The influence of landscape composition and configuration on bat-fly interaction networks

A influência da composição e configuração da paisagem nas redes de interação morcego-mosca

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Prof. Dr. Marco Aurelio Ribeiro de Mello
Orientador

To Oli, the future.

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SUMMARY

RESUMO

As mudanças provocadas pelo homem na composição e configuração da paisagem têm um impacto significativo na biodiversidade e nas interações entre as espécies, com implicações de longo alcance para a saúde e o funcionamento dos ecossistemas. Reconhecendo isto, os Objetivos de Desenvolvimento Sustentável (ODS) das Nações Unidas, particularmente o ODS 3 "Boa Saúde e Bem-Estar", enfatizam a interligação da saúde humana, animal e dos ecossistemas, e são alimentados por iniciativas como a One Health. Abordando esta preocupação global, a minha tese investiga como as mudanças na paisagem influenciam as comunidades ecológicas, focando nos morcegos e nos seus ectoparasitas como sistema modelo. Essas interações são de suma importância para a saúde pública, considerando os microrganismos transportados por ectoparasitas de morcegos, alguns dos quais podem se tornar patogênicos. No primeiro capítulo, publicado como um artigo de dados, conduzimos uma revisão sistemática de 174 estudos abrangendo desde o ano 1904 ao 2022, compilando um conjunto de dados de 3.984 interações entre morcegos e moscas em 650 locais Neotropicais. Este conjunto de dados, denominado BatFly, juntamente com metadados ricos, foi organizado de acordo com a filosofia tidy data para facilitar pesquisas futuras, incluindo informações sobre populações de morcegos e moscas, habitats e referências. No segundo capítulo, utilizando BatFly, exploramos os mecanismos subjacentes ao impacto das mudanças na paisagem nas interações morcego-mosca. Com base na Hipótese Integrativa de Especialização (IHS), levantamos a hipótese de que as características da paisagem influenciam indiretamente a estrutura da rede através da heterogeneidade dos recursos, considerando os morcegos como os recursos utilizados pelas moscas (consumidores). Nossa análise, empregando modelagem de equações estruturais, revelou que a cobertura florestal e o formato das manchas afetam indiretamente a estrutura da rede de morcegos por meio da diversidade de recursos. Especificamente, o formato da mancha influenciou positivamente a heterogeneidade dos recursos, enquanto a cobertura florestal teve um impacto negativo. Nosso estudo contribui com uma ferramenta valiosa para investigar questões ecológicas em várias escalas espaciais e níveis organizacionais. Além disso, sublinha a capacidade preditiva do IHS na compreensão dos efeitos da paisagem na organização comunitária, oferecendo conhecimentos cruciais para a conservação das espécies de morcegos, das suas interações e dos seus serviços ecossistêmicos.

Palavras-chave

Antagonismo, Chiroptera, especialização, interações interespecíficas, moscas de morcegos, morcegos neotropicais, Nycteribiidae, paisagem, redes parasita-hospedeiro, Streblidae.

ABSTRACT

Human-driven changes in landscape composition and configuration significantly impact biodiversity and species interactions, with far-reaching implications for ecosystem health and functioning. Recognizing this, the United Nations' Sustainable Development Goals (SDGs), particularly SDG 3 "Good Health and Wellbeing," emphasize the interconnectedness of human, animal, and ecosystem health, and is powered by initiatives like One Health. Addressing this global concern, my thesis investigates how landscape changes influence ecological communities, focusing on bats and their ectoparasites as a model system. Those interactions are of paramount important for public health, considering the microorganisms carried by bat ectoparasites, some of which might become pathogenic. In the first chapter, published as a data paper, we conducted a systematic review of 174 studies spanning from 1904 to 2022, compiling a data set of 3,984 bat-fly interactions across 650 Neotropical sites. This dataset, named BatFly, alongside rich metadata, was organized according to the tidy data philosophy to facilitate further research, including information on bat and fly populations, habitats, and references. In the second chapter, using BatFly, we explored the mechanisms underlying the impact of landscape changes on bat-fly interactions. Drawing on the Integrative Hypothesis of Specialization (IHS), we hypothesized that landscape features indirectly influence network structure through resource heterogeneity, considering bats as the resources used by flies (consumers). Our analysis, employing structural equation modeling, revealed that forest cover and patch shape indirectly affect bat-fly network structure via resource diversity. Specifically, patch shape positively influenced resource heterogeneity, while forest cover had a negative impact. Our study contributes a valuable tool for investigating ecological questions across various spatial scales and organizational levels. Moreover, it underscores the predictive capacity of the IHS in understanding landscape effects on community organization, offering insights crucial for the conservation of bat species, their interactions, and their ecosystem services.

