

# Phyllostomid bats as key pollinators: a review on chiropterophily and conservation challenges

Morcegos filostomídeos como polinizadores-chave: uma revisão sobre quiropterofilia e desafios de conservação

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## ABSTRACT

This review explores the relation between pollination and chiropterophily, emphasizing phyllostomid bats as key pollinators, particularly in tropical and subtropical ecosystems. These bats play an essential role in chiropterophilous pollination syndromes, where plants have evolved specific morphological traits to attract nocturnal bats. Bibliometric data show us that during the period analyzed (2004–2024), 174 scientific articles were published, and Brazil emerged as the primary contributor to scientific production on chiropterophily. Although chiropterophily syndrome provides numerous ecological and economic benefits, its study presents significant challenges due to a variety of ecological, behavioral, and methodological factors. Several analyzed manuscripts highlight the critical interdependence between bats and plants and underscore the urgent need for conservation strategies to preserve the ecological integrity and sustainability of ecosystems. A number of studies also show how changes in the phenology of plant species can compromise plant-pollinator interactions, and highlight the increasing impacts of habitat fragmentation and urbanization on bats. Our data show that, although scientific production on chiropterophily has grown in recent years, the variations observed over time may reflect changes in research priorities, funding availability, and a lack of specialized researchers in the field.

**Keywords:** bat-plant interactions; bibliometric research; conservation; ecosystem services.

## RESUMO

Esta revisão explora a relação entre polinização e quiropterofilia, enfatizando morcegos filostomídeos como polinizadores-chave, particularmente em ecossistemas tropicais e subtropicais. Esses morcegos desempenham um papel essencial nas síndromes de polinização quiropterófilas, nas quais as plantas desenvolveram características morfológicas específicas para atrair morcegos noturnos. Dados bibliométricos nos mostram que, durante o período analisado (2004–2024), 174 artigos científicos foram publicados, e o Brasil emergiu como o principal contribuinte para a produção científica sobre quiropterofilia. Embora a síndrome quiropterofilia ofereça inúmeros benefícios ecológicos e econômicos, seu estudo apresenta desafios significativos em razão de uma variedade de fatores ecológicos, comportamentais e metodológicos. Vários manuscritos analisados destacam a interdependência crítica entre morcegos e plantas, e ressaltam a necessidade urgente de estratégias de conservação para preservar a integridade ecológica e a sustentabilidade dos ecossistemas. Diversos estudos também demonstram como mudanças na fenologia de espécies vegetais podem comprometer as interações planta-polinizador, e destacam os impactos crescentes da fragmentação de habitats e da urbanização sobre os morcegos. Nossos dados mostram que, embora a produção científica sobre quiropterofilia tenha crescido nos últimos anos, as variações observadas ao longo do tempo podem refletir mudanças nas prioridades de pesquisa, na disponibilidade de financiamento e na falta de pesquisadores especializados na área.

**Palavras-chave:** interações morcego-planta; pesquisa bibliométrica; conservação; serviços ecossistêmicos.

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## Introduction

The Atlantic Forest biome is the second-largest forested region in the Americas, covering Eastern Brazil, the Misiones region of Argentina, and parts of Eastern Paraguay. Given its proximity to the South American dry diagonal, the Atlantic Forest is an isolated forest biome with no direct borders with other forested regions (Ab'Saber, 1977; Galindo-Leal and Câmara, 2005). This biome is important for its extraordinary biodiversity, harboring approximately 20,000 plant species and 1,800 animal species. It is internationally recognized as one of the world's most significant biodiversity hotspots (Myers et al., 2000). However, extensive deforestation due to anthropogenic activities has resulted in fragmented and disrupted habitats, significantly impacting biodiversity. This degradation affects both fauna populations and structural and compositional shifts in plant communities (Jardim and Melo, 2020). Understanding the biodiversity and community structures of the Atlantic Forest and their ecological responses is crucial for conservation efforts, given the rapid and intense environmental changes this biome faces (Ribeiro et al., 2011).

