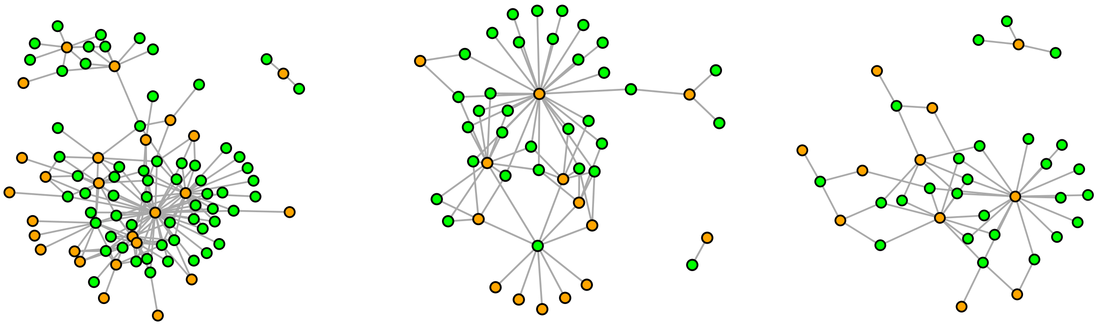
Universidade de São Paulo – USP

Instituto de Biociências

Programa de Pós-graduação em Ecologia

Interações tróficas em comunidades de serpentes: estrutura de redes e o papel das espécies

Trophic interactions in snake communities: network structure and the role of species



Daniela Pinto Coelho

São Paulo – SP

2022

Daniela Pinto Coelho

Interações tróficas em comunidades de serpentes: estrutura de redes e o papel das espécies

Trophic interactions in snake communities: network structure and the role of species

VERSÃO CORRIGIDA

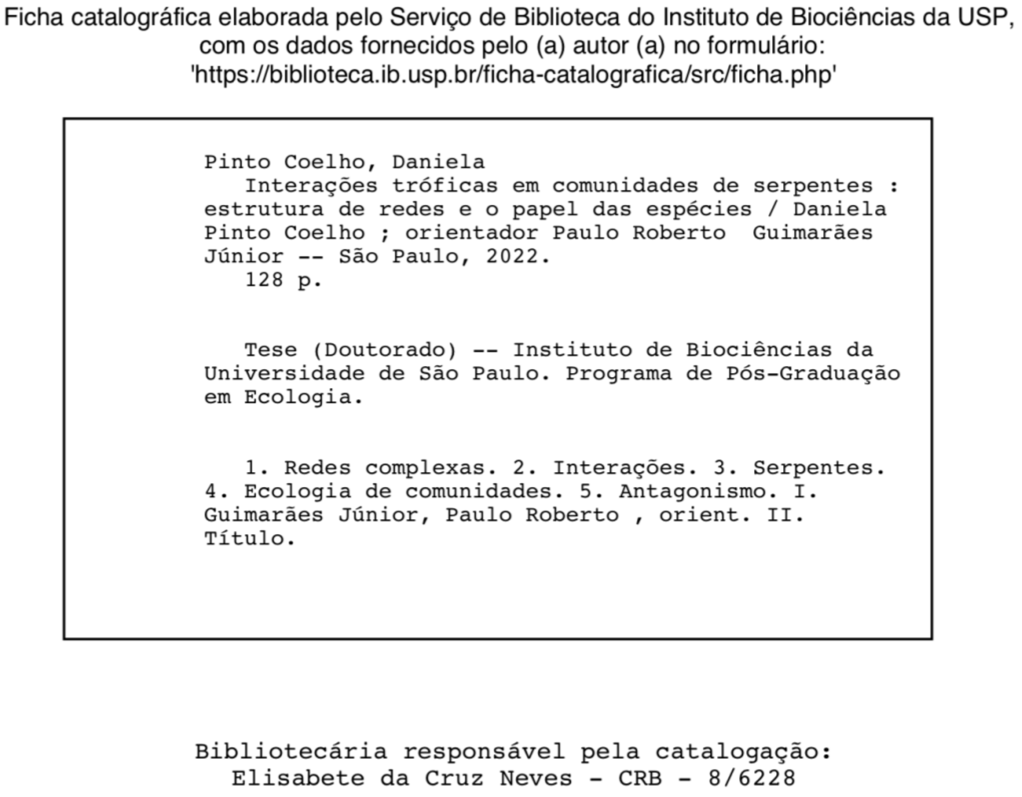
Tese apresentada ao Programa de Pós-Graduação em Ecologia da Universidade de São Paulo para a obtenção do título de Doutora em Ecologia.

Orientador: Paulo R. Guimarães Jr.

São Paulo – SP

2022

Ficha catalográfica



Ficha catalográfica elaborada pelo Serviço de Biblioteca do Instituto de Biociências da USP,
com os dados fornecidos pelo (a) autor (a) no formulário:
'https://biblioteca.ib.usp.br/ficha-catalografica/src/ficha.php'

Pinto Coelho, Daniela
Interações tróficas em comunidades de serpentes : estrutura de redes e o papel das espécies / Daniela Pinto Coelho ; orientador Paulo Roberto Guimarães Júnior -- São Paulo, 2022.
128 p.

Tese (Doutorado) -- Instituto de Biociências da Universidade de São Paulo. Programa de Pós-Graduação em Ecologia.

1. Redes complexas. 2. Interações. 3. Serpentes. 4. Ecologia de comunidades. 5. Antagonismo. I. Guimarães Júnior, Paulo Roberto , orient. II. Título.

Bibliotecária responsável pela catalogação:
Elisabete da Cruz Neves - CRB - 8/6228

Comissão Julgadora:

Profa. Dra. Carolina Reigada Montoya

Profa. Dra. Sabrina Borges Lino Araújo

Profa. Dra. Thais Barreto Guedes da Costa

Prof. Dr. Paulo R. Guimarães Jr.
Orientador

Dedicatória

Dedico esta tese a minha querida e amada tia Rita (*in memoriam*), por tanto me inspirar com sua garra, dedicação e esforço com os estudos.

Epígrafe

“A natureza é um enorme jogo de xadrez
disputado por deuses, e que temos o privilégio
de observar. As regras do jogo são o que
chamamos de física fundamental,
e compreender essas regras é a nossa meta”
Richard Feyman

Agradecimentos

A construção da minha tese foi algo que envolveu uma ampla rede de interações entre pessoas das mais diversas familiaridades. O meu doutorado foi uma construção conjunta, favorecida por uma rede de apoio formada por pessoas inspiradoras, que me ajudaram a construir cada degrau que eu precisei subir até chegar a esse produto final.

Primeiramente, eu gostaria de agradecer aos pais mais maravilhosos que a vida poderia ter me dado, Márcia e José Antônio, que sempre foram grandes admiradores da minha profissão e apoiadores das minhas escolhas. As minhas queridas irmãs, Anne e Paulinha, por serem sempre tão parceiras, divertidas e presentes. A Gláucio, meu irmãozão, que por muitas vezes foi como um pai, sempre preocupado e zeloso com o meu bem estar. As minhas sobrinhas, Mila e Mel, por quem eu tenho tanto afeto. Agradeço a Ernani, meu parceiro de vida, companheiro de tantos momentos, que foi uma peça fundamental nesse emaranhado de idas e vindas, altos e baixos e diferentes direções que a nossa vida tomou.

Um agradecimento especial ao Glauco Machado, um dos melhores professores e pesquisadores que eu tive a felicidade de interagir, pois sem o seu “apadrinhamento“ dificilmente eu teria a oportunidade de integrar o Miúdo`s Lab.

Ao meu orientador, o Miúdo, também conhecido como Paulo Guimarães, o meu agradecimento vai muito além dos mais diversos ensinamentos científicos. Agradeço ao Miúdo por, desde os primeiro momentos, ter segurado na minha mão e me conduzido de uma forma que eu jamais esquecerei. Com o Miúdo eu aprendi sobre respeito e empatia. Aprendi que ciência se faz com empenho e dedicação e também aprendi que “a mesa sempre estará cheia” e que aprender a se organizar é uma tarefa essencial para lidar com os desafios que estão por vir. Aprendi como cooperar, como buscar ajuda e também aprendi que eu preciso respeitar o meu tempo e manter a minha mente saudável. Acredito que as pessoas escolhem a orientação do Miúdo, não apenas pelo grande pesquisador que ele é, mas pelo conjunto de qualidades pessoais que ele possui. Com o Miúdo eu vivi uma relação de respeito mútuo, cooperação, inúmeras trocas de experiências pessoais e profissionais e muito aprendizado acadêmico, e esse ambiente me motivou a oferecer o que há de melhor em mim.

Agradeço aos amigos do Miúdo`s Lab e da Lage, pela construção de um espaço de trabalho super saudável. Agradeço especialmente ao Camacho, Pinguim, Danilo e Leandro, que tanto me ajudaram com os códigos do R, ao Taio, Irina, Marília, Andrés, Coral, Pam, Pam

Pam, Ana, Erika, Carol e Débora, pelos tantos momentos divertidos compartilhados, onde eu muito aprendi sobre a vida, o universo e tudo mais.

Agradeço ao Paulo Enrique (Popito), que desde o meu mestrado vêm me ajudando nessa longa jornada acadêmica. Agradeço aos coordenadores, professores e funcionárias do PPG em Ecologia, especialmente ao Paulo Inácio, por ser tão doce e gentil, e a Vera, Shirlene e Erika, essas mulheres maravilhosas que são exemplos de gentileza, eficiência e organização. Agradeço ao Márcio Martins e a Laura Alencar, que embarcaram comigo nessa jornada, compondo meu comitê de acompanhamento e, juntamente com a Kate Maia, colaboraram enormemente para que essa tese ficasse mais rica.

Agradeço a Melina, Kate e Paulinha Assis, essas brilhantes pesquisadoras, que tanto me inspiram e que se tornaram as minhas "santas desatadoras dos nós", verdadeiros oráculos da soluções de problemas, me ajudando em tantos e tantos momentos de dificuldade. Muito obrigada meninas, pela sempre disposição em me ajudar. A Mila, Bruno, Dinha e Pri, meus amigos da Bahia, que foram minha primeira rede de apoio, me auxiliando em absolutamente tudo que eu precisei, facilitando demais o meu processo de adaptação à São Paulo. Obrigada por essa amizade valiosa! As minhas companheiras de república, Pri, Juju, Duda e Gabi, agradeço pelos momentos compartilhados. Em especial, a Juju, que além de muito me ajudar a desvendar os códigos de R, foi sempre uma grande parceira. Aos colegas do PPG em Ecologia, que muito somaram para fazer desse programa algo diferenciado, promovendo eventos lindos como o EcoEncontros. a EcoEscola e o Café Existencial. Aos meus queridos amigos e amigas da Bahia, especialmente Breno, Mimi, Fila, Tiko e Lori, pelos muitos anos de amizade. Aos Percoço e aos Legais. A equipe da Eco.logic, especialmente a Thais, pela confiança e parceria nesses tantos anos de amizade. A Rejâne Lira, Tânia Brazil e Yukari pelos muitos ensinamentos durante os meus primeiros passos acadêmicos.

Agradeço à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) – Código de Financiamento 001, pelo financiamento da bolsa, à Universidade de São Paulo por fornecer toda estrutura, à Comissão de Pós Graduação (CPG) e ao Programa de excelência acadêmica (PROEX), pelas verbas concedidas, que me proporcionaram frequentar bons eventos científicos.

Agradeço a Alexandra Elbakyan, idealizadora do Sci-Hub, por lutar pelo fornecimento de acesso gratuito e irrestrito a todo o conhecimento científico já publicado em periódicos ou livros.

Por fim, agradeço às serpentes, animais tão belos e que tanto me inspiram!

Índice

Resumo geral

Em comunidades ecológicas, espécies são conectadas por interações. Interações ecológicas formam redes e a organização dessas redes pode ter importantes implicações para conservação, afetando potencialmente a robustez dos sistemas ecológicos à perda de espécies. Neste contexto, é essencial compreender a estrutura das interações ecológicas ao nível da comunidade, e como essas interações influenciam os papéis desempenhados pelas diferentes espécies. A fim de compreender como as redes de interações moldam as comunidades, a abordagem de redes fornece um conjunto de ferramentas para visualizar e descrever sistemas ecológicos inteiros. Um dos sistemas ecológicos mais amplamente estudados são as redes de interações tróficas. Utilizando serpentes como modelo de estudo, esta tese teve por objetivo compreender como redes de interações tróficas moldam a estrutura de comunidades serpentes-presas. No primeiro capítulo, nós investigamos a estrutura da rede trófica de uma comunidade rica e bem estudada de serpentes amazônicas. Nossos resultados revelaram que a estrutura da rede é parcialmente resultante do fato de espécies de maior tamanho se alimentarem de maior diversidade de presas e, portanto, promovendo estrutura aninhada, enquanto que serpentes com estilos de vida específicos e se alimentando de recursos distintos, promoveram modularidade. Simulações de remoção de espécies indicaram que a estrutura aninhada foi favorecida principalmente pela presença de cinco espécies da família Boidae (família de grandes serpentes constritoras), que devido ao seu tamanho corporal e estilos de vida generalistas conectaram módulos formados por outras serpentes e recursos na rede. No segundo capítulo, nós caracterizamos 24 redes serpentes-presas, amplamente distribuídas. Estudamos a associação entre latitude, atributos da comunidade (riqueza, diversidade taxonômica e variação de tamanho corporal entre serpentes) e estrutura de rede. Também avaliamos a importância diferencial dos recursos alimentares na dieta das serpentes. Nossos resultados mostraram que a estrutura das redes foi em geral aninhada, moderadamente conectada e não modular. A latitude influenciou apenas a variação de tamanho entre as serpentes, que juntamente com a riqueza, influenciaram apenas o aninhamento. Também observamos que redes de regiões tropicais foram mais aninhadas do que as de regiões temperadas. A análise da centralidade dos recursos indicou que anfíbios, lagartos ou pequenos mamíferos representam os recursos centrais na dieta das serpentes ao longo das múltiplas redes. Por fim, no terceiro capítulo, nós investigamos como diferentes atributos biológicos (tamanho do corpo, estilo de vida e história filogenética) podem revelar a importância das serpentes em 23 redes serpentes-presa.

Utilizando métricas de centralidade e análises de efeitos indiretos, nossos resultados indicaram que, em geral, maiores tamanhos corporais, estilos de vida aquáticos e semi-arbóreos e linhagens das grandes serpentes constritoras, apresentaram maior associação com as centralidades do grau e por intermédio, que também foram as métricas que mais contribuíram para a transmissão dos efeitos indiretos nas redes. Ao integrar análises de redes de interações com dados de história natural, história evolutiva das linhagens, atributos das comunidades e atributos biológicos das espécies, foi possível compreender, nesta tese, como as comunidades de serpentes estão estruturadas com base no uso dos recursos alimentares e quais atributos biológicos fazem de uma serpente uma espécie-chave dentro da comunidade.

Palavras-chave: Aninhamento, atributos biológicos, betweenness, Boidae, centralidade, closeness, conectância, efeitos indiretos, espécies-chave, latitude, modularidade e tamanho do corpo.

Abstract

In ecological communities, species are connected by interactions. Ecological interactions form networks and the organization of these networks can have important implications for conservation, potentially affecting the robustness of ecological systems to the loss of species. In this context, it is essential to understand the structure of ecological interactions at the community level, and how these interactions influence the roles played by different species. In order to understand how networks of interactions shape communities, the network approach provides a set of tools for visualizing and describing entire ecological systems. One of the most widely studied ecological systems is the networks of trophic interactions. Using snakes as a study model, this thesis aimed to understand how networks of trophic interactions shape the structure of snake-prey communities. In the first chapter, we investigated the trophic network structure of a rich and well-studied community of Amazonian snakes. Our results revealed that the structure of the network is partially a result of the fact that larger species feed on a greater diversity of prey and, therefore, promoting nested structure, while snakes with specific lifestyles and feeding on different resources, promoted modularity. Species removal simulations indicated that the nested structure was favored mainly by the presence of five species of the Boidae family (family of large constrictor snakes), which, due to their body size and generalist lifestyles, connected modules formed by other snakes and resources in the network. In the second chapter, we characterized 24 snake-prey networks, widely distributed. We studied the association between latitude, community attributes (richness, taxonomic diversity and body size variation among snakes) and network structure. We also evaluated the differential importance of food resources in the snakes' diet. Our results showed that the structure of the networks was in general nested, moderately connected and non-modular. Latitude only influenced size variation among snakes, which together with richness only influenced nestedness. We also observed that networks from tropical regions were more nested than those from temperate regions. The resource centrality analysis indicated that amphibians, lizards or small mammals represent the central resources in the snakes' diet along the multiple networks. Finally, in the third chapter, we investigated how different biological attributes (body size, lifestyle and phylogenetic history) might reveal the importance of snakes in 23 snake-prey networks. Using metrics of centrality and analysis of indirect effects, our results indicated that, in general, larger body sizes, aquatic and semi-arboreal lifestyles and lineages of the great constrictor snakes were more associated with degree and betweenness centralities, which were also the metrics that most contributed to the transmission of indirect effects on the networks. By integrating analysis of interaction networks with data from natural history, evolutionary history of lineages, community attributes and biological attributes of species, it was possible to understand, in this thesis, how snake communities are structured based on the use of food resources and which biological attributes make a snake a key species within the community.

Key-word: Betweenness, biological attributes, body size, Boidae, centrality, closeness, connectance, indirect effects, key species, latitude, modularity, nestedness.

Introdução geral

Indivíduos de todas as espécies dependem de interações ecológicas para obter alimento, se reproduzir ou se proteger contra inimigos naturais (Thompson, 2005). Como consequência, as interações ecológicas representam um componente chave para compreender a biodiversidade, potencialmente moldando tanto a organização dos ecossistemas (Estes & Palmisano 1974), quanto características das espécies que interagem (Galetti et al. 2013). Portanto, o conhecimento sobre a forma como as interações ecológicas se organizam na natureza é essencial para a compreensão dos diferentes níveis de organização dos sistemas ecológicos (Guimarães 2020).

Interações ecológicas formam redes que conectam populações de diferentes espécies em uma localidade (Bascompte & Jordano, 2013). A organização dessas redes pode ter importantes implicações para conservação, influenciando potencialmente a robustez dos sistemas ecológicos à perda de espécies (Schmitz & Beckerman, 2007). Neste contexto, é essencial compreender a estrutura das interações ecológicas ao nível da comunidade, e como essas interações afetam os papéis desempenhados pelas diferentes espécies (Cohen et al. 1993, Cagua et al. 2019).

O padrão estrutural das redes ecológicas e como sua estrutura influencia a dinâmica e a estabilidade dos ecossistemas é um assunto amplamente discutido por ecólogos, desde o clássico trabalho de Paine (1966). Estudos mostram que nem todas as espécies desempenham papéis equivalentes na estrutura das redes. Por exemplo, Estes & Palmisiano (1974) mostraram como a extinção local de populações de lontras marinhas (*Enhydra lutris*) na região do Alasca, impulsionou uma cascata trófica de reduções drásticas na abundância de algumas das espécies envolvidas na rede de interações local. A caça da lontra implicou em aumento substancial de uma das suas presas, o ouriço-do-mar (*Strongylocentrotus* sp). Consequentemente, a explosão populacional dos ouriços, implicou na drástica redução de uma espécie de macroalga marinha consumida pelos ouriços, a *kelps* (Laminariales), que formam florestas submarinas na região. A redução das florestas de *kelps* implicou na perda de importantes abrigos para diversas espécies, assim como na diminuição da produtividade primária na região, influenciando toda a cadeia pesqueira. Desta forma, a perda de uma espécie pode implicar em uma cascata de extinções, atingindo não apenas as espécies que interagem diretamente, mas todas as espécies associadas à rede de interações (Pires et al. 2020).

A fim de compreender como as interações entre as espécies moldam sistemas ecológicos inteiros, a abordagem de rede fornece um conjunto de ferramentas para visualizar e descrever sistemas ecológicos (Poisot et al. 2016). Padrões de rede não aleatórios podem representar as impressões digitais de processos ecológicos e evolutivos, responsáveis por moldar a complexidade dos sistemas ecológicos (Guimarães 2020). Padrões de rede incluem a variação no número de interações por espécie (Sinclair et al. 2003), a variação na força das interações (Ings et al. 2009), os papéis das espécies dentro das assembleias de interação (Anderson & Sukhdeo 2011), ou o formação de grupos de espécies (Rezende et al. 2009). Assim, o conjunto de métricas utilizadas pela abordagem de redes pode permitir inferências sobre o papel ecológico de espécies individuais dentro das comunidades (Cirtwill et al. 2018) e estimar como a propagação de efeitos diretos e indiretos na rede afetaria a robustez dos sistemas ecológicos para perda de espécies (Schmitz & Beckerman 2007, Pires et al. 2020).

Um dos sistemas ecológicos mais amplamente estudados são as redes de interações tróficas (Paine 1966, Cohen et al. 1993). Interações tróficas podem ser descritas como redes bipartidas na qual um conjunto de nós representa os consumidores e o outro conjunto de nós representa seus recursos alimentares; as ligações entre os dois conjuntos de nós indicam o uso dos recursos alimentares pelos consumidores (Cohen et al. 1993, Pires et al. 2011). A estrutura de uma rede pode ser descrita por métricas que caracterizam como as interações estão distribuídas e organizadas entre os diferentes nós que compõem a rede (Bascompte & Jordano 2013). Por exemplo, a conectância, uma medida de densidade das interações, está associada ao grau médio de especialização e ao grau de similaridade da dieta entre consumidores (Tinker et al., 2012; Bascompte & Jordano, 2007). A presença de um núcleo de espécies generalistas tende a formar redes mais conectadas nas quais especialistas tendem a interagir com subconjuntos dos recursos consumidos pelos generalistas, levando a uma estrutura aninhada (Bascompte et al. 2003, Lewinsohn et al. 2006). Por outro lado, a presença de grupos de espécies especializadas em consumir determinados tipos de recursos leva a formação de módulos alimentares, conduzindo a uma estrutura modular (Rezende et al. 2009). Assim, a estrutura das redes tróficas pode refletir diferentes padrões no uso dos recursos alimentares pelos consumidores (Ings et al. 2009).

Os padrões estruturais das redes podem ser influenciados pela história evolutiva associada às características das espécies, como por exemplo, o tamanho do corpo, o estilo de vida ou a linhagem das espécies interagentes (Woodward et al. 2005, Rezende et al. 2009, Pinto-Coelho et al. 2021). O aninhamento em redes tróficas geralmente está associado à hierarquia do tamanho do corpo entre os predadores (Sinclair et al. 2003, Woodward et al. 2005, Stouffer et al. 2011, Ceron et al. 2019, Pinto-Coelho et al. 2021), mas também há evidências para o surgimento de padrões aninhados associados a estrutura filogenética entre táxons relacionados (Cattin et al. 2004) e às diferenças nas abundâncias entre espécies que interagem (Krishna et al. 2008). Já a estrutura modular também pode derivar de interações mediadas pelo tamanho do corpo, pela história filogenética, por estrutura espacial (Prado & Lewinsohn 2004, Rezende et al. 2009) ou pelo estilo de vida (Pinto-Coelho et al. 2021). No entanto, em redes empíricas, redes tróficas podem apresentar tanto padrão aninhado, quanto modular, simultaneamente (Fortuna et al. 2010, Pinheiro et al. 2018; Valverde et al. 2020; Pinto-Coelho et al. 2021).

Além das métricas que associam a estrutura da rede aos processos ecológicos que moldam as comunidades, a abordagem de redes possui um conjunto de métricas que permite mensurar diferentes aspectos relacionados ao papel individual das espécies (Delmas et al. 2018). A importância de um nó pode ser capturado, por exemplo, por métricas de centralidade, que permitem inferir a importância relativa de um nó dentro da rede (Sazima et al. 2010). Assim, relacionar como a estrutura das redes é influenciada pelo papel das espécies e como o papel das espécies é influenciado pelos seus atributos biológicos pode fornecer importantes descobertas sobre como os padrões não aleatórios de redes podem representar as impressões digitais de processos ecológicos e evolutivos que moldam sistemas ecológicos (Guimarães, 2020). Por exemplo, Sebastián-González et al. (2020), estudando a estrutura de redes de vertebrados necrófagos em ambientes com diferentes graus de antropização, identificaram que o aninhamento é negativamente afetado pelo grau de antropização e que redes mais aninhadas são mais eficientes na ciclagem de nutrientes. A estrutura aninhada se mostrou mais associada a um conjunto de espécies-chave, que por apresentarem características mais peculiares, agem como facilitadores para os demais necrófagos, favorecendo maiores taxas de consumo. Por exemplo, espécies com maior capacidade de localizar carcaças, funcionam como indicadores da localização, assim como espécies com maior capacidade de perfurar tecidos duros, permitem que necrófagos menores acessem o recurso, possibilitando um aumento na eficiência na ciclagem de nutrientes. Assim, a presença dessas espécies chave é capaz de modificar a estrutura das interações.

Utilizando interações entre serpentes e suas presas como modelo de estudo, esta tese teve por objetivo compreender como redes de interações tróficas moldam a estrutura de comunidades ecológicas. Serpentes são animais estritamente carnívoros, que desenvolveram adaptações morfológicas, fisiológicas e comportamentais para matar e engolir suas presas inteiras (Greene, 1983). As características relacionadas aos seus diferentes hábitos alimentares e sistemas defensivos, fazem das cobras um bom modelo estudo modelo para compreender como as interações tróficas organizam a estrutura da comunidade (Shine & Bonnet 2000). Pesquisas usando serpentes como modelos de estudo têm sido desenvolvidas no intuito de compreender como características ecológicas, interações interespecíficas, uso do hábitat e história evolutiva influenciam as interações tróficas atuais de diferentes espécies (Alencar et al., 2013, 2017, Bellini et al., 2015, Colston et al., 2010, Klaczko et al., 2016, Martins et al., 2001). Além disso, algumas espécies (por exemplo, as dos gêneros *Bothrops*, *Crotalus*, *Lachesis* e *Micrurus*) são de importância médica (Campbell & Lamar, 1989) e o conhecimento sobre sua ecologia trófica pode favorecer estudos com foco em saúde pública, uma vez que sua dieta pode se relacionar com a química dos seus venenos (Daltry et al., 1996, Davies & Arbuckle, 2019).

Assim, esta tese foi dividida em três capítulos. No PRIMEIRO CAPÍTULO nós investigamos a estrutura de uma rede trófica de uma comunidade rica e bem estudada de serpentes amazônica, composta por 62 espécies de serpentes e 24 categorias de recursos alimentares. Nossos resultados revelaram que a estrutura da rede resulta da presença de espécies de maior tamanho, se alimentando de maior diversidade de presas e, portanto, promovendo estrutura aninhada, enquanto que serpentes com estilos de vida específicos e se alimentando de recursos distintos, promoveram padrão modular. Simulações de remoção de espécies indicaram que a estrutura aninhada foi favorecida principalmente pela presença de cinco espécies da família Boidae (família de grandes serpentes constritoras, como a sucuri e a jiboia), que devido ao seu tamanho corporal e estilos de vida generalistas conectaram módulos alimentares na rede. Este estudo destacou as maneiras particulares pelas quais os traços das espécies afetaram a estrutura das interações entre consumidores e recursos no nível da comunidade. Este trabalho foi publicado no meu segundo ano de doutorado. Pinto-Coelho, D, Martins, M. & Guimarães, P.R.Jr. 2021. Ecology and Evolution, 11:6558–6568. doi: 10.1002/ece3.7508.

No SEGUNDO CAPÍTULO, a fim de compreender a associação entre estrutura de redes e o gradiente ambiental, nós caracterizamos 24 redes serpentes-presas, amplamente distribuídas. Usamos uma análise de rotas para estudar a associação entre latitude, atributos da comunidade (riqueza, diversidade taxonômica e variação de tamanho corporal entre serpentes) e estrutura de rede. Também avaliamos a importância diferencial dos recursos alimentares na dieta das comunidades de serpentes. Nossos resultados mostraram que a estrutura das redes era em geral aninhada, moderadamente conectada e não modular. A latitude influenciou apenas a variação de tamanho entre cobras, que junto com a riqueza afetou apenas o aninhamento. Também observamos que redes de regiões tropicais foram mais aninhadas do que as de regiões temperadas. A análise da centralidade dos recursos indicou resultados congruentes, mostrando que anfíbios, lagartos ou pequenos mamíferos representam os recursos centrais na dieta das serpentes. Neste capítulo nós concluímos que redes serpentes-presa não apresentaram variações consistentes ao longo do gradiente latitudinal.

Por fim, no TERCEIRO CAPÍTULO, nós analisamos o papel individual das serpentes nas interações tróficas. Nós investigamos como diferentes atributos biológicos (tamanho do corpo, estilo de vida e história filogenética) podem revelar a importância das serpentes em 23 redes serpentes-presa. Utilizamos métricas de centralidade e análises de efeitos indiretos para estimar a importância das serpentes e revelar qual dessas métricas melhor captura efeitos em cascata que podem se propagar pela estrutura das interações analisadas. Nossos resultados indicaram que, em geral, maiores tamanhos corporais, linhagens de grandes serpentes constritoras, e os estilos de vida aquáticos e semi-arbóreos foram os atributos que apresentaram maior associação com as centralidades de grau e intermédio (betweenness), que também foram as métricas que mais contribuíram para a transmissão dos efeitos indiretos nas redes.

Referências Bibliográficas

Alencar, L.R.V., Gaiarsa, M.P. & Martins, M. 2013. The evolution of diet and microhabitat use in pseudoboine snakes. South American Journal of Herpetology, 8, 60–66. https://doi.org/10.2994/SAJH-D-13-00005.1

Alencar, L.R.V., Martins, M., Burin, G. & Quental, T.B. 2017. Arboreality constrains morphological evolution but not species diversification in vipers. Proc. R. Soc. B. 284, 20171775. http://dx.doi.org/10.1098/rspb.2017.1775

Anderson, T.K. & Sukhdeo, M.V.K. 2011. Host Centrality in Food Web Networks Determines Parasite Diversity. PLoS ONE 6, 10, e26798.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences of the United States of America, 100, 9383–9387.

Bascompte, J. & Jordano, P. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. Annu. Rev. Ecol. Evol. Syst., 38, 567–593.

Bellini, G.P., Giraudo, A.R, Arzamendia, V. & Etchepare, E.G. 2015. Temperate snake community in South America: Is diet determined by phylogeny or ecology? PLoS One, 10, 1–15. https://doi.org/10.1371/ journal.pone.0123237

Cagua E.F., Wootton, K.L. & Stouffer, D.B. 2019. Keystoneness, centrality, and the structural controllability of ecological networks. Journal of Ecology, 107, 1779–1790.

Campbell, J.A. & Lamar, W.W. 1989. The Venomous Reptiles of Latin America. Ithaca: Cornell Univ. Press.

Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R. & Gabriel, J.P. 2004 Phylogenetic constraints and adaptation explain food-web structure. *Nature*, 427, 835–839.

Ceron, K. et al. 2019. Global patterns in anuran–prey networks: structure mediated by latitude. Oikos, 1–12.

Cirtwill, A.R., Roslin, T., Rasmussen, C., Olesen, J.M. & Stouffer, D. B. 2018. Between-year changes in community composition shape species' roles in an Arctic plant-pollinator network. Oikos 127, 1163–1176. doi: 10.1111/oik.05074

Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldaña, J. 1993. Body Sizes of Animal Predators and Animal Prey in Food Webs. Journal of Animal Ecology, 62, 1, 67-78.

Colston, T.J., Costa, G.C. & Vitt, L.J. 2010. Snake diets and the deep history hypothesis. Biological Journal of the Linnean Society, 101, 476–486. https://doi.org/10.1111/j.1095-8312.2010.01502.x

Daltry, J.C., Wüster, W. & Thorpe, R. S. 1996. Diet and snake venom evolution. Nature, 379, 6565, 537–540. https://doi. org/10.1038/379537a0

Davies, E.L. & Arbuckle, K. 2019. Coevolution of snake venom toxic activities and diet: Evidence that ecological generalism favours tox- icological diversity. Toxins, 11, 711. https://doi.org/10.3390/toxin s11120711

Delmas, E., Besson, M., Brice, M.H., Burkle, L.A., Riva, G.V.D., Fortin, M.J, Gravel, D., Guimarães, P.R. Hembry, D.A., Newman, E.A., Pires, M.M., Yeakel, J.D. & Poisot, T. 2018. Analysing ecological networks of species interactions. Biol. Rev.

Estes, J.A. & Palmisano, J.F. 1974. Sea otters: their role in structuring nearshore communities. Science, 185, 1058–1060.

Fortuna, M.A., Stouffer, D.B., Olesen, J.M., Jordano, P., Mouillot, D., Krasnov, B.R., Poulin, R. & Bascompte, J. 2010. Nestedness versus modularity in ecological networks: Two sides of the same coin? Journal of Animal Ecology, 79, 811–817. doi.org/10.1111/j.1365-2656.2010.01688.x

Galetti, M. et al. 2013. Functional Extinction of Birds Drives Rapid Evolutionary Changes in Seed Size. Science 340, 1086-1090.

Greene, H.W. 1983. Dietary correlates of the origin and radiation of snakes. Amer. Zool. 23: 431–441.

Guimarães, P.R. 2020. The structure of ecological networks across levels of organization. Annual Review of Ecology, Evolution, and Systematics, 51, 433–460.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren, P.H. & Woodward, G. 2009. Ecological networks – beyond food webs. Journal of Animal Ecology, 78, 253–269.

Klaczko, J., Sherratt, E. & Setz, E.Z.F. 2016. Are diet preferences associated to skulls shape diversification in xenodontine snakes? PLoS One, 11, 1–12. doi.org/10.1371/journal.pone.0148375

Krishna, A., Guimarães Jr., P.R., Jordano, P. & Bascompte, J. 2008. A neutral-niche theory of nestedness in mutualistic networks. Oikos, 117, 1609–1618. https://doi.org/10.1111/j.1600-0706.2008.16540.x

Lewinsohn, T. M., Prado, P.I., Jordano, P. & Bascompte, J. 2006. Structure in plant-animal interaction assemblages. Oikos 113, 174–184.

Martins, M., Araujo, M.S., Sawaya, R.J., & Nunes, R. 2001. Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (Bothrops). Journal of Zoology, 254, 529–538.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist, pp. 65–75.

Pinheiro, R.B.P., Felix, G.M.F., Dormann, C.F. & Mello, M.A.R. 2019. A new model explaining the origin of different topologies in interaction networks. Ecology, 100, e02796. https://doi.org/10.1002/ecy.2796

Pinto-Coelho, D., Martins, M. & Guimarães Jr., P.R. 2021. Network analyses reveal the role of large snakes in connecting feeding guilds in a species-rich Amazonian snake community. Ecology and Evolution, 11, 6558-6568.

Pires, M.M., Guimarães Jr., P.R., Araújo, M.S., Giaretta, A.A., Costa, J.C.L. & Reis, S.F. 2011. The nested assembly of individual-resource networks. Journal of Animal Ecology, 80, 896–903.

Pires M.M., O'Donnell J.L., Burkle L.A., Díaz-Castelazo C., Hembry D.H., Yeakel J.D., Newman E.A., Medeiros L.P., de Aguiar M.A.M. & Guimarães Jr., P.R. 2020. The indirect paths to cascading effects of extinctions in mutualistic networks. Ecology, 101, e03080. doi: 10.1002/ecy.3080.

Poisot, T., Stouffer, D.B. & Kéfi, S. 2016. Describe, understand and predict: why do we need networks in ecology? Functional Ecology, 30, 1878–1882.

Prado, P.I. & Lewinsohn, T.M. 2004. Compartments in insect-plant associations and their consequences for community structure. Journal of Animal Ecology 73, 1168–1178.

Rezende, E.L., Albert, E.M., Fortuna, M.A. & Bascompte, J. 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. Ecol. Lett., 12, 779–788.

Sazima C., Guimarães Jr., P.R., Reis, S.F. & Sazima I. 2010. What makes a species central in a cleaning mutualism network? Oikos, 119, 1319–1325.

Schmitz, O.J. & Beckerman, A.P. 2007. Food Webs. Encyclopedia of Life Sciences, John Wiley & Sons.

Sebastián-González et al. 2020. Network structure of vertebrate scavenger assemblages at the global scale: drivers and ecosystem functioning implications. Ecography, 43, 1–13, 2020 doi: 10.1111/ecog.05083.

Shine, R., & Bonnet, X. 2000. Snakes: A new ‘model organism’ in ecolog- ical research? Trends in Ecology & Evolution, 15, 221–222. https://doi. org/10.1016/S0169-5347(00)01853-X

Sinclair, A.R.E., Mduma, S., Brashares, J.S. 2003. Patterns of predation in a diverse predator-prey system. Nature, 425, 288-290.

Stouffer, D.B. et al. 2011. The role of body mass in diet contiguity and food-web structure. J. Anim. Ecol., 80, 632–639.

Thompson, J.N. 2005. The Geographic Mosaic of Coevolution. University of Chicago Press, Chicago.

Tinker, M.T., Guimarães Jr., P.R., Novak, M., Marquitti, F.M.D., Bodkin, J.L., et al. 2012. Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. Ecol. Lett., 15, 475–83

Valverde, S., Vidiella, B., Montañez, R., Fraile, A., Sacristán, S. & García-Arenal, F. 2020. Coexistence of nestedness and modularity in host-pathogen infection networks. Nature Ecology and Evolution, 4, 568-577.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J., Olesen, J., Valido, A., & Warren, P. 2005. Body size in ecological networks. Trends in Ecology & Evolution, 20, 402–409. https://doi.org/10.1016/j.

Capítulo 1

Network analyses reveal the role of large snakes in connecting feeding guilds in a species-rich Amazonian snake community

Daniela Pinto-Coelho, Marcio Martins, and Paulo R. Guimarães Junior

Ecology and Evolution (2021), 11:6558–6568.

Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, Cidade Universitária, 05508-900, São Paulo, SP, Brazil. Daniela Pinto Coelho (https://orcid.org/0000-0001-8706-5066), Marcio Martins (https://orcid.org/0000-0001-8108-6309) and Paulo Roberto Guimarães Junior (https://orcid.org/0000-0001-9161-8305)

*Author for correspondence: danipcoelho@usp.br

Abstract

In ecological communities, interactions between consumers and resources lead to the emergence of ecological networks and a fundamental problem to solve is to understand which factors shape network structure. Empirical and theoretical studies on ecological networks suggest predator body size is a key factor structuring patterns of interaction. Because larger predators consume a wider resource range, including the prey consumed by smaller predators, we hypothesized that variation in body size favors the rise of nestedness. In contrast, if resource consumption requires specific adaptations, predators are expected to consume distinct sets of resources, thus favoring modularity. We investigate these predictions by characterising the trophic network of a species-rich Amazonian snake community (62 species). Our results revealed an intricate network pattern resulting from larger species feeding on higher diversity of prey and therefore promoting nestedness, whereas snakes with specific lifestyles and feeding on distinct resources, promoting modularity. Species removal simulations indicated that the nested structure is favored mainly by the presence of five species of the family Boidae, which because of their body size and generalist lifestyles connect modules in the network. Our study highlights the particular ways traits affect the structure of interactions among consumers and resources at the community level.

Keywords: Body size, Boidae, complex networks, *Eunectes murinus*, nestedness, modularity, trophic interaction.

Introduction

Interactions between species are a key component for understanding biodiversity (Abram 1987). In fact, individuals of all species rely upon ecological interactions to obtain food, to breed, or to protect against natural enemies (Thompson 2005). Ecological interactions form networks that connect populations of different species in a locality (Bascompte and Jordano 2013). The organisation of these networks may have important conservation implications, potentially affecting the robustness of ecological systems to species loss (Schmitz and Beckerman 2007). In this context, it is essential to understand how factors that influence the interactions between individuals affect the structure of networks at the level of ecological communities.

The structure of several ecological networks generally deviates from what is expected for networks in which individuals interact randomly, i.e., the interaction is proportional to the product of species abundances (Krishna et al. 2008). These deviations from expected network structure suggest that factors such as the characteristics of interacting individuals and environmental conditions influence the structural patterns of ecological networks at the community level. Among the traits that may affect network structure is body size, which is directly associated with the ability of individuals to consume resources (Stouffer et al. 2011). At the species level, there are strong evidence that diet width, i.e., the number of different resources that organisms of a given species feed on, vary with species mean body size, as observed in mammals (Sinclair et al. 2003), frogs (Ceron et al. 2019), fish (Rezende et al. 2009), and birds (Gliwicz 2008). If on average the larger the predator, the greater its ability to kill larger prey we should expect that, at the species level, larger average body sizes to be correlated with a larger number of resource types consumed by predator species (i.e., large predator species will have a diet that include both small and large prey) (Sinclair et al. 2003). Furthermore, if only body size were influencing the capacity to consume a wider range of resources, it is expected that the diet of the smaller predator species will be a subset of the items of the larger predator species's diet, leading to nested ecological networks (Sinclair et al. 2003, Woodward et al. 2005, Stouffer et al. 2011).

On the other hand, food resources are not homogeneously distributed in environments and the degree of specialisation in the consumption of distinct sets of prey may require distinct adaptations (Schoener 1968, Covich and McDowell 1996). For instance, the *Anolis* lizards of South Bimini islands divide habitat and the food resources according to lizard average size classes, in which larger lizard species usually eat larger food items than smaller lizard species (see Schoener 1968). Thus, we can expect that due to the restrictions related to prey handling, prey detection, or nutritional yield, larger predators are predisposed to disregard smaller prey (Mittelbach 1981, Arnold 1993, Arim et al. 2010). In this sense, deviations from the perfectly nested pattern are expected, enabling the formation of semi-isolated groups (modules) in the network. Networks with a modular structure have stimulated much interest due to its possible evolutionary and ecological consequences (Ings et al. 2009). For instance, modules may represent coevolutionary units (Thompson 2005) and increase the stability of ecological networks, thus providing a potential mechanism through which complexity arise and persist in ecological communities (Krause et al. 2003, Ings et al. 2009).

Here, we explore the trophic network organisation of a community Amazonian snakes. Many snakes are top-level carnivores that perform important roles in ecosystems (Yanosky et al. 1996). Indeed, snakes have been used as a model system in studies on the effect of ecological interactions on diversity (Martins et al. 2001, Colston et al. 2010, Alencar et al. 2013, Bellini et al. 2015, Klaczko et al. 2016, Alencar et al. 2017). These studies explore how ecological traits, interspecific interactions, habitat use, and evolutionary history influence the current trophic interactions of different species. Furthermore, as snakes evolved morphological and behavioral adaptations to kill and ingest their prey whole (Greene 1983), traits related to different dietary habits of species make snakes a model study system to understand how trophic interactions organise community structure (Shine and Bonnet 2000). In addition, some species (e. g. those in the genera *Bothrops, Crotalus, Lachesis* and *Micrurus*) are of medical importance (Campbell and Lamar 1989) and knowledge about their trophic ecology may favor studies focusing on public health, e.g., diet patterns are related to poison chemistry (see Daltry et al. 1996, Davies and Arbuckle 2019).

Motivated by understanding the trophic organisation pattern of snake communities, we here use as a model a rich and well-studied community of Amazonian snakes (Martins and Oliveira 1998). We characterised the structure of the interaction network between snakes and their food resources. We expected that if only snake body size were shaping network patterns at the species level, the structure would be nested; on the other hand, if specialization in resource consumption were driving patterns of resource use across snakes, modularity would be expected. We then evaluated the role of different snake species and the effect of snakes' habitat use (referred to here as a lifestyle) in shaping the network structure.

Methods

The network structure of interactions between snakes and their food resources

We analysed the snake diet derived from a long-term study carried out in a Central Amazonia site on the natural history of forest snakes (Martins and Oliveira 1998). We described the resource use by snakes as an interaction matrix **A** in which if a snake *i* feeds on a given resource *j* the matrix is filled with 1 and zero otherwise. The matrix **A** defines a bipartite network in which one set of nodes is represented by snake species, the other set of nodes by resource types and the links describe interactions between snake species and food resource types. Our food resources are not described at species level but at coarse categories such as small mammals, medium mammals and big mammals (see details in Supplementary material - dataset). Similar approach led to insights in the study of food webs (Cohen 1977) and individual-based networks (Araújo et al. 2008). In fact, there is no intrinsically correct level of description when characterizing an ecological network (Guimarães 2020). We opted for these coarse categories because they are in agreement with (i) the evidence that snakes are specialized in broad categories of resources, e.g., serpentiform organisms that include snakes, amphisbaenians, and caecilians (see Martins and Oliveira 1998); (ii) the level of detail available from the diet analyses of snakes. Having said that, to verify if our level of network description affects our analyses we performed a set of sensitivity analyses (details below).

We used four metrics to characterise the structure of the interactions network analysed: (i) degree distribution, which is the description on how the number of food resources a given snake can feed on (the degree) varies across snake species; (ii) connectance (*C*), which is the proportion of all possible interactions actually recorded in the network. Connectance values range from 0 (non-connected network) to 1 (maximum connectance); (iii) modularity (*M*), a measure of the extent to which the network is formed by groups (modules) of snake species in which snake within a module overlap in much of their resources, whereas snakes in different modules show no or weak resource use overlap; and (iv) nestedness (*N*), which consists of an interaction pattern in which the specialists interact with sets of resources with which the generalists also interact. Detailed descriptions of the metrics are available in the Supplementary material Appendix 1.

