



Review of studies about bat-fly interactions inside roosts, with observations on partnership patterns for publications

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Abstract

Pressures from anthropogenic disturbances have triggered a wealth of studies focusing on the assessment and mitigation of the negative impacts of these disturbances on inter and intraspecific ecological interactions, including bats and bat flies in their roosts. The heterogeneity of research methods employed for these studies and the scientific imbalance between countries may constrain advances and the consolidation of the knowledge on this subject. We reviewed the literature regarding bat and bat-ectoparasite interactions in roosts assessing global research trends and patterns of author collaborative work to be able to identify key questions for future studies and potential initiatives to improve the knowledge on this subject. Current information available has mostly come from the Americas and is predominantly focused on the recognition and description of parasite-host interactions between bats and bat flies. Our findings suggest the value of increasing collaboration for future research, as several countries with largely diverse environments and high organismal richness are disconnected from the countries that produce the most publications in this area, and/or have low records of publications. These regions are in the Global South, mostly in South American and African countries. We suggest that more collaborative networks may increase scientific production in the area, and that investing in local research development and enhancing partnerships for publications may strengthen the field. These research programs and collaborations are key for the development of conservation strategies for bats and bat flies, for their roosts, and for understanding bat and bat-ectoparasite interactions.

Keywords Parasitism · Cave · Streblidae · Nycteribiidae · Collaborative work

Introduction

Anthropogenic disturbance interfere in ecological interactions, resulting in losses such as local extinction of species and degraded ecological functions (Cisneros et al. 2015;

Carvalho et al. 2020; Ramírez-Mejía et al. 2020) as it has been observed for bat (Mammalia: Chiroptera) and bat fly (Diptera: Streblidae, Nycteribiidae) interactions (Ramalho et al. 2021). Negative effects to bat hosts, such as roost disruption and habitat fragmentation, may affect in interspecific interactions and also local and/or regional ecosystems (Pilosof et al. 2012; Bolívar-Cimé et al. 2018). Effects of environmental impacts on bat-plant interactions for feeding and for roosting are apparently better understood than those between bats and their ectoparasites (Oliveira et al. 2019; Hemprich-Bennett et al. 2021; Tormanen and Garrie 2021). Although most studies about bat and bat-ectoparasite interactions are historically descriptive, they provide crucial data to understand the host-parasite dynamics across diverse environments (Patterson et al. 2007; Fagundes et al. 2017; Salinas-Ramos et al. 2018). Studies focusing on the ecology of bat-parasite relationships in their roosts are scarce even though they are essential to the knowledge of pathogenic cycles of bats and their bat flies (Morse et al. 2012b; Abundes-Gallegos et al. 2018).

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Diurnal roosts offer climatic stability to bats, protection from predators, optimal conditions for the bat's reproduction, and social interactions (Kunz 1982; Kunz et al. 2012; Tuttle and Moreno 2005). Roosts used by bats can be temporary (e.g., leaves, foliage) or permanent (e.g., caves, rock outcrops) (Voss et al. 2016; Garbino and Tavares 2018) and appear to be essential for the development of interactions of bat flies and their hosts. Several species of bats are gregarious, many of them forming groups or colonies roosting in caves (Vargas-Mena et al. 2020), which may facilitate the creation and maintenance of ideal conditions for the bat flies' life cycle. Indeed, the development of the flies is limited by the microclimatic conditions of the shelter (Dittmar et al. 2009; Morse et al. 2012a) and by the bats' ability to avoid the parasitism (Reckardt and Kerth 2007). As part of its reproductive cycle, each female bat fly may deposit a prepupa in a roost wall surface, from which the pupa develops in approximately 3 weeks (Dick and Patterson 2007). As soon as the pupa hatches, the young fly needs to find a host to be able to survive (Dittmar et al. 2009) as it will perish in a few hours away from their hosts (Overal 1980; Fritz 1983).