Ecosystems function through the interactions between biotic, abiotic, and structural elements, which contribute to ecosystem services of ecological and economic value (Ferraz et al., 2019). Among the most crucial ecosystem services is pollination, which facilitates the reproduction of plant species and directly supports the diversity and structure of native plant communities. Pollination also plays a vital role in agriculture, with approximately 75% of food crops requiring pollinators for reproduction (Wolowski et al., 2016). It also helps to sustain ecological guilds that depend on floral resources, such as herbivores and seed-eating animals (Potts et al., 2006). Economically, pollination is fundamental for agricultural and biofuel production, significantly influencing seed development, increasing and enhancing the physical characteristics of food (Lamim-Guedes, 2014; Wolowski et al., 2016). Cross-pollination carried out by pollinators not only promotes fruiting and improves the quality of fruits and seeds but also increases the genetic variability of plants, which is crucial for genetic improvement and resistance to pests and diseases (Valois et al., 1996) (Figure 1).

Animal-mediated pollen dispersal accounts for about 90% of angiosperm reproduction. Among vertebrate pollinators, birds, bats, non-flying mammals, and reptiles are responsible for pollinating 3 to 15% of known angiosperm species. In Brazil, around 338 species of vertebrates act as effective or potential pollinators (Buzato et al., 2011; Fischer et al., 2014). Plants develop specific floral characteristics to attract vertebrate pollinators, such as colors, odors, flower shapes, nectar production, and timing of flower opening. These characteristics are described as pollination syndromes, directly aligned with morphological, sensory, and physiological traits of the pollinators (Fischer et al., 2014). Plants adapted for chiropterophily have evolved traits to attract bats as pollinators, including nocturnal anthesis, typically subtle coloration (white, green, or sometimes reddish or brown shades), strong

odors resembling fermentation, and abundant nectar production rich in hexose and pollen (Fleming et al., 2009; Raven et al., 2014). Furthermore, flowers adapted to chiropterophily tend to be large, robust, and located in positions easily accessible to bats, such as branches, tree trunks, or suspended from long stems. These flowers are typically tubular, bell-shaped, or brush-like, radially symmetrical, fleshy, and have a large opening (Fleming et al., 2009). Chiropterophily syndrome is an ecological phenomenon essential for various ecosystems. Given the wide range of plant species that rely on bats for pollination, this syndrome has a direct impact on the diversity and conservation of many plant species.

The order Chiroptera is a highly specialized group of mammals with 1,466 extant species (Mammal Diversity Database, 2023). These mammals play crucial roles in Neotropical ecosystems, constituting the second-largest order of mammals globally. Brazil ranks fourth among South American countries with the largest number of bat species, behind Colombia, Ecuador, and Peru, with 186 species recorded (Díaz et al., 2021; Pacheco et al., 2021; Ramírez-Chaves et al., 2022; Simmons and Cirranello, 2025). From these, 115 are associated with the Atlantic Forest biome (Abreu et al., 2024; Garbino et al., 2024).

In Brazil, species of the family Phyllostomidae, such as the great fruit-eating bat (*Artibeus lituratus*), are vital pollinators of native plants and play a key role in maintaining biodiversity in tropical ecosystems (Florez-Montero et al., 2022). Bats of this family have diverse diets reflecting their morphological and adaptive variability (Reis et al., 2007). The diverse feeding behaviors are linked to a range of morphological and physiological adaptations, enabling them to exploit different food resources and play varied ecological roles. Studies indicate that while nectarivorous bats are highly efficient pollinators, insectivorous and carnivorous bats also contribute to pollination by consuming pollen rich in proteins and lipids, which complement their diets (Fischer et al., 2014). This diversity in feeding habits highlights the critical role of bats as pollinators in multiple ecosystems.