Keywords

Antagonism, bat flies, Chiroptera, host-parasite network, landscape, Neotropical bats, Nycteribiidae, specialization, species interactions, Streblidae.

RESUMEN

Los cambios provocados por el hombre en la composición y configuración del paisaje impactan significativamente la biodiversidad y las interacciones entre especies, con implicaciones de gran alcance para la salud y el funcionamiento de los ecosistemas. Al reconocer esto, los Objetivos de Desarrollo Sostenible (ODS) de las Naciones Unidas, en particular el ODS 3 "Buena salud y bienestar", enfatizan la interconexión de la salud humana, animal y de los ecosistemas, y están impulsados por iniciativas como One Health. Abordando esta preocupación global, mi tesis investiga cómo los cambios del paisaje influyen en las comunidades ecológicas, centrándose en los murciélagos y sus ectoparásitos como sistema modelo. Esas interacciones son de suma importancia para la salud pública, considerando los microorganismos transportados por los ectoparásitos de los murciélagos, algunos de los cuales podrían volverse patógenos. En el primer capítulo, publicado como un artículo de datos, realizamos una revisión sistemática de 174 estudios que abarcan desde 1904 hasta 2022, compilando un conjunto de datos de 3984 interacciones entre murciélagos y moscas en 650 sitios neotropicales. Este conjunto de datos, denominado BatFly, junto con metadatos enriquecidos, se organizó de acuerdo con la filosofía de datos ordenados (tidy data) para facilitar futuras investigaciones, incluida información sobre poblaciones, hábitats y referencias de murciélagos y moscas. En el segundo capítulo, utilizando BatFly, exploramos los mecanismos subyacentes al impacto de los cambios del paisaje en las interacciones entre murciélagos y moscas. Basándonos en la Hipótesis Integrativa de Especialización (IHS), planteamos la hipótesis de que las características del paisaje influyen indirectamente en la estructura de la red a través de la heterogeneidad de los recursos, considerando a los murciélagos como los recursos utilizados por las moscas (consumidores). Nuestro análisis, que emplea modelos de ecuaciones estructurales, reveló que la cubierta forestal y la forma de los parches afectan indirectamente la estructura de la red de moscas murciélago a través de la diversidad de recursos. Específicamente, la forma de los parches influyó positivamente en la heterogeneidad de los recursos, mientras que la cubierta forestal tuvo un impacto negativo. Nuestro estudio aporta una herramienta valiosa para investigar cuestiones ecológicas en varias escalas espaciales y niveles organizacionales. Además, subraya la capacidad predictiva del IHS para comprender los efectos del paisaje en la organización de las comunidades, ofreciendo conocimientos cruciales para la conservación de las especies de murciélagos, sus interacciones y sus servicios ecosistémicos.

Palabras claves

Antagonismo, especialización, huésped-parásito, moscas de los murciélagos, murciélagos neotropicales, Nycteribiidae, paisaje, quirópteros, redes de interacción, Streblidae.

GENERAL INTRODUCTION

The human population is constantly growing, leading to an increase in its demands for space and food. Consequently, the frontiers of human activities are quickly expanding, transforming natural landscapes into mosaics of human-modified landscapes. These human-driven changes in landscape composition (i.e., the proportion of natural and human-made habitats), and configuration (i.e., the spatial arrangement of habitat remnants) ultimately affect ecosystem functioning (Gottdenker et al., 2014). For example, the decrease in the amount of natural habitat in the composition of a landscape is one of the main drivers of biological diversity loss (Estavillo et al., 2013), and has also been associated with emerging diseases related to changes in host-parasite relationships (Gottdenker et al., 2014). Therefore, the fast human population growth poses a significant threat not only to diversity but also to human survival (Faust et al., 2018; Newbold et al., 2015).