We used Q_B metric, defined by Barber (2007), to characterise modularity, with values ranging from 0 (non-modular network) to 1 (completely modular). A simulated annealing algorithm (Guimerà & Amaral 2005) was used to optimise the Q_B value. Modularity analyses were performed using the Modular program (Marquitti et al. 2014). All the above and the following analyses were performed using R version 3.5.1 (R Core Team 2018), with the exception of modularity. We performed a set of sensitivity analyses to verify if our results are dependent on our approach to compute modularity (Supplementary material Appendix 1).

The NODF metric was used to characterise the nestedness degree (Almeida-Neto et al. 2008) and its values ranges from 0 (non-nested network) to 100 (perfect nestedness). The degree of nestedness and modularity were then compared with a theoretical benchmark provided by the null model 2 of Bascompte et al. (2003) (see detailed description in Supplementary material Appendix 1). We generated 1000 null model matrices to estimate nestedness and modularity. If a network shows a degree of nestedness or modularity larger than expected by the null model 2, then there is evidence of ecological or evolutionary processes acting on the network organisation that goes beyond those shaping the degree of specialisation of the snake species (e.g, Bascompte et al. 2003).

In order to highlight the unique inferences provided by the network approach, we compared the results of the network analysis with the results of a multivariate analysis. Multivariate analysis methods are widely used in ecology due to their ability to analyse complex systems registered in an interaction matrix (Prado et al. 2002). Among the several types of multivariate analyses, we chose correspondence analysis (CA) because of its ability to reveal reciprocal relationships between two sets of equal interest (Greenacre 1984; Lewinsohn and Prado 2008), in our case, snakes and their food resources.

The role of snake species in network structure

If the network of interactions analysed follows the organisation pattern structured by body mass (i.e. presenting higher nestedness than expected by the null model 2), we hypothesized snake average body mass to be positively correlated with the number of resources consumed by the snake species. To explore this prediction, we investigate the association between average body mass and the role of species in the network structure. We recorded the estimates of the average body mass of each snake species in our network (data available in Feldman et al. 2016). Average body mass was log-transformed prior to analysis (Supplementary material Appendix 2 Table A1).

In order to understand the individual contribution of each species of snake to nestedness, we used a jackknife resampling approach in which we removed a snake species and recomputing the degree of nestedness. We repeated the procedure for all snake species in the network and then we computed a change in nestedness: $\Delta N_i = N - N_i$, in which N is the degree of nestedness of the complete network and N_i is the degree of nestedness after the removal of a snake species i. If body size is shaping the contribution to nestedness, we should expect that the ΔN_i will assume increasingly positive values as larger snakes are removed from the network, indicating that nestedness is higher in the presence of these larger snake species.

The relationship between lifestyles and network structure

Because dietary specialisation in snakes can be related to habitat occupation (see Martins et al. 2002, Alencar et al. 2017), we expect snake lifestyles to affect the degree of dietary specialisation (e.g., an aquatic snake would rely upon aquatic prey). If this is true, the distribution of lifestyles in the different modules will not be random. We evaluated this prediction using two analyses. First, we analysed the frequency of snake lifestyles in different modules. We estimated the probability of the observed number of species of a given lifestyle in a given module be reproduced by randomly assigning species across modules, but preserving the number of snake species in each lifestyle and the number of snake species in each module (n = 1000 randomisations). Then, we analysed the dissimilarity on lifestyles between modules. To do so, we used the Bray-Curtis index, available in the vegan package in R (Oksanen et al. 2018) (see detailed description in Supplementary material Appendix 1). Dissimilarity between a pair of modules range from 0 (modules are identical in the composition of lifestyles) to 1 (no lifestyle occurs in both modules).

Sensitivity analyses focuses on the level of resource resolution

Sampling effects may affect the description of network patterns. Therefore, we performed a sensitivity analysis to explore how robust is the description of network patterns to changes in our dataset. We add information to the use of resources by snakes by using data from other Amazonian regions, based on evidence that there is no significant intraspecific variation on the snake's diet across different localities in Amazonia (Martins and Oliveira, 1998; Supplementary material Appendix 1 and Appendix 2 Table A1).

Snake diet often include food resources that are mainly consumed and resources that are only eventually consumed. We performed a sensitivity analysis to check if the patterns reported in our study are robust enough when considering the presence or absence of secondary resources in the snake diet. We described two matrices of interactions: (1) a matrix in which only main resources were considered; (2) and a matrix in which both main and secondary resources were considered. We defined if a resource is main or secondary according to information about snake diet preferences available in Martins and Oliveira (1998). Then, we calculate the nestedness and modularity values in the presence and absence of secondary resources. The nestedness values of the two networks were compared with a null model generated with 5,000 random removals of food resources from each of the analysed networks. Finally, we calculated whether there was a significant difference between the nestedness of the network in the presence and absence of secondary resources.

Because taxonomic resolution might influence the detection of patterns in the network (Rezende et al. 2009), we performed another sensitivity analysis to check if the type of resource categorization could affect the network patterns. Thus, we described two other matrices of interaction with different degrees in the resources taxonomic resolution: less specific network (Supplementary material Appendix 1 Figure A2 and Appendix 3 Table A1) and more specific network (Supplementary material Appendix 1 Figure A3 and Appendix 4 Table A1).

Results

Network structure

We recorded 163 interactions between 62 snake species and 26 food resources (Figure 1 and Supplementary material Appendix 1 Figure A6) that were heterogeneously distributed among snake species, where most of them had few interactions (56.45% snake species interacted with one or two resource categories) and few species had many interactions (6.45% interacted with more than five resources; Supplementary material Appendix 1 Figure A1). The network structure show moderate connectance ($C = 0.101$) (Table 1), indicating that, from the variety of food items consumed by snakes, the species analysed use, on average, 2-3 resources. The snake-resource network also show significant nestedness ($N = 33.14$, $p < 0.01$), indicating that 1/3 of the interactions of the less connected species represent a subset of the interactions of the most connected species. Finally, the network also show significant modularity (M =

0.51, p = 0.03), indicating that the number of interactions within each modules is 51% larger than what is expected for a network with the same number of modules, the same number of interactions per species, but with random interactions between species.

Some snake species showed extreme specialisation, such as *Dipsas* spp., which feed exclusively on mollusks, and *Drepanoides anomalus* that rely upon eggs of squamate reptiles. Other species, such as *Atractus* spp., although specialist in the consumption of earthworms, may also feed on insects. Similarly, *Micrurus surinamensis* primarily consume fish but secondarily consume lizards and snakes. On the other hand, we found very generalist species, such as *Boa constrictor* and *Epicrates cenchria*, which interacted with six resource types, *Corallus hortulanus*, which interacted with eight resources and *Eunectes murinus*, the largest species of the network, which interacted with 11 resources. Among the food resources consumed by many snake species were lizards (24% of all interactions), anurans (16%), and small mammals (9%), comprising rodents and marsupials. Among the least consumed resources were large mammals (such as cervids), turtles and alligators, only consumed by *Eunectes murinus*, onychophorans only consumed by *Micrurus hemprichii*, gymnophiona only consumed by *M. lemniscatus*, and salamanders, which were only consumed by *Chironius fuscus* (Supplementary material Appendix 2 Table A1).

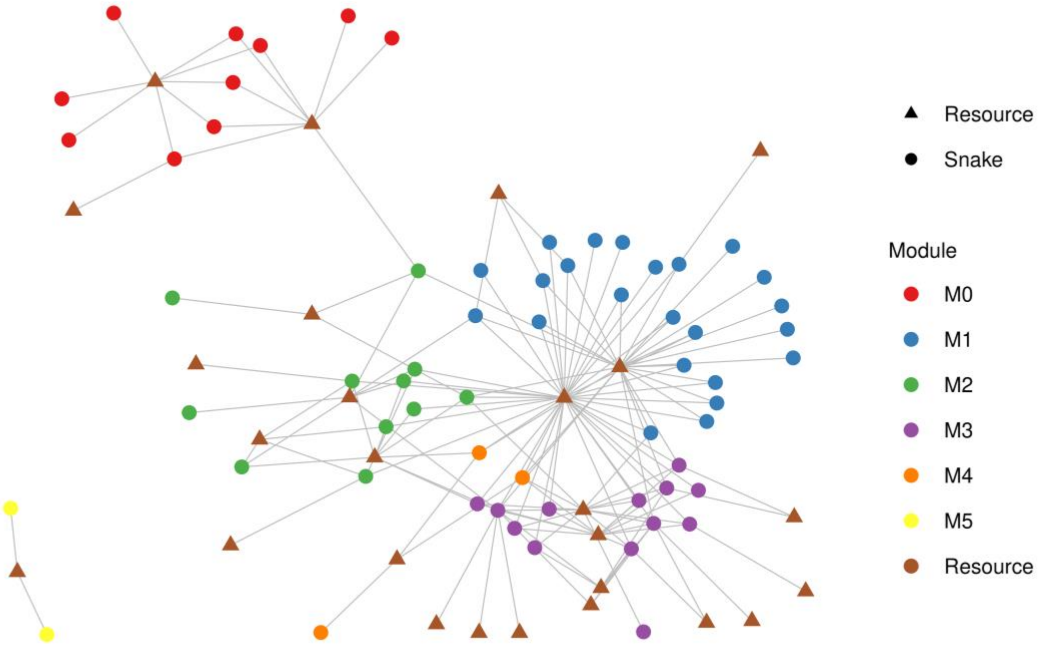


Figure 1: Network describing the interactions (lines) between species of Amazonian snakes (circles) and their food resources (triangle).

To assess whether there was a difference in network structure based only on the presence of primary resources in the snake diet, we removed all non-primary resources and reanalysed the network. Even after removing the secondary resources, network average degree and connectance remained within the same range values (Table 1). The results also indicated that there was no significant difference between the network nestedness values with and without the presence of secondary resources ($p = 0.147$). Even after the removal of non-primary items, the network remained significantly nested ($N = 29.46$, $p < 0.01$). In contrast, the modular structure was nonsignificant after removal of non-primary resources ($M = 0.47$, $p = 0.44$). Similarity, to check if the type of food resource categorization could affect the network patterns, we used the same metrics to analyse the more specific and the less specific networks. Our results for all, but connectance, hold with different levels of detail on resource description and all networks remained significantly nested and modular. Connectance was the only metric that values show large variation across levels of detail on resource description, and connectance increased (Supplementary material Appendix 1 Table A2).

Table 1: Relationship of the network structure analysis of interactions between Amazonian snakes and their food resources. S = snake species richness in the network; R = food resources richness (Note that with the removal of species from the network occurs the loss of interactions, which may reduce the number of resources); SD = average degree; C = connectivity; N = nestedness; Nrel = relative nestedness; M = modularity; Mrel = relative modularity; nM = number of food modules.

Web	S	R	SD	C	N	p N	Nrel	M	p M	nM	Mrel
Complete web	62	26	2.62	0.10	33.14	p < 0.01	0.94	0.51	p = 0.03	6	0.11
Without secondary resources	62	24	2.34	0.09	29.46	p < 0.01	0.93	0.48	p = 0.44	7	0.03
Without the 7 largest species	55	18	2.23	0.12	30.23	p < 0.01	0.69	0.53	p = 0.06	7	0.12
Without species of Boidae	57	19	2.26	0.12	30.42	p < 0.01	0.74	0.53	p = 0.01	7	0.13

Our results supported the prediction that there is a positive association between the number of resources consumed and average body size (slope = 1.41, $R^2 = 0.46$, $p < 0.01$, Figure 2A), indicating that in general the largest species of snakes showed a greater number of food interactions. Exceptions to this pattern were *Corallus caninus* ($k = 3$) and *Lachesis muta* ($k = 1$), both specialists in the consumption of mammals. Among the seven largest snake species, five of them (*Eunectes murinus, Boa constrictor*, *Epicrates cenchria*, *Corallus hortulanus*, and *Corallus caninus*) belong to the family Boidae. Thus, this family is over-represented among the set of heavier snakes in the network and our analysis may be biased by the confounding factors generated by all other traits shared by boid species. To circumvent this problem we explored if the correlation between average body mass and degree holds within speciose snake families. We performed correlation analyses between degree and average body mass for species of the family Colubridae and for those of the family Dipsadidae, the two largest snake families in the network. The results indicated that a positive correlation between average body mass and the number of resources consumed hold even for non-boid snakes and partially controlling for phylogenetic effects, there was (see Supplementary material Appendix 1 Figure A4 and A5).

The role of different species of snakes in network structure

The correlation between degree and average body mass suggest nestedness was driven by body size. In fact, there is a positive correlation between delta nestedness and average body mass (slope = 0.4, $R^2 = 0.37$, $p < 0.01$, Figure 2B), as well as between delta nestedness and degree (slope = 0.19, $R^2 = 0.46$, $p < 0.01$, Figure 2C), indicating that the largest snakes have a greater contribution to nestedness. We performed an removal analysis to further explore this pattern. We removed species with more outlier values of average body mass and recalculated the nestedness value. They were the seven largest snake species in the network (*Eunectes murinus, Boa constrictor, Lachesis muta, Epicrates cenchria, Corallus hortulanus, Corallus caninus* and *Spilotes pullatus*). If the largest snakes are key components contributing to nestedness, we expected that nestedness after removal of these species would be smaller than those generated by a null model in which we randomly remove any seven species from the network and recalculate the nestedness. Our results supported this prediction, indicating that the nestedness values were smaller after the removal of the seven largest snake species ($N = 30.23$, $p < 0.01$, $n = 1,000$ simulations of species removal).

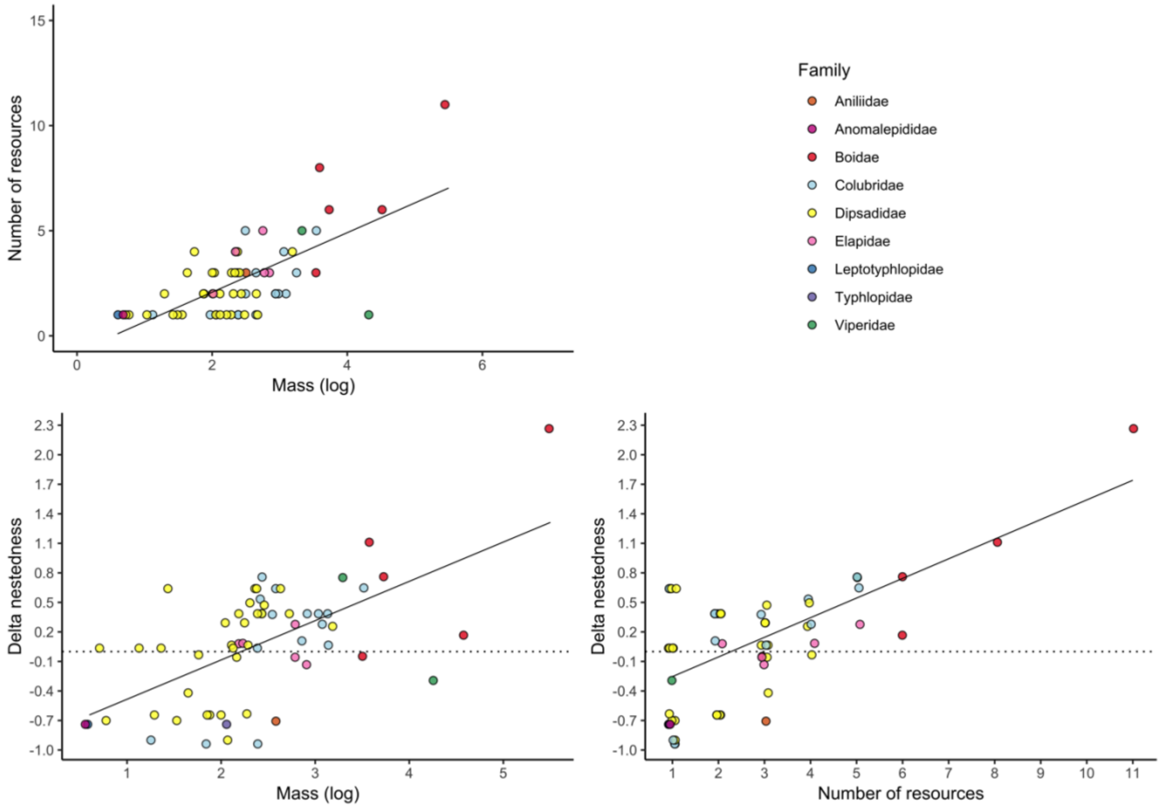


Figure 2: A) The number of categories of food resources consumed by different snake species is positively associated with the snake average body mass (slope = 1.41, $R^2 = 0.46$, $p < 0.01$) in a network of interactions between Amazonian snakes and their resources. . In simulations of species removal, B) changes in the level of nestedness are positively associated with the snake average body mass of the removed species (slope = 0.40, $R^2 = 0.37$, $p < 0.01$); C) as well as with the number of food resources (degree) (slope = 0.19, $R^2 = 0.46$, $p < 0.01$). Note the stronger, negative changes on nestedness are associated with Boidae snakes (red). Each point represents a species and the colors represent the different snake families. To avoid overlap, some points have been slightly offset from their original position on the x-axis.

The relationship between modularity and snake lifestyle

The network also presented a modular structure, in which the consumption of different resources divided the network into six different food modules (Table 1 and Supplementary material Appendix 1 Table A3). The formation of groups was also observed in our correspodence analysis, although a small number of groups were detected (Supplementary material Appendix 1). We expected that if the snake lifestyle was related to the formation of food modules, the distribution of lifestyles in the different modules would not be random. In fact, modules were associated with particular lifestyles, as indicated by significant or marginally significant probability values present in all modules but module 3 (Table 2). Module 3, was composed of species with the greatest variety in diet and lifestyle, such as boid snakes. Modules with more specific combinations of lifestyle and diet showed all significant or marginally significant probability values (Figure 3). Moreover, the formation of groupings based on diet and lifestyle occurred by species that specialise in the consumption of certain food resources, probably associated with their lifestyle. For example, the smallest module (number 5) was formed by only two arboreal species of the genus *Dipsas* that feed exclusively on mollusks; another module grouped species of terrestrial habits, such as *Drepanoides anomalus, Drymoluber dichrous,* and *Mastigodryas boddaerti,* which feed on squamate eggs, whereas another module grouped fossorial species, such as *Atractus* spp. that are specialists in preying upon earthworms. On the other hand, the remaining modules grouped species with varied lifestyles and generalist diets.

Table 2: Comparison between the real interaction matrix, the dissimilarity matrix, and the likelihood matrix of the lifestyle by food module of the network of interactions between Amazonian snakes and their food resources. Lines represent the six (0-5) food modules and columns represent the lifestyles of the snakes. Asterisks represent significant or marginally significant values of probability.

Real matrix

Modules	**Aquatic**	**Arboreal**	**Fossorial**	**Semi-arboreal**	**Semi-fossorial**	**Terrestrial**	**n species**
0	0	0	10	0	0	0	10
1	1	9	0	0	2	11	23
2	2	0	3	1	3	2	11
3	1	5	0	1	0	6	13
4	0	0	0	0	0	3	3
5	0	2	0	0	0	0	2
n species	4	16	13	2	5	22	62

Dissimilarity matrix

Modules	**0**	**1**	**2**	**3**	**4**	**5**
0	0	1	0.714	1	1	1
1	1	0	0.706	0.333	0.769	0.840
2	0.714	0.706	0	0.667	0.714	1
3	1	0.333	0.667	0	0.625	0.733
4	1	0.769	0.714	0.625	0	1
5	1	0.840	1	0.733	1	0

Probability matrix

Modules	**Aquatic**	**Arboreal**	**Fossorial**	**Semi-arboreal**	**Semi-fossorial**	**Terrestrial**
0	1	1	0*	1	1	1
1	0.839	0.06*	1	1	0.622	0.121
2	0.152	1	0.41	0.303	0.035*	0.969
3	0.647	0.197	1	0.386	1	0.276
4	1	1	1	1	1	0.027*
5	1	0.078*	1	1	1	1

As a consequence of the association between lifestyles and modular structure, modules often show dissimilar combinations of lifestyles. Dissimilarity values ranged from 0.33 to 1 (Table 2). The most dissimular module (Module 0) was composed exclusively of snakes with the fossorial lifestyle, such as the *Atractus* species, specialists in the consumption of earthworms. The most similar modules were modules 1 and 3, which as well as module 2 have the largest variety of lifestyles and food resources consumed by the snakes (Supplementary material Appendix 1 Table A3).

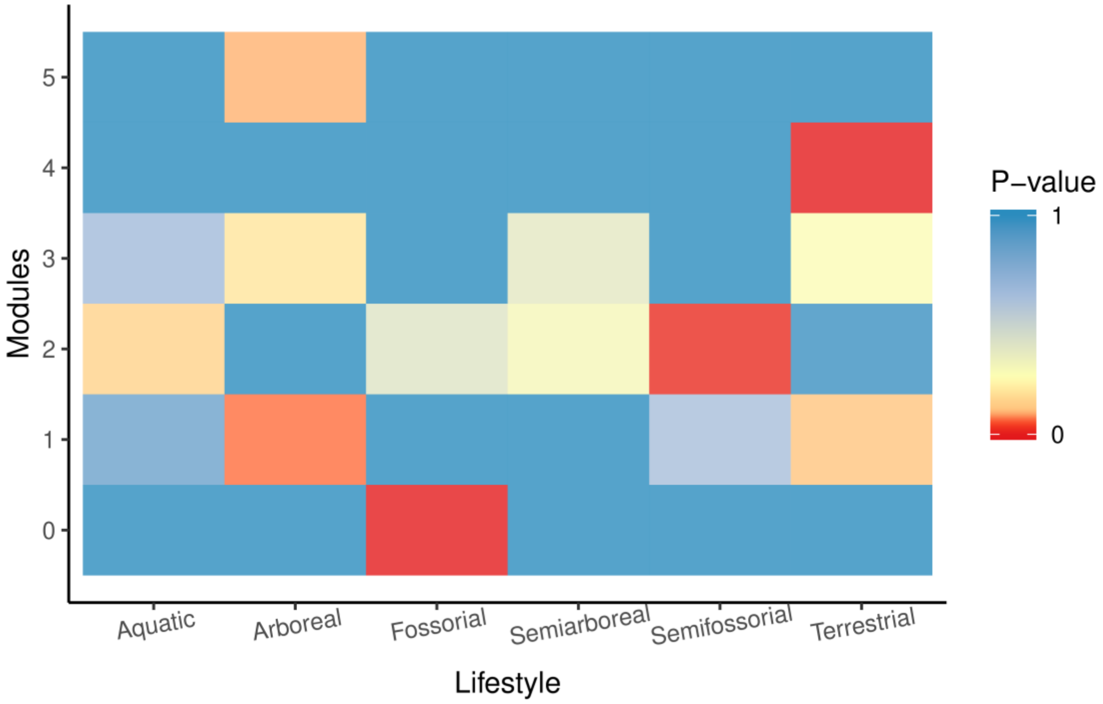


Figure 3: The probability of the observed number of species of a given lifestyle in a given module of being reproduced randomly. Red color indicates higher frequency, with a 95% confidence interval.

Discussion

Our results indicated that the network of interactions between snakes and their resources in a species-rich Amazonian community presented a combination of both nested and modular structure. Nestedness was related to average body mass of snakes, in which boid snakes connect food modules in the trophic network. The modular pattern, in turn, is associated to the different snake lifestyles, in which snakes that share similar habits usually consume similar resources available in their shared microhabitats.

The observed connectance of the network indicated that, given the variety of resources available in the environment, snake species consumed only a subset of these resources. This result suggests that most food resources may not be accessible to most species, suggesting forbidden interactions (Olesen et al. 2010) associated with possible restrictions related to lifestyle (see Savitzky 1983), as well as body size (Sinclair et al 2003, Woodward et al. 2005, Stouffer et al. 2011). For instance, arboreal snakes have morphological adaptations, such as a slender body and long tail, which may represent limitations to the consumption of large prey such as mammals (Martins et al. 2001, Alencar et al. 2013, Alencar et al. 2017). The analysis of network structure revealed that the patterns of resource use by different species lead, at the community level, to nestedness and modularity. Our results contrast with some studies on antagonistic networks that indicate opposite trends between nestedness and modularity (Thébault and Fontaine 2010, Pires and Guimarães 2012). Having said that, other studies simultaneously show levels of nestedness and modularity (Bellay et al. 2011, Flores et al. 2013, Pinheiro et al. 2019). The emergence of these combined network patterns is possible due to the low connectivity of the network (Lewinsohn and Prado 2006, Fortuna et al. 2010) and resource heterogeneity (Pinheiro et al. 2019) in Amazonian forests.

Several processes may explain the nested patterns, such as variations in species abundances (Lewinsohn and Prado 2006). One of the explanations for the nested pattern found in our study was the large size variation among species present in the network. The variation in snake body mass has led to a trophic hierarchy in which larger predators prey upon more resource items than smaller predators. This hierarchy was detected in several predator-prey interaction networks found in nature (Woodward et al. 2005, Smith and Mills 2008, Arim et al. 2010). This pattern indicates that predators have the potential to add resources sequentially as they increase in size, although this increment of larger resources may lead to the rejection of smaller, less nutritious or difficult to handle resources (Mittelbach 1981, Arnold 1993, Arim et al. 2010, Woodward et al. 2010). In addition to body size, skull morphology is also an important feature associated with diet and snake lifestyle (Pough and Groves 1983, Savitzky 1983, Klaczko et al. 2016). The larger the head of a snake, the greater the prey consumed (King 2002). Thus, future research that investigates emerging patterns arising from the association of both body size and skull morphology with the structure of trophic interaction networks could predict the processes, at the community-level, involved in the relationships between snakes and their food resources.

When analysing the contribution of each species to nestedness, we found that average body mass has a phylogenetic signal, with large species concentrated in a few clades. After removing larger species, mostly boids, the nestedness value decreases 8.78% although it still remains significant. The maintance of nestedness after the removal of large snakes might be a consequence of the number of resource - body mass association holds for smaller snake species, such colubrid and dipsadid snakes. Boids are efficient constrictors with generalist diets, that occupy diverse microhabitats, which allow them to consume a wide variety of food resources (Pizzato et al. 2009, Henderson and Pauers 2012). This combination of features may simultenouly explain why (i) boids act as hubs (species with many interactions) in the analysed network, and (ii) the decrease in nestedness when boids are removed from the network. Large predators, such as sharks, killer whales, lions, and birds of prey, often prey on diverse array of species (Sinclair et al. 2003), potentially connecting modules in networks (e.g., Rezende et al. 2009). The fact that a trophic network is connected implies that, at least from a theoretical point of view, indirect effects can propagate across species (Guimarães et al. 2017). As a consequence, the entire assemblage is more sensitive to change (see Andreazzi et al. 2018). In this sense, the highly connected species that create these links among guilds are candidates to play a key role to the ecological and evolutionary dynamics. This potential role is illustrated by our removal simulations that show the potential consequences of the removal of highly connected species to the structure of the network. Future research could test whether the presence of such large predators can also promote nestedness on predator-prey interaction networks.

The modular structure in ecological networks may be associated to factors such as the degree of specialisation among interacting species (Prado and Lewinsohn 2004, Lewinsohn and Prado 2006), habitat heterogeneity (Pimm and Lawton 1980), the phylogenetic relationship between species (Lewinsohn and Prado 2006), the convergence in a set of species traits (Olesen et al. 2007) or by a combination of factors (Donatti et al. 2011). We found that the consumption of specific resources is associated with more peculiar lifestyles. For instance, morphological adaptations to fossorial habit (e.g. less cranial mobility) hinder the consumption of prey larger than the snake's head size (Greene 1983, Savitzky 1983, Martins and Oliveira 1993). Accordingly, arboreal habits impose physical limitations on snake morphology and may restrict the consumption of larger prey, such as small mammals, favoring a diet based on lizards and/or frogs (Lillywhite and Henderson 1993, Martins et al. 2001, Martins et al. 2002, Alencar et al. 2013). Thus, we suggest that the modularity of the network we studied has emerged from the relationship between the lifestyles of snakes and the consumption of resources restricted to the habitats used by the species.

To sum up, we integrate network structure analyses with species removal simulations to evaluate the role of different snake species in the structure of a rich Amazonian snake community, and the mechanisms underlying the patterns found. The use of the network approach to understanding the organisation of ecological systems provides two sets of insights. First, nonrandom network patterns may represent the fingerprints of ecological and evolutionary processes shaping ecological systems (Guimarães 2020). In this sense, our quantitative predictions in terms of network descriptors allowed us to reveal how body size, past evolutionary history, and the lifestyles of snakes organise this species-rich snake assemblage. In this context, modularity is an example of a network descriptor that has been shown to better describe patterns of group organisation than other, more traditional multivariate approaches (Amaral and Guimerà 2005). Accordingly, network plots allow us to have a broader and faster visualisation of patterns that would be difficult to observe without using this approach (Marai et al. 2019). Figure 1, for example, allows us to quickly observe that there are two food items consumed by most species of snakes and that there are guilds that are completely specialised in the use of specific resources and others that are connected to the rest of the network by connector species. Second, network description allows us to infer about the robustness of ecological systems and their potential implications for biodiversity conservation (Schmitz and Beckerman 2007). For example, the presence of connector species allows us to infer about the possibility of the propagation of indirect effects in the network (Guimarães et al. 2017), which could affect species that do not directly interact with each other.

We encourage future studies to focus on understanding how community phylogenetic diversity may be associated with the modular structure (Rezende et al. 2009), as well as how the combination of traits associated with predator diet (e.g. its correlation with body size and skull shape) may contribute to the nested pattern and if geographic variation (environment type) can modify network structure (Pimm and Lawton 1980, Kortsch et al. 2019). This study points to the joint importance of the evolutionary history of lineages, body size, and their interacting resources to determine the structure, at the community scale, of the interactions between consumers and their resources.

Data Accessibility Statement

We declare that all data supporting the conclusions of this study (dataset, and supplementary information) are uploaded in Dryad (DOI https://doi.org/10.5061/dryad.f1vhhmgvt).

References

Andreazzi C. S, Guimarães Jr P. R., Melián, C. J. 2018. Eco-evolutionary feedback promotes fluctuating selection and long-term stability of antagonistic networks. – Proc. R. Soc. B 285: 20172596.

Abram, P. A. 1987. On classifying interactions between populations. – Oecologia 73: 272-281.

Alencar, L. R. V. et al. 2013. The Evolution of Diet and Microhabitat Use in Pseudoboine Snakes. – South Am. J. Herpetol. 8: 60–66.

Alencar, L. R. V. et al. 2017. Arboreality constrains morphological evolution but not species diversification in vipers. – Proc. Royal Soc. B 284: 20171775.

Almeida-Neto, M. et al. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. – Oikos 117: 1227–1239.

Araújo, M. S. et al. 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. – Ecology 89: 1981–1993.

Arim, M. et al. 2010. Food web structure and body size: trophic position and resource

Acquisition. – Oikos 119: 147-153.

Arnold, S. J. 1993. Foraging theory and prey size—predator-size relations in snakes. – In Seigel, R. A. and Collins, J. T. (eds.), Snakes: Ecology and Behavior. McGraw-Hill, New York, pp. 87–115.

Barber, M. J. 2007. Modularity and community detection in bipartite networks. – Phys. Rev. E 76: 066102.

Bascompte, J. et al. 2003. The nested assembly of plant-animal mutualistic networks. – PNAS 100: 9383–9387.

Bascompte, J. and Jordano, P. 2013. Mutualistic Networks. – Princeton: Princeton University Press.

Bellay, S. et al. 2011. A host-endoparasite network of Neotropical marine fish: are there organizational patterns? – Parasitology 138: 1945–1952.

Bellini, G. P. et al. 2015. Temperate Snake Community in South America: Is Diet Determined by Phylogeny or Ecology? – Plos One 10: 1-15.

Campbell, J. A. & Lamar, W. W. 1989. The Venomous Reptiles of Latin America. Ithaca: Cornell Univ. Press.

Ceron, K. et al. 2019. Global patterns in anuran–prey networks: structure mediated by latitude. – Oikos 00: 1–12.

Cohen, J. E. 1977. Food Webs and Niche Space. Princeton University Press, Princeton, New Jersey, USA.

Colston, T. J. et al. 2010. Snake diets and the deep history hypothesis. – Biol. J. Linn. Soc. 101: 476–486.

Covich, A. P. and McDowell, W. H. 1996. The stream community. – In Reagan D. P. and Waide, R. B. (eds), The food web of a tropical rainforest. University of Chicago Press, Chicago, Illinois, pp. 433–459.

Daltry, J. C., Wuster, W. and Thorpe, R. S. 1996. Diet and snake venom evolution. – Nature 379.

Davies, E. L. and Arbuckle, K. 2019. Coevolution of snake venom toxic activities and diet: Evidence that ecological generalism favours toxicological diversity. – Toxins 11: 711.

Donatti, C. I. et al. 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. – Ecol. Letters 14: 773–781.

Feldman, A. et al. 2016. Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. – Global Ecol. Biogeogr. 25: 187–197.

Flores, C. O. et al. 2013. Multi-scale structure and geographic drivers of cross-infection within marine bacteria and phages. – ISME J. 7: 520–532.

Fortuna, M. A. et al. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? – J. Anim. Ecol. 79: 811–817.

Gliwicz, J. 2008. Body Size Relationships between Avian Predators and Their Rodent Prey in a North-American Sagebrush Community. – Acta Ornithol. 43: 151-158.

Greenacre, M. J. 1984. Theory and applications of correspondence analysis. Academic Press, London.

Greene, H. W. 1983. Dietary correlates of the origin and radiation of snakes. – Amer. Zool. 23: 431–441.

Guimarães, P. R. et al. 2017. Indirect effects drive coevolution in mutualistic networks. – Nature 550: 511–14.

Guimarães, P. R. 2020. The structure of ecological networks across levels of organization. – Annual Review of Ecology, Evolution, and Systematics. 51: 433–60.

Guimerà, R. and Amaral, L. A. 2005. Functional cartography of complex metabolic networks. – Nature 433: 895–900.

Henderson, R. W. and Pauers, M. J. 2012. On the diets of neotropical treeboas (Squamata: Boidae: *Corallus*). – South Am. J. Herpetol. 7: 172-180.

Ings, T. C. et al. 2009. Ecological networks – beyond food webs. – J. Anim. Ecol. 78: 253-269.

King, R. B. 2002. Predicted and observed maximum prey size-snake size allometry. – Funct. Ecol. 16: 766-772.

Klaczko, J. et al. 2016. Are Diet Preferences Associated to Skulls Shape Diversification in Xenodontine Snakes? – PLoS One 11: 1-12.

Kortsch, S. et al. 2019. Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. – Ecography 42: 295–308.

Krause, A. E. et al. 2003. Compartments revealed in food-web structure. – Nature 426: 282–285.

Krishna, A. et al. 2008. A neutral-niche theory of nestedness in mutualistic networks. – Oikos 117: 1609–1618.

Lewinsohn, T. M. and Prado, P. I. 2006. Structure in plant-animal interaction assemblages. – Oikos 113: 174–184.

Lillywhite, H. B. and Henderson, R. W. 1993. Behavioral and functional ecology of arboreal snakes. – In: Seigel, R. A. and Collins, J. T. (eds.), Snakes: ecology and behavior. New York: McGraw-Hill, pp. 1-48.

Marai, G. E. et al. 2019. Ten simple rules to create biological network figures for communication. – PLoS Comput. Biol. 15(9): e1007244.

Marquitti, F. M. D. et al. 2014. MODULAR: Software for the autonomous computation of modularity in large network sets. – Ecography 37: 221–224.

Martins, M. and Oliveira, M. E. 1993. The snakes of the genus Atractus Wagler (Reptilia: Squamata: Colubridae) from the Manaus region, central Amazonia, Brazil. – Zool. Meded. 67: 21-40.

Martins, M. and Oliveira, M. E. 1998. Natural history of snakes in forests of the manaus region, Central Amazonia, Brazil. – Herpetol. Nat. History 6: 78-150.

Martins, M. et al. 2001. Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (Bothrops). – J. Zool. 254: 529-538.

Martins, M. et al. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers (Genus *Bothrops*). – In: Schuett, G. W. et al. (eds.), Biology of the vipers. Eagle Mountain Publishing, Eagle Mountain, pp. 307-328.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by Bluegills. – Ecology 62: 1370–1386.

Oksanen, J. et al. 2018. vegan: Community Ecology Package. R package version 2.5-2. https://CRAN.R-project.org/package=vegan.

Olesen, J. M. et al. 2007. The modularity of pollination networks. – PNAS. 104: 19891–19896.

Olesen, J. M. et al. 2010. Missing and forbidden links in mutualistic networks. – Proc. Royal Soc. B 278: 725-732.

Pimm, S. L. and Lawton, J. H. 1980. Are food webs compartmented? – J. Anim. Ecol. 49, 879–898.

Pinheiro, R. B. P. et al. 2019. A new model explaining the origin of different topologies in interaction networks. – Ecology 100: e02796.

Pires, M. M. and Guimarães, P. R. 2012. Interaction intimacy organizes networks of antagonistic interactions in different ways. – J. R. Soc. Interface 10: 20120649.

Pizzatto, L. et al. 2009. Food habits of Brazilian boid snakes: overview and new data, with special reference to *Corallus hortulanus*. – Amphibia-Reptilia 30: 533-544.

Pough, H. and Groves, J. D. 1983. Specializations of the Body Form and Food Habits of Snakes. – Am. Zool. 23: 443-454.

Prado, P. I. et al. 2002. Ordenação multivariada na ecologia e seu uso em ciências ambientais. – Ambiente & Sociedade 10: 1-15.

Prado, P. I. and Lewinsohn, T. M. 2004. Compartments in insect-plant associations and their consequences for community structure. – J. Anim. Ecol. 74: 1168-1178.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rezende, E. L. et al. 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. – Ecol. Lett. 12: 779–788.

Savitzky, A. H. 1983. Coadapted Character Complexes Among Snakes: Fossoriality, Piscivory, and Durophagy. – Am. Zool. 23: 397-409.

Schmitz, O. J. and Beckerman, A. P. 2007. Food Webs. Encyclopedia of Life Sciences, John Wiley & Sons.

Schoener, T. W. 1968. The Anolis Lizards of Bimini: Resource Partitioning in a Complex Fauna. – Ecology 49: 704-726.

Shine, R. and Bonnet, X. 2000. Snakes: a new ‘model organism’ in ecological research? – TREE 15: 221–222.

Sinclair, A. R. E. et al. 2003. Patterns of predation in a diverse predator–prey system. – Nature 425: 288-290.

Smith, N. O. and Mills, M. G. L. 2008. Predator–prey size relationships in an African large-mammal food web. – J. Anim. Ecol. 77: 173–183.

Stouffer, D. B. et al. 2011. The role of body mass in diet contiguity and food-web structure. – J. Anim. Ecol. 80: 632–639.

Thébault, E. and Fontaine, C. 2010. Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. – Science 329: 853-856.

Thompson, J. N. 2005. The Geographic Mosaic of Coevolution. University of Chicago Press, Chicago.

Woodward, G. et al. 2005. Body size in ecological networks. – TREE 20: 402-409.

Woodward, G. et al. 2010. Individual-based foodwebs: Species identity, body size and sampling effects. – Adv. Ecol. Res. 43: 211–266.

Yanosky, A. et al. 1996. Ecology of the snakes community at El Bagual Ecological Reserve, Northeastern Argentina. – Herpetol. Nat. Hist. 4(2): 97-110.

Capítulo 2

Drivers of the network structure of snake-prey interactions

Daniela Pinto-Coelho[1], Kate P. Maia[1], Laura R.V. Alencar[2], Marcio Martins[1] & Paulo R. Guimarães Jr[1].

[1]Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, Cidade Universitária, 05508-900, São Paulo, SP, Brazil.
[2]Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect St, New Haven, CT 06511.

Author for correspondence: danipcoelho@usp.br

Abstract

Trophic interactions form networks and the structure of these networks can reflect different patterns in the use of resources by consumers, thus shaping entire ecological systems. Specific patterns of networks can be influenced both by the biological attributes of the species and by the environment. We assess the structure of snake-prey networks and examine how different communities are structured based on the use of food resources along a latitudinal gradient. We characterized 24 widely distributed networks, based on the calculation of connectance, nestedness, and modularity. We used path analysis to study the association between latitude, community attributes (richness, taxonomic diversity, and body size variance among snakes), and network structure. We also used centrality metrics (degree, betweenness, and closeness) to assess the differential importance of food resources in the diet of snake communities. Our results showed that the structure of the networks was in general nested, moderately connected, and non-modular. Latitude only affected size variance between snakes ($\beta = -0.7$, $p < 0.01$), which together with richness only affected nestedness ($\beta = 1.73$, $p < 0.01$ for richness and $\beta = 0.69$, $p = 0.008$ for size variance). Networks from tropical regions were more nested than those from temperate regions ($F = 5.43$, $p = 0.02$). The centrality analysis indicated congruent results, showing that frogs, lizards, or small mammals represent the central resources, being consumed, on average, by 64% of the snakes. Our results indicated that snake-prey networks do not show consistent variations along the latitudinal gradient. This study points to the importance of combining data from the natural and evolutionary history of lineages with the approach of complex networks to determine, at the community scale, how interactions between consumers and their resources can be structured along the latitudinal gradient.

Keywords: body size, centrality, connectance, latitude, modularity, nestedness, richness, and taxonomic diversity.

Introduction

Individuals of all species rely upon trophic interactions to obtain resources (Thompson 2005). As a consequence, ecological interactions represent a key component of biodiversity, potentially shaping both the organization of ecosystems (Estes & Palmisano 1974) and the traits of interacting species (Galetti et al. 2013). Therefore, knowledge about ecological interactions is essential to understanding how ecological systems are organized at different levels of organization (Fontaine et al. 2011, Guimarães 2020).

At the community level, trophic interactions form networks that connect populations of different species in a given locality (Pringle & Hutchinson 2020). In order to understand the structure of these trophic networks, the network approach provides a set of tools to visualize and describe ecological systems (Poisot et al. 2016). Nonrandom network patterns may represent the fingerprints of ecological and evolutionary processes shaping ecological systems (Guimarães 2020). Network patterns include the variation in the number of interactions by species (Sinclair et al. 2003), variation in the strength of interactions (Ings et al. 2009), the roles of species within interacting assemblages (Anderson & Sukhdeo 2011), or the formation of groups of species (Rezende et al. 2009). In this way, the set of metrics used can allow inferences about the ecological role of individual species within the community (Cirtwill et al. 2018) and estimate how the propagation of direct and indirect effects on the network would affect the robustness of ecological systems to species loss (Schmitz & Beckerman 2007, Pires et al. 2020).

Trophic interactions can be described as a bipartite network in which one set of nodes represents consumers and the other set of nodes represents their food resources; the links between the two sets of nodes indicate the use of food resources by consumers (Cohen et al.

1993, Pires et al. 2011). The structure of trophic networks can reflect different patterns in the use of food resources by consumers (Ings et al. 2009). The presence of a core of generalist species tends to form more connected networks in which specialists tend to interact with subsets of the resources consumed by generalists, leading to a nested structure (Bascompte et al. 2003, Lewinsohn et al. 2006). On the other hand, the presence of groups of species specialized in consuming certain types of resources leads to a modular structure (Rezende et al. 2009). The network patterns can be influenced by the evolutionary history associated with the traits of species (e.g. body size) that determine the interactions in the network (Rezende et al. 2009), since related species may have similar dietary preferences (Fontaine & Thébault 2015). Nestedness in trophic networks is usually associated with the body size hierarchy between predators (Sinclair et al. 2003, Woodward et al. 2005, Stouffer et al. 2011, Ceron et al. 2019, Pinto-Coelho et al. 2021), but there is also evidence for the emergence of nested patterns associated with phylogenetic patterns between related taxa (Cattin et al. 2004) and differences in abundance across interacting species (Krishna et al. 2008). Modular structure can derive from interactions also mediated by body size, phylogenetic-structured traits, spatial structure (Prado & Lewinsohn 2004, Rezende et al. 2009), and lifestyle (Pinto-Coelho et al. 2021). In empirical networks, trophic networks may show nestedness and modularity simultaneously (Fortuna et al. 2010, Pinheiro et al. 2018; Valverde et al. 2020; Pinto-Coelho et al. 2021).

Specific network patterns are not only associated with the attributes of local species interactions but also with factors operating at broad spatial scales, such as climatic variations along the latitudinal gradient (Boyero et al. 2015, Zanata et al. 2017, Ceron et al. 2020). For most taxonomic groups the distribution of species richness is not homogeneous across the globe, being more concentrated in the tropics (Mittelbach et al. 2007, Schemske et al. 2009a). The greater species richness in the tropical region may favor specialization as new species introduce new resources and new interactions, expanding niche occupation opportunities (MacArthur 1969, Schemske et al. 2009b). Changes in species richness and patterns of specialization, in turn, affect network organization, leading to variation in network structure across space (Dunne et al. 2002, Bascompte et al. 2003, Schleuning et al. 2012, Morris et al. 2014). For example, Ceron et al. (2020) showed that in anuran-prey networks, reductions in species richness towards temperate regions increase nestedness and reduce modularity. Dalsgaard et al. (2011) and Zanata et al. (2017) showed that hummingbird–flower networks are more specialized in richer communities located in the tropical region. Showing opposite trends from previous studies, Schleuning et al. (2012) evaluating pollination and seed dispersal networks, and Dalsgaard et al. (2017) evaluating avian plant–frugivore networks, found that specialization decreased toward tropical latitudes. On the other hand, Morris et al. (2014) investigating host-parasitoid networks and de Araújo (2016) investigating plant-herbivore networks indicated that both are structured independently of latitude. These contrasting results indicate that the potential effects of latitude on the structure of interaction networks are still mostly unknown.