Studies focusing on bat and bat-fly interactions in their roosts can also play important roles for the conservation of the biodiversity associated to natural and artificial roosts. Some of the recent novelties about bats and bat-fly interactions include the study of fungal hyperparasitism on bat flies (Walker et al. 2018; Szentiványi et al. 2019, 2020), the detection of new pathogens in bats and in the bat flies including viruses and bacteria (Jansen Van Vuren et al. 2017; Stuckey et al. 2017; Abundes-Gallegos et al. 2018; Sándor et al. 2018), and the description of patterns of interaction (Lourenço and Palmeirim 2004; Lourenço 2008; Teixeira and Ferreira 2010). Studies of diurnal roosts of bats are essential for bat conservation and to minimize impacts in cave ecosystems (Kunz 1982; Marshall 1982; Vargas-Mena et al. 2020; Barros et al. 2021). On the other hand, most studies including bats and the bat and bat-ectoparasite data have been conducted in the open, outside bat roosts, when bats are out foraging. Over the course of a study on bat-ectoparasite ecological interactions in caves, we noticed a lacune for comparative data related to roosting ecology patterns associated to bats and bat-ectoparasite interactions. The scarcity of information on roosts, bat, and bat fly dynamics poses limitations to our ability to understand the biological cycles of the hosts and their parasites, and the importance of the roosts for these interactions, and consequently limits conservation actions for these systems.

Economic and scientific inequality contributes to restrict science production (Adams 2012, 2013; Gui et al. 2019) and partnerships between researchers from different countries promote engagement to scientific development, enabling collaboration, problem-solving, and to the visibility of results (Adams 2012, 2013; McManus et al.

2020). Programs improving the exchange among researchers have been developed worldwide (Adams 2012, 2013) but some countries are lagging behind, such as megadiverse countries from South America, Africa, and Asia, mostly lacking basic information regarding the biology of the bats and their interactions with ectoparasites (Phelps et al. 2019; Frick et al. 2020; Conenna et al. 2021; Mas et al. 2021). Thus, bibliometric information about studies of bat and bat-ectoparasite interactions in roosts, international partnership, and co-authorship networks may offer a useful overview and can potentially help to identify ways to increase international collaborations.

Our aim in this study was to compile published data and analyze the state-of-the-art of the bat and bat-ecosystem interactions in roosts, investigating global patterns and trends for future studies and learning about patterns of collaborative networks using bibliometric analyses. We were also interested in understanding the variation of the knowledge in the topic along time and spatially, considering the geopolitical distribution of the institutions of the lead authors. Based on our analyses, we comment on practices for boosting the knowledge on bat and bat-ectoparasite interactions across the globe.

Materials and methods

Literature search

We performed a bibliographic search using the ISI Web of Science (WoS) database and performed a search with the terms ((cav* OR "hot cav*" OR "bat cav*" OR roost OR shelter) AND bat* AND ("bat fl*" OR "ectoparasitic fl*" OR Streblidae OR Nycteribiidae)). We then saved all articles retrieved, departing from 1945 until October 29th, 2021. We choose to use only WoS database to avoid redundancy (Calver et al. 2017). We subsequently filtered the documents by examining each of them and saving every study containing records of bats and bat flies in our database.

After this first selection, we discriminated the distribution of bat and bat fly studies by roost types, separating in the categories: (i) records exclusively in caves; (ii) records in all types of roosts except caves (e.g., buildings, tunnels, bat boxes); and (iii) records in caves and any other roost. We then excluded studies mistakenly selected because they were conducted outside roosts and studies based on secondary data or not including field data on bats and bat flies. We followed a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram to guide our revisionary work (Moher et al. 2009) (Supplementary Material S1).

Data analysis

We built interaction networks for the collaborations and keywords compiled from the bibliometric data analyses using the software *VOSviewer* version 1.6.15 (van Eck and Waltman 2010). For each network, the node size represents the number of publications or keywords, and the link is the connection between items (i.e., countries or keywords). The cluster was calculated by using the association strength method (van Eck and Waltman 2010). For the construction of the collaboration network, we used the country of the lead author's affiliation.

Previous to the analyses, we merged the following terms “Cave” and “Caves”; “Chiroptera” and “Bats”; “Parasite load” and “Prevalence”; “Ectoparasite” and “Ectoparasites”; and “Bat flies” and “Bat fly” to avoid redundancy. We considered that the keyword “Parasite load” is a generic way to represent distinctly named parasitological indexes that all relate the number of parasites/host, such as “Prevalence,” “Mean Intensity,” and “Mean Abundance.” We assumed that keywords cited at least three times in different studies may represent an incipient publication pattern and used these keywords to build the interaction network. We evaluated the relationships between the number of links, in this case, of partnerships and the number of publications through a linear regression in the R environment software (R Core Team 2022).

