* 2003; Bolnick *et al.* 2007). Previous evidence suggests that these trade-offs in thin-toed frogs do not arise from morphology (Araújo *et al.* 2007). Thus we speculate that behavioral plasticity (propensity to risky behaviors, prey recognition) (Toscano *et al.* 2016) and/or differences in digestive performance between individuals (Hooker, Van Leeuwen & Adams 2017) may play an important role in constraining individuals' diets. Unravelling whether and how functional trade-offs shape individual niches and, ultimately, fitness variation is an important step for future studies.

Individuals of thin-toed frogs also varied largely in the direction of their trajectories, although this variation did not affect individual fitness. In practical terms, variation in niche trajectory direction indicates that individuals change their trophic positions ($\delta^{15}N$, vertical shift) and/or ultimate sources of carbon that might be associated with different food chains ($\delta^{13}C$, horizontal shift) (Dalerum & Angerbjörn 2005; Newsome *et al.* 2007). Therefore, our results

suggest that there is no single optimal direction of niche change for all individuals, which agrees with the idea that functional trade-offs drive within-population diet variation (Bolnick *et al.* 2003). In spite of this variation in the direction of trajectories, we observed some species-specific patterns. Males and females of *L. chaquensis* relocated their niches towards upper positions in the food web, meaning that conspecifics tended to shift towards higher trophic positions. Conversely, niche trajectories of *L. podicipinus* females showed a uniform circular distribution, suggesting that individuals diversified their diets rather than converging on specific prey types. These distinct patterns of niche directionality may be associated with two complementary and non-mutually exclusive mechanisms. First, because *L. chaquensis* are larger than *L. podicipinus*, the latter should be more gape constrained to capture and ingest large-sized prey, which tend to occupy relatively higher positions in food webs (e.g. centipedes, large spiders, small vertebrates) (Costa-Pereira *et al.* 2018a; Costa-Pereira *et al.* 2018b). Thus *L. podicipinus* could be biomechanically limited in their ability to move to higher positions in the isotopic niche space, which in turn may constitute a competitive refugia niche space for *L. chaquensis*, explaining the orientation of their niche trajectories. Additionally, because both *L. podicipinus* and *L. chaquensis* share small-sized prey (Costa-Pereira *et al.* 2018b), competition should prevent diet convergence of *L. podicipinus* individuals, resulting in the observed pattern of circular dispersion across niche trajectories. Indeed, individual trophic specialization is predicted to arise via negative density dependence (Araújo, Bolnick & Layman 2011; Tinker *et al.* 2012). Altogether, these findings indicate that the dispersion of individual trajectories in the niche space may reveal patterns of trophic variation that are not captured by niche trajectory length, which may bring new insights on how processes operating at the scale of individuals and interspecific differences may interact to determine niche variation.

### *Effects of niche trajectories on fitness*

Our results indicate that higher trophic flexibility resulted in higher fitness than consistent diets over the time period of the study. However, individual diets were significantly less flexible than random. While these results may appear counterintuitive at first glance, they are consistent with two major theoretical lines aiming to explain individual niche variation. A solid theoretical and empirical body of evidence indicates that a constant and more specialized diet is advantageous because individuals that shift diets or foraging behaviors often times incur in costs resulting from functional trade-offs in prey capture or digestion (see *Variation in individual niche trajectories*)

(MacArthur 1972; Bolnick *et al.* 2003; Patrick & Weimerskirch 2014; Hooker, Van Leeuwen & Adams 2017). In line with this expectation, our null models indicate that large trophic flexibility is restricted in thin-toed frogs. Conversely, because generalist individuals have access to a broader variety of resources, classic foraging theory predict that individuals' niche should fluctuate to include the whole set of resources used by the population, particularly in variable environments (Roughgarden 1972; Taper & Case 1985). Therefore, our results seem to conciliate these two apparently conflicting bodies of theory by suggesting that, within the potential foraging limitations imposed by functional trade-offs, individuals that managed to vary more their diets over time exhibit higher fitness.