In this paper, we evaluate the structure of trophic interactions among snakes and their prey. Snakes are ectothermic vertebrates with the greatest species richness concentrated in the tropical region (Uetz et al. 2022). The ability to constrict and poison, beyond cranial mobility, allows the snakes to kill prey of varying sizes and ingest them whole (Greene 1983, Campbell & Lamar 1989). As a consequence, there is a considerable diversity of food habits and hunting strategies (Greene 2001, Cundall & Greene 2000). Some species are top predators, playing an important role in the structure of communities (Yanosky et al. 1996), such as large constrictor species, such as anacondas and pythons, that have generalist food habits, consuming a variety of food resources (Pinto-Coelho et al. 2021, Luiselli et al. 1998), whereas other species have extremely specialized food habits, such as the snail-eating snakes (tribe Dipsadini), which rely exclusively upon mollusks (Arteaga et al. 2018). Due to the variation in the degree of diet specialization, and the existence of robust natural history studies, snake assemblages can represent a study case for testing hypotheses about how general are network patterns observed in other groups of predators, such as mammals (Sinclair et al. 2003), birds (Gliwicz 2008), fishes (Rezende et al. 2009), and frogs (Ceron et al. 2019).

First, we examine how different snake communities are structured based on the use of food resources along a latitudinal gradient. Our main goal was to analyze the overall structure of the snake-prey interaction networks and to evaluate the influence of size hierarchy between predators, taxonomic diversity, species richness, and latitude in the observed patterns. Based on the highest snake richness is in the tropical region (Uetz et al. 2022) and that metrics can be affected by variations in network size (Dunne et al. 2002, Bascompte et al. 2003, Schleuning et al. 2012, Morris et al. 2014), we expect to find qualitative variations in the structure of snake-prey networks along the latitudinal gradient. Variations in the presence of links within networks along environmental gradients may be driven by turnover in species composition (Pellissier et al. 2018, Ceron et al. 2022). Since higher richness values can favor specialization (Schemske et al. 2009), causing the network to have proportionally fewer interactions by species, we expected networks located in the tropical region should be significantly nested, with lower connectance values and significantly modular in comparison to networks located in the temperate region.

Methods

Dataset

Our dataset includes 24 interaction networks between snakes and their food resources (Table S1 - supplementary material). We searched for studies in the Web of Science database (<https://webofknowledge.com/>) using the keywords "Snake*" AND "Trophic OR Feed* OR Diet*", "Snake*" AND "Assemblage OR Communit*", and " Snake*" AND "Autoecol*" which were published until 2019. We selected studies of the ecology of snake communities that preferably presented data on the diet of snakes and that covered a wide geographical coverage. Most analyzed networks were from the tropical region, as a consequence of bias generated by the greater number of studies on the ecology of snake communities for the tropics. Furthermore, as snakes are ectothermic vertebrates, communities located in colder regions have low species richness which affects the formation of networks of interactions (Wallach et al. 2014, Uetz et al. 2022). We classified the studies that matched our criteria based on a sampling effort category, seeking to select only those studies that include a representative sample of the local snake community. The sampling effort category was based on the sampling effort and sampling sufficiency for each of the selected studies (see Appendix 1).

For each selected study, we extracted information about the richness of snake species, the number of food resources, the sampling effort, and geographical information about the study site (Table S1). In dietary studies, snake food resources are usually classified into coarse categories (e.g. lizards, amphibians, Squamata eggs, earthworms, rodents). As snakes feed on irregular intervals, the presence of food items in the stomach, as well as their identification to the species level may be hampered (Secor & Diamond 2000). Having said that, there is evidence that these categories reflect the scale of specialization of snakes, i.e., snakes are often specialized in consuming broad categories of resources, e.g., serpentiform organisms, which include other snakes, elongated fishes, caecilians, or elongated lizards (Martins & Oliveira 1998). In this sense, it is important to emphasize there is no intrinsically correct level of description of ecological interactions when characterizing ecological networks (Guimarães 2020), and a similar level of description is often used in the study of food webs (Cohen 1977) and individual-based networks (Araújo et al. 2008). Due to the variation in the quality of diet information across studies (e.g. number of stomachs analyzed or observations of predation in the field), we complemented the dataset of food resources consumed by snake species with a second approach. Since evidence suggests that there is no significant intraspecific geographic variation in the diet of snakes in terms of these broad categories (Martins et al. 2002) we supplemented each community's database with diet data from the literature for the same type of environment as the community studied (e.g. for communities in the Amazon region, we use secondary diet's data from the Amazon region) (see details in Appendix 1 - Datasets).

For each network, we described the resource used by snakes as a binary interaction matrix **A** in which if a snake i feeds on a given resource j, $a_{ij} = 1$, and if i does not feed on j a_{ij} = 0.

Controlling the effect of network size

The network size (species richness + number of resource types) often affect network descriptors (Dunne et al. 2002, Bascompte et al. 2003, Dalsgaard et al. 2011, Spiesman & Inouye 2013, Morris et al. 2014, Guimarães 2020). Because we would like to partition out the drivers shaping species richness and the number of resources from those affecting patterns of interaction, we control the effect of network size on network structure. To reduce the size bias we use the standardized values of the metrics by calculating a z-score. For example, for nestedness: z-score = (N - $\underline{x}$) / sd, where N is the nestedness value of the network, $\underline{x}$ is the mean of the nestedness of the null model and sd is the standard deviation of the nestedness of the null model.

Controlling the effect of sampling effort

Network description may be strongly affected by sampling effort and, therefore, in the detectability of interactions (Morris et al. 2014, Pringle & Hutchinson 2020). To reduce the sampling bias we summarized the sampling data from each study into a sampling effort category (mentioned above), ranging from 1 to 5, where 1 represents unsatisfactory sampling and 5 satisfactory samplings. We excluded all studies that were classified in category 1, keeping only those classified in categories 2 (n = 1), 3 (n = 5), 4 (n = 13) and 5 (n = 5).

Descriptors of network structure

Network metrics are able to simplify and aggregate the heterogeneity of ecological systems, revealing patterns (Guimarães 2020). Thus, we used six metrics to characterize the structure of each network: (i) *Network size* is the total number of nodes in the network, *i.e.*, the number of snake species and of the categories of food resources; (ii) *Degree distribution* which is the distribution describing the number of food resources consumed by each species of snake (the degree of each snake species); (iii) *Connectance* (*C*) describes the ratio of the number of interactions recorded relative to the possible number of network interactions, ranging from 0 (non-connected network) to 1 (fully connected network); (iv) *Nestedness* (*N*) is the pattern in which specialist species interact with sets of resources with which the generalists interact. To calculate nestedness we used the NODF metric (nestedness metric based on overlap and decreasing fill) (Almeida-Neto et al. 2008) in the "bipartite" package (<www.r-project.org>) (see details in Appendix 1). The nestedness values range from 0 (non-nested network) to 100 (perfectly nested); (v) *Modularity (M)* measures the extent to which the network is organized in groups of interacting species, measuring the number and level of isolation of these groups. The network will be modular when interactions within a module are denser than between modules (Olesen et al. 2007). We used Q_B metric, defined by Barber (2007), to characterize modularity, with values ranging from 0 (non-modular network) to 1 (highly modular). A simulated annealing algorithm (Guimerà & Amaral 2005) was used to optimize the Q_B value. Modularity analyses were performed using the Modular program (Marquitti et al. 2014); (vi) the number of isolated subsets of interacting species and resources (components). The components describe subsets of the nodes of the network in which there are indirect and direct paths connecting all nodes of the subset. In networks, it is expected to emerge a single, large component (the "giant component"), in which most of the nodes (species and resources) are linked to each other through direct and mainly indirect pathways. The presence of a giant component is associated with features of the degree distribution that can be described by a connectivity parameter (see Appendix I).

The levels of nestedness and modularity were compared with a theoretical benchmark provided by the null model 2 of Bascompte et al. (2003). We generated 1000 null matrices to estimate nestedness and only 100 to estimate modularity since the calculation of modularity is computationally intensive. If a network shows a level of nestedness or modularity larger than expected by the null model 2, then there is evidence of ecological or evolutionary processes acting on the network organization that goes beyond those shaping the variation in the number of resources consumed by snake species (e.g, Bascompte et al. 2003). Detailed descriptions of the metrics are available in supplementary material Appendix 1.

In order to compare the structure of snake-prey networks with other types of ecological networks, we also calculated nestedness, modularity, and connectance for a set of networks available in the database of the Web of Life and the Interaction Web Database (Table S2).

Path analysis to assess the association of the environment and community attributes on network structure

We use path analysis (Wright 1934) to assess the effect of latitude on the network structure. Path analysis allows inferring causality between a set of variables indicating whether the inferred relationships between variables are well supported by the conceptual model (Shipley 2004). We selected a set of causal variables related to community attributes (richness, taxonomic diversity, and body size variance) that can be affected by latitude (environmental variable) and that can shape the structure of network interactions (nestedness, modularity, and connectance). The standardized path coefficients (beta) represent the rate of change in the dependent variable (network structure) for every one standard deviation increase in the predictor variable (community attributes). Since one of the limitations of the path analysis is the sample size, it was necessary to remove the Rome network from the analyses, due to its small size (Table S1).

Among the community attributes, we used snake richness in the network. The taxonomic diversity of snake species for each network analyzed was obtained by calculating the taxonomic diversity index Δ^+ (Clarke & Warwick 1998). The Δ^+ index captures the taxonomic relatedness of the species in each sample through the taxonomic “distance” between any two organisms chosen at random from the sample (details in the supplementary material Appendix 1). For practical comparisons, Δ^+ is shown not to be dependent, on average, on the degree of sampling effort involved in the data collection. We used the variation in body mass to characterize the snake community. Snake body size is associated with multiple aspects of the life history of a given snake species (Pinto-Coelho et al. 2021). To characterize variation of body mass across species in a network, we first compute the estimates of the average body mass of each snake species that make up each network (data available in Feldman et al. 2016). Then, we calculated the coefficient of variation of the average body mass across snake species. In order to compare, all variables used in the path analysis were standardized by calculating the z-score. The path analysis was performed using the lavaan package in R (Rosseel 2012). All the above-mentioned analyses were carried out using R version 4.2.1 (R Core Team 2022), with the exception of modularity.

Analyzing the diet composition between networks

First, we want to understand whether the composition of the food resources of the smaller networks is nested within the composition of the larger networks. For that, we calculate the nestedness value from a binary matrix that describes the use of food resources by snakes in different communities. In this matrix, the rows represent the food resource categories and the columns of the communities. Resource usage within the community has been marked with 1 (at least one snake species uses that resource) and 0 otherwise.

Since not all food resources of a network of interactions are of equal ecological importance within communities (Sazima et al. 2010), to understand the role of resources in the snake diet, we investigate which resources are central and which represent more specialized food habits. To explore this issue we calculated three centrality metrics, degree centrality, betweenness centrality, and closeness centrality (Newman 2003), which together will seek to capture different ways of measuring patterns in the use of resources by snakes in the analyzed networks (Delmas et al. 2018). The degree centrality (DC) of a given resource is a normalized measure of its number of interactions, in which the degree centrality of a resource *i* is:

$$\mathrm{DC}_i = \frac{ki}{(N-1)},$$

where *N* is the network size (number of resources + species richness). Highly consumed resources will have high DC values.

Betweenness centrality (BC) describes the number of times a resource *l* lies on the shortest paths among other pairs of nodes (*i*, *j*) in the network. Thus, BC is given by:

$$\mathrm{BC_l} = \sum_i \sum_j \frac{p_{ilj}}{p_{ij}}$$

$$i \neq j \neq l,$$

where, $\sum_i \sum_j p(ij)$, is the number of shortest paths between all pairs of nodes in the network, no matter if both nodes describe resources, both nodes describe snake species or a node describe a resource and the other snake species; $\sum_i \sum_j p(ilj)$ is the number of shortest paths that pass through resource *l*. BC allows us to access the importance of each resource in connecting different parts of the network (Dáttilo and Rico-Gray 2018). Resources with BC values close to one are those that often are part of the shortest path between other nodes. Finally, closeness centrality (CC) is a measure based on counting the length of the smallest path (*d*) between a node and all other nodes in the network. CC is given by:

$$CC_i = \frac{N - 1}{\sum_j d_{(ij)}}$$

in which $d(ij)$ is the length of the smallest path, in number of links, connecting i and j. The node with the highest CC value is considered the closest to all other nodes in the network.

Results

Descriptors of networks structure

We analyzed 24 networks of snakes and their prey spread across four continents (South and North America, Africa, and Europe), representing a wide range of species richness, taxonomic diversity, prey category, and habitat types (Figure 1 and Table S1). Snake species richness varies widely across sites, from 5 to 62. Similarly, the number of resources used by snakes varies from 4 to 24. Snake species richness and the number of resources were correlated ($R^2 = 0.71$, $F = 54.84$, $p < 0.01$, Figure S1), indicating that the greater the number of snake species, the greater the width of the snake diet niche.

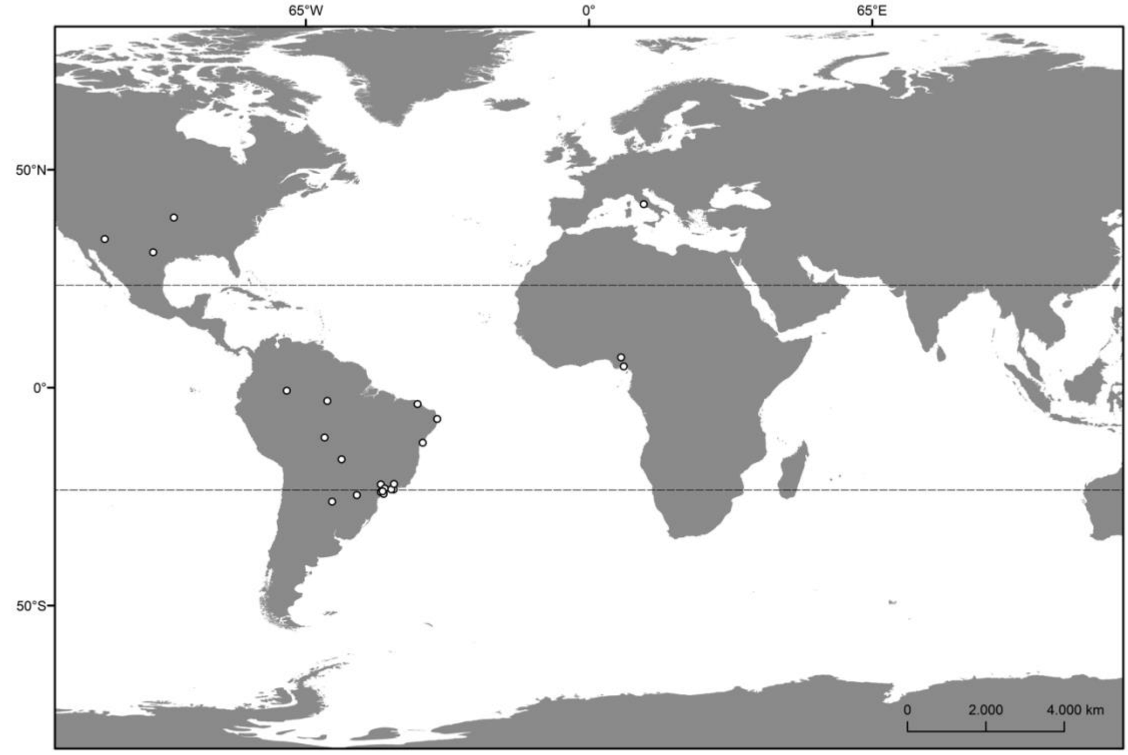


Figure 1: Distribution of the 24 snake-prey networks analyzed in the study.

The average number of resources used by a snake species shows low variation, ranging from 2 to 3.42 (2.69 ± 0.39). Having said that, there is a lot of within-site variation in the number of resources used across snake species. In all sites, there are multiple snake species feeding on one or two resources ("specialists") and at least one species that feeds on at least five resources ("highly connected species", Table 1). Accordingly, the degree distribution, which describes the probability of a snake species using *k* resources in a given site, indicates that, in all networks, the proportion of "specialists" and "highly connected species (generalists)" varied widely across networks. For instance, all networks located in the temperate region of the northern hemisphere had a lower proportion of specialist species compared to tropical networks. Furthermore, there is a consistent correlation between the proportion of specialists in relation to generalists and latitude, indicating that in the tropical region there is a higher concentration of specialist snakes ($R^2 = 0.18$, $F = 4.99$, d.f = 22, $p < 0.03$, Figure S2a) and in the temperate region there is a higher concentration of generalist snakes ($R^2 = 0.20$, $F = 5.56$, d.f = 22, $p < 0.02$, Figure S2b). Despite the correlation between species richness and the number of resource types, the networks with the highest proportion of highly connected species are those of smaller numbers of snake species and/or resources, such as Roma, Japi, and Kansas. These networks are not poor in snake species and resources due to sampling bias, as all three were categorized with high sampling effort (Table S1).

Network connectance ranged from 0.11 to 0.6 (0.2 ± 0.09, Table 1), with most networks (n = 22) presenting values between 0.11 to 0.26 and only two networks (Kansas and Roma) presenting much higher connectance values (0.38, and 0.6, respectively). The nestedness z-score ranged from -1.27 to 8.96 (3.98 ± 2.56 for the entire dataset, n = 24, Table 1), with most networks (n = 19) being more nested than expected by the null model. On the other hand, only one network (Manaus, Amazon region) was more modular than expected by the null model (Manaus z-score = 8.88, $p < 0.01$, n = 100 null model replicates). The modularity z-score ranged from -1.35 to 2.43 (-0.21 ± 0.93 for the entire dataset, n = 24) and the number of food modules ranged from 3 to 8 (Table 1). Thus, most networks show levels of modularity that are expected by the observed variation in the resource use across species, i.e., modularity was reproduced by the null model. Having said that, in most sites groups of snake species feed on resources that no other snake species use, forming isolated groups ("network components") from the rest of the network. The number of network components ranged from 1 (n = 4) to 5 (n = 1), with most networks (n = 19) presented 2 to 3 components. All networks, regardless of their number of components, showed the formation of a large component (the "giant component") encompassing most of the species and resources in the system, which indicates that there is a core of resources that are at least partially shared by most snake species. The number of snake species and resource types (nodes) inside the giant component of the network ranged from 67 to 100%, with just a single network having less than 80% of the nodes in the giant component (Figure 2). In general, additional isolated components represented a few snake species with highly specialized food habits, such as snakes feeding on mollusks or earthworms.

Table 1: Information on the network size, C = connectance, N = nestedness (p-value, z-score, and relative nestedness), M = modularity (p-value, z-score, and relative modularity), Number of modules, and number of components, of the 24 snakes-prey networks.

Code	Zone	Size	C	N	pN	zN	Nrel	M	pM	zM	Mrel	Modules	Ncomp
Arizona	Temperate	35	0.25	48.58	0.00	2.84	0.29	0.32	0.74	-0.61	-0.05	4	3
Bagual	Temperate	46	0.17	48.52	0.00	6.34	0.81	0.39	0.89	-1.21	-0.09	7	2
Bahia	Tropical	64	0.16	45.85	0.00	7.72	0.77	0.38	0.80	-0.77	-0.04	6	2
Carlos Botelho	Tropical	62	0.14	34.47	0.00	5.62	0.63	0.44	0.71	-0.72	-0.05	7	3
Ceará	Tropical	33	0.21	35.78	0.09	1.57	0.25	0.39	0.73	-0.71	-0.07	6	2
Chacoan	Tropical	38	0.22	44.79	0.00	3.33	0.43	0.36	0.80	-0.74	-0.06	7	3
Chico Mendes	Tropical	43	0.21	46.21	0.00	4.12	0.49	0.34	0.85	-1.06	0.13	6	3
Ejule	Tropical	30	0.17	27.36	0.00	2.73	0.44	0.57	0.10	1.35	0.03	5	3
Eket	Tropical	36	0.18	30.34	0.08	1.87	0.25	0.46	0.33	0.31	-0.13	7	1
Espigao	Tropical	76	0.13	38.96	0.00	8.96	0.85	0.43	0.29	0.66	0.03	5	3
Igarape	Tropical	66	0.12	38.85	0.00	7.19	0.90	0.45	0.34	0.26	0.02	6	2
Itirapina	Tropical	52	0.13	25.19	0.00	3.87	0.41	0.45	0.94	-1.35	-0.09	8	2
Japi	Tropical	26	0.25	48.31	0.00	3.14	0.40	0.33	0.89	-1.01	-0.01	6	2
Jureia	Tropical	40	0.18	38.44	0.00	4.59	0.56	0.41	0.75	-0.72	-0.06	4	3
Kansas	Temperate	21	0.38	48.46	0.24	0.64	0.08	0.30	0.49	-0.12	-0.02	4	2
Manaus	Tropical	86	0.11	34.77	0.00	8.88	0.88	0.50	0.00	2.43	0.14	5	2
Pantanal	Tropical	38	0.18	43.49	0.00	5.00	0.70	0.41	0.78	-0.84	-0.08	6	3
Paraíba	Tropical	41	0.21	36.98	0.00	2.88	0.26	0.39	0.32	0.42	0.03	5	5
Picinguaba	Tropical	39	0.20	44.68	0.00	4.41	0.52	0.36	0.87	-1.19	-0.10	5	4
Roma	Temperate	9	0.60	43.75	0.94	-1.27	-0.30	0.25	0.34	0.03	0.01	3	1
Santa Virginia	Tropical	38	0.21	35.72	0.01	2.52	0.30	0.42	0.42	0.10	0.01	6	4
Serra do Papagaio	Tropical	38	0.18	34.94	0.00	3.50	0.48	0.38	0.81	-0.97	-0.09	6	1
Tapirai	Tropical	59	0.17	36.89	0.00	5.25	0.54	0.43	0.56	-0.14	-0.01	6	1
Texas	Temperate	35	0.21	26.90	0.52	-0.11	-0.01	0.44	0.09	1.40	0.11	6	2

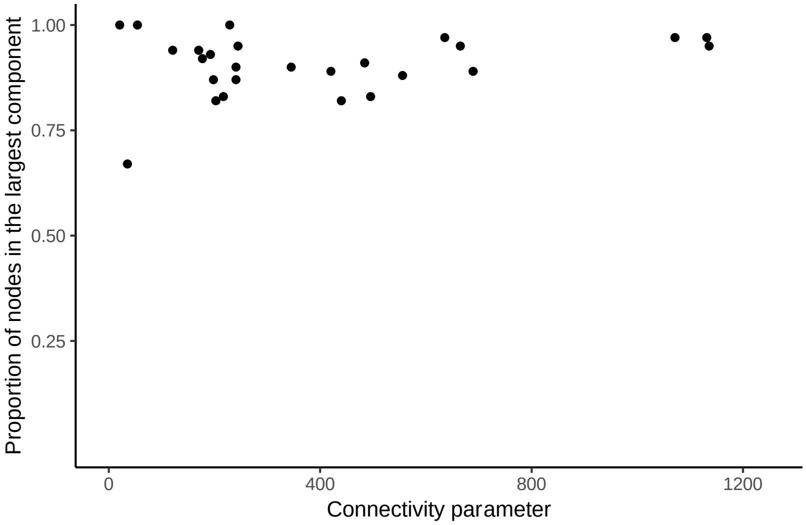


Figure 2: Graph showing the relationship between the proportion of nodes in the largest component of the network (giant component) and a connectivity parameter (algebraic connectivity) that depends on the distribution of interactions by species. According to Guimarães (2020), snake-prey networks are in a supercritical state where most nodes are connected by direct or indirect routes (see Appendix 1).

When comparing the snake-prey networks with other interaction networks described in the literature, the connectance values of snake-prey networks (0.11 to 0.6) are similar to different types of ecological networks but anemone-fish networks (0.3 to 0.67, $p < 0.01$) (Figure 3). There was no consistent difference in z-score nestedness values between snake-prey networks (-1.38 to 8.48) and all other types of ecological networks. Accordingly, snake-prey networks show levels of z-score modularity (-1.35 to 2.43) that are similar to all types of ecological networks but food-webs (0.43 to 10.5, $p = 0.02$).

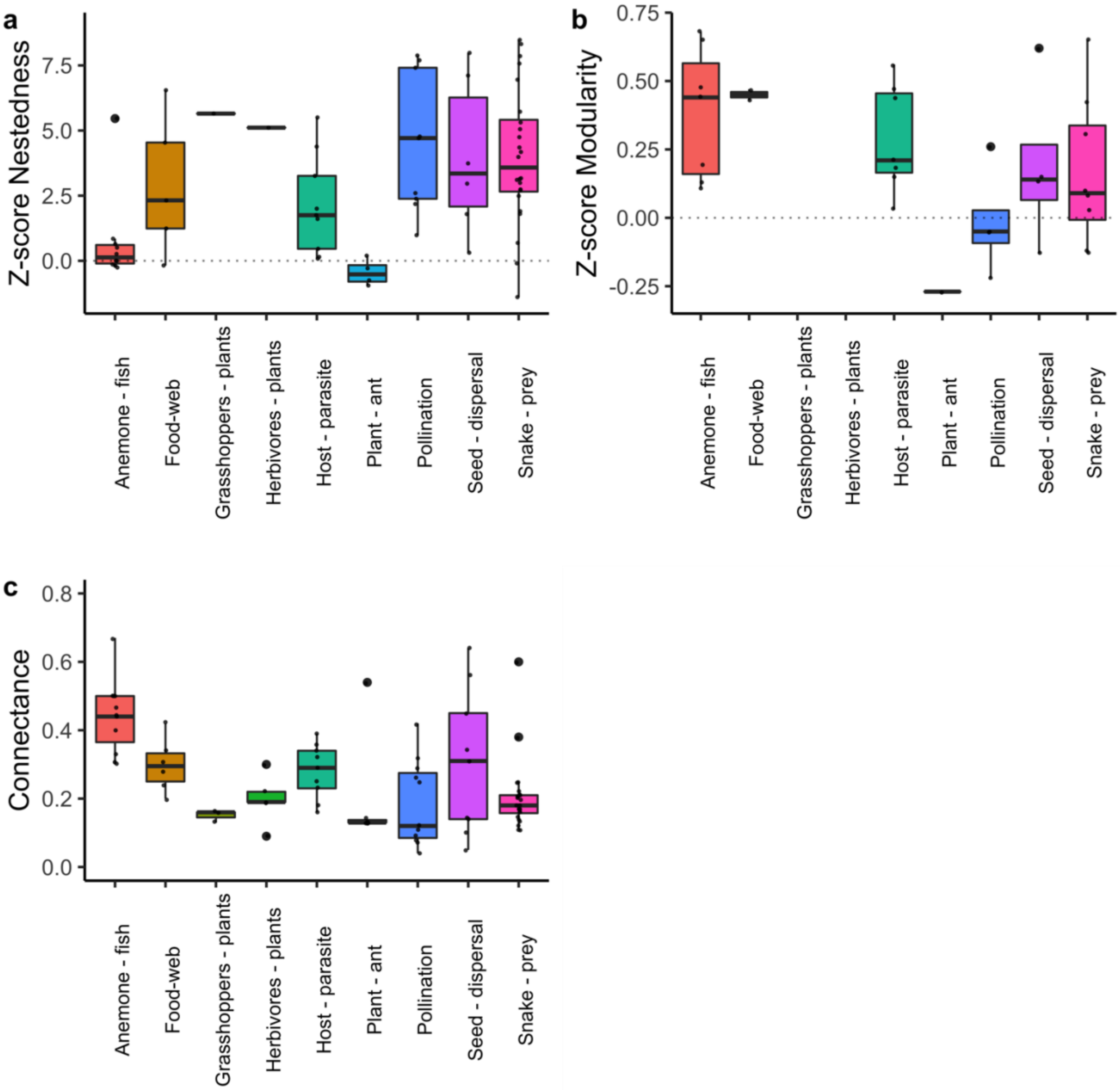


Figure 3: Boxplots comparing the values of the a) z-score of nestedness, b) z-score of modularity, and c) connectance between mutualistic and antagonistic interaction networks. The upper and lower limits of the box are the quartiles and the black band within each box represents the median. For the connectance, the only type of network that differed significantly from the snake-prey networks was the anemone-fish ($p < 0.01$), for the modularity it was the food-web ($p = 0.02$) and for the nestedness there was no consistent difference among the types of analyzed networks.

Path analysis to assess the association of the environment and community attributes on network structure

We now turn our attention to the association between the environmental variable (latitude), community attributes (richness, taxonomic diversity, and body size variance), and the network structure (connectance, nestedness, and modularity). The results of the path analysis showed that the structure of the network is partially affected by the latitude (Figure 4). Latitude negatively affected body size variance among snakes ($\beta = -0.7$, $p < 0.01$), but not species richness ($\beta = -0.36$, $p = 0.07$), nor the taxonomic diversity of the networks ($\beta = 0.16$, $p = 0.19$). Nestedness was positively affected by both species richness ($\beta = 1.73$, $p < 0.01$) and body size variance among snakes ($\beta = 0.69$, $p = 0.008$), but not by taxonomic diversity ($\beta = 0.67$, $p = 0.14$). It is important to highlight that among the communities that are not significantly nested are those of smaller size (Table 1). Connectance and modularity were not affected by either the environmental variable or the community attributes.

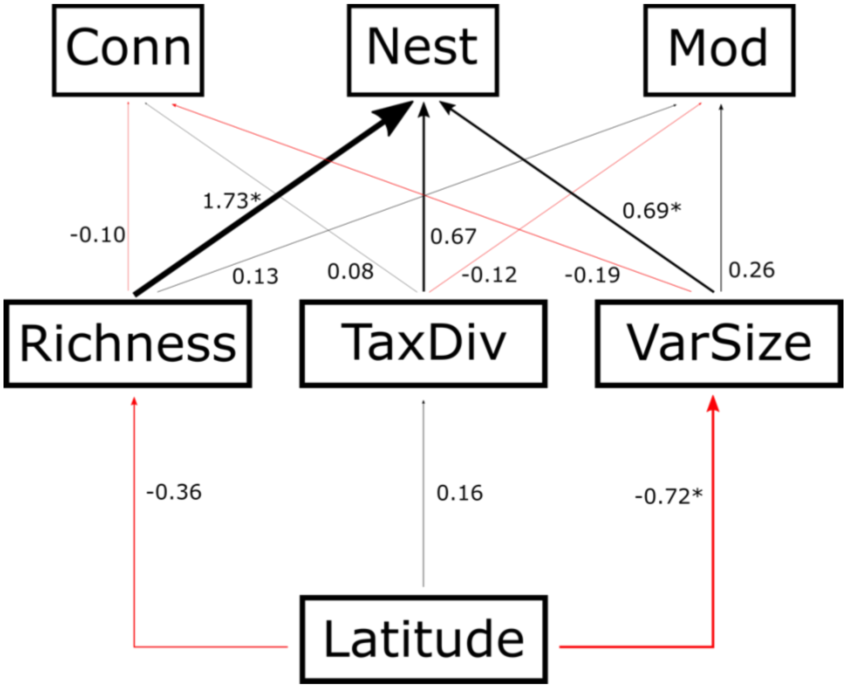


Figure 4: Path diagrams of the effects of causal variables on the network structure. Richness: number of snake species; TaxDiv: taxonomic diversity (Δ^+); VarSize: size variance among snakes; Conn: connectance; Nest: nestedness; Mod: modularity. The color of the arrows indicates the type of influence (black positive effect and red negative effect) and the width the size of the effect. Numbers indicate beta values and asterisks indicate that the relationship is significant. The values of R^2 are: connectance (0.19), nestedness (0.72), modularity (0.12), richness (0.12), taxonomic diversity (0.07) and size variance (0.45). All values were standardized by calculating the z-score.

Thus, latitude does not seem to exert a strong influence on the structure of interaction networks snake-prey and the only metric that was consistently influenced by species richness and body size variation among snakes was nestedness. When comparing the sets of networks between tropical and temperate regions, we observed that the latitudinal gradient influenced only the nestedness, with the networks from the tropical region being more nested than the networks from the temperate region (F = 5.43, p = 0.02). Connectance (F = 2.8, p = 0.11) and modularity (F = 0.09, p = 0.77) do not show consistent differences between regions (Figure 5).

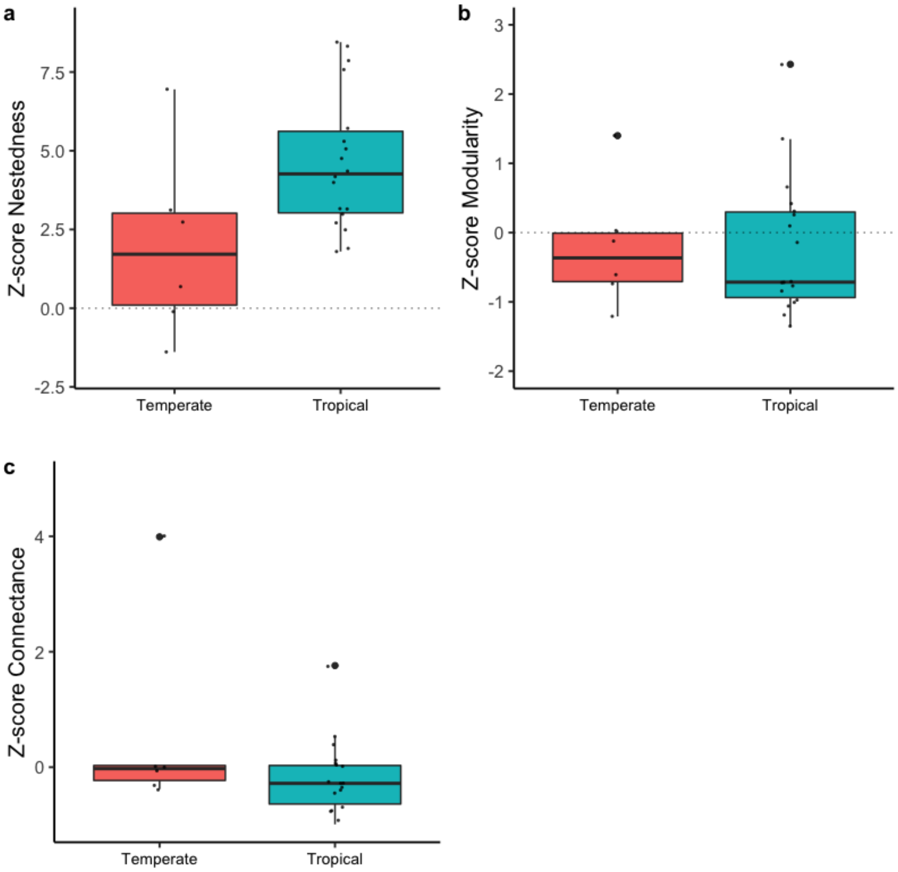


Figure 5: Boxplot indicating the relationship of metric values between networks located in the Tropical (n = 19) and Temperate (n = 5) regions. The only significant relationship was between a) nestedness values (F =5.43, p = 0.02). For b) modularity (F = 0.09, p = 0.77) and c) connectance (F = 2.8, p = 0.11) there was no consistent relationship. The upper and lower limits of the box are the quartiles and the black band within each box represents the median.

Analyzing the diet composition between networks

The results of the nestedness analysis between the networks of different snake communities indicate that the food resources contained in the smaller networks form a subset of the resources contained in the larger networks (NODF = 76.06, null model average = 60.20 ± 1.76, $p < 0.01$). The number of food resources between networks ranged from 4 to 24 and some resources were present in all networks, such as anurans, lizards, small mammals (which include rodents and marsupials), and Passeriformes. The centrality metrics for each snake-prey network indicated congruent results, showing anurans, lizards or small mammals represent the central resources, being consumed by, on average, 64% of the snakes that make up each network. The resources that represented more specialized food habits, being present in a few networks, but not necessarily as an isolated component, were crayfish (n = 1, Texas), Chelonian eggs (n = 1, Texas), scorpions (n = 1, Itirapina), spiders (n = 2, Itirapina and Paraíba), and onychophorans (n = 2, Manaus and Igarapé). Resources that appear predominantly in isolated components are mollusks (n = 16 networks), consumed exclusively by only five genera of snakes, and earthworms (n = 9 networks) consumed exclusively by only four genera of snakes.

Discussion

Understanding how trophic interactions are organized is essential in a world where global anthropogenic changes affect the structure of ecological communities (Donohue et al. 2017). Studies of trophic interactions using the network approach have revealed key aspects in the ecology of interactions, such as understanding the association between network structure and community stability (Thébault & Fontaine 2010, Robinson & Strauss 2020). Our study, analyzing 24 snake-prey networks, indicated that the network structure was generally nested, moderately connected, non-modular, and partially structured by a latitudinal gradient and body mass variation across snake species.

The snake-prey networks showed wide variation in snake richness and number of resources as well as in the number of interactions. As a consequence, connectance, a measure of the density of interactions, varies considerably across networks. Despite this variation in the density of interactions between networks, the connectance values remained, in general, moderate (0.2 ± 0.09), indicating that each snake species consumed only a subset of the food resources used by the community. Moderate values of connectance are expected for trophic interactions and the high connectances observed in the Roma and Kansas networks may reflect the small set of resources available to snakes in these localities. From a network perspective, few resource types imply low network size and, in ecological networks, there is a strong inverse association between network size and connectance, i.e., small ecological networks are often cohesive (Dunne et al. 2002, Thébault & Fontaine 2010). Small network sizes may indicate subsampling or poor taxonomic resolution (Pringle and Hutchinson 2020). However, the Kansas network, for example, has the largest sampling effort among the 24 networks analyzed, with more than 30 years of data collected and more than 22,000 specimens recorded (Fitch 1982) and the species richness of the Roma network reflects the low diversity of snakes in the Mediterranean region (Capizzi et al. 1995).

The network patterns that emerged from the variation in the number of resources consumed by snake species were derived from a combination of supergeneralist and specialized food habits (see Mariani et al. 2019). Snakes are important predators of terrestrial, arboreal, aquatic, fossorial, and even marine fauna, feeding on prey that vary widely in both taxonomic categories (e.g., annelids, crustaceans, arthropods, mollusks, and all major vertebrate groups) and size (from 20 to more than 100% of its weight) (Cundall & Greene 2000, Vieira-de-Alencar et al. 2022). Species such as the large constrictors of the Boidae and Pythonidae family feed on a wide variety of food resources, from large prey (e.g. big mammals) consumed only by larger snakes, to central resources consumed by most species in the network (e.g. anurans and lizards), including specialists. Although most networks present the formation of isolated food groups, i.e., extremely specialized food habits, the pattern of interaction in which specialists feed on subsets of resources also consumed by generalists emerges in a nested structure (Bascompte et al. 2003). The reasons behind the emergence of nestedness in ecological networks have been widely debated (Ulrich et al. 2009, Mariani et al. 2019). Nested structures have already been reported for snake-prey networks as a result of a hierarchy of body sizes among snakes (Pinto-Coelho et al. 2021). In general, predator body size is an important predictor of trophic network structure as it influences the predator's ability to kill prey of varying sizes (Sinclair et al. 2003, Woodward et al. 2005, Rezende et al. 2009, Brose et al. 2019, Ceron et al. 2019, Dudczak et al. 2021). Our results agree with this pattern, indicating that nested structure of the snake-prey networks was influenced by the body size variance among snakes.

Theoretical studies have indicated that the nested structure in trophic networks may imply a decrease in network persistence (Thébault & Fontaine 2010). The nested structure allows species to connect by direct and indirect ways, emerging in the formation of a large component, observed in all snake-prey networks analyzed. Connected networks can have deep consequences for eco-evolutionary feedback and cascading effects, which can propagate through various species in the community (Guimarães 2020). For example, the local extinction of sea otters has resulted in an increase in the population of sea urchins and a consequent reduction in kelp forests, affecting all primary productivity in Alaska (Estes & Palmisano 1974). It is possible that cascading effects in snake-prey interaction networks deviate from the expected for other trophic networks since snakes have unusual dietary patterns compared to other ectothermic vertebrates (Greene 2001, Luiselle 2006). Food is the most obvious limiting resource and some snake species in confinement can go more than a year without food (McCue et al. 2012). Starving snakes can exhibit various potentially adaptive strategies for tolerating food limitations, not being forced to migrate because of variations in the abundance of their preferred prey; they reduce reproduction and start to consume alternative prey (Fitch 1982, see McCue et al. 2012). Thus, in nearly 30 years of studying snake-prey interactions, Fitch (1982) suggested that snake populations are one of the most stable components of biotic communities and likely exert stabilizing effects on the community as a whole.

The nestedness was also influenced by the variations in snake richness between the analyzed networks where the networks from the tropical regions were more nested than those from temperate regions. Furthermore, networks from tropical regions have a higher proportion of specialists than networks from temperate regions. In fact, nested structures are positively correlated with the species richness of the network (Bascompte et al. 2003) and the highest richness of snakes occurs in the tropical region (Costa et al. 2021, Uetz et al. 2022). More species-rich regions may favor specialization as new species introduce new resources that imply new interactions, expanding niche occupation opportunities (MacArthur 1969, Schemske et al. 2009b). However, despite the greater diversity of resources in the tropical region, which could favor a modular structure due to a greater tendency toward specialization, our results show that even specialized snakes are often dependent on central resources, consumed by most snakes in networks. Even with isolated food modules in most networks, the general pattern did not prove to be modular. The only exception was the Manaus network, which has the largest guild of worm-eating snakes and other invertebrates, where modularity was associated with the fossorial lifestyle (see Pinto-Coelho et al. 2020).

In conclusion, our results indicate that snake-prey networks do not show consistent variations along the latitudinal gradient. Despite the maintenance of general patterns, some deviations were found. These deviations can be attributed to aspects such as ecological and evolutionary factors (e.g., the natural history of ecological interactions at the individual level) that affect the average number of interactions per species, as well as variations in the number of interactions between species, which can imply changes in the organization of the network at the community level (Dunne et al. 2002, Guimarães 2020). Thus, processes such as the level of intimacy of interaction between interacting species can modulate the general organization of interactions, explaining the absence of more consistent effects of latitude on the structure of snake-prey networks (Fontaine et al. 2011, Pires & Guimarães 2013, Hembry et al 2018). This study points to the importance of combining data from the natural and evolutionary history of lineages with the approach of complex networks to determine, at the community scale, how interactions between consumers and their resources can be structured along the latitudinal gradient.

References

Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Loyola, R.D. & Ulrich, W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos, 117, 1227– 1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Anderson, T.K. & Sukhdeo, M.V.K. 2011. Host centrality in food web networks determines parasite diversity. PLoS ONE, 6, e26798.

Arteaga, A., Salazar-Valenzuela, D., Mebert, K., Peñafiel, N., Aguiar, G., Sánchez-Nivicela, J.C., Pyron, R.A., Colston, T.J., Cisneros-Heredia, D.F., Yánez-Muñoz, M.H., Venegas, P.J., Guayasamin, J.M. & Torres-Carvajal, O. (2018) 2018. Systematics of South American snail-eating snakes (Serpentes, Dipsadini), with the description of five new species from Ecuador and Peru. ZooKeys, 766, 79–147.

Araújo, M.S., Guimarães, P.R., Svanbäck, R., Pinheiro, A., Guimarães, P., Reis, S.F.D. & Bolnick, D.I. 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. Ecology, 89, 1981-1993.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences of the United States of America, 100, 9383–9387.

Boyero, L., Pearson, R.G., Swan, C.M., Hui, C., Albariño, R.J., Arunachalam, M., Callisto, M., Chará, J., Chará-Serna, A.M., Chauvet, E., Cornejo, A., Dudgeon, D., Encalada, A.C., Ferreira, V., Gessner, M.O., Gonçalves Jr, J.F., Graça, M.A.S., Helson, J.E., Mathooko, J.M., McKie, B.G., Moretti, M.S. & Yule, C.M. 2015. Latitudinal gradient of nestedness and its potential drivers in stream detritivores. Ecography, 38, 949-955. 10.1111/ecog.00982.

Campbell, J.A. & Lamar, W.W. 1989. The venomous reptiles of Latin America. Cornell University Press, Ithaca.

Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R. & Gabriel, J.P. 2004 Phylogenetic constraints and adaptation explain food-web structure. Nature, 427, 835–839.

Ceron, K., Oliveira-Santos, L.G.R., Souza, C.S., Mesquita, D.O., Caldas, F.L., Araujo, A.C. & Santana, D.J. 2019. Global patterns in anuran–prey networks: structure mediated by latitude. Oikos, 128, 1537-1548.

Ceron, K., Provete, D.B., Pires, M.M., Araujo, A.C., Blüthgen, N. & Santana, D.J. 2022. Differences in prey availability across space and time lead to interaction rewiring and reshape a predator-prey metaweb. Ecology, e3716. doi.org/10.1002/ecy.3716

Cirtwill, A.R., Roslin, T., Rasmussen, C., Olesen, J.M. & Stouffer, D.B. 2018. Between-year changes in community composition shape species' roles in an Arctic plant-pollinator network. Oikos, 127, 1163–1176. doi: 10.1111/oik.05074

Clarke, K.R. & Warwick, R.M. 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology, 35, 523–531.

