

Bats in Habitats, Bats as Habitats: An integrative ecological framework for understanding synergistic interactions across levels of community organization

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Abstract

Global biodiversity and ecosystem function are the result of complex networks of interactions and feedbacks between animals and their environments, which in turn are affected by the interactions and feedbacks between animals and the organisms they host. Understanding these complex networks, including the main drivers of and responses to ecological and environmental changes and their global implications, requires adopting a systems-based perspective. We advocate for this approach by characterizing a framework centered around bats, a globally-distributed mammalian order, and their dual roles as both inhabitants of ecosystems and as habitats themselves. Like other organisms, bats interact with habitats by providing ecosystem services that impact the survival and distribution of other species, and may be affected by such factors as land use change, climate change, fluctuations in food availability, and hunting pressure. Habitat conditions (e.g. food availability, temperature, etc.) can affect the physiological condition of individuals, which in turn can affect the prevalence and/or virulence of hosted organisms and potential pathogens (e.g. ectoparasites, bacteria, viruses, fungi, and protozoa). In addition, the interactions among individuals (e.g. co-roosting, migration, etc.) influence the habitat connectivity for their hosted organisms (e.g. opportunities for dispersal). Bats have a unique relationship with infectious disease, both biological and cultural. With this in mind, when applied to bats this framework has special importance to how we understand and apply the One Health concept, whereby healthy natural environments foster both human and animal health, which in turn also promotes healthy environments. By leveraging a hierarchical approach among these different levels of biological organization, we can arrive at a clearer picture of the specific threats facing bats—as well as the risk of pathogen spillover to humans and other domesticated and wild animals generated by disrupting this delicate balance—and identify possible measures to mitigate adverse impacts. Thus, to understand these complex interactions and their implications for conservation, ecosystem health, and human health, we need a new ecological framework that recognizes that changes in habitats not only affect macrofauna and the ecosystem services they provide, but also have the potential to cascade through the diversity and evolution of the organisms they host. This review provides a case study for the application of this framework, which is extensible to other organisms with their own unique relationships with habitats and as habitats.

Keywords: Systems ecology, network ecology, microbiome, habitat, community ecology

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1. INTRODUCTION

Biology is becoming more interdisciplinary as our understanding of the integrative relationships between biological systems and levels of organization grows. Darwin described a “Tangled Bank” of organisms that interact with and depend upon each other in complex ways (Darwin, 1859), ultimately resulting in observed patterns of global biodiversity. While Darwin recognized that these phenomena are governed by biological laws, we now seek to generate mechanistic explanations for the complex properties of hierarchical biological systems by understanding how these and other laws intersect and interact. The fields of systems biology and systems ecology, in which species and ecological interactions are thought of in terms of networks, provide a modern approach both to disentangle the “complex web of life” and to understand it holistically.

Given the inherent complexity of these relationships, one way of applying a systems approach is to use a single species or taxonomic group as a node and work to understand it at multiple scales of biological organization. Biologists are accustomed to viewing species as either residents of ecosystems, or as ecosystems themselves when the focus is on their interactions with the parasites and other organisms they host. By examining a single macrofaunal clade as a node, we can link the concepts, research systems, and innovations developed for studying the interactions of members of that clade with their habitats, with those concepts, research systems, and innovations developed for studying the organisms that use that clade as their hosts. In this review, we develop a framework in which a single cosmopolitan clade of mammals can be studied across these nested levels of organization, from the broader habitat, to the host animals, to the organisms they host. This framework provides new conceptual insights by bringing together empirical and theoretical work bridging levels of organization, and can serve as a foundation for a better understanding of synergistic interactions across levels of community organization.

Different niche concepts reflect the differences in perspectives and approaches taken to study the biological context of species in ecosystems. A unified framework would incorporate all of these aspects as well as the ways in which changes at one level in the hierarchy may alter population and community dynamics as well as niches of organisms at other levels. For the purpose of this paper, “habitat” is defined as the collection of resources an organism or

population of organisms uses to survive, including physical surroundings (e.g. caves, structures, moisture, temperature), and biotic factors (e.g. food, interspecies competition, or host availability). The habitat is distinct from the overall environment by being species-specific, while the environment is the physical context in which habitats are formed. Habitats are also distinct from, though a part of, the species' niche. A species' multidimensional niche may be thought of as a hypervolume containing the set of conditions and resources needed for a species to persist, and is influenced by the habitat in which it lives, as well as the network of interactions a species has with other members of the community sharing a habitat (Grinnell, 1917; Hutchinson, 1957). This articulation does not acknowledge the bidirectional feedbacks between species and their habitats, while the Eltonian conception of the niche recognizes that species may also change their environments and thus, their habitats (Elton, 1927).

Here, we synthesize current understanding of feedbacks and interactions across various biological levels. Bats (Order Chiroptera) provide a useful model system for illustrating this framework due to their wide distribution, incredible ecological diversity, and comparatively well-studied interactions with microbes and parasites. Our ability to study these aspects of biology has also increased exponentially thanks to technological advances including next-generation sequencing, computational modeling, and the ability to track individual animals over their lifetimes at both fine and broad spatial scales. We advocate for the development of study designs that integrate multiple organizational scales from the outset, rather than reconstructing these interactions from cross-sectional studies. We begin by reviewing existing knowledge on bidirectional feedbacks between bats and their respective habitats (Table 1). Next, we explore the concept of bats as habitats for other organisms. Given that the goal of this paper is to use bats as a model to demonstrate a systems framework that makes explicit connections between levels, and illustrates knowledge gaps within the system, we do not attempt to exhaustively list everything known about bats at all scales of biological organization. Finally, we use the "Bats in Habitats, Bats as Habitats" synthesis to highlight significant knowledge gaps in a systems framework and propose future research directions. The goal is to develop a framework generalized enough to be extensible to other biological systems. Ultimately, this approach aims to enhance our comprehension of the "Tangled Bank," elucidating underlying mechanisms and identifying threats to bats and other species with whom they interact.

2. Bats in Habitats

2.a. Habitat determines bat community composition and dispersal

To understand the broadest level of organization, the level of a species' interactions with its habitat, it is useful to consider the species' multidimensional niche. The main drivers of species distributions vary depending on the spatial scale, species' traits, and evolutionary history. For example, at a coarse scale, bat richness is mainly affected by climate, while habitat structure tends to have an effect on a smaller scale (Estrada-Villegas, McGill & Kalko, 2012; Meramo *et al.*, 2025). Both are impacted by the evolutionary history of the clade, for example through the opening of new feeding niches in Phyllostomidae (Potter *et al.*, 2021; Hall *et al.*, 2021) or hybridization (e.g. *Myotis*; Foley *et al.*, 2024). The effects of environmental gradients

such as latitude, precipitation, temperature, and elevation are correlated such that variation along each of these axes produces emergent properties that define ecosystems.

Bat distribution and richness are influenced by these factors, with each species having a unique relationship to these variables that forms their multidimensional niche (**Fig. 1**). Generally, bat species richness increases toward the equator, where temperature and primary productivity are higher (Stevens, 2004). However, physiological limits on bat distributions vary significantly among species, making it difficult to establish definitive distribution rules (McNab, 1973; Dunbar & Brigham, 2010; Haarsma & Siepel, 2013; Becker *et al.*, 2019). Elevational gradients are an illustrative example of this challenge: despite commonalities among mountain slopes at the same latitude (e.g. oxygen concentration and temperature), there is no clear pattern between species diversity and elevation. Bats' sensitivity to temperature and humidity is related to their small size and high surface-to-volume ratio (McCain, 2007). Increasing temperatures can also indirectly promote bat richness by increasing food resource availability (i.e., fruit, nectar, and insects). This results in species richness and functional diversity varying in disparate ways along elevational gradients, related to relative humidity (McCain, 2007), temperature (Sivault *et al.*, 2023), water availability (Korine *et al.*, 2016), food resource availability, and other factors.

At a smaller scale, habitat structure, including heterogeneity and canopy cover, can affect the occurrence of certain foraging guilds (e.g. open-space vs. edge-space foragers), due to echolocation and maneuverability challenges in cluttered environments (Denzinger & Schnitzler, 2013; Suarez-Rubio, Ille & Bruckner, 2018; Senawi & Kingston, 2019; Yoh *et al.*, 2020). Vegetation complexity and habitat/resource diversity locally enhance bat species richness, as spatially heterogeneous conditions provide a greater diversity of suitable niches (Aguirre, 2002; Zortéa & Alho, 2008; Pereira *et al.*, 2009; Martins *et al.*, 2022). Feedback between adaptations in wing morphology, echolocation, and vegetation affect foraging success (Norberg & Rayner, 1987; Jones *et al.*, 2006; Denzinger *et al.*, 2016). Moreover, roost availability is crucial to determining bat occurrences, sometimes even more so than availability of prey (Avila-Flores & Medellín, 2004; Voss *et al.*, 2016; Suominen *et al.*, 2023). Local resource availability is also an important determinant of bat occurrence, including for migratory species, which can be exposed to different resource regimes across their migration paths (Richter & Cumming, 2006; Flaquer *et al.*, 2009). Simultaneously, bats are also important influencers of local resource availability for other organisms.

2.b. Bat community composition impacts ecosystem structure and function

As highlighted in Table 1, bats wield considerable influence on their own and other species' realized niches— the set of conditions actually used by an organism (Connell, 1961). For example, certain species of bats produce significant amounts of nitrogen, phosphorus, and potassium deposits in guano beneath their aggregations (Ferreira, 2019; Pimentel *et al.*, 2022). The largest aggregations of living vertebrates are found in caves (Furey & Racey, 2016), with large bat colonies functioning as a sink for up to 39% of the total forest nitrogen budget in some regions (Lundberg, McFarlane & Van Rentergem, 2022). Bat guano affects many aspects of cave biogeochemistry, including the bioavailability of organic and inorganic nutrients, the physical cave structure, and the diversity of invertebrate communities in the caves (Ferreira, 2019; Sakoui *et al.*, 2020; Piló *et al.*, 2023). Bat caves typically harbor great diversity and abundance of cave dwelling organisms, including some entirely dependent on the guano, known

as guanophiles (Ferreira, 2019). Furthermore, the heat from the guano fermentation process and the combined body heat of resident animals impact the cave microclimate (Mitchell, 1965).

Apart from altering their physical and chemical habitats, bats also take part in biotic interactions that can play out at local, ecosystem, and evolutionary scales. Plant-visiting bats provide important ecological services by facilitating reproductive success and recruitment of new seedlings (Kunz *et al.*, 2011; Aziz *et al.*, 2021). As an example, 63% of the basal area of native woody plants in plots in Mauritius came from seeds dispersed by the threatened native flying fox, *Pteropus niger* (Florens *et al.*, 2017). Indeed, pteropodid fruit bats are key to Pacific island flora due to long range dispersal of large seeded plants, although this relationship may break down at low population sizes (McConkey & Drake, 2006). Bats provide pollination services to more than 500 angiosperm species worldwide (Fleming, Geiselman & Kress, 2009), which is key to reproductive success and genetic exchange between plants and can drive plant evolution (Santana *et al.*, 2021). Columnar cacti and agaves are dominant plant elements in arid and semi-arid habitats of the Americas, which rely heavily on bats for pollination and thus sexual reproduction (Kunz *et al.*, 2011; Kasso & Balakrishnan, 2013). In Sulawesi, fruit bats are also the main pollinators of durian, estimated to contribute US\$117/ha in economic value (Sheherazade, Ober & Tsang, 2019).

Ecosystem services provided by bats are of particular importance in island systems, in which bats may constitute a large majority of the mammalian assemblage, in some cases being the only native mammals (Fleming & Racey, 2010). The high vagility of bats allows them to actively disperse to islands, including remote oceanic systems that do not have pre-existing biota. These ecosystem services are strongly related to the maintenance and stability of their ecosystems (Kingston, Florens & Vincenot, 2023). In concert with birds, bats play an important role as long-distance seed dispersers that promote island forest regeneration after significant loss due to natural disasters (Whittaker & Jones, 1994; Hjerpe, Hedenås & Elmquist, 2001; Scanlon *et al.*, 2018). The plant species brought by bats to islands include many pioneering plant species (e.g. figs; Whittaker & Jones, 1994; Thornton *et al.*, 2001; Oleksy *et al.*, 2017) important to both primary and secondary succession. Some plants become wholly dependent on flying foxes (tribe Pteropodini sensu (Bergmans, 1997)) for dispersal in island systems despite these plant species being common in continental landscapes (Cox *et al.*, 1991). Additionally, while doves and pigeons contribute to seed dispersal in Pacific island systems, flying foxes provide the main avenue of large seed dispersal (McConkey & Drake, 2015). In Tonga, the species diversity of plants consumed by pigeons is 40% less than bats, while on other islands, both contribute equally to seed dispersal but consume a different set of plant species (Meehan, McConkey & Drake, 2002; McConkey *et al.*, 2004).

However, not all bat-plant interactions are positive (Table 1); tent-making bats antagonistically affect some plants by damaging leaves to build temporary roosts, and *Pteropus* can cause similar damage on tree roosts when used consistently (Vardon *et al.*, 1997). Other bats such as *Centurio senex* are seed predators that do not increase germination success (Nogueira & Peracchi, 2003; Rodríguez-Herrera, Rodríguez & Otárola, 2018). On the mutualistic side, even if bats are not directly using plant products, their presence alone can benefit plants. For example, the aerial pitcher plant *Nepenthes rafflesiana* gains a significant portion of its foliar nitrogen from the feces of *Kerivoula hardwickii* (Grafe *et al.*, 2011). Trees that host bats are also known to benefit from the nutrients of their excrements (Duchamp, Sparks & Swihart, 2010;

Voigt, Borissov & Kelm, 2015). Thousands of these interactions occur at local scales across the globe; while it is beyond the scope of this review to cover them all exhaustively, other reviews (e.g. (Aziz *et al.*, 2021; Ramírez-Fráncel *et al.*, 2022; González-Gutiérrez *et al.*, 2022) are useful starting points.