Results

We initially retrieved 116 studies and filtered to 66 (first year with study record) covering a 25-year interval (1996–2021) with an average number of publications of 3.5 studies/year, and peaks of publication between 2006 and 2021 (Fig. 1) (Supplementary Material S2 for *VOSviewer*). Most studies were published from 2015 on ($n=36$; 54%) with a sharp drop in 2020 ($n=3$; 4%). Approximately 2.5 studies/year were published in average from 1996 to 2014, and the rate of publications doubled up to 5.14 from 2015 on. A larger number of publications were concentrated in the years of 2017 and 2018 (Fig. 1). Studies carried out exclusively in caves were more frequent ($n=38$; 57%), followed by studies in other type of roosts ($n=19$; 29%) and in both caves and other type of roosts ($n=9$; 14%).

Collaborative research led to the formation of 14 clusters composed of 36 countries (Fig. 2A). Only five clusters contained publications restricted to authors from the same country (Australia, India, Iran, Slovakia, and Philippines), and except for Iran ($n=2$ studies) these countries were represented by a single study each. The countries with larger number of publications were the USA ($n=25$ studies), Mexico ($n=10$ studies), Brazil ($n=9$ studies), and Madagascar

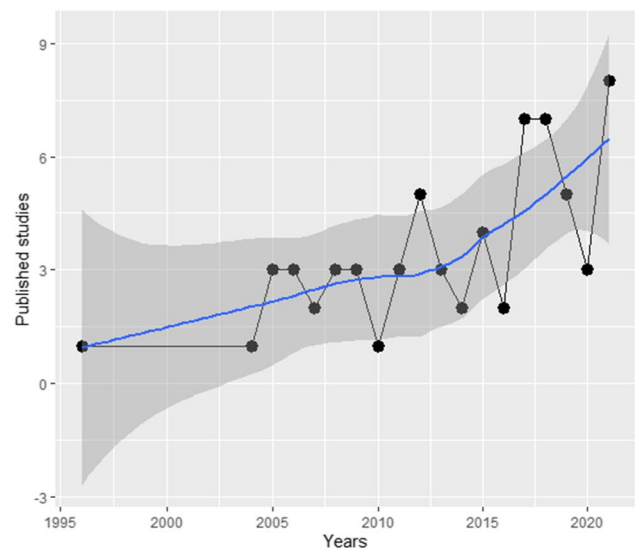


Fig. 1 Number of publications about bats and bat-flies in roosts per year (1996 to 2021). The blue line is the data trend curve

($n=6$ studies). Most studies published by researchers based in the USA and Brazil were published from 2014 to 2015, while publications of researchers based in Madagascar and Mexico were more recent, starting to appear in the literature database in 2016 and 2018, respectively (Fig. 2B). The USA, Mexico, Brazil, and Madagascar represent approximately 76% of all publications and the production led by US-based researchers accounted for the largest share of all global production (39%).

Countries accounting for a larger number of publications tend to have more connections with other clusters ($R^2=0.70$; $P\leq 0.001$; $df=34$) (Fig. 3A). The US institutions have the highest international network, connecting with five clusters (36%) and with a total of 17 countries represented in their collaborative publications (47%) (Fig. 2A), and this substantial network appear to reinforce partnerships ($R^2=0.27$; $P\leq 0.001$; $df=33$) (Fig. 3B). Following the USA, Mexico is the second in productions and connections, respectively ten studies and five connections to other clusters followed by Brazil and Madagascar, with nine and six publications, respectively and both with two connections. Some clusters are formed by two or three isolated countries, such as Poland and Turkey, which may indicate a trend to specific, regional partnerships (Fig. 2A). Furthermore, there appears to occur constant collaborations between researchers or study groups, e.g., Mexico, Costa Rica, Brazil, and Argentina which, together with Russia, form a cluster. Another example is the cluster formed by France, Cambodia, and Gabon (Fig. 2A).

