

**UNIVERSIDADE FEDERAL DE SÃO CARLOS
CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
PROGRAMA DE PÓS-GRADUAÇÃO EM CONSERVAÇÃO DA
FAUNA**

GEDIMAR PEREIRA BARBOSA

**Ecologia de Morcegos do Parque Estadual Carlos Botelho: Estrutura
da Comunidade e Interações com Plantas em Área de Mata Atlântica**

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2018**

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Dissertação apresentada ao Programa de Pós-Graduação em Conservação da Fauna como parte dos requisitos para obtenção do título de Mestre Profissional em Conservação da Fauna.

Orientador: Dr. Vlamir José Rocha

**SÃO CARLOS
2018**



UNIVERSIDADE FEDERAL DE SÃO CARLOS

Centro de Ciências Biológicas e da Saúde
Programa de Pós-Graduação em Conservação da Fauna

Folha de Aprovação

Assinaturas dos membros da comissão examinadora que avaliou e aprovou a Defesa de Dissertação de Mestrado do candidato Gedimar Pereira Barbosa, realizada em 25/05/2018:

Prof. Dr. Wlamir Jose Rocha
UFSCar

Profa. Dra. Kayna Agostini
UFSCar

Prof. Dr. Diego Casallas-Pabón
UNICAMP

Dedico este trabalho aos meus pais, Ademar e Maria, que, mesmo sem estudo algum, são meus eternos professores.

AGRADECIMENTOS

Ao meu orientador Prof. Dr. Vlamir José Rocha, por contribuir mais uma vez para minha formação e me auxiliar nesse novo desafio. Deixo esse ciclo com aprendizagens que extrapolam a academia, e que, com toda certeza, levarei por toda a vida

Ao mestrando Vinícius Cardoso e orientador Fabrício Rassi, pelo convite e pela oportunidade de poder desenvolver esse trabalho no PECB, que foi uma fonte de conhecimento e experiências que contribuíram bastante na minha forma de pensar minha atuação. Agradeço também pela parceria em campo, no desenvolvimento e execução de todo o projeto, e também pelas discussões e idéias sempre pertinentes ao trabalho e futuro na pesquisa com os morcegos.

À Dra. Angela Corrêa, por ter carinhosamente aceitado participar desse projeto desde o início, por ter me auxiliado com as questões botânicas e por todo o apoio e parceria na identificação dos tipos polínicos, junto ao Instituto de Botânica de São Paulo.

À Dra Kayna Agostini e Dr. Diego Casallas pela revisão, correção e discussão de ideias no trabalho final. As contribuições de vocês foram pertinentes não apenas para esse trabalho, mas também para meu futuro profissional.

Ao pessoal do Parque Estadual Carlos Botelho, que nos receberam sempre de portas abertas, auxiliando de forma técnica e logística para que este projeto acontecesse. Deixo aqui meus sinceros agradecimentos principalmente à Márcio, Kátia, Anderson, Willian, Édipo e Danilo, aos gestores José Luiz Camargo Maia e Pietro Scarascia por todo apoio e confiança no período inicial do projeto, e à gestora Stéfanie Kissajikian pelo apoio e confiança na parte final dos trabalhos de campo.

Aos amigos, antigos e aqueles que eu tive o prazer de conhecer durante esse trabalho, que disponibilizaram uma semana para nos auxiliar em campo e dividir momentos de bastante crescimento, Diego, Jiraya, Luisa, André, Rodrigo S., Gabriel, Augusto, Gabriela, Sosténes, Rodrigo P., Helen e Caio, sem a ajuda de vocês nada disso teria acontecido.

Ao amigo Gabriel Storolli, pela disponibilidade em ajudar sempre, apoio durante o mestrado e conversas produtivas sobre os morcegos e outras questões relativas ao nosso trabalho.

À pesquisadora Mariana Landis, pelas informações preciosas sobre o PECB e auxílio na escolha dos pontos de amostragem.

Aos professores que durante o mestrado, por meio de conversas e discussão de idéias, contribuíram para o meu desenvolvimento profissional e deste trabalho, Prof. Dr. Alexandre Colato, Profa. Dra. Roberta Nocelli, Profa. Dra. Alexandra Sanchez, Profa. Dra. Julianna Rondineli, Prof. Dr. Pedro Galetti, Prof. Dr. Marcelo Schlindwein, Profa. Msc. Kátia Rancura, Prof. Dr. Luiz Moschini, Prof. Msc. Fabrício Rassi e Prof. Dr. João Batista da Cruz.

Ao Programa de Pós Graduação em Conservação da Fauna e à Universidade Federal de São Carlos, pela possibilidade de formação e enriquecimento na minha carreira, através do PPG.

À Fundação Parque Zoológico de São Paulo, pela bolsa de mestrado concedida, pelas disciplinas e possibilidade de conhecer o Zoológico e participar um pouco da vivência com toda equipe técnica e demais funcionários.

À secretaria do PPGCFau, na pessoa do Roque, por todo auxílio com questões pertinentes ao andamento do mestrado e disponibilidade em ajudar sempre.

Aos amigos da turma de mestrado-2016 do PPGCFau, pelos momentos construtivos e engraçados que vivemos juntos, durante as disciplinas no Zoológico de São Paulo.

À Dinorah Evangelista e ao Alojamento do Instituto de Botânica, que cederam a possibilidade de moradia durante o período de disciplinas na cidade de São Paulo.

Aos amigos da República Caverna, da UFSCar Lagoa do Sino, por me receberem e cederem moradia durante o período de disciplinas em Campina do Monte Alegre.

À Valéria e Itacir, que abriram as portas de sua casa para mim, me ajudaram durante o período do mestrado em Araras e ainda me ajudam sempre que possível.

À minha família, Ademar, Maria, Gismar, Gislene, Márcio, Gisele, Laura, Alice e Pedro, que mais uma vez viveram, sofreram, aprenderam e venceram tudo isso comigo. Obrigado a todos vocês que nunca desistiram de mim, que nunca hesitaram em me apoiar e me levantar nos momentos de queda. Não sei o que seria de mim sem vocês. Muito obrigado!

À minha noiva, Marina, que, mesmo se eu vivesse outras vidas e outros tempos, eu não conseguiria agradecer o suficiente. Obrigado por cuidar de mim sempre, pelo seu carinho, pelas conversas filosóficas, pelos momentos de consciência e por me ensinar a *“olhar para as estrelas acima e não para os meus pés...”*. Obrigado por aprender comigo, por me ensinar e por dividir comigo a paixão pela ciência. Sem dúvida, *“... dividir um planeta e uma época com você”* é a melhor coisa que já me aconteceu.

Não poderia jamais, deixar de agradecer a todos os cientistas, mulheres e homens que dedicam suas vidas ao árduo trabalho de decifrar e proteger a natureza. Profissionais cujos trabalhos estão citados nessa dissertação, o conhecimento que vocês produziram até aqui foi o meu verdadeiro norte durante todo esse mestrado.

“As gerações dos mortais assemelham-se às folhas das árvores, que, umas, os ventos atiram no solo, sem vida; outras, brotam na primavera, de novo, por toda a floresta viçosa. Desaparecem ou nascem os homens da mesma maneira.”

- HOMERO (Ilíada, VI, 146-149)

RESUMO

Apesar da histórica exploração e fragmentação de sua área nativa, a Mata Atlântica abriga ainda uma significativa diversidade de espécies animais. Em vista de sua importância para a manutenção da fauna, conhecer a diversidade de espécies e como estas interagem entre si e com o ambiente físico em áreas estratégicas da Mata Atlântica, é fundamental para medidas eficazes de manejo e conservação das espécies. Desta forma, este estudo teve como objetivo analisar a comunidade de morcegos no Parque Estadual Carlos Botelho (PECB), uma unidade de conservação com alto grau de preservação da Mata Atlântica e que ainda não possui nenhum estudo ecológico com este grupo. Para isso, avaliamos dois aspectos: (1) qual a influência da altitude local na abundância, riqueza e diversidade de espécies de morcegos no PECB e; (2) como é estruturada a rede de interações entre morcegos e plantas (flores e frutos) no Parque. Apesar de variar consideravelmente em abundância e composição das espécies, a riqueza e diversidade alfa de morcegos parece não sofrer influência da variação de altitude encontrada na área do PECB (1000 m). Medidas de diversidade beta indicam que a variação encontrada na composição de morcegos entre os pontos de menor e maior altitude, é impulsionada mais pela substituição de espécies entre as áreas (*spatial turnover*), do que pela desagregação ordenada de assembleias de um mesmo *pool* de espécies (*nestedness*). Através da análise de uma rede multicamada de interações entre morcegos e plantas no PECB, foi possível verificar um padrão aninhado (NODF = 0,62, $p < 0.0001$) e pouca sobreposição nas interações entre morcegos e flores e morcegos e frutos. Os resultados mostraram ainda, que os morcegos *A. geoffroyii*, *C. perspicillata* e *A. caudifer* são centrais, atuando como espécies-chave para a manutenção da estrutura da rede de interações. Além de preencher uma lacuna importante para o PECB, avaliando a diversidade de morcegos em uma área sem estudos com esse grupo até o presente momento, os resultados apresentados aqui reforçam a importância de se analisar a diversidade de espécies em escalas espaciais. Além disso, auxiliam para um melhor entendimento das interações entre morcegos e plantas na Mata Atlântica, e quais espécies são centrais para a manutenção dessas interações. Sugerimos que estratégias locais de conservação mais eficazes precisam ir além de dados locais de diversidade, mas sim, considerar também variações espaciais e as interações entre as diferentes espécies que compõem os sistemas naturais.

Palavras-chave: Diversidade; gradiente altitudinal; polinização; dispersão de sementes.

ABSTRACT

Despite the historical exploitation and fragmentation of its native area, the Atlantic Forest still houses a significant diversity of wildlife species. Due to its importance for the maintenance of fauna representatives, getting knowledge of species diversity, and how they interact with each other and with the physical environment in strategic Atlantic Forest areas, is fundamental for effective species management and conservation plans. Thus, this study aimed to analyze the bat community from Carlos Botelho State Park (CBSP), a protected area with a high preserved Atlantic Forest and no ecological studies with bats until now. For this, we evaluated two aspects: (1) what is the influence of local altitude on bat abundance, species richness and diversity at CBSP and; (2) how the interaction network between bats and plants (flowers and fruits) is structured at the Park. In spite of varying considerably in abundance and species composition, species richness and alpha diversity of bats does not seem to be influenced by altitudinal variation found at CBSP area (1000 m). Measures of beta diversity indicate that the variation found in bat species composition between lower and higher altitude is driven more by species replacement between points (*spatial turnover*), than by orderly disaggregation of assemblages from the same species pool (*nestedness*). Through the analysis of a multilayer network of bat-plant interactions at CBSP, we found a nestedness pattern of interaction (NODF = 0.62, $p < 0.0001$) and few overlap on interactions between bats and flowers and bats and fruits. The results also showed that the bats *A. geoffroyii*, *C. perspicillata* and *A. caudifer* are central, acting as keystone species for the structure and maintenance of interaction network. In addition to filling an important knowledge gap for CBSP, by evaluating the bat species diversity in an area with no studies with bats until now, the results presented here reinforce the important of analyzing species diversity at spatial scales. Besides that, they help us to better understand the structure of bat-plant interaction networks in Atlantic Forests, and also which bat species are central to maintain these interactions. We suggest that more effective local conservation strategies should go beyond local diversity data, and also consider spatial variation and data on interactions between different species that comprise the natural systems.

Keywords: Diversity; altitudinal gradient; pollination; seed dispersal.

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INTRODUÇÃO GERAL

A biodiversidade global enfrenta o que parece ser a maior crise ambiental da história da humanidade. Considerado o sexto período de extinção em massa, o Antropoceno já é símbolo histórico da perda de biodiversidade e impactos diretos nos ecossistemas em consequência da atividade humana no planeta (DIRZO et al., 2014; PÉREZ-MÉNDEZ et al., 2016; PRIMACK, 2010; JOHNSON et al., 2017). Em meio a esse cenário, o processo de defaunação é eminente, e a perda de espécies animais já é associada com eventos que vão desde co-extinções de espécies em interação até a perda de serviços ecossistêmicos críticos à humanidade (CAMARGO-SANÁBRIA et al., 2015; DIRZO et al., 2014; KOERNER et al., 2016; PÉREZ-MÉNDEZ et al., 2016; PRIMACK, 2010; YOUNG et al., 2014).

Apesar ainda da incerteza sobre a realidade, estima-se o número de espécies animais no planeta varie de 7,8 a 8,7 milhões (SCHEFFERS et al., 2012; MORA et al., 2011). Desse número, é provável que algo em torno de 11.000 e 58.000 espécies animais sejam extintas anualmente (SCHEFFERS et al., 2012; MORA et al., 2013). Números mais precisos são apresentados para ecossistemas terrestres, onde a União Internacional para a Conservação da Natureza (IUCN em inglês) estima que 338 vertebrados terrestres tenham sido extintos desde o ano de 1500 (IUCN, 2015). As causas aparentes desta extinção oscilam entre a exploração excessiva da fauna (caça e comércio ilegal), perda de habitats naturais e a necessidade de políticas efetivas de proteção à biodiversidade (YOUNG et al., 2014).

No Brasil, as relações entre defaunação e fragmentação de habitats naturais são bastante estreitas. A conversão de floresta nativa em áreas urbanas e agricultáveis, como a cana-de-açúcar, a soja e as pastagens (DURIGAN et al., 2007; FEARNSSIDE, 2001; TONHASCA-JR., 2005), tem restringido integrantes da fauna a porções cada vez menores de floresta, isolando populações e impactando diretamente as espécies animais (ANDREAZI et al., 2009; CHIARELLO, 2000; GALLETI; SAZIMA, 2006; LAURANCE; VASCONCELOS, 2009; LYRA-JORGE et al., 2008; PRADO et al., 2006). Neste contexto de fragmentação e perda de espécies, um dos biomas mais afetados no país é a Mata Atlântica, que, outrora ocupava total ou parcialmente 17 estados brasileiros, hoje se encontra reduzida a aproximadamente 27% de sua área original (CAMPANILI; SCHAFER, 2010).

Apesar da intensa exploração e fragmentação de sua área nativa, é estimado que a Mata Atlântica abrigue ainda cerca de 20.000 espécies de plantas, 900 espécies de

aves, 370 espécies de anfíbios, 359 espécies de peixes, 298 espécies de mamíferos e 270 espécies de répteis (CAMPANILI; SCHAFER, 2010; MOREIRA-LIMA, 2013; PAGLIA et al., 2012). Além disso, o bioma ainda é a casa do maior número de espécies ameaçadas no Brasil, fornecendo abrigo à aproximadamente 70% das espécies de vertebrados e 50% das espécies de plantas em risco de extinção (CAMPANILI; SCHAFER, 2010). Tal importância deu a Mata Atlântica o título de uma das regiões ecológicas mais ricas em termo de diversidade biológica do planeta, incluindo o bioma entre os 25 *hotspots* mundiais para conservação da biodiversidade (MYERS et al., 2000).

Considerando a importância da Mata Atlântica para a manutenção da biodiversidade (CAMPANILI; SCHAFER, 2010), principalmente em vista de um processo acelerado de defaunação a nível global (DIRZO et al., 2014), medidas de conservação do bioma são imprescindíveis. No entanto, embora informações sobre a fauna da Mata Atlântica brasileira, incluindo aves (HASUI et al., 2017), médios e grandes mamíferos (LIMA et al., 2017), pequenos mamíferos (BOVENDORP et al., 2017) e morcegos (MUYLAERT et al., 2017) tenham sido compiladas por cientistas em ações conjuntas, muitas lacunas de conhecimento básico sobre os padrões ecológicos de espécies em diferentes áreas ainda existem. Nesse contexto, o conhecimento sobre aspectos das comunidades animais, bem como o estudo das áreas de grande diversidade de espécies, podem ser grandes aliados para a conservação (PRIMACK, 2010).