Cohen, J.E. 1977. Food Webs and Niche Space. Princeton University Press, Princeton.

Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldana, J. 1993. Body sizes of animal predators and animal prey in food webs. Journal of Animal Ecology, 62, 67-78.

Cundall, D. & Greene, H.W. 2000. Feeding in snakes. In *Feeding: form, function, and evolution in tetrapod vertebrates*, ed. Schwenk, K., pp. 293-333. Academic Press, New York.

Dalsgaard, B., Trøjelsgaard, K., Martín González, A.M., Nogués-Bravo, D., Ollerton, J., Petanidou, T., Sandel, B., Schleuning, M., Wang, Z., Rahbek, C., Sutherland, W.J., Svenning, J.-C. & Olesen, J. M. 2013. Historical climate-change influences modularity and nestedness of pollination networks. Ecography, 36, 1331-1340.

de Araújo, W.S. 2016. Global patterns in the structure and robusteness of plant-herbivore networks. Frontiers of Biogeography, 8, e31053.

Delmas, E., Besson, M., Brice, M.H., Burkle, L.A., Dalla Riva, G.V., Fortin, M.J., Gravel, D., Guimarães, P.R., Hembry, D.H., Newman, E.A., Pires, M.M., Yeakel, J.D. & Poisot, T. 2018. Analysing ecological networks of species interactions. Biological Reviews, 94, 16-36.

Donohue, I., Petchey, O.L., Kéfi, S., Génin, A., Jackson, A.L., Yang, Q. & O'Connor, N.E. 2017. Loss of predator species, not intermediate consumers, triggers rapid and dramatic extinction cascades. Global Change Biology, 23, 2962-2972.

Dudcsak, A.C., de la Torre, G.M., Euclydes, L., Campião, K.M. 2021. The roles of anurans in antagonistic networks are explained by life-habit and body-size. Integrative Zoology, 17, 530-542.

Dunne J.A., Williams R.J. & Martinez N.D. 2002. Food-web structure and network theory: the role of connectance and size. Proceedings of the National Academy of Sciences, 99, 12917-12922. doi.org/10.1073/pnas.1924076

Estes, J.A. & Palmisano, J.F. 1974. Sea otters: their role in structuring nearshore communities. Science, 185, 1058–1060.

Feldman, A., Sabath, N., Pyron, R., Mayrose, I. & Meiri, S. 2016. Body sizes and diversification rates of lizards, snakes, amphisbaenians, and the tuatara. Global Ecology and Biogeography, 25, 187–197.

Fiedler, M. 1975. A property of eigenvectors of nonnegative symmetric matrices and its application to graph theory. Czechoslovak Mathematical Journal, 25, 619–633.

Fitch, H. S. 1982. Resources of a snake community in prairie-woodland habitat of northeastern Kansas. Pages 83-97 in Herpetological communities: A symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists League, August 1977. Wildlife Research Reports 12. 239 pp. U. S. Fish and Wildlife Service, Washington, D. C.

Fontaine, C., Guimarães, P.R., Kéfi, S., Loeuille, N., Memmott, J.J., van der Putten, W.H., van Veen, F.J.F. & Thébault, E. 2011. The ecological and evolutionary implications of merging different types of networks. Ecology Letters, 14, 1170–1181. https://doi.org/10.1111/j.1461-0248.2011.

Fontaine, C. & Thébault, E. 2015. Comparing the conservatism of ecological interactions in plant-pollinator and plant-herbivore networks. Population Ecology, 57, 29–36.

Fortuna, M.A., Stouffer, D.B., Olesen, J.M., Jordano, P., Mouillot, D., Krasnov, B.R., Poulin, R. & Bascompte, J. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? Journal of Animal Ecology, 79, 811–817.

Fraga, R.D., Lima, A.P., Prudente, A.L.D.C. & Magnusson, W.E. 2013. Guia de cobras da região de Manaus, Amazônia Central. Editora INPA, Manaus.

Galetti, M., Guevara, R., Côrtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labecca, F., Ribeiro, T., Carvalho, C.S., Collevatti, R.G., Pires, M.M., Guimarães, P.R., Brancalion, P.H., Ribeiro, M.C. & Jordano, P. 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. Science, 340, 1086-1090.

Gliwicz, J. 2008. Body size relationships between avian predators and their rodent prey in a North-American sagebrush community. Acta Ornithologica, 43, 151–158. https://doi.org/10.3161/000164508X 395261.

Greene, H.W. 1983. Dietary correlates of the origin and radiation of snakes. American Zoologist, 23, 431-441.

Greene, H.W. 2001. Snakes: the evolution of mystery in nature. University of California Press, Berkeley.

Guimarães, P.R. 2020. The structure of ecological networks across levels of organization. Annual Review of Ecology, Evolution, and Systematics, 51, 433–460.

Guimerà, R. & Nunes Amaral, L.A. 2005. Functional cartography of complex metabolic networks. Nature, 433, 895–900. https://doi. org/10.1038/nature03288.

Hembry, D.H., Raimundo, R.L.G., Newman, E.A., Atkinson, L., Guo, C., Guimarães P.R. & Gillespie, R.G. 2018. Does biological intimacy shape ecological network structure? A test using a brood pollination mutualism on continental and oceanic islands. Journal of Animal Ecology, 87, 1160-1171. doi: 10.1111/1365-2656.12841.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, CF., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren P.H. & Woodward, G. 2009. Ecological networks – beyond food webs. Journal of Animal Ecology, 78, 253–269.

Jordán, F., Liu, W.C. & Davis, A.J. 2006. Topological keystone species: measures of positional importance in food webs. Oikos, 112, 535–546.

Krishna, A., Guimarães, P.R., Jordano, P. & Bascompte, J. 2008. A neutral-niche theory of nestedness in mutualistic networks. Oikos, 117, 1609–1618. https://doi.org/10.1111/j.1600-0706.2008.16540.x

Lewinsohn, T.M., Prado, P.I., Jordano, P. & Bascompte, J. 2006. Structure in plant-animal interaction assemblages. Oikos, 113, 174–184.

Luiselli, L., Akani, G.C. & Capizzi, D. 1998a. Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria. Journal of Zoology, 246, 125-133.

Luiselli, L. & Angelici, F.M. 1998b. Sexual size dimorphism and natural history traits are correlated with intersexual dietary divergence in royal pythons (*Python regius*) from the rainforests of southeastern Nigeria. Italian Journal of Zoology, 65, 183–185.

MacArthur, R.H. 1969. Patterns of communities in the tropics. Biological Journal of the Linnean Society, 1, 19–30.

Mariania, M.S., Renc, Z.M., Bascompte, J. & Tessone, C.J. 2019. Nestedness in complex networks: observation, emergence, and implications. Physics Reports, 813, 1-90.

Marquitti, F.M.D., Guimarães, P.R., Pires, M.M. & Bittencourt, L.F. 2014. MODULAR: Software for the autonomous computation of modularity in large network sets. Ecography, 37, 221–224. doi.org/10.1111/j.1600-0587.2013.00506.x

Martins, M. & Oliveira, M.E. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History, 6, 78–150.

Martins, M., Marques, O.A. & Sazima, I. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers (Genus *Bothrops*). In *Biology of the vipers*, ed. Schuett, G.W., pp. 307–328. Eagle Mountain Publishing, USA.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A., McCain, C.M., McCune, A.R., McDade, L.A., McPeek, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M. & Turelli, M. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters, 10, 315–331.

Morris, R.J., Gripenberg, S., Lewis, O.T. & Roslin T. 2014. Antagonistic interaction networks are structured independently of latitude and host guild. Ecology Letters, 17, 340–349.

Newman, M.E.J. 2003. The structure and function of complex networks. SIAM Review, 45, 167–256.

Ollerton, J. 2006. “Biological barter”: patterns of specialization compared across different mutualisms. In *Plant–Pollinator Interactions: From Specialization to Generalization*, eds. Waser, N.M. & Ollerton, J., pp. 411–35. University Chicago Press, Chicago.

Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. 2007. The modularity of pollination networks. Proceedings of the National Academy of Sciences, 104, 19891–19896.

Pellissier, L., Albouy, G., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M.A., Melián, C.J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N.E. & Gravel, D. 2018. Comparing species interaction networks along environmental gradients. Biological Reviews, 93, 785–800.

Pinheiro, R.B.P., Felix, G.M.F., Dormann, C.F. & Mello, M.A.R. 2019. A new model explaining the origin of different topologies in interaction networks. Ecology, 100, e02796. https://doi.org/10.1002/ecy.2796

Pinto-Coelho, D., Martins, M., Guimarães, P. R. 2021. Network analyses reveal the role of large snakes in connecting feeding guilds in a species-rich Amazonian snake community. Ecology and Evolution, 11, 6558-6568.

Pires, M.M. & Guimarães, P.R. 2013. Interaction intimacy organizes networks of antagonistic interactions in different ways. Journal of the Royal Society Interface 10, 20120649.

Pires, M.M., Guimarães, P.R., Araújo, M.S., Giaretta, A.A., Costa, J.C.L. & dos Reis, S.F. 2011. The nested assembly of individual-resource networks. Journal of Animal Ecology, 80, 896–903.

Pires, M.M., O'Donnell. J.L., Burkle, L.A., Díaz-Castelazo, C., Hembry, D.H., Yeakel, J.D., Newman, E.A., Medeiros, L.P., de Aguiar, M.A.M. & Guimarães, P.R. 2020. The indirect paths to cascading effects of extinctions in mutualistic networks. Ecology, 101, e03080. doi: 10.1002/ecy.3080.

Pizzatto, L., Marques, O.A.V. & Facure, K. 2009. Food habits of Brazilian boid snakes: overview and new data, with special reference to *Corallus hortulanus*. Amphibia-Reptilia, 30, 533-544.

Pizzatto, L., Oliveira, J.L., Marques, O.A.V. & Martins, M. 2018. Body shape and food habits of South American goo-eater snakes of the genus *Sibynomorphus*. South American Journal of Herpetology, 13, 300–307.

Poisot, T., Stouffer, D.B. & Kéfi, S. 2016. Describe, understand and predict: why do we need networks in ecology? Functional Ecology, 30, 1878–1882.

Prado, P.I. & Lewinsohn, T.M. 2004. Compartments in insect-plant associations and their consequences for community structure. Journal of Animal Ecology, 73, 1168–1178.

Pringle, R.M. & Hutchinson, M.C. 2020. Resolving food-web structure. Annual Review of Ecology, Evolution and Systematics, 51, 55–80.

Pyron, R.A., Burbrink, F.T. & Wiens, J.J. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology, 13, 93.

R Core Team 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-proje ct.org/

Rezende, E.L., Albert, E.M., Fortuna, M.A. & Bascompte, J. 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. Ecology Letters, 12, 779–788.

Rosseel, Y. 2012. lavaan: An R package for structural equation modeling. Journal of Statistical Software, 48, 1–36. https://www.jstatsoft.org/v48/i02/

Savitzky, A.H. 1983. Coadapted character complexes among snakes: fossoriality, piscivory, and durophagy. American Zoologist, 23, 397– 409. https://doi.org/10.1093/icb/23.2.397

Sazima, C., Guimarães, P.R., Reis, S.F. & Sazima, I. 2010. What makes a species central in a cleaning mutualism network? Oikos, 119, 1319–1325.

Schmitz, O.J. & Beckerman, A.P. 2007. Food webs. Encyclopedia of Life Sciences, John Wiley & Sons.

Schemske, D.W. 2009a. Biotic interactions and speciation in the tropics. In *Speciation and Patterns of Diversity,* eds. Butlin, R.K., Bridle, J.R., Schluter, D., pp. 219–39. Cambridge Univ. Press, Cambridge.

Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. 2009b. Is there a latitudinal gradient in the importance of biotic interactions? Annual Review in Ecology, Evolution and Systematics, 40, 245–269.

Schleuning, M., Fründ, J., Klein, A.M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G.K.S., Bazarian, S., Bohning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D.M., Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C.N., Kreft, H., Morris, R.J., Sandel, B., Sutherland, W.J., Svenning, J.-C., Tscharntke, T., Watts, S., Weiner, C.N., Werner, M., Williams, N.W., Winqvist, C., Dormann, C.F. & Bluthgen, N. 2012. Specialization of mutualistic interaction networks decreases toward tropical latitudes. Current Biology, 22, 1925–1931.

Secor, S.M. & Diamond, J.M. 2000. Evolution of regulatory responses to feeding in snakes. Physiological and Biochemical Zoology, 73, 123–141.

Shi, J. & Malick, J. 2000. Normalized cuts and image segmentation, IEEE. Transactions on Pattern Analysis and Machine Intelligence, 22, 888-905.

Shipley, B. 2000. Cause and correlation in biology: a user’s guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge.

Sinclair, A.R.E., Mduma, S. & Brashares, J.S. 2003. Patterns of predation in a diverse predator-prey system. Nature, 425, 288-290.

Spiesman, B.J. & Inouye, B.D. 2013. Habitat loss alters the architecture of plant-pollinator interaction networks. Ecology, 94, 2688–2696.

Solé, R.V., Montoya, J.M., 2001. Complexity and fragility in ecological networks. Proceedings of the Royal Society B, 268, 2039–2045.

Stouffer, D.B., Rezende, E.L. & Amaral, L.A.N. 2011. The role of body mass in diet contiguity and food-web structure. Journal of Animal Ecology, 80, 632–639.

Thébault, E. & Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science, 329, 853–856.

Thompson, J. N. 2005. The geographic mosaic of coevolution. University of Chicago Press, Chicago.

Uetz, P., Freed, P, Aguilar, R. & Hošek, J. (eds.). 2022. The Reptile Database, http://www.reptile-database.org, accessed [April 27, 2022].

Ulrich, W., Almeida-Neto, M. & Gotelli, N.J. 2009. A consumer's guide to nestedness analysis. Oikos, 118, 3-17.

Valverde, S., Vidiella, B., Montañez, R., Fraile, A., Sacristán, S. & García-Arenal, F. 2020. Coexistence of nestedness and modularity in host-pathogen infection networks. Nature Ecology and Evolution, 4, 568-577.

Vidal, N., Marin, J., Morini, M., Donnellan, S., Branch, W.R., Thomas, R., Vences, M., Wynn, A., Cruaud, C. & Hedges, S.B. 2010. Blindsnake evolutionary tree reveals long history on Gondwana. Biology Letters, 6, 558–561.

Vieira-Alencar, J.P.S., Furtado, L.O., Felicio, G.R., Pinto-Coelho, D. & Carmignotto, A.P. 2022. First predation record on the invasive lagomorph *Lepus europaeus* (Leporidae) by *Boa constrictor* (Boidae) in a southern Brazilian cerrado protected area. Revista Latinoamericana de Herpetología, 5. doi.org/10.22201/fc.25942158e.2022.2.318

Zanata, T.B. Dalsgaard, B. O., Passos, F. C., Cotton, P. A., Roper, J. J., Maruyama, P. K., et al. 2017. Global patterns of interaction specialization in bird–flower networks. Journal of Biogeography, 44, 1891–1910.

Wallach, V., Williams, K. L. & Boundy, J. 2014. Snakes of the world. A catalogue of living and extinct species. CRC Press, New York.

Webb, C.O., Ackerly, D., McPeek, M. & Donoghue, M. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics, 33, 475–505.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J., Olesen, J., Valido, A. & Warren, P. 2005. Body size in ecological networks. Trends in Ecology & Evolution, 20, 402–409. https://doi.org/10.1016/j.

Wright, S.L. 1934. Annals of Mathematical Statistics 5, 161.

Yanosky, A.A., Dixon, J.R. & Mercolli, C. 1996. Ecology of the snakes community at El Bagual Ecological Reserve, Northeastern Argentina. Herpetological Natural History, 4, 97-110.

Appendix 1

A detailed description of methods and network metrics used in our study.

The classification of the selected studies in the "sampling effort category" (Table S1), followed a qualitative criterion, developed by the specialist snake researcher, Márcio Martins, who considered three main observations: (i) the sampling effort, (ii) the size of the study area, (iii) the biome in which the study was developed. Based on these elements, we extrapolated the expected number of species expected for each study area and, when comparing with the number of species recorded by the study, we created the "sampling effort category", which ranged from 0-5. Only studies classified above 3 were considered.

(a) Degree distribution

The degree of a snake species is the total number of food resources that a snake consumes. The degree distribution is a description of how the number of consumed food resources varies across snake species.

(b) Connectance

The connectance is the proportion of all possible interactions actually recorded in the network:

$$C = I / SR$$

where I is the number of interactions recorded among snake species and their food resources, S is the number of snake species in the network, and R is the number of food resources in the network. Connectance values range from 0 (non-connected network) to 1 (maximum connectance).

Table S1: Information on the network code, country, environment type, geographical coordinates (decimal degrees), size study area, sampling period, sampling effort, number of species and specimens of snakes recorded, number of snake species expected for the study area, number of food resources categories, number of interactions, network size, data source, and sampling effort category of the 24 networks interactions between snakes and their food resources. *Based on Fraga et al. 2013. Guia de Cobras da Região de Manaus, Amazônia Central. Manaus: Editora INPA.

Code	Country	Environment	Latitude	Longitude	Area	No. snake specimens	No. snake species	Expected no. species	No. food resources	No. of interactions	Source information	Sampling effort category
Manaus	Brazil	Amazon rainforest	NA	NA	10,000 ha	552	62	66*	24	170	Martins & Oliveira (1998)	4
Espigao	Brazil	Amazon rainforest	-11.5000	-60.6667	4,000 ha	462	54	~60	22	155	Bernarde & Abe (2006)	4
Carlos Botelho	Brazil	Atlantic rainforest	-24.0000	-47.7500	37,793 ha	216	47	~50	15	101	Forlani et al. (2010)	4
Bahia	Brazil	Restinga	-12.7122	-37.6278	220 km along the coast	194	46	~50	18	132	Marques et al. (2016)	4
Tapirai	Brazil	Atlantic rainforest	-23.8167	-47.3333	15 fragments ranging from 3 - 150 ha	240	45	~50	14	104	Condez et al. (2009)	4
Igarape	Brazil	Amazon rainforest	-7.9556	-72.0769	200 ha	NA	42	~60	24	120	Bernarde et al. (2011)	3
Itirapina	Brazil	Cerrado	-22.2500	-47.7500	2,300 ha	755	35	~35	17	77	Sawaya et al. (2008)	5
Bagual	Argentina	Humid Chaco	-26.1814	-58.9442	3,463 ha	313	31	~35	15	79	Yanosky et al. (1996)	4
Chico Mendes	Brazil	Amazon rainforest	-0.7411	-69.3525	10 ha	63	28	~60	15	89	França et al. (2017)	2
Paraiba	Brazil	Atlantic rainforest	-7.2335	-34.8060	843 ha	151	27	~35	14	81	Sampaio et al. (2018)	3
Picinguaba	Brazil	Atlantic rainforest	-23.3833	-44.8333	4,000 ha	282	26	~30	13	69	Hartmann et al. (2009)	4
Santa Virginia	Brazil	Atlantic rainforest	23°22’S	45°07’W	4,400 ha	148	26	~30	12	64	Hartmann et al. (2009)	4
Chacoan	Argentina	Mosaic vegetation	-24.6833	-53.2500	800,000 ha	1,966	25	~25	13	72	Bellini et al. (2015)	5
Jureia	Brazil	Atlantic rainforest	NA	NA	NA	305	25	~30	15	66	Marques & Sazima (2004)	4
Pantanal	Brazil	Pantanal	-16.5000	-56.7500	NA	242	25	~28	13	58	Strussmann & Sazima (1993)	4
Serra do Papagaio	Brazil	Atlantic rainforest	-22.1425	-44.7286	22,900 ha	90	24	~35	14	61	Menezes et al. (2018)	3

Code	Country	Environment	Latitude	Longitude	Area	No. snake specimens	No. snake species	Expected no. species	No. food resources	No. of interactions	Source information	Sampling effort category
Eket	Africa	Moist rainforest	4.8333	7.9833	100 ha	237	23	~30	13	55	Luiselli et al. (1998)	3
Arizona	United States	Desert	NA	NA	~ 7,770 ha	NA	22	~25	13	73	Gates (1957)	4
Ceara	Brazil	Caatinga	-3.8184	-39.3374	823 ha	636	22	~22	11	51	Mesquita et al. (2013)	5
Texas	United States	Bottomland deciduous forest	NA	NA	2,300 ha	621	20	~25	15	64	Ford & Lancaster (2007)	4
Ejule	Africa	Savanna	6.9000	7.3833	NA	79	18	~25	12	36	Akani et al. (1999)	3
Japi	Brazil	Atlantic rainforest	-23.1833	-46.8667	35,000 ha	270	13	~20	13	43	Sazima & Haddad (1992)	4
Kansas	United States	Mosaic vegetation	38.9586	-95.2439	239 ha	22,093	12	12	9	41	Fitch (1982)	5
Roma	Italy	Mediterranean	42.0500	12.5833	100 ha	129	5	~5	4	12	Capizzi et al. (1995)	5

(c) Modularity

The modularity is a measure of the extent to which the network is formed by groups (modules) of snake species in which snake within a module overlap in much of their resources, whereas snakes in different modules show no or weak resource use overlap. We used Q_B metric, defined by Barber (2007), to characterise modularity, with values ranging from 0 (non-modular network) to 1 (completely modular):

$$QB = \frac{1}{2I} \sum_{i,j}^{S+R} \left(A_{ij} - P_{ij}\right) \delta\left(g_i, g_j\right),$$

where, I is the number of interactions; A_{ij} is a square and symmetric matrix describing the interactions among snakes and resources, in which $a_{ij} = a_{ji} = 1$ if a snake species i feeds on a resource j and zero otherwise; P_{ij} is the probabilities in the null model that an interaction exists between vertices i and j; and $\delta\left(g_i, g_j\right) = 1$ if nodes (snakes or resources) i and j are assigned to the same module and zero otherwise. In the null model, the probability there is an interaction between a snake species and a resource is proportional to the products of the degree of both the resource and the snake species. A simulated annealing algorithm (Guimerà & Amaral 2005) was used to optimise the Q_B value. Modularity analyses were performed using the Modular program (Marquitti et al. 2014).

(d) *Nestedness*

The nestedness is an interaction pattern in which the specialists interact with sets of resources with which the generalists also interact. The NODF (nestedness metric based on overlap and decreasing fill) metric was used to characterize the nestedness degree (Almeida-Neto et al. 2008) and its values ranges from 0 (non-nested network) to 100 (perfect nestedness):

$$\text{NODF} = \frac{\sum_{i,j}^{S} N_{ij} + \sum_{d,f}^{R} N_{df}}{S(S-1) + R(R-1)},$$

Where N_{ij} is the pairwise degree of nestedness (Almeida-Neto et al. 2008) calculated for snake species i and j and N_{df} is the pairwise degree of nestedness between resources *d* and *f*.

(e) *Null model*

We compared the degree of nestedness and modularity with a theoretical benchmark provided by the null model 2 of Bascompte et al. (2003). In this null model 2, the probability of a species of snake *i* interact with a resource *j* is

$$Pij = \frac{1}{2}\left(\frac{ki}{R} + \frac{kj}{S}\right) ,$$

in which k_i (k_j) is the degree of the snake species *i* (resource *j*), *R* is the number of resource types in the network, and *S* is the snake species richness. We chose the null model 2 because the probability of interaction is proportional to the number of interactions (degree), therefore allowing us to investigate if the levels of modularity and nestedness are higher than expected by the variation in number of resource types across snake species.

(f) Taxonomic diversity index (Δ^+)

The taxonomic diversity index (Δ^+) was calculated as the average taxonomic "distance" between any two snake species randomly chosen from the sample. This distance can be understood as the length of the path that connects these two species, traced by a Linnean or phylogenetic classification of the complete set of snake species involved in each sample (each of the analyzed networks). The taxonomic diversity index was usually developed for samples with species abundance information. However, for samples with only species presence and absence information, the original formula is reduced to:

$$\Delta^+ = [\Sigma\Sigma_{i<i} w_{ij}] / [s\ (s-1)/2]$$

where, w_{ij} is the "distinctness weight" given to the path length linking snakes *i* and *j* in the hierarchical classification, and *s* is the number of species present in the network; w = 1 (same genus species), w = 2 (same family but different genus), w = 3 (same suborder but different family), w = 4 (same order but different suborder), w = 5 (same subclass but different order), and w = 6 (different subclass). Additional details in Clarke & Warwick (1998).

(g) On network components

It is known that for many classes of random networks, there is a critical point separating disconnected networks formed by multiple components from networks with a giant component. This critical point is controlled by a connectivity parameter associated with the degree distribution (reviewed in Guimaraes 2020). For random bipartite networks with fixed degree distribution (e.g., a degree distribution that follows the same degree distribution of an empirical network), the giant component is expected to emerge if $c_1 = \langle k2 \rangle - 2\langle k \rangle > 0$ where $\langle k2 \rangle$ is the average of the square of the degrees of the nodes in the network. For random networks with fixed degree distribution showing bipartivity, the emergence of a giant component occurs if

$c_2 = \sum_{i=1}^{MI} \sum_{j=1}^{MJ} ij\ (ij - i - j)\, pij > 0$, where MI(MJ) is the largest degree recorded in set I(J), i=1 j=1 and pi (pj) is the frequency of nodes with a degree equal to i (j) (Newman et al. 2001). The connectivity parameter increases with the mean and variance of the degree distribution, favoring the emergence of a giant component. Additional details on Guimarães (2020).

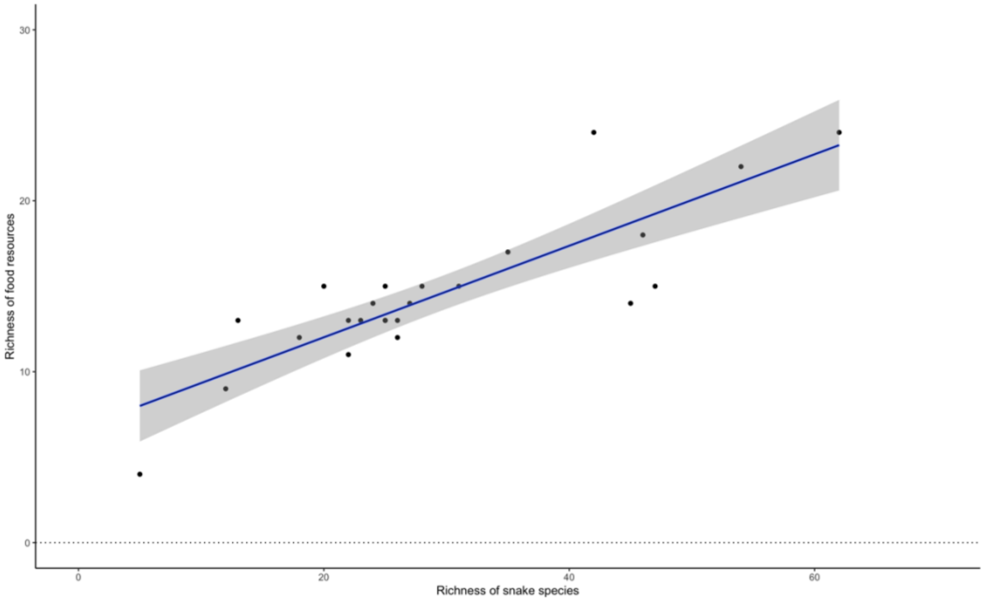


Figure S1: Consistent positive correlation between the richness of snake species and food resources ($R^2 = 0.71$, $p < 0.01$). Each point represents a network, the blue line the direction of the relationship, and the gray band the confidence interval.

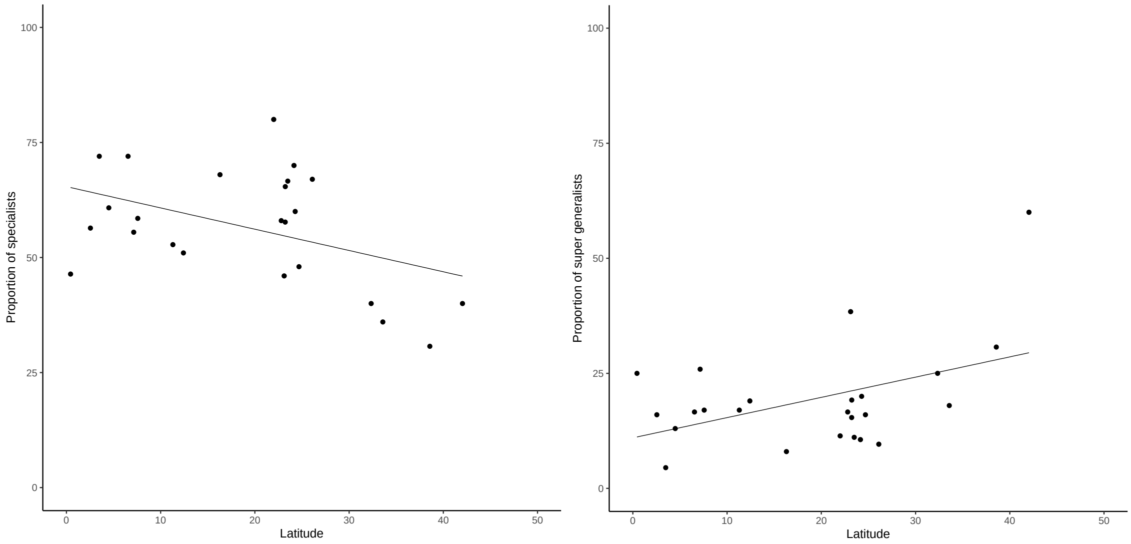


Figure S2: Relationship showing the effect of latitude on the proportion of specialist snakes in relation to super generalists in the analyzed networks. a) Negative correlation between latitude and proportion of specialists (R^2 = 0.18, $p < 0.03$) and b) Positive correlation between latitude and proportion of super generalists (R^2 = 0.20 $p < 0.02$).

References

Akani , G. C., Barieenee, I. F., Capizzi, D. & Luiselli, L. 1999. Snake communities of moist rainforest and derived savanna sites of Nigeria: biodiversity patterns and conservation priorities. Biodiversity and Conservation, 8, 629–642.

Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. 2008. A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. Oikos, 117, 1227– 1239. doi.org/10.1111/j.0030-1299.2008.16644.x

Barber, M. J. 2007. Modularity and community detection in bipartite networks. Physical Review E, 76, 066102. https://doi.org/10.1103/ PhysRevE., 76.066102

Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences of the United States of America, 100, 9383–9387. doi.org/10.1073/pnas.1633576100

Bellini, G. P., Giraudo, A. R., Arzamendia, V., & Etchepare, E. G. 2015. Temperate snake community in South America: Is diet determined by phylogeny or ecology? PLoS One, 10, 1–15. https://doi.org/10.1371/ journal.pone.0123237

Bernarde, P. S. & Abe, A. S. 2006. A snake community at Espigão do Oeste, Rondônia, southwestern Amazon, Brazil. South American Journal of Herpetology, 1, 2, 102-113.

Bernarde, P. S., Machado, R. A. & Turci, L. C. B. 2011. Herpetofauna da área do Igarapé Esperança na Reserva Extrativista Riozinho da Liberdade, Acre – Brasil. Biota Neotrop., 11, 3.

Capizzi, D., Luiselli, L., Capula, M. & Rugiero, L. 1995. Feeding habits of a mediterranean community of snakes in relation to prey availability. Rev. Eco/. (Terre Vie), 50.

Clarke, K.R. & Warwick, R.M. 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology, 35, 523–531

Condez, T. H., Sawaya, R. J. & Dixo, M. 2009. Herpetofauna dos remanescentes de Mata Atlântica da região de Tapiraí e Piedade, SP, sudeste do Brasil. Biota Neotrop., 9, 1, 157-185.

Ford, N. B & Lancaster, D. L. 2007. The Species-Abundance Distribution of Snakes in a Bottomland Hardwood Forest of the Southern United States. Journal of Herpetology, 41, 3, 385-393.

Fitch, H. S. 1982. Resources of a snake community in prairie-woodland habitat of northeastern Kansas. Pages 83-97 in Herpetological communities: A symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists League, August 1977. Wildlife Research Reports 12. 239 pp. U. S. Fish and Wildlife Service, Washington, D. C.

Forlani, M. C., Bernardo, P. H., Haddad, C. B. F. & Hussam, Z. 2010. Herpetofauna do Parque Estadual Carlos Botelho, São Paulo, Brasil. Biota Neotropica, 10, 3, 265-309.

França, D. P .F., Freitas, M. A., Ramalho, W. P . & Bernarde, P. S. 2017. Diversidade local e influência da sazonalidade sobre taxocenoses de anfíbios e répteis na Reserva Extrativista Chico Mendes, Acre, Brasil. Iheringia, Série Zoologia, 107, e2017023.

Gates, G. O. 1957. A Study of the Herpetofauna in the Vicinity of Wickenburg, Maricopa County, Arizona. Transactions of the Kansas Academy of Science, 60, 4, 403-418.

Guimarães, P. R. (2020). The structure of ecological networks across levels of organization. Annual Review of Ecology, Evolution, and Systematics, 51, 433–460.

Guimerà, R., & Nunes Amaral, L. A. (2005). Functional cartography of complex metabolic networks. Nature, 433, 895–900. https://doi. org/10.1038/nature03288

Hartmann, P. A., Hartmann, M. T. & Martins, M. 2009. Ecology of a snake assemblage in the Atlantic Forest of southeastern Brazil. Papeis Avulsos de Zoologia. 49, 27, 343-360.

Luiselli, L., Akani, G. C. & Capizzi, D. 1998. Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria. J. Zool., Lond. 246, 125-133.

Marquitti, F. M. D., Guimarães, P. R., Pires, M. M., & Bittencourt, L. F. (2014). MODULAR: Software for the autonomous computation of modularity in large network sets. Ecography, 37, 221–224. https:// doi.org/10.1111/j.1600-0587.2013.00506.x

Marques, O. A. V. & Sazima, I. 2004. História natural dos répteis da Estação Ecológica Juréia-Itatins. In Estação Ecológica Juréia-Itatins: ambiente físico, flora e fauna (O.A.V. Marques & W. Duleba, eds.). Holos, Ribeirão Preto. p. 257-277.

Marques, R., Mebert, K., Fonseca, E., Rödder, D., Solé, M. & Tinôco, M. S. 2016. Composition and natural history notes of the coastal snake assemblage from Northern Bahia, Brazil. ZooKeys, 611, 93–142.

Martins, M., & Oliveira, M. E. (1998). Natural history of snakes in for- ests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History, 6, 78–150.

Menezes, F. A. M., Abegg, A. D., Silva, B. R., Franco, F. L., & Feio, R. N. 2018. Composition and natural history of the snakes from the Parque Estadual da Serra do Papagaio, southern Minas Gerais, Serra da Mantiqueira, Brazil. ZooKeys 797: 117–160.

Mesquita, P. C. M. D., Passos, D. C., Borges-Nojosa, D. M. & Cechin, S. Z. 2013. Ecologia e história natural das serpentes de uma área de caatinga no nordeste brasileiro. Papeis Avulsos de Zoologia. 53, 8, 99-113.

Sampaio, I. L. R., Santos, C. P., França, R. C., Pedrosa, I. M. M. C., Solé, M. & França, F. G. R. 2018. Sampaio Ecological diversity of a snake assemblage from the Atlantic Forest at the south coast of Paraíba, northeast Brazil. ZooKeys, 787, 107–125.

Sazima, I. & Haddad, C. F. B. 1992. Répteis da Serra do Japi: notas sobre história natural. Pp. 212-236, In: L. P. C. Morellato (Ed.}, História natural da Serra do Japi: ecologia e preservação de uma área florestal no sudeste do Brasil. Ed. Unicamp e FAPESP, Campinas.

Sawaya, R. J., Marques, O. A. V. & Martins, M. 2008. Composição e história natural das serpentes de Cerrado de Itirapina, São Paulo, sudeste do Brasil. Biota Neotrop., 8, 2, 127-149.

Strussmann, C. & Sazima, I. 1993. The snake assemblage of the Pantanal at Poconé, Western Brazil: Faunal composition and ecological summary. Studies on Neotropical Fauna and Environment, 28, 3, 157-168.

Yanosky, A., Dixon, J. R. & Mercolli, C. 1996. Ecology of the snake community at El Bagual ecological reserve, northeastern Argentina. Herpetological Natural History, 4, 2, 97-110.

Capítulo 3

Attributes shaping the centrality of snake species in predator-prey networks

Daniela Pinto-Coelho, Kate P. Maia & Paulo R. Guimarães Jr.

Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, Cidade Universitária, 05508-900, São Paulo, SP, Brazil.

Author for correspondence: danipcoelho@usp.br

Abstract

One key concept in network ecology is centrality. Centrality measures allow identifying the importance of species to the structure of an ecological network. Since centrality varies across species, identifying which attributes make a species central may help us to understand how interacting assemblages are organized by ecological and evolutionary processes. In the present study, we investigated how different biological attributes (i.e. body size, lifestyle, and phylogenetic history) might explain the variation in the importance of snakes within and across 23 snake-prey networks. We use four measures of centrality to estimate the importance of snakes to network structure, exploring which of these measures is more relevant in describing the indirect effects that propagate in the networks analyzed. We observed that all centrality measures were correlated with each other (R^2 ranging from 0.8 to 0.22, $p < 0.01$ in all cases). Principal component analysis (PCA) revealed a greater association between degree and betweenness centralities (PC1) and between closeness and Fiedler centralities (PC2). The large values of degree and betweenness centralities are associated with larger body sizes, with the families of large constrictor snakes, and with aquatic and semi-arboreal lifestyles. In contrast, central species by closeness and Fiedler centralities did not show strong associations with large sizes or more generalist lifestyles. Moreover, we also show that small-sized species and non-generalist lifestyles also play important roles, essentially in connecting sectors in the network. Degree and betweenness centralities were the metrics that contributed most strongly to the transmission of indirect effects in the networks. We concluded that degree and betweenness centralities represented the most relevant metrics for indicating key species in snake-prey networks for the spreading of cascading effects.

Key-words: betweenness, body size, centrality, closeness, degree, Fiedler, indirect effects, key species, biological traits.

Introduction

Understanding the structure of ecological interactions and how these interactions affect the roles played by different species is one of the main goals of ecology (Cohen et al. 1993, Cagua et al. 2019). Ecological interactions form networks and the structural pattern of these networks affect their dynamics and stability (Solé & Montoya 2001, Dunne et al. 2002, Tylianakis et al. 2010, Pires et al. 2020). For example, in networks of scavenger vertebrates, more nested structures favor increases in consumption rates due to facilitation processes generated by the presence of key species (Sebastián-González et al. 2020). Because the distribution of interactions across species is not homogeneous in a network, not all species play equivalent roles in the network (Sazima et al. 2010, González et al. 2010).

The importance of species in the structure of interaction networks can be captured by different centrality metrics (Delmas et al. 2018). This set of metrics measures different aspects related to the importance of a node within the network (Estrada 2007). For example, degree centrality (Freeman, 1977) is a simple measure of counting the number of interactions of a node, estimating its direct influence. Closeness centrality (Freeman et al. 1979) measures the proximity of a species to all other species in the network in terms of direct and indirect pathways. Betweenness centrality (Freeman, 1977) describes the number of times a species finds itself on the path between two other species in the network. Several other metrics have been proposed in the network literature in order to quantify the relative importance of nodes in interactions (see further details in Delmas et al. 2018, Sazima et al. 2010, González et al. 2010, Mello et al. 2014). Since species do not have equivalent importance in trophic communities, it is fundamental to determine which biological attributes affect their levels of centrality (Sazima et al. 2010).

A fundamental problem to solve is to connect the structural importance of individual species to its potential dynamical consequences. For example, the loss of central predators can have cascading effects within the community, depending on their relevance in the network structure (Jordán et al. 2006), as indicated by how the local extinction of sea otters in Alaska affected all primary production in the region (Estes & Palmasiano 1974). Moreover, in a network, there are multiple alternative routes for the proliferation of indirect effects (Guimarães et al. 2017). Indirect effects can have profound consequences for the dynamics of ecological communities (Tylianakis et al. 2010, Pires et al. 2020). Thus, a challenge for the ecology of interactions is to understand which characteristics of species make them fundamental to structure and, consequently, to the dynamics of complex ecological systems.

Several species attributes have been associated with their role in interaction networks. The body size (Sinclair et al. 2003, Woodward et al. 2005, Rezende et al. 2009, Ceron et al. 2019; Pinto-Coelho et al. 2021), the trophic level (Sazima et al. 2010), the level of specialization in the diet (Mello et al. 2014), the lifestyle (Pinto-Coelho et al. 2021), the abundance (Lewinsohn et al., 2006) or the phylogenetic history (Rezende et al. 2009) may play a fundamental role in determining the importance of the species. In general, generalist species play central roles in networks (González et al. 2010, Guimarães et al. 2011, Palacio et al. 2016), since the loss of these species can alter the dynamics of communities, promoting cascades of extinctions (Solé & Montoya 2001, Pires et al. 2020).

In this paper, we use snake-prey networks to investigate how biological attributes (e.g. body size, lifestyle, and phylogenetic history) are associated with the role of a snake in predator-prey networks. To do so, we use snake-prey networks to investigate two main questions: (i) what biological attributes (e.g. body size, lifestyle, and phylogenetic history) drive snakes to become central in predator-prey networks, and (ii) which centrality metric best captures the transmission of indirect effects in the analyzed networks. We integrated analysis of network patterns, information on natural history of the snakes, and cascade effect simulations to explore these two questions. We expected, based on the results of chapters 1 and 2 of this thesis, that body size will be positively associated with centrality but this association will be modulated by lifestyle and phylogenetic history. Having said that, the best centrality metrics to describe the propagation of cascading effects will depend on the idiosyncratic aspects of the network structure. We hope that our findings can be useful for other types of interactions.

Methods

Dataset

We analyzed 23 widely distributed snake-prey interaction networks derived from published studies available on the Web of Science (all details of the dataset are available in the supplementary material in chapter 2 Appendix 1). In snake-prey networks, snake species and prey categories are represented as nodes and predator-prey interactions by links (see Pinto-Coelho et al. 2020). Datasets were organized as a binary interaction matrix **A (**adjacency matrix), where if a snake *i* feeds on a given prey *j*, $a_{ij} = 1$, and if snake species *i* does not feed on *j* $a_{ij} = 0$. We decided to use binary data in our analysis, i.e. to only compute the presence or absence of interactions between snakes and their food resources, due to limitations in the availability of detailed snake diet data (see details in Pinto-Coelho et al. 2021).

Centrality metrics

In this study, to infer the importance of snake species in the network structure we used three usual centrality metrics: (1) degree centrality, (2) closeness centrality, and (3) betweenness centrality, and (4) Fiedler centrality, based on Fiedler vector (Fiedler 1975, Shi & Malick 2000, Newman 2003). We chose to use these four metrics because (i) they represent distinct concepts of centrality, (ii) are associated with interaction patterns and processes relevant to ecological systems, and (iii) may be able to identify candidate lists of key species (Jórdan et al. 2006, Sazima et al. 2010, Mello et al. 2014, Delmas et al. 2018).

The degree centrality (DC) of a given snake is a normalized measure of its number of interactions, in which the degree centrality of a snake *i* is:

$$\mathrm{DC}_i = \frac{ki}{(N-1)},$$

where *k* is the degree of the species *i*, i.e. the number of resources consumed by snake species, and *N* is the total number of network snakes. Highly connected snakes will have high degree centrality values (Figure 1). In contrast, low degree centrality values indicate snakes with few interactions, such as those with specialized food habits (Arteaga et al. 2018) or rare species (Machado-Filho et al. 2011).

Betweenness centrality (BC) describes the number of times a node *l* lies on the shortest paths among other pairs of nodes (*i*, *j*) in the network (Figure 1). Thus, betweenness centrality is given by:

$$\mathrm{BC_l} = \sum_i \sum_j \frac{p_{ilj}}{p_{ij}}$$

$$i \neq j \neq l\ ,$$

where, $\sum_i \sum_j p(ij)$, is the number of shortest paths between all pairs of nodes in the network, no matter if both nodes describe resources, both nodes describe snake species or a node describe a resource and the other snake species; $\sum_i \sum_j p(ilj)$ is the number of shortest paths that pass through resource *l*. Betweenness centrality allows us to access the importance of each node in connecting different parts of the network (Dáttilo and Rico-Gray 2018). Thus, a snake with a high value of betweenness centrality can be considered a central species for keeping the different nodes of the network interconnected, favoring the transmission of direct and indirect effects in the network (Guimarães et al. 2017). Species with high BC values also might potentially trigger co-extinctions cascades by connecting subgroups of interacting species in the networks (Barthélemy 2004).

Closeness centrality (CC) is a measure based on the shortest distances between the focal species and all other nodes in the (Figure 1). Closeness centrality is given by:

$$CC_i = \frac{N-1}{\sum_j d_{(ij)}}$$

in which d_{ij} is the shortest distance between the snake i and a node (snake or resource) j in the network, in the number of links. The snake with the highest closeness centrality value is considered the closest to all other nodes in the network. In an ecological context, a snake species has high closeness centrality when it feeds on prey consumed by many other snakes in the same network, and it has low closeness centrality, when its diet is more unique (Mello et al. 2014). Closeness centrality can be used to understand co-extinction cascades, since species with high CC values, if extinct, can trigger the disappearance of other species in the network (Rezende et al. 2007).