Fruit- and nectar-eating bats of the Phyllostomidae family are vital for pollination, consuming fruits, nectar, and pollen from various plants. Pollen grains adhere to the fur of these bats as they search for food, facilitating pollen transfer between flowers and promoting plant reproduction and genetic diversity (Fleming et al., 2009). Due to their size and specialized fur, bats efficiently transport pollen over long nocturnal flights. Some species can fly up to 50 kilometers in a single night, far exceeding the range of other pollinators like bees, highlighting bats' importance in pollinating numerous plant species (Esbérard, 2003; Reis et al., 2007) (Figure 2).

Despite the ecological and economic relevance of chiropterophily, studies on bat-mediated pollination in the Atlantic Forest remain scarce. This literature review aimed to bridge this gap by exploring the interactions between bats and plants, highlighting their role in biodiversity conservation and ecosystem stability.

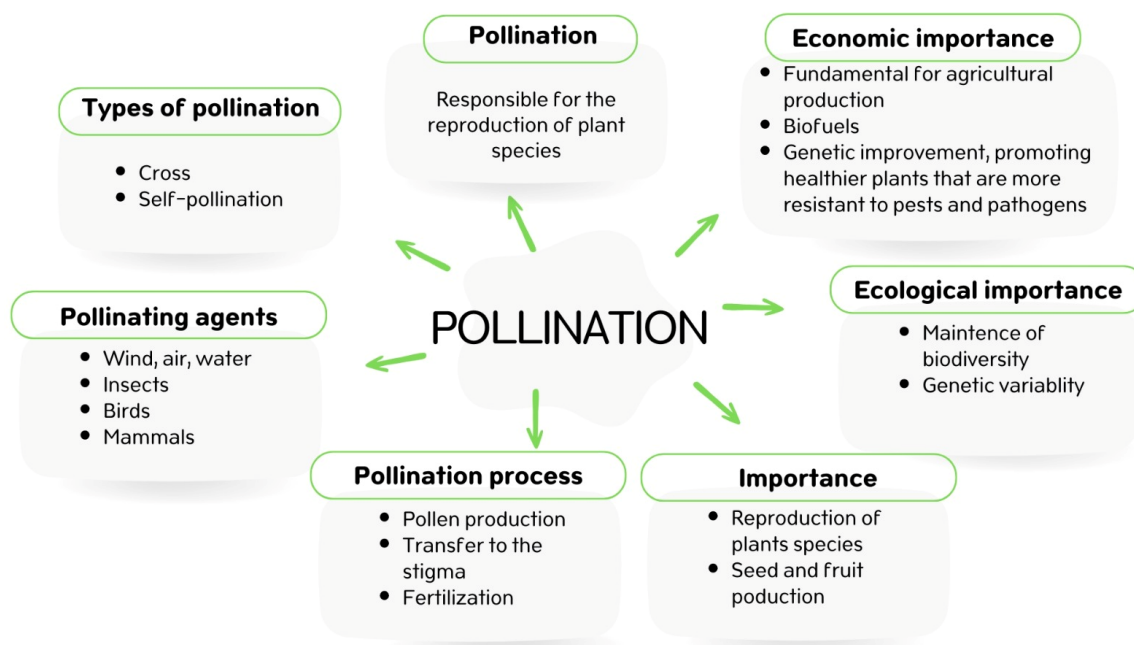


Figure 1 – Types of pollination, pollinating agents, pollination mechanisms, and the ecological and economic importance of pollination.