We identified 18 keywords distributed in five clusters, containing three main terms: “Bats,” “Ectoparasite,” and “Nycteribiidae” (Fig. 4A). The cluster in blue centralized by “Bats” connects most keywords that are restricted to caves

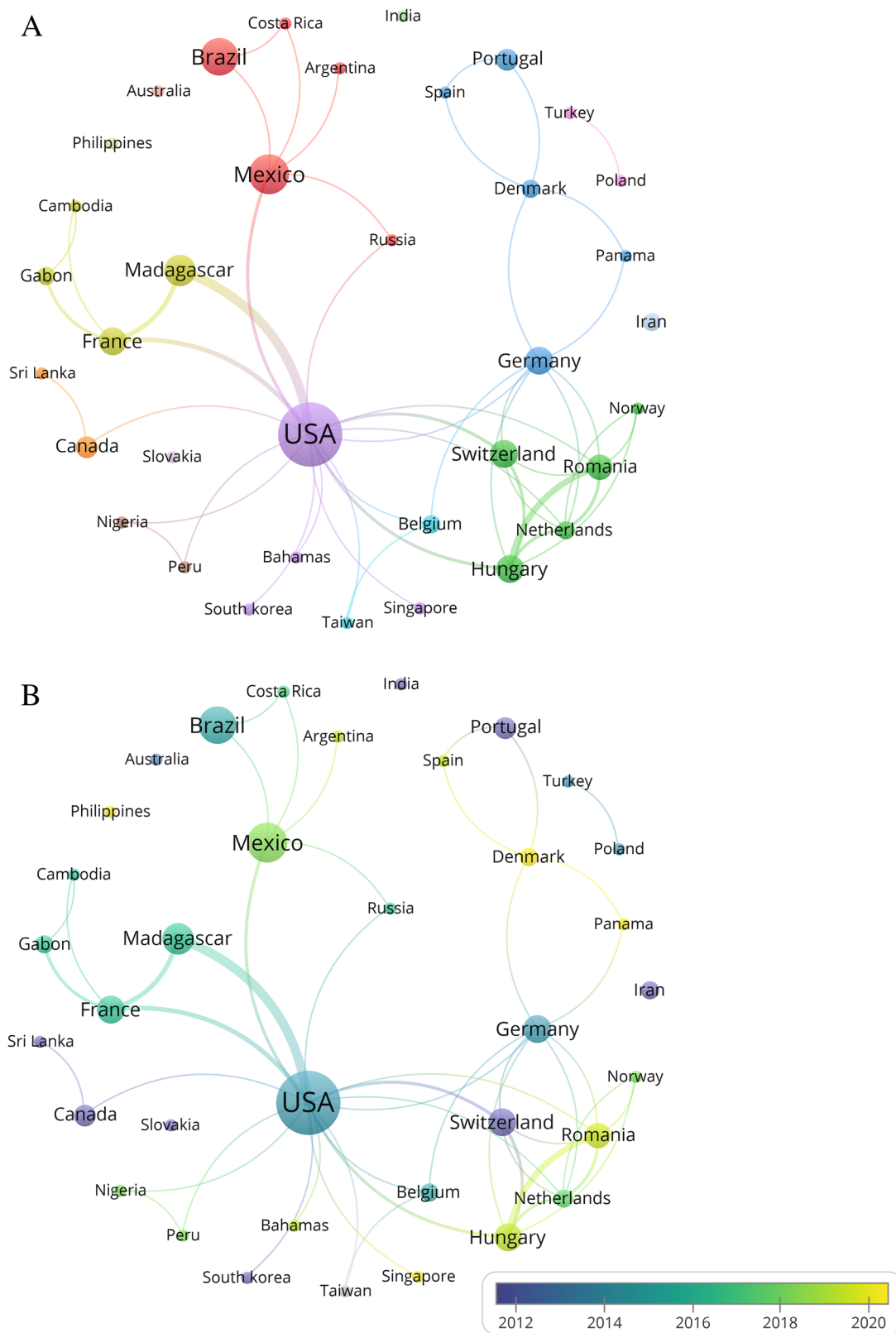
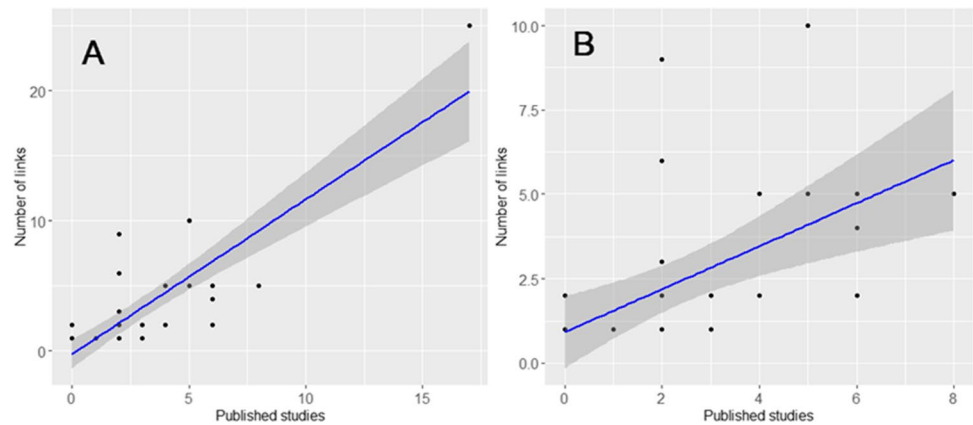