The overall positive relationship between niche trajectory length and individual-level fitness could be due to the higher feeding rate of predators when environmental prey availability fluctuates. Indeed, our study system is dynamic and gradual changes in temperature, humidity, and vegetation structure over the summer lead to shifts in the presence and abundance of important invertebrate prey for frogs, such as ants, spiders, and myriapods (Soares *et al.* 2013; Battirola *et al.* 2016; Santos-Silva *et al.* 2018). Therefore, these temporal changes in prey availability may provide the scope for temporal niche variation, favoring individuals that can plastically adjust their diets to the best foraging options at a given time. For example, according to their learning and performance foraging skills, individuals tend to adjust their diet to more abundant, more nutritive, and/or less risky resources (e.g. lower infection rates) (Werner & Hall 1974; Lee *et al.* 2006; Senior *et al.* 2015).

Evolutionary theory proposes that males and females are often subject to distinct selection pressures (Hayward & Gillooly 2011). For thin-toed frogs, males and females exhibited different fitness responses to variation in niche trajectories, which should be related to their different reproductive roles. For example, variation in reproductive investment was much higher and was explained by niche trajectory length for females. This is expected because the egg production and development is much more energetically costly than sperm production in a broad variety of organisms (Hayward & Gillooly 2011). Curiously, females with larger niche trajectories also had more parasites, which suggests that increased infection rates as novel resources are included in the diet may constitute an additional mechanism constraining females to shift their diets largely over time. Interestingly, body condition, which strongly responded to niche trajectory length, should also play an important role in determining reproductive success in thin-toed frogs, particularly for males. In many *Leptodactylus* species, males compete

for clasping females in amplexus (Heyer 1969; Prado, Uetanabaro & Haddad 2005) and larger forelimbs and better body condition may confer intrasexual reproductive advantages by enhancing resistance to fatigue (Navas & James 2007; Camurugi *et al.* 2017). Therefore, while we present evidence that temporally flexible diets result in higher fitness in both sexes of thin-toed frogs, the generality of this pattern should depend on system-specific sexual differences regarding behavior, nutritional requirements, and foraging priorities (Patrick & Weimerskirch 2014).

Beyond understanding the fitness consequences of individual variation in foraging strategies, a naturally following question is how these consequences scale to population-level processes. This is a relevant problem because most of community and population theory considers the effect of mean population demography rather than fitness magnitude and variation among individuals. Therefore, if temporal prey switching brings fitness disadvantages to individuals, populations composed of individuals with more consistent diets should present higher mean fitness, which favors population stability and persistency (May & Arthur 1972). More specifically, less obvious effects may arise if population-level fitness depends nonlinearly on individual diet niche consistency, hence populations with identical niche variation means but different variances will have distinct mean fitness (Jensen's inequality), which may have important consequences for demographic rates and community dynamics (Bolnick *et al.* 2011; Hart, Schreiber & Levine 2016; Ingram, Costa-Pereira & Araújo 2018). Therefore, determining the potentially nonlinear relationship between the temporal dimension of diet change and the population-fitness (e.g., growth rates) is a key direction for future studies.

Our findings add a new level of complexity to the understanding of ecological and evolutionary consequences of niche variation by demonstrating that temporal variation in foraging consistency within populations leads to distinct fitness payoffs. This mechanistic link between diet consistency and key fitness components within and across populations may bring new insights to species interaction studies that have traditionally overlooked niche and fitness variation within populations. We suggest that an important next step is to clarify whether and how functional tradeoffs determine shifts in individuals' niches and, consequently, individuals' contribution to population fitness. Specifically, experimental studies should test whether foraging variation is entirely behavioral or correlated with morphological and physiological traits. Determining whether such variation in foraging consistency arises as a simple consequence of cognitive constraints or heritable morphological variation in thin-toed frogs

and other taxa may open new avenues to potential eco-evolutionary implications to population adaptation and species interactions.