Consequently, the intricate relationship between a fast human population growth, human-driven changes in landscape composition and configuration (hereafter, simply "landscape changes"), and their impact on ecosystem functioning have become a global concern addressed in the United Nations' 17 Sustainable Development Goals (SDGs), which aim to pursue the harmonization of economic growth, social inclusion, and environmental protection (UN, 2015). SDG 3, "Good Health and Wellbeing," powered by initiatives like One Health, recognizes that human, animal, and ecosystem health are interdependent. It focuses on understanding and mitigating the impacts of human activities on the environment and their consequences on animal (both domestic and wild) and human health. To contribute to achieving SDG 3, it is essential to understand how species and their interactions are affected by landscape changes, in addition to potential impacts on our wellbeing.

Aiming to help in the global effort of achieving SDG 3, this thesis focuses on host-parasite interactions and how they might be affected by landscape changes, using as a model bats and their ectoparasites commonly known as bat flies.

Bat-fly interactions as a study model

Bats are the only mammals capable of flying, an adaptation that has influenced their diversification, life history, and interspecific interactions, allowing them to occur in a wide variety of ecosystems from almost every continent (Fleming et al., 2020; Peixoto et al., 2018). They feed on wide variety of resources, including vertebrates, insects, fruits, pollen, and blood. Therefore, they play important ecological roles and provide us vital ecosystem services, such as crop pollination, habitat regeneration, and pest suppression (Kunz et al., 2011; Ramírez-Fráncel et al., 2022). Additionally, bats are sensitive to environmental changes, especially those related to fragmentation, urbanization, and pollution (Russo et al., 2021).

Some bat species can survive in human-changed landscapes, showing varied responses associated with their feeding guild (Muylaert et al., 2016), aerial space use (Jung & Kalko, 2011), and foraging strategy (Bolívar-Cimé et al., 2013). For instance, some frugivorous bats tend to be favored by human interventions, such as edges or clearings, due to a higher fruit availability in those spaces. Conversely, carnivorous bats tend to be the most vulnerable to human changes because forest loss decreases food, shelter, and safe flying space availability for them (Mendes & Srbek-Araujo, 2021). Also, landscape changes can alter bat-parasite interactions (Bolívar-Cimé et al., 2018).

In the realm of parasitic interactions, it should be noted that bats establish a myriad of associations with microorganisms, including some that might be pathogenic to bats, other animals, and humans (Allocati et al., 2016). Therefore, bats are recognized as natural reservoirs of many viruses, bacteria, and fungi, playing a crucial role in the dynamics of emerging infectious diseases (Szentivanyi et al., 2023). One of the most conspicuous bat parasites are bat flies, which belong to the families Streblidae and Nycteribiidae.

Bat flies (henceforth, just "flies") are blood feeding ectoparasites that live in the fur and membranes of their hosts (Rothschild & Theodor, 1967). They are found exclusively on bats, which represent their whole world, providing them with both habitat and food, and sharing a tight evolutionary history with them (Dick & Dittmar, 2014). Consequently, both fly families exhibit intricate morphological and ecological adaptations for living on their bat hosts (Dick & Dittmar, 2014). For instance, those flies present a reduction or total absence of eyes and modifications in their legs to remain attached to their host. Particularly, nycteribiid flies lack wings, and their leg position gives them a spider-like appearance (Rothschild & Theodor, 1967). Although in streblid flies there are different degrees of wing development, their ability to fly is reduced to an upward spiraling clumsy pattern or forward-directed short glides, even in species with fully developed wings. Nevertheless, their walking agility on their host is outstanding (Dittmar et al., 2015).

Due those adaptations, flies spend almost their entire lives on their bat hosts. In fact, only females leave their host to deposit their offspring, as pre-pupae, on a substrate near bat roosts. When a fly emerges from its pupa, it must quickly find and colonize a new host to survive (Dittmar et al., 2009). Without access to food, adult the flies perish within hours (Dittmar et al., 2015). Due to their life history as blood-feeding parasites, flies carry a high diversity of microorganisms. For example, they transmit bacteria from the *Bartonella* group, which are considered pathogenic to humans, to other flies and bats (Morse et al., 2012; Reeves & Lloyd, 2019).