Fig. 2 Collaborative networks for the study of bats and bat-ectoparasite interaction in roosts, including studies primarily produced by researchers affiliated to institutions based in 34 countries, **A** total number of publications and **B** number of publications along time. The

size of the nodes represents the number of publications per country, and the lines indicate connections between countries. The scale of years refers to figure **B** with the darker color representing older publications in the last 20 years

Fig. 3 Relationships between the number of collaborative research and published studies about bats and bat-ectoparasite interaction in roosts from 1996 to 2021. **A** all countries; **B** all countries except the USA



(e.g., Caves, Diversity, and *Bartonella*) and connects keywords related to the diversity and to the presence of microorganisms in bats and bat flies. The cluster in red, centered by “Ectoparasites,” connects most keywords related to general relationships between bats and ectoparasites found in the Neotropics, including several species of bats and parasites. The green cluster, centered by “Nycteribiidae,” connects keywords relative to more specific host-parasite interactions between Madagascar (i.e., endemic fruit bat *Rousettus madagascariensis* G. Grandidier, 1928) and their bat flies. The keywords “Bats” and “Nycteribiidae” are strong connectors between clusters (46 and 30 links, respectively).

Classical parasitological descriptors and indexes (e.g., parasite load, prevalence) were the main topics studied in 2011 (Fig. 4B). Starting from 2012 onwards, studies include research on pathogens related to bat and bat fly life cycles as indicated by the appearance of “*Bartonella*” as a keyword. This period is also marked by studies about co-occurrence and interactions of bat flies and other bat ectoparasites and the terms “Host specificity,” “Spinturnicidae,” and “Bat flies” were recurrent. In 2015, there appear the terms “Roost” and “Cave” in the publications. The most recent terms to emerge in the clusters are “Diversity,” “Host-parasite interactions,” “Madagascar,” and “Hippoboscoidea,” from 2017 onwards (Fig. 4B).