The aggregate effect of each of these local interactions between bats and plants can have profound impacts on the structure of their habitats at the ecosystem scale (**Fig. 1**). For example, the functional extirpation of vertebrate seed dispersers (i.e., birds and bats) led to a reduction in seed bank richness in Guam compared to Saipan and Rota—where these dispersers still exist—suggesting that bats play a significant role in structuring plant communities (Wandrag *et al.*, 2015). Across the tropics, ~80% of seed dispersal in general is performed by birds and bats (Howe & Smallwood, 1982). Bats produce dense and diverse seed shadows, and it appears that more diverse communities of frugivorous bats are linked to more diverse forests (Fleming & Heithaus, 1981; Muscarella & Fleming, 2007). However, there are important differences in the impacts of plant-visiting bats across the globe; for example, Neotropical fruit bats appear to be more specialized compared to Afrotropical bats (Dugger *et al.*, 2019), but Afrotropical bats exert enormous influence on forests, forming aggregations of millions of individuals not seen in the Neotropics (Richter & Cumming, 2006). While it is clear that bats influence their habitats by changing vegetation, what is not clear is the impact that this aggregate of seemingly specific bat-plant interactions has on global rules of life, in other words, the integration of these multi-scale interactions. Are Afrotropical forests less diverse than the Neotropics because their seed dispersers are less specialized, because the dispersers are themselves less diverse, or for a completely unrelated reason? How does this filter down to bat-hosted organisms; do they show similar patterns of diversity across tropical environments? Our proposed framework would help to shed light on these complicated phenomena.

Of around 1500 bat species recorded, about 70% are insectivorous (Kissling *et al.*, 2014; Mammalian Diversity Database, 2024). This highlights the role of bat assemblages in arthropod regulation and their importance in food web dynamics, both in natural and in human-altered landscapes. Experimental exclusion of bats from plants in lowland tropical forests in Panama resulted in 209% more insect herbivory on plants, indicating that bats are important top-down regulators of ecological food webs (Kalka, Smith & Kalko, 2008; Puig-Montserrat *et al.*, 2020; Tuneu-Corral *et al.*, 2023). In North America, aerial insectivores were shown to consume at least 160 known agricultural pests and pathogen vectors, with similar results reported in Europe (Aizpurua *et al.*, 2018; Maslo *et al.*, 2022). For example, it is estimated that bats provide between \$3.7–53 billion of direct insect pest control across the United States (Boyles *et al.*, 2011), and they have been shown to reduce crop damage resulting from pests and their associated microbes (Maine & Boyles, 2015).

However, it is less clear if bats exert the same intensity of pressure on pathogen vectors such as mosquitoes as they do on agricultural pests. Much of the work in this vein has focused on mosquitoes as a major global pathogen vector, and in some cases there is conflicting evidence on whether bats consume enough mosquitoes to meaningfully affect mosquito population sizes (Wray *et al.*, 2018; Puig-Montserrat *et al.*, 2020). Interestingly, the presence of bats alone, regardless of the number of mosquitoes they actually consume, may be sufficient to alter mosquito oviposition, thereby decreasing populations (Reiskind & Wund, 2009). Bats could also regulate populations of insect vectors other than mosquitoes (Perea *et al.*, 2024), but most

of these interactions have been poorly studied, and even less attention has been paid to the direct impacts of predation on pathogen vectors on infectious disease incidence.

Bat diets nonetheless can strongly vary by species but also temporally and spatially, including following insect pulses and emergence, so disentangling the role of these factors in regulating insect populations is imperative (Vesterinen *et al.*, 2018; O'Rourke *et al.*, 2022). The consumption of insects has been hypothesized as a mechanism by which new parasites and microorganisms can colonize bats (Gibson *et al.*, 2005; Hodo *et al.*, 2016; Bennett *et al.*, 2019; Rangel *et al.*, 2019). Some efforts to document bat diets globally have been initiated and could fill in many knowledge gaps between diet and parasitism (see (Tuneu-Corral *et al.*, 2023), but require further research effort. Without having detailed information about bat habitats and diets, we lack an important window into the diversity and mechanism of acquisition of bat-hosted organisms and the impacts of environmental change on food availability for bats. For example, the impacts of declining insect populations and diversity globally may vary depending on bat taxa, directly affecting the entire network of relationships between bats and their prey. This then would affect the populations of plants that the insects consume, with downstream impacts on the ecosystems that these plants contribute to.

2.c. Effects of anthropogenic change on bats in habitats

In addition to biotic and abiotic interactions, and like most other animal and plant species, bats and their habitats are being increasingly modified by a third force: human activity (Table 1, **Fig. 1**). In the last few centuries, humans have shaped ecosystems so quickly and extensively that many species do not have time to adapt. Some examples of how humans are altering bat habitats at large include, but are not limited to, habitat loss and degradation (e.g. land use change, fragmentation, and encroachment). In particular, these modifications affect bat distributions by limiting food resources and roosting sites, and in some cases contribute to bat mortality directly or indirectly (e.g. via stress). Anthropogenic change to bat habitats that forces bats to alter their ecology has contributed to the spillover of lethal viruses from bats to humans (Eby *et al.*, 2023). Our ability to predict how bats respond to these challenges is fundamentally constrained by our understanding of bat biology, especially as responses may be idiosyncratic among species. While an exhaustive treatise on the effect of anthropogenic change on bats and their habitats is beyond the scope of this review, interested readers should see “Bats in the Anthropocene” (Voigt & Kingston, 2016).

Habitat transformation can lead to reduced resource availability, contributing to reduced reproductive and survival rates of individual species, thus altering the ecosystem dynamics in which bats participate (Jones *et al.*, 2009; Meyer, Stevens & Blackwood, 2016; Nurul-Ain, Rosli & Kingston, 2017). Human alteration of landscapes can have profound impacts on roost availability and increasing rates of land use change will overall reduce habitat availability (Gonçalves *et al.*, 2021). In the Neotropics, roost specialists appear to be particularly vulnerable to habitat fragmentation compared to more generalist roosting species (Voss *et al.*, 2016; Herrera *et al.*, 2018). Similarly, in the Paleotropics, species that roost in forest structures (standing and fallen hollows, under leaves) are proving more vulnerable to forest loss than cave-dwelling species (Struebig *et al.*, 2008; Huang *et al.*, 2019). Despite this, disturbance at caves (limestone and phosphate mining, tourism, etc.) means many cave-dependent species may be living on borrowed time (Struebig *et al.*, 2008; Phelps *et al.*, 2016, 2018).

Humans can also directly influence the availability and quality of bat food resources. Application of chemical pesticides is associated with a decrease in nocturnal insect diversity compared to organic farms, resulting in decreased bat activity (Wickramasinghe *et al.*, 2004), and nectar-feeding bats are forced to change their feeding ecology to respond to agricultural replacement of native habitat (Eby *et al.*, 2023). However organic farming on its own has been found to be insufficient to support bat biodiversity, with landscape features such as hedges and rivers playing a more important role (Froidevaux, Louboutin & Jones, 2017). Simulation of associations between bats and plant species in the Brazilian savannah also found that extinction of certain plant species would result in co-extinction of several bat species (Oliveira *et al.*, 2019). However, not all bat species respond negatively to human activities; common vampire bat populations have expanded over the last century due to the presence of livestock in Central and South America (Becker *et al.*, 2018). Some fruit-eating bats also show higher body condition and reproduction *outside* of protected areas, likely due to the increase in pioneer plants in disturbed habitats (Oliveira *et al.*, 2017). Bats therefore appear to respond variably and in potentially location-, diet-, and species-specific ways to habitat loss and alteration.

Urbanization and its consequences can impact where bats are found on the landscape (Moretto *et al.*, 2023). Alteration of food and roosting resources can lead to bats abandoning parts of their previous range and moving into less suitable habitats (e.g. (Tait *et al.*, 2014). The impacts of artificial light at night can vary with species biology, with some bat species taking advantage of the concentration of insects under lights, while more light-sensitive species are pushed into increasingly concentrated areas of dark refugia (Cravens & Boyles, 2019). Experimental and observational evidence also suggests that fruit-eating bats change their foraging behaviors to avoid illuminated plants (Lewanzik & Voigt, 2014). Current literature is equivocal about the extent and direction of the effect of artificial light on bat movement, including nightly foraging and migration (Rowse *et al.*, 2016; Voigt *et al.*, 2018). Land use change can also have variable impacts on bat occupancy and activity; most studies find evidence of lower bat occupancy and richness in monoculture habitats (e.g. oil palm, coffee, and eucalyptus plantations), but some species may be able to use agricultural habitats if vegetative complexity or patches of natural habitat are retained in the landscape (Numa, Verdú & Sánchez-Palomino, 2005; Barlow *et al.*, 2007; Wordley *et al.*, 2015; Syafiq *et al.*, 2016; Buchholz, Kelm & Ghanem, 2021). Humans can also create new habitats for bats; many species aggregate in abandoned mines or buildings (van Schaik *et al.*, 2015b; Moran *et al.*, 2023), and this can even provide physiological advantages compared to natural roosts (Lausen & Barclay, 2006; Detweiler & Bernard, 2023). Bat traits such as geographic range, habitat preference, and diet can impact likelihood of anthropogenic roosting (Betke *et al.*, 2024). The emerging pattern suggests that while changes in land cover and agricultural intensification overwhelmingly reduce bat diversity, responses vary among foraging and roosting ensembles, and even among species within these groups (Kingston, 2013; Wordley *et al.*, 2015; Huang *et al.*, 2019; da Costa & Ramos Pereira, 2022). This variation in response again emphasizes a need to fill knowledge gaps on what individual species require to survive in the Anthropocene.

Bat health and mortality, including infectious disease, may also be indirectly influenced by human activities that cause an increase in stress, or change how bats interact with other organisms. Habitat fragmentation and roost disturbance can leave bats to persist in suboptimal habitats, which results in elevated markers of physiological stress (Edson *et al.*, 2015; Miguel *et*

et al., 2019). On the converse, roosting in human-made structures may have no physiological costs, or actually improve survival and thermoregulation (Lausen & Barclay, 2006; Allen *et al.*, 2011). In addition, while higher cortisol levels are generally assumed to be deleterious, in some cases they may have negligible effects on overall bat physiology (Miguel *et al.*, 2019). In other cases, chronic stress may lead to poorer health outcomes for bats, including lower white blood cell counts and decreased body mass (Seltmann *et al.*, 2017b). The effects of stress can even influence the communities of organisms harbored by bats; flying foxes with higher markers of nutritional stress showed subsequently higher seropositivity of Hendra virus (Plowright *et al.*, 2008), and periods of food scarcity are related to elevated shedding pulses of Hendra virus (Becker *et al.*, 2023). Habitat fragmentation is also associated with higher bacterial microbiome variation in vampire bats, which may indicate a destabilized microbial community (Ingala *et al.*, 2019). Whether this response is directly related to stress remains unknown. Overall, the interactions between bats, their habitat features, and the organisms they host are nuanced, with only a fraction of species and populations having been studied (Phelps & Kingston, 2018). Without a robust baseline of stress markers, physiological fitness, and microbial community members for all bat species, we are limited in our ability to understand thresholds that lead to worse health outcomes in each species (but see (Sandoval-Herrera *et al.*, 2021; Sánchez *et al.*, 2024).

In addition to altering the resources bats need to live, humans can also directly impact bat populations through actions that increase mortality or decrease reproductive success. Two important ways that humans intentionally decrease bat survival are via bushmeat hunting and retaliatory killing. Bats are often taken as bushmeat in the Paleotropics, particularly in low income countries with high deforestation rates, suggesting that poverty is associated with bat bushmeat harvesting (Tanalgo *et al.*, 2023). In other countries, people often have negative attitudes towards bats, supporting lethal control measures to limit their populations (Shapiro *et al.*, 2020). However, culling of bats can have unwanted consequences. In Latin America, vampire bats are major reservoirs of rabies virus, but culling of vampire bats actually increases rabies virus transmission by altering the demographic structure and dispersal of populations (Streicker *et al.*, 2012; Viana *et al.*, 2023). Important services carried out only by bats, such as pollination and seed dispersal on islands, can also be disrupted following retaliatory culls due to commercial fruit damage by fruit bats (Oleksy *et al.*, 2021). Unintentional killing of bats also impacts their populations; wind energy has been identified as an increasingly important threat to migratory bat species (Frick *et al.*, 2017; Thaxter *et al.*, 2017). Even mundane human activities, such as driving, can result in significant impacts on bat populations given the size of the human population and increasing number of vehicles in operation (Fensome & Mathews, 2016; Ramalho & Aguiar, 2020; Huang, Chen & Lin, 2021). Although the previously reviewed associations cover a wide range of bat biology as it relates to their habitats, ~18% of bat species are classified as “Data Deficient” by the International Union for Conservation of Nature and many others have not even been assessed, highlighting the need for more natural history studies to allow for predictive modeling of bat responses to anthropogenic change using the “Bats in/as Habitats” framework (Welch & Beaulieu, 2018; Frick, Kingston & Flanders, 2020).

3. Bats as Habitats

The biology of bats makes them unique habitats for a variety of other organisms, from macroscopic parasites to microbial organisms from all domains of life (Table 1). Here, we define bat-hosted organisms to be any organism that lives in or on bats for a major part of its life cycle. In turn, the biology of bat-hosted organisms is constrained by host traits, while also influencing the biology of the hosts themselves (**Fig. 2**). A few attributes of bat-hosted organisms that can feed back on host biology are their mode of transmission, their ecological relationships with hosts (e.g. commensal, pathogenic, or mutualistic), and relationships with other organisms that share the same bat host (e.g. co-transmission). Because these relationships are nested and hierarchical, they not only feed back among themselves, but also can be modulated by changes at the habitat level. Synthesis across these levels of biological organization is poorly understood and a key research gap in both bat biology and global health; “Bats in/as Habitats” provides a framework for integrating bat-associated organisms into a holistic understanding of bat biology.