Bats and flies share a special interaction. Its degree of specialization is particularly intriguing, as it determines how many host species can be used by each bat fly species (Dick & Patterson, 2007). Most fly species parasitize a single bat species (Dick, 2007) while some are known to parasitize a few congeneric species (Colín-Martínez et al., 2018). Some fly species can even parasitize several bat species and establish transient interactions, being found on hosts different from their usual ones (Dick & Gettinger, 2005). With the increasing availability of information about this interaction (Urbieta et al., 2022), it has become important to understand how changes in landscape composition and configuration affect bat-fly interactions (R. M. Mello et al., 2021).

Landscape and its effect on bat-fly interactions

It is currently known that human-driven processes that lead to landscape changes (e.g., habitat fragmentation and urbanization) influence bat-fly interactions (Heckley & Becker, 2023). Such human-driven processes are known to affect the species richness of both bats and flies, as well as their interactions, influencing the proportion of infested bats in a population (prevalence), as well as the average number of flies found on each bat (mean intensity), with idiosyncratic responses shown by different species (Bolívar-Cimé et al., 2018; Palheta et al., 2020).

So far, most information comes from studies with a patch-level approach, where the biological response (e.g., bat richness) is related to unique attributes of the sampled habitat patch (Regolin et al., 2021). A few studies with a landscape approach found that landscape composition and configuration could affect interaction specialization, but their conclusions are contradictory. For instance, a study found less specialized interactions between bats and flies in landscapes with a high degree of human-driven changes (Hernández-Martínez et al., 2019), while another found the opposite (R. M. Mello et al., 2021). Also, there are studies that found no differences in bat-fly interactions between landscapes with varying degrees of human-driven changes (Tlapaya-Romero et al., 2023; Urbieta et al., 2019). Those contradictory conclusions highlight the importance of understanding how the structure and dynamics of bat-fly interactions respond to landscape changes across different spatial scales and environmental gradients (R. M. Mello et al., 2021; Regolin et al., 2021).

The difficulty to establish a clear mechanism to predict these effects suggests the existence of an additional factor that modulates the influence of landscape composition and configuration on bat-fly interactions. That is what we aimed to uncover here. However, before we could delve into those relationships, it was necessary to synthesize the current knowledge on bat-fly interactions. Thus, we decided to begin by making a data paper.

Data papers as tools to address SDG 3

As a society, the challenges that we must overcome are not limited to biodiversity loss. There is also a loss of credibility in science as a solution to the problems that we currently face. This credibility crisis, particularly concerning topics related to climate change, land use change, and their effect on human wellbeing, is getting worse (Krause et al., 2019). This is a multifactorial issue, which could be mitigated by the Open Science framework based on reproducibility, transparency, exchange, and collaboration in science making, focusing on the availability and reuse of information, data, and tools (UNESCO, 2021).

Within the Open Science framework, data papers emerged as an outstanding incentive for collaboration and transparency between the multiple actors involved in science making. A data paper is defined as a scholarly publication of a searchable metadata document describing an online data set or database, published following standard academic practices (such as peer review), whose primary purpose is making available data in a structured human- and computer-readable format. Data papers are made following protocols that ensure clarity and transparency when reporting the data's source. For example, for data extracted from the literature, the Preferred Reporting Items for Systematic Review and Meta-Analyses (PRISMA) guidelines are the gold standard, which provide an efficient framework for reporting the criteria used to include or exclude data sources in the data paper (Page et al., 2021). There is also a nice extension to those guidelines focused on Ecology and Evolutionary Biology, known as PRISMA-EcoEvo (O'Dea et al., 2021). Overall, data papers synthesize a large amount of curated data along with rich metadata, which avoids duplication of efforts in data collection, promotes data reuse and reproducibility, and optimizes the efficient use of data (Chavan & Penev, 2011).

General objective and structure of this thesis

In this thesis, we aimed at understanding the mechanisms that shape host-parasite interactions in different landscapes, so we can predict how those interactions may respond to landscape changes. To do so, we used bats and their parasitic flies as a study model and structured this thesis in two chapters.