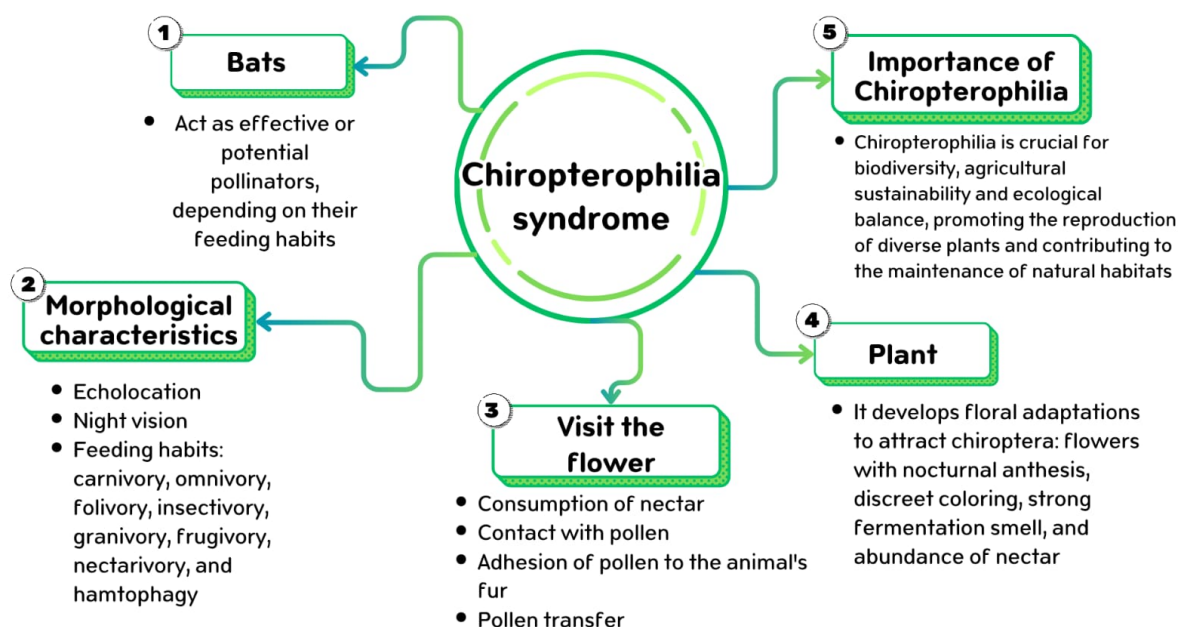


Figure 2 – Chiropterophily syndrome: bats and their morphological characteristics, flower visitation patterns, and plant traits developed to attract bats, emphasizing the ecological and economic significance of chiropterophily.

### Bibliometric data on chiropterophily

A scientometric review was conducted involving a quantitative analysis of scientific productions through indicators such as articles, books, and theses. This method aimed to assess the relevance of research and explore trends across various fields of knowledge. It helps to identify areas of interest, assess gaps or stagnation in specific fields, and determine the geographic concentration of topics. Such information is

crucial for directing financial resources efficiently. By understanding trends and gaps in research topics, resources can be optimized to promote relevant innovations and significant advances in strategic fields (Razera, 2016; Stefanuto et al., 2022).

The bibliometric survey was conducted using the Scopus, Web of Science, and PubMed databases. The terms “Phyllostomidae,” “Bat Pollination,” “Pollination,” “Bats and Pollen,” and “Chiropterophily and Atlantic

Forest” were employed, combined with the Boolean operators “AND” and “OR,” using quotation marks (“”) for compound keywords. The search was limited to scientific publications released in the past 20 years.

Document analysis was performed using the bibliometrix package within the RStudio environment (Aria and Cuccurullo, 2017). Although 2024 was still ongoing at the time of data collection, research from this year was included due to its current relevance. Exploratory research contextualized and identified the main trends in chiropterophily research, covering key themes, data, and developments in the field. This was followed by scientometric analysis, focusing on temporal trends in publication and authorship, as well as country collaborations on the topic. The review presented in the subsequent sections of this article was based on the publications highlighted by bibliometric analysis over the past 20 years.

During the period analyzed (2004–2024), 274 published documents were identified, 174 of which were scientific articles. The “author’s keywords” represent the primary themes investigated by researchers, totaling 170 terms (Table 1). Brazil emerged as the primary contributor to scientific production on chiropterophily, highlighting its prominent role in global research on this topic.