3.a. Bat biology influences hosted organism communities

Bat biology may influence hosted organisms in ways that are shared with other mammalian hosts, such as having high body temperature, fur, and non-nucleated blood. Some unusual aspects of bat biology compared to many other mammals are their cosmopolitan distribution and diversity, high vagility, long lifespans, use of heterothermy, and highly gregarious social systems. While we focus on the biology of bats in this review, it is important to note that other processes, such as conserved mammalian traits or overall taxonomic diversity, can also influence hosted organisms and have been reviewed elsewhere (Olival *et al.*, 2017; Carlson *et al.*, 2019; Shaw *et al.*, 2020; Mollentze & Streicker, 2020).

Bats are one of the most widely distributed and diverse groups of mammals on Earth, second only to rodents. At a broad scale, host taxonomic diversity is associated with higher diversity of zoonotic viruses, such that orders of mammals with more species harbor more zoonotic viruses (Mollentze & Streicker, 2020). However, there is often not a clear relationship between bat species identity and the organisms they host. While in other mammals the gut microbiome community reflects host phylogeny, in bats there is a stronger influence of diet and environment than host relatedness (Lutz *et al.*, 2019; Dai *et al.*, 2024). At finer scales, such as within a bat species or population, the relationships between host and hosted organism populations become more complex. In some cases, bat ectoparasite genetic population structure mirrors the genetic population structure of their bat hosts (Talbot *et al.*, 2016; Pejić *et al.*, 2022; McKee *et al.*, 2024). In other systems, bat ectoparasites lack genetic population structure even when host populations display structure (e.g. (Olival *et al.*, 2013; van Schaik *et al.*, 2018). The converse—where bat ectoparasites display population structure not evident among their bat hosts—can also occur (Speer *et al.*, 2019). Population-specific factors other than structure can also impact the organisms hosted by bats. Age structure, presence of anthropogenic food sources, and elevational gradients have also been shown to impact viral diversity, while in vampire bats, host genetic distances and colony size were found to have no effect (Bergner *et al.*, 2020). The conflicting evidence presented here suggests that certain “rules” governing these networks are not obvious from studying singular host species, and would benefit from a unified framework (**Fig. 2**).

Bats enjoy a cosmopolitan distribution in part because of their species diversity as well as their highly vagile nature. Bats are among the most mobile vertebrates on Earth, with some species embarking on long-distance migrations similar to those of whales or birds (Peel *et al.*, 2013; Welbergen *et al.*, 2020; Hurme *et al.*, 2022). As a result, bats have the ability to disperse their hosted organisms across a variety of biomes spread over large geographic scales. For example, some species have continental-scale migrations that have the potential to regularly move parasites over long distances (Popa-Lisseanu & Voigt, 2009; Peel *et al.*, 2013; Cryan, Stricker & Wunder, 2014); however, even rare vagrants might introduce parasites to new regions (Hamilton *et al.*, 2012). In addition to being able to move long distances, some bats form dense aggregations, while others roost in small groups or completely alone. This social behavior can have a strong impact on the sharing of hosted organisms, which has been extensively reviewed by (Webber & Willis, 2016). For example, co-roosting species in caves have a higher likelihood of pathogen sharing (Langwig *et al.*, 2012; Willoughby *et al.*, 2017). Ectoparasite prevalence and intensity can be affected by bat movement between summer and winter roosts, fall swarming behaviors, and formation of maternity colonies, which may in turn be mediated by anthropogenic change and climate variables, as discussed in section 4 (Webber, Czenze & Willis, 2015; Frank *et al.*, 2016; van Schaik & Kerth, 2017).

Traits of individual bat-hosted organisms may explain some of these patterns: for example, bat flies pupate in the roost and must locate an appropriate host within the roost after they emerge, while wing mites may rely more heavily on direct contact between bats to transfer between individual hosts (Pejić *et al.*, 2022), and some mites may use bats phoretically to reach new flowering plants (Tschapka & Cunningham, 2004). It is hypothesized that aspects of host behavior, such as fission/fusion dynamics and roost switching, are a parasitism avoidance strategy that works by interrupting direct contact between hosts (Reckardt & Kerth, 2007; Webber & Willis, 2016). Bat behavior and social systems can therefore influence ectoparasite dispersal and population structure, with bat species that roost in larger groups, intermix between colonies, or disperse over longer distances typically associated with less population structure among their ectoparasites, while ectoparasites of solo-roosting bats that disperse over shorter distances may display more genetic diversity overall and stronger levels of genetic population differentiation (Bruyndonckx *et al.*, 2009; van Schaik *et al.*, 2014). This might make those parasites more vulnerable to changes in their hosts or broader habitats, but few studies synthesize this information to evaluate extinction risk to microbes or parasites (but see (Speer, Dheilly & Perkins, 2020). Finally, for more ubiquitous organisms such as bacteria, host gregariousness can have a homogenizing effect on the microbiome. Concerted changes in fur and skin microbiota in colonies as a whole over time are linked to close contact between individuals, genetic factors, and environmental factors such as diet and climate (Lemieux-Labonté *et al.*, 2016; Avena *et al.*, 2016; Winter *et al.*, 2017; Kolodny *et al.*, 2019; Speer *et al.*, 2024). Bat dispersal thus impacts associated hosted organisms in specific ways that reflect the interaction between evolution, ecology, and behavior of bats and hosted organisms.

In addition to being social, many bat species also have remarkably long lifespans. These long lives, an average of 3.5 times longer than non-flying placental mammals of similar body mass (Wilkinson & South, 2002), represent an opportunity for long-term colonization—and perhaps *in situ* evolution— not found in other small mammals (Hughes *et al.*, 2018; Brook *et al.*,

2023). A proposed explanation for such long lifespans is that this feature evolved as a consequence of the metabolic changes associated with powered flight; although the mechanisms are still unclear, there is a relationship between longevity and ability to fly in both birds and mammals (Healy *et al.*, 2014). Other explanations, including predator release, are related to the evolution of flight but not necessarily as a physiological consequence (Brunet-Rossinni & Austad, 2004). For example, *Mystacina tuberculata*, endemic to New Zealand, frequently forages on the ground (Jones *et al.*, 2003) in support of the predator release hypothesis for the evolution of flight. As another proposed consequence of the metabolic demands of flight, bats have co-evolved unique immune repertoires that enable them to asymptotically host pathogens that would cause severe symptoms or death in other mammals (Brook & Dobson, 2015; Schountz *et al.*, 2017). It was previously hypothesized that bats have daily metabolic patterns that mimic fever, which might allow them to better tolerate viruses (O’Shea *et al.*, 2014), but current research suggests that viral tolerance is more likely a downstream effect of adaptations required for dealing with the metabolic stress of flight (Irving *et al.*, 2021; Toshkova *et al.*, 2024). These unique metabolic traits might be related, and may also allow bats to both host unique organisms and facilitate their evolution.

Finally, while bats are warm-blooded, they vary their core body temperatures over daily and seasonal time periods, and some species may even modulate the size of digestive organs, representing a dynamic and potentially challenging environment for the organisms they host (McGuire, Fenton & Guglielmo, 2013; Carey & Assadi-Porter, 2017). This unique combination of traits is reflected in the identity and diversity of bat-associated organisms, but direct relationships between host traits and the survival or persistence of hosted organisms remains poorly studied. For example, seasonal physiological changes have been shown to alter the gut microbial community, and in turn might also alter the metabolic capacity of those microbes to depend less on carbohydrates consumed during active foraging and more on lipids mobilized from fat stores (Xiao *et al.*, 2019; Liu *et al.*, 2023). Conversely, the drastic shift in host environment during hibernation is associated with changes at the immunological and metabolomic level that might seasonally remodel the function or composition of the microbial community (Carey & Assadi-Porter, 2017). As one illustrative example, hibernation of several Neartic bat species slows rabies virus replication and allows “overwintering” of the infection (George *et al.*, 2011; Davis *et al.*, 2016). The impact of seasonality on bat-microorganism interactions remains unclear, and might have important immunological consequences that inform questions about longevity (Wilkinson & Adams, 2019). As the multitrophic interactions of bats, their environments, and the organisms they host remains to be explored for many taxa (van Schaik, Dekeukeleire & Kerth, 2015a; Haelewaters *et al.*, 2021), further characterizing broader patterns in how bat-hosted organisms are constrained by host biology remains an important research priority amenable to study using the “Bats in/as Habitats” framework. While bats generally operate at the extreme edge of mammalian adaptation, the variation across bat species in vagility, lifespan, use of heterothermy, and gregariousness provides examples that also serve to illustrate how these traits in other mammals might influence the abilities of other species to host and share mammal-hosted organisms.

3.b. Hosted organisms influence bat health and survival

Like other mammals, bats host a range of organisms, including pathogenic, beneficial, and facultative associates which variably impact host bat populations (Table 1). One trait that sets bats apart from other mammals is their extraordinary resistance to some types of parasites or pathogens that are highly virulent in other animals (e.g. filoviruses and henipaviruses; Field *et al.*, 2011; Guito *et al.*, 2021). This trait enables them to act as reservoirs of pathogens, such as RNA viruses (Vazquez and Lauterbur *et al.*, 2024), rather than experiencing the population declines that these infections can precipitate in other animals. With limited exceptions, microbes are not a major cause of mortality in bats (O'Shea *et al.*, 2016). The most notable exception is *Pseudogymnoascus destructans*, the causative fungal agent of white-nose syndrome (WNS), which has led to severe, sustained bat mortality in the United States and Canada. Since its emergence in North America in 2007, WNS has driven previously abundant bat species to the edge of extinction (Cheng *et al.*, 2021; Hoyt, Kilpatrick & Langwig, 2021). Other types of endoparasites, including protozoan parasites and helminths, may induce bat mortality in cases of severe infection, but more often have sublethal effects. In most cases, ectoparasites do not cause bat mortality despite imposing energetic costs (Giorgi *et al.*, 2001), but act as important vectors of viruses (Ramírez-Martínez *et al.*, 2021), bacteria (McKee *et al.*, 2021), and protozoa (Szentiványi *et al.*, 2023) to their host bat species and potentially between bats and other animals (Szentiványi *et al.*, 2024). One exception is the paralysis tick, *Ixodes holocyclus*, which has contributed to population declines in the spectacled flying fox (*Pteropus conspicillatus*), first noted in the 1980s following a mass bat mortality event in eastern Australia (Buettnner *et al.*, 2013). The authors posited that a lack of native food sources drove a shift in the feeding ecology of *P. conspicillatus* towards invasive tobacco plants that supported greater infestation with paralysis ticks. In other mammals, ectoparasitism has been shown to impact environmental-scale processes by affecting host population size; for example, sarcoptic mange caused a dramatic population decline in the vicuña, restructuring trophic interactions and supplanting top-down effects by predators (Monk *et al.*, 2022). The link between parasite-driven population declines in bats and ecosystem-scale processes has not been well-studied and potential future studies to establish this link are limited by a lack of information about the biodiversity, systematics, and host-specificity of bat ectoparasites.

In addition to hosting organisms with deleterious or neutral health impacts, bats also have a normal microbiota that support their nutrition and health. For example, fruit-, blood-, and meat-eating bats have gut microbiota members that supplement their specialized diets with missing nutrients (Zepeda Mendoza *et al.*, 2018; Aizpurua *et al.*, 2021; Ingala *et al.*, 2021). Interestingly, these roles can be fulfilled by many microbes, suggesting that beneficial members may be highly interchangeable as long as they perform the same critical functions (Phillips *et al.*, 2017; Song *et al.*, 2019). Because bat microbiomes are often strongly linked to their local environment (Lutz *et al.*, 2019; Viquez-R *et al.*, 2021), it is essential to understand how perturbations in habitats may be reflected in the microbiota, especially if they disrupt beneficial functions contributed by these microbes. Further, there may be interactions among microbiota community members hosted by bats that can be mediated by the broader environment, such as the relationships of fungi from cave walls with bacterial and fungal microbiomes on bat skin (Ange-Stark *et al.*, 2023; Speer *et al.*, 2024).

Community-level interactions may involve ectoparasites hosting bacteria and viruses, interactions between microorganisms within the bat and ectoparasite hosts, and hyperparasitism (i.e., a parasite of a parasite). Ectoparasites themselves can be hosts to other organisms such as parasitic worms (e.g. filariae, helminths), protozoa (e.g. haemosporidian parasites, trypanosomes), bacteria (e.g. *Bartonella* spp.), viruses (e.g. Kanyawara virus) and fungi (e.g. Laboulbeniales) (Adam & Landau, 1973; Morse *et al.*, 2012; Reeves *et al.*, 2016; Goldberg *et al.*, 2017; Abundes-Gallegos *et al.*, 2018; Szentiványi *et al.*, 2018). The infection of a parasite with a different parasitism is a common phenomenon in nature though still largely understudied (Parratt & Laine, 2016; Haelewaters *et al.*, 2021). Infections with Laboulbeniales fungi or *Polychromophilus* parasites negatively impact the survival/lifespan of parasitic bat flies (Witsenburg, Schneider & Christe, 2015; Szentiványi *et al.*, 2020). Additionally, bat ectoparasites can transmit some of these microorganisms to their host bats and thus serve as vectors in the life cycle of certain microorganisms (e.g. blood parasites in nycteribiid bat flies of miniopterid bat species) or as mechanical vectors whereby microorganisms are transferred to bats when insects are consumed (Adam & Landau, 1973; Tendu *et al.*, 2022). Co-infections, simultaneous infections with multiple parasites in an individual host, are also common (Bordes & Morand, 2011; Szentiványi, Christe & Glaizot, 2019). Thus, bats are involved in multi-level parasitic systems and the ecology, behavior, and environment of bat species and their associated ectoparasites may shape these systems. Interactions among the trophic levels may be an important driver of microevolutionary processes (Szentiványi *et al.*, 2019; Haelewaters *et al.*, 2021), but these relationships need further investigation.