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# Supplementary Material

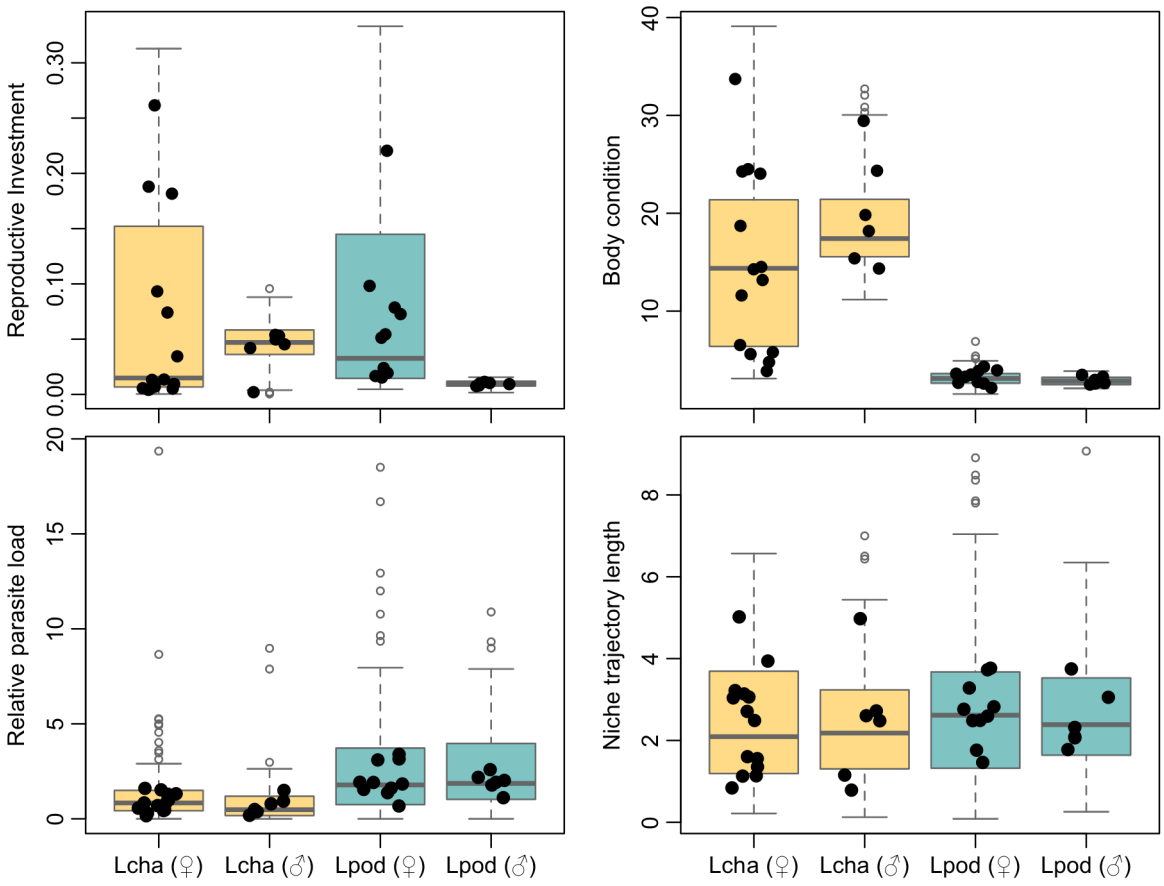



*Figure S1.* Boxplots showing variation in fitness components and niche trajectory length across individuals and sexes in two species of thin-toed frogs (*Leptodactylus chaquensis* [Lcha] and *L. podicipinus* [Lpod]). Black points represent the average value for each frog population.

# Conclusão geral

Ao longo dos quatro capítulos que compõem esta tese, estudei como e por que indivíduos de uma mesma espécie, que habitam o mesmo local, diferem no uso de recursos; bem como quais são as consequências ecológicas desse fenômeno. Mais do que documentar novos exemplos de variação individual de nicho em populações naturais, o que parece ser um fato incontestável na literatura atual (Araújo, Bolnick & Layman 2011; Layman, Newsome & Crawford 2015), demos um passo adiante ao elucidar padrões, causas e consequências da diversidade ecológica entre indivíduos em um contexto de múltiplas espécies que coexistem, aliando abordagens modernas e clássicas da teoria de nicho e de comunidades (Hutchinson 1957; Chesson 2000; Bolnick, Doebeli & Houle 2003).

No primeiro capítulo (Costa-Pereira *et al.* 2018b), elucidamos os mecanismos ecológicos que levam à variação de nicho entre indivíduos dentro de e entre espécies que coexistem. Pela primeira vez na literatura, conseguimos medir e testar simultaneamente os efeitos relativos dos quatro fatores ecológicos propostos pela teoria como causas importantes de especialização individual: competição intraespecífica, competição interespecífica, oportunidade ecológica e predação. Supreendentemente, encontramos que a especialização dos nichos individuais dentro e entre espécies é dependente do contexto ecológico ao longo desses gradientes, o que resulta na ausência de uma hierarquia consistente de especialização individual entre as espécies de rãs que estudamos. Já que diferenças no grau de variação individual de nicho entre espécies que coexistem levam a vantagens competitivas (Hart, Schreiber & Levine 2016), nossos resultados sugerem que gradientes ecológicos criam um mosaico de interações competitivas flexíveis na paisagem, o que tem potencial para afetar não somente padrões locais, mas também regionais de diversidade.