Brazil leads in scientific contributions to chiropterophily, largely due to its immense bat diversity and rich ecosystems that provide ideal research conditions. With approximately 186 recorded chiropteran species, the country represents a significant portion of global bat diversity (Abreu et al., 2024). The diversity of Brazilian biomes, such as the Amazon and Atlantic Forest, is home to numerous endemic and unknown species, encouraging intense scientific study in this area. Furthermore, renowned research institutions in Brazil, such as the National Museum and the Biosciences Institute at the University of São Paulo, have played a crucial role in advancing knowledge of the biology, ecology, and conservation of bats. Nevertheless, the use of the term “Chiropterophily and Atlantic Forest” in the bibliometric research might have biased this high number of publications for the country, since a large part of the forest is in Brazil, which naturally leads to a high number of studies related to chiropterophily within this geographic context.

Regarding published articles in the last 20 years, there is notable variation, with a significant increase observed in 2021, 2022, and 2023, and a lowest production recorded in 2012 and 2024 (to date) (Figure 3). In 2013, scientific output on chiropterophily increased significantly compared to the previous year. Although scientific production on chiropterophily has grown in recent years, the variations observed over time may reflect changes in research priorities, funding availability, and a lack of specialized researchers in the field, among other factors.

In terms of research contributions by country and international collaborations on chiropterophily, Brazil stands out significantly compared to other countries (Figures 4 and 5). Brazil leads chiropterophily research with 43 collaborations, reflecting its diverse ecosystems and ecological niches. The favorable environment for conducting various studies on chiropterophily includes the country’s diverse regions, such as the

Atlantic Forest, Cerrado, and Caatinga, which provide a rich landscape for studying how these bats adapt and behave in different habitats. Additionally, increasing urbanization and environmental changes in urban and peri-urban areas pose new challenges and research questions (Hasan et al., 2020). This wide range of environments and conditions in Brazil is critical for understanding bat biology and ecology, driving important discoveries in the field of chiropterophily. Besides Brazil, Mexico presents 28 collaborations and plays a key role in chiropterophily research.

The United States (USA) has 26 research collaborations on chiropterophily. Institutions such as the University of Florida and the University of Michigan, along with organizations like Bat Conservation International, play critical roles in advancing knowledge about bat pollination and other aspects of bat ecology. Germany, with 16 collaborations, also stands out for its significant investments in biological research. German research often focuses on advanced aspects of bat behavior, ecology, and conservation. The concentration of collaborations in certain countries reflects not only the diversity of chiropteran species but also the availability of research resources and the development of conservation policies. International collaboration is essential for understanding global aspects of bat ecology and conservation, especially considering their role in ecosystems and potential impacts on human health. However, continued investment in research and conservation is necessary to address emerging challenges, such as ecosystem conservation and climate change. A collaborative and integrated approach is crucial for addressing issues related to bat conservation and ecology.

**Table 1 – Main information resulted from the bibliometric analysis using the terms “Phyllostomidae,” “Bat Pollination,” “Pollination,” “Bats and Pollen,” and “Chiropterophily and Atlantic Forest” over the past 20 years from the Scopus, Web of Science, and PubMed databases.**

Description	
Documents	274
Time interval	2004–2024
Articles	174
Authors	896
Author’s keywords	1,011
Authors’ main keywords	
Animals	46
Pollination	37
Chiroptera	36
Chiropterophily	30
Bat pollination	21
Top countries of publications	
Brazil	43
Mexico	28
United States	26
Germany	16
India	11

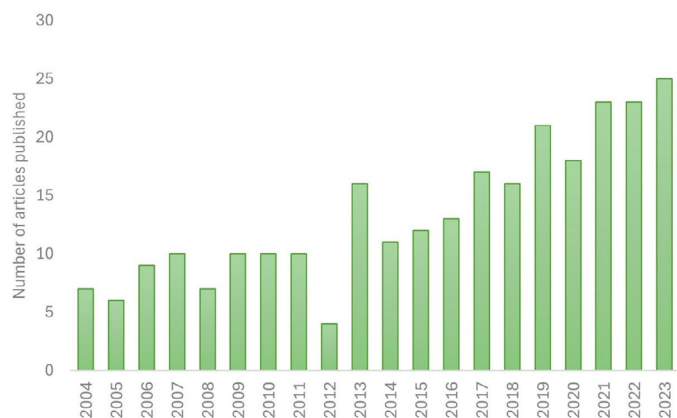


Figure 3 – Annual evolution of the number of publications from 2004 to 2023.