Interactions within a community of parasites and microorganisms exploiting the same host individual can be direct (e.g. competition for resources) or indirect (e.g. through immunological pathways; Pedersen & Fenton, 2007, 2019; Graham, 2008; Knowles *et al.*, 2013; Hellard *et al.*, 2015). For example, microbes may indirectly mediate host-parasite interactions (Speer, 2022); correlations have been found between the composition of bacterial communities on the skin of bats and the prevalence of dipteran ectoparasites (Lutz, Gilbert & Dick, 2022). Direct interactions can also occur; bat skin bacteria have been shown to have anti-fungal effects on the WNS pathogen, *P. destructans* (Lemieux-Labonté *et al.*, 2017). Ectoparasites may also actively avoid feeding on hosts with higher hemoparasite loads as an adaptive response given the negative effects of hemoparasites on bat fly survival (Witsenburg *et al.*, 2015). The result of these community-level interactions can be variable depending on whether the presence of one ectoparasite or microorganism affects the presence of other organisms (Hoarau, Mavingui & Lebarbenchon, 2020). However, without sufficient data on the microbiota and parasites hosted by bats, our understanding of these ecological relationships remains fundamentally limited.

Coinfections may be the result of direct interactions between the co-hosted organisms, or they may be incidental owing to a shared preference for an environment inhabited by bats or by some behavior that facilitates cotransmission (Patterson, Dick & Dittmar, 2007; Zacks, 2008; Winter *et al.*, 2017). If, for example, bat species in caves are common hosts of specific nycteribiid bat flies, they might also be common hosts of *Polychromophilus* (bat malaria) blood parasites. In contrast, tree-roosting bats may be less frequently parasitized by nycteribiids and therefore less common as hosts of *Polychromophilus* blood parasites (Sándor *et al.*, 2021). While tree-roosting pteropodids have also been recorded to have nycteribiid flies, they typically have a lower fly load than cave-roosting pteropodids (Maa, 1962; Allison, 1987). In areas where

different bat species aggregate together, nycteribiid flies and the microorganisms they host could infect other bat species, depending on the host-specificity of the ectoparasite species (Bajić *et al.*, 2023). Currently, it is difficult to tell whether coinfections are due to direct facilitation of one organism by another (either host–parasite or parasite–parasite), or whether organisms arrive at bat hosts due to broader factors in the environment. One such factor that may result in incidental coinfections relates back to bat vagility; a few studies in bats and birds suggest that rare malaria parasites may be spread to new hosts during migration events (Schaer *et al.*, 2019; de Angeli Dutra *et al.*, 2021; Sándor *et al.*, 2021). The relative contributions of within-host interactions vs. between-host spread are unclear and merit further investigation under a unified framework.

The existence of these community-level interactions within a single host individual, made more complex by the interactions of individual hosts with each other and their habitat, highlight the importance of regarding hosts as “habitats” for these communities of interacting organisms. This perspective of hosts as habitats opens the door more widely for exploring the impacts of host biology on hosted organism communities, and how environmentally-mediated changes to host biology can influence hosted organism communities and in turn their impact on host health. This is a required step for investigating the outside-in and inside-out feedbacks between environment, bat, and hosted organisms, as discussed further in section 4 below.

3.c. Effects of anthropogenic change on bats as habitats

Anthropogenic change may directly impact bat-hosted organisms or be filtered through hosts, therefore having profound effects on these microbial and parasite communities, above and beyond the scale of natural change. These filtering mechanisms may include physiological stress to the hosts, changes to the hosts’ population structure and dispersal patterns, and changes in overall host community diversity at the landscape level.

Host-mediated effects have been commonly observed in bat systems, with notable case studies having explored the role of habitat disturbance in shaping bat stress physiology and/or immunity in ways that affect bat-hosted organisms (Table 1). For example, studies of Neotropical bat communities in Belize have suggested exposure to heavy metals such as mercury suppress host innate immunity, in most cases increase the prevalence of intracellular bacteria (i.e., *Bartonella* and hemotropic mycoplasmas) through weakened neutrophil response (Becker *et al.*, 2021). Despite studies showing apparent correlations between environmental toxicants and the diversity of bat-hosted organisms (Korine *et al.*, 2017; Mehl *et al.*, 2021; Lobato-Bailón *et al.*, 2023), *direct* impacts on parasites (i.e., not mediated by impacts on the host) are difficult to show and represent a significant knowledge gap (**Fig. 3**). Similarly, studies in Malaysia have found elevated measures of physiological stress and inflammation in Palearctic bats roosting in disturbed habitats, which may manifest in shaping seasonal patterns of shedding for some (but not all) viruses (Seltmann *et al.*, 2017b, 2017a). Anthropogenic stress can also compound normal seasonal stress due to migration, breeding, or hibernation. Furthermore, studies in Australia have shown that poor-quality urban and agricultural habitats occupied by flying foxes outside their typical range are associated with increased shedding of Hendra virus, with effects most pronounced in periods of additional physiological stress (e.g. winters following food shortage events; Becker *et al.*, 2023; Eby *et al.*, 2023).

While direct anthropogenic disturbance can impact host stress, not all impacts on hosted organisms are the direct results of stress. In other cases, pressure from humans causes bats to alter patterns of dispersal or aggregation. For example, impacts on ectoparasite loads were found to be nuanced and context-specific, with cave complexity and population density of hosts interacting with disturbance (Phelps & Kingston, 2018). Intense disturbance of bats at caves (e.g. hunting, culling, intensive guano mining) can ultimately cause bats to abandon them as roosts (McCracken, 1986; Furey & Racey, 2016). In landscapes where suitable roosts are limited, this may increase aggregations at refugial roosts (those inaccessible to people), with consequences for transmission dynamics of host-associated microbes and parasites (Obitte, 2023).

Effects of anthropogenic change on bat-hosted organisms can also be detected at the coarsest scale—overall biodiversity loss. These effects are especially evident for habitat fragmentation and species loss from the landscape. For example, a study examining patterns in the microbiomes of bat flies in Brazil found that as habitat patch area decreased, the bacteria hosted by the bat flies demonstrated consistent, correlated changes in relative abundance. In contrast, microbiomes of bat flies in larger habitat patches showed heterogeneous associations (Speer *et al.*, 2022). These findings suggest that network interactions may be shaped by factors *two levels* removed (first through the bat fly hosting the microbes, and then through the bat hosting the parasite). Additionally, high host diversity can decrease the risk of infectious diseases spreading within biological communities—a phenomenon called the “dilution effect” (Keesing, Holt & Ostfeld, 2006). An example of the dilution effect can be seen with Lyme disease; when ticks feed on a great diversity of mammals, not all of them will be competent hosts for *Borrelia burgdorferi*, thus “diluting” the infection risk exerted by highly competent hosts (LoGiudice *et al.*, 2003; Keesing & Ostfeld, 2021). However, the dilution effect may be a phenomenon specific to particular types of host-pathogen interactions, and it is worth noting that tests of the dilution effect have very rarely been applied to bats and their hosted organisms (Cottontail, Wellinghausen & Kalko, 2009; Meyer *et al.*, 2024). Rigorously testing the dilution effect would require investigating changes in host abundance, overall biodiversity change, and variation in host competence, which requires a cohesive and integrative framework that we advocate for here. In addition to species diversity, other types of diversity (functional, spatial, genetic, etc.) can also play a role in mediating bat/bat-hosted organism interactions, but are comparatively understudied (Naeem, Duffy & Zavaleta, 2012).

Despite promising advances in understanding these processes, the mechanistic links between habitat disturbance, stress and immunity, and bat/bat-hosted organism interactions remain poorly understood, with a particular need to characterize the physiological changes in bats across habitats and over time (Gonzalez & Banerjee, 2022; Becker & Banerjee, 2023). In addition, there is a need to understand how disturbance influences bat movements and roosting ecology, as resultant changes to inter- and intra-specific interactions, primarily at roosts, can influence transmission dynamics and parasite cycles (Willoughby *et al.*, 2017; McKee *et al.*, 2019; Simonis & Becker, 2023). Even indirect or infrequent interactions (e.g. sharing roosts at different times) can modify pathogen transition dynamics (Hoyt *et al.*, 2018).

These integrations of bats, their habitats, and their hosted organisms have salient implications for global health. Degraded habitats can increase direct interactions between bats and humans or their domestic animals, but can also foster indirect interactions by increasing

habitat sharing. Additionally, deforestation and land use change increase the contact area between bats and other organisms (Eby *et al.*, 2023). Emerging evidence also suggests that the conversion of agricultural landscapes further feeds back by decreasing community diversity (e.g. monocultural plots), and that this has measurable changes in bat-hosted organism diversity (Alpizar *et al.*, 2021). Declines in habitat quality via land conversion may intersect with downstream effects, such as altering contacts between bats and other species, but the combined effect of these parameters on pathogen spread represents an ongoing knowledge gap.

4. A systems-based approach to complex interactions

A systems-based approach is one in which species and ecological interactions are thought of in terms of networks and analyzed holistically instead of in the traditional biologically reductive scope. This approach provides a way to understand the mechanisms and drivers of the complex interactions that make up global biodiversity. Because the relationships among environment, macrofauna, and hosted organisms are nested and hierarchical, they not only feed back among themselves, but can be modulated by changes at every level.

While bats may mediate the impact of the habitat on their hosted organisms and vice versa, it is also possible for changes at any of these levels to generate feedbacks that reverberate throughout the system (**Fig 3**). As cited previously, there are studies linking individual pieces of this network of interactions, but understanding these complex phenomena more broadly requires a systems-based approach. One way of thinking about relationships between bats, hosted organisms, and their environment is to consider bats as an extended phenotype for their hosted organisms, and those organisms as an extended phenotype of the bats. Another way is to think about individual bats as habitat patches, which requires considering metapopulation and metacommunity dynamics of the hosted organisms. As a hypothetical example, the environment can impact host stress responses (Seltmann *et al.*, 2017b), which can then change the composition of the gut microbiota (Stothart, Palme & Newman, 2019), which can then lead to decreased digestive efficiency (Aizpurua *et al.*, 2021; Ingala *et al.*, 2021), which ultimately may feed back on bat health *vis-a-vis* poorer body condition or immune response (Berman *et al.*, 2023). The knock-on effects of declining bat health could have global consequences if they result in a decrease in important ecosystem services that bats render or increased spillover of potentially zoonotic pathogens. While there are individual studies that address one or perhaps a few of these levels of change, there is no one study that links all of these processes even in a single host species.

While a large amount of research effort has been dedicated to studying individual elements of these interactions, important emergent properties will be lost unless the study is explicitly conceived as a *network* of interactions that is greater than the sum of its parts. The existence of both “missing links” and “forbidden links”, which are interactions that are not detected or *do not* occur, respectively, are important to understand, but not obvious unless the network is fully defined (Olesen *et al.*, 2010; Jordano, 2016). For example, there are developmental, physical limitations on bat skulls that prevent them from having certain shapes and might restrict their evolvability (Sorensen *et al.*, 2014). These “rules” are largely difficult to observe, but by using a network-level view, it may be possible to detect them through the shape and structure of the network. This kind of thinking has been applied to other ecological systems,

such as the ecological interactions of predators and prey on the Serengeti (Carroll, 2016), but has rarely been applied to the multi-tiered system of habitats, organisms, and the organisms they host.

A key facet that differentiates this paradigm from typical predator-prey or plant-pollinator interactions is that we do not often consider predators or pollinators as “ecosystems” in their own right, but rather part of some larger ecosystem. The reason that we need to consider environment-macrofauna-hosted organism connections more explicitly is because the macrofauna at the center of the network have their own behaviors and physiologies that can be impacted in both a top-down and also bottom-up fashion. This review has uncovered some knowledge gaps that can *only* be addressed through a framework that considers bats both as organisms within habitats and as habitats themselves. Similar knowledge gaps exist for other taxa that might be placed as the node of such a framework.

The basis of the mechanistic assembly in this system (e.g. genetics, physiology, development) is still poorly defined, and cannot be fully understood unless conceptualized as a network. In an applied sense, this limits our ability to make predictions about the system or its constituent parts. For example, how can we predict if rabies will become more widespread in Latin America after cutting down the Amazon rainforest if we do not understand the processes being impacted by this perturbation? If rabies transmission dynamics are a complex interplay among human activities, broader habitat quality, the intrinsic biology of bats, and functionality of beneficial microorganisms, then it will be difficult to make predictions about any of the links in that network if one does not fully sample all of the interactions among the constituent parts. To best study these knowledge gaps, it is thus necessary to incorporate the “Bats in/as Habitats” framework at the outset of study design.

This framework is also useful for approaching questions about climate change and disease. While the One Health concept addresses the links between habitat quality and ecosystem health, it often falls short of determining mechanistic drivers that influence specific risk factors within the system. A few of these mechanistic limitations are identified in the literature, including the conflation of native habitat loss and resource provisioning under “habitat loss”, and lack of understanding of interactions among pathogens both within and between hosts (Kessler *et al.*, 2018). Ultimately, a better understanding of mechanisms is what allows us to make better predictions. For example, the life cycles of bat-hosted organisms may mediate whether the effects of climate change are felt directly (e.g. parasites that spend time away from their host) or are mediated indirectly through the bat host (e.g. obligate intracellular viruses and bacteria). To date, no study integrates habitat disturbance with parasite ecology and host behavior to resolve these complex interactions, but such a study would shed light on the higher-order interactions between bats, their habitats, and the organisms they host (Gallana *et al.*, 2013).

An important caveat to the predictive value of this framework is that it may be jeopardized by the instability of climate change. While many of the changes we present are incremental, repeated and/or severe climate perturbations may produce stochastic and non-linear responses that are difficult to predict based on the data we already have (Oliveira *et al.*, 2022). Even if the current data are no longer useful for making predictions under these scenarios, the framework itself will remain useful as a conceptual basis for understanding the linkages that can be severed or altered under extreme climate conditions.

5. CONCLUSION

Having a conceptual framework to understand complex networks of interactions is an increasingly important goal in scientific research (e.g. the U.S. National Science Foundation's Big Ideas: "Rules of Life", the "One Health" concept, the United Nations Quadripartite). Researchers tend to develop highly specialized areas of expertise, but the proposed framework calls upon a wide variety of expertise to elucidate the larger picture and make connections across biological scales. What we advocate for in this review is ultimately a more explicit connection between levels of biological organization and an expansion of the term "ecosystem" to include the nested interactions reviewed here. An additional element of complexity that could be integrated in such a framework is understanding the relationships of organisms that are directly dependent on other organisms, but are not necessarily directly hosted by them (e.g. guanoophilic troglobionts that do not live on bats, but remain fully dependent on their existence). While we use bats as a model system to develop this framework, the end goal is a framework that is highly translational to other systems to predict risk factors and threats to other biological entities.