No segundo capítulo (Costa-Pereira *et al.* 2018a), mostramos que a intrigante variação no tamanho de predadores em relação a suas presas observada em diversas teias tróficas naturais pode não ser simplesmente 'ruído', como comumente é tratado na literatura. Nossos resultados sugerem que gradientes de limitação de presas são reguladores chave não somente da alometria de interações tróficas, mas também de sua variância intrapopulacional, o que é consistente com as previsões da Teoria do Forrageamento Ótimo. Ao mostrar que interações tróficas não seguem uma constante alométrica única, mas variam de forma previsível, nossos

resultados desafiam paradigmas das sólidas teorias metabólica e de teias alimentares, além de contribuir para um entendimento mais mecanístico das forças que estruturam as interações entre predadores e presas na natureza.

No terceiro capítulo, investigamos como os nichos de populações que coexistem variam e se sobrepõem em uma perspectiva multidimensional. Afinal, por definição, nichos são multidimensionais. Aplicamos um método recentemente proposto para modelar os componentes do nicho considerando variações intra- e interindividuais simultaneamente em duas dimensões. Como esperado pela teoria clássica de nicho, encontramos que populações em comunidades com maior diversidade de recursos disponíveis e menor número de potenciais espécies competidoras expandiram seus nichos. Contraintuitivamente, à primeira vista, nossos resultados sugerem que o generalismo trófico pode constituir uma estratégia para diminuir o grau de sobreposição de nicho relativo entre competidores, trazendo uma nova perspectiva à antiga questão de como tantas espécies generalistas conseguem coexistir em comunidades tropicais.

No quarto e último capítulo, investigamos se a variação individual de nicho resulta em diferenças intrapopulacionais de valor adaptativo. Especificamente, estudamos como a consistência trófica ao longo dos meses que antecedem a reprodução das rãs afeta a subsequente aptidão reprodutiva e somática de indivíduos. Curiosamente, as rãs tiveram dietas mais temporalmente consistentes do que seria esperado ao acaso, sugerindo que demandas conflitantes na busca, captura ou digestão de diferentes tipos de presas limitam a mudança temporal de dieta. Entretanto, aqueles indivíduos que conseguiram mudar mais suas dietas ao longo do tempo apresentaram maior investimento reprodutivo, melhor condição corpórea e menor carga parasitária. Esses resultados constituem um passo importante para entender como variações de valor adaptativo intrapopulacionais emergem a partir de decisões individuais de forrageio em comunidades naturais, o que pode ter implicações importantes para a teoria de coexistência de espécies.

Em conclusão, acredito que esta tese contribui para o entendimento (*i*) dos mecanismos que moldam diferenças de nicho trófico entre indivíduos e entre espécies que coexistem ao longo de gradientes ecológicos, bem como (*ii*) das implicações ecológicas desse fenômeno para a sobreposição interespecífica de nicho, coexistência de espécies e diferenças intrapopulacionais de valor adaptativo. Além disso, propomos algumas abordagens metodológicas novas que poderão ser úteis em posteriores estudos de redes tróficas, ecologia

isotópica e variação individual de dieta *per se*. Futuros estudos no sistema das rãs *Leptodactylus* poderão ajudar a esclarecer algumas hipóteses que foram levantadas ao longo dessa tese. Destaco três linhas que considero promissoras. Primeiro, seria interessante investigar os potenciais mecanismos biomecânicos, comportamentais e/ou fisiológicos subjacentes à variação individual de nicho. Segundo, um experimento para quantificar a magnitude relativa de competição intra- *vs*. interespecífica na presença de variação individual poderia estabelecer ligações mais sólidas entre os resultados do primeiro capítulo e as ideias da teoria moderna de coexistência. Por fim, mas não menos importante, como sugerimos no capítulo quatro, seria promissor investigar como a magnitude da variação de nicho dentro de populações se relaciona com o valor adaptativo entre populações, o que também poderia aproximar os resultados do primeiro e quarto capítulos ao ferramental teórico da abordagem moderna de coexistência. Espero que os resultados desta tese estimulem pesquisadores a buscar entender como características e decisões de indivíduos reverberam em dinâmicas de populações, comunidades e ecossistemas.

Fim.

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