Figure 4 – Countries' contributions to scientific production on chiropterophily. Darker shades indicate more significant contributions, highlighting countries with higher production and relevance. Lighter shades reflect fewer contributions, signaling countries with less research focus on this topic.

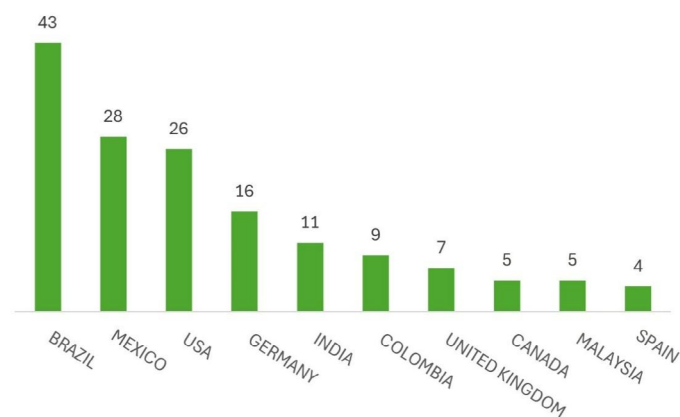


Figure 5 – Number of scientific contributions on chiropterophily by country. The values correspond to data from the selected bibliometric databases.

The ten most cited publications among the reviewed studies provided a comprehensive analysis of the interaction between bats and plants, highlighting the importance of these pollinators in maintaining biodiversity and ecosystem functionality. Kunz et al. (2011) and Willmer (2011) explored the impact of bats on ecosystem services, such as pollination and insect control, with implications for biodiversity and the economy. Fleming (2008, 2009) examined the role of fruit bats in plant

reproduction and the influence of bat pollination on ecosystem function. Muscarella and Fleming (2007) reviewed bat pollination and seed dispersal mechanisms, while Abrol (2011) analyzed the relationship between pollination and agricultural productivity, emphasizing the importance of pollinators for biodiversity conservation. Dick et al. (2007), Quesada et al. (2004) and Tschapka (2004) focused on bat-plant interactions in tropical and neotropical ecosystems. Finally, Rojas et al. (2011) discussed the diversification of feeding habits in the Phyllostomidae family.

Simultaneously, these studies highlighted the critical interdependence between bats and plants and underscored the urgent need for conservation strategies to preserve ecosystems' ecological integrity and sustainability. Bats play fundamental roles in ecosystem dynamics, acting as pollinators and seed dispersers. These functions are crucial for plant regeneration and environmental maintenance, directly influencing ecosystem structure and functionality. The loss of bats could compromise the reproduction and adaptability of chiropterophilous plants to environmental changes, ultimately affecting habitat integrity. These findings highlight the importance of implementing effective conservation measures to sustain ecosystem functionality and diversity.

### The ecological and economic importance of chiropterophily

Chiropterophily syndrome is an ecological phenomenon that plays a vital role in diverse ecosystems. Considering the wide variety of plant species that depend on chiropterans for pollination, chiropterophily syndrome directly impacts the diversity and conservation of flora. Fleming and Valiente-Banuet (2002) and Ghanem and Voigt (2012) emphasized that pollination by bats is essential for the survival of many plant species that sustain diversity in tropical ecosystems, since the ecosystem services provided by bats are crucial for maintaining biodiversity. Additionally, Kunz and Fenton (2003) highlighted that the loss of bat diversity directly affects the decline in plant diversity, making the conservation of pollinating bat species crucial for ensuring ecosystem resilience in the face of climate change.

In terms of ecosystem services, pollination is considered a regulatory service, providing benefits through the regulation of ecosystems and the support of life on Earth (Ferraz et al., 2019). Pollination by bats contributes significantly to maintaining ecosystem services, such as fruit and seed production, which serve as food for both other animal species and humans. Therefore, it represents a substantial service to ecosystems and the sustainability of agricultural communities.