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References

- Abundes-Gallegos, J., Salas-Rojas, M., Galvez-Romero, G., Perea-Martínez, L., Obregón-Morales, C.Y., Morales-Malacara, J.B., Chomel, B.B., Stuckey, M.J., Moreno-Sandoval, H., García-Baltazar, A., Noguera-Torres, B., Zuñiga, G. & Aguilar-Setién, A. (2018) Detection of Dengue Virus in Bat Flies (Diptera: Streblidae) of Common Vampire Bats, *Desmodus rotundus*, in Progreso, Hidalgo, Mexico. *Vector Borne and Zoonotic Diseases* **18**, 70–73.
- Adam, J.P. & Landau, I. (1973) Developmental stages of *Polychromophilus* sp., a parasite of insectivorous bats from the Congo-Brazzaville, in the nycteribiid fly *Penicillidia fulvida* Bigot 1889. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **67**, 5–6.
- Aguirre, L.F. (2002) Structure of a Neotropical Savanna Bat Community. *Journal of Mammalogy* **83**, 775–784.
- Aizpurua, O., Budinski, I., Georgiakakis, P., Gopalakrishnan, S., Ibañez, C., Mata, V., Rebelo, H., Russo, D., Szodoray-Parádi, F., Zhelyazkova, V., Zrnčić, V., Gilbert, M.T.P. & Alberdi, A. (2018) Agriculture shapes the trophic niche of a bat preying on multiple pest arthropods across Europe: Evidence from DNA metabarcoding. *Molecular Ecology* **27**, 815–825.
- Aizpurua, O., Nyholm, L., Morris, E., Chaverri, G., Herrera Montalvo, L.G., Flores-Martinez, J.J., Lin, A., Razgour, O., Gilbert, M.T.P. & Alberdi, A. (2021) The role of the gut microbiota in the dietary niche expansion of fishing bats. *Animal Microbiome* **3**, 76.
- Allen, L.C., Turmelle, A.S., Widmaier, E.P., Hristov, N.I., McCracken, G.F. & Kunz, T.H. (2011) Variation in Physiological Stress between Bridge- and Cave-Roosting Brazilian Free-Tailed Bats. *Conservation Biology* **25**, 374–381.
- Allison, F.R. (1987) Notes on the bat flies (Diptera: Nycteribiidae) of Australian Megachiroptera (Pteropodidae). *Australian Mammalogy* **10**, 111–113. CSIRO PUBLISHING.
- Alpizar, P., Risely, A., Tschapka, M. & Sommer, S. (2021) Agricultural Fast Food: Bats Feeding in Banana Monocultures Are Heavier but Have Less Diverse Gut Microbiota. *Frontiers in Ecology and Evolution* **9**.
- de Angeli Dutra, D., Fillion, A., Fecchio, A., Braga, É.M. & Poulin, R. (2021) Migrant birds disperse haemosporidian parasites and affect their transmission in avian communities. *Oikos* **130**, 979–988.
- Ange-Stark, M., Parise, K.L., Cheng, T.L., Hoyt, J.R., Langwig, K.E., Frick, W.F., Kilpatrick, A.M., Gillece, J., MacManes, M.D. & Foster, J.T. (2023) White-nose syndrome restructures bat skin microbiomes. *Microbiology Spectrum* **11**, e02715-23.
- Avena, C.V., Parfrey, L.W., Leff, J.W., Archer, H.M., Frick, W.F., Langwig, K.E., Kilpatrick, A.M., Powers, K.E., Foster, J.T. & McKenzie, V.J. (2016) Deconstructing the Bat Skin Microbiome: Influences of the Host and the Environment. *Frontiers in Microbiology* **7**.
- Avila-Flores, R. & Medellín, R.A. (2004) Ecological, Taxonomic, and Physiological Correlates of Cave Use by Mexican Bats. *Journal of Mammalogy* **85**, 675–687.
- Aziz, S.A., McConkey, K.R., Tanalgo, K., Sritongchuay, T., Low, M.-R., Yong, J.Y., Mildenstein, T.L., Nuevo-Diego, C.E., Lim, V.-C. & Racey, P.A. (2021) The Critical Importance of Old World Fruit Bats for Healthy Ecosystems and Economies. *Frontiers in Ecology and Evolution* **9**.
- Bajić, B., Werb, O., Budinski, I., Blagojević, J., Schaer, J. & van Schaik, J. (2023) Non-invasive investigation of *Polychromophilus* parasite infections in bat populations in Serbia using bat flies. *Parasites & Vectors* **16**, 170.
- Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., et al. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences* **104**, 18555–18560.

- Becker, D.J. & Banerjee, A. (2023) Coupling field and laboratory studies of immunity and infection in zoonotic hosts. *The Lancet Microbe* **4**, e285–e287.
- Becker, D.J., Czirják, G.Á., Volokhov, D.V., Bentz, A.B., Carrera, J.E., Camus, M.S., Navara, K.J., Chizhikov, V.E., Fenton, M.B., Simmons, N.B., Recuenco, S.E., Gilbert, A.T., Altizer, S. & Streicker, D.G. (2018) Livestock abundance predicts vampire bat demography, immune profiles and bacterial infection risk. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373**, 20170089. Royal Society.
- Becker, D.J., Eby, P., Madden, W., Peel, A.J. & Plowright, R.K. (2023) Ecological conditions predict the intensity of Hendra virus excretion over space and time from bat reservoir hosts. *Ecology Letters* **26**, 23–36.
- Becker, D.J., Nachtmann, C., Argibay, H.D., Botto, G., Escalera-Zamudio, M., Carrera, J.E., Tello, C., Winiarski, E., Greenwood, A.D., Méndez-Ojeda, M.L., Loza-Rubio, E., Lavergne, A., de Thoisy, B., Czirják, G.Á., Plowright, R.K., et al. (2019) Leukocyte Profiles Reflect Geographic Range Limits in a Widespread Neotropical Bat. *Integrative and Comparative Biology* **59**, 1176–1189.
- Becker, D.J., Speer, K.A., Korstian, J.M., Volokhov, D.V., Droke, H.F., Brown, A.M., Baijnauth, C.L., Padgett-Stewart, T., Broders, H.G., Plowright, R.K., Rainwater, T.R., Fenton, M.B., Simmons, N.B. & Chumchal, M.M. (2021) Disentangling interactions among mercury, immunity and infection in a Neotropical bat community. *Journal of Applied Ecology* **58**, 879–889.
- Bennett, A.J., Bushmaker, T., Cameron, K., Ondzie, A., Niama, F.R., Parra, H.-J., Mombouli, J.-V., Olson, S.H., Munster, V.J. & Goldberg, T.L. (2019) Diverse RNA viruses of arthropod origin in the blood of fruit bats suggest a link between bat and arthropod viromes. *Virology* **528**, 64–72.
- Bergmans, W. (1997) Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 5. The genera *Ussonycteris* Andersen, 1912, *Myonycteris* Matschie, 1899 and *Megaloglossus* Pagenstecher, 1885; general remarks and conclusions; annex: key to all species. *Beaufortia* **47**, 11–90.
- Bergner, L.M., Orton, R.J., Benavides, J.A., Becker, D.J., Tello, C., Biek, R. & Streicker, D.G. (2020) Demographic and environmental drivers of metagenomic viral diversity in vampire bats. *Molecular Ecology* **29**, 26–39.
- Berman, T.S., Weinberg, M., Moreno, K.R., Czirják, G.Á. & Yovel, Y. (2023) In sickness and in health: the dynamics of the fruit bat gut microbiota under a bacterial antigen challenge and its association with the immune response. *Frontiers in Immunology* **14**.
- Betke, B.A., Gottdenker, N.L., Meyers, L.A. & Becker, D.J. (2024) Ecological and evolutionary characteristics of anthropogenic roosting ability in bats of the world. *iScience* **27**.
- Bordes, F. & Morand, S. (2011) The impact of multiple infections on wild animal hosts: a review. *Infection Ecology & Epidemiology* **1**, 7346.
- Boyles, J.G., Cryan, P.M., McCracken, G.F. & Kunz, T.H. (2011) Economic Importance of Bats in Agriculture. *Science* **332**, 41–42.
- Brook, C.E. & Dobson, A.P. (2015) Bats as ‘special’ reservoirs for emerging zoonotic pathogens. *Trends in Microbiology* **23**, 172–180.
- Brook, C.E., Rozins, C., Guth, S. & Boots, M. (2023) Reservoir host immunology and life history shape virulence evolution in zoonotic viruses. *PLOS Biology* **21**, e3002268.
- Brunet-Rossinni, A.K. & Austad, S.N. (2004) Ageing Studies on Bats: A Review. *Biogerontology* **5**, 211–222.
- Bruyndonckx, N., Henry, I., Christe, P. & Kerth, G. (2009) Spatio-temporal population genetic structure of the parasitic mite *Spinturnix bechsteini* is shaped by its own demography and the social system of its bat host. *Molecular Ecology* **18**, 3581–3592.
- Buchholz, S., Kelm, V. & Ghanem, S.J. (2021) Mono-specific forest plantations are valuable bat habitats: implications for wind energy development. *European Journal of Wildlife*

Research **67**, 1.

- Buettner, P.G., Westcott, D.A., Maclean, J., Brown, L., McKeown, A., Johnson, A., Wilson, K., Blair, D., Luly, J., Skerratt, L., Muller, R. & Speare, R. (2013) Tick Paralysis in Spectacled Flying-Foxes (*Pteropus conspicillatus*) in North Queensland, Australia: Impact of a Ground-Dwelling Ectoparasite Finding an Arboreal Host. *PLOS ONE* **8**, e73078.
- Carey, H.V. & Assadi-Porter, F.M. (2017) The Hibernator Microbiome: Host-Bacterial Interactions in an Extreme Nutritional Symbiosis. *Annual Review of Nutrition* **37**, 477–500.
- Carlson, C.J., Zipfel, C.M., Garnier, R. & Bansal, S. (2019) Global estimates of mammalian viral diversity accounting for host sharing. *Nature Ecology & Evolution* **3**, 1070–1075.
- Carroll, S.B. (2016) *Serengeti rules: the quest to discover how life works and why it matters*. Princeton University Press.
- Cheng, T.L., Reichard, J.D., Coleman, J.T.H., Weller, T.J., Thogmartin, W.E., Reichert, B.E., Bennett, A.B., Broders, H.G., Campbell, J., Etchison, K., Feller, D.J., Geboy, R., Hemberger, T., Herzog, C., Hicks, A.C., et al. (2021) The scope and severity of white-nose syndrome on hibernating bats in North America. *Conservation Biology* **35**, 1586–1597.
- Connell, J.H. (1961) The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle *Chthamalus Stellatus*. *Ecology* **42**, 710–723.
- da Costa, C.F. & Ramos Pereira, M.J. (2022) Aerial insectivorous bats in the Brazilian-Uruguayan savanna: Modelling the occupancy through acoustic detection. *Frontiers in Ecology and Evolution* **10**.
- Cottontail, V.M., Wellinghausen, N. & Kalko, E.K.V. (2009) Habitat fragmentation and haemoparasites in the common fruit bat, *Artibeus jamaicensis* (Phyllostomidae) in a tropical lowland forest in Panamá. *Parasitology* **136**, 1133–1145.
- Cox, P.A., Elmqvist, T., Pierson, E.D. & Rainey, W.E. (1991) Flying Foxes as Strong Interactors in South Pacific Island Ecosystems: A Conservation Hypothesis. *Conservation Biology* **5**, 448–454.
- Cravens, Z.M. & Boyles, J.G. (2019) Illuminating the physiological implications of artificial light on an insectivorous bat community. *Oecologia* **189**, 69–77.
- Cryan, P.M., Stricker, C.A. & Wunder, M.B. (2014) Continental-scale, seasonal movements of a heterothermic migratory tree bat. *Ecological Applications* **24**, 602–616.
- Dai, W., Leng, H., Li, J., Li, A., Li, Z., Zhu, Y., Li, X., Jin, L., Sun, K. & Feng, J. (2024) The role of host traits and geography in shaping the gut microbiome of insectivorous bats. *mSphere* **9**, e00087-24.
- Darwin, C. (1859) *The Origin of Species by Means of Natural Selection*, 6th edition.
- Davis, A.D., Morgan, S.M.D., Dupuis, M., Poulliott, C.E., Jarvis, J.A., Franchini, R., Clobridge, A. & Rudd, R.J. (2016) Overwintering of Rabies Virus in Silver Haired Bats (*Lasiurus noctivagus*). *PLOS ONE* **11**, e0155542.
- Denzinger, A., Kalko, E.K.V., Tschapka, M., Grinnell, A.D. & Schnitzler, H.-U. (2016) Guild Structure and Niche Differentiation in Echolocating Bats. In *Bat Bioacoustics* (eds M.B. Fenton, A.D. Grinnell, A.N. Popper & R.R. Fay), pp. 141–166. Springer, New York, NY.
- Denzinger, A. & Schnitzler, H.-U. (2013) Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology* **4**.
- Detweiler, L.W. & Bernard, R.F. (2023) Wildlife Use of Anthropogenic Structures: A Comprehensive Review of Bridge Use by Bats. *Acta Chiropterologica* **25**, 135–157.
- Duchamp, J.E., Sparks, D.W. & Swihart, R.K. (2010) Exploring the “nutrient hot spot” hypothesis at trees used by bats. *Journal of Mammalogy* **91**, 48–53.
- Dugger, P.J., Blendinger, P.G., Böhning-Gaese, K., Chama, L., Correia, M., Dehling, D.M., Emer, C., Farwig, N., Fricke, E.C., Galetti, M., García, D., Grass, I., Heleno, R., Jacomassa, F.A.F., Moraes, S., et al. (2019) Seed-dispersal networks are more specialized in the Neotropics than in the Afrotropics. *Global Ecology and Biogeography* **28**, 248–261.