Ecological networks can be composed of multiple components, i.e., isolated groups of connected species. Such components may be more prone to break in specific points as a result of the loss of specific interactions, further generating new isolated components. These key interactions can be identified with the Fiedler vector (Fiedler 1975, see below). The Fiedler vector is the eigenvector associated with the smallest non-zero eigenvalue of the network's Laplacian matrix. The Laplacian matrix is defined as L = D - A, where D is the degree matrix, a matrix in which all off-diagonal elements are zero and diagonal elements are equal to the degree of that species, and A is the adjacency matrix. The Fiedler vector has length equal to S, the number of network species, and contains a positive or a negative value for each network species, dividing the component in two sets. The Fiedler vector allows one to divide the largest component of the network in two sets and it is the underlying approach to some classical methods to find groups in networks ("spectral partitioning"). We define Fiedler centrality as the number of interactions connecting the two sets of the largest component in the network that are held by a given species. The Fiedler centrality of a given species is the number of interactions of this species established with species with opposite signed values in the Fiedler vector. The Fiedler vector proves to be useful in computer science, being applied to algorithms for partitioning the nodes of a graph (Fiedler 1975, Shi & Malick 2000). Using the Fiedler vector to measure the importance of nodes in networks of ecological interactions may allow insights that may not be captured by traditional centrality metrics, such as DC, CC, or BC. Since Fiedler centrality captures only the number of interactions between sectors that a species has, there will be a tendency for the existence of many zeros in the matrix, referring to those species restricted to only one sector of the network. Thus, in order to understand the contribution of central species by Fiedler to the transmission of indirect effects in the network, we performed an one-way ANOVA with Tukey's posthoc test to investigate the possible existence of consistent differences between interconnecting or not interconnecting sectors of the network (Appendix 1 Figure S1).

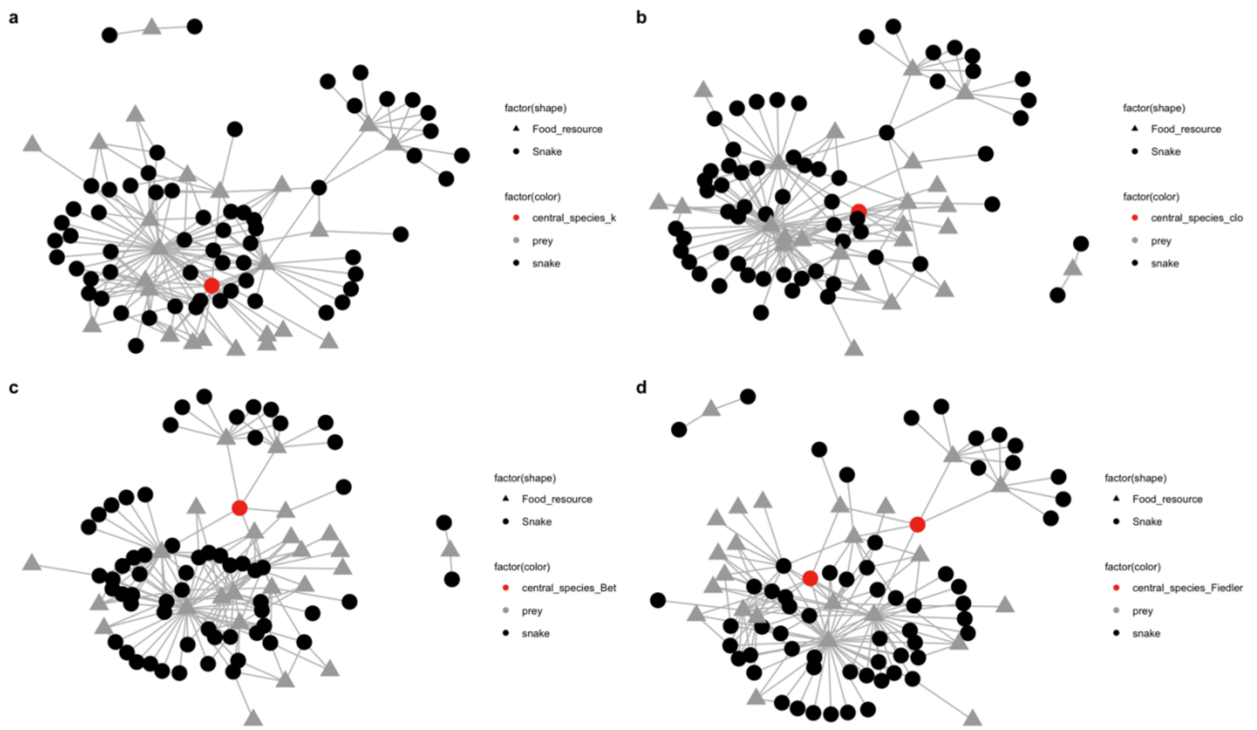


Figure 1: Graph of the snake-prey network referring to Manaus site. Circles represent snakes, triangles represent food resources, and lines represent interactions. Red circles represent the central species, indicating how different species can assume equivalent or different central roles depending on the measured centrality metric. a) Degree centrality; b) Closeness centrality; c) Betweenness centrality; and d) Fiedler centrality.

Centrality metrics can be strongly correlated (Wutchy & Stadler 2003, Sazima et al. 2010). To investigate a possible correlation between the centrality metrics used in this study and to extract independent centrality measures that incorporate the effects of the centrality measures used, we performed a principal component analysis (PCA). We use the scores associated with the main axes of PCA (here called PC1 and PC2) as two statistically independent generalized centrality indices. If PC1 and PC2 retain most of the information regarding centrality metrics, it becomes possible to relate their scores to species traits, in order to understand which biological attributes are associated with the importance of snakes in the network (Sazima et al. 2010). However, divergences in the ranking of the central role of different species can be derived from across-network variations in the ranges of the centrality values (see Estrada 2007). We circumvent this issue by standardizing all centrality measures by calculating the z-score, both within and between networks.

Ecological traits

To investigate what makes some snakes more important than others to the structure of the network, we tested the relationship between PCA scores with three snake biological attributes: body mass, lifestyle, and phylogenetic history (Appendix 1 Table S1). Body mass and lifestyle have already been associated with the structure of snake-prey interactions (see Pinto-Coelho et al. 2021, Chapter 1). Body mass is recognized as an important attribute in predator-prey networks, since, at the species level, the larger the body mass, the greater the predator's ability to consume prey of varying sizes (Sinclair et al., 2003, Woodward et al. 2005, Stouffer et al., 2011, Pinto-Coelho et al. 2021). Average body mass for each species was obtained from Feldman et al. (2016) and was log-transformed prior to analysis. The snake lifestyle, i.e., the habitat the snake uses, represents an important attribute associated with the degree of specialization in the consumption of food resources (Alencar et al. 2013, Pinto-Coelho et al. 2021). Lifestyle data were obtained directly from the databases. Since the degree of dietary conservatism may be associated with the phylogenetic history of the species, we used the snake family as a proxy for its evolutionary history (Martins et al. 2002, Colston et al. 2010, Bellini et al. 2015). The family data were obtained from Costa et al. (2021) and Uetz et al. (2022).

We performed simple linear regressions between the PCA scores and the body mass and one-way ANOVAs between the PCA scores and lifestyle, and between PCA scores and the family identity. In this way, we will be able to explore which snake species and their biological attributes are of central importance to the network structure.

Analyzing the influence of the centrality on the flow of indirect effects in the network

In order to understand how the centrality of a snake affects its contribution to the information flow in the network, we calculated the ability of each species to affect other network species through indirect interactions, hereafter T_{out_i}, following Pires et al. (2020). To do so, we first calculated the matrix T of total (direct and indirect) effects of each network (Guimarães et al. 2007). A network can be represented by adjacency matrix, A, in which both snake species i (or the resource i) is depicted by both row and column i. From A, we can calculate the dependence of each snake species *i* on each resource *j* as:

$$W_{ij} = \frac{a_{ij}}{\sum_k a_{ik}}$$

The dependence matrix W sums to 1, meaning that each row describes the relative contribution of a given resource for snake diet or the relative contribution of each snake for the consumption of a given resource. To rescale dependencies, we multiplied W by R, a diagonal matrix in which the diagonal assumed values ranging from 0.1 to 0.9: Q = RD. These values can be interpreted as different levels of snake dependence on network resources for survival as well as the resource depletion by snake consumption. Pairwise dependencies in Q correspond to direct paths (of length $m = 1$) connecting species. The strength of paths of length $m = 2$ connecting species can be obtained by computing $Q^2 = QQ$. Likewise, the strength of paths of length m by computing $Q^m = QQ$. To calculate the sum of paths of any length in a network, the matrix of total (direct and indirect) effects can be computed as $T = (I-Q)^{-1}$, where I is the identity matrix. From T, T_{out} (the ability of each snake species to affect other network nodes through indirect interactions) is the mean for each column of T corresponding to a snake species (for additional details see Pires et al. 2020). All the analyzes mentioned above were performed using R version 4.2.1 (R Core Team, 2022).

Results

The 23 analyzed networks had, on average, 45 ± 16 nodes and 81 ± 34 interactions (mean ± sd). Overall, 280 snake species and 28 categories of food resources were analyzed. The number of resources consumed by snake species (degree) ranged from one to 12. Most species (57.9%, n = 404) are specialists, consuming up to two food resources, while only 7.7% (n = 54) are super generalists, consuming at least six different resources (Appendix 1 Figure S2). The z-score of the centrality metrics for all networks ranged from -1.27 to 4.65 for degree centrality, from -0.87 to 6.7 for betweenness centrality, from -5.57 to 1.85 for closeness centrality, and from -0.95 to 7.02 for Fiedler centrality. The body mass of snakes ranged from 1.95 g (the tiny fossorial species *Epictia borapeliotes*) to 345 kg (the large constrictor *Eunectes murinus*). The snakes analyzed belong to 14 different families and are grouped into seven lifestyles (see Appendix 1 Table S1 - *Dataset*).

All centrality metrics were correlated with each other and R^2 values ranged from 0.8 to 0.22, with $p < 0.01$ in all cases (Figure S3). The strongest correlation was detected between degree and betweenness centralities. The results of the PCA analysis indicated that the two main axes together retained 80% of the variation (PC1 = 59.7% and PC2 = 20.4%). Betweenness centrality and degree centrality were more and positively associated with PC1 (loading = 0.58 and 0.57, respectively), while closeness and Fiedler centralities were more associated with PC2 (loading = 0.79 and -0.57, respectively), although in different directions: positive values indicate high scores of closeness centrality whereas negative values indicate high scores of Flider's centrality. Thus, positive values related to PC1 were more strongly associated with the number of resources consumed (degree centrality), as well as the position of intermediating interactions (betweenness centrality) (Figure 2a). On the other hand, positive values of PC2 were more related to the proximity of the species to all other nodes of the network through indirect paths (closeness centrality), while negative values indicate a greater intermediary of interactions, mainly between different sectors of the network (Fiedler centrality). PC1 scores ranged from -3.12 to 7.76, while PC2 scores ranged from -4.87 to 1.27. Despite the dispersion in the distribution of data between the PCA axes (Figure 2a), the variation between the different networks was uniform (Figure 2b), indicating the PC scores were not affected by idiosyncratic aspects of each network.

When analyzing the relationship between biological attributes and species centrality, we observed that body mass was positively correlated with PC1 ($R^2 = 0.21$; $p < 0.01$, slope = 0.9; Figure 3a) and with the PC2 ($p < 0.01$; slope = 0.24; Figure 3b), although the association with PC2 was very weak ($R^2 = 0.04$). This indicates that larger snakes generally feed on many food resources and also play the role of intermediating interactions between other nodes in the network. In contrast, size does not seem to exert a strong influence on species that are located closer to all other nodes in the network or that mediate interactions between sectors of the network. For example, the species that presented the highest closeness centrality value was *Masticophis flagelum*, a terrestrial species of the Colubridae family that weighs less than 1,5 kg, while the species that presented the highest centrality value by Fiedler was *Erythrolamprus breviceps*, a tiny terrestrial snake of the Dipsadidade family, which weighs only 45g (Table S1).

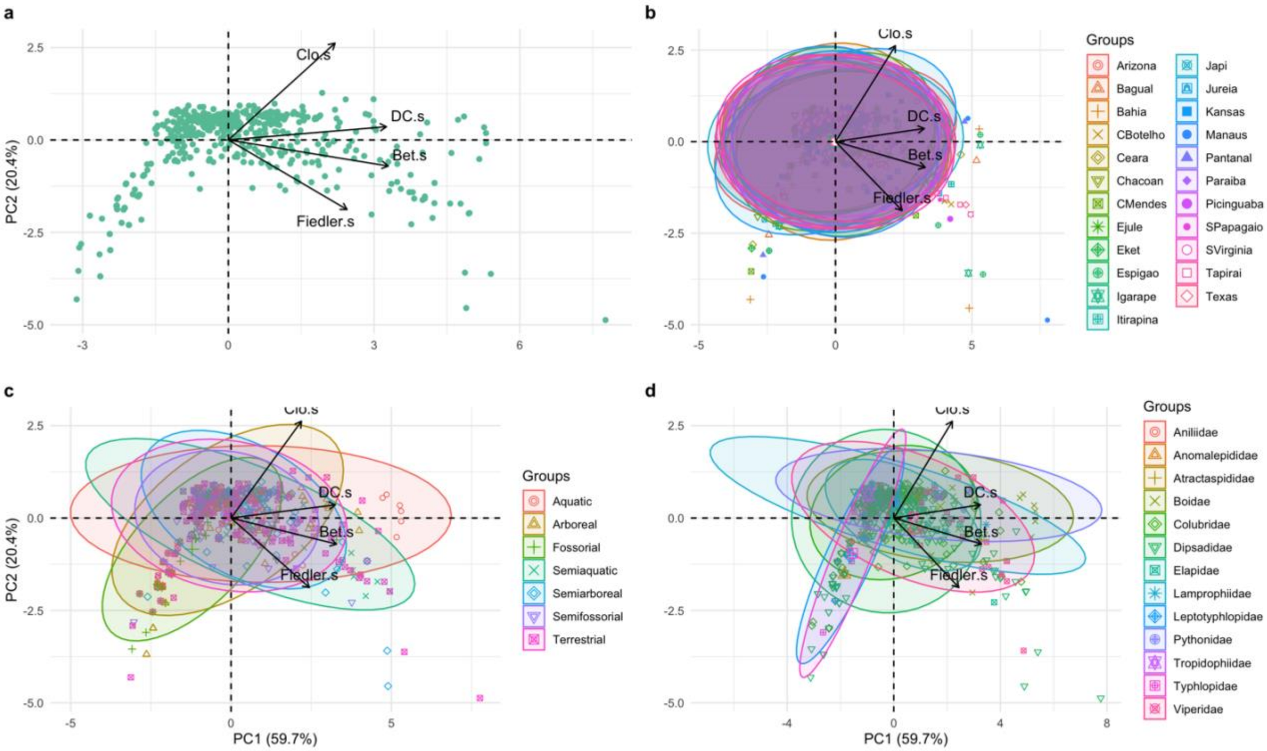


Figure 2: PCA analysis indicating: a) the association of metrics with the PC1 and PC2 axes; b) the effect of standardizing the centrality measures by calculating the z-score, indicating the PC scores were not affected by idiosyncratic aspects of each network; association between the PC1 and PC2 axes with c) lifestyle and d) snake families.

No lifestyle showed a strong association with the PCA axes ($p < 0.01$, F = 9.8, df = 6, Table S2), however, the aquatic and semi-arboreal lifestyles show a slight association with metrics related to PC1 (degree and betweenness centralities) (Figure 2c and Figure 4a). The only lifestyles that showed consistent differences were fossorial with all others ($p < 0.01$ in all cases) and terrestrial-aquatic (p = 003). The large constrictor snakes of the Boidae and Phytonidae families showed a strong association with degree centrality (Figure 5, $p < 0.01$, F = 8.93, df = 12). In fact, the aquatic Boidae *Eunectes murinus* and *E. notaeus*, presented the highest degree centrality values. The fossorial lifestyle, represented mainly by the lineage of small snakes from the families Typhlopidae, Leptotyphlopidae, and Anomalepididae, specialists in the consumption of earthworms and small insects, was negatively associated with the PC1 and PC2 axis, indicating peripheral roles in the networks (Figures 2c, 2d, 4 and 5). Finally, no lifestyle or family were strongly associated with Fiedler centrality (negative values of PC2), indicating that species with different biological attributes may be important in connecting sectors of the network.

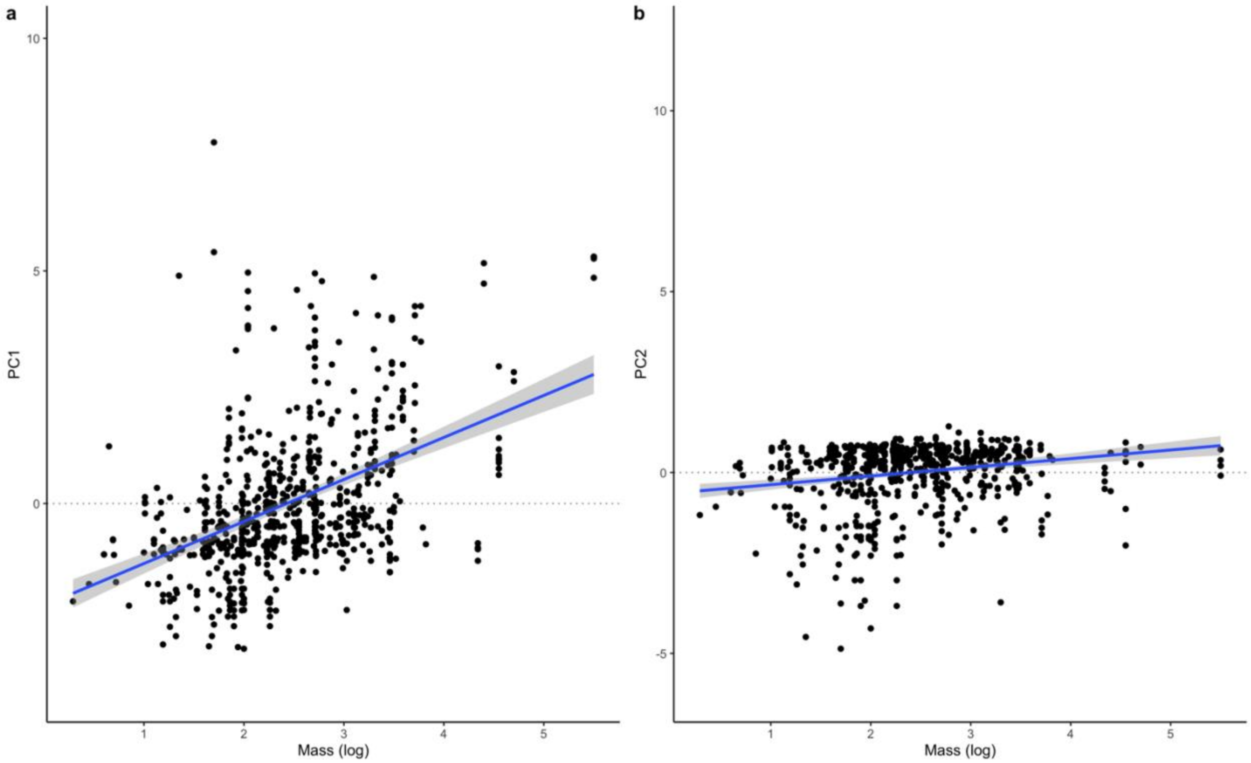


Figure 3: Positive correlation between body mass (transformed log) and a) PC1 axis ($R^2 = 0.21$; $p < 0.01$, slope = 0.9), and b) PC2 axis ($R^2 = 0.04$, $p < 0.01$; slope = 0.24). Each point represents a snake species, the blue line the direction of the relationship, and the gray band the confidence interval. To avoid overlapping, some points have been slightly shifted from their original position on the x-axis.

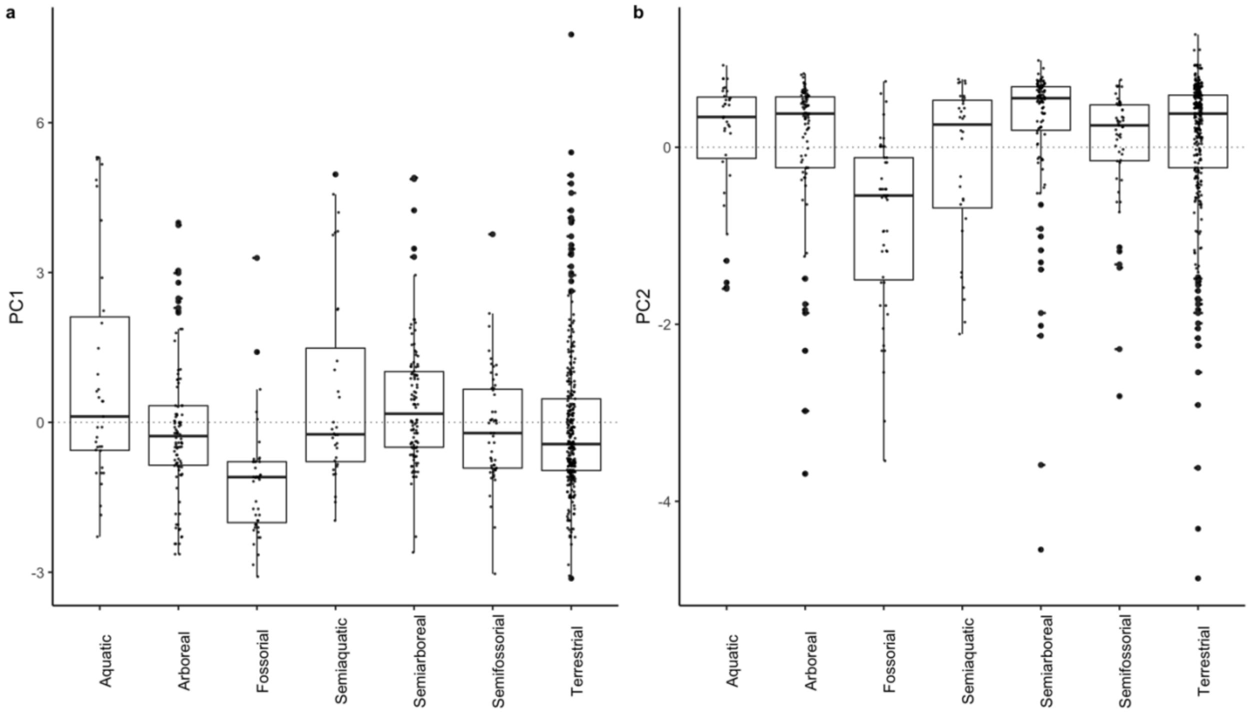


Figure 4: Boxplot representing the relationship between the snakes' lifestyle and the a) PC1 and b) PC2 axes. Each point represents a snake species; the upper and lower limits of the box are the quartiles and the black band within each box represents the median. To avoid overlapping, some points have been slightly shifted from their original position on the x-axis.

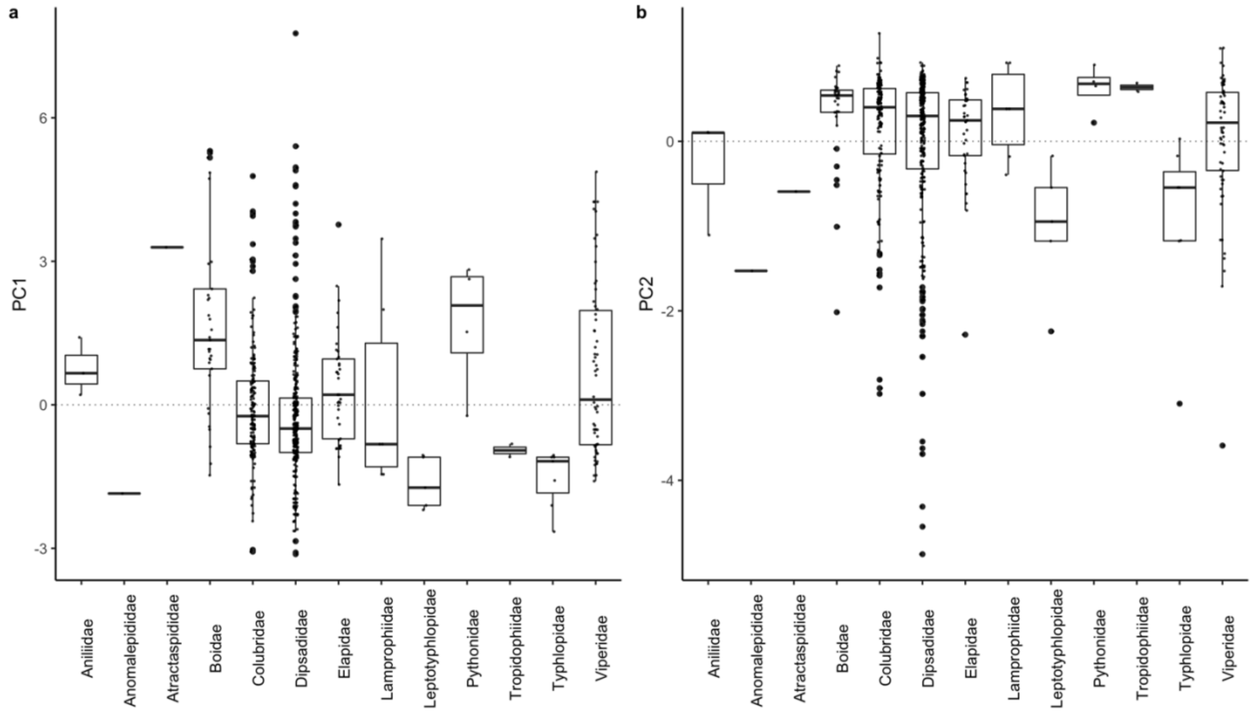


Figure 5: Boxplot representing the relationship between the snakes' Families and the a) PC1 and b) PC2 axes. Each point represents a snake species; the upper and lower limits of the box are the quartiles and the black band within each box represents the median. To avoid overlapping, some points have been slightly shifted from their original position on the x-axis.

The relationship between centrality and indirect effects indicated positive associations between all metrics (Figure 6). However, species that consume a lot of food resources ($R^2 = 0.4$; $p < 0.01$, slope = 5.37, Figure 6a) and that occupy positions of intermediary interactions between other nodes ($R^2 = 0.31$; $p < 0.01$, slope = 4.75, Figure 6b), contributed more strongly, indicating that degree and betweenness centralities better capture the transmission of indirect effects in the snake-prey networks.

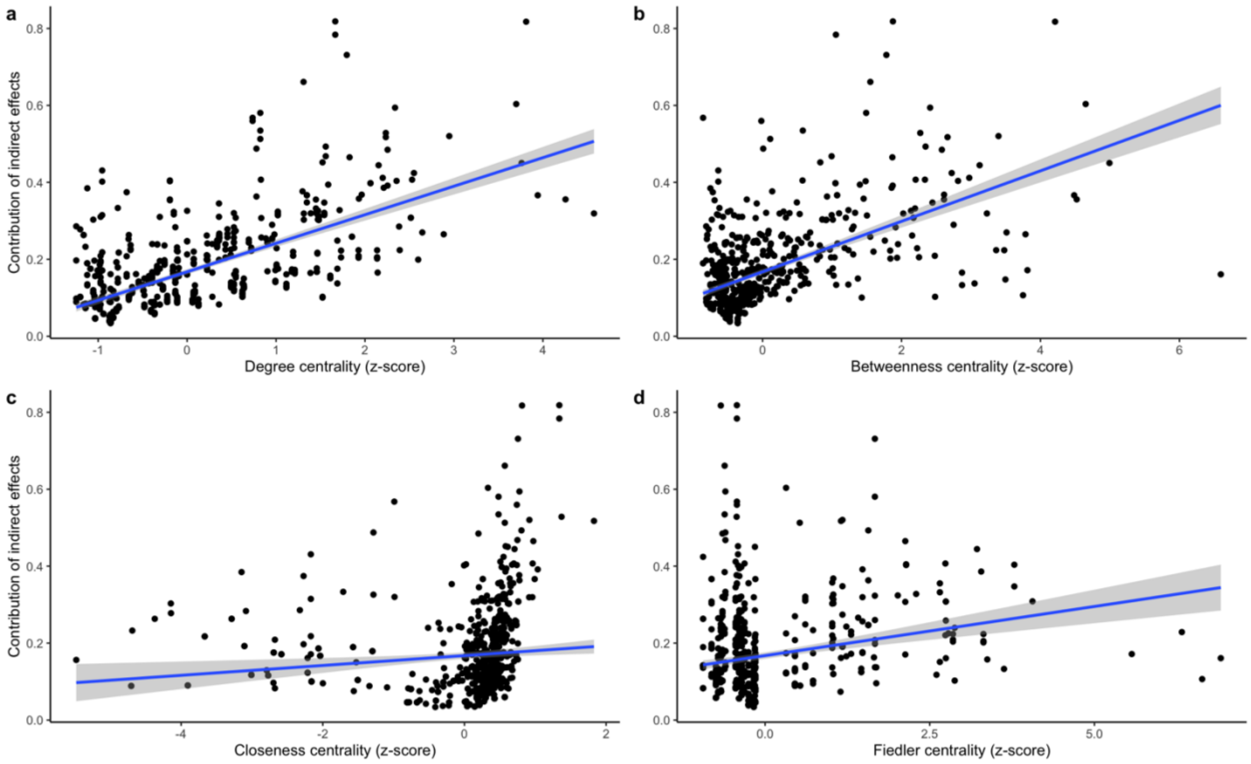


Figure 6: Positive relationship between centrality metrics and indirect effects on networks. a) Degree centrality ($R^2 = 0.4$; $p < 0.01$, slope = 5.37); b) Betweenness centrality ($R^2 = 0.31$; $p < 0.01$, slope = 4.75); c) Closeness centrality ($R^2 = 0.012$; $p = 0.003$, slope = 0.93); and d) Fiedler centrality ($R^2 = 0.05$; $p < 0.01$, slope = 1.85). Each point represents a snake species, the blue line the direction of the relationship, and the gray band the confidence interval. To avoid overlapping, some points have been slightly shifted from their original position on the x-axis.

Discussion

Our analysis showed the existence of a correlation between the four centrality metrics (degree, betweenness, closeness, and Fiedler centralities) used to infer the importance of snake species in trophic networks. The degree centrality was the metric that presented the highest correlation with the other metrics. The notion that the greater the number of interactions of a given species, the smaller its average distance from other network species, produces generally high correlations, between the degree and the other centrality metrics (Jordán et al. 2006, Estrada, 2007, Sazima et al. 2010). This pattern can be explained by the combination of a nested structure, with the presence of a giant component, both observed in snake-prey interactions (Chapter 2 of this thesis). Nested networks present a core of highly connected species that are usually close to other network species either by direct or indirect pathways (Bascompte et al. 2003, Sazima et al. 2010, Guimarães 2020). Thus, in nested networks where centrality metrics are strongly correlated, indicating that the same species can be central in different ways (Sazima et al. 2010). In this sense, our study showed that despite the correlation between all centrality metrics, the highest correlation was between degree and betweenness centralities. This indicates that snake species are central because as a result of consuming a lot of resources, these species are also central due to their position in-between many other node pairs, but not necessarily because they connect network sectors or are close to other network nodes. This result suggests that, in nested systems such as snake-prey networks, the same set of species might be strongly influential in multiple ways to ecological dynamics associated with cascading effects.

The association between the centrality metrics and the species' biological attributes indicates that the body mass of snakes is positively associated with the number of resources consumed and with their role of intermediating interactions. The positive correlation between the degree and body mass is well-known for trophic networks (Sinclair et al. 2003, Gliwicz 2008, Rezende et al. 2009, Ceron et al. 2019) including snake-prey networks (Pinto-Coelho et al. 2021). These large species with several resources, however, do not necessarily connect sectors in the network. For instance, the largest species in the Bahia network, the anaconda *Eunectes murinus*, which weighs an average of 345 kg and feeds on 12 different resources, has high values for degree, closeness, and betweenness centralities, but does not show any interactions with species in the opposite network sector. Conversely, the small *Thamnodynastes pallidus*, which weighs an average of 22.26 g and feeds on two resources, is the species with the most cross-sector interactions in the network. Therefore, despite the significant correlations between centrality metrics, the association between body mass and some centrality metrics is only limited, indicating that organisms of different sizes can occupy central roles in networks (Mello et al. 2014).

Species' lifestyles and evolutionary history have also been related to their degree of specialization in the consumption of food resources (Savitzky 1983, Martins et al. 2001, Rezende et al. 2009, Pinto-Coelho et al. 2021). Here, we found that species with aquatic or semi-arboreal lifestyles and within the families Boidae or Pythonidae consistently occupy central network roles. The Boidae and Pythonidae families belong to a lineage of large constrictor snakes, with generalist feeding habits, and which occupy a variety of macrohabitats (Luiselli et al. 1998, Pizzato et al., 2009, Henderson & Pauers, 2012, Pyron et al. 2013). This combination of characteristics - wide range of resources and habitats - could explain the high frequency with which Boidae species, especially anacondas, occupy central network roles. Large predators often act as hubs, species with a large number of interactions that connect modules in the network (Rezende et al., 2009, Pinto-Coelho et al. 2021). Connected networks favor the propagation of indirect effects (Guimarães 2020, Pires et al. 2020). Thus, species with high degree and betweenness centralities are good candidates to play key roles in the ecological dynamics of predator-prey communities.

We also found that some lineages and lifestyles did not show strong associations with any of the centrality metrics investigated. The lineages encompassing the Colubridae and Dipsadidae families are the largest (in number of species) and most ecologically diverse lineages of Neotropical snakes, with species that vary widely in body size, lifestyle, and food habits (Costa et al. 2021, Uetz et al. 2022). Approximately 80% of the species analyzed by our study belong to one of these two families, which explains the large variance observed in the data, with the consequent absence of consistent patterns for what. The fossorial lifestyle, instead, which is represented by uniform lineages of worm-like snakes, most of them with reduced vision, small sizes, and very specialized food habits (Vidal et al. 2010) showed no association with the analyzed centrality metrics. Thus, it is likely that lineages with extreme specialization may not occupy central roles in networks.

We conclude that degree and betweenness centralities represent the most relevant metrics to identify key species in snake-prey networks. Species with high centrality by degree and betweenness were more consistently associated with the lineage of large constrictor snakes. However, we also show that some species with smaller body sizes and specialist lifestyles also played key roles, such as those connecting different network sectors. The loss of highly connected species - those feeding on a diversity of prey – has profound consequences for the persistence of trophic networks (Solé & Montoya 2001, Dunne et al. 2002). However, only considering species' degrees as a measure of centrality simplifies the complexity of the analyzed communities. Additional central roles, defined by alternative metrics, may be consistently occupied by species with distinct attributes/evolutionary histories. Disregarding some of these "modes of centrality" may also disregard the importance of some species in mediating indirect effects, preventing a better understanding of the functioning of ecological systems (Estrada 2007, Pires et al. 2020). The component associated with the role of the snakes in connecting sectors in the network, as well as in being indirectly close to these groups, is not being mapped solely by the degree and betweenness centrality. The great diversity of snakes' lifestyles and evolutionary histories demonstrates that not only the large and highly-connected contribute to the structural organization and ecological dynamics of snake-prey communities. Our results also emphasize the importance of food habits and other species' biological attributes in the organization of predator-prey networks. Body size, lifestyle, and phylogenetic history showed to be important attributes to determine the centrality of snakes in ecological networks.

References

Alencar, L.R.V., Gaiarsa, M.P. & Martins, M. 2013. The evolution of diet and microhabitat use in pseudoboine snakes. South American Journal of Herpetology, 8, 60–66. https://doi.org/10.2994/SAJH-D-13-00005.1.

Alencar, L.R.V., Martins, M., Burin, G. & Quental, T.B. 2017. Arboreality constrains morphological evolution but not species diversification in vipers. Proceedings of the Royal Society B, 284, 20171775. http://dx.doi.org/10.1098/rspb.2017.1775

Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Loyola, R.D. & Ulrich, W. 2008. A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. Oikos, 117, 1227– 1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Anderson, T.K. & Sukhdeo, M.V.K. 2011. Host Centrality in Food Web Networks Determines Parasite Diversity. PLoS ONE, 6, e26798.

Arteaga, A., Salazar-Valenzuela, D., Mebert, K., Peñafiel, N., Aguiar, G., Sánchez-Nivicela, J.C., Pyron, R.A., Colston, T.J., Cisneros-Heredia, D.F., Yánez-Muñoz, M.H., Venegas, P.J., Guayasamin, J.M. & Torres-Carvajal, O. 2018. Systematics of South American snail-eating snakes (Serpentes, Dipsadini), with the description of five new species from Ecuador and Peru. ZooKeys, 766, 79–147.

Araújo, M.S., Guimarães, P.R., Svanbäck, R., Pinheiro, A., Guimarães, P., Reis, S.F.D. & Bolnick, D.I. 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. Ecology, 89, 1981-1993.

Barthélemy, M. 2004. Betweenness centrality in large complex networks. European Physical Journal B, 38, 163–168.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences of the United States of America, 100, 9383–9387.

Bellini, G.P., Giraudo, A.R., Arzamendia, V. & Etchepare, E.G. 2015. Temperate snake community in South America: is diet determined by phylogeny or ecology? PLoS One, 10, 1–15. https://doi.org/10.1371/ journal.pone.0123237

Boyero, L., Pearson, R.G., Swan, C.M., Hui, C., Albariño, R.J., Arunachalam, M., Callisto, M., Chará, J., Chará-Serna, A.M., Chauvet, E., Cornejo, A., Dudgeon, D., Encalada, A.C., Ferreira, V., Gessner, M.O., Gonçalves Jr, J.F., Graça, M.A.S., Helson, J.E., Mathooko, J.M., McKie, B.G., Moretti, M.S. & Yule, C.M. 2015. Latitudinal gradient of nestedness and its potential drivers in stream detritivores. Ecography, 38, 949-955. 10.1111/ecog.00982.

Cagua, E.F., Wootton, K.L. & Stouffer, D.B. 2019. Keystoneness, centrality, and the structural controllability of ecological networks. Journal of Ecology, 107, 1779–1790.

Campbell, J.A. & Lamar, W.W. 1989. The venomous reptiles of Latin America. Cornell University Press, Ithaca.

Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R. & Gabriel, J.P. 2004. Phylogenetic constraints and adaptation explain food-web structure. Nature, 427, 835–839.

Ceron, K., Oliveira-Santos, L.G.R., Souza, C.S., Mesquita, D.O., Caldas, F.L., Araujo, A.C. & Santana, D.J. 2019. Global patterns in anuran–prey networks: structure mediated by latitude. Oikos, 128, 1537-1548.

Ceron, K., Provete, D.B., Pires, M.M., Araujo, A.C., Blüthgen, N. & Santana, D.J. 2022. Differences in prey availability across space and time lead to interaction rewiring and reshape a predator-prey metaweb. Ecology, 103, e3716. doi.org/10.1002/ecy.3716

Cirtwill, A.R., Roslin, T., Rasmussen, C., Olesen, J.M. & Stouffer, D.B. 2018. Between-year changes in community composition shape species' roles in an Arctic plant-pollinator network. Oikos, 127, 1163–1176. doi: 10.1111/oik.05074

Clarke, K.R. & Warwick, R.M. 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology, 35, 523–531.

Cohen, J.E. 1977. Food webs and niche space. Princeton University Press, Princeton.

Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldaña, J. 1993. Body sizes of animal predators and animal prey in food webs. Journal of Animal Ecology, 62, 67-78.

Colston, T.J., Costa, G.C. & Vitt, L. J. 2010. Snake diets and the deep history hypothesis. Biological Journal of the Linnean Society, 101, 476– 486. https://doi.org/10.1111/j.1095-8312.2010.01502.x

Cundall, D. & Greene, H.W. 2000. Feeding in snakes. In *Feeding: form, function, and evolution in tetrapod vertebrates*, ed. Schwenk, K., pp. 293-333. Academic Press, New York.

Dalsgaard, B., Trøjelsgaard, K., Martín González, A.M., Nogués-Bravo, D., Ollerton, J., Petanidou, T., Sandel, B., Schleuning, M., Wang, Z., Rahbek, C., Sutherland, W.J., Svenning, J.-C. & Olesen, J. M. 2013. Historical climate-change influences modularity and nestedness of pollination networks. Ecography, 36, 1331-1340.

de Araújo, W.S. 2016. Global patterns in the structure and robusteness of plant-herbivore networks. Frontiers of Biogeography, 8, e31053.

Delmas, E., Besson, M., Brice, M.H., Burkle, L.A., Dalla Riva, G.V., Fortin, M.J., Gravel, D., Guimarães, P.R., Hembry, D.H., Newman, E.A., Pires, M.M., Yeakel, J.D. & Poisot, T. 2018. Analysing ecological networks of species interactions. Biological Reviews, 94, 16-36.

Donohue, I., Petchey, O.L., Kéfi, S., Génin, A., Jackson, A.L., Yang, Q. & O'Connor, N.E. 2017. Loss of predator species, not intermediate consumers, triggers rapid and dramatic extinction cascades. Global Change Biology, 23, 2962-2972.

Dudcsak, A.C., de la Torre, G.M., Euclydes, L., Campião, K.M. 2021. The roles of anurans in antagonistic networks are explained by life-habit and body-size. Integrative Zoology, 17, 530-542.

Dunne J.A., Williams R.J. & Martinez N.D. 2002. Food-web structure and network theory: the role of connectance and size. Proceedings of the National Academy of Sciences, 99, 12917-12922. doi.org/10.1073/pnas.1924076

Dupont, Y.L. & Olesen, J.M. 2009. Ecological modules and roles of species in heathland plant–insect flower visitor networks. Journal of Animal Ecology, 78, 346–353.

Estes, J.A. & Palmisano, J.F. 1974. Sea otters: their role in structuring nearshore communities. Science, 185, 1058–1060.

Estrada, E. 2007. Characterization of topological keystone species local, global and ‘‘meso-scale’’ centralities in food webs. Ecological Complexity, 4, 48–57.

Feldman, A., Sabath, N., Pyron, R., Mayrose, I. & Meiri, S. 2016. Body sizes and diversification rates of lizards, snakes, amphisbaenians, and the tuatara. Global Ecology and Biogeography, 25, 187–197.

Fiedler, M. 1975. A property of eigenvectors of nonnegative symmetric matrices and its application to graph theory. Czechoslovak Mathematical Journal, 25, 619–633.

Fontaine, C., Guimarães, P.R., Kéfi, S., Loeuille, N., Memmott, J.J., van der Putten, W.H., van Veen, F.J.F. & Thébault, E. 2011. The ecological and evolutionary implications of merging different types of networks. Ecology Letters, 14, 1170–1181. https://doi.org/10.1111/j.1461-0248.2011.

Fontaine, C. & Thébault, E. 2015. Comparing the conservatism of ecological interactions in plant-pollinator and plant-herbivore networks. Population Ecology, 57, 29–36.

Freeman, L.C. 1977. A set of measures of centrality based on betweenness. Sociometry, 40, 35.

Freeman, L.C., Roeder, D. & Mulholland, R.R. 1979. Centrality in social networks: ii. experimental results. Social Networks, 2, 119–141.

Galetti, M., Guevara, R., Côrtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labecca, F., Ribeiro, T., Carvalho, C.S., Collevatti, R.G., Pires, M.M., Guimarães, P.R., Brancalion, P.H., Ribeiro, M.C. & Jordano, P. 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. Science, 340, 1086-1090.

Gliwicz, J. 2008. Body size relationships between avian predators and their rodent prey in a North-American sagebrush community. Acta Ornithologica, 43, 151–158. https://doi.org/10.3161/000164508X 395261.

González, A.M.M., Dalsgaard, B. & Olesen, J.M. 2010. Centrality measures and the importance of generalist species in pollination networks. Ecological Complexity, 7, 36–43.

Greene, H.W. 1983. Dietary correlates of the origin and radiation of snakes. American Zoologist, 23, 431-441.

Greene, H.W. 2001. Snakes: the evolution of mystery in nature. University of California Press, Berkeley.

Guimarães, P.R., Jordano, P. & Thompson, J.N. 2011. Evolution and coevolution in mutualistic networks. Ecology Letters, 14, 877–885.

Guimarães, P.R. 2020. The structure of ecological networks across levels of organization. Annual Review of Ecology, Evolution, and Systematics, 51, 433–460.

Guimerà, R. & Nunes Amaral, L.A. 2005. Functional cartography of complex metabolic networks. Nature, 433, 895–900. https://doi. org/10.1038/nature03288.

Hembry, D.H., Raimundo, R.L.G., Newman, E.A., Atkinson, L., Guo, C., Guimarães P.R. & Gillespie, R.G. 2018. Does biological intimacy shape ecological network structure? A test using a brood pollination mutualism on continental and oceanic islands. Journal of Animal Ecology, 87, 1160-1171. doi: 10.1111/1365-2656.12841.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, CF., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren P.H. & Woodward, G. 2009. Ecological networks – beyond food webs. Journal of Animal Ecology, 78, 253–269.

Jordán, F., Liu, W.C. & Davis, A.J. 2006. Topological keystone species: measures of positional importance in food webs. Oikos, 112, 535–546.