Conforme já mencionado, a Mata Atlântica é representada por uma grande diversidade de espécies animais (CAMPANILI; SCHAFER, 2010). Segundo Primack (2010), identificar as localidades de maior diversidade ecológica é o primeiro desafio dos cientistas na busca de medidas efetivas de conservação das espécies. Em um senso mais amplo, a diversidade pode ser representada basicamente pelo número de espécies presentes em um determinado local (MAGURRAN, 2004). Essa forma restrita de tratar a diversidade, igualando-a ao conceito de riqueza de espécies, foi bastante utilizada em estudos iniciais sobre as comunidades, e ainda é utilizada por alguns autores (MAGURRAN, 2004). Considerando que a contagem de todas as espécies em uma comunidade, principalmente em relação à fauna, é uma tarefa árdua e praticamente impossível, diferentes formas quantitativas de se indicar a diversidade de espécies, considerando outras características das comunidades além da riqueza, foram desenvolvidas (MAGURRAN, 2004).

Apesar de hoje existirem uma infinidade de índices diferentes para mensurar a diversidade ecológica, de uma forma geral, medidas adotadas pelos cientistas consideram três diferentes escalas geográficas. A diversidade alfa (α) é uma medida quantitativa de diversidade local e é bastante utilizada em estudos que visam à comparação de diferentes localidades, de forma a auxiliar na seleção daquelas prioritárias a conservação (MAGURRAN, 2004; PRIMACK, 2010). A diversidade gama (γ) é aplicada a uma escala maior, onde objetiva-se estabelecer uma medida de diversidade para uma região ou continente, permitindo assim a comparação de diferentes paisagens em domínios geográficos amplos (PRIMACK, 2010). Por fim, a diversidade beta (β) é entendida como um link entre a diversidade alfa e gama, e representa a taxa pela qual a composição de espécies varia ao longo de gradientes ambientais ou geográficos (MAGURRAN, 2004). Considerando uma perspectiva conservacionista, a diversidade beta é uma medida central, pois ajuda a entender os processos que estruturam e mantêm a diversidade no espaço, fornecendo subsídios para um melhor planejamento de ações de conservação (SOCOLAR et al., 2016).

O fato de a diversidade não se restringir apenas a um local em particular demonstra a necessidade de se entender como as espécies respondem a diferentes modificações no ambiente físico, de forma a prever respostas das comunidades (PRIMACK, 2010). A estrutura da paisagem, ciclos anuais de temperatura, precipitação e outras variáveis físicas, influenciam na capacidade de um ambiente em sustentar as comunidades biológicas, afetando diretamente na distribuição das espécies e nas interações entre elas (GASTON; BLACKBURN, 2000; LOMOLINO, 2001; PIANKA, 1966; PRIMACK, 2010). Assim, entender como as comunidades se reorganizam em vista a modificações no ambiente físico é uma das principais questões em áreas da ecologia e conservação (GASTON; BLACKBURN, 2000; LOMOLINO, 2001; PIANKA, 1966; PRIMACK, 2010; STEVENS, 2013; WILLIG & SELCER 1989).

Dentro do contexto de modificações no ambiente, comunidades animais ao longo de gradientes de altitude têm sido amplamente estudadas com objetivo de se avaliar respostas das espécies a variações em condições físicas (CURRAN et al., 2012; KATTAN; FRANCO, 2004; McCAIN, 2007; McCAIN, 2010; SORIANO, 2000; PATTERSON et al, 1996; WILLIG; PRESLEY 2016). Isso ocorre porque gradientes de altitude oferecem um grande potencial para se testar hipóteses e criar cenários de processos globais em escalas locais. De forma geral, os estudos indicam que a riqueza e diversidade de espécies das comunidades animais tendem a sofrer um declínio com o

aumento da altitude (CURRAN et al., 2012; KATTAN; FRANCO, 2004; PATTERSON et al, 1996). No entanto, é possível verificar também que em algumas comunidades, valores de riqueza e diversidade são baixos em altitudes reduzidas e elevadas, apresentando um pico em médias altitudes (McCAIN, 2007; McCAIN, 2010). Embora muitas explicações sejam prováveis, estudos destacam o forte potencial da variação na temperatura como fator responsável pela resposta das comunidades a variação na altitude (McCAIN, 2007; SORIANO, 2000).

Além de impactar na riqueza e diversidade de espécies, outra consequência iminente atribuída ao atual cenário de defaunação refere-se a possíveis perdas ou reorganizações em redes de interações ecológicas (JOHNSON et al., 2017; PÉREZ-MÉNDEZ et al., 2016; YOUNG et al., 2014). As espécies relacionam-se entre si por meio de antagonismos (ex. presa-predador) e mutualismos (ex. planta-polinizador), formando complexas redes de interações essenciais para o equilíbrio dos ecossistemas. Embora estudos apontem para os efeitos de modificações antrópicas na estrutura dessas redes (PÉREZ-MÉNDEZ et al., 2016), a maioria das ações conservacionistas é direcionada ainda apenas em um contexto isolado de espécies, ignorando totalmente a estrutura das interações entre essas espécies (TYLIANASKIS et al., 2010).

Não se deve, por tanto, entender que ações de conservação direcionadas às espécies sejam dispensáveis, mas sim, que estas sejam desenvolvidas de forma a abranger importantes aspectos das interações entre elas. Tylianaskis e colaboradores (2010) recorrem ao fato de que as interações são mais do que a soma de seus componentes, logo, para que a conservação seja eficaz e abranja a estrutura das redes de interação, se faz necessário conservar a co-ocorrência de espécies que interagem entre si. O entendimento de que a conservação das espécies vegetais não depende apenas do manejo de suas populações, mas também de seus polinizadores e dispersores de sementes, é um exemplo (KEARNS; INOUE, 1997; TREJO-SALAZAR et al., 2016).

Nesse contexto, entender a estrutura das redes de interação entre animais e plantas é fundamental para se pensar em medidas mais eficazes de conservação de forma local e global. Interações como a dispersão de sementes e a polinização afetam drasticamente a dinâmica populacional das espécies de animais e plantas, e a forma como essas interações são estruturadas tem um papel fundamental na manutenção da biodiversidade e funções ecossistêmicas (BASCOMPTE et al, 2003; BASCOMPTE; JORDANO, 2007; BASTOLLA et al, 2009; FORTUNA; BASCOMPTE 2006; OLESEN et al., 2007).

As redes de interação entre animais e plantas podem estruturar-se de formas não aleatórias, como as redes aninhadas e modulares (BASCOMPTE et al., 2003; BASCOMPTE; JORDANO, 2007; LEWINSOHN et al., 2006). Redes aninhadas, onde espécies pouco conectadas (poucas interações) são ligadas a subconjuntos de espécies mais conectadas (muitas interações), são conhecidas por proverem uma estrutura mais coesa, evitando o isolamento de espécies, permitindo maior estabilidade à rede e contribuindo para a manutenção da biodiversidade (BASCOMPTE et al., 2003; BASCOMPTE; JORDANO, 2007). Em redes modulares, as espécies formam subconjuntos (módulos) e tendem a interagir com maior frequência entre elas, verificando-se pouca interação entre diferentes módulos (LEWINSOHN et al., 2006; OLESEN et al., 2007). Em seus estudos, Olesen e colaboradores (2007) descrevem a importância de espécies-chaves em redes modulares, atribuindo possíveis cascatas de extinções à perda dessas espécies e, em consequência, de suas interações entre diferentes módulos.

Além do entendimento sobre a estrutura das redes de interações, conhecer as espécies-chave nessas redes é fundamental para prever possíveis reorganizações ou perdas em cenários de mudanças ambientais (LEWINSOHN; CAGNOLO, 2012; MELLO et al., 2015, OLESEN et al., 2007). O conceito original de espécie-chave (*keystone species* em inglês) foi descrito por Paine (1969) para classificar aquelas espécies com desproporcional importância, em relação a sua abundância, para a estrutura de uma comunidade. Desde a proposição desta classificação, o conceito de espécie-chave foi aplicado a diferentes atribuições (MILLS et al., 1993; POWER et al., 1996; BROSE et al., 2005) e, recentemente, MELLO et al. (2015) forneceram dados ecológicos sobre os fatores que fazem uma espécie ser considerada espécie-chave em redes mutualísticas envolvendo plantas e frugívoros. Para tal, os autores determinaram a importância relativa de cada espécie para a estrutura da rede, através de medidas de centralidade aplicadas às redes de interação animal-planta (MELLO et al., 2015).

Dentre os animais cuja diversidade impacta diretamente as funções ecossistêmicas, devido principalmente às estreitas relações que estes sustentam com uma infinidade de espécies vegetais em áreas florestais, destaca-se o grupo dos morcegos (BREDET et al., 2012; FLEMING et al., 2009; FLEMING; HEITHAUS, 1981; PIJL, 1975; VOGEL, 1969). Representando aproximadamente 25% dos mamíferos brasileiros (PAGLIA et al., 2012), os morcegos são considerados importantes indicadores de integridade funcional em uma comunidade (MEDELLÍN et al., 2000).

Ao explorar recursos de diferentes formas, esses animais desempenham papéis ecológicos indispensáveis nas florestas tropicais (KALKO, 1998), auxiliando na manutenção dos ecossistemas através da polinização e dispersão de sementes de espécies vegetais, bem como, do controle de populações de insetos (AGUIAR; ANTONINI, 2008; BREDT et al., 2012; CLEVELAND et al., 2006; FLEMING et al., 2009; FLEMING; HEITHAUS, 1981; PIJL, 1975; VOGEL, 1969).

Os morcegos podem explorar recursos alimentares das espécies de plantas de três formas diferentes: através do consumo de partes vegetativas, como as folhas (CORDERO-SCHMIDT et al., 2016; KUNZ; INGALLS, 1994; ZORTÉA; MENDES, 1993); consumo de frutos e sementes (BREDT et al., 2012; GIANNINI; KALKO, 2000; SALDAÑA-VÁZQUEZ et al., 2013) e; consumo de néctar, pólen e estruturas florais (FLEMING et al., 2009; KOOPMAN, 1981; MUCHHALA; JARRÍN-V, 2002; WINTER; HELVERSEN, 2003). No Brasil e em outras áreas tropicais, os morcegos representam importantes polinizadores, devido principalmente à sua capacidade de voo e volume corporal (FLEMING et al., 2009). Como dispersores de sementes, morcegos frugívoros podem interagir com pelo menos 542 espécies de plantas zoocóricas, pertencentes a mais de 50 famílias (BREDT et al., 2012). Durante seu forrageamento, esses morcegos podem carregar as sementes por aproximadamente 10 km de distância da planta-mãe (HEITHAUS et al., 1975).

Essa ampla variedade de níveis tróficos também propiciou aos morcegos ocuparem diferentes habitats (KALKO, 1998). No entanto, assim como outros representantes da fauna, os morcegos também apresentam limitações em sua distribuição em função de variações no ambiente físico (PATTERSON, et al., 1996; SORIANO, 2000; STEVENS, 2013; WILLIG; PRESLEY, 2016). Variações na riqueza e diversidade de morcegos em relação a gradientes de altitude foram documentadas por diversos pesquisadores, indicando declínio da diversidade com aumento da altitude (CURRAN et al., 2012; MARTINS et al., 2015; PATTERSON et al., 1996) e também, picos médios de diversidade em gradientes estudados (MCCAIN, 2007; SÁNCHEZ-CORDERO, 2001). Mudanças na diversidade de morcegos podem ser atribuídas a fenômenos como o clima, heterogeneidade de habitats, produtividade, partição de nicho e processos evolutivos (CISNEROS et al., 2014; CURRAN et al., 2012; DUNN; WATERS, 2012; MCCAIN, 2007; MARTINS et al., 2015; SÁNCHEZ; GIANNINI, 2014). Entre esses, o clima parece ocupar posição de destaque nas modificações

observadas na comunidade de morcegos ao longo de gradientes de altitude (MCCAIN, 2007; SORIANO, 2000).

Considerando a importância dos morcegos para os ecossistemas tropicais, torna-se evidente a necessidade de se estudar esse animais em áreas de Mata Atlântica. Embora recentemente informações sobre os morcegos desse bioma tenham sido disponibilizadas por vários pesquisadores em formato de *data paper* (MUYLAERT et al., 2017), no cenário de defaunação no qual nos encontramos (DIRZO et al., 2014), muitos esforços ainda são necessários com este grupo na Mata Atlântica, abordando inclusive localidades não amostradas, fatores físicos que podem influenciar na diversidade de espécies e também, as interações entre os morcegos e plantas em áreas estratégicas para conservação.

Nesse contexto, o Parque Estadual Carlos Botelho (PECB) é uma unidade de conservação com cerca de 37.000 ha de Mata Atlântica em excelente estado de preservação que carece de estudos sobre a comunidade de morcegos local. Desde que foi protegido como Parque Estadual no ano de 1892, o PECB é considerado um dos mais importantes remanescentes de Mata Atlântica do território nacional, devido em grande parte ao seu status de conservação e importância para manutenção da biodiversidade (SÃO PAULO, 2008). Mesmo assim, os morcegos do PECB começaram a ser amostrados apenas no ano de 2016 (CLÁUDIO et al., *dados não publicados*), e até o presente momento, este é o primeiro estudo abordando aspectos ecológicos da comunidade de morcegos do Parque.

OBJETIVOS

O objetivo geral deste trabalho foi investigar aspectos ecológicos da comunidade de morcegos (Mammalia, Chiroptera) do Parque Estadual Carlos Botelho (PECB), avaliando como a altitude pode influenciar na estrutura da comunidade de morcegos, e também descrever como as interações entre morcegos e plantas são estruturadas na área do Parque. Para isso, os seguintes objetivos específicos foram divididos em dois capítulos independentes:

- I. Avaliar como a altitude presente no PECB influencia nos padrões de abundância, riqueza e diversidade de espécies (Capítulo 1);
- II. Avaliar como as variáveis temperatura e umidade podem afetar a estrutura da comunidade de morcegos do Parque (Capítulo 1);

- III. Descrever a estrutura de interações entre morcegos e plantas no PECB, utilizando uma abordagem de rede de interações multicamada que considera as interações morcego-flor e morcego-fruto (Capítulo 2);
- IV. Avaliar se a estrutura das interações morcego-planta numa perspectiva multicamada segue o mesmo padrão, quando consideramos apenas redes de interações morcego-flor e morcego-fruto (Capítulo 2);
- V. Descrever quais espécies de morcegos são consideradas espécies-chave, ou seja, centrais para a manutenção da rede de interações (Capítulo 2).

HIPÓTESES

Considerando que variações no ambiente físico afetam diretamente as espécies animais (KATTAN; FRANCO, 2004; McCAIN, 2007; McCAIN, 2010; SORIANO, 2000; WILLIG; PRESLEY 2016), se a altitude presente no PECB exercer influência sobre a comunidade de morcegos, espera-se que:

I- a estrutura da comunidade modifique-se em relação à altitude, apresentando diferentes padrões na composição, abundância, riqueza e diversidade de espécies entre a porção baixa e alta do Parque (CURRAN et al., 2012; MCCAIN, 2007; SORIANO, 2000; PATTERSON et al., 1996).

II- a variação de temperatura presente no Parque ajude a explicar possíveis influências na estrutura da comunidade de morcegos em diferentes altitudes (McCAIN, 2007; SORIANO, 2000).

Considerando que as redes de interação morcegos-planta, avaliadas separadamente como redes de dispersão de sementes ou polinização, podem apresentar diferentes níveis de modularidade ou aninhamento (MELLO et al., 2011a; MELLO et al., 2011b; MORA-BELTRÁN; LÓPEZ-ARÉVALO, 2018), espera-se que:

III. a rede de interação entre morcegos e plantas avaliada sob uma perspectiva de rede multicamada ajude a confirmar a real estrutura das interações morcego-planta no PECB (COSTA et al. 2016; PILOSOF et al. 2017).

IV. a rede de interações apresente espécies-chave para a manutenção da sua estrutura, e que podem ser definidas pelo nível de centralidade que estas apresentam em relação às demais (MELLO et al., 2015).