- Dunbar, M.B. & Brigham, R.M. (2010) Thermoregulatory variation among populations of bats along a latitudinal gradient. *Journal of Comparative Physiology B* **180**, 885–893.
- Eby, P., Peel, A.J., Hoegh, A., Madden, W., Giles, J.R., Hudson, P.J. & Plowright, R.K. (2023) Pathogen spillover driven by rapid changes in bat ecology. *Nature* **613**, 340–344.
- Edson, D., Field, H., McMichael, L., Jordan, D., Kung, N., Mayer, D. & Smith, C. (2015) Flying-Fox Roost Disturbance and Hendra Virus Spillover Risk. *PLOS ONE* **10**, e0125881.
- Elton, C.S. (1927) *Animal ecology*. In pp. 1–256. Macmillan Co, New York.
- Estrada-Villegas, S., McGill, B.J. & Kalko, E.K.V. (2012) Climate, habitat, and species interactions at different scales determine the structure of a Neotropical bat community. *Ecology* **93**, 1183–1193.
- Fensome, A.G. & Mathews, F. (2016) Roads and bats: a meta-analysis and review of the evidence on vehicle collisions and barrier effects. *Mammal Review* **46**, 311–323.
- Ferreira, R.L. (2019) Chapter 57 - Guano communities. In *Encyclopedia of Caves (Third Edition)* (eds W.B. White, D.C. Culver & T. Pipan), pp. 474–484. Academic Press.
- Field, H., Jong, C. de, Melville, D., Smith, C., Smith, I., Broos, A., Kung, Y.H. (Nina), McLaughlin, A. & Zeddeman, A. (2011) Hendra Virus Infection Dynamics in Australian Fruit Bats. *PLOS ONE* **6**, e28678.
- Flaquer, C., Puig-Montserrat, X., Goiti, U., Vidal, F., Curcó, A. & Russo, D. (2009) Habitat selection in *Nathusius' pipistrelle* (*Pipistrellus nathusii*): the importance of wetlands. *Acta Chiropterologica* **11**, 149–155.
- Fleming, T.H., Geiselman, C. & Kress, W.J. (2009) The evolution of bat pollination: a phylogenetic perspective. *Annals of Botany* **104**, 1017–1043.
- Fleming, T.H. & Heithaus, E.R. (1981) Frugivorous Bats, Seed Shadows, and the Structure of Tropical Forests. *Biotropica* **13**, 45–53.
- Fleming, T.H. & Racey, P.A. (eds) (2010) *Island Bats: Evolution, Ecology, and Conservation*. University of Chicago Press, Chicago, IL.
- Florens, F.B.V., Baider, C., Marday, V., Martin, G.M.N., Zmanay, Z., Oleksy, R., Krivek, G., Vincenot, C.E., Strasberg, D. & Kingston, T. (2017) Disproportionately large ecological role of a recently mass-culled flying fox in native forests of an oceanic island. *Journal for Nature Conservation* **40**, 85–93.
- Foley, N.M., Harris, A.J., Bredemeyer, K.R., Ruedi, M., Puechmaille, S.J., Teeling, E.C., Criscitiello, M.F. & Murphy, W.J. (2024) Karyotypic stasis and swarming influenced the evolution of viral tolerance in a species-rich bat radiation. *Cell Genomics* **4**.
- Frank, H.K., Mendenhall, C.D., Judson, S.D., Daily, G.C. & Hadly, E.A. (2016) Anthropogenic impacts on Costa Rican bat parasitism are sex specific. *Ecology and Evolution* **6**, 4898–4909.
- Frick, W.F., Baerwald, E.F., Pollock, J.F., Barclay, R.M.R., Szymanski, J.A., Weller, T.J., Russell, A.L., Loeb, S.C., Medellín, R.A. & McGuire, L.P. (2017) Fatalities at wind turbines may threaten population viability of a migratory bat. *Biological Conservation* **209**, 172–177.
- Frick, W.F., Kingston, T. & Flanders, J. (2020) A review of the major threats and challenges to global bat conservation. *Annals of the New York Academy of Sciences* **1469**, 5–25.
- Froidevaux, J.S.P., Louboutin, B. & Jones, G. (2017) Does organic farming enhance biodiversity in Mediterranean vineyards? A case study with bats and arachnids. *Agriculture, Ecosystems & Environment* **249**, 112–122.
- Furey, N.M. & Racey, P.A. (2016) Conservation Ecology of Cave Bats. In *Bats in the Anthropocene: Conservation of Bats in a Changing World* (eds C.C. Voigt & T. Kingston), pp. 463–500. Springer International Publishing, Cham.
- Gallana, M., Ryser-Degiorgis, M.-P., Wahli, T. & Segner, H. (2013) Climate change and infectious diseases of wildlife: Altered interactions between pathogens, vectors and hosts. *Current Zoology* **59**, 427–437.

- George, D.B., Webb, C.T., Farnsworth, M.L., O'Shea, T.J., Bowen, R.A., Smith, D.L., Stanley, T.R., Ellison, L.E. & Rupprecht, C.E. (2011) Host and viral ecology determine bat rabies seasonality and maintenance. *Proceedings of the National Academy of Sciences* **108**, 10208–10213.
- Gibson, K.E., Rikihisa, Y., Zhang, C. & Martin, C. (2005) Neorickettsia risticii is vertically transmitted in the trematode Acanthatrium oregonense and horizontally transmitted to bats. *Environmental Microbiology* **7**, 203–212.
- Giorgi, M.S., Arlettaz, R., Christe, P. & Vogel, P. (2001) The energetic grooming costs imposed by a parasitic mite (Spinturnix myoti) upon its bat host (Myotis myotis). *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**, 2071–2075.
- Goldberg, T.L., Bennett, A.J., Kityo, R., Kuhn, J.H. & Chapman, C.A. (2017) Kanyawara Virus: A Novel Rhabdovirus Infecting Newly Discovered Nycteribiid Bat Flies Infesting Previously Unknown Pteropodid Bats in Uganda. *Scientific Reports* **7**, 5287.
- Gonçalves, F., Sales, L.P., Galetti, M. & Pires, M.M. (2021) Combined impacts of climate and land use change and the future restructuring of Neotropical bat biodiversity. *Perspectives in Ecology and Conservation* **19**, 454–463.
- Gonzalez, V. & Banerjee, A. (2022) Molecular, ecological, and behavioral drivers of the bat-virus relationship. *iScience* **25**, 104779.
- González-Gutiérrez, K., Castaño, J.H., Pérez-Torres, J. & Mosquera-Mosquera, H.R. (2022) Structure and roles in pollination networks between phyllostomid bats and flowers: a systematic review for the Americas. *Mammalian Biology* **102**, 21–49.
- Grafe, T.U., Schöner, C.R., Kerth, G., Junaidi, A. & Schöner, M.G. (2011) A novel resource–service mutualism between bats and pitcher plants. *Biology Letters* **7**, 436–439.
- Graham, A.L. (2008) Ecological rules governing helminth–microparasite coinfection. *Proceedings of the National Academy of Sciences* **105**, 566–570.
- Grinnell, J. (1917) The Niche-Relationships of the California Thrasher. *The Auk* **34**, 427–433.
- Guito, J.C., Prescott, J.B., Arnold, C.E., Amman, B.R., Schuh, A.J., Spengler, J.R., Sealy, T.K., Harmon, J.R., Coleman-McCray, J.D., Kulcsar, K.A., Nagle, E.R., Kumar, R., Palacios, G.F., Sanchez-Lockhart, M. & Towner, J.S. (2021) Asymptomatic Infection of Marburg Virus Reservoir Bats Is Explained by a Strategy of Immunoprotective Disease Tolerance. *Current Biology* **31**, 257-270.e5.
- Haarsma, A.-J. & Siepel, H. (2013) Macro-evolutionary trade-offs as the basis for the distribution of European bats. *Animal Biology* **63**, 451–471.
- Haelewaters, D., Dick, C.W., Cocherán Pittí, K.P., Dittmar, K. & Patterson, B.D. (2021) Bats, Bat Flies, and Fungi: Exploring Uncharted Waters. In *50 Years of Bat Research* (eds B.K. Lim, M.B. Fenton, R.M. Brigham, S. Mistry, A. Kurta, E.H. Gillam, A. Russell & J. Ortega), pp. 349–371. Springer International Publishing, Cham.
- Hall, R.P., Mutumi, G.L., Hedrick, B.P., Yohe, L.R., Sadier, A., Davies, K.T.J., Rossiter, S.J., Sears, K., Dávalos, L.M. & Dumont, E.R. (2021) Find the food first: An omnivorous sensory morphotype predates biomechanical specialization for plant based diets in phyllostomid bats. *Evolution* **75**, 2791–2801.
- Hamilton, P.B., Cruickshank, C., Stevens, J.R., Teixeira, M.M.G. & Mathews, F. (2012) Parasites reveal movement of bats between the New and Old Worlds. *Molecular Phylogenetics and Evolution* **63**, 521–526.
- Healy, K., Guillerme, T., Finlay, S., Kane, A., Kelly, S.B.A., McClean, D., Kelly, D.J., Donohue, I., Jackson, A.L. & Cooper, N. (2014) Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20140298.
- Hellard, E., Fouchet, D., Vavre, F. & Pontier, D. (2015) Parasite–Parasite Interactions in the Wild: How To Detect Them? *Trends in Parasitology* **31**, 640–652.

- Herrera, J.P., Duncan, N., Clare, E., Fenton, M.B. & Simmons, N. (2018) Disassembly of fragmented bat communities in Orange Walk District, Belize. *Acta Chiropterologica* **20**, 147–159.
- Hjerpe, J., Hedenâs, H. & Elmquist, T. (2001) Tropical Rain Forest Recovery from Cyclone Damage and Fire in Samoa. *Biotropica* **33**, 249–259.
- Hoarau, A.O.G., Mavingui, P. & Lebarbenchon, C. (2020) Coinfections in wildlife: Focus on a neglected aspect of infectious disease epidemiology. *PLOS Pathogens* **16**, e1008790.
- Hodo, C.L., Goodwin, C.C., Mayes, B.C., Mariscal, J.A., Waldrup, K.A. & Hamer, S.A. (2016) Trypanosome species, including *Trypanosoma cruzi*, in sylvatic and peridomestic bats of Texas, USA. *Acta Tropica* **164**, 259–266.
- Howe, H.F. & Smallwood, J. (1982) Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics* **13**, 201–228.
- Hoyt, J.R., Kilpatrick, A.M. & Langwig, K.E. (2021) Ecology and impacts of white-nose syndrome on bats. *Nature Reviews Microbiology* **19**, 196–210.
- Hoyt, J.R., Langwig, K.E., White, J.P., Kaarakka, H.M., Redell, J.A., Kurta, A., DePue, J.E., Scullon, W.H., Parise, K.L., Foster, J.T., Frick, W.F. & Kilpatrick, A.M. (2018) Cryptic connections illuminate pathogen transmission within community networks. *Nature* **563**, 710–713.
- Huang, J.C.-C., Chen, W.-J. & Lin, T.-E. (2021) Landscape and Species Traits Co-Drive Roadkills of Bats in a Subtropical Island. *Diversity* **13**, 117.
- Huang, J.C.-C., Rustiati, E.L., Nusalawo, M. & Kingston, T. (2019) Echolocation and roosting ecology determine sensitivity of forest-dependent bats to coffee agriculture. *Biotropica* **51**, 757–768.
- Hughes, G.M., Leech, J., Puechmaille, S.J., Lopez, J.V. & Teeling, E.C. (2018) Is there a link between aging and microbiome diversity in exceptional mammalian longevity? *PeerJ* **6**, e4174.
- Hurme, E., Fahr, J., Network, E.M., Eric-Moise, B.F., Hash, C.T., O'Mara, M.T., Richter, H., Tanshi, I., Webala, P.W., Weber, N., Wikelski, M. & Dechmann, D.K.N. (2022) Fruit bat migration matches green wave in seasonal landscapes. *Functional Ecology* **36**, 2043–2055.
- Hutchinson, G.E. (1957) Population studies-animal ecology and demography-concluding remarks. In *Cold Spring Harbor symposia on quantitative biology* pp. 415–427. Cold Spring Harbor Lab Press.
- Ingala, M.R., Becker, D.J., Bak Holm, J., Kristiansen, K. & Simmons, N.B. (2019) Habitat fragmentation is associated with dietary shifts and microbiota variability in common vampire bats. *Ecology and Evolution* **9**, 6508–6523.
- Ingala, M.R., Simmons, N.B., Dunbar, M., Wultsch, C., Krampis, K. & Perkins, S.L. (2021) You are more than what you eat: potentially adaptive enrichment of microbiome functions across bat dietary niches. *Animal Microbiome* **3**, 82.
- Irving, A.T., Ahn, M., Goh, G., Anderson, D.E. & Wang, L.-F. (2021) Lessons from the host defences of bats, a unique viral reservoir. *Nature* **589**, 363–370.
- Jones, G., Jacobs, D., Kunz, T., Willig, M. & Racey, P. (2009) Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research* **8**, 93–115.
- Jones, G., Parsons, S., Zhang, S., Stadelmann, B., Benda, P. & Ruedi, M. (2006) Echolocation calls, wing shape, diet and phylogenetic diagnosis of the endemic Chinese bat *Myotis pequinus*. *Acta Chiropterologica* **8**, 451–463.
- Jones, G., Webb, P.I., Sedgeley, J.A. & O'Donnell, C.F.J. (2003) Mysterious *Mystacina*: how the New Zealand short-tailed bat (*Mystacina tuberculata*) locates insect prey. *Journal of Experimental Biology* **206**, 4209–4216.
- Jordano, P. (2016) Sampling networks of ecological interactions. *Functional Ecology* **30**, 1883–1893.