Lewinsohn, T.M., Prado, P.I., Jordano, P. & Bascompte, J. 2006. Structure in plant-animal interaction assemblages. Oikos, 113, 174–184.

Luiselli, L., Akani, G.C. & Capizzi, D. 1998a. Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria. Journal of Zoology, 246, 125-133.

MacArthur, R.H. 1969. Patterns of communities in the tropics. Biological Journal of the Linnean Society, 1, 19–30.

Machado-Filho, P.R., Duarte, M.R., Carmo, L.F. & Franco, F. 2011. New record of *Corallus cropanii* (Boidae, Boinae): a rare snake from the Vale do Ribeira, State of São Paulo, Brazil. Salamandra, 47, 112-115.

Mariania, M.S., Renc, Z.M., Bascompte, J. & Tessone, C.J. 2019. Nestedness in complex networks: observation, emergence, and implications. Physics Reports, 813, 1-90.

Marquitti, F.M.D., Guimarães, P.R., Pires, M.M. & Bittencourt, L.F. 2014. MODULAR: Software for the autonomous computation of modularity in large network sets. Ecography, 37, 221–224. doi.org/10.1111/j.1600-0587.2013.00506.x

Martín González, A.M., Daalsgard, B. & Olesen, J.M. 2009. Centrality measures and the importance of generalist species in pollination networks. Ecological Complexity, 7, 36-43. doi:10.1016/j.ecocom.2009.03.008.

Martins, M. & Oliveira, M.E. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. Herpetological Natural History, 6, 78–150.

Martins, M., Marques, O.A. & Sazima, I. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers (Genus *Bothrops*). In *Biology of the vipers*, ed. Schuett, G.W., pp. 307–328. Eagle Mountain Publishing, USA.

Mello, M.A.R., Rodrigues, F.A., Costa, L.F., Kissling, W.D., Şekercioğlu, Ç.H., Marquitti F.M.D. & Kalko, E.K.V. 2014. Keystone species in seed dispersal networks are mainly determined by dietary specialization. Oikos, 124, 1031–1039, doi: 10.1111/oik.01613.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A., McCain, C.M., McCune, A.R., McDade, L.A., McPeek, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M. & Turelli, M. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters, 10, 315–331.

Morris, R.J., Gripenberg, S., Lewis, O.T. & Roslin T. 2014. Antagonistic interaction networks are structured independently of latitude and host guild. Ecology Letters, 17, 340–349.

Newman, M.E.J. 2003. The structure and function of complex networks. SIAM Review, 45, 167–256.

Ollerton, J. 2006. "Biological barter": patterns of specialization compared across different mutualisms. In *Plant–Pollinator Interactions: From Specialization to Generalization*, eds. Waser, N.M. & Ollerton, J., pp. 411–35. University Chicago Press, Chicago.

Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. 2007. The modularity of pollination networks. Proceedings of the National Academy of Sciences, 104, 19891–19896.

Palacio, R.D., Valderrama-Ardila, C. & Kattan, G.H. 2016. Generalist species have a central role in a highly diverse plant–frugivore network. Biotropica, 48, 349–355. 10.1111/btp.12290.

Pellissier, L., Albouy, G., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M.A., Melián, C.J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N.E. & Gravel, D. 2018. Comparing species interaction networks along environmental gradients. Biological Reviews, 93, 785–800.

Pimm, S.L. 2002. Food webs. University of Chicago Press, Chicago.

Pinheiro, R.B.P., Felix, G.M.F., Dormann, C.F. & Mello, M.A.R. 2019. A new model explaining the origin of different topologies in interaction networks. Ecology, 100, e02796. https://doi.org/10.1002/ecy.2796

Pinto-Coelho, D., Martins, M., Guimarães, P. R. 2021. Network analyses reveal the role of large snakes in connecting feeding guilds in a species-rich Amazonian snake community. Ecology and Evolution, 11, 6558-6568.

Pires, M.M. & Guimarães, P.R. 2013. Interaction intimacy organizes networks of antagonistic interactions in different ways. Journal of the Royal Society Interface 10, 20120649.

Pires, M.M., Guimarães, P.R., Araújo, M.S., Giaretta, A.A., Costa, J.C.L. & dos Reis, S.F. 2011. The nested assembly of individual-resource networks. Journal of Animal Ecology, 80, 896–903.

Pires, M.M., O'Donnell. J.L., Burkle, L.A., Díaz-Castelazo, C., Hembry, D.H., Yeakel, J.D., Newman, E.A., Medeiros, L.P., de Aguiar, M.A.M. & Guimarães, P.R. 2020. The indirect paths to cascading effects of extinctions in mutualistic networks. Ecology, 101, e03080. doi: 10.1002/ecy.3080.

Pizzatto, L., Marques, O.A.V. & Facure, K. 2009. Food habits of Brazilian boid snakes: overview and new data, with special reference to *Corallus hortulanus*. Amphibia-Reptilia, 30, 533-544.

Pizzatto, L., Oliveira, J.L., Marques, O.A.V. & Martins, M. 2018. Body shape and food habits of South American goo-eater snakes of the genus *Sibynomorphus*. South American Journal of Herpetology, 13, 300–307.

Poisot, T., Stouffer, D.B. & Kéfi, S. 2016. Describe, understand and predict: why do we need networks in ecology? Functional Ecology, 30, 1878–1882.

Prado, P.I. & Lewinsohn, T.M. 2004. Compartments in insect-plant associations and their consequences for community structure. Journal of Animal Ecology, 73, 1168–1178.

Pringle, R.M. & Hutchinson, M.C. 2020. Resolving food-web structure. Annual Review of Ecology, Evolution and Systematics, 51, 55–80.

R Core Team 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-proje ct.org/

Rezende, E.L., Lavabre, J.E., Jordano, P. & Bascompte, J. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. Nature, 448, 925–928.

Rezende, E.L., Albert, E.M., Fortuna, M.A. & Bascompte, J. 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. Ecology Letters, 12, 779–788.

Rosseel, Y. 2012. lavaan: An R package for structural equation modeling. Journal of Statistical Software, 48, 1–36. https://www.jstatsoft.org/v48/i02/

Sazima, C., Guimarães, P.R., Reis, S.F. & Sazima, I. 2010. What makes a species central in a cleaning mutualism network? Oikos, 119, 1319–1325.

Schmitz, O.J. & Beckerman, A.P. 2007. Food webs. Encyclopedia of Life Sciences, John Wiley & Sons.

Schemske, D.W. 2009a. Biotic interactions and speciation in the tropics. In *Speciation and Patterns of Diversity*, eds. Butlin, R.K., Bridle, J.R., Schluter, D., pp. 219–39. Cambridge Univ. Press, Cambridge.

Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. 2009b. Is there a latitudinal gradient in the importance of biotic interactions? Annual Review in Ecology, Evolution and Systematics, 40, 245–269.

Schleuning, M., Fründ, J., Klein, A.M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G.K.S., Bazarian, S., Bohning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D.M., Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C.N., Kreft, H., Morris, R.J., Sandel, B., Sutherland, W.J., Svenning, J.-C., Tscharntke, T., Watts, S., Weiner, C.N., Werner, M., Williams, N.W., Winqvist, C., Dormann, C.F. & Bluthgen, N. 2012. Specialization of mutualistic interaction networks decreases toward tropical latitudes. Current Biology, 22, 1925–1931.

Sebastián-González, E., Morales-Reyes, Z., Botella, F., Naves-Alegre, L., Pérez-García, J.M., Mateo-Tomás, P., Olea, P.P., Moleón, M., Barbosa, J.M., Hiraldo, F., Arrondo, E., Donázar, J.A., Cortés-Avizanda, A., Selva, N., Lambertucci, S.A., Bhattacharjee, A., Brewer, A., Anadón, J.D., Abernethy, E., Rhodes, O.E., Turner, K., Beasley, J.C., DeVault, T.L., Ordiz, A., Wikenros, C., Zimmermann, B., Wabakken, P., Wilmers, C.C., Smith, J.A., Kendall, C.J., Ogada, D., Buechley, E.R., Frehner, E., Allen, M.L. Wittmer, H.U., Butler, J.R.A., du Toit, J.T., Read, J., Wilson, D., Jerina, K., Krofel, M., Kostecke, R., Inger, R., Samson, A., Naves-Alegre, L. & Sánchez-Zapata, J.A. 2020. Network structure of vertebrate scavenger assemblages at the global scale: drivers and ecosystem functioning implications. Ecography, 43, 1143-55.

Secor, S.M. & Diamond, J.M. 2000. Evolution of regulatory responses to feeding in snakes. Physiological and Biochemical Zoology, 73, 123–141.

Shi, J. & Malick, J. 2000. Normalized cuts and image segmentation, IEEE. Transactions on Pattern Analysis and Machine Intelligence, 22, 888-905.

Shipley, B. 2000. Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge.

Sinclair, A.R.E., Mduma, S. & Brashares, J.S. 2003. Patterns of predation in a diverse predator-prey system. Nature, 425, 288-290.

Spiesman, B.J. & Inouye, B.D. 2013. Habitat loss alters the architecture of plant-pollinator interaction networks. Ecology, 94, 2688–2696.

Solé, R.V., Montoya, J.M., 2001. Complexity and fragility in ecological networks. Proceedings of the Royal Society B, 268, 2039–2045.

Stouffer, D.B., Rezende, E.L. & Amaral, L.A.N. 2011. The role of body mass in diet contiguity and food-web structure. Journal of Animal Ecology, 80, 632–639.

Thébault, E. & Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science, 329, 853–856.

Thompson, J.N. 2005. The geographic mosaic of coevolution. University of Chicago Press, Chicago.

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. 2010. Conservation of species interaction networks. Biological Conservation, 143, 2270–2279. https://doi.org/10.1016/j.biocon.2009.12.004

Uetz, P., Freed, P, Aguilar, R. & Hošek, J. (eds.). 2022. The Reptile Database, http://www.reptile-database.org, accessed [April 27, 2022].

Ulrich, W., Almeida-Neto, M. & Gotelli, N.J. 2009. A consumer's guide to nestedness analysis. Oikos, 118, 3-17.

Valverde, S., Vidiella, B., Montañez, R., Fraile, A., Sacristán, S. & García-Arenal, F. 2020. Coexistence of nestedness and modularity in host-pathogen infection networks. Nature Ecology and Evolution, 4, 568-577.

Vieira-Alencar, J.P.S., Furtado, L.O., Felicio, G.R., Pinto-Coelho, D. & Carmignotto, A.P. 2022. First predation record on the invasive lagomorph *Lepus europaeus* (Leporidae) by *Boa constrictor* (Boidae) in a southern Brazilian cerrado protected area. Revista Latinoamericana de Herpetología, 5. doi.org/10.22201/fc.25942158e.2022.2.318

Zanata, T.B. Dalsgaard, B.O., Passos, F.C., Cotton, P.A., Roper, J.J., Maruyama, P.K., Fischer, E., Schleuning, M., Martín González, A.M., Vizentin-Bugoni, J., Franklin, D.C., Abrahamczyk, S., Alárcon, R., Araujo, A.C., Araújo, F.P., Azevedo-Junior, S.M., Baquero, A.C., Böhning-Gaese, K., Carstensen, D.W., Chupil, H., Coelho, A.G., Faria, R.R., Hořák, D., Ingversen, T.T., Janeček, S., Kohler, G., Lara, C., Las-Casas, F.M.G., Lopes, A.V., Machado, A.O., Machado, C.G., Machado, I.C., Maglianesi, M.A., Malucelli, T.S., Mohd-Azlan, J., Moura, A.C., Oliveira, G.M., Oliveira, P.E., Ornelas, J.F., Riegert, J., Rodrigues, L.C., Rosero-Lasprilla, L., Rui, A.M., Sazima, M., Schmid, B., Sedláček, O., Timmermann, A., Vollstädt, M.G.R, Wang, Z., Watts, S., Rahbek, C. & Varassin, I.G. 2017. Global patterns of interaction specialization in bird–flower networks. Journal of Biogeography, 44, 1891–1910.

Wutchy, S. & Stadler, P.F. 2003. Centers of complex networks. Journal of Theoretical Biology, 223, 45–53.

Wallach, V., Williams, K.L. & Boundy, J. 2014. Snakes of the world. A catalogue of living and extinct species. CRC Press, New York.

Webb, C.O., Ackerly, D., McPeek, M. & Donoghue, M. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics, 33, 475–505.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J., Olesen, J., Valido, A. & Warren, P. 2005. Body size in ecological networks. Trends in Ecology & Evolution, 20, 402–409. https://doi.org/10.1016/j.

Wright, S.L. 1934. Annals of Mathematical Statistics 5, 161.

Yanosky, A.A., Dixon, J.R. & Mercolli, C. 1996. Ecology of the snakes community at El Bagual Ecological Reserve, Northeastern Argentina. Herpetological Natural History, 4, 97-110.

Appendix 1

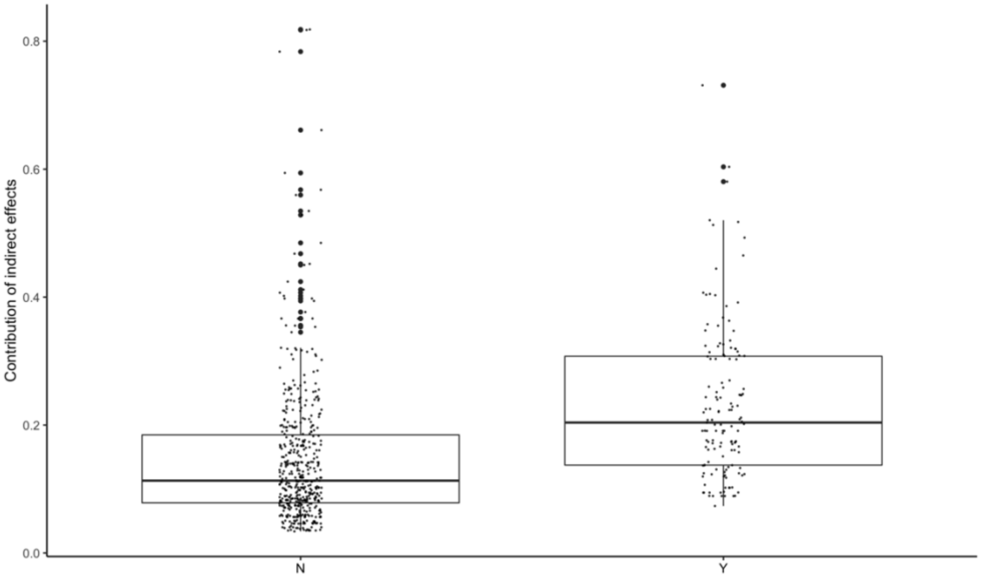


Figure S1: The contribution of central species by Fiedler to the transmission of indirect effects in the network indicated consistent differences between interconnecting and not interconnecting sectors of the network.

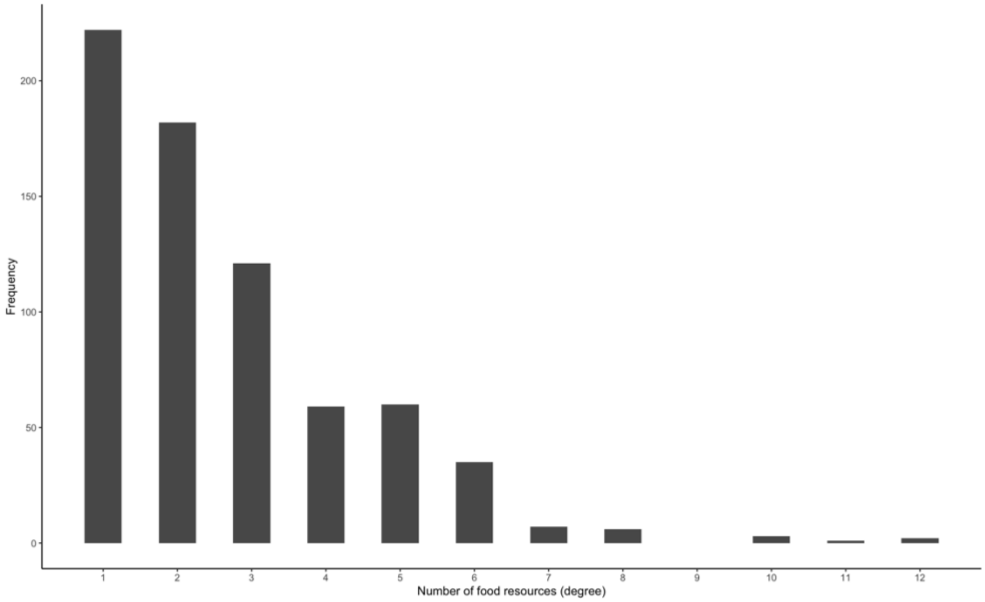


Figure S2: Degree histogram indicating the relationship between the frequency of the number of resources consumed by snake species (degree) in all networks analyzed in this study.

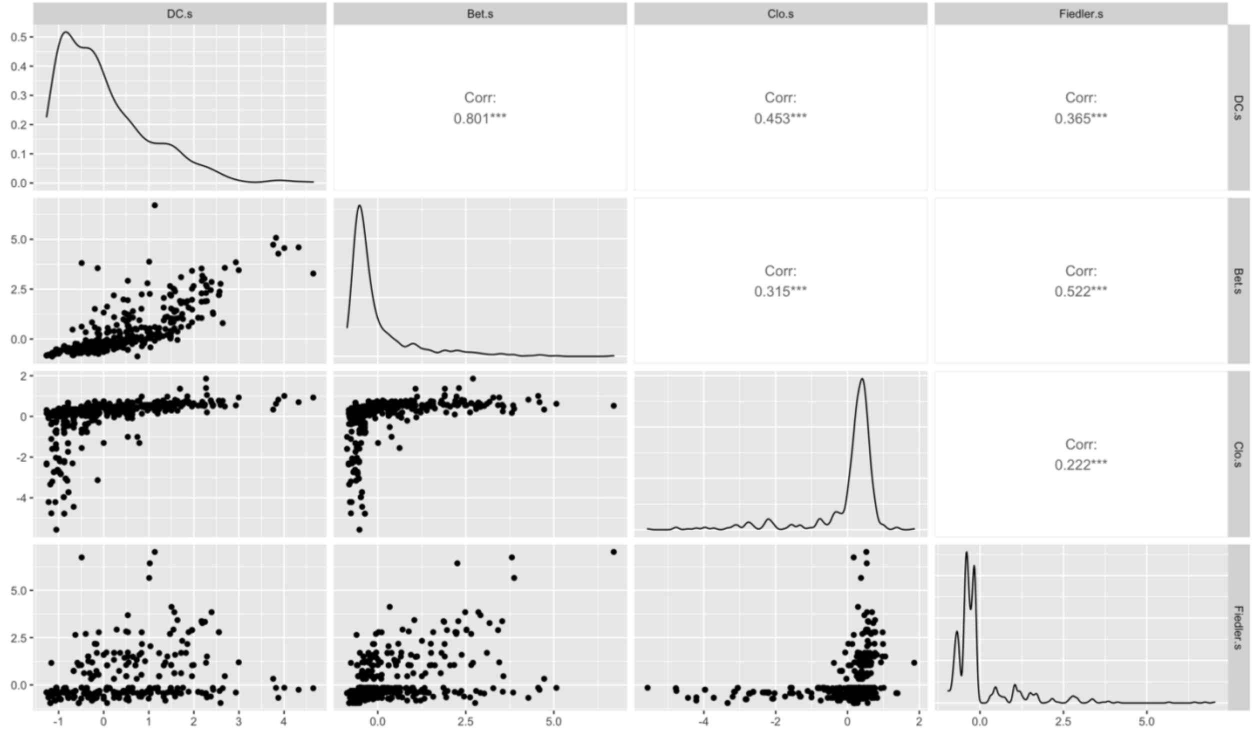


Figure S3: Correlations indicating positive associations between all centrality metrics used in this study. DC.s = degree centrality, Bet.s = betweenness centrality, Clo.s = closeness centrality, and Fiedler.s = Fiedler centrality. Metric values were weighted by calculating the z-score. Asterisks indicate $p < 0.01$.

Table S1: Dataset indicating the network code, snake species, degree (k), values standardized by the z-score of the centrality metrics used in this study (degree (DC.s), betweenness (Bet.s), closeness (Clo .s), and Fiedler), the logarithmized body mass, the lifestyle, the family to which the snake belongs and the values of scores referring to the two main axes of PCA (PC1 and PC2).

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Arizona	*Arizona elegans*	4	0.368	-0.383	0.437	-0.439	2.700	Semiarboreal	Colubridae	-0.031	-0.714
Arizona	*Crotalus atrox*	3	-0.108	-0.542	0.123	-0.439	3.790	Terrestrial	Viperidae	-0.517	-0.450
Arizona	*Crotalus cerastes*	4	0.368	-0.383	0.437	-0.439	2.500	Terrestrial	Viperidae	-0.031	-0.714
Arizona	*Crotalus mitchellii*	3	-0.108	-0.542	0.123	-0.439	3.110	Terrestrial	Viperidae	-0.517	-0.450
Arizona	*Crotalus molossus*	3	-0.108	-0.542	0.123	-0.439	3.110	Terrestrial	Viperidae	-0.517	-0.450
Arizona	*Crotalus scutulatus*	3	-0.108	-0.509	-0.301	-0.439	3.140	Terrestrial	Viperidae	-0.663	-0.108
Arizona	*Diadophis punctatus*	3	-0.108	0.110	0.609	2.781	2.070	Semifossorial	Dipsadidae	1.434	1.130
Arizona	*Hypsiglena torquata*	1	-1.059	-0.592	-0.301	-0.439	1.770	Terrestrial	Viperidae	-1.256	-0.023
Arizona	*Lampropeltis getula*	8	2.270	2.306	1.393	-0.439	2.880	Terrestrial	Viperidae	2.989	-1.102
Arizona	*Masticophis bilineatus*	6	1.319	0.141	0.786	-0.439	2.650	Semiarboreal	Colubridae	0.953	-0.981
Arizona	*Masticophis flagellum*	8	2.270	2.705	1.858	1.171	3.120	Terrestrial	Viperidae	4.093	-0.472
Arizona	*Micruroides euryxanthus*	1	-1.059	-0.592	-1.363	-0.439	1.970	Terrestrial	Elapidae	-1.667	0.815
Arizona	*Phyllorhynchus decurtatus*	1	-1.059	-0.592	-2.031	-0.439	1.330	Terrestrial	Colubridae	-1.925	1.342
Arizona	*Pituophis melanoleucus*	1	-1.059	-0.542	0.123	-0.439	2.980	Terrestrial	Colubridae	-1.063	-0.347
Arizona	*Rena humilis*	1	-1.059	-0.592	-1.530	-0.439	1.040	Fossorial	Leptotyphlopidae	-1.732	0.947
Arizona	*Rhinocheilus lecontei*	4	0.368	0.080	0.609	-0.439	2.530	Terrestrial	Colubridae	0.304	-0.752
Arizona	*Salvadora hexalepis*	4	0.368	-0.010	0.437	-0.439	2.220	Terrestrial	Colubridae	0.185	-0.635
Arizona	*Sonora occipitalis*	1	-1.059	-0.592	-1.530	-0.439	1.140	Fossorial	Colubridae	-1.732	0.947
Arizona	*Sonora semiannulata*	2	-0.584	-0.249	0.275	1.171	1.260	Terrestrial	Colubridae	0.132	0.456
Arizona	*Tantilla atriceps*	1	-1.059	-0.592	-1.530	-0.439	0.450	Terrestrial	Colubridae	-1.732	0.947
Arizona	*Thamnophis cyrtopsis*	5	0.843	2.239	0.978	2.781	2.650	Terrestrial	Colubridae	3.357	1.189
Arizona	*Trimorphodon lambda*	4	0.368	-0.330	0.275	-0.439	2.220	Terrestrial	Colubridae	-0.063	-0.576
Bagual	*Amerotyphlops brongersmianus*	1	-0.781	-0.447	-0.465	-0.680	1.260	Fossorial	Typhlopidae	-1.180	-0.029
Bagual	*Atractus reticulatus*	1	-0.781	-0.447	-3.726	-0.680	1.320	Fossorial	Dipsadidae	-2.442	2.543
Bagual	*Bothrops alternatus*	3	0.228	-0.216	0.338	1.327	3.380	Terrestrial	Viperidae	0.707	0.415
Bagual	*Bothrops neuwiedi*	2	-0.277	-0.331	0.311	0.324	2.720	Terrestrial	Viperidae	-0.091	-0.103
Bagual	*Chironius quadricarinatus*	2	-0.277	-0.325	0.377	-0.680	2.270	Semiarboreal	Colubridae	-0.494	-0.722
Bagual	*Clelia clelia*	2	-0.277	-0.421	-0.031	0.324	3.240	Terrestrial	Dipsadidae	-0.275	0.148
Bagual	*Dipsas turgida*	1	-0.781	-0.447	-3.726	-0.680	1.680	Terrestrial	Dipsadidae	-2.442	2.543
Bagual	*Erythrolamprus almadensis*	1	-0.781	-0.447	0.114	-0.680	1.770	Terrestrial	Dipsadidae	-0.956	-0.486
Bagual	*Erythrolamprus jaegerii*	2	-0.277	-0.125	0.180	-0.680	1.800	Semiaquatic	Dipsadidae	-0.454	-0.524
Bagual	*Erythrolamprus miliaris*	3	0.228	0.005	0.417	-0.680	2.040	Semiaquatic	Dipsadidae	0.003	-0.737
Bagual	*Erythrolamprus poecilogyrus*	4	0.732	0.009	0.443	1.327	1.830	Terrestrial	Dipsadidae	1.167	0.325

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Bagual	*Eunectes notaeus*	10	3.760	4.726	0.338	0.324	4.400	Aquatic	Boidae	5.167	0.516
Bagual	*Helicops leopardinus*	2	-0.277	-0.278	0.154	-0.680	1.990	Aquatic	Dipsadidae	-0.553	-0.535
Bagual	*Hydrodynastes gigas*	7	2.246	1.887	0.588	3.334	3.340	Aquatic	Colubridae	4.044	1.584
Bagual	*Leptodeira annulata*	1	-0.781	-0.447	0.114	-0.680	2.960	Arboreal	Dipsadidae	-0.956	-0.486
Bagual	*Leptophis ahaetulla*	2	-0.277	-0.325	0.377	-0.680	2.960	Arboreal	Colubridae	-0.494	-0.722
Bagual	*Lygophis dilepis*	1	-0.781	-0.447	0.114	-0.680	1.650	Terrestrial	Dipsadidae	-0.956	-0.486
Bagual	*Lygophis flavifrenatus*	2	-0.277	-0.343	0.311	0.324	1.920	Terrestrial	Dipsadidae	-0.098	-0.105
Bagual	*Micrurus frontalis*	2	-0.277	-0.421	-0.031	0.324	2.770	Semifossorial	Elapidae	-0.275	0.148
Bagual	*Mussurana bicolor*	3	0.228	-0.109	0.417	0.324	2.250	Terrestrial	Dipsadidae	0.368	-0.193
Bagual	*Oxyrhopus guibei*	2	-0.277	-0.325	0.377	-0.680	2.550	Terrestrial	Dipsadidae	-0.494	-0.722
Bagual	*Oxyrhopus rhombifer*	2	-0.277	-0.325	0.377	-0.680	2.110	Terrestrial	Dipsadidae	-0.494	-0.722
Bagual	*Palusophis bifossatus*	4	0.732	0.100	0.377	0.324	2.650	Terrestrial	Colubridae	0.763	-0.172
Bagual	*Paraphimophis rusticus*	3	0.228	-0.109	0.417	0.324	3.150	Terrestrial	Dipsadidae	0.368	-0.193
Bagual	*Philodryas aestiva*	2	-0.277	-0.325	0.377	-0.680	2.230	Semiarboreal	Dipsadidae	-0.494	-0.722
Bagual	*Philodryas olfersii*	4	0.732	0.470	0.443	1.327	2.660	Semiarboreal	Dipsadidae	1.435	0.423
Bagual	*Philodryas patagoniensis*	6	1.742	1.256	0.561	2.330	2.710	Terrestrial	Dipsadidae	2.947	0.957
Bagual	*Phimophis guerini*	1	-0.781	-0.447	0.114	-0.680	2.510	Terrestrial	Dipsadidae	-0.956	-0.486
Bagual	*Psomophis obtusus*	1	-0.781	-0.447	0.114	-0.680	1.360	Terrestrial	Dipsadidae	-0.956	-0.486
Bagual	*Taeniophallus occipitalis*	1	-0.781	-0.447	0.114	-0.680	1.610	Semifossorial	Dipsadidae	-0.956	-0.486
Bagual	*Xenodon merremii*	1	-0.781	-0.447	0.114	-0.680	2.230	Terrestrial	Dipsadidae	-0.956	-0.486
Bahia	*Amerotyphlops brongersmianus*	1	-1.050	-0.520	-1.588	-0.150	1.260	Fossorial	Typhlopidae	-1.582	1.170
Bahia	*Boa constrictor*	5	1.197	0.133	0.136	-0.150	4.550	Semiarboreal	Boidae	0.752	-0.293
Bahia	*Bothrops leucurus*	3	0.073	-0.240	0.545	-0.150	3.560	Semiarboreal	Viperidae	0.049	-0.574
Bahia	*Chironius bicarinatus*	2	-0.489	-0.472	0.314	-0.150	2.720	Semiarboreal	Colubridae	-0.497	-0.380
Bahia	*Chironius carinatus*	4	0.635	-0.122	0.598	-0.150	2.860	Semiarboreal	Colubridae	0.461	-0.651
Bahia	*Chironius exoletus*	3	0.073	-0.111	0.350	-0.150	2.550	Semiarboreal	Colubridae	0.048	-0.392
Bahia	*Chironius flavolineatus*	2	-0.489	-0.472	0.314	-0.150	2.270	Semiarboreal	Colubridae	-0.497	-0.380
Bahia	*Clelia plumbea*	3	0.073	-0.308	0.172	-0.150	3.270	Terrestrial	Dipsadidae	-0.134	-0.294
Bahia	*Corallus hortulanus*	6	1.759	1.001	0.687	-0.150	3.590	Arboreal	Boidae	1.790	-0.604
Bahia	*Crotalus durissus*	1	-1.050	-0.520	-0.681	-0.150	3.460	Terrestrial	Viperidae	-1.232	0.455
Bahia	*Drymarchon corais*	5	1.197	0.502	0.741	-0.150	3.140	Terrestrial	Colubridae	1.200	-0.691
Bahia	*Drymoluber dichrous*	2	-0.489	-0.472	0.314	-0.150	2.360	Terrestrial	Colubridae	-0.497	-0.380
Bahia	*Epicrates assisi*	1	-1.050	-0.520	-0.681	-0.150	3.270	Semiarboreal	Boidae	-1.232	0.455
Bahia	*Erythrolamprus aesculapii*	1	-1.050	-0.520	-0.823	-0.150	2.140	Terrestrial	Dipsadidae	-1.287	0.567
Bahia	*Erythrolamprus almadensis*	1	-1.050	-0.520	0.012	-0.150	1.770	Terrestrial	Dipsadidae	-0.963	-0.092
Bahia	*Erythrolamprus miliaris*	6	1.759	1.866	0.598	-0.150	2.040	Semiaquatic	Dipsadidae	2.258	-0.350
Bahia	*Erythrolamprus poecilogyrus*	2	-0.489	-0.472	0.314	-0.150	1.830	Terrestrial	Dipsadidae	-0.497	-0.380

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Bahia	*Erythrolamprus reginae*	3	0.073	-0.111	0.350	-0.150	1.990	Terrestrial	Dipsadidae	0.048	-0.392
Bahia	*Erythrolamprus viridis*	2	-0.489	-0.472	0.314	-0.150	1.770	Terrestrial	Dipsadidae	-0.497	-0.380
Bahia	*Eunectes murinus*	10	4.006	4.557	1.007	-0.150	5.540	Aquatic	Boidae	5.265	-0.343
Bahia	*Helicops angulatus*	3	0.073	-0.193	0.101	-0.150	2.250	Aquatic	Dipsadidae	-0.096	-0.213
Bahia	*Helicops leopardinus*	2	-0.489	-0.413	0.048	-0.150	1.990	Aquatic	Dipsadidae	-0.566	-0.158
Bahia	*Imantodes cenchoa*	2	-0.489	-0.472	0.314	-0.150	2.710	Arboreal	Dipsadidae	-0.497	-0.380
Bahia	*Lachesis muta*	1	-1.050	-0.520	-0.681	-0.150	4.340	Terrestrial	Viperidae	-1.232	0.455
Bahia	*Leptodeira annulata*	3	0.073	-0.289	0.456	-0.150	2.270	Arboreal	Dipsadidae	-0.013	-0.514
Bahia	*Leptophis ahaetulla*	2	-0.489	-0.472	0.314	-0.150	2.960	Arboreal	Colubridae	-0.497	-0.380
Bahia	*Micrurus corallinus*	3	0.073	-0.028	0.261	-0.150	2.390	Semifossorial	Elapidae	0.062	-0.304
Bahia	*Micrurus ibiboboca*	2	-0.489	-0.450	-0.806	-0.150	2.700	Semifossorial	Elapidae	-0.917	0.508
Bahia	*Oxybelis aeneus*	2	-0.489	-0.472	0.314	-0.150	2.530	Arboreal	Colubridae	-0.497	-0.380
Bahia	*Oxyrhopus petolarius*	4	0.635	-0.194	0.101	-0.150	3.100	Terrestrial	Dipsadidae	0.226	-0.274
Bahia	*Oxyrhopus trigeminus*	4	0.635	-0.225	0.225	-0.150	2.300	Terrestrial	Dipsadidae	0.256	-0.379
Bahia	*Palusophis bifossatus*	5	1.197	0.179	0.741	-0.150	2.650	Terrestrial	Colubridae	1.012	-0.760
Bahia	*Philodryas nattereri*	5	1.197	0.179	0.741	-0.150	2.530	Terrestrial	Dipsadidae	1.012	-0.760
Bahia	*Philodryas olfersii*	3	0.073	-0.272	0.456	-0.150	2.660	Semiarboreal	Dipsadidae	-0.004	-0.511
Bahia	*Philodryas patagoniensis*	5	1.197	0.179	0.741	-0.150	2.710	Terrestrial	Dipsadidae	1.012	-0.760
Bahia	*Phimophis guerini*	1	-1.050	-0.520	-0.219	-0.150	2.510	Terrestrial	Dipsadidae	-1.053	0.091
Bahia	*Pseudoboa nigra*	3	0.073	-0.240	0.545	-0.150	2.720	Terrestrial	Dipsadidae	0.049	-0.574
Bahia	*Sibynomorphus neuwiedi*	1	-1.050	-0.520	-5.569	-0.150	2.000	Terrestrial	Dipsadidae	-3.123	4.311
Bahia	*Siphlophis compressus*	1	-1.050	-0.520	-0.219	-0.150	2.620	Arboreal	Dipsadidae	-1.053	0.091
Bahia	*Spilotes pullatus*	5	1.197	0.297	0.652	-0.150	3.480	Arboreal	Colubridae	1.047	-0.665
Bahia	*Spilotes sulphureus*	2	-0.489	-0.511	-0.646	-0.150	3.190	Arboreal	Colubridae	-0.891	0.368
Bahia	*Taeniophallus occipitalis*	3	0.073	-0.289	0.456	-0.150	1.610	Semifossorial	Dipsadidae	-0.013	-0.514
Bahia	*Tantilla melanocephala*	2	-0.489	0.620	-1.552	-0.150	1.190	Semifossorial	Colubridae	-0.586	1.324
Bahia	*Thamnodynastes pallidus*	2	-0.489	3.810	0.172	6.742	1.350	Semiarboreal	Dipsadidae	4.897	4.546
Bahia	*Xenodon merremii*	1	-1.050	-0.520	0.012	-0.150	2.230	Terrestrial	Dipsadidae	-0.963	-0.092
Bahia	*Xenodon rabdocephalus*	2	-0.489	-0.355	0.048	-0.150	2.080	Terrestrial	Dipsadidae	-0.532	-0.145
CBotelho	*Atractus trihedrurus*	1	-0.875	-0.534	-2.250	-0.401	2.320	Fossorial	Dipsadidae	-1.854	1.528
CBotelho	*Bothrops jararaca*	5	2.171	1.052	0.542	-0.401	3.310	Semiarboreal	Viperidae	1.892	-0.665
CBotelho	*Bothrops jararacussu*	5	2.171	2.288	0.570	3.368	3.710	Terrestrial	Viperidae	4.242	1.711
CBotelho	*Chironius bicarinatus*	3	0.648	-0.079	0.514	-0.401	2.720	Semiarboreal	Colubridae	0.352	-0.720
CBotelho	*Chironius exoletus*	1	-0.875	-0.534	0.431	-0.401	2.550	Semiarboreal	Colubridae	-0.817	-0.586
CBotelho	*Chironius flavolineatus*	1	-0.875	-0.534	0.431	-0.401	2.270	Semiarboreal	Colubridae	-0.817	-0.586
CBotelho	*Chironius foveatus*	2	-0.113	-0.397	0.431	-0.401	2.970	Semiarboreal	Colubridae	-0.301	-0.639
CBotelho	*Clelia plumbea*	3	0.648	-0.131	0.403	1.484	3.270	Terrestrial	Dipsadidae	1.090	0.425

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
CBotelho	*Dipsas alternans*	1	-0.875	-0.534	-2.194	-0.401	1.900	Arboreal	Dipsadidae	-1.832	1.484
CBotelho	*Dipsas petersi*	1	-0.875	-0.534	-2.194	-0.401	NA	Arboreal	Dipsadidae	-1.832	1.484
CBotelho	*Echinanthera amoena*	1	-0.875	-0.534	0.431	-0.401	1.650	Terrestrial	Dipsadidae	-0.817	-0.586
CBotelho	*Echinanthera cephalostriata*	2	-0.113	-0.026	0.431	-0.401	1.630	Terrestrial	Dipsadidae	-0.086	-0.560
CBotelho	*Echinanthera cyanopleura*	3	0.648	-0.064	0.514	-0.401	1.610	Terrestrial	Dipsadidae	0.361	-0.716
CBotelho	*Echinanthera undulata*	1	-0.875	-0.534	0.431	-0.401	1.650	Terrestrial	Dipsadidae	-0.817	-0.586
CBotelho	*Erythrolamprus aesculapii*	2	-0.113	-0.314	0.403	0.541	2.140	Terrestrial	Dipsadidae	0.142	-0.066
CBotelho	*Erythrolamprus atraventer*	1	-0.875	-0.534	0.431	-0.401	1.590	Terrestrial	Dipsadidae	-0.817	-0.586
CBotelho	*Erythrolamprus jaegeri*	2	-0.113	-0.181	0.431	-0.401	1.800	Semiaquatic	Dipsadidae	-0.176	-0.593
CBotelho	*Erythrolamprus miliaris*	5	2.171	3.535	0.570	3.368	2.040	Semiaquatic	Dipsadidae	4.965	1.976
CBotelho	*Erythrolamprus poecilogyrus*	1	-0.875	-0.534	0.431	-0.401	1.830	Terrestrial	Dipsadidae	-0.817	-0.586
CBotelho	*Erythrolamprus typhlus*	1	-0.875	-0.534	0.431	-0.401	2.050	Terrestrial	Dipsadidae	-0.817	-0.586
CBotelho	*Liotyphlops beui*	1	-0.875	-0.534	-2.250	-0.401	1.320	Fossorial	Anomalepididae	-1.854	1.528
CBotelho	*Lygophis meridionalis*	2	-0.113	-0.181	0.431	-0.401	1.980	Terrestrial	Dipsadidae	-0.176	-0.593
CBotelho	*Micrurus corallinus*	3	0.648	1.394	0.291	-0.401	2.390	Semifossorial	Elapidae	1.120	-0.230
CBotelho	*Oxyrhopus clathratus*	2	-0.113	-0.510	0.375	-0.401	1.980	Terrestrial	Dipsadidae	-0.388	-0.619
CBotelho	*Oxyrhopus guibei*	2	-0.113	-0.510	0.375	-0.401	2.550	Terrestrial	Dipsadidae	-0.388	-0.619
CBotelho	*Oxyrhopus rhombifer*	3	0.648	-0.131	0.403	1.484	2.110	Terrestrial	Dipsadidae	1.090	0.425
CBotelho	*Oxyrhopus trigeminus*	2	-0.113	-0.510	0.375	-0.401	2.300	Terrestrial	Dipsadidae	-0.388	-0.619
CBotelho	*Phalotris mertensi*	2	-0.113	-0.443	0.263	-0.401	2.720	Fossorial	Dipsadidae	-0.393	-0.517
CBotelho	*Philodryas olfersii*	4	1.409	0.210	0.514	-0.401	2.660	Semiarboreal	Dipsadidae	0.956	-0.740
CBotelho	*Philodryas patagoniensis*	5	2.171	1.869	0.570	3.368	2.710	Terrestrial	Dipsadidae	3.999	1.622
CBotelho	*Sibynomorphus mikanii*	1	-0.875	-0.534	-2.194	-0.401	1.860	Terrestrial	Dipsadidae	-1.832	1.484
CBotelho	*Sibynomorphus neuwiedi*	1	-0.875	-0.534	-2.194	-0.401	2.000	Terrestrial	Dipsadidae	-1.832	1.484
CBotelho	*Simophis rhinostoma*	1	-0.875	-0.534	0.431	-0.401	2.050	Terrestrial	Colubridae	-0.817	-0.586
CBotelho	*Siphlophis longicaudatus*	2	-0.113	-0.314	0.403	0.541	1.750	Arboreal	Dipsadidae	0.142	-0.066
CBotelho	*Sordellina punctata*	1	-0.875	-0.534	-2.250	-0.401	1.680	Aquatic	Dipsadidae	-1.854	1.528
CBotelho	*Spilotes pullatus*	6	2.931	3.846	0.542	-0.401	3.480	Arboreal	Colubridae	3.949	-0.154
CBotelho	*Taeniophallus affinis*	3	0.648	1.077	0.542	1.484	NA	Terrestrial	Dipsadidae	1.844	0.572
CBotelho	*Taeniophallus bilineatus*	2	-0.113	-0.303	0.514	-0.401	1.010	Terrestrial	Dipsadidae	-0.214	-0.685
CBotelho	*Taeniophallus occipitalis*	2	-0.113	-0.303	0.514	-0.401	1.610	Semifossorial	Dipsadidae	-0.214	-0.685
CBotelho	*Taeniophallus persimilis*	2	-0.113	-0.303	0.514	-0.401	1.170	Semifossorial	Dipsadidae	-0.214	-0.685
CBotelho	*Thamnodynastes hypoconia*	2	-0.113	-0.303	0.514	-0.401	1.750	Semiarboreal	Dipsadidae	-0.214	-0.685
CBotelho	*Tomodon dorsatus*	1	-0.875	-0.534	-2.194	-0.401	1.980	Terrestrial	Dipsadidae	-1.832	1.484
CBotelho	*Tropidodryas serra*	3	0.648	-0.064	0.514	-0.401	2.260	Semiarboreal	Dipsadidae	0.361	-0.716
CBotelho	*Tropidodryas striaticeps*	3	0.648	-0.064	0.514	-0.401	2.030	Semiarboreal	Dipsadidae	0.361	-0.716
CBotelho	*Tropidophis paucisquamis*	1	-0.875	-0.534	0.431	-0.401	1.310	Arboreal	Tropidophiidae	-0.817	-0.586