Fleming and Muchhala (2008) highlighted the importance of chiropterophily in sustaining ecosystem services across many habitats. Ghanem and Voigt (2012) emphasized that bat pollination is crucial for environmental stability in the face of climate change. By pollinating a variety of plants, bats promote greater diversity and resilience in plant communities, allowing plants to better adapt to changing environmental conditions. In other words, the presence of bats as pollinators enhances plant health and adaptability, strengthening ecosystems' ability to remain balanced and adjust to natural disturbances and climate change.

Chiropterophily also plays a fundamental role in maintaining plants' biodiversity, particularly in tropical and subtropical ecosystems where night-blooming plants are predominantly pollinated by bats. These specialized pollinators are essential for the reproduction of numerous native plant species in complex ecosystems and support diverse food webs. The interaction between bats and plants ensures the perpetuation of these plant species and also promotes the integrity and resilience of natural habitats by providing food and shelter for a wide range of organisms. The extinction or reduction of bat populations can lead to a significant decline in plant diversity, negatively affecting habitat structure and resource availability for other animal species (Kunz and Fenton, 2003).

In addition to their crucial role in pollination, bats are essential for seed dispersal, facilitating the regeneration of forests and other natural habitats. This process is vital for maintaining the structure and biodiversity of ecosystems, since it allows native plants to establish in new areas and recover in disturbed environments. Studies demonstrate that seed-dispersing bats contribute significantly to the recovery of degraded areas and the expansion of vegetation cover, helping restore ecosystems and promote biodiversity (Regolin et al., 2020; Corá et al., 2024; Silva et al., 2024;). The mutual dependence between bats and native plants underscores the importance of conserving these pollinators for preserving biodiversity and the health of ecosystems. Recent studies indicate that changes in the distribution of plant species that bats are dependent on may disrupt their functions, such as pollination services, possibly presenting negative effects on the pollination potential and plant reproduction (Zamora-Gutierrez et al., 2021).

Considering the significant economic value of some plant species that exhibit chiropterophily syndrome, bat pollination directly influences the quality and quantity of agricultural production, promoting the economic viability of these crops. Kunz et al. (2011) highlighted the importance of bat pollination in agave crops used for tequila production. Garibaldi et al. (2013) reported that bats' contribution to the pollination of various plant species enhances fruit and seed productivity, regardless of bee abundance, demonstrating their value in maintaining and increasing agricultural yields. Thus, chiropterophily emerges as a critical component in the complex ecological web, linking the vitality of natural ecosystems with economic sustainability. The role of bats in pollination and seed dispersal supports not only the diversity and health of natural environments but also ensures the production and quality of various agricultural crops.

### Challenges in the research of chiropterophily

Although chiropterophily syndrome provides numerous ecological and economic benefits, its study presents significant challenges due to various ecological, behavioral, and methodological factors. The first challenge in investigating bats is their nocturnal behavior and high mobility, which makes it difficult to observe and analyze their interactions with plants. Numerous papers highlight bats' behavior and ability to travel long distances as limiting factors in researchers' efforts to monitor their pollination interactions. Furthermore, the lack of night

visibility and the need for specialized equipment to observe bats are significant barriers to studying chiropterophily (Fleming et al., 2009; Kunz et al., 2011; Frick et al., 2019).

Another factor complicating the study of chiropterophily is the diversity of species and ecosystems. The abundance of bat species and variations in ecosystems where pollination interactions occur make it difficult to generalize results. Therefore, study approaches must be adapted to each species and specific ecosystem, as noted by Fleming and Muchhala (2008) and Ghanem and Voigt (2012). Ecological interactions vary significantly between different habitats, complicating data extrapolation from one region to another. Additionally, the variability in bat-pollinated flowers and differences in pollination techniques across species add complexity to chiropterophily studies.