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ARTIGOS PRODUZIDOS

Os dois capítulos desta dissertação referem-se aos artigos produzidos a partir desta pesquisa. O primeiro artigo, intitulado “*Analysis of bat species diversity at two contrasting altitudes in a protected Atlantic Forest area, Southeastern Brazil*” teve o objetivo de investigar se a altitude encontrada no Parque Estadual Carlos Botelho exerce alguma influência na riqueza, composição e diversidade de espécies de morcegos da Mata Atlântica. O segundo, intitulado “*Among flowers and fruits: a multilayer network of bat-plant interactions in a Brazilian Atlantic Forest*”, objetivou investigar a estrutura de interações entre morcegos e plantas no Parque, bem como, identificar quais espécies de morcegos são espécies-chave nessa estrutura. Ambos os artigos foram preparados para a submissão na revista *Journal of Tropical Ecology* (Cambridge University Press), e estão formatados de acordo com as normas da mesma.

CAPÍTULO 1

Analysis of bat species diversity at two contrasting altitudes in a protected Atlantic Forest area, Southeastern Brazil

Gedimar P. Barbosa^{1,2*}, Vinícius C. Cláudio^{1,2}, Vlamir J. Rocha³, Fabrício B. Rassy²

¹ Universidade Federal de São Carlos, Centro de Ciências Biológicas e da Saúde, São Carlos, SP, Brazil.

² Fundação Parque Zoológico de São Paulo, São Paulo, SP, Brazil.

³ Universidade Federal de São Carlos, Centro de Ciências Agrárias. Araras, SP, Brazil.

Abstract

Understanding how environment affects biological communities is crucial for biodiversity conservation strategies. Although altitudinal variation is known to affect bat fauna in different ways, only few studies in Brazil are found addressing this issue. Here, changes on bat species diversity were investigated between two different altitudinal bands in Carlos Botelho State Park (CBSP), a well preserved Atlantic Forest in southeastern Brazil. Despite varying considerably in abundance and composition, patterns of bat richness and alpha diversity did not vary according to altitude, and measures of beta diversity components indicate that variation in species composition between altitudes is driven more by species replacement than by orderly disaggregation of assemblages from the same species pool. We confirm that the altitudinal variation found within CBSP (30 to 1000 m) does not affect bat community structure, as the values of richness and diversity did not change according to altitude. However, we also suggest that the accentuated decline in air temperature from lower to upper altitudes can explain the decline in abundance and changes in species composition within the Park.

Keywords: community structure, species richness, elevation gradients, spatial turnover, biodiversity conservation.

INTRODUCTION

Understanding the spatial patterns of biodiversity in response to environment is vital to forecast changes in communities and to inform conservation priorities (Socolar *et al.* 2016, Willig & Presley 2016). Since patterns of distribution that shape communities are outcomes of interactions between a range of ecological, geological and evolutionary process (Gaston & Blackburn 2000, Lomolino 2001, Pianka, 1966), perceive how species diversity change in relation to these patterns has been a major

issue in ecological studies (Gaston & Blackburn 2000, Lomolino 2001, Pianka 1966, Stevens 2013, Willig & Selcer 1989). In light of this, altitudinal gradients provide a suitable field to test hypothesis on how patterns of biodiversity change to a range of different taxa.

Bat diversity at distinct altitudes has been extensively studied and, in general, the effects of altitude on richness and diversity fall into two major categories: (i) the clinal pattern, in which richness is higher at lower areas and presents a decline with elevation (Curran *et al.* 2012, Martins *et al.* 2015, Patterson *et al.* 1996), and the (ii) modal pattern, in which richness reaches a peak at medium elevations (McCain 2007, Sánchez-Cordero 2001). Several factors arise to explain this change in species richness from lower to upper sites, such as differences in climate, habitat heterogeneity, productivity, evolutionary process and niche partitioning (Cisneros *et al.* 2014, Curran *et al.* 2012, Dunn & Waters 2012, McCain 2007, Martins *et al.* 2015, Sánchez & Giannini 2014).

Although well studied elsewhere, Brazil still lacks research addressing the differences on bat species diversity caused by variation on altitudinal patterns (Bordignon & França 2009, Dias *et al.* 2008, Lopes *et al.* 2017, Martins *et al.* 2015). Despite showing varied results, the studies conducted until now state the presence of spatial turnover of bat species between different altitudes. However, no measurements of this fraction of beta diversity (Harrison *et al.* 1992) are shown in these studies to confirm the assumption of spatial turnover as a driver of diversity variation.

Beta diversity can be understood as the extent to which diversity changes between two or more spatial unities (Magurran 2004). According to Harrison *et al.* (1992) and Baselga (2010), beta diversity may be partitioned into different measures, reflecting two different phenomena: (i) nestedness, which occurs when assemblages with smaller number of species are subsets of richer assemblages; and (ii) spatial turnover, in which species in one assemblage are replaced by others as consequence of species sorting and spatial or historical constraints (Baselga 2010, Gaston & Blackburn 2000, Harrison *et al.* 1992).

In this context, the Carlos Botelho State Park is a protected area that covers a mountainous portion of Atlantic Forest in southeastern Brazil, with altitude ranging from 30 to 1000 m within its domain. Even though available literature indicates that markedly changes in bat species richness and diversity occur above 1000 m (Bordignon & França 2009, Cisneros *et al.* 2014, Curran *et al.* 2012, Dias *et al.* 2008, Lopes *et al.*

2017, Martins *et al.* 2015, Patterson *et al.* 1996), Carlos Botelho State Park provides a great opportunity to evaluate how bat communities are affected by altitude within this range. Considering the challenging task of conserving species in elevation gradients of tropical forests (Willig & Presley 2016) and the current status of Atlantic Forest preservation in Brazil (SOS Mata Atlântica & INPE 2018), this information can be useful to target actions towards a more efficient species conservation at local scales (Socolar *et al.* 2016, Willig & Presley 2016).

Thus, the present study aimed to investigate bat species diversity at lower and upper areas within Carlos Botelho State Park, an Atlantic Forest with no ecological studies conducted on bat fauna until now. For this, we assessed bat species richness and abundance, as well as local and regional measures of species diversity at different altitudes within the Park. If altitudinal differences found in the study area affect patterns of bat species diversity (CURRAN *et al.*, 2012; MCCAIN, 2007; SORIANO, 2000; PATTERSON *et al.*, 1996), we predict that (1) species richness and abundance will decrease with increasing elevation; (2) measures of alpha diversity will be different between altitude locations; (3) and high beta diversity at the study site, measured as spatial turnover and/ or nestedness in species assemblage. If climate variation found in study site influences species diversity patterns (McCAIN, 2007; SORIANO, 2000), we predict that (4) decreasing ambient temperature and relative humidity will result in a decline in species abundance and richness.

METHODS

Study area

Carlos Botelho State Park (hereafter CBSP) is a protected area located in São Paulo (24° 06' 55" - 24° 14' 41" S and 47° 47' 18" - 48° 07' 17" W), with 37,644 ha in a continuous massif called "Serra de Paranapiacaba" in southeastern Brazil (Figure 1). The Park covers a mountainous and steep relief, with altitudes ranging from 30 m (lower part) to 1000 m (upper part). The vegetation is predominantly dense montane and submontane Atlantic Rain Forest, with the upper part characterized by humid montane forest and the lower part characterized as lowland evergreen forest (Lima *et al.* 2011). Forest formations vary between well-preserved stretches with continuous canopy above 20 m, to secondary formations with smaller and more opened canopy (Lima *et al.* 2011).

The topographic pattern is the main drive of variations in air temperature at the study area. February is considered the hottest month, with temperatures around 28°C in the lowlands and 19°C in the upper parts. The lowest temperatures are recorded in July, around 17°C in the lowlands and 11°C in higher elevations. Annually, the lower portion of the Park presents average temperatures ranging from 21°C to 23°C, while at higher elevations the average temperature falls between 15°C and 19°C (SÃO PAULO 2008). The average rainfall varies between 1,700 and 2,400 mm, with predominance of rainfalls during the summer. Along the rainy trimester, the total percentage of precipitation in lowland areas range from 37% to 43% and from 31 to 41% for portions of the Serra de Paranapiacaba. Due to its geomorphologic characteristics, the Park does not show water deficit, presenting no dry months along the year (SÃO PAULO 2008).

The CBSP houses a relevant diversity of life (SÃO PAULO, 2008) and is considered a priority area for the conservation of nature, since it constitutes a well-preserved portion of the Brazil's Atlantic forest, an important hotspot for biodiversity conservation (Meyers *et al.*, 2000). Despite its relevance, the Park lacks studies on bat fauna, and although there is a detailed species list by Cláudio *et al.* (unpublished data), this is the first study addressing ecological aspects of bat diversity at CBSP.

Sampling sites

We studied bat diversity in two different sites (upper and lower part) covering contrasting altitudes within CBSP (Figure 1). Each site contained 15 mist net points, which were chosen considering altitude, logistic, suitability to capture methods and accessibility, since the Park has a great portion of intangible areas of difficult access. The choice for different capture points occurred to avoid sampling the same point in consecutive days, as it may influence bat activity and capturing rate by mist nets (Marques *et al.* 2013).

The upper part was sampled 18 times during the study, and its altitude ranged from 650 to 850 m. On the other hand, 21 samples were taken on the lower part, where the altitude ranged from 45 to 250 m. The small variation on the number of samples taken per site occurred because sample nights carried out in presence of heavy rain were excluded from the analyses.

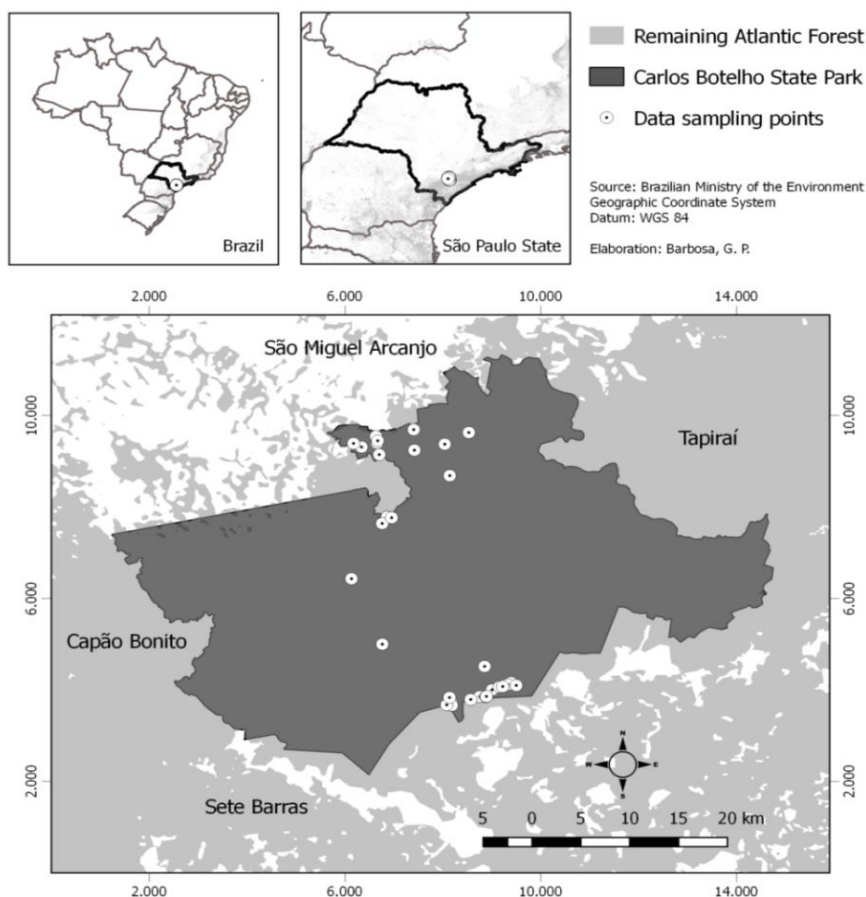


Figure 1. Location of Carlos Botelho State Park, a massive Atlantic forest area in southeastern Brazil. White dots in the map represent different mist-net points where bat species were sampled.

Bat sampling

Capture and handling protocols followed the guidelines of the American Society of Mammalogists (Sikes et al. 2016). We carried out field work between October 2016 and September 2017, sampling both sites twice a month. Bats were captured through mist-nets set up in natural openings, trails, passages, near and over streams and rivers. In each sampling night we used 10 ground nets and one canopy net (size: 9 x 2.5 m; mesh, 20 mm), that remained opened during a four hour period, starting at dusky, and checked every 20 min. All samples were made during the new moon phase to avoid lunar phobia (Morrison 1978, Saldaña-Vázquez & Munguía-Rosas 2013), and the sampling effort was calculated according to Straube & Bianconi (2002).

Sampled individuals were aged, and checked for sex and reproductive status. External measurements and qualitative diagnostic characters were taken from all captured bats to help on species identification. Field identification was based on the

keys provided by Gardner (2008), Reis *et al.* (2013) and López-Baucells *et al.* (2016). Two voucher specimens were taken from all species, fixed with 10% of buffered formalin, preserved in 70% alcohol and deposited in the Coleção de Vertebrados da Universidade Federal de São Carlos – *campus* Sorocaba (ZSP; Sorocaba, SP, Brazil) and in the Museu Nacional, Universidade Federal do Rio de Janeiro (MN; Rio de Janeiro, RJ, Brazil). Except for the vouchers, pregnant females and young individuals, all recorded bats were marked with individual plastic collars and released in the same place they were captured. All research reported in this manuscript is adhered to Brazil's legal requirements under the licenses provided by the Biodiversity Authorization and Information System (SISBIO/ICMBIO 54.381-1/2016), and the Technical and Scientific Committee from São Paulo Forestry Institute (COTEC/SMA-IF 260108-006.479/2016).

Species diversity analyses

Data from a single night of sampling constituted a sample unity. Species richness estimators build on abundance (ACE, Chao 1 and M-M) and incidence (ICE and Chao 2, first- and second-order Jackknife, and the Bootstrap estimator) were computed based in 100 randomizations of sampling order in EstimateS 9.1 (Cowell 2013). The choice for a species richness estimator to be employed at each study site followed the framework proposed by Brose & Martinez (2004) (see Supplementary information S1).

To compare species richness between lower and upper parts of the Park, sample-based rarefaction/ extrapolation (RE) curves with 95% interval was computed with R software (RStudio Team 2015), using the R package “*iNEXT*” (Hsieh & Chao 2016). The “*iNEXT*” RE curves are produced based on Hill numbers quantification of species diversity of an assemblage (Chao *et al.* 2014), and presented here as $q = 0$, which represents species richness as a measure of diversity. We also used richness estimates and curves to investigate undersampling in our dataset, as a major concern in ecological studies refers to data biases caused by sample incompleteness.

We assessed alpha diversity parameters by calculating Fisher's α value for each site, using the R package “*vegan*” (version 2.4-4). Since the abundance distributions did not deviate significantly from the log series distribution ($p > 0.05$ - see Supplementary information S2), Fisher's α measure was chosen because it provides a robust and comprehensible description of the diversity of a community and is relatively unaffected

by sample size (Magurran 2004). An independent – samples t-test was then conducted to compare values of Fisher’s α obtained in both sites.

Since differences in species composition among habitats (beta diversity) may represent two distinct processes – nestedness and spatial turnover (Harrison *et al.* 1992) – we calculated total beta diversity and the portions of the two components according to Baselga (2010). In this approach, total beta diversity is calculated as the Sørensen dissimilarity index (β_{sor}), the spatial turnover is described as the Simpson dissimilarity index (β_{sim}) and the nestedness component of beta diversity (β_{nes}) is obtained by the difference between β_{sor} and β_{sim} (Baselga 2010). Total beta diversity and its fractions were obtained using the R package “*betapart*” (Baselga & Orme 2012).

Environmental variables

In addition to measures of altitude recorded with a handheld GPS (Garmin), we quantified environmental variables (air temperature and relative humidity) known to play a role in altitude-diversity relationships. Data on air temperature and relative humidity was recorded for each sampling night at every 15 minute interval, using a data logger (Instrutemp – model ITLOG 80) placed near to the nets on the same habitat bats were captured. These data were averaged across the entire sampling night and represented as average nightly air temperature (°C) and average nightly relative humidity (%) for analyses (see Supplementary information S3).

We used independent – samples t-tests to assess whether temperature and humidity differed between sampling sites. The relationship between these variables and bat abundance (number of individuals captured) and species richness (number of species captured) was also tested using simple linear regressions. All analyses and graphical representations were performed in R software environment.

RESULTS

We captured a total of 333 bats belonging to 27 species, 19 genera and three families (see Supplementary information S4, S5, S6). Recaptures (10 individuals) are already excluded from the total number (Table 1). Phyllostomidae were the most representative family with 21 species and 306 individuals, followed by Vespertilionidae with five species and 26 individuals, and Molossidae with one individual from a single species. The number of observed species richness differed markedly across sampling sites (Table 1). A pattern on the distribution of bat species indicates a strong association

between Phyllostomidae bats and lower elevations (20 species recorded among 21), when compared to Vespertilionidae (only *Myotis nigricans* recorded among five species). On the other hand, at the upper part, only 10 among 21 Phyllostomidae species were recorded while all Vespertilionidae bats in the sample were captured at this altitude.

Table 1. Bat species recorded at Carlos Botelho State Park, Brazil. Captures are divided by site, including totals and sampling effort applied for each site. Trophic guild classification followed Kalko *et al.* 1996, as aerial insectivore (AI), carnivore (C), frugivore (F), gleaning (G), nectarivore (N) and sanguivore (S).

Species	Trophic guild	Individuals captured		Total
		Lower part	Upper part	
Family Phyllostomidae				
Subfamily Micronycterinae				
<i>Lamproncycteris brachyotis</i> (Dobson, 1879)	G	1	0	1
<i>Microncycteris microtis</i> Miller, 1898	G	2	0	2
<i>Microncycteris schimdtorum</i> Sanborn, 1935	G	1	0	1
Subfamily Desmodontinae				
<i>Desmodus rotundus</i> (E. Geoffroy, 1810)	S	5	13	18
<i>Diphylla ecaudata</i> Spix, 1823	S	2	2	4
Subfamily Phyllostominae				
<i>Mimon bennettii</i> (Gray, 1838)	G	1	0	1
<i>Trachops cirrhosus</i> (Spix, 1823)	C	2	1	3
Subfamily Glossophaginae				
<i>Anoura caudifer</i> (E. Geoffroy, 1818)	N	20	5	25
<i>Anoura geoffroyi</i> (E. Geoffroy, 1838)	N	18	9	27
Subfamily Carollinae				
<i>Carollia perspicillata</i> (Linnaeus, 1758)	F	68	20	88
Subfamily Glyphonycterinae				
<i>Glyphonycteris sylvestris</i> Thomas, 1896	G	2	0	2
Subfamily Stenodermatinae				
<i>Artibeus fimbriatus</i> Gray, 1838	F	28	17	45
<i>Artibeus lituratus</i> (Olfers, 1818)	F	7	3	10
<i>Artibeus obscurus</i> (Schinz, 1821)	F	31	0	31
<i>Dermanura cinerea</i> (Gervais, 1856)	F	7	0	7
<i>Platyrrhinus lineatus</i> (E. Geoffroy, 1810)	F	1	0	1
<i>Platyrrhinus recifinus</i> (Thomas, 1901)	F	1	0	1
<i>Pygoderma bilabiatum</i> (Wagner, 1843)	F	0	3	3
<i>Sturnira lilium</i> (E. Geoffroy, 1810)	F	9	21	30
<i>Sturnira tildae</i> de la Torre, 1959	F	5	0	5
<i>Vampyressa pusilla</i> (Wagner, 1843)	F	1	0	1
Family Vespertilionidae				
Subfamily Vespertilioninae				
<i>Eptesicus taddeii</i> Miranda, Bernardi & Passos, 2006	AI	0	2	2

<i>Lasiurus ebenus</i> Fazzolari-Corrêa, 1994	AI	0	1	1
Subfamily Myotinae				0
<i>Myotis nigricans</i> (Schinz, 1821)	AI	13	7	20
<i>Myotis riparius</i> Handley, 1960	AI	0	2	2
<i>Myotis ruber</i> (E. Geoffroy, 1806)	AI	0	1	1
Family Molossidae				0
Subfamily Molossinae				0
<i>Molossops neglectus</i> Williams & Genoways, 1980	AI	0	1	1
Total number of captures		225	108	333
Observed species richness		21	16	27
Sampling effort (m ² .h)		20,430	17,550	37,980

According to the richness estimator chose (first-order Jackknife), true richness are beyond the observed for the lower ($S_{est} = 26.71 \pm 2.02$; mean coverage = 82.17%) and upper part ($S_{est} = 19.78 \pm 1.71$; mean coverage = 84.38%), and also for CBSP as a whole ($S_{est} = 35.76 \pm 2.59$; mean coverage = 76.27%). The estimates corroborate with the analyses of RE curves (Figure 2), which display both sites in a stage of accumulation, and extrapolation of data shows that more sampling would be necessary to reach an asymptote. No statically significant differences were found regarding to the number of species found in both sites (Figure 2), indicating the same richness patterns between upper and lower parts of the Park.

As noted for species richness, measures of local diversity did not differentiate between sites ($t = -0.678$, $df = 18.429$, $p > 0.05$), showing similar results at the upper ($\alpha = 5.19$) and lower part ($\alpha = 5.67$) of CBSP. The total beta diversity, measured as the Sørensen dissimilarity index, showed a value of $\beta_{sor} = 0.459$. When this value is partitioned in the two fractions of beta diversity, one can note that spatial turnover plays a major role in the communities' dissimilarity found ($\beta_{sim} = 0.375$), while nestedness is almost inexistent ($\beta_{nes} = 0.084$).

Nightly air temperature was higher at the lower part of the Park ($t = 2.603$, $df = 35.547$, $p < 0.05$), while nightly relative humidity did not show variation between sites ($t = 1.495$, $df = 26.225$, $p > 0.05$) (Figure 3). Air temperature was positively related to bat abundance per night ($R^2 = 0.111$, $p < 0.05$), but showed no relation to bat species richness ($R^2 = 0.012$, $p > 0.05$) (Figure 4). Also, variation in relative humidity did not show relation to bat abundance ($R^2 = 0.001$, $p > 0.05$) and richness ($R^2 = 0.042$, $p > 0.05$) across sampling nights (Figure 4).

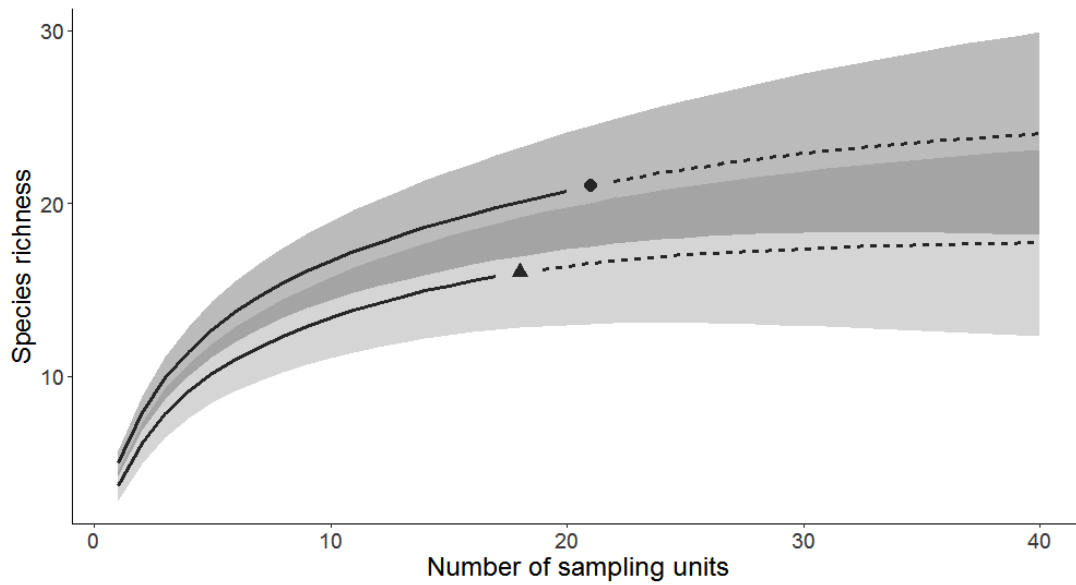


Figure 2. Sample-based rarefaction/ extrapolation curves for bat assemblages at two sites with different altitude in Carlos Botelho State Park, Brazil. Circle and triangle denote lower part and upper part of the Park, respectively. Confidence intervals are shaded. Solid line = interpolation; dashed line = extrapolation.

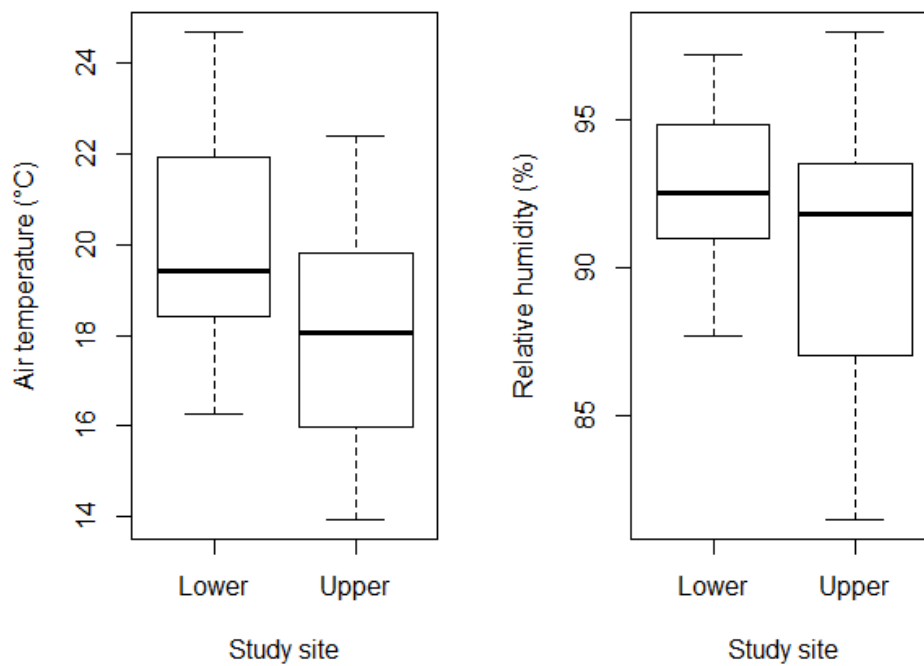


Figure 3. Distribution of average nightly air temperature (°C) and relative humidity (%) between two sites with different altitude at Carlos Botelho State Park, Brazil.

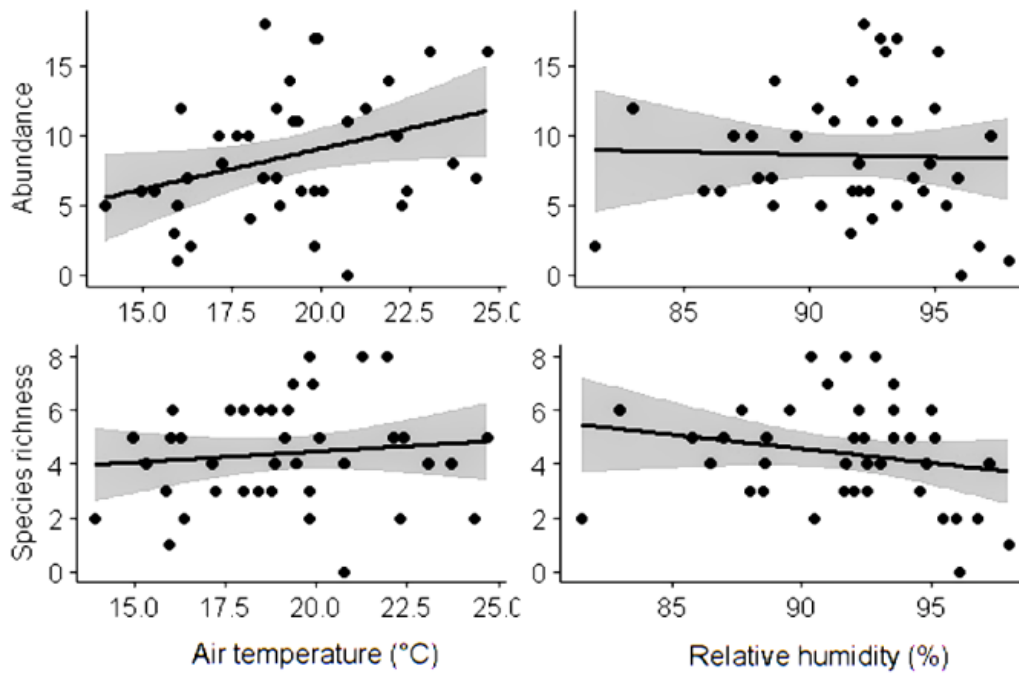


Figure 4. Relationship between observed bat abundance and species richness, and average nightly air temperature (°C) and relative humidity (%) at Carlos Botelho State Park, Brazil. Confidence intervals are shaded.

DISCUSSION

Species diversity at contrasting altitudes

In general, studies that point to a negative relationship between bat diversity and altitude show that a markedly decrease in bat richness is usually found on sites above 1000 m of altitude (Cisneros *et al.* 2014, Curran *et al.* 2012, Patterson *et al.* 1996). This is also true for the few studies available in Brazilian area (Bordignon & França 2009, Dias *et al.* 2008, Lopes *et al.* 2017, Martins *et al.* 2015). Our results corroborated with these studies on this matter, as the highest point within CBSP does not exceeds 1000 m, the altitudinal differences sampled within the Park seem to play no role on the patterns structuring bat richness and diversity.

Differences in species composition indicate spatial turnover as a source of variation between upper and lower altitudes. It implies that species absence between different locations at CBSP is not a result of orderly disaggregation of assemblages from the same species pool (Gaston & Blackburn 2000, Meyer & Kalko 2008, Patterson *et al.* 1996), but rather because of species replacement due to selective differentiation processes as species sorting, spatial constraints or historical dynamics (Gaston & Blackburn 2000, López-González *et al.* 2012, Stevens *et al.* 2007, Svenning *et al.* 2011). As already stated, non-exclusive factors such as climate variation, habitat

heterogeneity, and evolutionary process (Cisneros *et al.* 2014, Curran *et al.* 2012, Dun & Waters 2012, McCain 2007, Martins *et al.* 2015, Sánchez & Giannini 2014) are involved in this difference in species composition.

In our study, the small range of variation in humidity, which can be related to the lack of dry season at the study area, did not affect bat community in any way. Although not addressed deeply in this study, we assume that water availability may not be a source of variation in bat species diversity at CBSP, as found in other studies (McCain 2007, Salsamendi *et al.* 2012). On the other hand, as predicted, accentuated temperature variation has a major effect on bat abundance in CBSP, which might explain differences in species abundance and composition between altitudes sampled. Intra-specific effects of ambient temperature in bat populations may include changes in bat activity (Wolbert *et al.* 2014) reproductive patterns (Mello *et al.* 2009), foraging strategies and roosting behavior (Dietz & Kalko 2006).

At community level, ambient temperature might influence bat species richness indirectly by fluctuation in food resources, which includes changes in prey abundance (Brooks *et al.* 2017, Müller *et al.* 2012, Sherwin *et al.*, 2012) and fruit availability (Pereira *et al.* 2010, Sherwin *et al.* 2012). Despite not working as a driver of species richness in general, the fluctuation in temperature might have acted as a source of variation in species captured at both sites. This is noted in the reduced number of Phyllostomidae and increased number of Vespertilionidae species at higher altitudes, a pattern already found in other studies addressing bat communities in high elevations (McCain 2007, Martins *et al.* 2015, Soriano 2000).

According to Soriano (2000) and Espinosa (2006), differences in species distribution can be explained by metabolic rates and thermoregulatory responses of different body size species. Resource variation also plays an important role in this matter. While fruit eating bats may face limiting food resources due to plant diversification and resource variation at high elevations, aerial insectivores seem to present adaptations to cold environmental conditions, as many species occupy cloudy forests and are well distributed outside the tropics (Espinosa 2006, Soriano 2000).

Potential bias in findings

A potential source of bias arise from our study as rarefaction/extrapolation (RE) curves indicate that observed species inventory was incomplete at both sites. Also, the predominance of Phyllostomidae may be a bias of the capture method based almost

entirely in ground mist nets, which favors the capture of Phyllostomidae bats in detriment of other families (Simmon & Voss 1998).

Although we believe that temperature has a major role in species variation found between altitudes sampled at CBSP, we did not account for the effects of other important variables involved in altitude-diversity relationship (Cisneros *et al.* 2014, Curran *et al.* 2012, Dunn & Waters 2012, McCain, 2007, Martins *et al.* 2015, Sánchez & Giannini 2014) to investigate this further, as they may operate in interaction.

Distribution of bat species richness along altitudinal gradients may present two patterns: declining species richness with elevation and a mid-elevation peak in species richness (McCain 2007, Willig & Presley 2016). Despite changes in species composition (spatial turnover), we did not observe a significant decrease on species richness due to altitude at CBSP. However, as mid domain effects of altitude on species richness could not be assessed due to logistic reasons, new studies would be necessary to clarify this assumption, taking into consideration mid altitudes within CBSP.

Conservation implications

According to Willig & Presley (2016), the high diversity, presence of rare and endemic species and spatial turnover found in elevation gradients of tropical forests make conservation a challenging task, reinforcing the need of ecological research and target conservation actions. Thus, quantifying spatial patterns of biodiversity and understanding mechanisms that mould them are crucial, as they can reveal spatial scaling of diversity loss and mechanisms of regional diversity organization and maintenance (Socolar *et al.* 2016, Willig & Presley 2016).

The Carlos Botelho State Park (CBSP) is a well preserved Atlantic forest area, protected as a State Park, with a huge relevance on conservation of wildlife species and its interactions (SÃO PAULO 2008). The high presence of bats from subfamilies as Phyllostominae, Glyphonycterinae and Micronycterinae (this study) corroborates with this assumption, as these bats are sensitive to disturbance and their presence indicate high ecosystem integrity (Medellín *et al.* 2000)..

Considering the importance of bats on ecosystems, the fact that bat fauna from CBSP started being surveyed (Cláudio *et al.* unpublished data) and studied recently (the present work), since its recognition as a State Park in 1982 (SÃO PAULO 2008), rises concern about the need to improve wildlife studies in protected and non-protected areas in Brazil. Analysis of species diversity in a spatial scale at CBSP can optimize

conservation management, in order to guarantee that conservation priorities capture the variation in site-specific risks of losing species.

CONCLUSION

Altitudinal variation affects the structure of natural communities by causing changes on its abundance, species richness and diversity. Due to a range of circumstances working in interaction, as differences in climate, habitat heterogeneity and evolutionary process, bat richness and diversity usually decline with increasing altitude. At CBSP, a well-preserved Atlantic Forest in southeastern Brazil, the altitudinal variation found (30 to 1000 m) did not affect patterns of bat richness and diversity, showing that community structure remains similar between lower and upper parts of the Park. Changes in species composition between sites, mainly among Phyllostomidae and Vespertilionidae species, indicate the presence of species turnover. Among the variables tested, substantial differences in air temperature was significantly related to the decline on abundance of these bats from lower to upper areas. Despite increasing the knowledge on the ecology and conservation of bats, more research is needed to understand other aspects of bat ecology within CBSP, considering its importance on the conservation of biodiversity from Brazilian Atlantic Forest.

ACKNOWLEDGEMENTS

We are thankful to the staff of Carlos Botelho State Park for the logistical support. GPB and VCC had received MSc scholarships from Programa de Pós-Graduação em Conservação da Fauna and Fundação Parque Zoológico de São Paulo.

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SUPPLEMENTARY INFORMATION

Analysis of bat species diversity at two contrasting altitudes in a protected Atlantic Forest area, Southeastern Brazil

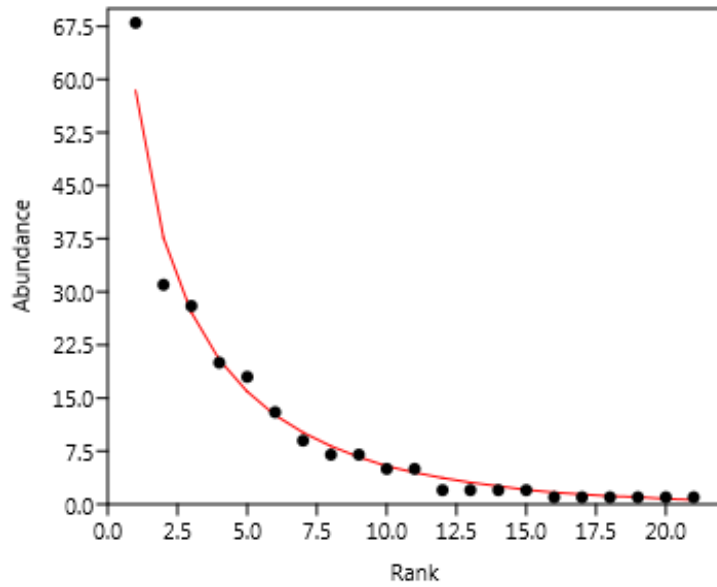
Additional tables and figures

S1. Site-specific, non-parametric species richness estimates. F1 and F2, refer to singletons and doubletons respectively. Q1 and Q2 refer to unique and duplicates respectively.

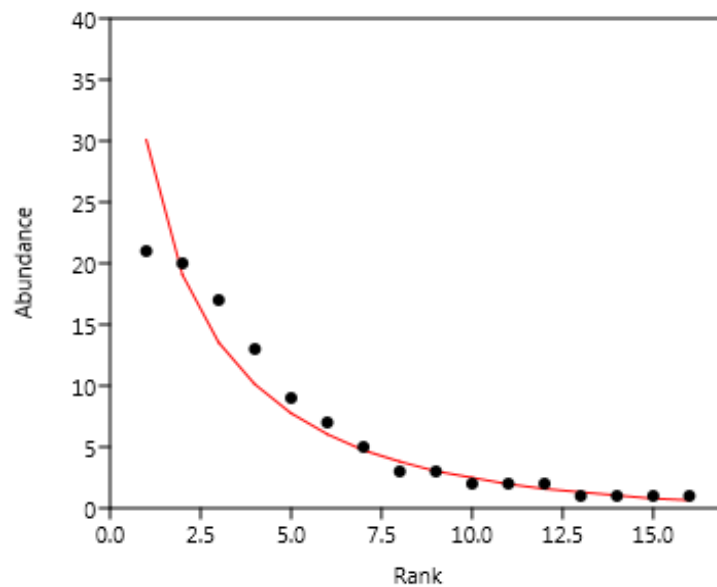
Data properties	Lower part	Upper part	CBSP
S _{obs}	21	16	27
N	225	108	333
F1	6	4	9
F2	4	3	4
Q1	6	4	9
Q2	4	4	5
ACE	27.48	19.86	40.32
ICE	25.67	19.25	40.28
Chao 1	23.99	17.49	34.18
Chao 2	23.86	17.13	32.84
Jack 1	26.71	19.78	35.76
Jack 2	28.70	19.99	39.68
Boot	23.66	17.96	30.98
M-M	24.16	20.23	29.84
Coverage (%)	82.17	84.38	76.27
Estimator choice	Jack 1	Jack 1	Jack 1
S _{est}	26.71	19.78	35.76

S2. Rank abundance plots illustrating shape of bat abundance distributions at Carlos Botelho State Park. Both lower (a) and upper part (b) distributions follow a log-series model.

a) $\alpha = 5.66$; deviation from log-series: $\chi^2 = 4.777$, $p = 0.9798$



b) $\alpha = 5.191$; deviation from log-series: $\chi^2 = 5.141$, $p > 0.7424$



S3. Data on air temperature and relative humidity recorded at each sample unity during the 39 nights of bat sampling at Carlos Botelho State Park, Brazil.

Sampling Site	Altitude (m)	Average air temperature (°C)	Average relative Humidity (%)
Lower part	45	19.81	92.81
Lower part	46	23.06	93.00
Lower part	50	17.12	97.19
Lower part	50	24.68	95.13
Lower part	51	21.92	91.69
Lower part	51	17.66	87.69
Lower part	52	23.71	94.81
Lower part	52	20.75	92.50
Lower part	52	19.43	91.69
Lower part	54	18.75	95.00
Lower part	61	19.90	93.50
Lower part	66	17.98	89.50
Lower part	75	18.44	92.19
Lower part	75	19.35	91.00
Lower part	82	21.25	90.36
Lower part	92	18.75	88.00
Lower part	96	22.29	95.44
Lower part	105	16.27	94.13
Lower part	105	24.34	95.94
Lower part	170	18.00	92.50
Lower part	220	18.40	88.50
Upper part	650	22.13	87.00
Upper part	650	19.20	93.50
Upper part	709	14.95	92.00
Upper part	729	15.98	97.94
Upper part	739	13.95	90.50
Upper part	750	17.24	92.00
Upper part	754	18.87	88.56
Upper part	769	20.75	96.06
Upper part	769	19.82	94.56
Upper part	775	22.41	85.81
Upper part	787	16.35	81.50
Upper part	800	20.06	92.38
Upper part	806	15.35	86.50
Upper part	810	19.11	88.63
Upper part	820	15.87	91.63
Upper part	820	19.83	96.75
Upper part	836	16.00	93.50
Upper part	848	16.05	83.00

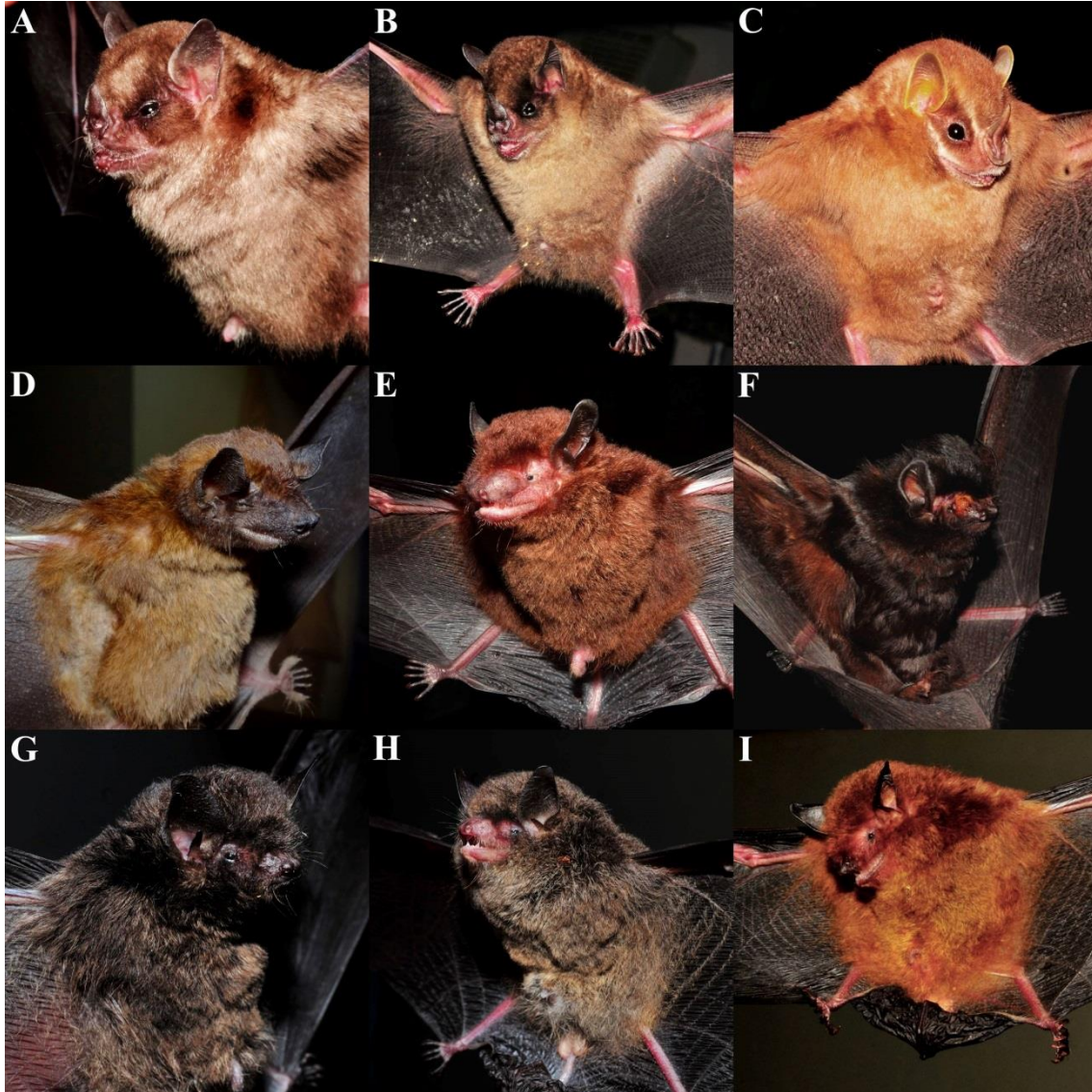
S4. Bats species captured at Carlos Botelho State Park, Brazil. *Lamproncyteris brachyotis* (A); *Micronycteris microtis* (B); *Micronycteris schmidtorum* (C); *Desmodus rotundus* (D); *Diphylla ecaudata* (E); *Mimon bennettii* (F); *Trachops cirrhosus* (G); *Anoura caudifer* (H); *Anoura geoffroyi* (I).



S5. Bats species captured at Carlos Botelho State Park, Brazil. *Carollia perspicillata* (A); *Glyphonycteris sylvestris* (B); *Artibeus fimbriatus* (C); *Artibeus lituratus* (D); *Artibeus obscurus* (E); *Dermanura cinerea* (F); *Platyrrhinus lineatus* (G); *Platyrrhinus recifinus* (H); and *Pygoderma bilabiatum* (I).



S6. Bats species captured at Carlos Botelho State Park, Brazil. *Sturnira lilium* (A); *Sturnira tildae* (B); *Vampyressa pusilla* (C); *Molossops neglectus* (D); *Eptesicus taddeii* (E); *Lasiurus ebenus* (F); *Myotis nigricans* (G); *Myotis riparius* (H); and *Myotis ruber* (I).



CAPÍTULO 2

Among flowers and fruits: a multilayer network of bat-plant interactions in a Brazilian Atlantic Forest.

Gedimar P. Barbosa^{1,2*}, Angela M. S. Corrêa³, Vinícius C. Cláudio^{1,2}, Vlamir J. Rocha⁴,
Fabrício B. Rassy²

¹ Universidade Federal de São Carlos, Centro de Ciências Biológicas e da Saúde, São Carlos, SP, Brazil.

² Fundação Parque Zoológico de São Paulo, São Paulo, SP, Brazil.

³ Instituto de Botânica, São Paulo, SP, Brazil.

⁴ Universidade Federal de São Carlos, Centro de Ciências Agrárias. Araras, SP, Brazil.

Abstract

Networks of interaction between bat and plant species have always been analyzed based on a single interaction or resource type at a time. However, as bats feed on a diversity of plant resources, we provided empirical data to evaluate the structure of bat-plant interactions through a multilayer network perspective. At a well-preserved Atlantic Forest area in southeastern Brazil, we found that bats and plants form a nested interaction network, when considering bat-flower and bat-fruit interactions within a multilayer network. This nestedness was already described for seed dispersal and pollination interactions, in studies based on a single interaction network. As the degrees of nestedness and modularity varied considerably between networks of different interactions, the analysis through a multilayer perspective can be useful to better describe bat-plant interactions as a whole. Beyond detecting structural differences across interaction networks, our study also shows that common bat species as *A. geoffroyii*, *C. perspicillata* and *A. caudifer* play a keystone role in the local community structure, being responsible for a large number of connections and also for keeping different parts of the network bound.

Keywords: Community structure; keystone species; pollination; seed dispersal; conservation.

INTRODUCTION

The structure of animal-plant interactions have always been an important issue in ecological studies. Interactions as seed dispersal and pollination drastically affect population dynamics of the interacting species, and understand the way they are structured plays a vital role for the maintenance of biodiversity and function of ecosystems (Bascompte *et al.* 2003, Bascompte & Jordano 2007, Bastolla *et al.* 2009,

Fortuna & Bascompte 2006, Olesen *et al.* 2007). Despite different animal-plant interactions can occur simultaneously, most empirical data available in this field focus on networks mediated by a single resource or single interaction type at a time.

In this context, recent advances in the network theory have provided an approach that provides the possibility of linking different types of interactions, different communities, and different temporal and spatial networks into a single multilayer network (Pilosof *et al.* 2017). This approach has been applied in empirical studies to better understand the complexity of the interactions between ant species and different plant resources (Costa *et al.* 2016), the consequences of mutualistic and antagonistic interactions between mammals and seeds (Genrich *et al.* 2016) and the spatial structure of seed-dispersal networks (Timóteo *et al.* 2018).

Among mammals, bats are well-known to feed on different plant resources (Bredt *et al.* 2012, Kalko 1998), which makes them an efficient model to evaluate the structure of animal-plant networks under a multilayer perspective. Bat species that rely on plants to feed, obtain resources through the consumption mainly of fruits (Bredt *et al.* 2012, Giannini & Kalko 2004, Saldaña-Vázquez *et al.* 2013), flower composites as nectar and pollen (Fleming *et al.* 2009, Koopman 1981, Muchhala & Jarrín-V 2002, Winter & Helversen 2003) and leaves (Cordero-Schmidt *et al.* 2016, Kunz & Ingalls 1994, Zortéa & Mendes 1993). However, to this date, the structure of interaction networks among bats and plants have been analyzed based on a single type of interaction, presenting either pollination (Cordero-Schmidt 2016, Mora-Beltrán & López-Arévalo 2018) or seed dispersal networks (Mello *et al.* 2011a, Mello *et al.* 2011b, Mello *et al.* 2015) separately.

Animal-plant networks structures usually present nonrandom patterns of interaction, as nestedness and modularity (Bascompte *et al.* 2003, Bascompte & Jordano 2007, Lewinsohn *et al.* 2006, Olesen *et al.* 2007). In nested networks, species with fewer interactions are connected to subsets of species with more interactions (Bascompte *et al.* 2003, Bascompte & Jordano 2007). It provides a high cohesion and more resistant structure, which provides alternative routes to avoid damage caused by perturbation (Bascompte *et al.* 2003). In modular networks, species form subsets (modules) that are more likely to interact within themselves than between subsets (Lewinsohn *et al.* 2006, Olesen *et al.* 2007). These modules may be the result of habitat heterogeneity or phylogenetic and functional restraints (Lewinsohn *et al.* 2006, Olesen *et al.* 2007), which lead to nonrandom patterns of aggregation.

The available literature on bat-plant network structure are more restrained to the interaction between bats and fruits (Mello *et al.* 2011a, Mello *et al.* 2011b, Mello *et al.* 2015), and data on the network structure of interactions between bats and flowers are more scarce (Cordero-Schmidt 2016, Mora-Beltrán & López-Arévalo 2018). Both types of interaction present high nested networks (Cordero-Schmidt 2016, Mello *et al.* 2011b, Mora-Beltrán & López-Arévalo 2018), but degrees of modularity are also described for seed dispersal networks (Mello *et al.* 2011a).

Besides understanding plant-animal network structure, identifying the keystone species that are essential to the maintenance of this structure is also primordial from a conservation perspective. The original concept of keystone species was proposed by Paine (1969) to categorize species with disproportional importance to community structure, in relation to their abundances. Since then, many versions of the concept of keystone species were derived (Mills *et al.* 1993, Power *et al.* 1996, Brose *et al.* 2005), and recently, Mello *et al.* (2015) provided data on ecological factors that lead a species to become a keystone in plant-animal mutualistic networks. For this, the authors measured the centrality of frugivore species to determine their relative importance to the network structure (Mello *et al.* 2015).

Thus in the present study we aimed to (1) describe the structure of bat-plant interactions in a well-preserved Atlantic Forest in Southeastern Brazil, exploring different interaction types through a multilayer network perspective, to (2) understand how this structure varies from patterns described to date for bat-plant networks when interactions with different resource types are considered, and to (3) identify which bat species are central to the maintenance of the network structure described. Despite some studies have applied multilayer networks to describe network structure at different types of interactions and resources (Costa *et al.* 2016, Genrich *et al.* 2016), to our knowledge, this is the first study to consider the bats-plant interactions on a multilayer network perspective.

METHODS

Study area

Carlos Botelho State Park (hereafter CBSP) is a protected area located in São Paulo (24° 06' 55" - 24° 14' 41" S and 47° 47' 18" - 48° 07' 17" W), with 37,644 ha in a continuous massif called "Serra de Paranapiacaba" in southeastern Brazil (Figure 1).

The Park covers a mountainous and steep relief, with altitudes between 30 m (lower part) and 1000 m (upper part). The vegetation is predominantly dense montane and submontane Atlantic Forest, with the upper part characterized mainly by humid montane forest and the lower part characterized as lowland evergreen forest (Lima *et al.* 2011). Forest formations vary between well-preserved stretches with continuous canopy above 20 m, to secondary formations with smaller and more open canopy (Lima *et al.* 2011). The CBSP houses a relevant diversity of life (SÃO PAULO, 2008) and is considered a priority area for the conservation of nature, since it constitutes a well-preserved portion of the Brazil's Atlantic Forest, an important hotspot for biodiversity conservation (Meyers *et al.* 2000). Despite its relevance, the Park lacks studies on bat fauna, and this is the first study addressing ecological aspects of bat-plant species interactions in CBSP.

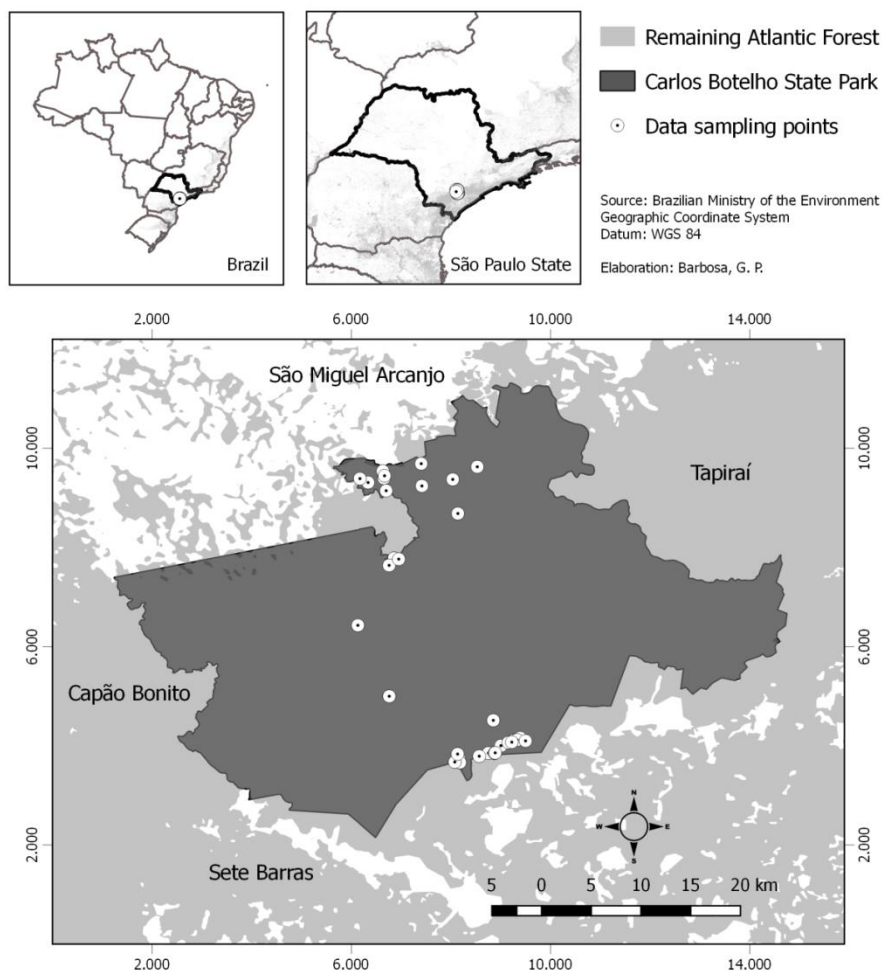


Figure 1. Location of Carlos Botelho State Park, a massive Atlantic Forest area in southeastern Brazil. White dots in the map represent the 30 different points where data on bat-plant interactions were recorded during the study.

Bat sampling

We sampled bats along two altitudinal bands covering contrasting elevations within the Park. Bat captures occurred at 30 different points (Figure 1), chosen considering logistic, suitability to capture methods and accessibility, since the Park has a great portion of intangible areas of difficult access. Capture points ranged from 50 to 250 m altitude at the lower altitude of the Park, and from 650 to 850 m at the higher altitude portion.

Field work was carried out four nights per month, between October 2016 and September 2017. Animal capture and handling protocols followed the guidelines of the American Society of Mammalogists (Sikes *et al.* 2011). Individual bats were captured through mist-nets set up in natural openings, trails, passages, near and over streams and rivers. In each sampling night we used 10 ground nets (size: 9 x 2.5 m; mesh, 20 mm), that remained opened during a four hour period, starting at dusky, and checked every 20 min. External measurements were taken from all captured bats, and data recorded combined to the keys provided by Gardner (2008), Reis *et al.* (2013) and López-Baucells *et al.* (2016), in order to correctly identify the species. After data collection, animals were marked with individual plastic collars and released in the same place they were captured. Bat sampling effort was calculated according to Straube & Bianconi (2002). All research reported in this manuscript is adhered to Brazil's legal requirements under the licenses provided by the Biodiversity Authorization and Information System (SISBIO/ICMBIO 54.381-1/2016), and the Technical and Scientific Committee from Forestry Institute (COTEC/SMA-IF 260108-006.479/2016).

Data on bat-flower interaction

To obtain data on the interaction between bats and flowers, we used a fine brush dipped in distilled water to collect pollen grains from the heads and bodies of Phyllostomidae bats sampled, according to MacSwiney *et al.* (2017). The pollen was stored in 10ml Falcon tubes containing 5ml of distilled water. In order to avoid sampling contamination, a separated and identified brush and tube were used for each species, and pollen grains were collected from the bats stuck in the nets, before handling the animals and collecting other type of data. The samples were later prepared according to the acetolysis method provided by Erdtman (1960), and analyzed with an Olympus BX50 microscope coupled to an Olympus SC30 video camera, in order to identify and take photomicrographs of pollen samples. The software CellSens Standard

1.5 (Olympus 2013) was also used to analyze the images produced. For samples with abundant pollen, a maximum of 300 grains were counted for each sample. As pollen grains are usually not distinguishable by its morphology, the identification was limited by pollen types, which refers commonly to several species from a same genus (Barth 1989). To correctly identify the pollen types, we used the reference collection of the Research Center in Palynology from the Institute of Botany (IBT) in São Paulo, and also relevant pollen catalogs provided by Melhem *et al.* (1984, 2003) and Roubik & Moreno (1991).

Data on bat-fruit interaction

Data on fruits consumed by bat species were obtained by seed analysis, collected from fecal samples during bat capture and handling. In order to maximize data collection on the seeds eaten, Phyllostomidae bats captured in the nets were also kept in individual cloth bags up to 30 minutes after captured, and feces were collected from the bags after bats were released. The droppings from each bat were stored in individual paper bags with information on bat species and date of collection. The fecal samples were later dried, and those containing seeds were counted and analyzed using a stereomicroscope. To correctly identify the consumed items, we used the material provided by Bredt *et al.* (2012), Lima *et al.* (2016), Lorenzi (1992, 1998, 2009) and also the seed collection of the Wildlife Lab from Federal University of São Carlos *campus* in Araras, São Paulo. In order to present the data and build the networks, the plant species were identified to the genus level, as of the pollen types obtained in the study.

Network analysis

A binary multilayer network was built to describe the structure of bat-plant interactions, in which animals and plants were connected to one another by both records of flower interaction (presence of pollen on bat's head and body) and fruit interaction (presence of seeds in bat's fecal samples). Two layers (subnetworks) were derived from this multilayer, characterized by bat-flower and bat-fruit interactions. We used the “*Kamada–Kawai separate components*” method to draw the graphs in Pajek 5.02a (Batagelj & Mrvar 1998). We also used Pajek 5.02a to measure the connectance, as the proportion of realized interactions of the total possible in each network.

The network structures were accessed by measures of nestedness and modularity. The Nestedness metric based on Overlap and Decreasing Fill index (NODF) was calculated with the software ANINHADO 3.0 to measure the degree of

nestedness (Almeida-Neto *et al.* 2008). NODF values were normalized in order to vary from 0 (non-nested) to 1 (perfectly nested). The degree of modularity was calculated using the index M based on Simulated Annealing, considering the function proposed by Barber (2007), with the software MODULAR 1.0 (Marquitti *et al.* 2014). The index M ranges from 0 (no subgroups) to 1 (totally separated subgroups). We used a Monte Carlo procedure to estimate the significance of nestedness and modularity, generating 1000 random matrices from the original matrix, using the Null Model II of Bascompte *et al.* (2003). This null model considers that the probability of occurrence of an interaction is proportional to the number of interactions of both animal and plant species (Bascompte *et al.* 2003). After simulations, we defined P value by testing the results of our network against the results obtained by the null distributions.

We accessed the relative importance of each animal species to the network structure by measuring centrality metrics, which are applied in ecological studies to identify keystone species (Mello *et al.* 2015). Three centrality metrics were calculated according to Mello *et al.* (2015) and Genrich *et al.* (2016) in Pajek 5.02a (relative degree, closeness centrality and betweenness centrality). Relative degree is measured to represent a species' niche breadth, by calculating the number of interactions one species have in relation to the total number of possible interactions it could have in the network (Mello *et al.* 2015). Closeness centrality measures the species niche's commonness, by calculating the proximity of a species to all other species in the network. A species with high closeness centrality interacts to species in contact with many others in a network (Mello *et al.* 2015). Lastly, betweenness centrality measures the importance of a species as a connector within the network. A species with a high value of betweenness centrality is assumed to have an important role in keeping different parts of the network bound (Mello *et al.* 2015).

RESULTS

A sampling effort of 35,100 m².h resulted in 269 bat specimens captured (recaptures already excluded), representing 17 Phyllostomidae species. A total of 43 different pollen types were recorded in association with 11 bat species (see Supplementary information S1, S2 and S3). A total of 121 fecal samples were collected during bat capture, in which 85 samples (70%) produced by six bat species contained seeds of 21 plant species from eight genera.

The multilayer network contained 107 links (Figure 2). The bat-fruit and bat-flower interaction layers did not overlap too much: 45.4% of all bats were recorded consuming fruits and interacting with flowers, but only 8.5% of the plant genera were present in both subnetworks. Of the 107 connections observed in the multilayer network, only seven links (6.5%) were repeated (Figure 2), which means the same animal species interacting with flowers and consuming fruits from the same plant genera. Those were: *Carolia perspicillata* and *Ficus*; *Artibeus fimbriatus* and *Ficus*; *A. fimbriatus* and *Cecropia*; *Artibeus obscurus* and *Ficus*; *A. obscurus* and *Piper*; *Sturnira lilium* and *Piper* and; *S. lilium* and *Solanum*.

The multilayer network had a high and significant nested pattern, with lower degree of modularity when compared to the bat-flower and bat-fruit networks (Table 1). The network formed by the interactions between bats and fruits was also significant nested, but presented a high modularity degree when compared to the multilayer network (Table 1, Figure 3). The bat-flower interaction network had a lower but significant value of nestedness, presenting more modularity degree than the other networks (Table 1, Figure 3). In general, values of connectance were low for the three networks (Table 1).

Centrality metrics varied considerably within groups and networks (Table 2). In the multilayer network, the bat species *Anoura geoffroyi*, *C. perspicillata* and *Anoura caudifer*, presented the higher niche's breadths, evidenced by the values of relative degree obtained (1.0, 0.71, 0.67) respectively. These same bat species are also pointed out to interact with plants that share connections with different animal species (closeness centrality - 0.49, 0.44, 0.43, respectively) and for being important connectors keeping different parts of the network bound (betweenness centrality - 0.46, 0.25, 0.22, respectively).

Among the plants, the genera with higher relative degrees were *Marcgravia* and *Piper* (0.38 each), followed by *Ficus* (0.33). Regarding to closeness centrality, the genera *Marcgravia*, *Piper* and *Mucuna* stand out with the higher values (0.52, 0.48, 0.47) respectively. Different from bat species, plant genera did not show to work as a connector binding the network, in which the higher values of betweenness centrality occurred for *Marcgravia* (0.16), *Piper* and *Ficus* (0.10 each).

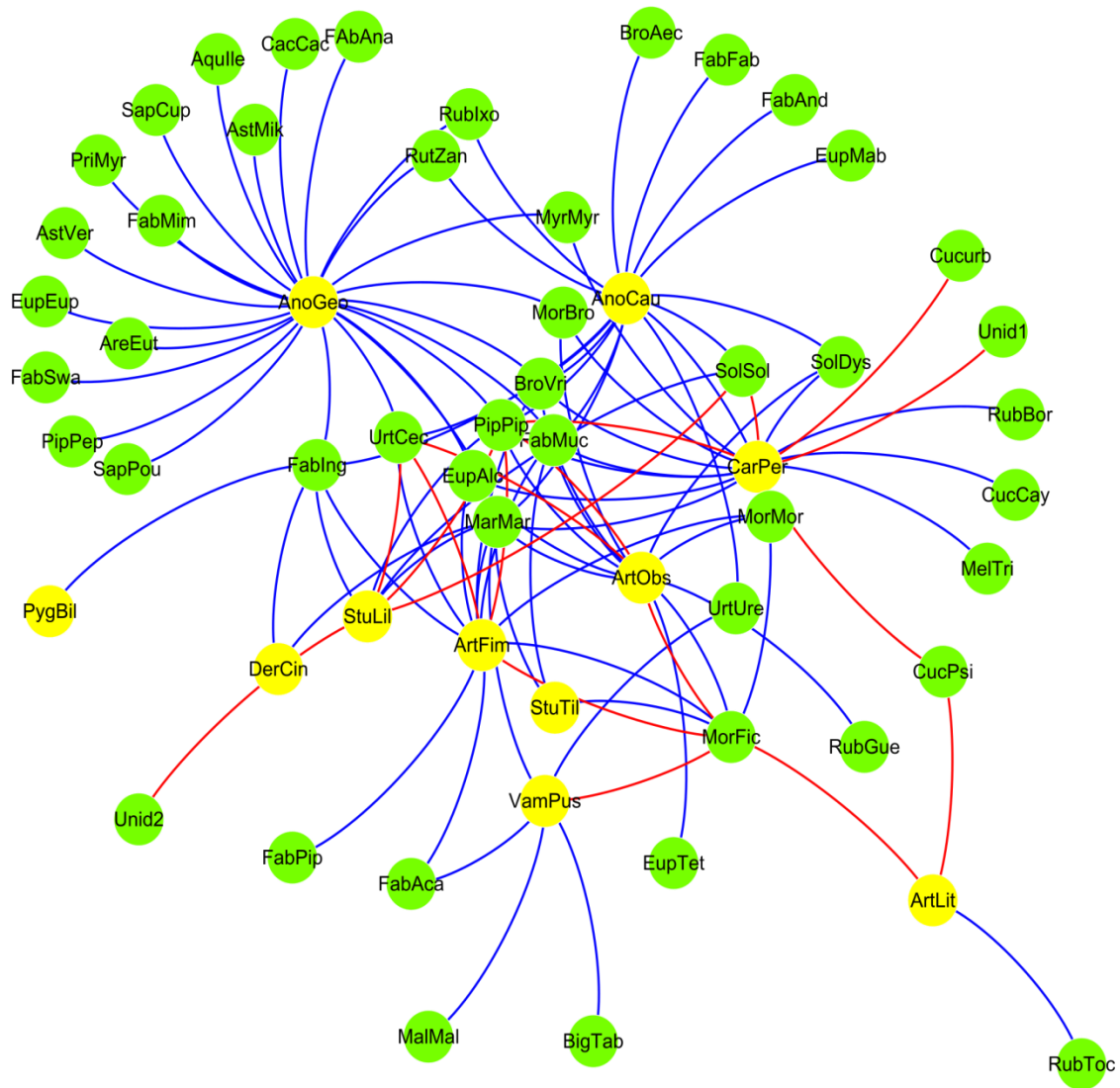


Figure 2. Binary multilayer network of bat-plant interactions recorded at Carlos Botelho State Park. Yellow and green circles (nodes) represent bat species and plant genera, respectively. Blue and red lines (connections) represent bat-flower and bat-fruit interactions, respectively. See Table 2 for node codes.

Table 1. Structural metrics calculated for the multilayer network (ML) of bat-plant interaction, and the layers of bat-flower (FL) and bat-fruit (FR) interaction.

Network descriptors	ML	FL	FR
Nestedness (NODF) *	0.62	0.37	0.47
Modularity (M) **	0.32	0.41	0.35
Number of modules	5	7	4
Connectance	0.21	0.19	0.37

* All bat-plant networks were significantly nested ($p < 0.0001$).

** No bat-plant networks showed modular pattern of interaction ($p > 0.05$).

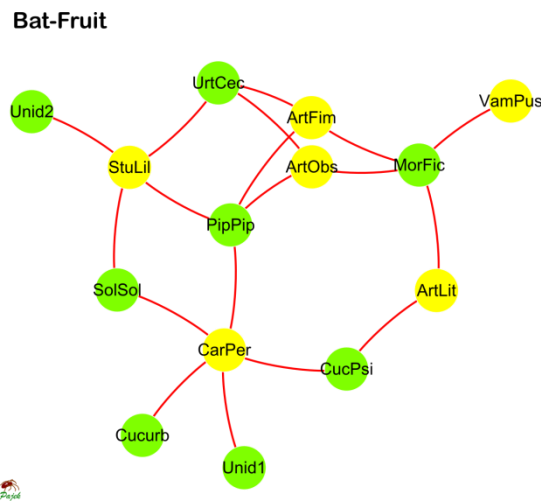
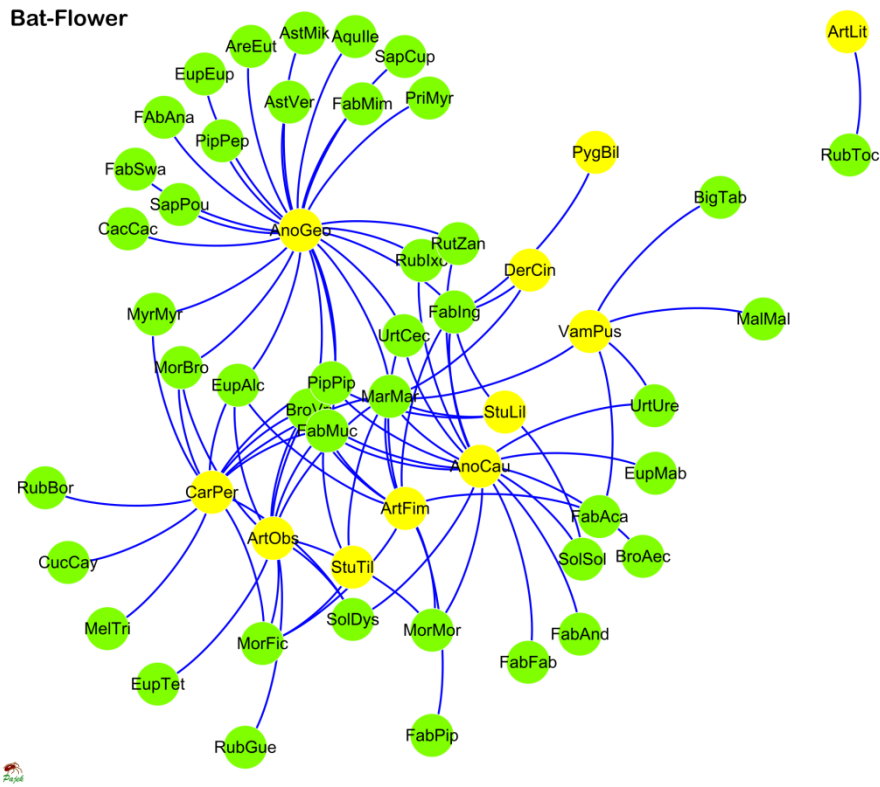


Figure 3. Network layers formed by interactions between bats and plants with flower and fruit resources. Yellow and green circles (nodes) represent bat species and plant genera, respectively. Blue and red lines (connections) represent bat-flower and bat-fruit interactions, respectively. See Table 2 for node codes.

Table 2. Centrality metrics calculated considering the values measured in the multilayer network (ML) of bat-plant interaction, and the layers of bat-flower (FL) and bat-fruit (FR) interaction.

Group	Code	Relative degree			Closeness			Betweenness		
		ML	FL	FR	ML	FL	FR	ML	FL	FR
Bat nodes*										
<i>Anoura caudifer</i>	AnoCau	0.67	0.67	0.00	0.43	0.44	0.00	0.22	0.25	0.00
<i>Anoura geoffroyi</i>	AnoGeo	1.00	1.00	0.00	0.49	0.51	0.00	0.46	0.48	0.00
<i>Artibeus fimbriatus</i>	ArtFim	0.54	0.42	0.60	0.41	0.40	0.46	0.11	0.10	0.13
<i>Artibeus lituratus</i>	ArtLit	0.13	0.04	0.40	0.28	0.04	0.38	0.04	0.00	0.07
<i>Artibeus obscurus</i>	ArtObs	0.58	0.46	0.60	0.41	0.40	0.46	0.12	0.11	0.13
<i>Carollia perspicillata</i>	CarPer	0.71	0.50	1.00	0.44	0.40	0.50	0.25	0.14	0.42
<i>Dermanura cinerea</i>	DerCin	0.08	0.08	0.00	0.35	0.35	0.00	0.00	0.00	0.00
<i>Pygoderma bilabiatum</i>	PygBil	0.04	0.04	0.00	0.30	0.30	0.00	0.00	0.00	0.00
<i>Sturnira lilium</i>	StuLil	0.33	0.17	0.80	0.37	0.36	0.43	0.05	0.01	0.23
<i>Sturnira tildae</i>	StuTil	0.13	0.13	0.00	0.36	0.35	0.00	0.00	0.00	0.00
<i>Vampyressa pusilla</i>	VamPus	0.25	0.21	0.20	0.38	0.36	0.30	0.08	0.08	0.00
Plant nodes**										
<i>Ilex</i>	AquIlle	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Euterpe</i>	AreEut	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Mikania</i>	AstMik	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Vernonia</i>	AstVer	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Tabebuia</i>	BigTab	0.04	0.04	0.00	0.28	0.26	0.00	0.00	0.00	0.00
<i>Aechmea</i>	BroAec	0.04	0.04	0.00	0.30	0.30	0.00	0.00	0.00	0.00
<i>Vriesea</i>	BroVri	0.21	0.21	0.00	0.46	0.46	0.00	0.04	0.05	0.00
Cactaceae	CacCac	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Cayaponia</i>	CucCay	0.04	0.04	0.00	0.30	0.29	0.00	0.00	0.00	0.00
<i>Alchornea</i>	EupAlc	0.17	0.17	0.00	0.42	0.41	0.00	0.03	0.03	0.00
Euphorbiaceae	EupEup	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Mabea</i>	EupMab	0.04	0.04	0.00	0.30	0.30	0.00	0.00	0.00	0.00
<i>Tetrorchidium</i>	EupTet	0.04	0.04	0.00	0.29	0.28	0.00	0.00	0.00	0.00
<i>Acacia</i>	FabAca	0.08	0.08	0.00	0.30	0.30	0.00	0.00	0.01	0.00
<i>Anadenanthera</i>	FabAna	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Andira</i>	FabAnd	0.04	0.04	0.00	0.30	0.30	0.00	0.00	0.00	0.00
Fabaceae	FabFab	0.04	0.04	0.00	0.30	0.30	0.00	0.00	0.00	0.00
<i>Inga</i>	FabIng	0.25	0.25	0.00	0.42	0.43	0.00	0.07	0.08	0.00
<i>Mimosa</i>	FabMim	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Mucuna</i>	FabMuc	0.25	0.25	0.00	0.47	0.47	0.00	0.06	0.06	0.00
<i>Piptadenia</i>	FabPip	0.04	0.04	0.00	0.29	0.28	0.00	0.00	0.00	0.00
<i>Swartzia</i>	FabSwa	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
Malvaceae	MalMal	0.04	0.04	0.00	0.28	0.26	0.00	0.00	0.00	0.00
<i>Marcgravia</i>	MarMar	0.38	0.38	0.00	0.52	0.52	0.00	0.16	0.19	0.00
<i>Trichilia</i>	MelTri	0.04	0.04	0.00	0.30	0.29	0.00	0.00	0.00	0.00
<i>Brosimum</i>	MorBro	0.13	0.13	0.00	0.40	0.39	0.00	0.02	0.02	0.00
<i>Ficus</i>	MorFic	0.33	0.17	0.8	0.37	0.33	0.41	0.10	0.01	0.24

Table 2 (continued). Centrality metrics calculated considering the values measured in the multilayer network (ML) of bat-plant interaction, and the layers of bat-flower (FL) and bat-fruit (FR) interaction

Group	Code	Relative degree			Closeness			Betweenness		
		ML	FL	FR	ML	FL	FR	ML	FL	FR
Moraceae	MorMor	0.13	0.13	0.00	0.34	0.34	0.00	0.01	0.01	0.00
Myrtaceae	MyrMyr	0.08	0.08	0.00	0.38	0.37	0.00	0.01	0.01	0.00
<i>Peperomia</i>	PipPep	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Piper</i>	PipPip	0.38	0.21	0.8	0.48	0.45	0.54	0.10	0.05	0.33
<i>Myrsine</i>	PriMyr	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Borreria</i>	RubBor	0.04	0.04	0.00	0.30	0.29	0.00	0.00	0.00	0.00
<i>Guetarda</i>	RubGue	0.04	0.04	0.00	0.29	0.28	0.00	0.00	0.00	0.00
<i>Ixora</i>	RubIxo	0.08	0.08	0.00	0.37	0.38	0.00	0.01	0.01	0.00
<i>Tocoyena</i>	RubToc	0.04	0.04	0.00	0.22	0.04	0.00	0.00	0.00	0.00
<i>Zanthoxylum</i>	RutZan	0.08	0.08	0.00	0.37	0.38	0.00	0.01	0.01	0.00
<i>Cupania</i>	SapCup	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Pouteria</i>	SapPou	0.04	0.04	0.00	0.33	0.34	0.00	0.00	0.00	0.00
<i>Dysochroma</i>	SolDys	0.13	0.13	0.00	0.36	0.35	0.00	0.01	0.01	0.00
<i>Solanum</i>	SolSol	0.17	0.08	0.4	0.36	0.31	0.41	0.01	0.00	0.07
<i>Cecropia</i>	UrtCec	0.25	0.13	0.6	0.43	0.41	0.41	0.04	0.02	0.08
<i>Urera</i>	UrtUre	0.08	0.08	0.00	0.33	0.32	0.00	0.01	0.01	0.00
Psiguria	CucPsi	0.08	0.00	0.4	0.31	0.00	0.41	0.01	0.00	0.09
Cucurbitacea	Cucurb	0.04	0.00	0.2	0.30	0.00	0.34	0.00	0.00	0.00
Unidentified 1	Unid1	0.04	0.00	0.2	0.30	0.00	0.34	0.00	0.00	0.00
Unidentified 2	Unid2	0.04	0.00	0.2	0.27	0.00	0.31	0.00	0.00	0.00

* Bat nodes are represented at the species level.

** Plant nodes are represented at the genus level, except for some representatives of Cucurbitacea, Moraceae, Fabaceae, Euphorbiaceae and Malvaceae.

DISCUSSION

A total of 47 different plant genera showed interaction with bats, either involving fruit, flower or both plant resources. Some of the interactions recorded are well known associations between bats and plants in the past literature, as *Carollia* with *Pipper* (Bredt *et al.* 2012, Saldaña-Vázquez *et al.* 2013, Thies & Kalko 2004), *Artibeus* with *Ficus* and *Cecropia* (Bredt *et al.* 2012, da Silva *et al.* 2008, Saldaña-Vázquez *et al.* 2013), *Sturnira* with *Solanum* (Bredt *et al.* 2012, Mello *et al.* 2008, Saldaña-Vázquez *et al.* 2013), *Anoura* with *Marcgravia*, *Mucuna*, *Vriesea* and *Inga* (Fleming *et al.* 2009, Kaehler *et al.* 2005, Muchhala & Jarrín-V 2002, Ortega & Alarcón-D 2008, Sazima *et al.* 1999).

Despite almost half of the bat species interacted with both fruits and flowers, only few genera of plants were recorded in both layers of the network. These findings reinforce the assumption that some bats are able to switch their food sources, due to intrinsic (e.g. reproduction and social status) and extrinsic (e.g. seasonality and distribution) factors that affect foraging behavior (Bredt *et al.* 2012, Bohlender *et al.* 2018, Giannini & Kalko 2004, Mello *et al.* 2009, Ortega & Alarcón-D 2008, Santana *et al.* 2011, Thies *et al.* 2006). The results also suggest that, in general, different food resources available to bat species come from different levels and structures within plant genera.

The structural metrics calculated for the multilayer network and its derived layers showed different values, however, only values of nestedness were significant. According to Bascompte *et al.* (2003), nestedness is well-known in plant-animal mutualistic networks due to factors that mold species interaction, as adaptive, phenotypic and phenological aspects. This pattern is believed to be important from a conservation perspective because it plays an important role in the network stability and the maintenance of biodiversity (Bascompte *et al.* 2003; Bastolla *et al.* 2009, Okuyama & Holland 2008, Tylianaskis *et al.* 2010). In a scenario where a specialist species goes extinct in a nested network, the remaining plant species that interacted with this specialist can still interact with generalist species, keeping the ecosystem functions stable (Fortuna & Bascompte 2006, Okuyama & Holland 2008).

Even though nestedness was significant at both layers that comprised the multilayer network, one can note that differences in structure arise from the analysis of the networks separately. From the multilayer to the bat-fruit and bat-flower interaction, the structure tends to gradually change from a nested to a more modular pattern. Our results corroborate with previous studies on the nested structure of bat-plant networks (Cordero-Schmidt 2016, Mello *et al.* 2011b, Mora-Beltrán & López-Arévalo 2018), and also confirm a degree of modularity already described from seed dispersal networks (Mello *et al.* 2011a).

When comparing the networks, the bat-flower interaction network seems to be more modular than the other. Modularity in plant-pollinator networks are related to the temporal variation in species phenology in communities, in which pollinator exchanges along the time and short flowering favor the formation of interaction subsets among the species (Martín-González *et al.* 2012). In addition, morphological, phylogenetic and functional restraints are also drives of modularity in plant-pollinator networks (Olesen

et al. 2007), linking the formation of modules by the association of specific pollinators and plants (Martín-González *et al.* 2012). However, the detection of modules in plant-pollinator networks are less likely to occur when studies are focused in community interaction subsets (e.g. bat-plant only) (Freitas *et al.* 2014), which helps to explain why modularity was not significant in our bat-flower interaction network.

Another goal of this study was to find out which bat species are more important to the local network structure, by combining different measures of centrality (Mello *et al.* 2015). Although tricky, assessing the relative importance of species in a network can be a powerful way to identify keystones (Lewinsohn and Cagnolo 2012, Mello *et al.* 2015), those critically important species in which organization and maintenance of communities rely on (Paine 1969). Taking that into account, our results place the bats *A. geoffroyi*, *C. perspicillata* and *A. caudifer* as keystone species in the local network structure, responsible for a large number of interactions and for keeping different parts of the entire network bound.

According to Mello *et al.* (2015), keystone species in seed dispersal networks are mainly determined by dietary specializations. Our results also corroborates with that assumption, as the keystone bats in our local network are pointed out as specialists due to the evolution of foraging strategies and functional skull morphology (Koopman 1981, Santana & Dummont 2009, Santana *et al.* 2012). The genus *Anoura* are specialized nectarivores considered to be potential pollinators of native vegetal species (Koopman 1981, Muchhala & Jarrín-V 2002, Ortega & Alarcón-D 2008, Sazima *et al.* 1999), with morphological and behavioral adaptations to nectar feeding, as long and narrow snouts, and greatly lengthened tongue papillae (Koopman 1981, Ortega & Alarcón-D 2008, Winter & Helversen 2003).

The genus *Carollia*, on the other hand, does not present a highly specialized feeding apparatus, allowing them to include a large portion of insects in their diet (Santana & Dummont 2009). However, the relationship between *Carollia* foraging strategies and the distribution of preferred food sources is so strait, that one might consider their behavioral adaptation as a specialized food habit. As already discussed, bats within this genus have a strong preference for plants of the genus *Piper* (Bredt *et al.* 2012, Giannini & Kalko 2004, Thies & Kalko 2004, Thies *et al.* 2006), and so present adaptations that narrow the association between *Carollia* and these plant species.

CONCLUSION

Networks of interaction between bat and plant species have always been analyzed based on a single interaction or resource type at a time. Through the analysis of a multilayer network considering different interactions between bats and plants, we confirmed the nested structure of bat-plant interactions already described for seed dispersal and pollination separately. However, modularity seems to be higher in bat-flower interactions, following a pattern generally described for plant-pollinator networks. Thus, we suggest that the structural patterns described for bat-plant interactions are changeable depending on the type of interaction considered, and that the multilayer network presents a pattern closer to seed dispersal than pollination interaction networks. The keystone species, central to the maintenance of the network structure, are very common bat species to the Atlantic Forest, with dietary, morphological and behavioral specializations. Despite coming from the analysis of a single community, these results help us to better understand the complexity of bat-plant interaction networks. However, we support the idea that new studies should be made considering different interactions between bats and plants in other Atlantic Forest areas.

ACKNOWLEDGEMENTS

We are thankful to the staff of Carlos Botelho State Park and the staff of the Research Center in Palynology from the Institute of Botany (IBT). GPB and VCC had received MSc scholarships from Programa de Pós-Graduação em Conservação da Fauna and Fundação Parque Zoológico de São Paulo.

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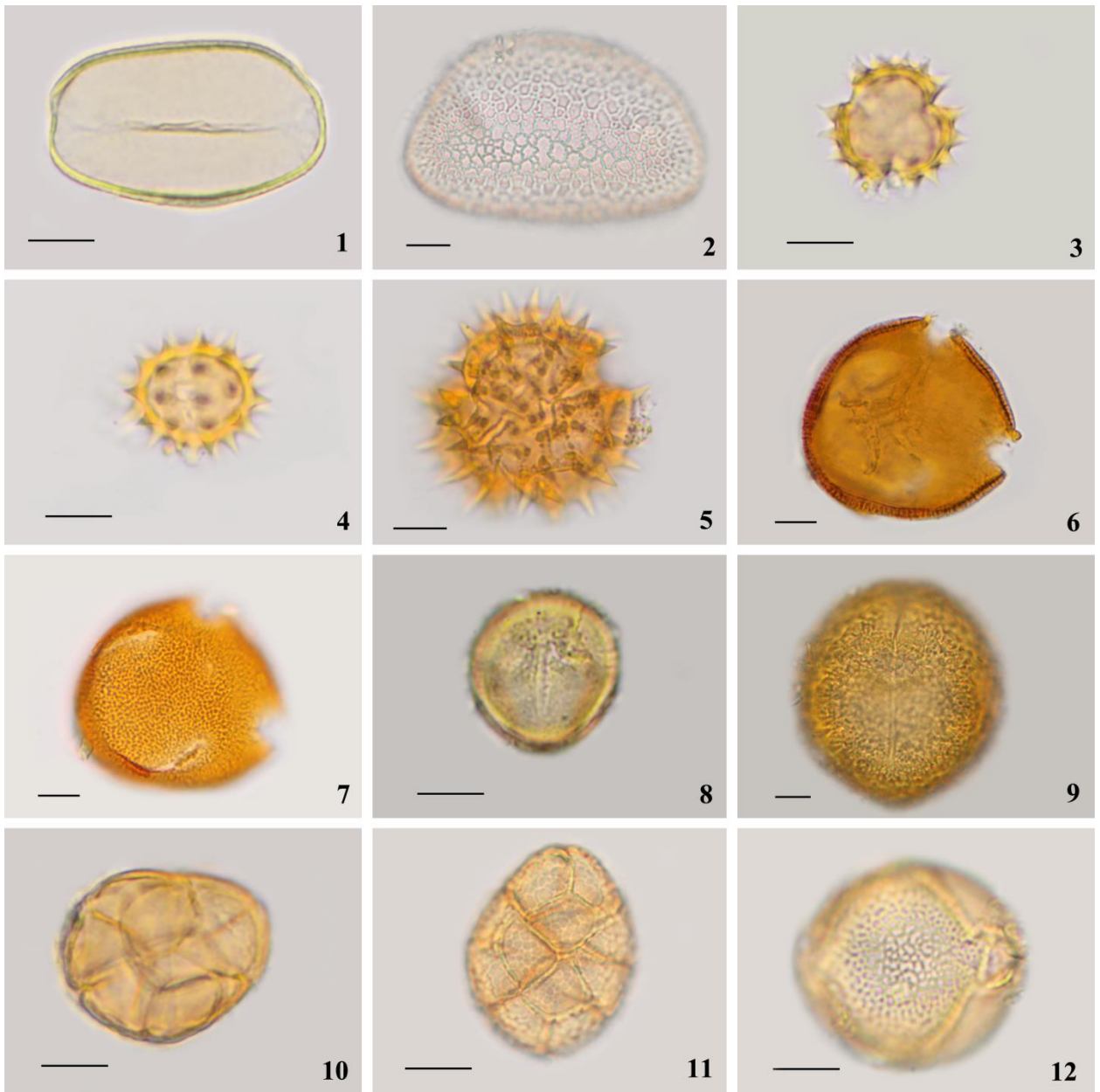
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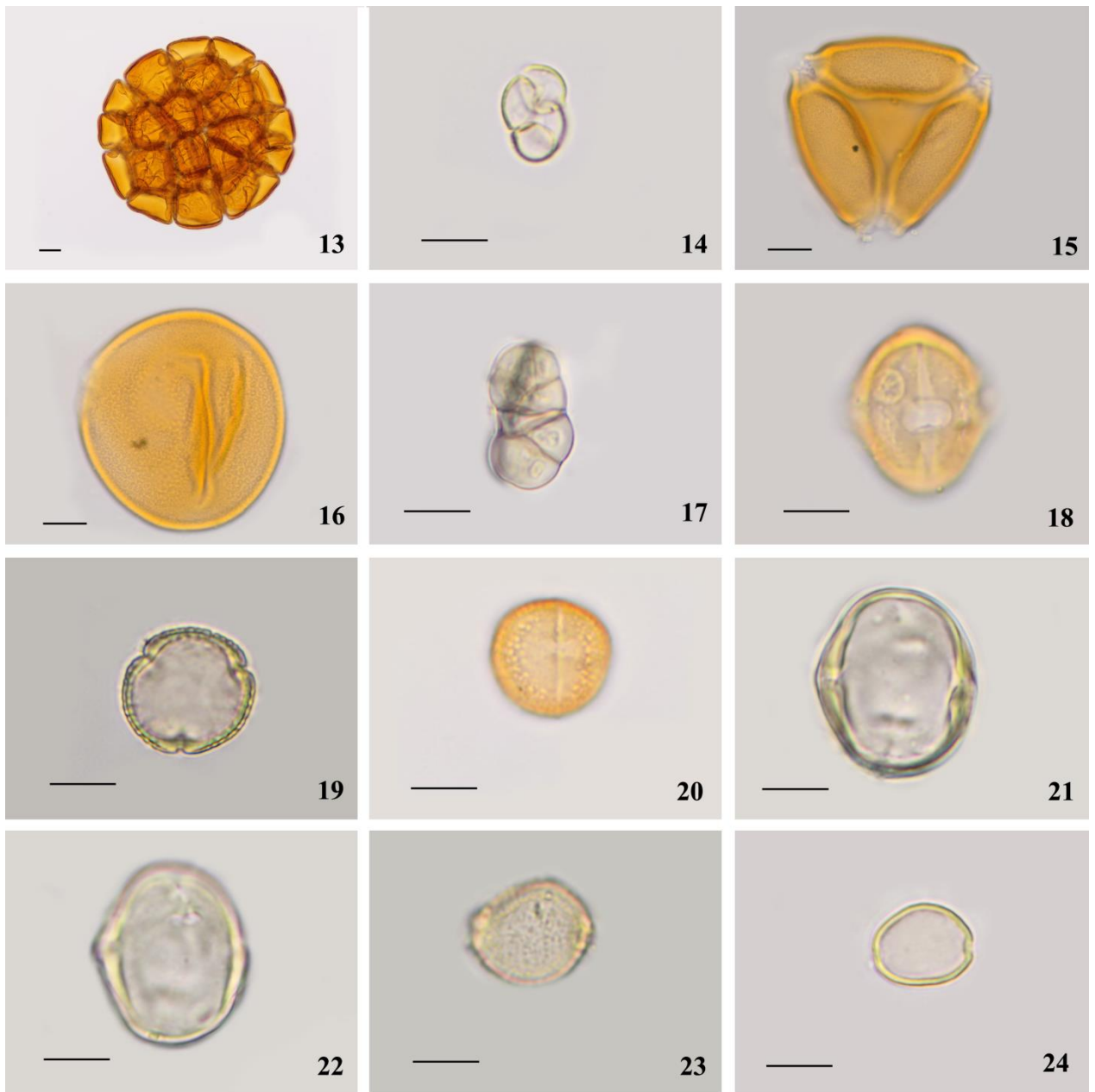
SUPPLEMENTARY INFORMATION

Among flowers and fruits: a multilayer network of bat-plant interactions in a Brazilian Atlantic Forest.

S1: Photomicrography (scale = 10 μm) of pollen grains on bats' fur at Carlos Botelho State Park: 1. Arecaceae: *Euterpe edulis*; 2. Bromeliaceae: *Vriesea*; 3-5. Asteraceae: *Baccharys* (3. polar view and 4. equatorial view) and 5. *Vernonia*; 6 – 7. Cactaceae (6. shape and 7. ornamentation); 8- 9. Euphorbiaceae: 8. *Alchornea* and 9. *Mabea*; 10 – 12. Fabaceae: 10. *Acacia*, 11. *Anadenanthera* and 12. *Andira*.



S2: Photomicrography (scale = 10 μm) of pollen grains on bats' fur at Carlos Botelho State Park: 13 – 18. Fabaceae: 13. *Inga*, 14. *Mimosa*, 15 – 16. *Mucuna* (15. polar view and 16. equatorial view). 17. *Piptadenia* and 18. *Swartzia*; 19 – 20. Marcgraviaceae: *Marcgravia* (19. polar view and 20. equatorial view); 21- 22. Meliaceae: *Trichilia* (21. shape in equatorial view and 22. colpus in equatorial view). 23 – 24. Moraceae: 23. *Brosimum*. 24. *Ficus*.



S3: Photomicrography (scale = 10 μm) of pollen grains on bats' fur at Carlos Botelho State Park: 25. Myrtaceae; 26 – 27. Piperaceae: 26. *Peperomia* and 27. *Piper*; 28. Primulaceae: *Myrsine*; 29 – 30. Rubiaceae: 29. *Ixora* and 30. *Tocoyena*; 31. Rutaceae: *Zanthoxylum*; 32. Sapindaceae: *Cupania*; 33 – 34. Sapotaceae: *Pouteria*; 35 – 36. Solanaceae: *Dysochromaviridiflorum* (35. Polar view and 36. colpus in equatorial view).