- Kalka, M.B., Smith, A.R. & Kalko, E.K.V. (2008) Bats Limit Arthropods and Herbivory in a Tropical Forest. *Science* **320**, 71–71.
- Kasso, M. & Balakrishnan, M. (2013) Ecological and Economic Importance of Bats (Order Chiroptera). *International Scholarly Research Notices* **2013**, 187415.
- Keesing, F., Holt, R.D. & Ostfeld, R.S. (2006) Effects of species diversity on disease risk. *Ecology Letters* **9**, 485–498.
- Keesing, F. & Ostfeld, R.S. (2021) Dilution effects in disease ecology. *Ecology Letters* **24**, 2490–2505.
- Kessler, M.K., Becker, D.J., Peel, A.J., Justice, N.V., Lunn, T., Crowley, D.E., Jones, D.N., Eby, P., Sánchez, C.A. & Plowright, R.K. (2018) Changing resource landscapes and spillover of henipaviruses. *Annals of the New York Academy of Sciences* **1429**, 78–99.
- Kingston, T. (2013) Response of bat diversity to forest disturbance in Southeast Asia – insights from long-term research in Malaysia. In pp. 169–195.
- Kingston, T., Florens, F.B.V. & Vincenot, C.E. (2023) Large Old World Fruit Bats on the Brink of Extinction: Causes and Consequences. *Annual Review of Ecology, Evolution, and Systematics* **54**, 237–257.
- Kissling, W.D., Dalby, L., Fløjgaard, C., Lenoir, J., Sandel, B., Sandom, C., Trøjelsgaard, K. & Svenning, J.-C. (2014) Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution* **4**, 2913–2930.
- Knowles, S.C.L., Fenton, A., Petchey, O.L., Jones, T.R., Barber, R. & Pedersen, A.B. (2013) Stability of within-host–parasite communities in a wild mammal system. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20130598.
- Kolodny, O., Weinberg, M., Reshef, L., Harten, L., Hefetz, A., Gophna, U., Feldman, M.W. & Yovel, Y. (2019) Coordinated change at the colony level in fruit bat fur microbiomes through time. *Nature Ecology & Evolution* **3**, 116–124.
- Korine, C., Adams, R., Russo, D., Fisher-Phelps, M. & Jacobs, D. (2016) Bats and water: anthropogenic alterations threaten global bat populations. *Bats in the Anthropocene: Conservation of bats in a changing world*, 215–241.
- Korine, C., Pilosof, S., Gross, A., Morales-Malacara, J.B. & Krasnov, B.R. (2017) The effect of water contamination and host-related factors on ectoparasite load in an insectivorous bat. *Parasitology Research* **116**, 2517–2526.
- Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences* **1223**, 1–38.
- Langwig, K.E., Frick, W.F., Bried, J.T., Hicks, A.C., Kunz, T.H. & Kilpatrick, A.M. (2012) Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecology Letters* **15**, 1050–1057.
- Lausen, C.L. & Barclay, R.M.R. (2006) Benefits of Living in a Building: Big Brown Bats (*Eptesicus fuscus*) in Rocks versus Buildings. *Journal of Mammalogy* **87**, 362–370.
- Lemieux-Labonté, V., Simard, A., Willis, C.K.R. & Lapointe, F.-J. (2017) Enrichment of beneficial bacteria in the skin microbiota of bats persisting with white-nose syndrome. *Microbiome* **5**, 115.
- Lemieux-Labonté, V., Tromas, N., Shapiro, B.J. & Lapointe, F.-J. (2016) Environment and host species shape the skin microbiome of captive neotropical bats. *PeerJ* **4**, e2430.
- Lewanzik, D. & Voigt, C.C. (2014) Artificial light puts ecosystem services of frugivorous bats at risk. *Journal of Applied Ecology* **51**, 388–394.
- Liu, S., Xiao, Y., Wang, X., Guo, D., Wang, Y. & Wang, Y. (2023) Effects of Microhabitat Temperature Variations on the Gut Microbiotas of Free-Living Hibernating Animals. *Microbiology Spectrum* **11**, e00433-23.
- Lobato-Bailón, L., García-Ulloa, M., Santos, A., Guixé, D., Camprodon, J., Florensa-Rius, X.,

- Molleda, R., Manzano, R., P. Ribas, M., Espunyes, J., Dias-Alves, A., Marco, I., Migura-Garcia, L., Martínez-Urtaza, J. & Cabezón, O. (2023) The fecal bacterial microbiome of the Kuhl's pipistrelle bat (*Pipistrellus kuhlii*) reflects landscape anthropogenic pressure. *Animal Microbiome* **5**, 7.
- LoGiudice, K., Ostfeld, R.S., Schmidt, K.A. & Keesing, F. (2003) The ecology of infectious disease: Effects of host diversity and community composition on Lyme disease risk. *Proceedings of the National Academy of Sciences* **100**, 567–571.
- Lundberg, J., McFarlane, D. & Van Rentergem, G. (2022) The nitrogen dynamics of Deer Cave, Sarawak, and the role of bat caves as biogeochemical sinks in Tropical Moist Forests. *International Journal of Speleology* **51**, 205–221.
- Lutz, H.L., Gilbert, J.A. & Dick, C.W. (2022) Associations between Afrotropical bats, eukaryotic parasites, and microbial symbionts. *Molecular Ecology* **31**, 1939–1950.
- Lutz, H.L., Jackson, E.W., Webala, P.W., Babyesiza, W.S., Kerbis Peterhans, J.C., Demos, T.C., Patterson, B.D. & Gilbert, J.A. (2019) Ecology and Host Identity Outweigh Evolutionary History in Shaping the Bat Microbiome. *mSystems* **4**, 10.1128/msystems.00511-19.
- Maa, T.C. (1962) Records and Descriptions of Nycteribiidae and Streblidae (Diptera). *Pacific Insects* **4**, 417–436.
- Maine, J.J. & Boyles, J.G. (2015) Bats initiate vital agroecological interactions in corn. *Proceedings of the National Academy of Sciences* **112**, 12438–12443. Proceedings of the National Academy of Sciences.
- Mammalian Diversity Database (2024) Mammal Diversity Database (Version 1.12.1). Dataset, Zenodo. <https://zenodo.org/records/10595931> [accessed 19 November 2024].
- Martins, A.C.M., Oliveira, H.F.M., Zimbres, B., Sá-Neto, R.J. & Marinho-Filho, J. (2022) Environmental heterogeneity and water availability shape the structure of phyllostomid bat assemblages (Mammalia: Chiroptera) in the northeastern Amazon forest. *Forest Ecology and Management* **504**, 119863.
- Maslo, B., Mau, R.L., Kerwin, K., McDonough, R., McHale, E. & Foster, J.T. (2022) Bats provide a critical ecosystem service by consuming a large diversity of agricultural pest insects. *Agriculture, Ecosystems & Environment* **324**, 107722.
- McCain, C.M. (2007) Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography* **16**, 1–13.
- McConkey, K.R. & Drake, D.R. (2006) Flying Foxes Cease to Function as Seed Dispersers Long Before They Become Rare. *Ecology* **87**, 271–276.
- McConkey, K.R. & Drake, D.R. (2015) Low redundancy in seed dispersal within an island frugivore community. *AoB PLANTS* **7**, plv088.
- McConkey, K.R., Drake, D.R., Franklin, J. & Tonga, F. (2004) Effects of Cyclone Waka on flying foxes (*Pteropus tonganus*) in the Vava'u Islands of Tonga. *Journal of Tropical Ecology* **20**, 555–561.
- McCracken, G.F. (1986) Why are we losing our Mexican free-tailed bats. *Bats* **3**, 1–2.
- McGuire, L.P., Fenton, M.B. & Guglielmo, C.G. (2013) Phenotypic flexibility in migrating bats: seasonal variation in body composition, organ sizes and fatty acid profiles. *Journal of Experimental Biology* **216**, 800–808.
- McKee, C.D., Bai, Y., Webb, C.T. & Kosoy, M.Y. (2021) Bats are key hosts in the radiation of mammal-associated *Bartonella* bacteria. *Infection, Genetics and Evolution* **89**, 104719.
- McKee, C.D., Krawczyk, A.I., Sándor, A.D., Görföl, T., Földvári, M., Földvári, G., Dekeukeleire, D., Haarsma, A.-J., Kosoy, M.Y., Webb, C.T. & Sprong, H. (2019) Host Phylogeny, Geographic Overlap, and Roost Sharing Shape Parasite Communities in European Bats. *Frontiers in Ecology and Evolution* **7**.
- McKee, C.D., Peel, A.J., Hayman, D.T.S., Suu-Ire, R., Ntiamoa-Baidu, Y., Cunningham, A.A., Wood, J.L.N., Webb, C.T. & Kosoy, M.Y. (2024) Ectoparasite and bacterial population genetics and community structure indicate extent of bat movement across an island

- chain. *Parasitology* **151**, 708–721.
- McNab, B.K. (1973) Energetics and the Distribution of Vampires. *Journal of Mammalogy* **54**, 131–144.
- Meehan, H.J., McConkey, K.R. & Drake, D.R. (2002) Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. *Journal of Biogeography* **29**, 695–712.
- Mehl, C., Schoeman, M.C., Sanko, T.J., Bezuidenhout, C., Mienie, C.M.S., Preiser, W. & Vosloo, D. (2021) Wastewater treatment works change the intestinal microbiomes of insectivorous bats. *PLOS ONE* **16**, e0247475.
- Meramo, K., Vasko, V., Pietikäinen, T.-M., Laine, V.N., Ovaskainen, O. & Lilley, T.M. (2025) Tree-volume and forest age increase bat species diversity in boreal urban landscape. *Landscape Ecology* **40**, 1–18.
- Meyer, A.D., Stevens, D.F. & Blackwood, J.C. (2016) Predicting bat colony survival under controls targeting multiple transmission routes of white-nose syndrome. *Journal of Theoretical Biology* **409**, 60–69.
- Meyer, M., Melville, D.W., Baldwin, H.J., Wilhelm, K., Nkrumah, E.E., Badu, E.K., Oppong, S.K., Schwensow, N., Stow, A., Vallo, P., Corman, V.M., Tschapka, M., Drosten, C. & Sommer, S. (2024) Bat species assemblage predicts coronavirus prevalence. *Nature Communications* **15**, 2887.
- Miguel, P.H., Kerches-Rogeri, P., Niebuhr, B.B., Souza Cruz, R.A., Cezar Ribeiro, M. & Cruz Neto, A.P. da (2019) Habitat amount partially affects physiological condition and stress level in Neotropical fruit-eating bats. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **237**, 110537.
- Mitchell, H.A. (1965) Investigations of the Cave Atmosphere of a Mexican Bat Colony. *Journal of Mammalogy* **45**, 568–577.
- Mollentze, N. & Streicker, D.G. (2020) Viral zoonotic risk is homogenous among taxonomic orders of mammalian and avian reservoir hosts. *Proceedings of the National Academy of Sciences* **117**, 9423–9430.
- Monk, J.D., Smith, J.A., Donadío, E., Perrig, P.L., Crego, R.D., Fileni, M., Bidder, O., Lambertucci, S.A., Pauli, J.N., Schmitz, O.J. & Middleton, A.D. (2022) Cascading effects of a disease outbreak in a remote protected area. *Ecology Letters* **25**, 1152–1163.
- Moran, M.L., Steven, J.C., Williams, J.A. & Sherwin, R.E. (2023) Bat use of abandoned mines throughout Nevada. *Wildlife Society Bulletin* **47**, e1468.
- Moretto, L., Coleman, J.L., Davy, C.M., Fenton, M.B., Korine, C. & Patriquin, K.J. (2023) *Urban Bats: Biology, Ecology, and Human Dimensions*. Springer Nature.
- Morse, S.F., Olival, K.J., Kosoy, M., Billeter, S., Patterson, B.D., Dick, C.W. & Dittmar, K. (2012) Global distribution and genetic diversity of *Bartonella* in bat flies (Hippoboscoidea, Streblidae, Nycteribiidae). *Infection, Genetics and Evolution* **12**, 1717–1723.
- Muscarella, R. & Fleming, T.H. (2007) The Role of Frugivorous Bats in Tropical Forest Succession. *Biological Reviews* **82**, 573–590.
- Naeem, S., Duffy, J.E. & Zavaleta, E. (2012) The Functions of Biological Diversity in an Age of Extinction. *Science* **336**, 1401–1406.
- Nogueira, M.R. & Peracchi, A.L. (2003) Fig-Seed Predation by 2 Species of Chiroderma: Discovery of a New Feeding Strategy in Bats. *Journal of Mammalogy* **84**, 225–233.
- Norberg, U.M. & Rayner, J.M.V. (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* **316**, 335–427.
- Numa, C., Verdú, J.R. & Sánchez-Palomino, P. (2005) Phyllostomid bat diversity in a variegated coffee landscape. *Biological Conservation* **122**, 151–158.
- Nurul-Ain, E., Rosli, H. & Kingston, T. (2017) Resource availability and roosting ecology shape reproductive phenology of rain forest insectivorous bats. *Biotropica* **49**, 382–394.