In the first chapter, we have written and published a data paper with information on bat-fly interactions extracted from 177 studies with various scopes, including taxonomic reviews, checklists, and assessments of species interactions. The database, named BatFly, includes information from 650 sites distributed from the northern frontier of the Neotropics (including Mexico, southern USA, and the Caribbean) to southern South America. By making those data available in an online repository, the scientific community can access and use it to address multiple research questions.

In the second chapter, by using information from BatFly, we have focused on understanding how bat-fly interactions are affected by landscape changes, using a network approach (M. A. R. Mello & Muylaert, 2020). Our main goal was to understand the factors that could influence this relationship, and also to reconcile conflicting results from previous studies and predict crucial outcomes.

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CONCLUDING REMARKS

In this thesis, we aimed at understanding the mechanisms that shape host-parasite interactions in the light of global changes. Specifically, how landscape composition and configuration shape the structure of host-parasite networks. To do so, we used a remarkable study model: the antagonistic relationship between bats and their ectoparasite streblid and nycteribiid flies. However, before we could delve into understanding this effect, we had the need to first synthesize knowledge of such interactions.

Synthesizing and finding gaps

In the first chapter we aimed at synthesizing and making accessible all records of bat–fly interaction found in the literature, along with three completely new datasets. As a result, we created BatFly (Zapata-Mesa et al., 2024), the largest existing database of interactions between Neotropical bats and their ectoparasite flies, with records of over 3,000 interactions from Southern USA to northern Argentina.

Bat-fly interactions are frequently studied at local scales, where they are reported to be highly host-specific, with most fly species parasitizing a single bat species (Colín-Martínez et al., 2018). However, the Neotropical-scale network, which we were able to build by using BatFly, was highly interconnected. This is an indication that fly species might have a larger fundamental niche than previously thought. In other words, they might have the potential to parasitize a larger number of bat species than recorded so far. Consequently, there might be key ecological factors to be investigated, which strongly limit bat-fly interactions at smaller scales.

With a series of studies published from 1904 to 2022, BatFly has allowed us to see that there has been an evident growth in the interest for studying this parasitic system since the beginning of the current millennium. In addition to temporal trends, BatFly also shows gaps in the spatial distribution of the localities where these interactions have been studied and recorded. For example, the largest and clearest gap we were able to detect is located in the Amazon and Cerrado, since most records from Brazil come from the southeastern region, associated with remnants of the Atlantic Forest. Given the current threats that both the Amazon and Cerrado are currently facing (Albert et al., 2023; Rodrigues et al., 2022), the need for directed sampling on these regions becomes imperative.

Given the size and quality of the data available in BatFly, it is possible to use it to address research questions at different levels of ecological organization and spatial scales. Thus, BatFly might also foster collaborations and partnerships. By using BatFly and sharing your findings with stakeholders, conservation organizations, government agencies, and communities together we can work more effectively to address environmental challenges, protect biodiversity, understand disease transmission dynamics, assess health risks, and, therefore, achieve some of UN's Sustainable Development Goals.

Using our database

In the second chapter, by using the database built in the first chapter, we aimed at understanding the mechanisms by which landscape composition and configuration affect the structure of interactions between bats and flies. To do so, we harnessed the Integrative Hypothesis of Specialization as a framework, and learned that resource heterogeneity, measured as bat functional and phylogenetic diversity, mediates the indirect effects of landscape composition and configuration on the topology of bat-fly networks.

Although in other studies the mechanism by which the landscape affected this interaction was yet to be revealed, the importance of bats for the persistence of this interaction had been pointed out before. In a previous study that evaluated the effects of human-driven landscape composition and configuration on the topology of bat-fly networks, it was suggested that the diversity of flies mirrored the diversity of hosts (Ramalho et al., 2021), an idea that is supported by our findings.

Finally, this thesis served as an empirical test of the Integrative Hypothesis of Specialization (IHS) (Pinheiro et al., 2019), as a comprehensive model to explain the drivers of host-parasite interactions at human-driven landscape composition and configuration, providing insight that could help to predict zoonotic outbreaks and address UN's SDG 3, "Good Health and Wellbeing" (UN, 2015).

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