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
CBotelho	*Xenodon merremii*	1	-0.875	-0.534	0.431	-0.401	2.230	Terrestrial	Dipsadidae	-0.817	-0.586
CBotelho	*Xenodon neuwiedii*	1	-0.875	-0.534	0.431	-0.401	1.980	Terrestrial	Dipsadidae	-0.817	-0.586
Ceara	*Apostolepis cearensis*	1	-1.072	-0.742	-0.747	-0.826	0.720	Semifossorial	Dipsadidae	-1.690	0.079
Ceara	*Boa constrictor*	4	1.368	1.090	0.263	-0.826	4.550	Semiarboreal	Boidae	1.163	-0.591
Ceara	*Boiruna sertaneja*	2	-0.259	-0.361	0.118	-0.826	3.120	Terrestrial	Dipsadidae	-0.668	-0.610
Ceara	*Crotalus durissus*	2	-0.259	-0.649	0.118	-0.826	3.460	Terrestrial	Viperidae	-0.835	-0.671
Ceara	*Epicrates assisi*	4	1.368	1.090	0.263	-0.826	3.270	Semiarboreal	Boidae	1.163	-0.591
Ceara	*Erythrolamprus mossoroensis*	2	-0.259	0.837	-0.209	-0.826	2.460	Semiaquatic	Dipsadidae	-0.100	-0.097
Ceara	*Erythrolamprus poecilogyrus*	1	-1.072	-0.742	-0.267	-0.826	1.830	Terrestrial	Dipsadidae	-1.504	-0.299
Ceara	*Erythrolamprus viridis*	2	-0.259	-0.383	0.496	1.193	1.770	Terrestrial	Dipsadidae	0.335	0.232
Ceara	*Leptodeira annulata*	2	-0.259	-0.383	0.496	1.193	2.270	Arboreal	Dipsadidae	0.335	0.232
Ceara	*Leptophis ahaetulla*	2	-0.259	-0.383	0.496	1.193	2.960	Arboreal	Colubridae	0.335	0.232
Ceara	*Lygophis dilepis*	1	-1.072	-0.742	-0.267	-0.826	1.650	Terrestrial	Dipsadidae	-1.504	-0.299
Ceara	*Micrurus ibiboboca*	3	0.555	1.218	0.191	-0.826	2.700	Semifossorial	Elapidae	0.742	-0.419
Ceara	*Oxybelis aeneus*	2	-0.259	-0.383	0.496	1.193	2.530	Arboreal	Colubridae	0.335	0.232
Ceara	*Oxyrhopus trigeminus*	2	-0.259	-0.649	0.118	-0.826	2.300	Terrestrial	Dipsadidae	-0.835	-0.671
Ceara	*Palusophis bifossatus*	2	-0.259	-0.438	0.191	1.193	2.650	Terrestrial	Colubridae	0.185	0.461
Ceara	*Philodryas nattereri*	6	2.995	3.451	0.932	1.193	2.530	Terrestrial	Dipsadidae	4.592	0.352
Ceara	*Philodryas olfersii*	4	1.368	0.501	0.663	1.193	2.660	Semiarboreal	Dipsadidae	1.845	0.112
Ceara	*Pseudoboa nigra*	2	-0.259	-0.550	0.053	-0.826	2.720	Terrestrial	Dipsadidae	-0.803	-0.599
Ceara	*Psomophis joberti*	2	-0.259	-0.383	0.496	1.193	1.130	Terrestrial	Dipsadidae	0.335	0.232
Ceara	*Tantilla melanocephala*	1	-1.072	-0.742	-4.212	-0.826	1.190	Semifossorial	Colubridae	-3.031	2.812
Ceara	*Thamnodynastes phoenix*	3	0.555	0.089	0.583	1.193	NA	Semiarboreal	Dipsadidae	1.108	0.175
Ceara	*Xenodon merremii*	1	-1.072	-0.742	-0.267	-0.826	2.230	Terrestrial	Dipsadidae	-1.504	-0.299
Chacoan	*Atractus reticulatus*	1	-1.182	-0.808	-3.340	-0.957	1.320	Fossorial	Dipsadidae	-2.851	2.048
Chacoan	*Bothrops alternatus*	3	0.075	-0.562	0.282	-0.957	3.380	Terrestrial	Viperidae	-0.585	-0.892
Chacoan	*Bothrops diporus*	5	1.333	2.058	0.481	1.036	2.840	Terrestrial	Viperidae	2.590	0.501
Chacoan	*Dipsas turgida*	1	-1.182	-0.808	-3.340	-0.957	1.680	Terrestrial	Dipsadidae	-2.851	2.048
Chacoan	*Erythrolamprus jaegerii*	2	-0.554	-0.514	0.202	-0.957	1.800	Semiaquatic	Dipsadidae	-0.949	-0.751
Chacoan	*Erythrolamprus poecilogyrus*	4	0.705	-0.135	0.431	1.036	1.830	Terrestrial	Dipsadidae	0.939	0.143
Chacoan	*Erythrolamprus semiaureus*	2	-0.554	-0.626	0.202	-0.957	2.230	Aquatic	Dipsadidae	-1.014	-0.775
Chacoan	*Helicops infrataeniatus*	2	-0.554	-0.626	0.202	-0.957	2.230	Aquatic	Dipsadidae	-1.014	-0.775
Chacoan	*Helicops leopardinus*	2	-0.554	-0.626	0.202	-0.957	1.990	Aquatic	Dipsadidae	-1.014	-0.775
Chacoan	*Hydrodynastes gigas*	7	2.591	2.766	0.560	-0.957	3.340	Aquatic	Colubridae	2.895	-0.675
Chacoan	*Leptophis ahaetulla*	2	-0.554	-0.699	0.202	-0.957	2.960	Arboreal	Colubridae	-1.056	-0.790
Chacoan	*Lygophis anomalus*	1	-1.182	-0.808	0.172	-0.957	1.920	Semiaquatic	Dipsadidae	-1.492	-0.722
Chacoan	*Micrurus altirostris*	3	0.075	0.309	0.033	1.036	2.680	Semifossorial	Elapidae	0.681	0.619

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Chacoan	*Micrurus pyrrhocryptus*	3	0.075	0.309	0.033	1.036	2.990	Semifossorial	Elapidae	0.681	0.619
Chacoan	*Mussurana bicolor*	3	0.075	-0.165	0.391	1.036	2.250	Terrestrial	Dipsadidae	0.545	0.235
Chacoan	*Palusophis bifossatus*	4	0.705	0.520	0.431	1.036	2.650	Terrestrial	Colubridae	1.318	0.282
Chacoan	*Paraphimophis rusticus*	3	0.075	-0.590	0.093	1.036	3.150	Terrestrial	Dipsadidae	0.183	0.380
Chacoan	*Philodryas aestiva*	2	-0.554	-0.708	0.242	-0.957	2.230	Semiarboreal	Dipsadidae	-1.046	-0.823
Chacoan	*Philodryas olfersii*	4	0.705	-0.135	0.431	1.036	2.660	Semiarboreal	Dipsadidae	0.939	0.143
Chacoan	*Philodryas patagoniensis*	6	1.962	1.478	0.521	1.036	2.710	Terrestrial	Dipsadidae	2.630	0.279
Chacoan	*Thamnodynastes chaquensis*	1	-1.182	-0.808	0.172	-0.957	1.980	Terrestrial	Dipsadidae	-1.492	-0.722
Chacoan	*Thamnodynastes hypoconia*	2	-0.554	-0.570	0.351	1.036	1.750	Semiarboreal	Dipsadidae	-0.066	0.249
Chacoan	*Thamnodynastes strigatus*	5	1.333	0.934	0.481	1.036	1.980	Terrestrial	Dipsadidae	1.938	0.263
Chacoan	*Xenodon dorbingyi*	3	0.075	1.622	0.391	1.036	1.980	Terrestrial	Dipsadidae	1.581	0.615
Chacoan	*Xenodon merremii*	1	-1.182	-0.808	0.172	-0.957	2.230	Terrestrial	Dipsadidae	-1.492	-0.722
CMendes	*Atractus albuquerquei*	1	-1.161	-0.761	-4.765	-0.317	1.940	Fossorial	Dipsadidae	-3.088	3.542
CMendes	*Boa constrictor*	6	1.504	0.341	0.293	4.125	4.550	Semiarboreal	Boidae	2.948	2.016
CMendes	*Chironius carinatus*	2	-0.628	-0.602	0.174	2.644	2.860	Semiarboreal	Colubridae	0.496	1.300
CMendes	*Chironius exoletus*	1	-1.161	-0.761	-0.379	1.163	2.550	Semiarboreal	Colubridae	-0.753	0.922
CMendes	*Chironius multiventris*	2	-0.628	-0.569	0.362	-0.317	3.130	Semiarboreal	Colubridae	-0.687	-0.518
CMendes	*Chironius scurrulus*	2	-0.628	-0.569	0.362	-0.317	3.050	Semiarboreal	Colubridae	-0.687	-0.518
CMendes	*Clelia clelia*	5	0.971	0.044	0.293	-0.317	3.240	Terrestrial	Dipsadidae	0.559	-0.506
CMendes	*Corallus batesii*	2	-0.628	-0.725	0.105	-0.317	3.820	Arboreal	Boidae	-0.877	-0.349
CMendes	*Corallus hortulanus*	8	2.570	2.375	0.708	-0.317	3.590	Arboreal	Boidae	2.988	-0.510
CMendes	*Drepanoides anomalus*	2	-0.628	-0.234	0.046	-0.317	2.030	Terrestrial	Dipsadidae	-0.615	-0.198
CMendes	*Drymarchon corais*	6	1.504	0.928	0.639	-0.317	3.140	Terrestrial	Colubridae	1.511	-0.648
CMendes	*Drymoluber dichrous*	4	0.438	0.985	0.500	-0.317	2.360	Terrestrial	Colubridae	0.879	-0.412
CMendes	*Epicrates cenchria*	6	1.504	1.027	0.639	-0.317	3.660	Semiarboreal	Boidae	1.569	-0.627
CMendes	*Erythrolamprus dorsocorallinus*	1	-1.161	-0.761	-0.379	-0.317	1.730	Terrestrial	Dipsadidae	-1.390	0.083
CMendes	*Erythrolamprus oligolepis*	1	-1.161	-0.761	-0.379	-0.317	1.990	Terrestrial	Dipsadidae	-1.390	0.083
CMendes	*Helicops angulatus*	4	0.438	1.981	0.569	-0.317	2.250	Aquatic	Dipsadidae	1.484	-0.255
CMendes	*Hydrops triangularis*	1	-1.161	-0.761	-1.110	-0.317	1.850	Aquatic	Dipsadidae	-1.673	0.659
CMendes	*Leptophis ahaetulla*	3	-0.095	0.231	0.431	-0.317	2.960	Arboreal	Colubridae	0.110	-0.460
CMendes	*Micrurus annellatus*	2	-0.628	-0.675	0.046	-0.317	2.070	Semifossorial	Elapidae	-0.871	-0.292
CMendes	*Micrurus lemniscatus*	5	0.971	2.794	0.362	-0.317	2.750	Semifossorial	Elapidae	2.181	0.024
CMendes	*Oxybelis fulgidus*	2	-0.628	-0.715	0.046	-0.317	2.920	Arboreal	Colubridae	-0.894	-0.300
CMendes	*Oxyrhopus melanogenys*	3	-0.095	-0.658	0.174	-0.317	2.250	Terrestrial	Dipsadidae	-0.505	-0.447
CMendes	*Oxyrhopus petolarius*	3	-0.095	-0.658	0.174	-0.317	3.100	Terrestrial	Dipsadidae	-0.505	-0.447
CMendes	*Philodryas viridissima*	3	-0.095	-0.374	0.431	-0.317	2.430	Arboreal	Dipsadidae	-0.241	-0.589
CMendes	*Phrynonax polylepis*	4	0.438	-0.285	0.234	-0.317	3.030	Terrestrial	Colubridae	0.039	-0.472

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
CMendes	*Pseudoboa coronata*	4	0.438	-0.443	0.234	-0.317	2.310	Terrestrial	Dipsadidae	-0.052	-0.505
CMendes	*Spilotes pullatus*	5	0.971	0.370	0.569	-0.317	3.480	Arboreal	Colubridae	0.855	-0.655
CMendes	*Xenodon severus*	1	-1.161	-0.761	-0.379	-0.317	2.990	Terrestrial	Dipsadidae	-1.390	0.083
Ejule	*Afronatrix anoscopus*	3	0.792	0.009	-1.306	-0.612	2.040	Semiaquatic	Colubridae	-0.310	0.600
Ejule	*Atractaspis aterrima*	4	1.584	2.384	0.818	1.592	1.920	Fossorial	Atractaspididae	3.292	0.593
Ejule	*Bitis gabonica*	1	-0.792	-0.631	0.673	-0.612	3.460	Terrestrial	Viperidae	-0.823	-0.927
Ejule	*Boaedon fuliginosus*	1	-0.792	-0.631	0.673	-0.612	2.500	Terrestrial	Lamprophiidae	-0.823	-0.927
Ejule	*Boaedon lineatus*	1	-0.792	-0.631	0.673	-0.612	2.290	Terrestrial	Lamprophiidae	-0.823	-0.927
Ejule	*Causus maculatus*	1	-0.792	-0.631	-1.320	-0.612	2.270	Terrestrial	Viperidae	-1.595	0.646
Ejule	*Crotaphopeltis hotamboeia*	1	-0.792	-0.631	-1.320	-0.612	1.820	Semiaquatic	Colubridae	-1.595	0.646
Ejule	*Dasypeltis sp*	1	-0.792	-0.631	-1.739	-0.612	NA	Terrestrial	Colubridae	-1.757	0.976
Ejule	*Dipsadoboa duchesnii*	1	-0.792	-0.631	-1.320	-0.612	2.440	Arboreal	Colubridae	-1.595	0.646
Ejule	*Dispholidus typus*	2	0.000	-0.125	0.673	1.592	2.750	Arboreal	Colubridae	0.874	0.345
Ejule	*Echis ocellatus*	2	0.000	-0.258	0.746	1.592	2.210	Terrestrial	Viperidae	0.824	0.259
Ejule	*Elapsoidea semiannulata*	1	-0.792	-0.631	0.442	-0.612	1.870	Fossorial	Elapidae	-0.913	-0.745
Ejule	*Grayia smythii*	2	0.000	-0.471	-1.306	-0.612	1.680	Semiaquatic	Colubridae	-1.042	0.583
Ejule	*Limaformosa crossi*	3	0.792	0.943	0.789	1.592	2.450	Terrestrial	Lamprophiidae	1.991	0.395
Ejule	*Naja nigricollis*	2	0.000	-0.258	0.746	1.592	3.440	Terrestrial	Elapidae	0.824	0.259
Ejule	*Psammophis phillipsi*	1	-0.792	-0.631	0.529	-0.612	2.860	Terrestrial	Dipsadidae	-0.879	-0.813
Ejule	*Python regius*	4	1.584	1.010	0.760	-0.612	3.210	Terrestrial	Pythonidae	1.524	-0.903
Ejule	*Python sebae*	5	2.375	2.450	0.789	-0.612	4.700	Terrestrial	Pythonidae	2.825	-0.705
Eket	*Afronatrix anoscopus*	3	0.534	0.695	0.200	-0.657	2.040	Semiaquatic	Colubridae	0.504	-0.440
Eket	*Aparallactus modestus*	1	-1.221	-0.789	-4.210	-0.657	1.650	Terrestrial	Colubridae	-3.070	2.912
Eket	*Atheris squamiger*	2	-0.343	-0.659	0.080	-0.657	2.400	Arboreal	Viperidae	-0.831	-0.539
Eket	*Bitis gabonica*	1	-1.221	-0.789	-0.083	-0.657	3.460	Terrestrial	Viperidae	-1.473	-0.343
Eket	*Bitis nasicornis*	2	-0.343	-0.156	0.665	1.503	3.460	Terrestrial	Viperidae	0.616	0.331
Eket	*Boaedon virgatus*	5	2.290	1.903	1.051	1.503	2.950	Terrestrial	Lamprophiidae	3.470	0.179
Eket	*Calabaria reinhardti*	1	-1.221	-0.789	-0.083	-0.657	2.720	Semifossorial	Boidae	-1.473	-0.343
Eket	*Crotaphopeltis hotamboeia*	2	-0.343	-0.156	0.665	1.503	1.820	Semiaquatic	Colubridae	0.616	0.331
Eket	*Dendroaspis jamesoni*	4	1.412	1.119	0.974	1.503	3.420	Arboreal	Elapidae	2.482	0.168
Eket	*Dipsadoboa duchesnii*	2	-0.343	-0.408	0.261	1.503	2.440	Arboreal	Colubridae	0.314	0.596
Eket	*Grayia smythii*	2	-0.343	-0.638	0.028	-0.657	1.680	Semiaquatic	Colubridae	-0.839	-0.493
Eket	*Hapsidophrys smaragdinus*	2	-0.343	-0.408	0.261	1.503	2.170	Terrestrial	Colubridae	0.314	0.596
Eket	*Limaformosa crossi*	1	-1.221	-0.789	-0.032	-0.657	2.450	Terrestrial	Lamprophiidae	-1.453	-0.383
Eket	*Mehelya poensis*	1	-1.221	-0.789	-0.032	-0.657	2.590	Terrestrial	Lamprophiidae	-1.453	-0.383
Eket	*Naja melanoleuca*	3	0.534	0.656	0.742	1.503	3.440	Terrestrial	Elapidae	1.620	0.348
Eket	*Naja nigricollis*	2	-0.343	-0.576	0.200	-0.657	3.440	Terrestrial	Elapidae	-0.736	-0.616

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Eket	*Natriciteres fuliginoides*	3	0.534	0.394	-1.003	-0.657	1.430	Semiaquatic	Colubridae	-0.136	0.445
Eket	*Natriciteres variegata*	3	0.534	1.945	0.200	-0.657	0.650	Semiaquatic	Colubridae	1.229	-0.175
Eket	*Psammophis phillipsi*	2	-0.343	-0.576	0.200	-0.657	2.860	Terrestrial	Dipsadidae	-0.736	-0.616
Eket	*Python regius*	3	0.534	-0.529	0.140	-0.657	3.210	Terrestrial	Pythonidae	-0.229	-0.653
Eket	*Python sebae*	5	2.290	2.622	0.200	-0.657	4.700	Terrestrial	Pythonidae	2.628	-0.220
Eket	*Thelotornis kirtlandii*	2	-0.343	-0.729	-0.341	-0.657	2.590	Arboreal	Colubridae	-1.035	-0.221
Eket	*Toxicodryas blandingii*	3	0.534	-0.552	-0.083	-0.657	3.200	Arboreal	Colubridae	-0.329	-0.482
Espigao	*Amerotyphlops reticulatus*	1	-0.886	-0.479	-0.410	-0.255	2.000	Fossorial	Typhlopidae	-1.054	0.172
Espigao	*Anilius scytale*	4	0.535	0.670	-0.063	1.715	2.500	Fossorial	Aniliidae	1.409	1.106
Espigao	*Atractus albuquerquei*	1	-0.886	-0.479	-0.641	-0.255	1.900	Fossorial	Dipsadidae	-1.144	0.354
Espigao	*Atractus latifrons*	2	-0.412	-0.411	-0.386	-0.255	1.700	Fossorial	Dipsadidae	-0.734	0.117
Espigao	*Atractus snethlageae*	2	-0.412	-0.411	-0.386	-0.255	1.900	Fossorial	Dipsadidae	-0.734	0.117
Espigao	*Boa constrictor*	6	1.482	0.020	0.330	-0.255	4.500	Semiarboreal	Boidae	0.879	-0.560
Espigao	*Bothrops atrox*	6	1.482	1.027	0.561	-0.255	3.300	Semiarboreal	Viperidae	1.553	-0.529
Espigao	*Bothrops bileneatus*	3	0.061	-0.274	0.469	-0.255	2.700	Arboreal	Viperidae	-0.052	-0.579
Espigao	*Chironius exoletus*	1	-0.886	-0.479	0.076	-0.255	2.500	Semiarboreal	Colubridae	-0.866	-0.211
Espigao	*Chironius multiventris*	2	-0.412	-0.387	0.422	-0.255	3.100	Semiarboreal	Colubridae	-0.407	-0.516
Espigao	*Chironius scurrulus*	2	-0.412	-0.387	0.422	-0.255	3.000	Semiarboreal	Colubridae	-0.407	-0.516
Espigao	*Clelia plumbea*	3	0.061	-0.341	0.307	-0.255	3.300	Terrestrial	Dipsadidae	-0.154	-0.466
Espigao	*Corallus caninus*	3	0.061	-0.359	0.261	-0.255	3.500	Arboreal	Boidae	-0.182	-0.433
Espigao	*Corallus hortulanus*	8	2.429	1.258	0.561	-0.255	3.600	Arboreal	Boidae	2.229	-0.582
Espigao	*Dendrophidion dendrophis*	1	-0.886	-0.479	0.076	-0.255	2.300	Arboreal	Colubridae	-0.866	-0.211
Espigao	*Dipsas castebyi*	1	-0.886	-0.479	-3.969	-0.255	1.800	Arboreal	Dipsadidae	-2.431	2.979
Espigao	*Dipsas indica*	1	-0.886	-0.479	-3.969	-0.255	2.300	Arboreal	Dipsadidae	-2.431	2.979
Espigao	*Dipsas pavonina*	1	-0.886	-0.479	-3.969	-0.255	1.900	Arboreal	Colubridae	-2.431	2.979
Espigao	*Drepanoides anomalus*	2	-0.412	-0.341	0.238	-0.255	2.000	Terrestrial	Dipsadidae	-0.452	-0.360
Espigao	*Drymarchon corais*	6	1.482	0.410	0.561	-0.255	3.100	Terrestrial	Colubridae	1.194	-0.660
Espigao	*Drymobius rhombifer*	1	-0.886	-0.479	0.214	-0.255	2.300	Terrestrial	Colubridae	-0.813	-0.320
Espigao	*Drymoluber dichrous*	4	0.535	0.168	0.492	-0.255	2.400	Terrestrial	Colubridae	0.485	-0.555
Espigao	*Epicrates cenchria*	6	1.482	0.302	0.515	-0.255	3.700	Semiarboreal	Boidae	1.114	-0.646
Espigao	*Erythrolamprus aesculapii*	3	0.061	-0.277	0.353	-0.255	2.100	Terrestrial	Dipsadidae	-0.099	-0.489
Espigao	*Erythrolamprus almadensis*	1	-0.886	-0.479	0.076	-0.255	1.800	Terrestrial	Dipsadidae	-0.866	-0.211
Espigao	*Erythrolamprus breviceps*	5	1.008	3.874	0.376	5.656	1.700	Terrestrial	Dipsadidae	5.405	3.623
Espigao	*Erythrolamprus reginae*	3	0.061	-0.201	0.446	-0.255	2.000	Terrestrial	Dipsadidae	-0.019	-0.546
Espigao	*Eunectes murinus*	12	4.323	4.595	0.700	-0.255	5.500	Aquatic	Boidae	5.304	-0.186
Espigao	*Helicops angulatus*	4	0.535	0.062	0.492	-0.255	2.300	Aquatic	Dipsadidae	0.423	-0.577
Espigao	*Hydrodynastes gigas*	2	-0.412	-0.383	0.191	-0.255	3.300	Aquatic	Colubridae	-0.494	-0.333

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Espigao	*Imantodes cenchoa*	2	-0.412	-0.387	0.422	-0.255	2.700	Arboreal	Dipsadidae	-0.407	-0.516
Espigao	*Lachesis muta*	1	-0.886	-0.479	-0.225	-0.255	4.300	Terrestrial	Viperidae	-0.983	0.026
Espigao	*Leptodeira annulata*	3	0.061	-0.201	0.446	-0.255	2.300	Arboreal	Dipsadidae	-0.019	-0.546
Espigao	*Leptophis ahaetulla*	3	0.061	-0.201	0.446	-0.255	3.000	Arboreal	Colubridae	-0.019	-0.546
Espigao	*Mastigodryas boddaerti*	5	1.008	0.248	0.492	-0.255	2.500	Terrestrial	Colubridae	0.802	-0.589
Espigao	*Micrurus hemprichii*	4	0.535	2.918	0.469	3.686	2.300	Semifossorial	Elapidae	3.766	2.281
Espigao	*Micrurus spixii*	3	0.061	-0.043	0.284	1.715	2.900	Semifossorial	Elapidae	0.858	0.732
Espigao	*Micrurus surinamensis*	3	0.061	-0.277	0.353	-0.255	2.700	Aquatic	Elapidae	-0.099	-0.489
Espigao	*Oxybelis fulgidus*	2	-0.412	-0.457	0.238	-0.255	2.900	Arboreal	Colubridae	-0.520	-0.385
Espigao	*Oxyrhopus melanogenys*	3	0.061	-0.416	0.261	-0.255	2.200	Terrestrial	Dipsadidae	-0.215	-0.445
Espigao	*Oxyrhopus petolarius*	3	0.061	-0.416	0.261	-0.255	2.300	Terrestrial	Dipsadidae	-0.215	-0.445
Espigao	*Philodryas argentea*	2	-0.412	-0.387	0.422	-0.255	2.500	Arboreal	Dipsadidae	-0.407	-0.516
Espigao	*Philodryas olfersii*	5	1.008	0.038	0.538	-0.255	2.700	Semiarboreal	Dipsadidae	0.698	-0.670
Espigao	*Phrynonax polylepis*	4	0.535	-0.104	0.284	-0.255	3.000	Terrestrial	Colubridae	0.247	-0.448
Espigao	*Rhinobothryum lentiginosum*	1	-0.886	-0.479	0.214	-0.255	2.600	Terrestrial	Colubridae	-0.813	-0.320
Espigao	*Siphlophis compressus*	1	-0.886	-0.479	0.214	-0.255	2.600	Arboreal	Dipsadidae	-0.813	-0.320
Espigao	*Siphlophis worontzowi*	1	-0.886	-0.479	0.214	-0.255	2.100	Arboreal	Dipsadidae	-0.813	-0.320
Espigao	*Spilotes pullatus*	5	1.008	0.086	0.492	-0.255	3.500	Arboreal	Colubridae	0.709	-0.623
Espigao	*Taeniophallus occipitalis*	2	-0.412	-0.387	0.422	-0.255	1.600	Semifossorial	Dipsadidae	-0.407	-0.516
Espigao	*Tantilla melanocephala*	1	-0.886	-0.479	-0.410	-0.255	1.200	Semifossorial	Colubridae	-1.054	0.172
Espigao	*Trilepida macrolepis*	1	-0.886	-0.479	-0.410	-0.255	1.000	Fossorial	Leptotyphlopidae	-1.054	0.172
Espigao	*Xenodon rabdocephalus*	1	-0.886	-0.479	0.076	-0.255	2.100	Terrestrial	Dipsadidae	-0.866	-0.211
Espigao	*Xenodon severus*	1	-0.886	-0.479	0.076	-0.255	3.000	Terrestrial	Dipsadidae	-0.866	-0.211
Espigao	*Xenopholis scalaris*	1	-0.886	-0.479	0.076	-0.255	1.100	Terrestrial	Dipsadidae	-0.866	-0.211
Igarape	*Anilius scytale*	4	0.555	0.633	0.111	-0.157	2.500	Fossorial	Aniliidae	0.661	-0.102
Igarape	*Atractus major*	1	-0.844	-0.538	-3.057	-0.157	2.000	Fossorial	Dipsadidae	-2.047	2.299
Igarape	*Atractus schach*	1	-0.844	-0.538	-3.057	-0.157	1.300	Fossorial	Dipsadidae	-2.047	2.299
Igarape	*Boa constrictor*	6	1.489	0.137	0.408	-0.157	4.550	Semiarboreal	Boidae	1.024	-0.542
Igarape	*Bothrops atrox*	5	1.022	2.261	0.536	6.429	3.300	Semiarboreal	Viperidae	4.871	3.590
Igarape	*Chironius carinatus*	2	-0.378	-0.456	0.302	-0.157	2.860	Semiarboreal	Colubridae	-0.431	-0.383
Igarape	*Chironius fuscus*	3	0.089	0.558	0.408	-0.157	2.600	Semiarboreal	Colubridae	0.465	-0.302
Igarape	*Chironius scurrulus*	2	-0.378	-0.466	0.387	-0.157	3.050	Semiarboreal	Colubridae	-0.404	-0.453
Igarape	*Clelia clelia*	5	1.022	0.249	0.430	-0.157	3.240	Terrestrial	Dipsadidae	0.829	-0.485
Igarape	*Corallus hortulanus*	8	2.422	1.330	0.515	-0.157	3.590	Arboreal	Boidae	2.292	-0.473
Igarape	*Dipsas catesbyi*	1	-0.844	-0.538	-3.057	-0.157	1.840	Arboreal	Dipsadidae	-2.047	2.299
Igarape	*Dipsas indica*	1	-0.844	-0.538	-3.057	-0.157	2.300	Arboreal	Dipsadidae	-2.047	2.299
Igarape	*Drepanoides anomalus*	2	-0.378	-0.260	0.302	-0.157	2.030	Terrestrial	Dipsadidae	-0.318	-0.342

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Igarape	*Drymarchon corais*	6	1.489	0.817	0.515	-0.157	3.140	Terrestrial	Colubridae	1.459	-0.482
Igarape	*Drymobius rhombifer*	2	-0.378	-0.466	0.387	-0.157	2.330	Terrestrial	Colubridae	-0.404	-0.453
Igarape	*Drymoluber dichrous*	4	0.555	0.560	0.451	-0.157	2.360	Terrestrial	Colubridae	0.750	-0.386
Igarape	*Erythrolamprus dorsocorallinus*	1	-0.844	-0.538	0.196	-0.157	1.730	Terrestrial	Dipsadidae	-0.788	-0.267
Igarape	*Erythrolamprus pygmaeus*	1	-0.844	-0.538	0.196	-0.157	0.690	Terrestrial	Dipsadidae	-0.788	-0.267
Igarape	*Erythrolamprus reginae*	3	0.089	-0.243	0.408	-0.157	2.000	Terrestrial	Dipsadidae	0.001	-0.472
Igarape	*Erythrolamprus taeniogaster*	2	-0.378	-0.406	0.260	-0.157	2.130	Semiaquatic	Dipsadidae	-0.419	-0.339
Igarape	*Erythrolamprus typhlus*	2	-0.378	-0.466	0.387	-0.157	2.100	Terrestrial	Dipsadidae	-0.404	-0.453
Igarape	*Eunectes murinus*	12	3.821	5.074	0.621	-0.157	5.500	Aquatic	Boidae	5.306	0.088
Igarape	*Helicops angulatus*	4	0.555	0.127	0.451	-0.157	2.250	Aquatic	Dipsadidae	0.499	-0.477
Igarape	*Imantodes cenchoa*	2	-0.378	-0.466	0.387	-0.157	2.700	Arboreal	Dipsadidae	-0.404	-0.453
Igarape	*Lachesis muta*	1	-0.844	-0.538	0.026	-0.157	4.300	Terrestrial	Viperidae	-0.854	-0.133
Igarape	*Leptodeira annulata*	3	0.089	-0.243	0.408	-0.157	2.300	Arboreal	Dipsadidae	0.001	-0.472
Igarape	*Leptophis ahaetulla*	3	0.089	-0.243	0.408	-0.157	2.960	Arboreal	Colubridae	0.001	-0.472
Igarape	*Micrurus hemprichii*	4	0.555	0.975	0.366	-0.157	2.300	Semifossorial	Elapidae	0.958	-0.230
Igarape	*Micrurus lemniscatus*	5	1.022	0.537	0.430	-0.157	2.750	Semifossorial	Elapidae	0.996	-0.424
Igarape	*Micrurus remotus*	1	-0.844	-0.538	0.026	-0.157	1.810	Semifossorial	Elapidae	-0.854	-0.133
Igarape	*Oxybelis fulgidus*	2	-0.378	-0.479	0.302	-0.157	2.920	Arboreal	Colubridae	-0.445	-0.388
Igarape	*Oxyrhopus melanogenys*	3	0.089	-0.404	0.366	-0.157	2.250	Terrestrial	Dipsadidae	-0.109	-0.473
Igarape	*Oxyrhopus occipitalis*	1	-0.844	-0.538	0.281	-0.157	2.340	Terrestrial	Dipsadidae	-0.755	-0.334
Igarape	*Oxyrhopus petolarius*	3	0.089	-0.404	0.366	-0.157	3.100	Terrestrial	Dipsadidae	-0.109	-0.473
Igarape	*Philodryas argentea*	2	-0.378	-0.466	0.387	-0.157	2.500	Arboreal	Dipsadidae	-0.404	-0.453
Igarape	*Phrynonax poecilonotus*	1	-0.844	-0.538	0.005	-0.157	3.030	Terrestrial	Colubridae	-0.862	-0.116
Igarape	*Siphlophis compressus*	1	-0.844	-0.538	0.281	-0.157	2.620	Arboreal	Dipsadidae	-0.755	-0.334
Igarape	*Spilotes pullatus*	5	1.022	0.289	0.451	-0.157	3.480	Arboreal	Colubridae	0.860	-0.493
Igarape	*Taeniophallus brevirostris*	1	-0.844	-0.538	0.281	-0.157	1.500	Terrestrial	Dipsadidae	-0.755	-0.334
Igarape	*Tantilla melanocephala*	1	-0.844	-0.538	-0.208	-0.157	1.200	Semifossorial	Colubridae	-0.944	0.052
Igarape	*Xenodon severus*	1	-0.844	-0.538	0.196	-0.157	2.990	Terrestrial	Dipsadidae	-0.788	-0.267
Igarape	*Xenopholis scalaris*	1	-0.844	-0.538	0.196	-0.157	1.100	Terrestrial	Dipsadidae	-0.788	-0.267
Itirapina	*Apostolepis dimidiata*	1	-0.807	-0.617	-0.303	-0.360	1.960	Fossorial	Dipsadidae	-1.093	-0.009
Itirapina	*Atractus pantostictus*	2	-0.135	0.302	0.312	-0.360	1.620	Fossorial	Dipsadidae	0.064	-0.371
Itirapina	*Boa constrictor*	4	1.211	0.458	0.421	-0.360	4.550	Semiarboreal	Boidae	0.968	-0.569
Itirapina	*Boiruna maculata*	3	0.538	0.022	0.487	2.788	2.870	Terrestrial	Dipsadidae	1.710	1.142
Itirapina	*Bothrops alternatus*	1	-0.807	-0.617	0.246	-0.360	3.380	Terrestrial	Viperidae	-0.880	-0.442
Itirapina	*Bothrops itapetiningae*	5	1.883	0.635	0.641	-0.360	2.150	Terrestrial	Viperidae	1.542	-0.777
Itirapina	*Bothrops moojeni*	6	2.556	2.207	0.773	2.788	3.770	Semiarboreal	Viperidae	4.244	1.164
Itirapina	*Bothrops pauloensis*	6	2.556	2.207	0.773	2.788	2.670	Terrestrial	Viperidae	4.244	1.164

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Itirapina	*Chironius flavolineatus*	1	-0.807	-0.617	0.246	-0.360	2.270	Semiarboreal	Colubridae	-0.880	-0.442
Itirapina	*Crotalus durissus*	2	-0.135	-0.586	0.356	-0.360	3.460	Terrestrial	Viperidae	-0.434	-0.594
Itirapina	*Epicrates crassus*	2	-0.135	-0.580	0.290	-0.360	3.210	Semiarboreal	Boidae	-0.456	-0.541
Itirapina	*Erythrolamprus jaegeri*	1	-0.807	-0.617	0.246	-0.360	1.800	Semiaquatic	Dipsadidae	-0.880	-0.442
Itirapina	*Erythrolamprus poecilogyrus*	2	-0.135	-0.332	0.487	-0.360	1.830	Terrestrial	Dipsadidae	-0.236	-0.644
Itirapina	*Helicops modestus*	3	0.538	1.200	0.290	-0.360	1.960	Aquatic	Dipsadidae	0.962	-0.235
Itirapina	*Lygophis meridionalis*	1	-0.807	-0.617	0.246	-0.360	1.980	Terrestrial	Dipsadidae	-0.880	-0.442
Itirapina	*Micrurus frontalis*	2	-0.135	3.552	0.246	-0.360	2.770	Semifossorial	Elapidae	1.923	0.372
Itirapina	*Oxyrhopus guibei*	2	-0.135	-0.586	0.356	-0.360	2.550	Terrestrial	Dipsadidae	-0.434	-0.594
Itirapina	*Oxyrhopus rhombifer*	2	-0.135	-0.586	0.356	-0.360	2.110	Terrestrial	Dipsadidae	-0.434	-0.594
Itirapina	*Phalotris lativittatus*	1	-0.807	-0.617	-0.303	-0.360	1.980	Fossorial	Dipsadidae	-1.093	-0.009
Itirapina	*Phalotris mertensi*	1	-0.807	-0.617	-0.303	-0.360	2.720	Fossorial	Dipsadidae	-1.093	-0.009
Itirapina	*Phalotris multipunctatus*	1	-0.807	-0.617	-0.303	-0.360	1.220	Fossorial	Dipsadidae	-1.093	-0.009
Itirapina	*Philodryas aestiva*	4	1.211	0.170	0.597	-0.360	2.230	Semiarboreal	Dipsadidae	0.869	-0.769
Itirapina	*Philodryas agassizii*	2	-0.135	-0.596	-3.135	-0.360	1.460	Terrestrial	Dipsadidae	-1.790	2.157
Itirapina	*Philodryas olfersii*	4	1.211	0.170	0.597	-0.360	2.660	Semiarboreal	Dipsadidae	0.869	-0.769
Itirapina	*Philodryas patagoniensis*	5	1.883	1.575	0.729	2.788	2.710	Terrestrial	Dipsadidae	3.475	1.136
Itirapina	*Phimophis guerini*	2	-0.135	-0.586	0.356	-0.360	2.510	Terrestrial	Dipsadidae	-0.434	-0.594
Itirapina	*Rhachidelus brazili*	2	-0.135	0.302	0.180	-0.360	2.770	Terrestrial	Dipsadidae	0.013	-0.267
Itirapina	*Sibynomorphus mikanii*	1	-0.807	-0.617	-3.157	-0.360	1.860	Terrestrial	Dipsadidae	-2.197	2.242
Itirapina	*Simophis rhinostoma*	1	-0.807	-0.617	0.246	-0.360	2.050	Terrestrial	Colubridae	-0.880	-0.442
Itirapina	*Taeniophallus occipitalis*	1	-0.807	-0.617	0.312	-0.360	1.610	Semifossorial	Dipsadidae	-0.855	-0.494
Itirapina	*Tantilla melanocephala*	1	-0.807	-0.617	0.070	-0.360	1.190	Semifossorial	Colubridae	-0.948	-0.303
Itirapina	*Thamnodynastes hypoconia*	1	-0.807	-0.617	0.246	-0.360	1.750	Semiarboreal	Dipsadidae	-0.880	-0.442
Itirapina	*Trilepida koppesi*	1	-0.807	-0.617	-3.157	-0.360	0.850	Fossorial	Leptotyphlopidae	-2.197	2.242
Itirapina	*Xenodon merremii*	1	-0.807	-0.617	0.246	-0.360	2.230	Terrestrial	Dipsadidae	-0.880	-0.442
Itirapina	*Xenodon nattereri*	2	-0.135	0.302	0.312	-0.360	1.560	Terrestrial	Dipsadidae	0.064	-0.371
Japi	*Bothrops jararaca*	5	0.836	0.588	0.489	-0.624	3.310	Semiarboreal	Viperidae	0.741	-0.704
Japi	*Chironius bicarinatus*	3	-0.152	-0.667	0.246	-0.624	2.720	Semiarboreal	Colubridae	-0.647	-0.673
Japi	*Chironius exoletus*	2	-0.646	-0.744	0.170	-0.624	2.550	Semiarboreal	Colubridae	-1.005	-0.576
Japi	*Crotalus durissus*	1	-1.140	-0.763	-0.293	-0.624	3.460	Terrestrial	Viperidae	-1.478	-0.161
Japi	*Dipsas bucephala*	1	-1.140	-0.763	-3.197	-0.624	1.700	Semiarboreal	Dipsadidae	-2.602	2.129
Japi	*Erythrolamprus aesculapii*	2	-0.646	-0.704	-0.347	-0.624	2.140	Terrestrial	Dipsadidae	-1.181	-0.160
Japi	*Erythrolamprus miliaris*	5	0.836	1.515	0.489	1.693	2.040	Semiaquatic	Dipsadidae	2.276	0.805
Japi	*Oxyrhopus guibei*	2	-0.646	-0.689	0.170	-0.624	2.550	Terrestrial	Dipsadidae	-0.973	-0.564
Japi	*Philodryas olfersii*	5	0.836	0.112	0.579	0.535	2.660	Semiarboreal	Dipsadidae	0.998	-0.220
Japi	*Philodryas patagoniensis*	7	1.824	1.811	0.768	1.693	2.710	Terrestrial	Dipsadidae	3.122	0.542

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Japi	*Spilotes pullatus*	6	1.330	1.576	0.579	-0.624	3.480	Arboreal	Colubridae	1.632	-0.619
Japi	*Taeniophallus affinis*	3	-0.152	-0.508	0.323	1.693	1.850	Terrestrial	Dipsadidae	0.472	0.613
Japi	*Xenodon neuwiedii*	1	-1.140	-0.763	0.026	-0.624	1.980	Terrestrial	Dipsadidae	-1.355	-0.413
Jureia	*Bothrops jararaca*	5	1.471	0.052	0.498	-0.368	3.310	Semiarboreal	Viperidae	0.908	-0.749
Jureia	*Bothrops jararacussu*	5	1.471	2.230	0.657	2.696	3.710	Terrestrial	Viperidae	3.551	1.325
Jureia	*Chironius bicarinatus*	3	0.224	-0.474	0.442	-0.368	2.720	Semiarboreal	Colubridae	-0.134	-0.682
Jureia	*Chironius exoletus*	2	-0.399	-0.607	0.414	-0.368	2.550	Semiarboreal	Colubridae	-0.579	-0.621
Jureia	*Chironius fuscus*	4	0.848	-0.367	0.470	-0.368	2.590	Semiarboreal	Colubridae	0.297	-0.748
Jureia	*Chironius multiventris*	1	-1.022	-0.644	0.330	-0.368	3.130	Semiarboreal	Colubridae	-0.990	-0.495
Jureia	*Corallus hortulanus*	6	2.095	1.066	0.535	-0.368	3.590	Arboreal	Boidae	1.868	-0.630
Jureia	*Dipsas indica*	1	-1.022	-0.644	-2.626	-0.368	2.260	Arboreal	Dipsadidae	-2.134	1.837
Jureia	*Echinanthera cyanopleura*	2	-0.399	-0.607	0.414	-0.368	1.610	Terrestrial	Dipsadidae	-0.579	-0.621
Jureia	*Echinanthera undulata*	1	-1.022	-0.644	0.330	-0.368	1.650	Terrestrial	Dipsadidae	-0.990	-0.495
Jureia	*Erythrolamprus aesculapii*	2	-0.399	-0.591	0.021	-0.368	2.140	Terrestrial	Dipsadidae	-0.722	-0.307
Jureia	*Erythrolamprus miliaris*	5	1.471	2.654	0.657	2.696	2.040	Semiaquatic	Dipsadidae	3.797	1.415
Jureia	*Helicops carinicaudus*	2	-0.399	-0.405	0.358	-0.368	2.240	Aquatic	Dipsadidae	-0.484	-0.534
Jureia	*Imantodes cenchoa*	2	-0.399	-0.607	0.414	-0.368	2.710	Arboreal	Dipsadidae	-0.579	-0.621
Jureia	*Micrurus corallinus*	3	0.224	2.187	0.096	-0.368	2.390	Semifossorial	Elapidae	1.276	0.157
Jureia	*Oxyrhopus clathratus*	2	-0.399	-0.617	0.273	-0.368	1.980	Terrestrial	Dipsadidae	-0.639	-0.512
Jureia	*Sibynomorphus neuwiedi*	1	-1.022	-0.644	-2.626	-0.368	2.000	Terrestrial	Dipsadidae	-2.134	1.837
Jureia	*Siphlophis pulcher*	2	-0.399	-0.052	0.414	2.696	2.220	Semiarboreal	Dipsadidae	1.061	1.233
Jureia	*Sordellina punctata*	2	-0.399	0.340	-0.522	-0.368	1.680	Aquatic	Dipsadidae	-0.391	0.318
Jureia	*Spilotes pullatus*	6	2.095	1.066	0.535	-0.368	3.480	Arboreal	Colubridae	1.868	-0.630
Jureia	*Taeniophallus bilineatus*	3	0.224	-0.239	0.442	-0.368	1.010	Terrestrial	Dipsadidae	0.003	-0.632
Jureia	*Thamnodynastes strigatus*	1	-1.022	-0.644	0.330	-0.368	1.980	Terrestrial	Dipsadidae	-0.990	-0.495
Jureia	*Tomodon dorsatus*	1	-1.022	-0.644	-2.626	-0.368	1.980	Terrestrial	Dipsadidae	-2.134	1.837
Jureia	*Tropidodryas serra*	3	0.224	-0.522	0.442	-0.368	2.260	Semiarboreal	Dipsadidae	-0.161	-0.692
Jureia	*Xenodon neuwiedii*	1	-1.022	-0.644	0.330	-0.368	1.980	Terrestrial	Dipsadidae	-0.990	-0.495
Kansas	*Agkistrodon contortrix*	7	1.692	1.906	1.361	-0.435	3.100	Terrestrial	Viperidae	2.415	-1.097
Kansas	*Carphophis vermis*	1	-1.141	-0.871	-1.597	-0.435	1.190	Fossorial	Dipsadidae	-1.965	0.952
Kansas	*Coluber constrictor*	7	1.692	1.072	1.361	-0.435	2.780	Terrestrial	Colubridae	1.932	-1.274
Kansas	*Crotalus horridus*	2	-0.669	-0.815	-0.372	-0.435	3.520	Terrestrial	Viperidae	-1.187	-0.054
Kansas	*Diadophis punctatus*	3	-0.197	0.584	0.022	2.175	2.070	Semifossorial	Dipsadidae	1.171	1.360
Kansas	*Lampropeltis calligaster*	5	0.748	-0.019	0.752	-0.435	2.460	Terrestrial	Colubridae	0.522	-0.924
Kansas	*Lampropeltis triangulum*	3	-0.197	-0.231	0.486	-0.435	2.780	Terrestrial	Colubridae	-0.246	-0.657
Kansas	*Nerodia sipedon*	1	-1.141	-0.691	0.022	-0.435	3.030	Aquatic	Colubridae	-1.234	-0.288
Kansas	*Pantherophis obsoletus*	5	0.748	-0.871	-1.006	-0.435	3.110	Arboreal	Colubridae	-0.653	0.282