- Obitte, B. (2023) Why hunt: the socio-ecological drivers and ecological consequences of bat hunting in an Afrotropical system.
- Oleksy, R., Giuggioli, L., McKetterick, T.J., Racey, P.A. & Jones, G. (2017) Flying foxes create extensive seed shadows and enhance germination success of pioneer plant species in deforested Madagascan landscapes. *PLOS ONE* **12**, e0184023.
- Oleksy, R.Z., Ayady, C.L., Tatayah, V., Jones, C., Froidevaux, J.S.P., Racey, P.A. & Jones, G. (2021) The impact of the Endangered Mauritian flying fox *Pteropus niger* on commercial fruit farms and the efficacy of mitigation. *Oryx* **55**, 114–121.
- Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C. & Jordano, P. (2010) Missing and forbidden links in mutualistic networks. *Proceedings of the Royal Society B: Biological Sciences* **278**, 725–732.
- Olivai, K.J., Dick, C.W., Simmons, N.B., Morales, J.C., Melnick, D.J., Dittmar, K., Perkins, S.L., Daszak, P. & DeSalle, R. (2013) Lack of population genetic structure and host specificity in the bat fly, *Cyclopodia horsfieldi*, across species of *Pteropus* bats in Southeast Asia. *Parasites & Vectors* **6**, 231.
- Olivai, K.J., Hosseini, P.R., Zambrana-Torrel, C., Ross, N., Bogich, T.L. & Daszak, P. (2017) Host and viral traits predict zoonotic spillover from mammals. *Nature* **546**, 646–650.
- Oliveira, H.F.M., de Camargo, N.F., Gager, Y. & Aguiar, L.M.S. (2017) The Response of Bats (Mammalia: Chiroptera) to Habitat Modification in a Neotropical Savannah. *Tropical Conservation Science* **10**, 1940082917697263.
- Oliveira, H.F.M., Camargo, N.F., Gager, Y., Muylaert, R.L., Ramon, E. & Martins, R.C.C. (2019) Protecting the Cerrado: where should we direct efforts for the conservation of bat-plant interactions? *Biodiversity and Conservation* **28**, 2765–2779.
- Oliveira, H.F.M., Pinheiro, R.B.P., Varassin, I.G., Rodríguez-Herrera, B., Kuzmina, M., Rossiter, S.J. & Clare, E.L. (2022) The structure of tropical bat-plant interaction networks during an extreme El Niño-Southern Oscillation event. *Molecular Ecology* **31**, 1892–1906.
- O'Rourke, D., Rouillard, N.P., Parise, K.L. & Foster, J.T. (2022) Spatial and temporal variation in New Hampshire bat diets. *Scientific Reports* **12**, 14334.
- O'Shea, T.J., Cryan, P.M., Cunningham, A.A., Fooks, A.R., Hayman, D.T.S., Luis, A.D., Peel, A.J., Plowright, R.K. & Wood, J.L.N. (2014) Bat Flight and Zoonotic Viruses. *Emerging Infectious Diseases* **20**, 741–745.
- O'Shea, T.J., Cryan, P.M., Hayman, D.T.S., Plowright, R.K. & Streicker, D.G. (2016) Multiple mortality events in bats: a global review. *Mammal Review* **46**, 175–190.
- Parratt, S.R. & Laine, A.-L. (2016) The role of hyperparasitism in microbial pathogen ecology and evolution. *The ISME Journal* **10**, 1815–1822.
- Patterson, B.D., Dick, C.W. & Dittmar, K. (2007) Roosting habits of bats affect their parasitism by bat flies (Diptera: Streblidae). *Journal of Tropical Ecology* **23**, 177–189.
- Pedersen, A.B. & Fenton, A. (2007) Emphasizing the ecology in parasite community ecology. *Trends in Ecology & Evolution* **22**, 133–139.
- Pedersen, A.B. & Fenton, A.N.D.Y. (2019) Wild rodents as a natural model to study within-host parasite interactions. In *Wildlife Disease Ecology: Linking Theory to Data and Application* pp. 58–90. Cambridge University Press.
- Peel, A.J., Sargan, D.R., Baker, K.S., Hayman, D.T.S., Barr, J.A., Cramer, G., Suu-Ire, R., Broder, C.C., Lembo, T., Wang, L.-F., Fooks, A.R., Rossiter, S.J., Wood, J.L.N. & Cunningham, A.A. (2013) Continent-wide panmixia of an African fruit bat facilitates transmission of potentially zoonotic viruses. *Nature Communications* **4**, 2770.
- Pejić, B., Budinski, I., van Schaik, J. & Blagojević, J. (2022) Sharing roosts but not ectoparasites: high host-specificity in bat flies and wing mites of *Miniopterus schreibersii* and *Rhinolophus ferrumequinum* (Mammalia: Chiroptera). *Current Zoology* **68**, 507–516.
- Perea, S., Meinecke, C.D., Larsen-Gray, A.L., Greene, D.U., Villari, C., Gandhi, K.J.K. & Castleberry, S.B. (2024) Winter diet of bats in working forests of the southeastern U.S.

- Coastal Plain. *Scientific Reports* **14**, 12778.
- Pereira, M.J.R., Marques, J.T., Santana, J., Santos, C.D., Valsecchi, J., De Queiroz, H.L., Beja, P. & Palmeirim, J.M. (2009) Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load. *Journal of Animal Ecology* **78**, 1163–1171.
- Phelps, K., Jose, R., Labonite, M. & Kingston, T. (2016) Correlates of cave-roosting bat diversity as an effective tool to identify priority caves. *Biological Conservation* **201**, 201–209.
- Phelps, K., Jose, R., Labonite, M. & Kingston, T. (2018) Assemblage and Species Threshold Responses to Environmental and Disturbance Gradients Shape Bat Diversity in Disturbed Cave Landscapes. *Diversity* **10**, 55.
- Phelps, K.L. & Kingston, T. (2018) Environmental and biological context modulates the physiological stress response of bats to human disturbance. *Oecologia* **188**, 41–52.
- Phillips, C.D., Hanson, J., Wilkinson, J.E., Koenig, L., Rees, E., Webala, P. & Kingston, T. (2017) Microbiome Structural and Functional Interactions across Host Dietary Niche Space. *Integrative and Comparative Biology* **57**, 743–755.
- Piló, L.B., Calux, A., Scherer, R. & Bernard, E. (2023) Bats as ecosystem engineers in iron ore caves in the Carajás National Forest, Brazilian Amazonia. *PLOS ONE* **18**, e0267870.
- Pimentel, N.T., da Rocha, P.A., Pedroso, M.A. & Bernard, E. (2022) Estimates of insect consumption and guano input in bat caves in Brazil. *Mammal Research* **67**, 355–366.
- Plowright, R.K., Field, H.E., Smith, C., Divljan, A., Palmer, C., Tabor, G., Daszak, P. & Foley, J.E. (2008) Reproduction and nutritional stress are risk factors for Hendra virus infection in little red flying foxes (*Pteropus scapulatus*). *Proceedings of the Royal Society B: Biological Sciences* **275**, 861–869.
- Popa-Lisseanu, A.G. & Voigt, C.C. (2009) Bats on the Move. *Journal of Mammalogy* **90**, 1283–1289.
- Potter, J.H.T., Davies, K.T.J., Yohe, L.R., Sanchez, M.K.R., Rengifo, E.M., Struebig, M., Warren, K., Tsagkogeorga, G., Lim, B.K., dos Reis, M., Dávalos, L.M. & Rossiter, S.J. (2021) Dietary Diversification and Specialization in Neotropical Bats Facilitated by Early Molecular Evolution. *Molecular Biology and Evolution* **38**, 3864–3883.
- Puig-Montserrat, X., Flaquer, C., Gómez-Aguilera, N., Burgas, A., Mas, M., Tuneu, C., Marquès, E. & López-Baucells, A. (2020) Bats actively prey on mosquitoes and other deleterious insects in rice paddies: Potential impact on human health and agriculture. *Pest Management Science* **76**, 3759–3769.
- Ramalho, D.F. & Aguiar, L.M.S. (2020) Bats on the road — a review of the impacts of roads and highways on bats. *Acta Chiropterologica* **22**, 417–433.
- Ramírez-Francel, L.A., García-Herrera, L.V., Losada-Prado, S., Reinoso-Flórez, G., Sánchez-Hernández, A., Estrada-Villegas, S., Lim, B.K. & Guevara, G. (2022) Bats and their vital ecosystem services: a global review. *Integrative Zoology* **17**, 2–23.
- Ramírez-Martínez, M.M., Bennett, A.J., Dunn, C.D., Yuill, T.M. & Goldberg, T.L. (2021) Bat Flies of the Family Streblidae (Diptera: Hippoboscoidea) Host Relatives of Medically and Agriculturally Important “Bat-Associated” Viruses. *Viruses* **13**, 860.
- Rangel, D.A., Lisboa, C.V., Novaes, R.L.M., Silva, B.A., Souza, R. de F., Jansen, A.M., Moratelli, R. & Roque, A.L.R. (2019) Isolation and characterization of trypanosomatids, including *Crithidia mellificae*, in bats from the Atlantic Forest of Rio de Janeiro, Brazil. *PLOS Neglected Tropical Diseases* **13**, e0007527.
- Reckardt, K. & Kerth, G. (2007) Roost selection and roost switching of female Bechstein’s bats (*Myotis bechsteinii*) as a strategy of parasite avoidance. *Oecologia* **154**, 581–588.
- Reeves, W.K., Beck, J., Orlova, M.V., Daly, J.L., Pippin, K., Revan, F. & Loftis, A.D. (2016) Ecology of Bats, Their Ectoparasites, and Associated Pathogens on Saint Kitts Island. *Journal of Medical Entomology* **53**, 1218–1225.
- Reiskind, M.H. & Wund, M.A. (2009) Experimental Assessment of the Impacts of Northern Long-Eared Bats on Ovipositing *Culex* (Diptera: Culicidae) Mosquitoes. *Journal of*

- Medical Entomology* **46**, 1037–1044.
- Richter, H.V. & Cumming, G.S. (2006) Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *Journal of Zoology* **268**, 35–44.
- Rodríguez-Herrera, B., Rodríguez, M.E. & Otárola, M.F. (2018) Ecological Networks between Tent-Roosting Bats (Phyllostomidae: Stenodermatinae) and the Plants Used in a Neotropical Rainforest. *Acta Chiropterologica* **20**, 139–145.
- Rowse, E.G., Lewanzik, D., Stone, E.L., Harris, S. & Jones, G. (2016) Dark matters: the effects of artificial lighting on bats. In *Bats in the Anthropocene: Conservation of bats in a changing world* pp. 187–213.
- Sakoui, S., Derdak, R., Addoum, B., Serrano-Delgado, A., Soukri, A. & El Khalfi, B. (2020) The Life Hidden Inside Caves: Ecological and Economic Importance of Bat Guano. *International Journal of Ecology* **2020**, 9872532.
- Sánchez, C.A., Phelps, K.L., Frank, H.K., Geldenhuys, M., Griffiths, M.E., Jones, D.N., Kettenburg, G., Lunn, T.J., Moreno, K.R., Mortlock, M., Vicente-Santos, A., Viquez-R, L.R., Kading, R.C., Markotter, W., Reeder, D.M., et al. (2024) Advances in understanding bat infection dynamics across biological scales. *Proceedings of the Royal Society B: Biological Sciences* **291**, 20232823.
- Sándor, A.D., Péter, Á., Corduneanu, A., Barti, L., Csősz, I., Kalmár, Z., Hornok, S., Kontschán, J. & Mihalca, A.D. (2021) Wide Distribution and Diversity of Malaria-Related Haemosporidian Parasites (*Polychromophilus* spp.) in Bats and Their Ectoparasites in Eastern Europe. *Microorganisms* **9**, 230.
- Sandoval-Herrera, N., Paz Castillo, J., Herrera Montalvo, L.G. & Welch Jr., K.C. (2021) Micronucleus Test Reveals Genotoxic Effects in Bats Associated with Agricultural Activity. *Environmental Toxicology and Chemistry* **40**, 202–207.
- Santana, S.E., Kaliszewska, Z.A., Leiser-Miller, L.B., Lauterbur, M.E., Arbour, J.H., Dávalos, L.M. & Riffell, J.A. (2021) Fruit odorants mediate co-specialization in a multispecies plant–animal mutualism. *Proceedings of the Royal Society B: Biological Sciences* **288**, 20210312.
- Scanlon, A.T., Petit, S., Tuiwawa, M. & Naikatini, A. (2018) Response of primary and secondary rainforest flowers and fruits to a cyclone, and implications for plant-servicing bats. *Global Change Biology* **24**, 3820–3836.
- Schaer, J., Boardman, W.S.J., McKeown, A., Westcott, D.A., Matuschewski, K. & Power, M. (2019) Molecular investigation of *Hepatozoon* parasites in the Australian flying fox *Pteropus poliocephalus* across its distribution range. *Infection, Genetics and Evolution* **75**, 103978.
- van Schaik, J., Dekeukeleire, D., Gazaryan, S., Natradze, I. & Kerth, G. (2018) Comparative phylogeography of a vulnerable bat and its ectoparasite reveals dispersal of a non-mobile parasite among distinct evolutionarily significant units of the host. *Conservation Genetics* **19**, 481–494.
- van Schaik, J., Dekeukeleire, D. & Kerth, G. (2015a) Host and parasite life history interplay to yield divergent population genetic structures in two ectoparasites living on the same bat species. *Molecular Ecology* **24**, 2324–2335.
- van Schaik, J., Janssen, R., Bosch, T., Haarsma, A.-J., Dekker, J.J.A. & Kranstauber, B. (2015b) Bats Swarm Where They Hibernate: Compositional Similarity between Autumn Swarming and Winter Hibernation Assemblages at Five Underground Sites. *PLOS ONE* **10**, e0130850.
- van Schaik, J. & Kerth, G. (2017) Host social organization and mating system shape parasite transmission opportunities in three European bat species. *Parasitology Research* **116**, 589–599.
- van Schaik, J., Kerth, G., Bruyndonckx, N. & Christe, P. (2014) The effect of host social system on parasite population genetic structure: comparative population genetics of two

- ectoparasitic mites and their bat hosts. *BMC Evolutionary Biology* **14**, 18.
- Schountz, T., Baker, M.L., Butler, J. & Munster, V. (2017) Immunological Control of Viral Infections in Bats and the Emergence of Viruses Highly Pathogenic to Humans. *Frontiers in Immunology* **8**.
- Seltmann, A., Corman, V.M., Rasche, A., Drosten, C., Czirják, G.Á., Bernard, H., Struebig, M.J. & Voigt, C.C. (2017a) Seasonal Fluctuations of Astrovirus, But Not Coronavirus Shedding in Bats Inhabiting Human-Modified Tropical Forests. *EcoHealth* **14**, 272–284.
- Seltmann, A., Czirják, G.Á., Courtiol, A., Bernard, H., Struebig, M.J. & Voigt, C.C. (2017b) Habitat disturbance results in chronic stress and impaired health status in forest-dwelling paleotropical bats. *Conservation Physiology* **5**, cox020.
- Senawi, J. & Kingston, T. (2019) Clutter negotiating ability in an ensemble of forest interior bats is driven by body mass. *Journal of Experimental Biology*, jeb.203950.
- Shapiro, H., Willcox, A., Tate, M. & Willcox, E. (2020) Can Farmers and Bats Co-exist? Farmer Attitudes, Knowledge, and Experiences with Bats in Belize. *Human–Wildlife Interactions* **14**.
- Shaw, L.P., Wang, A.D., Dylus, D., Meier, M., Pogacnik, G., Dessimoz, C. & