



Universidade Federal do Amapá

Pró-Reitoria de Pesquisa e Pós-Graduação



Programa de Pós-Graduação em Biodiversidade Tropical

Mestrado e Doutorado

UNIFAP / EMBRAPA-AP / IEPA / CI-Brasil

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FATORES AMBIENTAIS QUE DETERMINAM A RIQUEZA,
DIVERSIDADE TAXONÔMICA, FUNCIONAL E FILOGENÉTICA DE
MORCEGOS EM UMA FLORESTA DE TERRA FIRME
PRESERVADA NO NORDESTE DA AMAZÔNIA BRASILEIRA

MACAPÁ, AP

2021

MARCELO MARTINS FERREIRA

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TAXONÔMICA, FUNCIONAL E FILOGENÉTICA DE MORCEGOS EM UMA
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BRASILEIRA

Dissertação de mestrado apresentada ao
Programa de Pós-graduação em
Biodiversidade Tropical (PPGBIO) da
Universidade Federal do Amapá, como
requisito parcial à obtenção do título de
Mestre em Biodiversidade Tropical.

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Carvalho

MACAPÁ, AP

2021

Dados Internacionais de Catalogação na Publicação (CIP)
Biblioteca Central da Universidade Federal do Amapá
Jamile da Conceição da Silva – CRB-2/1010

Ferreira, Marcelo Martins.

Fatores ambientais que determinam a riqueza, diversidade taxonômica, funcional e filogenética de morcegos em uma floresta de terra firme preservada no nordeste da Amazônia brasileira. / Marcelo Martins Ferreira, orientador, José Júlio de Toledo, coorientador, William Douglas de Carvalho. – Macapá, 2021.
92 f.

Dissertação (Mestrado) – Universidade Federal do Amapá, Coordenação do Programa de Pós-Graduação em Biodiversidade Tropical.

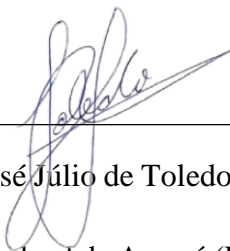
1. Morcego. 2. Morcegos filostomídeos. 3. Diversidade alfa. 4. Floresta tropical. 5. Biodiversidade. I. Toledo, José Júlio de, orientador. II. Carvalho, William Douglas de, coorientador. III. Fundação Universidade Federal do Amapá. IV. Título.

599.4 F383f
CDD. 22 ed.

MARCELO MARTINS FERREIRA

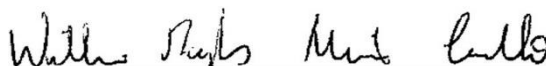
FATORES AMBIENTAIS QUE DETERMINAM A RIQUEZA, DIVERSIDADE
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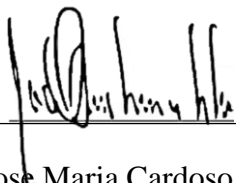
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Aprovada em 30 de julho de 2021, Macapá, AP, Brasil

AGRADECIMENTOS

A minha família, em especial aos meus pais Maria das Graças Martins e José Caetano Soares Ferreira, que sempre me apoiaram e me incentivaram a continuar minha formação acadêmica.

A Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES – processo nº 88882.430000/2019-01) Brasil, pela bolsa de mestrado concedida.

A Universidade Federal do Amapá e ao Programa de Pós-graduação em Biodiversidade Tropical – PPGBio, que me proporcionaram suporte técnico e logístico para que esta obra fosse realizada.

Aos meus orientadores, Dr. William Douglas de Carvalho e o Dr. José Júlio de Toledo, pela ORIENTAÇÃO, sua paciência, dicas, ensinamentos, e sobre tudo, por me ajudarem a amadurecer no âmbito acadêmico e profissional.

Aos meus colegas e professores do PPGBio, por todo conhecimento e bons momentos compartilhados dentro e fora das salas de aulas. A professora Fernanda Michalski, pelo apoio logístico logo que cheguei na cidade de Macapá.

A minha pequena família Amapaense (os Moshos) Andrea Bárcenas Garcia, Marisol Alfaro, Cassiano Martins e Bruna Xavier, pela tolerância, acolhimento, apoio emocional, suportes variados e pelos bons momentos compartilhados.

A Gustavo Silveira, Cledinaldo Marques, Cremilson Marques, Raimundão e Dona Vita pelo auxílio na amostragem e logística para a realização das atividades de campo. Assim como aos moradores da FLOTA-AP e guarda parques da FLONA-AP (José e Jorge) por sua acolhida durante minha estadia.

Ao Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) pelo auxílio logístico e autorizações para a realização deste estudo.

Ao Dr. José Maria Cardoso da Silva, Dra. Maria João Veloso da Costa Ramos Pereira e a Dra. Luciana de Moraes Costa, por se disporem de tempo e aceitarem o convite para a banca examinadora desta dissertação de mestrado.

Finalmente, aos *MORCEGOS* por me apresentarem a um universo enigmático, mas cheio de encantamentos e curiosidades.

GRATIDÃO A TODOS VOCÊS!!!!

RESUMO

Ferreira, Marcelo Martins. Fatores ambientais que determinam a riqueza, diversidade taxonômica, funcional e filogenética de morcegos em uma floresta de terra firme preservada no nordeste da Amazônia brasileira. Macapá, 2021. Dissertação (Mestre em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitoria de Pesquisa e Pós-Graduação - Universidade Federal do Amapá.

Variações nas condições ambientais ao longo de gradientes desempenham um papel importante na distribuição das espécies por meio da filtragem ambiental de características morfológicas e fisiológicas, mas seus efeitos na diversidade de morcegos permanecem pouco entendidos. O objetivo principal deste estudo foi distinguir como a estrutura da vegetação (obstrução da vegetação, altura do dossel e área basal), topografia do terreno e distância para o corpo d'água mais próximo afetam as três dimensões da diversidade alfa (dimensões taxonômica, funcional e filogenética), além da predominância de alguns traços funcionais da comunidade de morcegos filostomídeos em uma área de floresta de terra firme preservada no nordeste da Amazônia brasileira. Após um total de 77.760 m² .h de esforço amostral, que resultou na captura de 279 morcegos pertencentes a 28 espécies, demonstramos que em áreas mais distantes do corpo d'água, a assembleia de morcegos é muito mais rica em espécies e taxonomicamente e funcionalmente mais diversa. A riqueza taxonômica também foi influenciada positivamente pela elevação do terreno. No entanto, não houve efeito de nenhuma das variáveis medidas sobre a diversidade filogenética. Contrariando as nossas expectativas, a massa média de morcegos foi influenciada positivamente pela área basal da floresta. Em conjunto, nossos resultados demonstram que variações sutis nas condições ambientais de um mesmo gradiente em escala local, são suficientes para direcionar as principais dimensões da diversidade alfa de morcegos.

Palavras-chave: Chiroptera; diversidade alfa; traços funcionais; floresta tropical; filtro ambiental; morcegos filostomídeos; topografia; estrutura da vegetação; distância para o corpo d'água.

ABSTRACT

Ferreira, Marcelo Martins. Environmental factors that determine the richness, taxonomic, functional and phylogenetic diversity of bats in a preserved terra firme forest in the northeast of the Brazilian Amazon. Macapá, 2021. Dissertação (Mestre em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitoria de Pesquisa e Pós-Graduação - Universidade Federal do Amapá.

Variations in environmental conditions along gradients play an important role in species distributions through environmental filtering of morphological and physiological characteristics, however, their effects on bat diversity remain poorly understood. The main objective of this study was to investigate how vegetation structure (vegetation obstruction, canopy height and basal area), terrain topography and distance to the nearest watercourse affect both the three dimensions of alpha diversity (taxonomic, functional and phylogenetic), and the predominance of some functional traits, in the Phyllostomid bat community in an area of terra firme forest in the northeastern Brazilian Amazon. A total of 77,760 m² .h of sampling effort resulted in the capture of 279 bats belonging to 28 species. Based on these data, we demonstrate that in areas that are more distant from watercourses, the bat assemblage is much richer in species and is taxonomically and functionally more diverse. Taxonomic richness was also positively influenced by terrain elevation. However, there was no effect of any of the measured variables on phylogenetic diversity. Contrary to our expectations, the average body mass of bats was positively influenced by the basal area of the forest. Taken together, our results demonstrate that subtle variations in the environmental conditions at a local scale have an influence on the main dimensions of Phyllostomid bat alpha diversity.

Keywords: Chiroptera; alpha diversity; functional traits; tropical forest; environmental filter; phyllostomid bats; topography; vegetation structure; Distance to the watercourse.

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1. INTRODUÇÃO GERAL

1.1. FATORES AMBIENTAIS QUE ESTRUTURAM AS COMUNIDADES DE ANIMAIS

Os animais percebem o ambiente por meio da disponibilidade de recursos e por isso procuram melhores locais para se alimentarem, abrigarem e reproduzirem (MacArthur e Pianka 1966, Carr e Macdonald 1986, Capaverde et al. 2018). Fatores como disponibilidade de alimento (August 1983, Lambert et al. 2006, Dodd et al. 2008, Capaverde et al. 2018), estrutura da vegetação (MacArthur e MacArthur 1961, Kerr e Packer 1997, Poulsen 2002, Williams et al. 2002), disponibilidade de água (Rojas-Ahumada et al. 2012) e relevo (Curran et al. 2012, Carvalho et al. 2019) podem ser cruciais para o estabelecimento de espécies. Esse processo é definido como seleção ideal de habitat, e prediz que os indivíduos podem se locomover livremente no habitat para maximizar a aptidão individual (Holt 1985), podendo afetar os padrões de riqueza e distribuição das assembleias em um gradiente florestal (Lambert et al. 2006, Rojas-Ahumada et al. 2012).

Estrutura da vegetação, topografia, proximidade aos corpos d'água e disponibilidade de alimento, frequentemente, explicam a distribuição de espécies (Williams et al. 2002, Pereira et al. 2009, Bueno et al. 2012, Capaverde et al. 2018). Mudanças na estrutura física e taxonômica da vegetação influenciam no movimento, nos locais de abrigo e nidificação e disponibilidade de alimento para os animais (Castagneyrol and Jactel 2012). Além disso, gradientes topográficos com até 3.000 m apresentam grandes variações de temperatura, precipitação e radiação solar (Willig and Presley 2015), que criam vários tipos de habitats e influenciam na distribuição de espécies. No entanto, variações mais sutis na topografia (<100 m) também resultam em alterações nas comunidades vegetais (Pansonato 2012, Schietti et al. 2014), o que afeta a distribuição dos animais (Menin et al. 2007, Fraga et al. 2011). Além da topografia, a influência das margens de rios também afeta a distribuição dos animais devido à disponibilidade de alimentos nesses ambientes (Marques et al. 2012).

A relevância das características ambientais para estruturação das assembleias tem sido demonstrada para vários grupos de animais. Em escala local em um gradiente de floresta tropical, Williams et al. (2012), demonstraram que as estruturas das assembleias de pequenos mamíferos não voadores estão intimamente relacionadas com a estrutura da vegetação, de modo que, a riqueza de pequenos mamíferos aumentava de acordo a

complexidade da vegetação. Lees and Peres (2008) demonstraram que fatores como cobertura do dossel, área basal e altura da vegetação afetam a distribuição de mamíferos de médios e grande porte. Outros trabalhos realizados com assembleias de aves (Poulsen 2002, Oliveira et al. 2019), anfíbios, répteis (Atauri e Lucio 2001, Fraga et al. 2011), e morcegos (Estrada-Villegas et al. 2012) também evidenciaram o efeito da estrutura da paisagem na distribuição e diversidade de espécies. No entanto, são poucos os estudos que vão além da dimensão taxonômica (e.g., riqueza, abundâncias e composição de espécies) para tentar explicar os principais fatores que estruturam as assembleias de animais (Oliveira et al. 2019). Incorporar outras dimensões da diversidade de espécies pode nos dar uma maior compreensão de como os fatores ambientais estão direcionando essas dimensões e estruturando as assembleias de animais dentro de um gradiente ambiental (Cisneros et al. 2014, Oliveira et al. 2019).

1.2. ABORDAGEM MULTIDIMENSIONAL PARA MENSURAR A BIODIVERSIDADE

Identificar e compreender os padrões que estruturam a biodiversidade são alguns dos principais objetivos de estudos ecológicos (Connor e Simberloff 1979, MacArthur 1984, Lawton 1999, Pavoine e Bonsall 2011, Magurran 2013, Arnan et al. 2017, Dambros et al. 2020). Assim, mensurando a biodiversidade, estudos buscam determinar quais fatores espaciais, ambientais e temporais estruturam os diferentes padrões de distribuição de espécies, tanto em escala local como global (Chase e Leibold 2002, Leibold et al. 2004, Kreft e Jetz 2007). A mensuração da biodiversidade não deve simplesmente quantificar um conjunto de diferentes espécies e a uniformidade de suas abundâncias (diversidade taxonômica) (DeJong 1975), mas sim mensurar a biodiversidade através de uma abordagem multifacetada, incluindo diferentes escalas no espaço e no tempo, além das características funcionais das espécies (e.g., diversidade funcional) e diferentes linhagens evolutivas [e.g., diversidade filogenética (Pavoine e Bonsall 2011)]. No entanto, conhecemos muito sobre padrões taxonômicos da biodiversidade, porém com grandes lacunas no conhecimento relacionado às dimensões funcional e filogenética (Pavoine e Bonsall 2011, Swenson 2013, Aguirre et al. 2016, Arnan et al. 2017). Atualmente, esse viés em relação à dimensão taxonômica da biodiversidade tem sido suprimido com o advento de diferentes ferramentas para se mensurar as diferentes dimensões da diversidade, considerando diferentes índices ecológicos (Pla et al. 2012, Cardoso et al. 2014, Chao et al. 2014, Melo et al. 2014, Moreno et al. 2018).

Dentre as três dimensões da biodiversidade, a diversidade funcional reflete as características morfológicas, fisiológicas e ecológicas encontrada em uma determinada comunidade (Petchey e Gaston 2006), oferecendo uma visão mecanicista para a resistência, resiliência e funcionamento do ecossistema. Já a diversidade filogenética reflete diferenças evolutivas entre as espécies com base nos tempos desde a divergência de um ancestral comum (Faith 1992, Webb et al. 2002) e representa uma estimativa abrangente das diferenças ecológicas e fenotípicas filogeneticamente conservadas entre as espécies (Cavender-Bares et al. 2009). Quando usadas em conjunto, as três dimensões da biodiversidade, temos resultados muito mais robustos e interpretativos sobre os diferentes padrões de diversidade, nos permitindo discutir também sobre como o meio interfere na função ecológica e na história evolutiva das espécies (Leibold 1995, Larson e Losos 1996, Webb 2000, Webb et al. 2002, Fukami et al. 2005, Cadotte et al. 2013, Swenson 2013, Cisneros et al. 2015, Ramos Pereira et al. 2018, Carvalho et al. 2020). Portanto, o uso das múltiplas dimensões da diversidade em estudos ecológicos pode nos ajudar a entender os diferentes padrões evolutivos das espécies, assim como suportar de forma robusta diferentes diretrizes direcionadas à conservação de habitats e espécies (Vane-Wright et al. 1991, Faith 1996, Cadotte et al. 2011, Freitas e Mantovani 2017, Tucker et al. 2017).

Abordagens multidimensionais também podem nos trazer informações mais robustas para entender como fatores ambientais, como a filtragem ambiental, afetam a formação das comunidades de espécies (Pavoine e Bonsall 2011). Em geral, espere-se uma correlação positiva entre as dimensões taxonômica, funcional e filogenética, visto que, um aumento na diversidade de espécies pode refletir em mais linhagens e características funcionais acumuladas na comunidade (Losos 2008). No entanto, os mecanismos que direcionam variações na riqueza de espécies podem não ser os mesmos responsáveis pela variação nas características funcionais e filogenéticas (Cisneros et al. 2014).

Maior riqueza taxonômica ao longo de um gradiente ambiental, em relação aos componentes funcional e filogenético, deve-se a filtragem ambiental que atua nas espécies que compartilham características funcionais semelhantes (ou histórias filogenéticas semelhantes), as quais serão importantes para a persistências das espécies (e linhagens) em um determinado habitat (Hermant et al. 2012, Cisneros et al. 2014, Farneda et al. 2015, Frank et al. 2017). Em tais cenários, a capacidade de lidar com o filtro ambiental específico é compartilhado em espécies mais estritamente relacionadas da comunidade (Kraft et al. 2007, De Pauw et al. 2021). No entanto, espécies de diferentes

linhagens filogenéticas podem adquirir a capacidade de se adaptar a filtragem ambiental de forma independente, levando a uma maior diversidade filogenética em relação a riqueza de espécies (De Pauw et al. 2021). Isso mostra que diferentes aspectos da diversidade podem ser direcionados por condições ambientais contrastantes e em diferentes direções (De Pauw et al. 2021), evidenciando a importância de olhar além da dimensão taxonômica, utilizando abordagens que quantificam a diversidade funcional e filogenética.

1.3. MORCEGOS E SUA IMPORTÂNCIA PARA VISUALIZAR PADRÕES ECOLÓGICOS NA AMAZÔNIA

Morcegos possuem um elevado número de espécies e guildas alimentares bem conhecidas (Kalko et al. 1996, Emmons e Feer 1997, Simmons e Voss 1998, Schnitzler e Kalko 2001, Giannini e Kalko 2004, Fenton e Simmons 2015, Reis et al. 2017, López-Baucells 2018), além de serem bastante sensíveis à mudanças na paisagem (Stevens et al. 2007). Sendo assim, os morcegos são de grande interesse para estudos que visam avaliar os efeitos de mudanças ambientais na seleção do habitat. Por exemplo, morcegos respondem a gradientes de elevação topográficos (Capaverde et al. 2018), a variações no clima (Estrada-Villegas et al. 2012), e sua riqueza e abundância de espécies são influenciadas pela estrutura do habitat. Portanto, isso permite relacionar distribuição de espécies com características ambientais (Colombo 2017).

Estrutura da vegetação pode determinar diferentes assimetrias no uso de habitats. Por exemplo, morcegos com adaptações morfológicas para forrageio em habitats abertos têm dificuldades em forragear em locais com vegetação densa (Norberg e Rayner 1987, Muller et al. 2012). Provavelmente, isso deve estar relacionado ao comportamento de voo dos morcegos (Bobrowiec et al. 2014), pois morcegos que possuem um voo rápido devido a um maior aspecto e carga relativa da asa, vão voar preferencialmente em espaços abertos, enquanto que espécies que possuem um voo altamente manobrável, devido a menor carga alar e menor aspecto de asa são mais favorecidas em locais com vegetação densa (Siemers e Swift 2005, Muller et al. 2012). Sendo assim, a estrutura da vegetação se comporta como um filtro, selecionando as espécies de maior manobrabilidade (Stockwell 2001, Marciente et al. 2015).

A disponibilidade de alimento também se mostra como um fator determinante na dinâmica populacional de morcegos. Isso é demonstrado no estudo de Ramos Pereira et al. (2010), onde constatou-se que uma maior oferta de frutas na época de cheia contribuiu

para uma variação na abundância de morcegos frugívoros (*Carollia perspicillata* e *Artibeus planirostris*) dentro e entre florestas de várzea, igapó e floresta de terra firme não inundada. Outro estudo, realizado por (Oliveira et al. 2015), mostrou que a atividade de *Pteronotus parnellii* foi maior em áreas não ripárias, devido a maior biomassa de insetos, do que em áreas ripárias

Gradientes topográficos também podem influenciar os padrões de distribuições de morcegos (Stein et al. 2014). Por exemplo, Carvalho et al. (2019) demonstraram que a diversidade de morcegos diminuiu acentuadamente com o incremento da elevação. Esses padrões de distribuição de morcegos em gradientes altitudinais têm sido demonstrados, principalmente, em altitudes de até 3.000 m (Bejarano-Bonilla et al. 2007, Carvalho et al. 2019), pois apresentam grandes variações de temperatura, precipitação e radiação solar (Willig e Presley 2015). No entanto, ao longo das terras baixas amazônicas, variação mais sutil na topografia (< 100) resultam em alterações nas comunidades vegetais (Pansonato et al. 2012, Schiatti et al. 2014), com conseqüente influência na distribuição de vertebrados, incluindo morcegos (Kabat et al. 2007, Menin et al. 2007, e Fraga 2011).

Topografia, estrutura da vegetação e disponibilidade de alimento já são bem documentados como preditores da diversidade e estrutura da comunidade de morcegos na Amazônia (Marques et al. 2012, Muller et al. 2012, Silva 2012, Marciente et al. 2015, Bobrowiec e Tavares 2017, Carvalho et al. 2019). Todavia, estes estudos focaram em ambientes muito diferentes. Por exemplo, diferenças nas comunidades de morcegos entre terra firme e várzea (Bobrowiec et al. 2014), terra firme, savanas e campinaranas (Carvalho et al. 2018) e entre terra firme, várzea e igapó (Ramos Pereira et al. 2009, Marques et al. 2012). Neste caso, a composição das espécies pode estar relacionada a cada tipo de vegetação e, portanto, ocultando variações dentro de cada ambiente (Tews et al. 2003, Capaverde Junior 2015). Entretanto, pouco se conhece sobre os direcionadores da diversidade e estrutura da comunidade de morcegos em um mesmo gradiente ambiental (Marciente et al. 2015, Capaverde et al. 2018, Pereira et al. 2019). Em um mesmo gradiente, é possível que variações mais sutis de um mesmo tipo de vegetação possam influenciar na diversidade e composição de morcegos em uma escala mais local (Ober e Hayes 2008, Estrada-Villegas et al. 2012, Capaverde Junior 2015).

Apesar de diferentes estudos terem sido realizados em um mesmo gradiente ambiental nos últimos anos (Marciente et al. 2015, Capaverde et al. 2018, Pereira et al. 2019), nenhum desses estudos avaliou simultaneamente as dimensões taxonômica, funcional e filogenética. Portanto, nosso objetivo neste estudo é distinguir como a estrutura da

vegetação (obstrução da vegetação, área basal e altura do dossel), altitude e distância para o corpo d'água mais próximo afetam as três dimensões da diversidade alfa (dimensão taxonômica, funcional e filogenética), além da predominância de alguns traços funcionais (massa corporal, morfologia da asa e nível trófico) da comunidade de morcegos filostomídeos em uma área de floresta de terra firme preservada no nordeste da Amazônia brasileira.

2. PREDIÇÕES

- O aumento da obstrução da vegetação leva a uma diminuição nas dimensões da diversidade alfa de morcegos ao nível do sub-bosque, pois dificulta a manobrabilidade e ecolocalização dos morcegos filostomídeos (Hagen e Sabo 2011, Marciente et al. 2015).
- Área basal é um indicador de poleiros, abrigos e disponibilidade de alimentos (Aguirre et al. 2003, Carbone et al. 2013, Minor e Kobe 2019). Devido a isso, esperamos que um incremento em seu valor influencie positivamente nas dimensões da diversidade alfa de morcegos filostomídeos.
- Esperamos que altura do dossel afete positivamente as dimensões da diversidade alfa de morcegos filostomídeos, pois um dossel mais alto apresenta maior variação vertical das condições ambientais como biomassa vegetal, temperatura, umidade e luz (Bazzaz 1975, Parker et al. 1995, Clark et al. 2008), gerando diferentes formas de aproveitar os recursos disponíveis.
- Esperamos que o aumento da elevação influencie positivamente as dimensões da diversidade alfa, pois áreas mais elevadas tendem a ter maior complexidade da vegetação [e.g., maior riqueza de espécies de plantas e estrutura da vegetação lenhosa (Jankowski et al. 2013, Rodrigues et al. 2014, Toledo et al. 2017)], e isso, por sua vez, reflete em uma maior diversidade de abrigos e alimentos para os morcegos filostomídeos.
- Os solos são mais arenosos, encharcados e pouco oxigenados em áreas próximas aos corpos d'água, o que limita o crescimento de muitas espécies de plantas afetando a diversidade de recursos como alimentos e abrigos para os morcegos filostomídeos nessas regiões (Costa et al. 2005). Devido a essas condições, esperamos uma relação positiva da distância do corpo d'água com as dimensões da diversidade alfa de morcegos filostomídeos.
- Em relação aos traços funcionais da comunidade, morcegos com maior massa corporal, aspecto e carga relativa da asa tendem a ter menor capacidade de

manobrabilidade durante o voo e, por isso, são favorecidos em ambientes mais abertos. Assim, espécies com estas características utilizarão mais os locais com menor grau de obstrução de sub-bosque, área basal, áreas com maior altura do dossel, áreas menos elevadas e mais próximas dos corpos d'água (Sleep e Brigham 2003, Ober e Hayes 2008, Hanspach et al. 2012, Marinello e Bernard 2014, Blakey et al. 2017).

- Nós também esperamos que morcegos animalívoros, que em geral apresentam valores menores de aspecto da asa e carga relativa da asa, sejam mais associados a ambientes mais obstruídos com maior grau de obstrução do sub-bosque, área basal, menor altura do dossel e em áreas mais elevadas e mais distantes dos corpos d'água (Norberg e Fenton 1988, Fenton et al. 1992, Medellín et al. 2000, Giannini e Kalko 2004, Bobrowiec e Gribel 2010, Marinello e Bernard 2014). Por outro lado, morcegos fitófagos que são mais generalistas, terão maior peso médio em ambientes menos complexos, áreas menos elevadas e próximas aos corpos d'água, devido a maior abundância de frutas nessas regiões (Marques et al. 2012).

3. OBJETIVOS

3.1. GERAL

Avaliar o efeito dos fatores ambientais sobre a diversidade alfa e a predominância de traços funcionais de *morcegos* filostomídeos em floresta de terra firme preservada no nordeste da Amazônia brasileira.

3.2. ESPECÍFICOS

- Avaliar o efeito da obstrução da vegetação, área basal, altura do dossel, altitude e distância até o curso d'água mais próximo sobre a diversidade alfa de morcegos filostomídeos de uma floresta de terra firme preservada no nordeste da Amazônia brasileira.
- Avaliar o efeito da obstrução da vegetação, área basal, altura do dossel, altitude e distância até o corpo d'água mais próximo sobre a predominância de alguns traços funcionais (massa corporal, morfologia da asa e nível trófico) de morcegos filostomídeos em uma floresta de terra firme preservada no nordeste da Amazônia brasileira.

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5. ARTIGO CIENTÍFICO

Bat diversity is driven by elevation and distance to the watercourse in *terra firme* forest in Northeastern Brazilian Amazon

Artigo submetido ao periódico “Journal of Tropical Ecology”

1 **Bat diversity is driven by elevation and distance to the watercourse in *terra firme***
2 **forest in Northeastern Brazilian Amazon**

3

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34 Running title: Bat diversity in Northeastern Brazilian Amazon

35

36 **Keywords:** Chiroptera, environmental filter, functional diversity, phylogenetic

37 diversity, Phyllostomid bats, taxonomic diversity, topography, vegetation structure

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51 **5.1. Abstract**

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53 Here we investigate the effect of five explanatory variables: distance to the watercourse,
54 terrain elevation, vegetation clutter, basal area, and canopy height on taxonomic,
55 functional, and phylogenetic α -diversity, and predominance of some functional traits
56 (body mass, wing morphology, and trophic level) of Phyllostomid bat assemblages in a
57 *terra firme* forest, Northeastern Brazilian Amazon. We have sampled bats using mist nets
58 in 15 permanent plots over 25 km² of continuous forest. We have captured 279 individuals
59 belonging to 28 species with a total of 77,760 m² .h of sampling effort. Our results have
60 showed that, in addition to increasing the richness of Phyllostomid bats as a function of
61 distance to the nearest watercourse, the assemblage also changes, with more diverse
62 taxonomic and functional groups in areas far to the watercourse. Furthermore, elevation
63 positively affects species richness, and the basal area of the forest positively influences
64 the average body mass of bats. Taken together, our results demonstrate that subtle
65 variations in the environmental conditions of the same gradient at a local scale are
66 sufficient to target the main components of the α -diversity of bats in primary forests.

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77 **5.2. Introduction**

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79 One of the main goals of ecology is to understand how environmental factor's
80 structure animal communities (Elton 2001; Guilherme *et al.* 2019; Lawton 1999; Leibold
81 1995; Magurran 2013; McGill *et al.* 2006). Different studies have tried to understand the
82 mechanisms that structure communities (Grinnell 1917; Levin 1992). Environmental
83 conditions, referring to niche theory, play an important role in the distribution of species
84 in a habitat through the environmental filtering of morphological, physiological, and
85 behavioral characteristics (Elton 2001; Keddy 1992; Rosenzweig 1987; Webb 2000),
86 generating differences in taxonomic, functional, and phylogenetic dimensions at different
87 scales (Baccaro *et al.* 2013; Carvalho *et al.* 2021; Guilherme *et al.* 2019; Poff 1997).

88 The relevance of different environmental characteristics, such as vegetation
89 structure, food availability, topography, and distance to the water, has been demonstrated
90 for amphibians and reptiles (Aauri & Lucio 2001; Fraga *et al.* 2011), birds (Bueno *et al.*
91 2012; Poulsen 2002), terrestrial mammals (Lees & Peres 2008; Williams *et al.* 2002), and
92 bats (Marciente *et al.* 2015; Pereira *et al.* 2019; Ramos Pereira *et al.* 2009). Among these
93 different groups of vertebrates, bats stand out, which have a high number of species and
94 feeding guilds (Emmons & Feer 1997; Kalko & Handley 2001; Kalko *et al.* 1996a; López-
95 Baucells 2018; Reis *et al.* 2017; Simmons & Voss 1998; Voss & Emmons 1996), and are
96 very sensitive to environmental gradients (Capaverde *et al.* 2018; Carvalho *et al.* 2021;
97 Meyer *et al.* 2016; Stevens *et al.* 2007).

98 One of the regions with the greatest richness and diversity of bats in the world is
99 the Amazon forest, which has at least 200 species described to date (López-Baucells
100 2018). In this tropical forest, topography and vegetation structure are already well
101 documented as predictors of bat community structure (Bobrowiec & Tavares 2017;
102 Carvalho *et al.* 2019; Marciente *et al.* 2015; Marques *et al.* 2012; Silva 2012). However,

103 several studies carried out in the region seeking to understand how ecological aspect's
104 structure bat assemblages are based on very different habitats: *terra firme versus*
105 floodplain (Bobrowiec *et al.* 2014), *terra firme versus savannas versus campinaranas*
106 (*Carvalho et al.* 2018), *terra firme versus floodplain versus igapó* (Ramos Pereira *et al.*
107 2009). In these cases, changes in species composition are abrupt due to the enormous
108 difference in the structure and species composition of the vegetation. On the other hand,
109 it is not well known how bat assemblages respond to finer changes in environmental
110 conditions within each habitat (Capaverde *et al.* 2018; Tews *et al.* 2003). It is possible
111 that more subtle variations of the same vegetation type can influence the diversity and
112 composition of bats at a local scale (Capaverde *et al.* 2018; Estrada-Villegas *et al.* 2012;
113 Ober & Hayes 2008). There are few studies that relate the composition and structure of
114 animal assemblages to environmental factors in the same continuous forest (Tews *et al.*
115 2003). In addition, there is still a huge gap in knowledge about the bat fauna in the
116 Amazon, as most of the studies carried out in this region are centered on a few areas,
117 generally with easier access, close to major urban centers such as Manaus, Belém or
118 Santarém (Delgado-Jaramillo *et al.* 2020). In general, these studies are focused on
119 epidemiological aspects (Costa *et al.* 2017; Filgueiras *et al.* 2019; Streicker & Allgeier
120 2016) and species inventories (Bernard & Fenton 2002; Sampaio *et al.* 2003), with few
121 studies analyzing the influence of food availability, vegetation structure, topography, and
122 proximity to water bodies on richness and taxonomic composition of bat (Bernard &
123 Valeria 2011; Capaverde *et al.* 2018; Marciente *et al.* 2015; Pereira *et al.* 2019). In
124 addition, to date, no study has simultaneously assessed the taxonomic, functional, and
125 phylogenetic dimensions of bat α -diversity in a continuous forest gradient in Amazon.

126 Multidimensional approaches that incorporate species diversity, functional traits
127 and phylogenetic trees can increase the detectability of ecological patterns (McGill *et al.*

128 2006) because the components of diversity can capture different variations in the
129 community. The mechanisms that give rise to variations in species richness may not be
130 the same ones responsible for the variation in functional and phylogenetic characteristics
131 (Cisneros *et al.* 2014). For example, Blanchet *et al.* (2014) demonstrated that the mean
132 annual water temperature and the distance of the river's upstream-downstream gradient
133 negatively affected the phylogenetic diversity of fish, while these same predictors
134 positively affected species richness. Graça *et al.* (2016) demonstrated that the relationship
135 between tropical butterflies and birds was evident when assessing the variation in
136 butterfly body size (functional component), but when analyzing species composition
137 (taxonomic component), there was no relationship. Therefore, the use of functional and
138 phylogenetic approaches, together with the taxonomic approach, provide more robust
139 information on the mechanisms that determine the variation in diversity along
140 environmental gradients (Cisneros *et al.* 2014; Freitas & Mantovani 2017).

141 In this study, we aim to distinguish how vegetation structure (vegetation clutter,
142 canopy height, and basal area), terrain elevation, and distance to the nearest watercourse
143 affect the three dimensions of α -diversity (taxonomic, functional, and phylogenetic) and
144 the predominance of some functional traits of the Phyllostomid bat assemblage in a
145 preserved *terra firme* forest area in the Northeastern Brazilian Amazon. We expect
146 vegetation clutter to be a physical barrier at the understory level for bats (Marciente *et al.*
147 2015), negatively affecting all dimensions of α -diversity. Basal area is an indicator of
148 perches, shelter, and food availability (Aguirre *et al.* 2003; Carbone *et al.* 2013; Minor &
149 Kobe 2019). Because of this, we hope that an increase in its value will reflect positively
150 on the dimensions of α -diversity. Tropical forests show considerable vertical variation in
151 plant extracts (Clark *et al.* 2008), temperature, humidity, and light (Parker *et al.* 1995)
152 from soil to canopy, and all this complexity of environmental factors generates different

153 strategies to take advantage of available resources (Bazzaz 1975). Therefore, considering
154 that vegetation structure is an important factor in the availability of shelter and food, we
155 expect an increase in the dimensions of α -diversity in the higher parts of the terrain. In
156 addition, soils are sandier, waterlogged and poorly oxygenated in areas close to water
157 bodies, which limits the growth of many plant species, affecting the diversity of resources
158 such as food and shelter for bats in these regions (Costa *et al.* 2005; Toledo *et al.* 2017).
159 Due to these conditions, we expect a positive relationship between the distance from the
160 nearest watercourse and the dimensions of α -diversity.

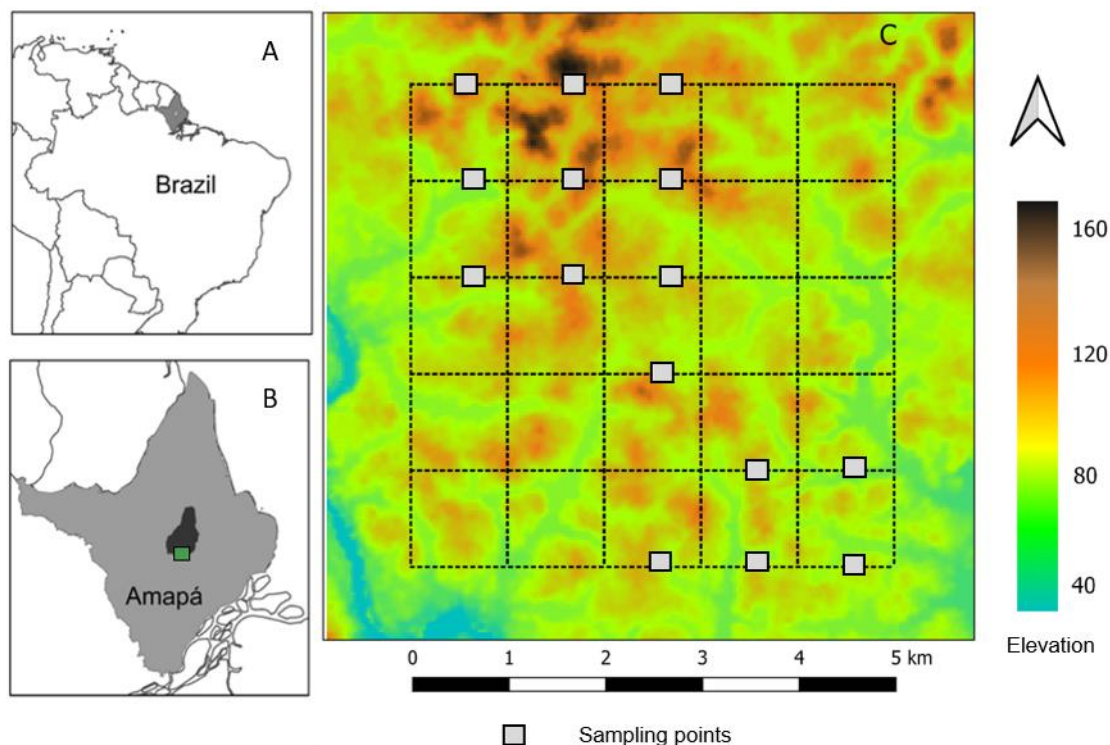
161 Regarding the functional traits of the bat assemblage, we expect higher values for
162 mean body mass, wing morphology (relative wing loading and wing aspect ratio) in
163 environments with fewer obstacles, which tend to have less vegetation clutter understory
164 obstruction, basal area, and a higher canopy. We also expect higher mean values for body
165 mass, wing aspect ratio and relative wing loading in lower parts and close to nearest
166 watercourses due to less vegetation clutter that favors bat navigation (Ober & Hayes 2008;
167 Sleep & Brigham 2003). Animalivorous bats have lower values for aspect and relative
168 wing loading (Marinello & Bernard 2014; Norberg & Fenton 1988), and these
169 characteristics make them to be more favored in environments with higher levels of
170 obstacles. Therefore, we expect a higher weight of bats at this trophic level in areas with
171 greater vegetation cluttering, basal area, and lower canopy height and in higher areas and
172 further away to watercourses, where vegetation is more obstructed (Oliveira *et al.* 2015).
173 On the other hand, phytophagous bats that are more generalists will have higher average
174 weight in less complex environments, less elevated areas and close to nearest
175 watercourses, due to the greater abundance of fruits in these areas (Marques *et al.* 2012).
176

177 **5.3. Methods**

178 **5.3.1. Study area**

179 The study was carried out in the Floresta Nacional do Amapá (FLONA of Amapá),
180 a conservation unit of sustainable use located in the extreme Northeast of the Brazilian
181 Amazon. FLONA of Amapá has 459,800 ha (Figure 1 - ICMBio 2016). The region's
182 climate is hot and humid, with temperatures ranging from 24 to 28 °C, and annual
183 precipitation ranging between 2,300 and 2,900 mm (Oliveira *et al.* 2010; Oliveira *et al.*
184 2020). The wet season, which lasts from February to May, concentrates 70% of the total
185 annual precipitation, which can exceed 500 mm/month. The dry season (September to
186 November) concentrates 30% of annual precipitation and is characterized by <250
187 mm/month (Oliveira *et al.* 2010; Oliveira *et al.* 2020).

188 Most of the FLONA of Amapá is located at elevations between 50 and 160 m a.s.l.
189 (ICMBio 2016), however in the Northwest and East portions, the elevation varies from
190 160 to 200 m a.s.l. The forest phytophysiology that makes up the FLONA of Amapá is
191 not homogeneous, the main types of vegetation are dense alluvial forest with uniform
192 canopy, dense ombrophilous forest with emerging canopy, dense ombrophilous forest
193 with emerging canopy, and dense ombrophilous forest with submontane canopy uniform,
194 with the last two being the most representative vegetation types in the region (ICMBio
195 2016).



196

197 **Figure 1.** Location of the study area in the state of Amapá, Brazil (a), southern part of the Amapá National
 198 Forest (b), highlighting the 15 sampling points (grey squared) in the permanent plots (solid line) of the
 199 Biodiversity Research Program (c).

200 5.3.2. Bat sampling

201 Sampling was carried out in 15 permanent plots installed in a system of trails
 202 established by the Brazilian Program for Research in Biodiversity (PPBio;
 203 <https://ppbio.inpa.gov.br/> - Figure 1). PPBio uses the RAPELD method (in Portuguese,
 204 RAP = rapid assessment protocol; PELD = long-term ecological survey) for sampling
 205 different biological groups (Magnusson *et al.* 2005). The trail system consists of 6 trails
 206 in the East-West direction and 6 trails in the North-South direction, covering an area of
 207 25 km². The trails allow access to 30 permanent plots systematically distributed at 1 km
 208 intervals on the East-West trails (Magnusson *et al.* 2013). The plots are 250 m long and
 209 follow the ground level curve, thus minimizing internal variations in soil and topography.
 210 The 15 plots were chosen to ensure the greatest variation in topography (elevation) and
 211 vegetation structure (e.g. diameter and height of trees) and distance to nearest

212 watercourses (Figure 1).

213 We have visited each plot twice during the less rainy period in the Northeastern
214 Brazilian Amazon, between November 15th and December 2nd, 2017, and once in the
215 rainy season, between February 27th and March 7th, 2018. During each visit (sampling
216 night), we have captured bats using eight mist nets (12×3 m in size and 14 mm mesh)
217 per plot. The nets were set up 15 minutes before sunset (~18h:00) at ground level and
218 remained open for six hours (~00h:00), being inspected every 30 minutes (Carvalho *et al.*
219 2016). The sampling effort was dimensioned following recommendations by Straube and
220 Bianconi (2002), reaching 5,184 m² .h per plot, totaling 77,760 m² .h.

221 After removing bats from the mist net, we have measured the length of the forearm
222 with a caliper and the body mass with a spring scale (Pesola brand and accuracy of
223 $\pm 0.3\%$). Afterwards, bats were identified in the field with the help of taxonomic keys and
224 descriptions (Lim & Engstrom 2001; López-Baucells 2018; Reis *et al.* 2013; Reis *et al.*
225 2017). Captured individuals were marked with a collar with individual identification
226 (Esbérard & Daemon 1999) and later released. We restricted our analyzes to bats of the
227 Phyllostomid ae family and the aerial insectivore *Pteronotus* sp. (family Mormoopidae),
228 because bats from other families are not commonly captured in ground-level mist nets
229 (Kalko *et al.* 1996a). All packages mentioned below were loaded in the R program,
230 version 3.6.1(R Development Core Team 2019).

231 **5.3.3. Forest structure**

232 We have estimated the vegetation clutter using the point-of-intercept sampling
233 method (Dias-Terceiro *et al.* 2015). This method consists of quantifying the number of
234 direct contacts by leaves and branches on a 1.5 m long stick raised vertically to 50 cm
235 above the ground (Bobrowiec & Tavares 2017; Dias-Terceiro *et al.* 2015). We counted
236 the number of points that touched the stick every 2 m in a 100 m stretch located in the
237 central track of the plot and in the same portion where the mist nets were installed. This

238 procedure to estimate the vegetation clutter was carried out in parallel with the mist nets,
 239 at a distance of 1 m, in order to minimize interferences caused by the removal of
 240 vegetation when the nets were placed. Thus, the vegetation clutter in each plot was
 241 represented by the total number of strokes on the stick over the 100 m.

242 Basal area (AB) and canopy height data were obtained through a vegetation
 243 structure inventory carried out previously in accordance with the protocol established by
 244 PPBio (Castilho *et al.* 2014). Trees with diameter at breast height (DBH) ≥ 1 cm and < 30
 245 cm were inventoried in an area of 2 x 250 m and trees ≥ 30 were sampled in an area and
 246 40 x 250 m in the plots. DBH was measured at 1.3 m above ground or at 50 cm above
 247 tabular roots or trunk irregularities. The basal area of the plot was calculated by adding
 248 the basal area values derived from the DBH_i of each tree, the following equation 1:

$$249 \quad AB = \sum_{i=1}^n \left[\pi \frac{DBH_i}{2} \right]^2 \quad (1)$$

250 where AB is the basal area in m^2 . The calculation was performed for trees with $1 \leq DBH$
 251 < 30 cm and $DBH \geq 30$ cm separately (due to sampling in different area sizes) and the
 252 basal areas were multiplied by 20 and 1 (respectively), then added together to provide an
 253 estimate per hectare.

254 The total height (from the base of the trunk to the top of the crown) was measured
 255 with a laser hypsometer (TruPulse® 360) in 1,156 trees (1 – 109 cm DBH) selected in 5
 256 plots. The height calculation was performed using the tangent method (Larjavaara &
 257 Muller-Landau 2013), using the distance and the lower and upper angles of the tree in
 258 relation to the operator. The relationship between total height and DBH was adjusted
 259 using the Michaelis Menten equation to generate an allometric model capable of
 260 predicting height using the equation 2:

$$261 \quad H = 51.1 \frac{DBH_i}{(25.1 + DBH_i)} \quad (2)$$

262 The equation 2 was then used to estimate the total height of the inventoried trees and the

263 mean height was calculated to represent the canopy height of the plot as a function of
264 DBH.

265 **5.3.4. Terrain elevation and distance to the nearest watercourse**

266 We use the geographic coordinates of the initial part of each plot to determine its
267 position and thus obtain the elevation through a digital elevation model (DEM) from the
268 Topodata project available at <http://www.webmapit.com.br/inpe/topodata/>, derived from
269 the Shuttle Radar Topography Mission – STRM. The distances to the nearest watercourse
270 were measured from the location of the plots and the network of river channels generated
271 with the DEM data. Using Quantum GIS 3.6.3 software and data from river channel
272 networks (Fill sinks modules), we have calculated the shortest distance from the central
273 point of each plot to the closest point of the river channel.

274

275 **5.3.5. Functional traits**

276 We chose four functional traits that have been related to the distribution of bats in
277 tropical forests (Castillo-Figueroa & Pérez-Torres 2021; Cisneros *et al.* 2014; Marciente
278 *et al.* 2015). The traits were obtained based on data collected during the manipulation of
279 bats and data from the literature, namely: body mass, trophic level, relative wing loading,
280 and wing aspect ratio.

281 Bat size may be a determining factor in habitat use (Hanspach *et al.* 2012; Ramos
282 Pereira *et al.* 2009). Large bats like *Artibeus lituratus* and *Phyllostomus hastatus* prefer
283 to forage on larger fruits that occur in the tree canopy, whereas small bats like *Carollia*
284 spp. prefer smaller fruits that are available in the lower forest strata (Kalko *et al.* 1996b;
285 Marques *et al.* 2012; Rex *et al.* 2011; Saldaña-Vázquez *et al.* 2013; Schaefer *et al.* 2002;
286 Shanahan & Compton (2001); Voigt 2010). Body mass was determined as the average of
287 the body mass of adult individuals of each species captured.

288 Both the relative wing loading (division of body mass by the wing area) wing

289 aspect ratio (division of the square of the wingspan by the wing area) directly influence
290 the maneuverability, agility, and flight speed of bats (Norberg & Rayner 1987), being
291 important predictors of habitat use in foraging (Muller *et al.* 2012; Norberg & Rayner
292 1987). Bats that have a low relative loading and a lower wing aspect ratio perform better
293 for foraging in places with more obstacles (Marinello & Bernard 2014; Silva 2012).
294 Species with these characteristics have wings capable of producing the high curvature
295 necessary to maintain lift in low-speed flights, favoring success in environments with
296 higher levels of obstruction (Stockwell 2001). Bats that have a high relative wing charge
297 and a high wing aspect ratio have constant high-speed flights and low energy costs
298 (Norberg & Rayner 1987). These characteristics favor flights in less obstructed
299 environments and over long distances in search of food (Norberg & Rayner 1987). Values
300 for relative loading and wing appearance were obtained from Marinello and Bernard
301 (2014).

302 Different animal trophic guilds are affected by the resource availability, and
303 therefore these animals look for areas with better chances of finding available food
304 (Capaverde *et al.* 2018; Carr & Macdonald 1986; MacArthur & Pianka 1966; Marciente
305 *et al.* 2015; Marinello & Bernard 2014; Oliveira *et al.* 2015; Silva 2012). We classify bats
306 into two trophic categories: animalivorous, which include insectivorous, carnivorous, and
307 hematophagous bats, and phytophagous, which include frugivorous and nectarivorous
308 bats (Giannini & Kalko 2004; Schnitzler *et al.* 2003).

309

310 **5.3.6. Alpha diversity**

311 We have quantified the taxonomic, functional, and phylogenetic dimensions of α -
312 diversity of bat assemblages sampled in each plot using Hill numbers (Chao *et al.* 2014a;
313 Hill 1973). Hill numbers are defined by the q parameter, which reflects their respective
314 sensitivity to relative species abundances, facilitating data comparison (Chiu & Chao

2014; Hill 1973; Roswell *et al.* 2021). Thus, as the q parameter increases, the diversity index becomes more sensitive to common species and less dependent on rare species (Chiu & Chao 2014). For Hill numbers, $q = 0$ equals species richness, as species abundances are not considered, and for $q = 2$, dominant species receive greater weight than rare species, representing the inverse of the dominance index by Simpson (Chiu & Chao 2014; Daly *et al.* 2018; Li 2018a). Thus, for each plot, the taxonomic, functional, and phylogenetic dimensions of α -diversity were quantified considering the variation of the parameter q ($q = 0$, $q = 2$), through the 'hillR' package (Li 2018b). Specifically, the taxonomic richness ($q = 0$) of each plot was estimated by constructing interpolated and extrapolated species accumulation curves using the 'iNEXT' package in R (Chao *et al.* 2014b; Hsieh *et al.* 2016). Comparisons were made with a sample size of 15 individuals, which is triple the size of the smallest sample. For functional diversity, Hill numbers incorporate functional distances between pairs of species from the functional characteristics of the species (Chao *et al.* 2019; Chiu & Chao 2014), while for phylogenetic diversity, Hill numbers incorporate a phylogenetic tree (Li 2018b). For phylogenetic diversity, we use a phylogenetic tree derived from a most current phylogeny (Upham *et al.* 2019).

332

333 **5.3.7. Community weighted indexes**

334 The use of weighted indices by the relative abundances of the species allows
335 evaluating changes in the mean values of the characteristics of the
336 assemblage/community (Lavorel *et al.* 2008). We have used the Community Weighted
337 Mean (CWM), which is the predominance of functional traits of the bat assemblages of
338 each plot using a weighted average of the functional trait for the community. The CWM
339 allows accessing the average value of functional traits for the community (in our case, the
340 bat assemblage of each plot), weighting this value by the relative abundances of the

341 species in the sample in question (Lavorel *et al.* 2008). We estimate the CWM through
342 the 'BAT' package (Cardoso *et al.* 2021).

343 **5.3.8. Data analysis**

344 We have evaluated the effect of vegetation clutter, terrain elevation, distance to
345 nearest watercourse, basal area, and canopy height on each of our response variables:
346 richness, taxonomic, functional and phylogenetic diversity, and CWM. For this, we use
347 Generalized Linear Models (GLM, Gaussian family). We selected models separately for
348 each q parameter ($q = 0$, $q = 2$) of α -diversity and for CWM, with all possible
349 combinations of predictor variables. Model residuals were tested for normality (Shapiro
350 Wilks, $p \geq 0.05$) and homoscedasticity (Breusch-Pagan test, $p \geq 0.05$). Based on this, we
351 had to take the square root of the nearest watercourse distance explanatory variable in the
352 selection of models with the CWM of the animalivorous and phytophagous trophic levels
353 and square the average body mass response variable so that the residuals of the models
354 followed a normal distribution.

355 To identify the predictor variables with greater explanatory support on the
356 response variables, the generated models were selected considering the Akaike
357 information criterion, corrected for small samples (AICc - corrected Akaike Information
358 Criterion), where the best model was the one with the lowest value of AICc. (Burnham &
359 Anderson 1998). Thus, the models that presented $\Delta AICc$ values < 2 were considered the
360 most supportive. Subsequently, we calculated the parameter estimates, importance and
361 the unconditional mean of the regression coefficients and their standard errors for each
362 predictor variable of the models with $\Delta AICc < 2$. The parameter estimates of the predictor
363 variables were only calculated for the model selections that they did not have the null
364 model as being the one with the greatest explanatory support ($\Delta AICc = 0$). These
365 estimates and model selection were made using the “Multi-model inference” package
366 (MuMIn), version 1.40.0 (Barton 2018).

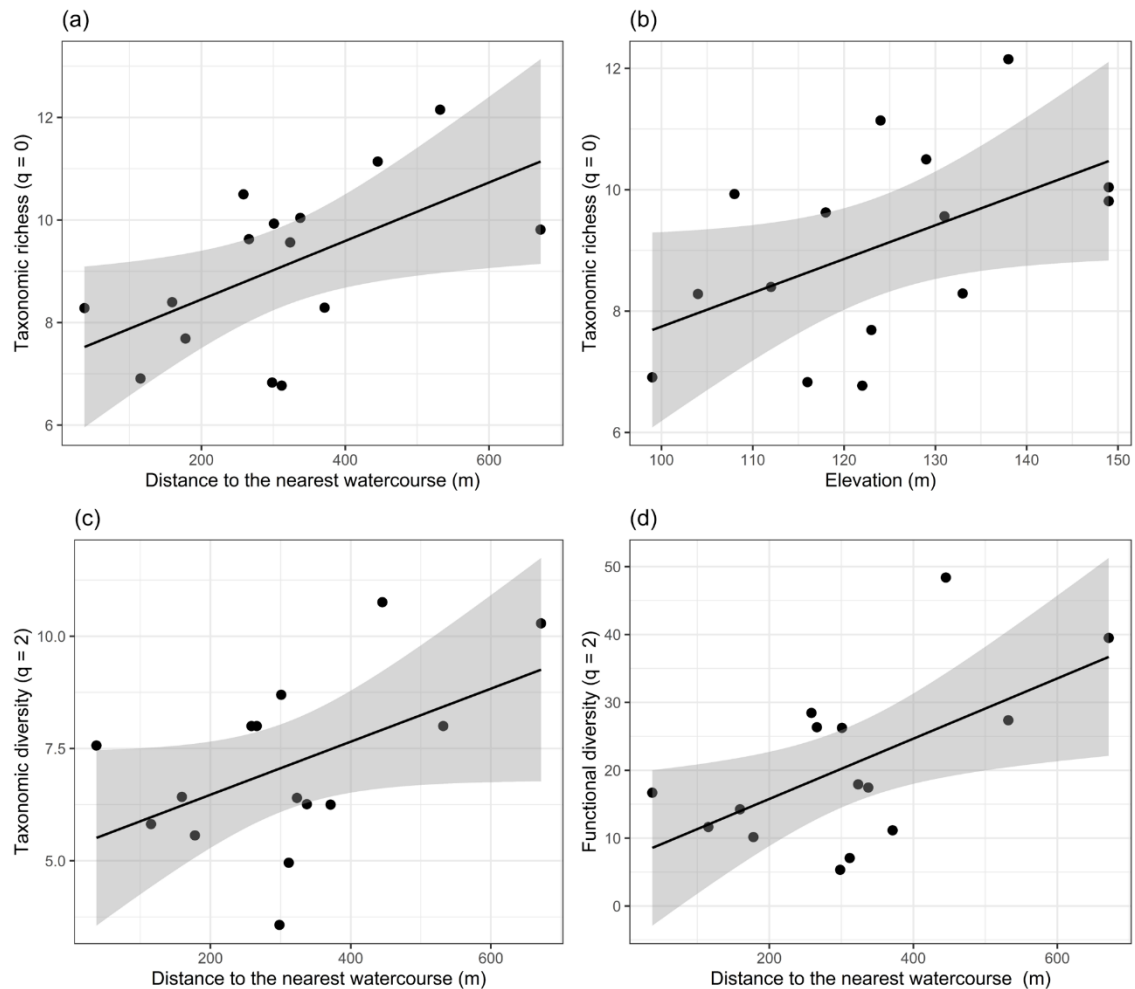
367

368 6. Results

369 We have captured 279 individuals belonging to 28 species and two families. The
370 most captured species were *Rhinophylla pumilio* (46 individuals), *Artibeus planirostris*
371 (44), *Artibeus lituratus* (31), and *Pteronotus* sp. (31). The species *R. pumilio* and *A.*
372 *planirostris* represented 32% of all captured bats. Phytophagous bats were more captured
373 (199 captures of 16 species) than animalivorous [80 captures of 12 species -
374 (Supplementary Material – Table S1)].

375 6.1. Environmental factors driving richness and alpha diversity components

376 Of the five predictor variables used for model selection, distance to the nearest
377 watercourse was the most important predictor (0.64) for taxonomic richness ($q = 0$),
378 followed by elevation (0.36). Taxonomic richness increased with distance to the nearest
379 watercourse and with elevation (Figure 2; Table 1). Taxonomic and functional diversity
380 also increased with distance to the nearest watercourse ($q = 2$; Figure 2; Table 1), this
381 being the most important predictor for taxonomic (0.62) and functional diversity (0.83).
382 No predictor variable explained phylogenetic richness ($q = 0$; (Supplementary Material –
383 Table S6)). For functional richness ($q = 0$) and phylogenetic diversity ($q = 2$), the null
384 model had the greatest explanatory support (Supplementary Material – Tables S6 and S7)



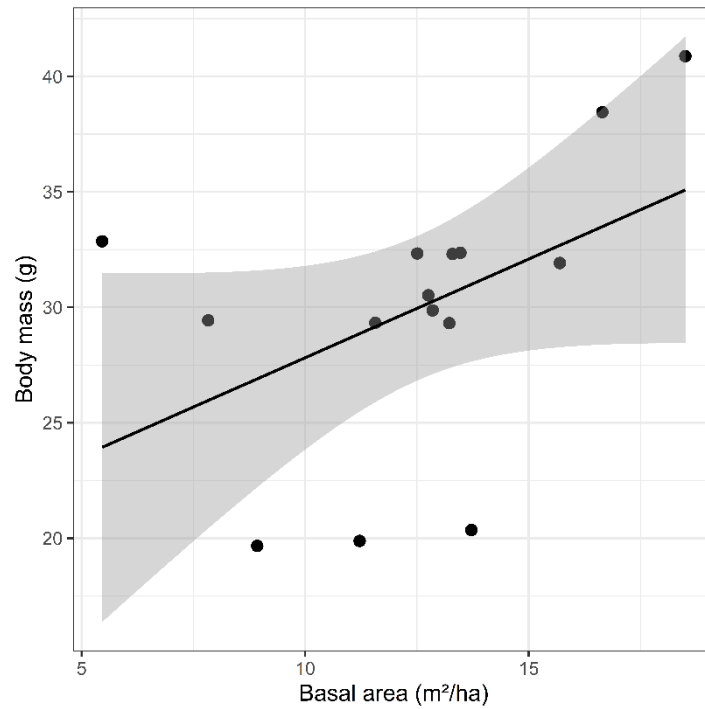
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386 **Figure 2.** Relationship between the variables selected as the best predictors for taxonomic richness ($q = 0$
 387 – a, b), taxonomic diversity ($q = 2$ – c), and functional diversity ($q = 2$ – d) in a community of Phyllostomid
 388 bats from the terra firme forest of Northern Brazilian Amazon. The straight line represents the model
 389 estimate and the gray area the 95% confidence interval.

390 **6.2. Environmental factors that drive the predominance of functional traits**

391 For CWM, only body mass did not have the null model with greater explanatory
 392 support ($\Delta AICc < 2$ - Supplementary Material – Table S8-S12)). For this functional trait,
 393 basal area and vegetation clutter were considered with greater explanatory support, with
 394 basal area being present in two of the best selected models (Supplementary Material –
 395 Table S8)). The basal area was more important (0.76), while the importance of vegetation
 396 clutter was (0.29) to predict the variation in mean body mass. However, there was a
 397 significant relationship only between basal area and mean body mass ($p = 0.05$ – Table

398 1). Thus, areas occupied by a greater number of large trees tend to have bat species with
 399 greater mean body mass (Figure 3).



400

401 **Figure 3.** Relationship between the mean body mass of Phyllostomid bat species (measured using the
 402 community weighted mean - CWM) and basal area in a terra firme forest in Northeastern Brazilian Amazon.
 403 The straight line represents the model estimate and the gray area the 95% confidence interval.

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412 **Table 1.** Estimates of parameters, standard error and unconditional regression coefficient
 413 (SE) of the set of models with $\Delta\text{AICc} < 2$ related to predictor variables with taxonomic
 414 richness ($q = 0$), taxonomic diversity ($q = 2$), functional diversity ($q = 2$), and with the
 415 CWM of the mean body mass. The predictors that enter the models are distance from the
 416 nearest watercourse – DNW; elevation – ELE; basal area – BA; vegetation clutter– VCL.
 417

Dependent variable	Predictor	Estimattion	Standard error	SE	Z-value	p-value
Taxonomic richness ($q = 0$)	DNW	0,91	0,37	0,18	1,64	0,02
	ELE	0,83	0,39	0,07	1,59	0,05
Taxonomic diversity ($q = 2$)	DNW	0,95	0,47	0,03	1,87	0,06
Functional diversity ($q = 2$)	DNW	7,12	2,73	1,77	12,47	0,02
CWM - average body mass (g)	BA	179,07	83,53	15,35	342,79	0,05
	VCL	-128,17	80,68	286,30	29,96	0,15

418

419 7. Discussion

420 We have found that terrain elevation and distance from the nearest watercourse
 421 are the predictors that drive the α -diversity of bat assemblages in *terra firme* forest in the
 422 Northeastern Brazilian Amazon. Specifically, we observed that bat taxonomic richness
 423 was positively influenced by terrain elevation and distance to the nearest watercourse. In
 424 addition, taxonomic and functional diversity was positively influenced by the distance to
 425 the nearest watercourse. Across the Amazon basin, terrain elevation and distance to water
 426 bodies have been shown to be important predictors of the richness and taxonomic

427 composition of bats (Bobrowiec & Tavares 2017; Capaverde *et al.* 2018), terrestrial
428 mammals (Kinap *et al.* 2021; Michalski *et al.* 2015), understory birds (Bueno *et al.* 2012;
429 Cintra & Naka 2012; Oliveira *et al.* 2019), amphibians and reptiles (Fraga *et al.* 2011;
430 Rojas-Ahumada *et al.* 2012; Tavares *et al.* 2019), and plants (Drucker *et al.* 2008; Schietti
431 *et al.* 2014). Therefore, as occurs in the Southwest and Central Amazon, variations in
432 terrain elevation and distance to the water bodies are crucial for structuring bat
433 assemblages at small scales in *terra firme* forests in Northeastern Brazilian Amazonia.

434 We have found that the taxonomic richness of bats increases with terrain elevation.
435 Subtle variations (< 100 m) in terrain elevation have been shown to be fundamental for
436 the structuring of bat assemblages (Bobrowiec & Tavares 2017; Capaverde *et al.* 2018),
437 as terrain elevation has a direct influence on the hydrological and edaphic characteristics
438 of the soil, playing an important role in determining the composition of the plant
439 assemblage (Costa *et al.* 2008; Schietti *et al.* 2014). For example, in Central Amazon, the
440 richness and abundance of palm trees and shrubs (Kinupp & Magnusson 2005; Rodrigues
441 *et al.* 2014) and the structure of woody vegetation (Castilho *et al.* 2006) tend to increase
442 with elevation of the terrain. In addition, tall trees (>70 m) are more frequent in higher
443 terrain (>100 m a.s.l.) in lowland Amazonian forests (Gorgens *et al.* 2021). A more
444 complex forest provides more niches and different ways to harness environmental
445 resources (Bazzaz 1975), greater availability of food, shelter, and nesting sites (Tews *et*
446 *al.* 2003). Thus, forests in in higher elevation areas tend to have a greater frequency of
447 large trees, which produce greater structural complexity, increasing the number of
448 available niches and allowing more bat species to coexist.

449 The lower value of taxonomic and functional diversity found for areas closer to
450 the watercourse may be due to the greater dominance of the frugivores *Rhinophylla*
451 *pumilio*, *Artibeus planirostris*, *Artibeus lituratus* and the insectivore *Pteronotus* sp. in

452 these regions. These species represented 54% of the total captures. Soils are more sandy
453 and poorly oxygenated in regions close to water bodies, which limits the growth of many
454 plant species in these regions (Costa *et al.* 2005; Pansonato *et al.* 2012; Rodrigues *et al.*
455 2014; Toledo *et al.* 2017). However, in the Amazon region, several plant species,
456 including pioneers such as *Ficus*, *Cecropia*, and *Vismia* manage to perpetuate under these
457 conditions (Ferreira 2000; Salo *et al.* 1986). Bats of the genera *Artibeus* and *Rhinophylla*
458 are known for their strong association with fruits of plants of these genera (Andrade *et al.*
459 2013; Giannini & Kalko 2004). In the FLONA of Amapá, during the present study, we
460 have observed a higher occurrence of *Ficus* spp., including fruiting, close to water
461 courses. In addition, natural erosion, and subsequent sediment deposition due to river
462 dynamics form sandbanks and create habitats of primary succession on riverbanks
463 (Peixoto *et al.* 2009). In these environments, the lesser competition for solar radiation and
464 the proximity to the water table, allows plants adapted to these conditions to allocate more
465 energy to fruit production (Van Schaik *et al.* 1993), consequently, plants of the genus
466 *Ficus* spp., *Cecropia*, *Piper* and *Vismia* on riverbanks offer a greater abundance of fruit
467 than in the forest interior (Marques *et al.* 2012). In addition to this fruit abundance for
468 frugivorous bats, habitats close to watercourses have a significant influence on insect
469 biomass and represent an important foraging habitat for many insectivorous bats (Fukui
470 *et al.* 2006; Hagen & Sabo 2011,2014; Holloway & Barclay 2000). Thus, all this
471 abundance of food for the bats *R. pumilio*, *A. planirostris*, *A. lituratus*, and *Pteronotus* sp.
472 in areas close to the watercourse, it may have contributed to the increase in the number
473 of individuals of these species, reducing the Simpson diversity values ($q = 2$), which in
474 turn is an index more sensitive to dominant species (Chiu & Chao 2014).

475 In addition to the increased dominance of a few species close to the watercourses,
476 the decrease in taxonomic richness may be one of the factors responsible for the lower

477 taxonomic diversity in these locations. The conditions that favor the dominance of some
478 species (e.g. high abundance of some food resources, less dense undergrowth) close to
479 watercourses may disfavor the existence of some species dependent on this forest extract
480 (Oliveira *et al.* 2015), reducing the taxonomic richness. Locations away from
481 watercourses may not have a great abundance of certain resources, but they may contain
482 a greater diversity of them, contemplating a greater number of bat species

483 Contrary to our expectations, only one functional trait of the bat assemblages was
484 influenced by environmental variables. The average body mass weighted by abundance
485 was higher in areas that had a larger basal area. Larger trees have a greater ability to
486 acquire and store nutrients and carbohydrates (Carbone *et al.* 2013) and tend to produce
487 more fruits (Minor & Kobe 2019). Thus, this greater availability of fruits reflects in a
488 greater biomass of primary consumers, such as bats (Ramos Pereira *et al.* 2009). In
489 addition, bat size can be an important and limiting criterion in habitat use (Hanspach *et*
490 *al.* 2012; Stockwell 2001). For example, locomotion through flight requires bat species
491 high rates of energy expenditure during foraging (Norberg & Rayner 1987; Voigt &
492 Holderied 2012) and larger bats have a higher absolute energy demand (Brown *et al.*
493 2004; Winter & Von Helversen 1998). Therefore, larger bats are more favored when
494 foraging in regions where the trees have a larger basal area, as the energy costs incurred
495 by the flight activity are offset by the greater availability of food in these regions.

496 Despite the low number of captures, compared to other studies carried out in *terra*
497 *firme* forest Capaverde *et al.* (2018); Carvalho *et al.* (2018) and Marciente *et al.* (2015),
498 our multidimensional approach proved to be efficient to understand the effect of
499 environmental filters on the distribution of bats in this Amazon ecosystem. Overall, our
500 study supports the hypothesis that variations in environmental factors in the same forest
501 habitat are sufficient to structure bat assemblages. Specifically, we show that increasing

502 distance to the nearest watercourse and small variations (< 50 m a.s.l) in the elevation
503 exerts a positive effect on the different components of the α -diversity of bats in *terra firme*
504 forest. Furthermore, only the average body mass stood out among the functional traits of
505 the bat assemblage (CWM), showing an association with the basal area of the forest.

506

507 **7.1. Implications for conservation**

508 Our study demonstrated that there is an increase in taxonomic and functional
509 diversity due to the increase in distance (up to 600 m) in relation to the nearest
510 watercourse. Brazilian environmental legislation only protects 30 m from the riparian
511 strip in streams <10 m wide (Brasil 2012). Therefore, if we consider our results, the
512 minimum strip of 30 m left on each side of the streams as Areas of Permanent Preservation
513 may not be sufficient for the preservation of different species of bats and, consequently,
514 of the ecosystem services provided by the group (e.g. seed dispersal). We have also found
515 a positive relationship between the mean body mass of bats and the basal area of trees,
516 which could be a variable to be considered in future management plans for selective
517 logging. Due to the increase in human population, and with it the increased demand for
518 timber resources (Kraxner *et al.* 2013), tropical forests are being degraded at an alarming
519 rate by selective logging (Asner *et al.* 2005; Hansen *et al.* 2013; Lindquist *et al.* 2012).
520 In Brazil, the current government has tried to make the bidding model and contracts for
521 forest concessions more flexible to make the process faster and more attractive
522 (Menegassi 2021). For example, the FLONA of Amapá started a process for logging in
523 an area of 226,000 hectares, which corresponds to almost half of this conservation unit
524 (Serviço Florestal Brasileiro 2019,2020). Therefore, it is necessary to promote forest
525 management plans that prioritize the preservation of biological and physical elements
526 such as large trees, which are the focus of current exploration, as well as hollow and dead
527 trees, which are crucial for the supply of food, perches, and shelters for the bat fauna.

528 **8. Acknowledgments**

529 MMF and WDC were supported, respectively, by master scholarships and post-
530 doctoral (PNPD/CAPES) of the Coordenação de Aperfeiçoamento de Pessoal de Nível
531 Superior (CAPES), Brazil. We thank Gustavo Silveira, Cledinaldo Marques, Cremilson
532 Marques, Raimundão and Dona Vita for their help in sampling and logistics for carrying
533 out activities in the field. We also thank Instituto Chico Mendes de Conservação da
534 Biodiversidade (ICMBio) for the logistical help and permissions to carry out this study.

535

536 **Competing interests declaration**

537 The author(s) declare none

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945

10. Supplementary material

Supplementary Material Table S1. List of bat species with their trophic categories, abundance in plots (N = 15) occurring in the study area of the Northeastern Brazilian Amazon.

Species	Animalivorous	Phytophagous
<i>Artibeus concolor</i>	-	2
<i>Artibeus lituratus</i>	-	31
<i>Artibeus obscurus</i>	-	14
<i>Artibeus planirostris</i>	-	44
<i>Carollia brevicauda</i>	-	10
<i>Carollia perspicillata</i>	-	10
<i>Chrotopterus auritus</i>	1	-
<i>Dermanura cinérea</i>	-	5
<i>Dermanura gnoma</i>	-	1
<i>Desmodus rotundus</i>	6	-
<i>Hsunnycteris thomasi</i>	-	10
<i>Lichonycteris degener</i>	-	3
<i>Lophostoma schulzi</i>	1	-
<i>Lophostoma silvícola</i>	7	-
<i>Mesophylla macconnelli</i>	-	4
<i>Micronycteris microtis</i>	1	-
<i>Mimon crenulatum</i>	8	-
<i>Phylloderma stenops</i>	-	7
<i>Phyllostomus elongatus</i>	10	-
<i>Pteronotus sp.</i>	31	-
<i>Rhinophylla pumilio</i>	-	46

<i>Sturnira tildae</i>	-	1
<i>Tonatia saurophila</i>	8	-
<i>Trachops cirrhosus</i>	3	-
<i>Trinycteris nicefori</i>	3	-
<i>Uroderma bilobatum</i>	-	9
<i>Vampyriscus bidens</i>	-	2
<i>Vampyrodes caraccioli</i>	1	-
Total	80	199
Grand total	279	

Supplementary Material Table S2. Models relating predictor variables to taxonomic richness ($q = 0$) of Phyllostomid bats in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	wi
DNW	3	-25,25	58,7	0,00	0,30
ELE	3	-25,82	59,8	1,14	0,17
NULL	2	-28,09	61,2	2,49	0,09
ELE+DNW	4	-25,09	62,2	3,50	0,05
VCL+DNW	4	-25,11	62,2	3,53	0,05
DNW+CH	4	-25,16	62,3	3,65	0,05
DNW+BA	4	-25,18	62,4	3,67	0,05
BA	3	-27,09	62,4	3,67	0,05
ELE+BA	4	-25,41	62,8	4,14	0,04
VCL+ELE	4	-25,79	63,6	4,90	0,03
ELE+CH	4	-25,82	63,6	4,95	0,03
CH	3	-27,97	64,1	5,43	0,02
VCL	3	-28,02	64,2	5,54	0,02
VCL+BA	4	-27,02	66,1	7,37	0,01
BA+CH	4	-27,08	66,2	7,48	0,01
VCL+ELE+DNW	5	-24,93	66,5	7,85	0,01

ELE+DNW+BA	5	-24,98	66,6	7,95	0,01
ELE+DNW+CH	5	-25,00	66,7	7,99	0,01
VCL+DNW+CH	5	-25,03	66,7	8,06	0,01
VCL+DNW+BA	5	-25,06	66,8	8,12	0,01
DNW+BA+CH	5	-25,07	66,8	8,13	0,01
ELE+BA+CH	5	-25,37	67,4	8,74	0,00
VCL+ELE+BA	5	-25,39	67,5	8,77	0,00
VCL+CH	4	-27,93	67,9	9,17	0,00
VCL+ELE+CH	5	-25,79	68,2	9,56	0,00
VCL+BA+CH	5	-27,02	70,7	12,03	0,00
VCL+ELE+DNW+CH	6	-24,86	72,2	13,55	0,00
VCL+ELE+DNW+BA	6	-24,87	72,2	13,55	0,00
ELE+DNW+BA+CH	6	-24,87	72,3	13,57	0,00
VCL+DNW+BA+CH	6	-24,98	72,5	13,77	0,00
VCL+ELE+BA+CH	6	-25,36	73,2	14,54	0,00
VCL+ELE+DNW+BA+CH	7	-24,78	79,6	20,87	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AICc, w_i – model weight (Akaike).

Supplementary Material Table S3. Models relating predictor variables to taxonomic diversity ($q = 2$) of Phyllostomid bats in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	Wi
DNW	3	-235,80	479,8	0,00	0,31
NULL	2	-237,86	480,7	0,95	0,19
ELE+DNW	4	-235,31	482,6	2,84	0,07
ELE	3	-237,41	483,0	3,24	0,06
VCL+DNW	4	-235,65	483,3	3,53	0,05
DNW+BA	4	-235,74	483,5	3,71	0,05
DNW+CH	4	-235,75	483,5	3,72	0,05
BA	3	-237,66	483,5	3,72	0,05
CH	3	-237,76	483,7	3,93	0,04
VCL	3	-237,83	483,8	4,07	0,04
ELE+BA	4	-237,34	486,7	6,91	0,01
ELE+CH	4	-237,39	486,8	7,01	0,01
VCL+ELE	4	-237,41	486,8	7,05	0,01
VCL+ELE+DNW	5	-235,17	487,0	7,22	0,01
ELE+DNW+BA	5	-235,21	487,1	7,31	0,01
ELE+DNW+CH	5	-235,25	487,2	7,38	0,01

BA+CH	4	-237,60	487,2	7,42	0,01
VCL+BA	4	-237,61	487,2	7,45	0,01
VCL+CH	4	-237,75	487,5	7,72	0,01
VCL+DNW+BA	5	-235,53	487,7	7,95	0,01
VCL+DNW+CH	5	-235,61	487,9	8,12	0,01
DNW+BA+CH	5	-235,70	488,1	8,28	0,01
ELE+BA+CH	5	-237,33	491,3	11,55	0,00
VCL+ELE+BA	5	-237,34	491,3	11,57	0,00
VCL+ELE+CH	5	-237,39	491,5	11,68	0,00
VCL+BA+CH	5	-237,57	491,8	12,04	0,00
VCL+ELE+DNW+BA	6	-234,97	492,4	12,68	0,00
VCL+ELE+DNW+CH	6	-235,12	492,7	12,96	0,00
ELE+DNW+BA+CH	6	-235,15	492,8	13,03	0,00
VCL+DNW+BA+CH	6	-235,49	493,5	13,71	0,00
VCL+ELE+BA+CH	6	-237,33	497,2	17,38	0,00
VCL+ELE+DNW+BA+CH	7	-234,93	499,9	20,09	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AICc, w_i – model weight (Akaike).

Supplementary Material Table S4. Models relating predictor variables with functional richness ($q = 0$) of Phyllostomid bats in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	Wi
NULL	2	-305,33	615,7	0,00	0,35
DNW	3	-304,73	617,6	1,98	0,13
VCL	3	-305,19	618,6	2,90	0,08
BA	3	-305,26	618,7	3,03	0,08
CH	3	-305,28	618,7	3,08	0,08
ELE	3	-305,33	618,8	3,17	0,07
ELE+DNW	4	-304,03	620,0	4,38	0,04
VCL+DNW	4	-304,19	620,4	4,72	0,03
DNW+BA	4	-304,77	621,5	5,78	0,02
DNW+CH	4	-304,73	621,5	5,79	0,02
VCL+CH	4	-305,10	622,2	6,52	0,01
VCL+BA	4	-305,13	622,3	6,58	0,01
VCL+ELE	4	-305,15	622,3	6,63	0,01
BA+CH	4	-305,23	622,5	6,78	0,01
ELE+BA	4	-305,26	622,5	6,84	0,01
ELE+CH	4	-305,28	622,6	6,90	0,01

VCL+ELE+DNW	5	-303,46	623,6	7,93	0,08
ELE+DNW+BA	5	-303,99	624,6	8,98	0,00
ELE+DNW+CH	5	-304,02	624,7	9,04	0,00
VCL+DNW+BA	5	-304,09	624,9	9,18	0,00
VCL+DNW+CH	5	-304,19	625,1	9,38	0,00
DNW+BA+CH	5	-304,72	626,1	10,44	0,00
VCL+BA+CH	5	-305,06	626,8	11,11	0,00
VCL+ELE+CH	5	-305,08	626,8	11,15	0,00
VCL+ELE+BA	5	-305,11	626,9	11,22	0,00
ELE+BA+CH	5	-305,22	627,1	11,44	0,00
VCL+ELE+DNW+BA	6	-303,29	629,1	13,40	0,00
VCL+ELE+DNW+CH	6	-303,46	629,4	13,76	0,00
ELE+DNW+BA+CH	6	-303,99	630,5	14,80	0,00
VCL+DNW+BA+CH	6	-304,09	630,7	15,02	0,00
VCL+ELE+BA+CH	6	-305,05	632,6	16,93	0,00
VCL+ELE+DNW+BA+CH	7	-303,29	636,6	20,90	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AICc, w_i – model weight (Akaike).

Supplementary Material Table S5. Models relating the predictor variables to the functional diversity ($q = 2$) of Phyllostomid bats in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	Wi
DNW	3	296,86	601,9	0,00	0,41
ELE+DNW	4	296,40	604,8	2,92	0,10
NULL	2	300,00	605,0	3,12	0,09
VCL+DNW	4	296,71	605,4	3,53	0,07
DNW+CH	4	296,84	605,7	3,79	0,06
DNW+BA	4	296,85	605,7	3,80	0,06
ELE	3	299,15	606,5	4,58	0,04
BA	3	299,52	607,2	5,33	0,03
CH	3	299,53	607,2	5,34	0,03
VCL	3	299,92	608,0	6,12	0,02
VCL+ELE+DNW	5	296,27	609,2	7,31	0,01
ELE+DNW+BA	5	296,38	609,4	7,53	0,01
ELE+DNW+CH	5	296,39	609,5	7,56	0,01
ELE+CH	4	298,92	609,8	7,95	0,01
ELE+BA	4	298,93	609,9	7,97	0,01
VCL+DNW+BA	5	296,67	610,0	8,12	0,01

VCL+DNW+CH	5	296,69	610,1	8,16	0,01
VCL+ELE	4	299,15	610,3	8,40	0,01
DNW+BA+CH	5	296,84	610,3	8,44	0,01
BA+CH	4	299,18	610,4	8,46	0,01
VCL+BA	4	299,40	610,8	8,90	0,01
VCL+CH	4	299,50	611,0	9,11	0,00
ELE+BA+CH	5	298,75	614,2	12,27	0,00
VCL+ELE+CH	5	298,92	614,5	12,61	0,00
VCL+ELE+BA	5	298,92	614,5	12,61	0,00
VCL+ELE+DNW+BA	6	296,19	614,9	12,99	0,00
VCL+BA+CH	5	299,12	614,9	13,02	0,00
VCL+ELE+DNW+CH	6	296,25	615,0	13,10	0,00
ELE+DNW+BA+CH	6	296,37	615,2	13,34	0,00
VCL+DNW+BA+CH	6	296,65	615,8	13,91	0,00
VCL+ELE+BA+CH	6	298,74	620,0	18,09	0,00
VCL+ELE+DNW+BA+CH	7	296,17	622,3	20,44	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AICc, w_i – model weight (Akaike).

Supplementary Material Table S6. Models relating predictor variables to phylogenetic richness ($q = 0$) of Phyllostomid bats in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	Wi
NULL	2	-221,99	449,0	0,00	0,40
DNW	3	-221,85	451,9	2,90	0,10
VCL	3	-221,88	451,9	2,94	0,09
CH	3	-221,99	452,2	3,17	0,08
ELE	3	-221,97	452,2	3,18	0,08
BA	3	-221,97	452,2	3,18	0,08
VCL+DNW	4	-221,58	455,2	6,17	0,02
ELE+DNW	4	-221,62	455,2	6,24	0,02
DNW+BA	4	-221,82	455,6	6,64	0,02
DNW+CH	4	-221,85	455,7	6,71	0,01
VCL+CH	4	-221,86	455,7	6,72	0,01
VCL+ELE	4	-221,87	455,7	6,75	0,01
VCL+BA	4	-221,88	455,8	6,76	0,01
ELE+CH	4	-221,99	456,0	6,99	0,01
BA+CH	4	-221,99	456,0	6,99	0,01
ELE+BA	4	-221,99	456,0	7,00	0,01

VCL+ELE+DNW	5	-221,35	459,4	10,37	0,00
VCL+DNW+BA	5	-221,45	459,6	10,58	0,00
ELE+DNW+BA	5	-221,55	459,8	10,78	0,00
VCL+DNW+CH	5	-221,58	459,8	10,83	0,00
ELE+DNW+CH	5	-221,61	459,9	10,89	0,00
DNW+BA+CH	5	-221,81	460,3	11,30	0,00
VCL+ELE+CH	5	-221,85	460,4	11,38	0,00
VCL+BA+CH	5	-221,86	460,4	11,38	0,00
VCL+ELE+BA	5	-221,87	460,4	11,41	0,00
ELE+BA+CH	5	-221,99	460,6	11,65	0,00
VCL+ELE+DNW+BA	6	-221,16	464,9	15,86	0,00
VCL+ELE+DNW+CH	6	-221,35	465,2	16,20	0,00
VCL+DNW+BA+CH	6	-221,45	465,4	16,41	0,00
ELE+DNW+BA+CH	6	-221,55	465,6	16,60	0,00
VCL+ELE+BA+CH	6	-221,85	466,2	17,21	0,00
VCL+ELE+DNW+BA+CH	7	-221,17	472,3	23,36	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AICc, w_i – model weight (Akaike).

Supplementary Material Table S7. Models relating predictor variables to phylogenetic diversity ($q = 2$) of Phyllostomid bats in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	Wi
NULL	2	-499,81	1004,6	0,00	0,28
DNW	3	-498,79	1005,8	1,14	0,16
CH	3	-499,04	1006,3	1,64	0,12
ELE	3	-499,25	1006,7	2,06	0,10
VCL	3	-499,69	1007,6	2,94	0,06
BA	3	-499,78	1007,7	3,13	0,06
DNW+CH	4	-498,46	1008,9	4,30	0,03
DNW+BA	4	-498,65	1009,3	4,69	0,03
ELE+CH	4	-498,74	1009,5	4,86	0,02
ELE+DNW	4	-498,78	1009,6	4,95	0,02
VCL+DNW	4	-498,79	1009,6	4,96	0,02
VCL+CH	4	-499,00	1010,0	5,39	0,02
BA+CH	4	-499,04	1010,1	5,46	0,02
VCL+ELE	4	-499,23	1010,5	5,84	0,02
ELE+BA	4	-499,24	1010,5	5,87	0,02
VCL+BA	4	-499,65	1011,3	6,69	0,01

DNW+BA+CH	5	-498,31	1013,3	8,67	0,00
VCL+DNW+CH	5	-498,45	1013,6	8,96	0,00
ELE+DNW+CH	5	-498,46	1013,6	8,96	0,00
VCL+DNW+BA	5	-498,64	1014,0	9,34	0,00
ELE+DNW+BA	5	-498,65	1014,0	9,35	0,00
ELE+BA+CH	5	-498,71	1014,1	9,47	0,00
VCL+ELE+CH	5	-498,73	1014,1	9,52	0,00
VCL+ELE+DNW	5	-498,78	1014,2	9,62	0,00
VCL+BA+CH	5	-499,00	1014,7	10,05	0,00
VCL+ELE+BA	5	-499,22	1015,1	10,50	0,00
VCL+DNW+BA+CH	6	-498,28	1019,1	14,45	0,00
ELE+DNW+BA+CH	6	-498,31	1019,1	14,50	0,00
VCL+ELE+DNW+CH	6	-498,45	1019,4	14,79	0,00
VCL+ELE+DNW+BA	6	-498,64	1019,8	15,16	0,00
VCL+ELE+BA+CH	6	-498,71	1019,9	15,30	0,00
VCL+ELE+DNW+BA+CH	7	-498,28	1026,6	21,94	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AICc, w_i – model weight (Akaike).

Supplementary Material Table S8. Models relating the predictor variables with the CWM of the mean body mass of Phyllostomid bats in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	wi
BA	3	-452,05	912,3	0,00	0,24
VCL+BA	4	-450,62	913,2	0,95	0,15
NULL	2	-454,31	913,6	1,35	0,12
VCL	3	-453,08	914,3	2,06	0,09
BA+CH	4	-451,30	914,6	2,31	0,08
ELE+BA	4	-451,73	915,5	3,18	0,05
DNW+BA	4	-451,91	915,8	3,54	0,04
CH	3	-454,12	916,4	4,12	0,03
DNW	3	-454,18	916,5	4,25	0,03
VCL+DNW	4	-452,27	916,5	4,25	0,03
ELE	3	-454,31	916,8	4,53	0,03
VCL+BA+CH	5	-450,14	917,0	4,67	0,02
VCL+ELE+BA	5	-450,57	917,8	5,53	0,02
VCL+DNW+BA	5	-450,59	917,9	5,57	0,02
VCL+ELE	4	-452,98	918,0	5,67	0,01
VCL+CH	4	-453,01	918,0	5,73	0,01

ELE+BA+CH	5	-451,15	919,0	6,67	0,01
DNW+BA+CH	5	-451,29	919,2	6,95	0,01
DNW+CH	4	-453,76	919,5	7,23	0,01
ELE+DNW	4	-453,92	919,8	7,55	0,01
ELE+DNW+BA	5	-451,73	920,1	7,84	0,01
ELE+CH	4	-454,10	920,2	7,91	0,01
VCL+DNW+CH	5	-451,89	920,4	8,14	0,00
VCL+ELE+DNW	5	-451,97	920,6	8,33	0,00
VCL+ELE+CH	5	-452,85	922,4	10,09	0,00
VCL+DNW+BA+CH	6	-450,01	922,5	10,24	0,00
VCL+ELE+BA+CH	6	-450,14	922,8	10,49	0,00
VCL+ELE+DNW+BA	6	-450,37	923,2	10,96	0,00
ELE+DNW+CH	5	-453,47	923,6	11,32	0,00
ELE+DNW+BA+CH	6	-451,08	924,7	12,37	0,00
VCL+ELE+DNW+CH	6	-451,56	925,6	13,33	0,00
VCL+ELE+DNW+BA+CH	7	-449,76	929,5	17,24	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AICc, w_i – model weight (Akaike).

Supplementary Material Table S9. Models relating predictor variables with CWM of phytophagous Phyllostomid bats in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	wi
NULL	2	13,42	-21,8	0,00	0,34
DNW	3	14,06	-19,9	1,90	0,13
CH	3	13,53	-18,9	2,95	0,08
VCL	3	13,44	-18,7	3,14	0,07
BA	3	13,44	-18,7	3,14	0,07
ELE	3	13,42	-18,7	3,18	0,07
ELE+DNW	4	15,10	-18,2	3,64	0,05
DNW+CH	4	14,69	-17,4	4,47	0,04
VCL+DNW	4	14,34	-16,7	5,15	0,03
DNW+BA	4	14,16	-16,3	5,52	0,02
ELE+DNW+CH	5	16,03	-15,4	6,44	0,01
BA+CH	4	13,58	-15,2	6,69	0,01
ELE+CH	4	13,54	-15,1	6,75	0,01
VCL+CH	4	13,54	-15,1	6,76	0,01
VCL+BA	4	13,46	-14,9	6,93	0,01
VCL+ELE	4	13,44	-14,9	6,96	0,01

ELE+BA	4	13,44	-14,9	6,96	0,01
VCL+ELE+DNW	5	15,48	-14,3	7,54	0,01
ELE+DNW+BA	5	15,38	-14,1	7,74	0,01
VCL+DNW+CH	5	14,97	-13,3	8,56	0,01
DNW+BA+CH	5	14,82	-13,0	8,87	0,00
VCL+DNW+BA	5	14,64	-12,6	9,21	0,00
VCL+BA+CH	5	13,58	-10,5	11,35	0,00
ELE+BA+CH	5	13,58	-10,5	11,35	0,00
VCL+ELE+CH	5	13,55	-10,4	11,39	0,00
VCL+ELE+DNW+CH	6	16,44	-10,4	11,47	0,00
ELE+DNW+BA+CH	6	16,42	-10,3	11,50	0,00
VCL+ELE+BA	5	13,46	-10,2	11,59	0,00
VCL+ELE+DNW+BA	6	16,19	-9,9	11,96	0,00
VCL+DNW+BA+CH	6	15,33	-8,2	13,67	0,00
VCL+ELE+DNW+BA+CH	7	17,35	-4,7	17,14	0,00
VCL+ELE+BA+CH	6	13,58	-4,7	17,17	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AICc, w_i – model weight (Akaike).

Supplementary Material Table S10. Models relating predictor variables with CWM of animal-eating Phyllostomid bats in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	wi
NULL	2	14,28	-23,6	0,00	0,32
CH	3	15,05	-21,9	1,63	0,14
VCL	3	14,64	-21,1	2,46	0,09
BA	3	14,42	-20,7	2,89	0,07
DNW	3	14,40	-20,6	2,94	0,07
ELE	3	14,29	-20,4	3,15	0,07
DNW+CH	4	15,64	-19,3	4,27	0,04
BA+CH	4	15,40	-18,8	4,76	0,03
VCL+CH	4	15,26	-18,5	5,03	0,03
ELE+CH	4	15,07	-18,1	5,42	0,02
VCL+DNW	4	15,02	-18,0	5,51	0,02
ELE+DNW	4	14,81	-17,6	5,94	0,02
VCL+BA	4	14,76	-17,5	6,03	0,02
VCL+ELE	4	14,64	-17,3	6,27	0,01
ELE+BA	4	14,49	-17,0	6,58	0,01
DNW+BA	4	14,46	-16,9	6,64	0,01

VCL+DNW+CH	5	16,24	-15,8	7,74	0,01
ELE+DNW+CH	5	16,16	-15,6	7,90	0,01
DNW+BA+CH	5	15,73	-14,8	8,77	0,00
VCL+BA+CH	5	15,56	-14,5	9,10	0,00
VCL+ELE+DNW	5	15,44	-14,2	9,33	0,00
ELE+BA+CH	5	15,40	-14,1	9,43	0,00
VCL+ELE+CH	5	15,32	-14,0	9,58	0,00
VCL+DNW+BA	5	15,03	-13,4	10,17	0,00
ELE+DNW+BA	5	14,84	-13,0	10,53	0,00
VCL+ELE+BA	5	14,77	-12,9	10,69	0,00
VCL+ELE+DNW+CH	6	16,77	-11,0	12,52	0,00
VCL+DNW+BA+CH	6	16,25	-10,0	13,56	0,00
ELE+DNW+BA+CH	6	16,21	-9,9	13,63	0,00
VCL+ELE+BA+CH	6	15,57	-8,6	14,92	0,00
VCL+ELE+DNW+BA	6	15,45	-8,4	15,16	0,00
VCL+ELE+DNW+BA+CH	7	16,77	-3,5	20,02	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AICc, w_i – model weight (Akaike).

Supplementary Material Table S11. Models relating the predictor variables with the CWM of the relative aspect of the wing of Phyllostomid bats in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	wi
NULL	2	3,31	-1,6	0,00	0,37
CH	3	3,75	0,7	2,31	0,12
BA	3	3,49	1,2	2,83	0,09
VCL	3	3,46	1,3	2,89	0,09
DNW	3	3,36	1,5	3,09	0,08
ELE	3	3,34	1,6	3,17	0,08
BA+CH	4	3,84	4,3	5,93	0,02
ELE+CH	4	3,83	4,3	5,96	0,02
VCL+CH	4	3,82	4,4	5,98	0,02
DNW+CH	4	3,75	4,5	6,12	0,02
VCL+BA	4	3,66	4,7	6,30	0,02
ELE+BA	4	3,53	4,9	6,55	0,01
ELE+DNW	4	3,51	5,0	6,59	0,01
VCL+ELE	4	3,50	5,0	6,62	0,01
DNW+BA	4	3,49	5,0	6,65	0,01

VCL+DNW	4	3,46	5,1	6,69	0,01
ELE+BA+CH	5	3,99	8,7	10,31	0,00
VCL+ELE+CH	5	3,95	8,8	10,38	0,00
VCL+BA+CH	5	3,93	8,8	10,42	0,00
ELE+DNW+CH	5	3,91	8,9	10,47	0,00
DNW+BA+CH	5	3,87	8,9	10,54	0,00
VCL+DNW+CH	5	3,83	9,0	10,62	0,00
VCL+ELE+BA	5	3,82	9,1	10,67	0,00
VCL+DNW+BA	5	3,69	9,3	10,90	0,00
VCL+ELE+DNW	5	3,63	9,4	11,02	0,00
ELE+DNW+BA	5	3,62	9,4	11,05	0,00
VCL+ELE+BA+CH	6	4,18	14,1	15,76	0,00
VCL+DNW+BA+CH	6	4,04	14,4	16,03	0,00
ELE+DNW+BA+CH	6	4,01	14,5	16,10	0,00
VCL+ELE+DNW+CH	6	3,99	14,5	16,12	0,00
VCL+ELE+DNW+BA	6	3,83	14,8	16,46	0,00
VCL+ELE+DNW+BA+CH	7	4,18	21,6	23,25	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AICc, w_i – model weight (Akaike).

Supplementary Material Table S12. Models relating the predictor variables with the CWM of the relative load of Phyllostomid bat wings in a terra firme forest gradient in Northeastern Brazilian Amazon. The models were listed according to the corrected Akaike information criterion (AICc), selecting those that presented values of $\Delta\text{AICc} < 2$ (in bold). The predictors that enter the models are distance to the nearest watercourse – DNW; elevation – ELE; canopy height – CH; basal area – BA; vegetation clutter – VCL.

Models	df	logLik	AICc	ΔAICc	wi
NULL	2	7,40	-9,8	0,00	0,34
VCL	3	7,84	-7,5	2,30	0,11
DNW	3	7,78	-7,4	2,41	0,10
BA	3	7,63	-7,1	2,71	0,09
CH	3	7,45	-6,7	3,08	0,07
ELE	3	7,40	-6,6	3,18	0,07
VCL+DNW	4	8,77	-5,5	4,25	0,04
ELE+DNW	4	8,33	-4,7	5,14	0,03
VCL+BA	4	8,05	-4,1	5,70	0,02
DNW+CH	4	8,03	-4,1	5,74	0,02
VCL+ ELE	4	7,89	-3,8	6,01	0,02
VCL+CH	4	7,85	-3,7	6,10	0,02
DNW+BA	4	7,83	-3,7	6,13	0,02
BA+CH	4	7,74	-3,5	6,32	0,01
ELE+BA	4	7,65	-3,3	6,50	0,01
ELE+CH	4	7,45	-2,9	6,89	0,01

VCL+ELE+DNW	5	9,35	-2,0	7,76	0,01
VCL+DNW+CH	5	8,98	-1,3	8,51	0,01
VCL+DNW+BA	5	8,77	-0,9	8,92	0,00
ELE+DNW+CH	5	8,61	-0,5	9,25	0,00
ELE+DNW+BA	5	8,35	0,0	9,76	0,00
DNW+BA+CH	5	8,09	0,5	10,28	0,00
VCL+BA+CH	5	8,09	0,5	10,29	0,00
VCL+ELE+BA	5	8,06	0,6	10,35	0,00
VCL+ELE+CH	5	7,92	0,8	10,62	0,00
ELE+BA+CH	5	7,74	1,2	10,98	0,00
VCL+ELE+DNW+CH	6	9,59	3,3	13,11	0,00
VCL+ELE+DNW+BA	6	9,37	3,8	13,56	0,00
VCL+DNW+BA+CH	6	8,98	4,5	14,34	0,00
ELE+DNW+BA+CH	6	8,64	5,2	15,02	0,00
VCL+ELE+BA+CH	6	8,10	6,3	16,09	0,00
VCL+ELE+DNW+BA+CH	7	9,60	10,8	20,59	0,00

Note: df – number of model parameters, logLik – log-likelihood, AICc – Akaike information criterion corrected for small samples, Δ AICc – difference between the AICc values of the model in question and the model with the lowest AIC, w_i – model weight (Akaike).

11. CONCLUSÕES

Nossa abordagem multidimensional mostrou-se uma ferramenta eficiente para compreender como os fatores ambientais influenciam as dimensões da diversidade alfa de morcegos em ecossistemas amazônicos.

Distância para o curso d'água mais próximo e elevação do terreno são preditores importantes para estruturação das assembleias de morcegos, que é composta por grupos taxonômicos e funcionais mais diversos em áreas mais elevadas e mais distantes dos corpos d'água.

A estrutura da vegetação exerce influência sobre a massa média dos morcegos, sendo que morcegos maiores têm maior peso nas assembleias que estão em locais com árvores com maior área basal.

Finalmente, nossa abordagem multidimensional nos permitiu discutir importantes implicações para a conservação dos morcegos e das florestas de terra firme da FLONA do Amapá. Especificamente, mudanças devem ser feitas na legislação ambiental relacionada às Áreas de Proteção Permanente (APP). Segundo nossos dados, a área mínima atual de APP parece não proteger onde há maior riqueza e diversidade de morcegos. Além disso, mudanças devem ocorrer nos planos de manejo para exploração de madeira em Florestas Nacionais, com uma revisão na quantidade da extração de árvores com maior área basal, afim de garantir a conservação da fauna de morcegos Amazônicos.

12. ANEXOS

Comprovante de submissão do artigo “**Bat diversity is driven by elevation and distance to the watercourse in *terra firme* forest in Northeastern Brazilian Amazon**” para o periodico Journal of Tropical Ecology.

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Journal Of Tropical Ecology

Manuscript ID
JTE-21-068

Title
Bat diversity is driven by elevation and distance to the watercourse in terra firme forest in Northeastern Brazilian Amazon

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Date Submitted
21-Jul-2021

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