Data collection methods also present obstacles. Techniques used in chiropterophily studies can be invasive and complex, requiring innovative approaches. Mist-net capture and handling of bats cause stress to the animals and result in direct consequences for their natural behavior, affecting data accuracy. Traditional direct observation methods are often ineffective given the nocturnal activity of bats, as evidenced by Fleming et al. (2009) and Frick et al. (2019).

Pollen identification faces considerable challenges due to the intrinsic variability and limitations of current techniques. The morphological diversity of pollen grains, which varies significantly between and within species, can make distinguishing between similar types extremely difficult (Taia, 2022). Additionally, grain degradation over time, often exacerbated by adverse environmental conditions, affects sample quality and analysis accuracy (Viertel and König, 2022). Advanced techniques such as scanning electron microscopy and high-resolution image analysis offer potential solutions but require a high level of expertise and technological investment (Smith and Brown, 2022).

The lack of comprehensive databases and the need for detailed knowledge of plant pollen morphology increase the complexity of the process. These challenges are amplified by variability within species and the difficulty of standardizing sample collection and preparation methods. Current techniques also face limitations in identifying pollen in advanced stages of decomposition or when mixed with other types of pollen. This requires continuous evolution in taxonomic approaches and improved analytical methods to ensure accurate and efficient identification (Herzschuh et al., 2022; Viertel and König, 2022). Advances in genetics and molecular biology, such as applying DNA sequencing for pollen identification are emerging as promising tools to overcome these limitations (Bell et al., 2016).

Finally, the impact of climate change and habitat loss further complicates chiropterophily studies, as these factors directly affect bat populations and the plants that depend on them for reproduction. Climate change alters the phenology of plant species, shifting flowering patterns and food resource availability for pollinating bats, complicating the analysis of their ecological interactions (Kunz et al., 2011). Studies such as those by Gómez-Ruiz and Lacher (2019) and Zamora-Gutierrez

rez et al. (2021) show how changes in the phenology of plant species can compromise plant-pollinator interactions, making these relationships more vulnerable and reinforcing the urgency of conservation strategies. Moreover, Ghanem and Voigt (2012) and Fleming and Valiente-Banuet (2002) state that habitat loss due to urbanization and the expansion of intensive agriculture reduces and isolates bat populations, limiting their range and pollination effectiveness. This negatively impacts the availability of plants exhibiting chiropterophily syndrome.

## Conclusions

Our data show that phyllostomid bats are pointed out as key pollinators, particularly in tropical and subtropical ecosystems. We observed that during the period analyzed (2004–2024), 174 scientific articles were published, and Brazil emerged as the primary contributor to scientific production on chiropterophily. However, the use of the term “Chiropterophily and Atlantic Forest” in the bibliometric research might have biased this high number of publications for the country. Although chiropterophily syndrome provides numerous ecological and economic benefits, its investigation presents significant challenges due to a variety of ecological, behavioral, and methodological factors. Several analyzed

manuscripts highlight the critical interdependence between bats and plants, and underscore the urgent need for conservation strategies to preserve the ecological integrity and sustainability of ecosystems. Additionally, some studies suggest that technological advances and new ecological approaches have significantly expanded our understanding of the behavior and movements of pollinating bats, especially in a context of rapid climate change. A number of studies also show how changes in the phenology of plant species can compromise plant-pollinator interactions, and highlight the increasing impacts of habitat fragmentation and urbanization on bats, pointing to the need for conservation strategies that consider not only natural environments but also habitats transformed by human action. Our data show that although scientific production on chiropterophily has grown in recent years, the variations observed over time may reflect changes in research priorities, funding availability, and a lack of specialized researchers in the field.

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## Authors' Contributions

**Piceta**, E.S.: conceptualization, data curation, formal analysis, writing – review & editing. **Primam**, G.L.: conceptualization, data curation, formal analysis, writing – review & editing. **Zanette**, G.: conceptualization, writing – review & editing. **Galiano**, D.: conceptualization, data curation, formal analysis, writing – review & editing.

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