Discussion

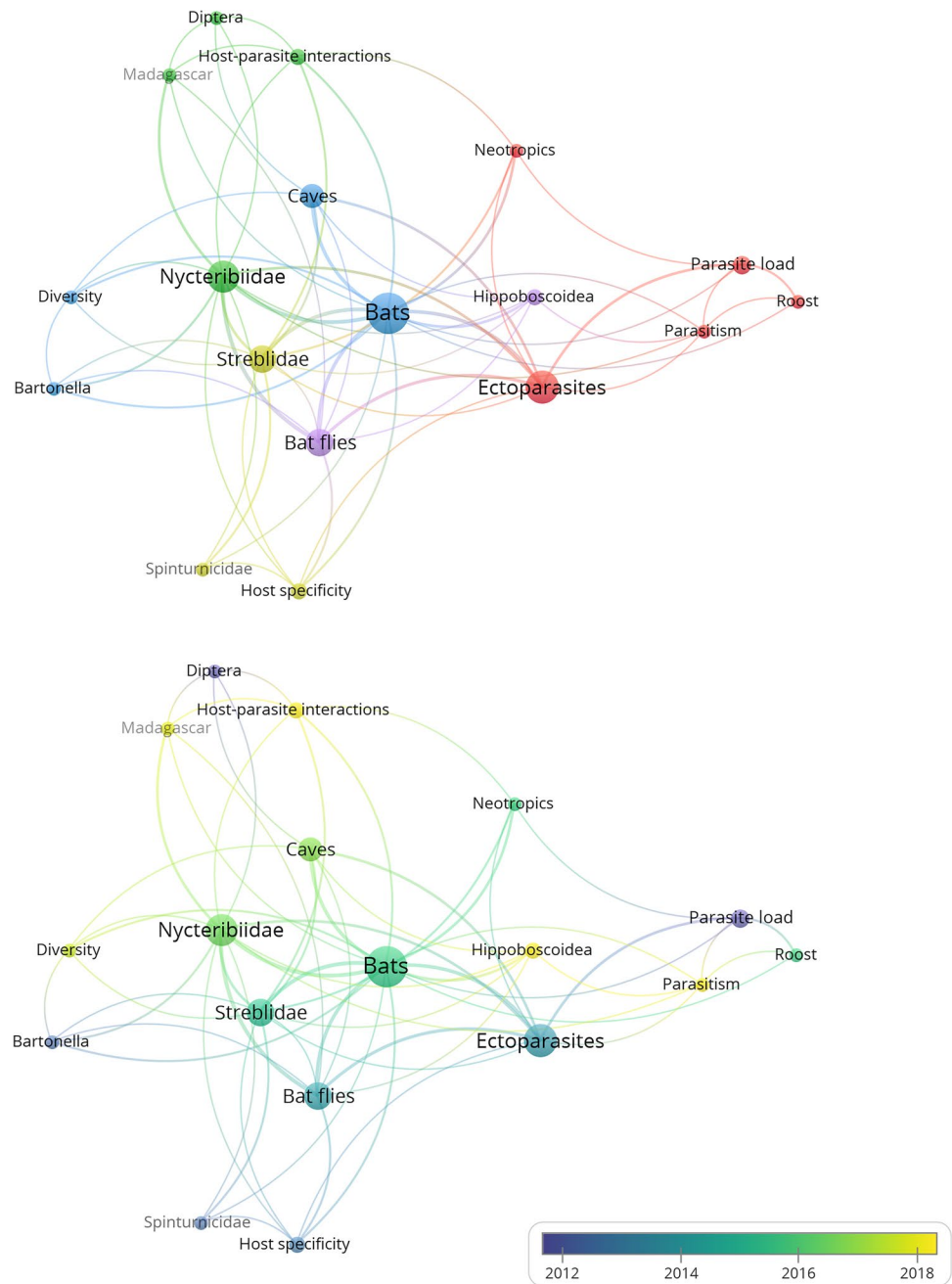
Research about ecology of roosting bats and their parasites has progressed slowly and increased recently (Zarazúa-Carbajal et al. 2016; Tlapaya-Romero et al. 2021). Early considerations about the importance of the roosts to the bat and bat-ectoparasite ecological interactions, with detailed descriptions about the reproduction and parasitism of bat flies appear in the studies of Wenzel and Tipton (1966) and Wenzel (1976). Stringer and Meyer-Rochow (1996) also contributed with data on bat and bat-ectoparasite

interactions in roosts. Almost a decade after, there appear in the literature data on cave bats’ ecology, bat roosting preferences, estimates of ectoparasite densities, and reproduction of the bat flies (Reeves et al. 2005; Ter Hofstede and Fenton 2005), about stable isotopes and bat and bat-ectoparasite relationships (Voigt and Kelm 2006), tests of variables potentially constraining the circulation of bat flies among bats (Lourenço and Palmeirim 2008), and on parasite’s specificity (Seneviratne et al. 2009). In this period, key findings and hypotheses concerning the bat, bat-ectoparasite, and roost interactions were consolidated, such as the high parasite specificity hypothesis, the recurrent findings of bat flies as hosts of pathogens, and the patterns of reproduction of bat flies in caves (Dittmar et al. 2009; Seneviratne et al. 2009).

Significant advances in the study of bat-ectoparasite interactions in their roosts have been made in the last 12 years, including data on the evolutionary history of bat flies (Lack et al. 2011), spatial and temporal effects on bat-fly reproduction (Dittmar et al. 2011), newly proposed parasitological indexes (Esbérard et al. 2012), and endosymbiosis (Morse et al. 2012a). In the second half of the 2010s decade, the use of interaction networks contributed to an alternative way to study the bat and bat-ectoparasite ecological interactions helping to build a broader understanding to studies including eco-epidemiology, endosymbiosis, and hyper-parasitism (Fagundes et al. 2017; Sándor et al. 2018; Jensen et al. 2019). From 2020 onwards, new data are added to the description of interactions within caves and to the reports of viruses found in bat-flies and in bats (Bennett et al. 2020; Hiller et al. 2021; Tlapaya-Romero et al. 2021).

The growth in number of publications along time was halted in the surge of the pandemics of the new coronavirus, SARS-CoV-2, which in a first view appear to have had overall negative effects in the scientific, non-medical production (Huh 2021). This scenario was complicated because of the limited access to research facilities and universities and of the constraints to fieldwork. On the other hand, perhaps the

Fig. 4 Keywords network of studies of bat and bat-ectoparasite interactions in diurnal roosts, considering keywords cited at least 3 times displaced as **A** cluster colors and **B** over time. The size of the node represents the number of occurrences of keywords, and the links indicate the connections among them. The scale of years refers to figure **B**, and goes from the dark green, older publications to yellow, recent publications



home-based work enabled to the writing and submission of more manuscripts (Aubry et al. 2021) as suggested by the peak of publications in 2021.

The global concern for detecting and studying pathogens (e.g., “*Bartonella*,” “Ebola”) and understanding their life cycles has contributed to increase the number of research groups working with these biological systems (Morse et al. 2012b; Stuckey et al. 2017). Most of these studies included few bat and ectoparasite individuals (< 50) for genetic and molecular analysis (Sándor et al. 2018). Apparently, caves have been the preferred study sites of researchers working

with zoonoses because they may concentrate many bats, ectoparasites, and guano. The term “Diversity” in roosts appears indirectly contemplated based on molecular studies (Jansen Van Vuren et al. 2017; Abundes-Gallegos et al. 2018) and directly, in species inventories (Barbier et al. 2018; Tlapaya-Romero et al. 2019). The publication of inventories of bats and their bat-ectoparasites is essential because they can indicate whether each roost should be viewed as a research target, depending on the focus of the research. The remarkable presence of the item “Streblidae” in the red cluster reinforces the dominance of studies

in American countries where the family reaches its higher diversity (Dick et al. 2016), and reinforces that this group as more specific to their host than are the nycteribiids.

Parasitological descriptors have been the starting point for studies of bat-ectoparasite interactions in roosts, which seems to coincide with the standardization of several parasitological and statistical terms used in this field (Bush et al. 1997). In the late 1990s, the use of several of these indices became popular in bat studies, and the further development of software to calculate them, and new indexes has expanded the use of these descriptors in different contexts (Reiczigel et al. 2019). However, we only found the use of indexes describing parasite loading for bat roosting ecology studies starting in the late 2000s, and mostly beginning in the 2010s decade. Prevalence, mean intensity infestation, and specificity have been the main metrics recorded in roosting bats (Teixeira and Ferreira 2010; Aguiar and Antonini 2011, 2016; Tlapaya-Romero et al. 2015), and provide basic information about interspecific interactions between ectoparasites and bats, infracommunities, and ectoparasite populations. However the absence of standardization for the use of these indexes, i.e., the minimum number of hosts, reliability of values, among others, generates misinterpretations about host-parasite relationships (Reiczigel et al. 2019). Although common in other studies (Lourenço et al. 2016), the use of these descriptors in roosting ecology is still incipient and may be useful to disentangle parasitic patterns and help setting methodological standardization for further research.

The expansion of the bat (green) cluster is a result of the exploration of new regions, hosts, and decentralization of studies. *Rousettus madagascariensis* is probably among the most studied bats in Madagascar, including ecological and epidemiological studies (Andrianaivoarivelo et al. 2012; Cardiff et al. 2012; Obame-Nkoghe et al. 2016; Ramanant-salama et al. 2019). The number of studies in roosts of Madagascar has increased in the last 10 years, most of them conducted in caves (Cardiff et al. 2012). The study of bat flies has then followed, and Madagascar is one of the countries that most publish about the theme.

The centralization of the cluster of “Nycteribiidae” highlights the focus of studies and diversity of this family in the Old World (Graciolli and Dick 2018), and the study of ectoparasite flies may favor the establishment of other lines of research. In this case, the term “Diptera” had been registered 5 years before the appearance of the term “Nycteribiidae,” and posteriorly, “cave” studies and “*Rousettus madagascariensis*” were recorded.

The inequality of collaboration between countries makes it difficult to consolidate and expand research on bat interactions in their roosts. In the Americas, the larger part of these studies was led by researchers based in the USA, Brazil, and Mexico. Our findings may indicate a positive effect of developing local research and promoting international

collaboration, i.e., boosting the ability to study the roosts and interaction as a consequence of the partnership. The USA has the greatest weight in interactions and connects the main clusters. Several advances in the research of bat and bat flies in this country, between 1960 and 1970, with emphasis on entomologists Dr. Vernon J. Tipton and Dr. Rupert L. Wenzel (Wenzel and Tipton 1966; Wenzel 1976). In this period, several new species and genera were described, and the first partnerships between researchers and institutions emerged. Since then, publications follow in a constant pace from the US research groups, highlighting the contributions of researchers Dr. Carl W. Dick, Dr. Katharina Dittmar, and Dr. Bruce Patterson. Similarly, the establishment of research in Central and South American countries has been strengthened with research groups from Mexico (e.g., Dr. Juan B. Morales-Malacara), Venezuela (e.g., Dr. Ricardo Guerrero), Brazil (e.g., Dr. Gustavo Graciolli), and Argentina (e.g., Dra. Analía G. Autino). A possible strategy to stimulate research in this topic is to promote partnerships between geographically close countries, e.g., Belgium, Germany, and Hungary. Countries far from the Americas and lacking partnerships, according to our data, lag in publications. Another constant scenario is the lack of collaboration between researchers of a same country. In all cases, it appears that collaboration connecting researchers and countries with the potential for studies of bats and their parasites in their roosts is beneficial to advance more rapidly the knowledge on the theme and to help avoiding lacunes leading to the crisis of the biodiversity (Bini et al. 2005).

For that matter, we emphasize that countries with more publications tend to form more partnerships with researchers from other countries independently of the research time (years) invested previously. Researchers (herein represented by countries) that started early with this theme of research—bat and bat-ectoparasite interactions in caves and other roosts—(e.g., Brazil) have similar contributions compared to researchers that began working later in the subject (e.g., Mexico). The USA, for example, had its first publication in this theme registered approximately in 2009, similarly to Brazil. Similarly, research conducted in Madagascar date as late as 2016 and counted with an expressive international collaborative network.

International partnership may help preventing local researchers from countries with less resources to perish or publishing only occasionally in the subject (Adams 2012, 2013). However, financial resource limitation to scientific research impair the emergence and development of technological innovations (Wagner et al. 2015; Whitley et al. 2018) and regardless of the willingness of the countries to collaborate, the lack of funding contributes to the countries’ distance from a “well-connected world” (Adams 2015).

The overview of the collaborative patterns for the studies on bat and bat-ectoparasite interactions in roosts reveals

heterogeneity, often concurrently with differences in terms of country development (Valente-Neto et al. 2021). In Brazil, for example, resources for research were severely cut over the last years, accounting for 92% of budget originally destined to Science and Technology (De Moura and De Camargo Junior 2017; Santos et al. 2019). Access to resources and misuse of this advantage can contribute for the so-called helicopter surveys (Rochmyaningsih 2018; Valente-Neto et al. 2021).

Mexico and Brazil have a high concentration of karstic areas still relatively little studied (Kunz 1982; Lewis 1995; Rodríguez-Durán and Soto-Centeno 2003; Medellín et al. 2017; De Oliveira et al. 2018; Téllez et al. 2018; De Sousa et al. 2021). Parallel to natural roosts, urban spaces offer a variety of artificial roosts for different studies involving bat and bat-fly interactions. Creating a global database on roosts, bats, and bat flies could also help to facilitate international collaboration and enhance the study of macroecological patterns for the interaction between bat and their bat flies in their roosts.

Conclusion

The recent use of bibliometric analyses has made it possible to identify patterns and trends in studies in different contexts considering collaborations between researchers over the globe. Here, we focus on understanding international collaboration patterns and trends in studies of bat and bat-ectoparasite interactions in roosts. Our results showed that studies on this area mainly involve cave roosts and mostly are carried out by the US, Mexican, and Brazilian researchers and institutions. In general, countries with more publications make more partnerships with other countries. We suggest that local research development and international collaboration can promote research improvement in countries that are disconnected in networks.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00436-022-07635-z>.

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Author contribution GLU and VCT conceived the study and wrote the original draft of the manuscript. GLU executed the literature search. GLU and VCT carried out all the formal analysis. GLU, VCT, and GG contributed to interpretation of data, writing, and reviewed the manuscript.

Data availability Not applicable.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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