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Kansas	*Pituophis melanoleucus*	3	-0.197	-0.702	-0.182	-0.435	2.980	Terrestrial	Colubridae	-0.778	-0.231
Kansas	*Storeria dekayi*	1	-1.141	-0.871	-1.597	-0.435	1.530	Terrestrial	Colubridae	-1.965	0.952
Kansas	*Thamnophis sirtalis*	3	-0.197	1.507	0.752	2.175	2.940	Aquatic	Colubridae	1.988	0.981
Manaus	*Amerotyphlops reticulatus*	1	-0.875	-0.364	-0.795	-0.174	2.000	Fossorial	Typhlopidae	-1.095	0.545
Manaus	*Anilius scytale*	4	0.632	-0.071	-0.095	-0.174	2.500	Fossorial	Aniliidae	0.209	-0.107
Manaus	*Atractus alphonsehogei*	1	-0.875	-0.364	-0.822	-0.174	0.700	Fossorial	Dipsadidae	-1.106	0.567
Manaus	*Atractus latifrons*	2	-0.372	-0.348	-0.768	-0.174	1.700	Fossorial	Dipsadidae	-0.787	0.474
Manaus	*Atractus major*	2	-0.372	-0.348	-0.768	-0.174	2.000	Fossorial	Dipsadidae	-0.787	0.474
Manaus	*Atractus poeppigi*	1	-0.875	-0.364	-0.822	-0.174	1.500	Fossorial	Dipsadidae	-1.106	0.567
Manaus	*Atractus schach*	2	-0.372	-0.348	-0.768	-0.174	1.300	Fossorial	Dipsadidae	-0.787	0.474
Manaus	*Atractus snethlageae*	2	-0.372	-0.348	-0.768	-0.174	1.900	Fossorial	Dipsadidae	-0.787	0.474
Manaus	*Atractus torquatus*	2	-0.372	-0.348	-0.768	-0.174	1.900	Fossorial	Dipsadidae	-0.787	0.474
Manaus	*Boa constrictor*	6	1.636	-0.048	0.282	-0.174	4.500	Semiarboreal	Boidae	0.944	-0.508
Manaus	*Bothrops atrox*	6	1.636	1.039	0.767	3.428	3.300	Semiarboreal	Viperidae	3.312	1.382
Manaus	*Chironius fuscus*	3	0.130	0.387	0.605	-0.174	2.600	Semiarboreal	Colubridae	0.458	-0.508
Manaus	*Chironius multiventris*	2	-0.372	-0.261	0.578	-0.174	3.100	Semiarboreal	Colubridae	-0.216	-0.570
Manaus	*Chironius scurrulus*	2	-0.372	-0.261	0.578	-0.174	3.000	Semiarboreal	Colubridae	-0.216	-0.570
Manaus	*Clelia clelia*	5	1.134	-0.089	0.282	-0.174	3.200	Terrestrial	Dipsadidae	0.632	-0.462
Manaus	*Corallus caninus*	3	0.130	-0.284	0.228	-0.174	3.500	Arboreal	Boidae	-0.077	-0.353
Manaus	*Corallus hortulanus*	8	2.640	0.795	0.767	-0.174	3.600	Arboreal	Boidae	2.196	-0.819
Manaus	*Dendrophidion dendrophis*	1	-0.875	-0.364	0.040	-0.174	2.300	Arboreal	Colubridae	-0.772	-0.113
Manaus	*Dipsas indica*	1	-0.875	-0.364	-4.780	-0.174	2.300	Arboreal	Dipsadidae	-2.637	3.689
Manaus	*Dipsas pavonina*	1	-0.875	-0.364	-4.780	-0.174	1.900	Arboreal	Dipsadidae	-2.637	3.689
Manaus	*Drepanoides anomalus*	2	-0.372	-0.275	0.174	-0.174	2.000	Terrestrial	Dipsadidae	-0.380	-0.254
Manaus	*Drymoluber dichrous*	4	0.632	0.117	0.659	-0.174	2.400	Terrestrial	Colubridae	0.610	-0.662
Manaus	*Epicrates cenchria*	6	1.636	0.369	0.713	-0.174	3.700	Semiarboreal	Boidae	1.353	-0.759
Manaus	*Epictia tenella*	1	-0.875	-0.364	-0.795	-0.174	0.600	Fossorial	Leptotyphlopidae	-1.095	0.545
Manaus	*Erythrolamprus aesculapii*	3	0.130	-0.145	0.524	-0.174	2.100	Terrestrial	Dipsadidae	0.118	-0.557
Manaus	*Erythrolamprus breviceps*	5	1.134	6.702	0.524	7.030	1.700	Terrestrial	Dipsadidae	7.765	4.871
Manaus	*Erythrolamprus pygmaeus*	1	-0.875	-0.364	0.040	-0.174	0.700	Terrestrial	Dipsadidae	-0.772	-0.113
Manaus	*Erythrolamprus reginae*	3	0.130	-0.120	0.605	-0.174	2.000	Terrestrial	Dipsadidae	0.164	-0.615
Manaus	*Erythrolamprus typhlus*	2	-0.372	-0.261	0.578	-0.174	2.100	Terrestrial	Dipsadidae	-0.216	-0.570
Manaus	*Eunectes murinus*	12	4.648	3.281	0.928	-0.174	5.500	Aquatic	Boidae	4.852	-0.635
Manaus	*Helicops angulatus*	4	0.632	0.187	0.686	-0.174	2.300	Aquatic	Dipsadidae	0.661	-0.668
Manaus	*Helicops hagmanni*	1	-0.875	-0.364	-0.311	-0.174	2.200	Aquatic	Dipsadidae	-0.908	0.163
Manaus	*Imantodes cenchoa*	2	-0.372	-0.261	0.578	-0.174	2.700	Arboreal	Dipsadidae	-0.216	-0.570
Manaus	*Lachesis muta*	1	-0.875	-0.364	-0.418	-0.174	4.300	Terrestrial	Viperidae	-0.949	0.248

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Manaus	*Leptodeira annulata*	3	0.130	-0.120	0.605	-0.174	2.300	Arboreal	Dipsadidae	0.164	-0.615
Manaus	*Leptophis ahaetulla*	3	0.130	-0.120	0.605	-0.174	3.000	Arboreal	Colubridae	0.164	-0.615
Manaus	*Mastigodryas boddaerti*	5	1.134	0.206	0.686	-0.174	2.500	Terrestrial	Colubridae	0.960	-0.718
Manaus	*Micrurus averyi*	2	-0.372	-0.337	0.201	-0.174	2.100	Semifossorial	Elapidae	-0.406	-0.289
Manaus	*Micrurus hemprichii*	4	0.632	0.466	0.228	-0.174	2.300	Semifossorial	Elapidae	0.646	-0.248
Manaus	*Micrurus lemniscatus*	5	1.134	0.601	0.578	-0.174	2.700	Semifossorial	Elapidae	1.147	-0.549
Manaus	*Micrurus spixii*	3	0.130	-0.181	0.228	-0.174	2.900	Semifossorial	Elapidae	-0.017	-0.331
Manaus	*Micrurus surinamensis*	3	0.130	-0.145	0.524	-0.174	2.700	Aquatic	Elapidae	0.118	-0.557
Manaus	*Oxybelis aeneus*	2	-0.372	-0.261	0.578	-0.174	2.500	Arboreal	Colubridae	-0.216	-0.570
Manaus	*Oxybelis fulgidus*	2	-0.372	-0.349	0.174	-0.174	2.900	Arboreal	Colubridae	-0.423	-0.270
Manaus	*Oxyrhopus melanogenys*	3	0.130	-0.319	0.228	-0.174	2.200	Terrestrial	Dipsadidae	-0.097	-0.360
Manaus	*Oxyrhopus formosus*	1	-0.875	-0.364	0.147	-0.174	2.300	Terrestrial	Dipsadidae	-0.730	-0.198
Manaus	*Philodryas argentea*	2	-0.372	-0.261	0.578	-0.174	2.500	Arboreal	Dipsadidae	-0.216	-0.570
Manaus	*Philodryas viridissima*	3	0.130	-0.160	0.632	-0.174	2.400	Arboreal	Dipsadidae	0.151	-0.645
Manaus	*Phrynonax polylepis*	4	0.632	-0.200	0.228	-0.174	3.000	Terrestrial	Colubridae	0.259	-0.389
Manaus	*Pseudoboa coronata*	4	0.632	-0.254	0.255	-0.174	2.300	Terrestrial	Dipsadidae	0.238	-0.422
Manaus	*Pseudoboa neuwiedii*	1	-0.875	-0.364	0.147	-0.174	2.400	Terrestrial	Dipsadidae	-0.730	-0.198
Manaus	*Rhinobothryum lentiginosum*	1	-0.875	-0.364	0.147	-0.174	2.600	Terrestrial	Colubridae	-0.730	-0.198
Manaus	*Siphlophis cervinus*	2	-0.372	-0.261	0.578	-0.174	2.300	Arboreal	Dipsadidae	-0.216	-0.570
Manaus	*Siphlophis compressus*	1	-0.875	-0.364	0.147	-0.174	2.600	Arboreal	Dipsadidae	-0.730	-0.198
Manaus	*Spilotes pullatus*	5	1.134	0.222	0.686	-0.174	3.500	Arboreal	Colubridae	0.969	-0.715
Manaus	*Spilotes sulphureus*	3	0.130	-0.319	0.228	-0.174	3.200	Arboreal	Colubridae	-0.097	-0.360
Manaus	*Taeniophallus brevirostris*	1	-0.875	-0.364	0.147	-0.174	1.500	Terrestrial	Dipsadidae	-0.730	-0.198
Manaus	*Taeniophallus nicagus*	1	-0.875	-0.364	0.040	-0.174	1.400	Semifossorial	Dipsadidae	-0.772	-0.113
Manaus	*Tantilla melanocephala*	1	-0.875	-0.364	-0.553	-0.174	1.200	Semifossorial	Colubridae	-1.001	0.354
Manaus	*Typhlophis squamosus*	1	-0.875	-0.364	-0.795	-0.174	0.600	Fossorial	Typhlopidae	-1.095	0.545
Manaus	*Xenodon rabdocephalus*	1	-0.875	-0.364	0.040	-0.174	2.100	Terrestrial	Dipsadidae	-0.772	-0.113
Manaus	*Xenopholis scalaris*	1	-0.875	-0.364	0.040	-0.174	1.100	Terrestrial	Dipsadidae	-0.772	-0.113
Pantanal	*Amerotyphlops brongersmianus*	1	-0.666	-0.443	-4.443	-0.683	1.260	Fossorial	Typhlopidae	-2.651	3.095
Pantanal	*Boa constrictor*	4	0.847	-0.102	0.133	2.163	4.550	Semiarboreal	Boidae	1.409	1.008
Pantanal	*Bothrops moojeni*	6	1.856	1.898	0.988	2.163	3.770	Semiarboreal	Viperidae	3.478	0.649
Pantanal	*Bothrops neuwiedi*	2	-0.161	-0.136	0.601	2.163	2.720	Terrestrial	Viperidae	0.992	0.740
Pantanal	*Chironius aff multiventris*	1	-0.666	-0.443	-0.156	0.740	3.130	Semiarboreal	Colubridae	-0.380	0.520
Pantanal	*Chironius quadricarinatus*	1	-0.666	-0.443	-0.156	0.740	2.270	Semiarboreal	Colubridae	-0.380	0.520
Pantanal	*Clelia clelia*	3	0.343	-0.273	0.196	0.740	3.240	Terrestrial	Dipsadidae	0.432	0.170
Pantanal	*Crotalus durissus*	1	-0.666	-0.443	-0.210	0.740	3.460	Terrestrial	Viperidae	-0.401	0.562
Pantanal	*Drymarchon corais*	2	-0.161	-0.164	0.394	0.740	3.140	Terrestrial	Colubridae	0.283	0.091

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Pantanal	*Erythrolamprus almadensis*	1	-0.666	-0.443	-0.156	0.740	1.770	Terrestrial	Dipsadidae	-0.380	0.520
Pantanal	*Erythrolamprus poecilogyrus*	1	-0.666	-0.443	-0.156	-0.683	1.830	Terrestrial	Dipsadidae	-0.992	-0.286
Pantanal	*Erythrolamprus reginae*	1	-0.666	-0.443	-0.156	-0.683	1.990	Terrestrial	Dipsadidae	-0.992	-0.286
Pantanal	*Eunectes notaeus*	10	3.873	4.278	0.826	-0.683	4.400	Aquatic	Boidae	4.728	-0.547
Pantanal	*Helicops leopardinus*	2	-0.161	-0.062	0.322	-0.683	1.990	Aquatic	Dipsadidae	-0.298	-0.637
Pantanal	*Hydrodynastes gigas*	3	0.343	0.401	0.745	-0.683	3.340	Aquatic	Colubridae	0.423	-0.926
Pantanal	*Leptophis ahaetulla*	2	-0.161	-0.215	0.529	-0.683	2.960	Arboreal	Colubridae	-0.306	-0.832
Pantanal	*Micrurus pyrrhocryptus*	1	-0.666	-0.443	-0.408	-0.683	2.990	Semifossorial	Elapidae	-1.090	-0.088
Pantanal	*Mussurana bicolor*	3	0.343	0.121	0.673	-0.683	2.250	Terrestrial	Dipsadidae	0.233	-0.929
Pantanal	*Oxyrhopus petolarius*	3	0.343	-0.359	0.079	-0.683	3.100	Terrestrial	Dipsadidae	-0.275	-0.562
Pantanal	*Palusophis bifossatus*	3	0.343	0.115	0.673	-0.683	2.650	Terrestrial	Colubridae	0.230	-0.930
Pantanal	*Pseudoboa nigra*	2	-0.161	-0.418	0.015	-0.683	2.720	Terrestrial	Dipsadidae	-0.623	-0.471
Pantanal	*Pseudoeryx plicalilis*	1	-0.666	-0.443	-0.552	-0.683	2.300	Terrestrial	Dipsadidae	-1.146	0.026
Pantanal	*Psomophis joberti*	2	-0.161	-0.215	0.529	-0.683	1.130	Terrestrial	Dipsadidae	-0.306	-0.832
Pantanal	*Thamnodynastes pallidus*	1	-0.666	-0.443	-0.156	-0.683	1.350	Semiarboreal	Dipsadidae	-0.992	-0.286
Pantanal	*Xenopholis cf undulatus*	1	-0.666	-0.443	-0.156	-0.683	1.380	Terrestrial	Dipsadidae	-0.992	-0.286
Paraiba	*Amerotyphlops brongersmianus*	1	-0.997	-0.723	-2.069	-0.723	1.260	Fossorial	Typhlopidae	-2.103	1.176
Paraiba	*Boa constrictor*	5	0.997	0.292	0.475	-0.723	4.550	Semiarboreal	Boidae	0.614	-0.830
Paraiba	*Bothrops leucurus*	6	1.496	0.874	0.624	1.052	3.560	Semiarboreal	Viperidae	2.059	0.129
Paraiba	*Chironius flavolineatus*	2	-0.499	-0.582	0.487	1.052	2.270	Semiarboreal	Colubridae	0.018	0.142
Paraiba	*Corallus hortulanus*	6	1.496	1.527	0.587	1.052	3.590	Arboreal	Boidae	2.423	0.297
Paraiba	*Crotalus durissus*	1	-0.997	-0.723	0.351	-0.723	3.460	Terrestrial	Viperidae	-1.167	-0.733
Paraiba	*Epicrates assisi*	3	0.000	-0.647	0.438	-0.723	3.270	Semiarboreal	Boidae	-0.517	-0.892
Paraiba	*Epictia borapeliotes*	1	-0.997	-0.723	-2.069	-0.723	0.290	Fossorial	Leptotyphlopidae	-2.103	1.176
Paraiba	*Erythrolamprus taeniogaster*	2	-0.499	-0.455	0.400	-0.723	2.130	Semiaquatic	Dipsadidae	-0.706	-0.769
Paraiba	*Helicops angulatus*	3	0.000	1.326	0.425	-0.723	2.250	Aquatic	Dipsadidae	0.622	-0.463
Paraiba	*Hydrodynastes gigas*	4	0.499	0.881	0.574	2.827	3.340	Aquatic	Colubridae	2.236	1.282
Paraiba	*Micrurus ibiboboca*	2	-0.499	-0.704	0.239	-0.723	2.700	Semifossorial	Elapidae	-0.913	-0.694
Paraiba	*Micrurus potyguara*	2	-0.499	-0.704	0.239	-0.723	2.310	Semifossorial	Elapidae	-0.913	-0.694
Paraiba	*Oxybelis aeneus*	2	-0.499	-0.582	0.487	1.052	2.530	Arboreal	Colubridae	0.018	0.142
Paraiba	*Oxyrhopus petolarius*	3	0.000	-0.647	0.438	-0.723	3.100	Terrestrial	Dipsadidae	-0.517	-0.892
Paraiba	*Oxyrhopus trigeminus*	3	0.000	-0.647	0.438	-0.723	2.300	Terrestrial	Dipsadidae	-0.517	-0.892
Paraiba	*Palusophis bifossatus*	4	0.499	0.004	0.587	1.052	2.650	Terrestrial	Colubridae	0.968	0.080
Paraiba	*Philodryas nattereri*	6	1.496	0.874	0.624	1.052	2.530	Terrestrial	Dipsadidae	2.059	0.129
Paraiba	*Philodryas olfersii*	6	1.496	0.874	0.624	1.052	2.660	Semiarboreal	Dipsadidae	2.059	0.129
Paraiba	*Philodryas patagoniensis*	7	1.994	2.655	0.649	1.052	2.710	Terrestrial	Dipsadidae	3.387	0.434
Paraiba	*Phimophis guerini*	1	-0.997	-0.723	0.351	-0.723	2.510	Terrestrial	Dipsadidae	-1.167	-0.733

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Paraiba	*Sibon nebulatus*	1	-0.997	-0.723	-2.094	-0.723	2.240	Arboreal	Dipsadidae	-2.113	1.196
Paraiba	*Sibynomorphus mikanii*	1	-0.997	-0.723	-2.094	-0.723	1.860	Terrestrial	Dipsadidae	-2.113	1.196
Paraiba	*Spilotes pullatus*	6	1.496	2.172	0.587	1.052	3.480	Arboreal	Colubridae	2.797	0.434
Paraiba	*Taeniophallus occipitalis*	1	-0.997	-0.723	0.388	-0.723	1.610	Semifossorial	Dipsadidae	-1.152	-0.762
Paraiba	*Tantilla melanocephala*	1	-0.997	-0.723	-2.069	-0.723	1.190	Semifossorial	Colubridae	-2.103	1.176
Paraiba	*Xenodon merremii*	1	-0.997	-0.723	0.388	-0.723	2.230	Terrestrial	Dipsadidae	-1.152	-0.762
Picinguaba	*Bothrops jararaca*	5	1.567	0.542	0.480	-0.455	3.310	Semiarboreal	Viperidae	1.203	-0.690
Picinguaba	*Bothrops jararacussu*	5	1.567	1.353	0.542	0.620	3.710	Terrestrial	Viperidae	2.159	0.042
Picinguaba	*Cercophis auratus*	2	-0.437	-0.610	0.382	-0.455	1.820	Semiarboreal	Dipsadidae	-0.652	-0.642
Picinguaba	*Chironius bicarinatus*	3	0.231	-0.429	0.409	-0.455	2.720	Semiarboreal	Colubridae	-0.154	-0.696
Picinguaba	*Chironius exoletus*	2	-0.437	-0.610	0.382	-0.455	2.550	Semiarboreal	Colubridae	-0.652	-0.642
Picinguaba	*Chironius foveatus*	2	-0.437	-0.593	0.284	-0.455	2.970	Semiarboreal	Colubridae	-0.680	-0.561
Picinguaba	*Chironius fuscus*	4	0.899	-0.221	0.444	-0.455	2.590	Semiarboreal	Colubridae	0.364	-0.752
Picinguaba	*Chironius laevicollis*	1	-1.104	-0.691	0.258	-0.455	2.720	Terrestrial	Colubridae	-1.130	-0.489
Picinguaba	*Clelia plumbea*	3	0.231	-0.263	0.284	1.695	3.270	Terrestrial	Dipsadidae	0.819	0.655
Picinguaba	*Dipsas indica*	1	-1.104	-0.691	-2.736	-0.455	2.260	Arboreal	Dipsadidae	-2.288	1.873
Picinguaba	*Dipsas sp*	1	-1.104	-0.691	-2.736	-0.455	NA	Semiarboreal	Dipsadidae	-2.288	1.873
Picinguaba	*Echinanthera cephalostriata*	1	-1.104	-0.691	0.258	-0.455	1.630	Terrestrial	Dipsadidae	-1.130	-0.489
Picinguaba	*Echinanthera undulata*	1	-1.104	-0.691	0.258	-0.455	1.650	Terrestrial	Dipsadidae	-1.130	-0.489
Picinguaba	*Erythrolamprus miliaris*	5	1.567	2.485	0.542	3.845	2.040	Semiaquatic	Dipsadidae	4.203	2.110
Picinguaba	*Helicops carinicaudus*	2	-0.437	-0.256	0.284	-0.455	2.240	Aquatic	Dipsadidae	-0.485	-0.489
Picinguaba	*Imantodes cenchoa*	2	-0.437	-0.610	0.382	-0.455	2.710	Arboreal	Dipsadidae	-0.652	-0.642
Picinguaba	*Micrurus corallinus*	3	0.231	1.095	-0.044	-0.455	2.390	Semifossorial	Elapidae	0.555	-0.015
Picinguaba	*Oxyrhopus clathratus*	2	-0.437	-0.647	0.195	-0.455	1.980	Terrestrial	Dipsadidae	-0.746	-0.502
Picinguaba	*Philodryas olfersii*	5	1.567	1.011	0.542	0.620	2.660	Semiarboreal	Dipsadidae	1.961	-0.030
Picinguaba	*Sibynomorphus neuwiedi*	1	-1.104	-0.691	-2.736	-0.455	2.000	Terrestrial	Dipsadidae	-2.288	1.873
Picinguaba	*Siphlophis pulcher*	2	-0.437	-0.455	0.258	0.620	2.220	Arboreal	Dipsadidae	-0.148	0.099
Picinguaba	*Spilotes pullatus*	6	2.235	3.023	0.515	-0.455	3.480	Arboreal	Colubridae	3.038	-0.262
Picinguaba	*Taeniophallus affinis*	3	0.231	0.392	0.480	1.695	1.850	Terrestrial	Dipsadidae	1.275	0.640
Picinguaba	*Taeniophallus bilineatus*	3	0.231	0.073	0.409	-0.455	1.010	Terrestrial	Dipsadidae	0.137	-0.589
Picinguaba	*Thamnodynastes strigatus*	3	0.231	-0.442	0.409	-0.455	1.980	Terrestrial	Dipsadidae	-0.161	-0.699
Picinguaba	*Xenodon neuwiedii*	1	-1.104	-0.691	0.258	-0.455	1.980	Terrestrial	Dipsadidae	-1.130	-0.489
SPapagaio	*Apostolepis assimilis*	1	-0.970	-0.648	-0.006	-0.418	1.460	Semifossorial	Dipsadidae	-1.114	-0.266
SPapagaio	*Atractus zebrinus*	1	-0.970	-0.648	-2.204	-0.418	1.750	Fossorial	Dipsadidae	-1.965	1.468
SPapagaio	*Boiruna maculata*	4	0.918	-0.069	0.559	-0.418	2.870	Terrestrial	Dipsadidae	0.523	-0.791
SPapagaio	*Bothrops fonsecai*	1	-0.970	-0.648	0.241	-0.418	2.810	Terrestrial	Viperidae	-1.019	-0.460
SPapagaio	*Bothrops jararaca*	5	1.547	1.450	0.590	-0.418	3.310	Semiarboreal	Viperidae	1.777	-0.561

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
SPapagaio	*Bothrops neuwiedi*	1	-0.970	-0.648	0.241	-0.418	2.720	Terrestrial	Viperidae	-1.019	-0.460
SPapagaio	*Chironius bicarinatus*	3	0.288	-0.440	0.487	-0.418	2.720	Semiarboreal	Colubridae	-0.081	-0.746
SPapagaio	*Chironius brazili*	1	-0.970	-0.648	0.354	-0.418	NA	Semiarboreal	Colubridae	-0.975	-0.549
SPapagaio	*Crotalus durissus*	2	-0.341	-0.550	0.446	-0.418	3.460	Terrestrial	Viperidae	-0.522	-0.669
SPapagaio	*Echinanthera cephalostriata*	2	-0.341	-0.298	0.374	1.254	1.630	Terrestrial	Dipsadidae	0.316	0.388
SPapagaio	*Erythrolamprus miliaris*	5	1.547	2.523	0.559	2.925	2.040	Semiaquatic	Dipsadidae	3.826	1.585
SPapagaio	*Gomesophis brasiliensis*	1	-0.970	-0.648	-2.204	-0.418	1.250	Semiaquatic	Dipsadidae	-1.965	1.468
SPapagaio	*Mussurana montana*	2	-0.341	-0.452	0.395	-0.418	2.400	Terrestrial	Dipsadidae	-0.484	-0.608
SPapagaio	*Oxyrhopus clathratus*	2	-0.341	-0.550	0.446	-0.418	1.980	Terrestrial	Dipsadidae	-0.522	-0.669
SPapagaio	*Oxyrhopus rhombifer*	3	0.288	-0.174	0.467	-0.418	2.110	Terrestrial	Dipsadidae	0.065	-0.673
SPapagaio	*Philodryas aestiva*	4	0.918	-0.069	0.559	-0.418	2.230	Semiarboreal	Dipsadidae	0.523	-0.791
SPapagaio	*Philodryas patagoniensis*	5	1.547	0.844	0.590	-0.418	2.710	Terrestrial	Dipsadidae	1.425	-0.690
SPapagaio	*Sibynomorphus mikanii*	1	-0.970	-0.648	-2.204	-0.418	1.860	Terrestrial	Dipsadidae	-1.965	1.468
SPapagaio	*Spilotes pullatus*	6	2.177	2.917	0.611	-0.418	3.480	Arboreal	Colubridae	2.996	-0.333
SPapagaio	*Taeniophallus affinis*	3	0.288	0.705	0.518	2.925	1.850	Terrestrial	Dipsadidae	2.034	1.367
SPapagaio	*Taeniophallus occipitalis*	2	-0.341	-0.571	0.467	-0.418	1.610	Semifossorial	Dipsadidae	-0.526	-0.690
SPapagaio	*Thamnodynastes strigatus*	4	0.918	0.567	0.559	1.254	1.980	Terrestrial	Dipsadidae	1.611	0.291
SPapagaio	*Tomodon dorsatus*	1	-0.970	-0.648	-2.204	-0.418	1.980	Terrestrial	Dipsadidae	-1.965	1.468
SPapagaio	*Xenodon merremii*	1	-0.970	-0.648	0.354	-0.418	2.230	Terrestrial	Dipsadidae	-0.975	-0.549
SVirginia	*Atractus sp*	1	-0.988	-0.578	-2.740	-0.455	NA	Fossorial	Dipsadidae	-2.158	1.888
SVirginia	*Bothrops jararaca*	5	1.716	0.601	0.493	-0.455	3.310	Semiarboreal	Viperidae	1.328	-0.704
SVirginia	*Bothrops jararacussu*	5	1.716	1.788	0.651	0.620	3.710	Terrestrial	Viperidae	2.540	0.032
SVirginia	*Cercophis auratus*	2	-0.312	-0.485	0.377	-0.455	1.820	Semiarboreal	Dipsadidae	-0.510	-0.624
SVirginia	*Chironius bicarinatus*	3	0.364	-0.299	0.398	-0.455	2.720	Semiarboreal	Colubridae	-0.006	-0.674
SVirginia	*Chironius exoletus*	2	-0.312	-0.485	0.377	-0.455	2.550	Semiarboreal	Colubridae	-0.510	-0.624
SVirginia	*Crotalus durissus*	1	-0.988	-0.578	0.007	-0.455	3.460	Terrestrial	Viperidae	-1.095	-0.279
SVirginia	*Dipsas alternans*	1	-0.988	-0.578	-2.719	-0.455	1.900	Arboreal	Dipsadidae	-2.149	1.871
SVirginia	*Echinanthera melanostigma*	1	-0.988	-0.578	0.260	-0.455	1.940	Terrestrial	Dipsadidae	-0.997	-0.479
SVirginia	*Echinanthera undulata*	1	-0.988	-0.578	0.260	-0.455	1.650	Terrestrial	Dipsadidae	-0.997	-0.479
SVirginia	*Elapomorphus quinquelineatus*	3	0.364	-0.086	0.208	-0.455	2.230	Semifossorial	Dipsadidae	0.044	-0.479
SVirginia	*Erythrolamprus aesculapii*	2	-0.312	-0.534	0.187	-0.455	2.140	Terrestrial	Dipsadidae	-0.612	-0.485
SVirginia	*Erythrolamprus atraventer*	1	-0.988	-0.578	0.260	-0.455	1.590	Terrestrial	Dipsadidae	-0.997	-0.479
SVirginia	*Erythrolamprus miliaris*	5	1.716	3.101	0.620	1.695	2.040	Semiaquatic	Dipsadidae	3.751	0.945
SVirginia	*Micrurus corallinus*	3	0.364	-0.086	0.208	-0.455	2.390	Semifossorial	Elapidae	0.044	-0.479
SVirginia	*Micrurus decoratus*	3	0.364	-0.086	0.208	-0.455	1.980	Semifossorial	Elapidae	0.044	-0.479
SVirginia	*Mussurana montana*	2	-0.312	-0.350	0.377	0.620	2.400	Terrestrial	Dipsadidae	0.030	0.013
SVirginia	*Oxyrhopus clathratus*	2	-0.312	-0.485	0.260	-0.455	1.980	Terrestrial	Dipsadidae	-0.555	-0.532

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
SVirginia	*Philodryas patagoniensis*	6	2.393	2.859	0.683	3.845	2.710	Terrestrial	Dipsadidae	4.949	1.989
SVirginia	*Sibynomorphus neuwiedi*	1	-0.988	-0.578	-2.719	-0.455	2.000	Terrestrial	Dipsadidae	-2.149	1.871
SVirginia	*Siphlophis pulcher*	2	-0.312	-0.350	0.377	0.620	2.220	Arboreal	Dipsadidae	0.030	0.013
SVirginia	*Taeniophallus affinis*	3	0.364	0.273	0.556	1.695	1.850	Terrestrial	Dipsadidae	1.312	0.540
SVirginia	*Taeniophallus persimilis*	1	-0.988	-0.578	0.260	-0.455	1.170	Semifossorial	Dipsadidae	-0.997	-0.479
SVirginia	*Thamnodynastes strigatus*	3	0.364	-0.208	0.430	-0.455	1.980	Terrestrial	Dipsadidae	0.059	-0.680
SVirginia	*Tropidodryas striaticeps*	4	1.040	0.030	0.461	-0.455	2.030	Semiarboreal	Dipsadidae	0.597	-0.727
SVirginia	*Xenodon neuwiedii*	1	-0.988	-0.578	0.260	-0.455	1.980	Terrestrial	Dipsadidae	-0.997	-0.479
Tapirai	*Atractus trihedrurus*	1	-0.955	-0.575	-2.836	-0.758	2.320	Fossorial	Dipsadidae	-2.305	1.789
Tapirai	*Atractus zebrinus*	1	-0.955	-0.575	-2.836	-0.758	1.750	Fossorial	Dipsadidae	-2.305	1.789
Tapirai	*Boiruna maculata*	4	1.230	0.279	0.345	1.679	2.870	Terrestrial	Dipsadidae	1.723	0.606
Tapirai	*Bothrops jararaca*	5	1.959	0.838	0.491	0.460	3.310	Semiarboreal	Viperidae	1.997	-0.159
Tapirai	*Bothrops jararacussu*	5	1.959	2.519	0.553	2.898	3.710	Terrestrial	Viperidae	4.045	1.530
Tapirai	*Chironius bicarinatus*	3	0.502	-0.181	0.449	0.460	2.720	Semiarboreal	Colubridae	0.555	-0.186
Tapirai	*Chironius exoletus*	1	-0.955	-0.575	0.304	-0.758	2.550	Semiarboreal	Colubridae	-1.090	-0.688
Tapirai	*Chironius flavolineatus*	1	-0.955	-0.575	0.304	-0.758	2.270	Semiarboreal	Colubridae	-1.090	-0.688
Tapirai	*Chironius quadricarinatus*	1	-0.955	-0.575	0.304	-0.758	2.270	Semiarboreal	Colubridae	-1.090	-0.688
Tapirai	*Clelia plumbea*	3	0.502	-0.014	0.345	0.460	3.270	Terrestrial	Dipsadidae	0.611	-0.068
Tapirai	*Crotallus durissus*	2	-0.227	-0.555	0.262	0.460	3.460	Terrestrial	Viperidae	-0.152	-0.039
Tapirai	*Dipsas alternans*	1	-0.955	-0.575	-2.816	-0.758	1.900	Arboreal	Dipsadidae	-2.297	1.772
Tapirai	*Echinanthera cephalostriata*	2	-0.227	-0.130	0.324	-0.758	1.630	Terrestrial	Dipsadidae	-0.406	-0.689
Tapirai	*Echinanthera cyanopleura*	3	0.502	-0.147	0.449	0.460	1.610	Terrestrial	Dipsadidae	0.574	-0.179
Tapirai	*Echinanthera melanostigma*	1	-0.955	-0.575	0.304	-0.758	1.940	Terrestrial	Dipsadidae	-1.090	-0.688
Tapirai	*Echinanthera undulata*	1	-0.955	-0.575	0.304	-0.758	1.650	Terrestrial	Dipsadidae	-1.090	-0.688
Tapirai	*Erythrolamprus aesculapii*	2	-0.227	-0.268	0.324	-0.758	2.140	Terrestrial	Dipsadidae	-0.486	-0.718
Tapirai	*Erythrolamprus atraventer*	1	-0.955	-0.575	0.304	-0.758	1.590	Terrestrial	Dipsadidae	-1.090	-0.688
Tapirai	*Erythrolamprus miliaris*	5	1.959	3.417	0.553	2.898	2.040	Semiaquatic	Dipsadidae	4.566	1.721
Tapirai	*Erythrolamprus poecilogyrus*	1	-0.955	-0.575	0.304	-0.758	1.830	Terrestrial	Dipsadidae	-1.090	-0.688
Tapirai	*Erythrolamprus typhlus*	1	-0.955	-0.575	0.304	-0.758	2.050	Terrestrial	Dipsadidae	-1.090	-0.688
Tapirai	*Micrurus corallinus*	3	0.502	0.352	0.116	-0.758	2.390	Semifossorial	Elapidae	0.210	-0.501
Tapirai	*Micrurus decoratus*	3	0.502	0.352	0.116	-0.758	1.980	Semifossorial	Elapidae	0.210	-0.501
Tapirai	*Micrurus frontalis*	2	-0.227	-0.516	0.116	-0.758	2.770	Semifossorial	Elapidae	-0.711	-0.607
Tapirai	*Oxyrhopus clathratus*	2	-0.227	-0.555	0.262	0.460	1.980	Terrestrial	Dipsadidae	-0.152	-0.039
Tapirai	*Oxyrhopus guibei*	2	-0.227	-0.555	0.262	0.460	2.550	Terrestrial	Dipsadidae	-0.152	-0.039
Tapirai	*Phalotris mertensi*	2	-0.227	-0.516	0.116	-0.758	2.720	Fossorial	Dipsadidae	-0.711	-0.607
Tapirai	*Philodryas aestiva*	2	-0.227	-0.555	0.262	0.460	2.230	Semiarboreal	Dipsadidae	-0.152	-0.039
Tapirai	*Philodryas olfersii*	4	1.230	0.062	0.470	0.460	2.660	Semiarboreal	Dipsadidae	1.121	-0.229

Code	Species	k	DC.s	Bet.s	Clo.s	Fiedler.s	Mass	Lifestyle	Family	PC1	PC2
Tapirai	*Philodryas patagoniensis*	5	1.959	1.967	0.553	2.898	2.710	Terrestrial	Dipsadidae	3.725	1.413
Tapirai	*Sibynomorphus mikanii*	1	-0.955	-0.575	-2.816	-0.758	1.860	Terrestrial	Dipsadidae	-2.297	1.772
Tapirai	*Siphlophis longicaudatus*	2	-0.227	-0.268	0.324	-0.758	1.750	Arboreal	Dipsadidae	-0.486	-0.718
Tapirai	*Spilotes pullatus*	6	2.687	3.569	0.491	0.460	3.480	Arboreal	Colubridae	3.998	0.343
Tapirai	*Taeniophallus affinis*	3	0.502	1.254	0.532	0.460	1.850	Terrestrial	Dipsadidae	1.419	0.053
Tapirai	*Taeniophallus bilineatus*	2	-0.227	-0.364	0.449	0.460	1.010	Terrestrial	Dipsadidae	0.031	-0.146
Tapirai	*Taeniophallus occipitalis*	2	-0.227	-0.364	0.449	0.460	1.610	Semifossorial	Dipsadidae	0.031	-0.146
Tapirai	*Taeniophallus persimilis*	2	-0.227	-0.364	0.449	0.460	1.170	Semifossorial	Dipsadidae	0.031	-0.146
Tapirai	*Thamnodynastes hypoconia*	2	-0.227	-0.364	0.449	0.460	1.750	Semiarboreal	Dipsadidae	0.031	-0.146
Tapirai	*Thamnodynastes rutilus*	2	-0.227	-0.315	0.324	-0.758	1.740	Semiaquatic	Dipsadidae	-0.514	-0.728
Tapirai	*Thamnodynastes strigatus*	4	1.230	0.556	0.470	0.460	1.980	Terrestrial	Dipsadidae	1.408	-0.124
Tapirai	*Tomodon dorsatus*	1	-0.955	-0.575	-2.816	-0.758	1.980	Terrestrial	Dipsadidae	-2.297	1.772
Tapirai	*Tropidodryas striaticeps*	4	1.230	0.062	0.470	0.460	2.030	Semiarboreal	Dipsadidae	1.121	-0.229
Tapirai	*Tropidophis paucisquamis*	1	-0.955	-0.575	0.304	-0.758	1.310	Arboreal	Tropidophiidae	-1.090	-0.688
Tapirai	*Xenodon neuwiedii*	1	-0.955	-0.575	0.304	-0.758	1.980	Terrestrial	Dipsadidae	-1.090	-0.688
Tapirai	*Xenopholis scalaris*	1	-0.955	-0.575	0.304	-0.758	1.100	Terrestrial	Dipsadidae	-1.090	-0.688
Texas	*Agkistrodon contortrix*	4	0.461	-0.040	0.516	1.436	3.096	Terrestrial	Viperidae	1.058	0.349
Texas	*Agkistrodon piscivorus*	4	0.461	1.308	0.516	-0.397	3.523	Semiaquatic	Viperidae	1.051	-0.404
Texas	*Coluber constrictor*	7	2.188	3.175	0.718	3.269	2.783	Terrestrial	Colubridae	4.780	1.724
Texas	*Crotalus horridus*	3	-0.115	0.487	0.313	-0.397	3.523	Terrestrial	Viperidae	0.166	-0.356
Texas	*Farancia abacura*	1	-1.266	-0.825	-2.361	-0.397	3.028	Aquatic	Dipsadidae	-2.289	1.599
Texas	*Heterodon nasicus*	4	0.461	-0.229	0.548	-0.397	2.703	Terrestrial	Dipsadidae	0.172	-0.755
Texas	*Heterodon platirhinos*	1	-1.266	-0.825	0.313	-0.397	2.387	Terrestrial	Dipsadidae	-1.254	-0.511
Texas	*Lampropeltis calligaster*	5	1.036	-0.417	0.462	-0.397	2.461	Terrestrial	Colubridae	0.360	-0.790
Texas	*Lampropeltis getula*	6	1.612	1.423	0.601	-0.397	2.878	Terrestrial	Colubridae	1.811	-0.570
Texas	*Lampropeltis triangulum*	3	-0.115	-0.749	0.409	-0.397	2.777	Terrestrial	Colubridae	-0.513	-0.695
Texas	*Masticophis flagellum*	5	1.036	0.307	0.548	2.047	3.123	Terrestrial	Colubridae	1.865	0.681
Texas	*Nerodia erythrogaster*	3	-0.115	-0.282	0.388	-0.397	3.159	Semiaquatic	Colubridae	-0.250	-0.578
Texas	*Nerodia fasciata*	3	-0.115	-0.282	0.388	-0.397	3.116	Semiaquatic	Colubridae	-0.250	-0.578
Texas	*Nerodia rhombifer*	2	-0.691	-0.806	0.004	-0.397	3.258	Semiaquatic	Colubridae	-1.033	-0.325
Texas	*Opheodrys aestivus*	1	-1.266	-0.825	0.153	-0.397	2.232	Arboreal	Colubridae	-1.316	-0.385
Texas	*Pantherophis obsoletus*	5	1.036	0.249	0.569	-0.397	3.108	Arboreal	Colubridae	0.788	-0.733
Texas	*Regina rigida*	2	-0.691	0.470	0.175	-0.397	2.128	Semiaquatic	Colubridae	-0.227	-0.189
Texas	*Storeria dekayi*	2	-0.691	-0.729	-2.308	-0.397	1.534	Terrestrial	Colubridae	-1.883	1.515
Texas	*Storeria occipitomaculata*	1	-1.266	-0.825	-2.308	-0.397	1.534	Terrestrial	Colubridae	-2.268	1.557
Texas	*Thamnophis proximus*	2	-0.691	-0.585	0.356	-0.397	2.750	Semiaquatic	Colubridae	-0.769	-0.556

Discussão Geral e Conclusões

Ao longo dos três capítulos que compõem esta tese eu abordei aspectos relacionados à estrutura e ao papel das espécies em redes de interações antagônicas, focando especificamente em interações serpentes-presas. Eu explorei como os principais padrões estruturais se relacionam com a história evolutiva das linhagens e com os atributos biológicos das espécies, principalmente referentes ao tamanho de corpo e ao estilo de vida. Eu também investiguei como o papel das espécies pode afetar a dinâmica da rede por meio dos efeitos indiretos.

No primeiro capítulo nós mostramos que a rede de interações entre serpentes e seus recursos em uma comunidade amazônica rica em espécies, apresentou uma combinação de estruturas aninhada e modular. O aninhamento foi explicado pelas variações de tamanho entre as serpentes que compõem a comunidade e simulações de remoção de espécies indicaram que espécies da família Boidae, a família das grandes serpentes constritoras, foram responsáveis por conectar módulos alimentares na rede trófica. O padrão modular, por sua vez, foi associado aos diferentes estilos de vida, uma vez que serpentes que compartilham hábitos de vida semelhantes costumam consumir recursos semelhantes disponíveis em seus microhabitats compartilhados.

No segundo capítulo nós mostramos que as 24 redes serpentes-presas analisadas, distribuídas em três continentes (Américas dos Norte e do Sul, África e Europa), não apresentaram variações estruturais consistentes ao longo do gradiente latitudinal, se mostrando, em geral, aninhadas, moderadamente conectadas e não modulares. Os padrões de rede que emergiram da variação no número de recursos consumidos pelas espécies de serpentes foram derivados de uma combinação de hábitos alimentares supergeneralistas e especializados. As serpentes são importantes predadores da fauna terrestre, arbórea, aquática, fossorial e até marinha, alimentando-se de presas que variam amplamente, tanto em categorias taxonômicas, quanto em tamanho. O único atributo da comunidade que se mostrou influenciado pela latitude foi a variação de tamanho entre as serpentes. Riqueza e diversidade taxonômica não variaram de forma consistente ao longo do gradiente latitudinal e o aninhamento foi a única métrica que se mostrou consistentemente afetada pela variação de tamanho e pela riqueza de serpentes, resultado que concorda com a literatura específica da área. Nossos resultados também indicaram que redes de regiões tropicais são mais aninhadas do que as de regiões temperadas. Esse resultado apresenta relação com os maiores valores de riqueza de serpentes em regiões tropicais, uma vez que aninhamento e riqueza de espécies são positivamente correlacionados. Por fim, mostramos também que, em geral, as serpentes compartilham os mesmos conjuntos de recursos e que anfíbios, lagartos ou pequenos mamíferos representaram os recursos centrais em todas as redes, sendo consumidos, em média, por 64% das serpentes em cada rede analisada.

No terceiro capítulo nós mostramos que alguns atributos biológicos são mais associados à posição central das serpentes nas redes. Em geral, serpentes de maior tamanho, que possuem os hábitos de vida aquático e semi-arborícola e que pertencem a linhagem de grandes serpentes constritoras, ocuparam mais frequentemente posições como espécies centrais. Grandes serpentes normalmente detém muitas interações e, em geral, quanto maior o número de interações de uma espécie, menor são suas distâncias médias para as demais espécies da rede. Essa relação justifica a posição central das serpentes de maior tamanho. Mostramos também que as centralidades do grau e de intermédio melhor capturam a importância das serpentes. No entanto, notamos que espécies menores também podem ocupar papéis centrais, especialmente em conectar diferentes setores da rede (centralidade de Fiedler). Assim, mostramos que papéis centrais em redes serpentes-presas podem ser ocupados por espécies com diferentes atributos e histórias evolutivas.

Finalmente, eu pude concluir que ao integrar análises de redes de interações com dados de história natural, história evolutiva das linhagens, atributos das comunidades e atributos biológicos das espécies, foi possível compreender como as comunidades de serpentes estão estruturadas com base no uso dos recursos alimentares e quais atributos biológicos fazem de uma serpente uma espécie chave dentro da comunidade. Os resultados da minha tese mostram que a estrutura das redes serpentes-presas apresenta padrões não aleatórios, que podem ser explicados por características moldadas por processos ecológicos e evolutivos.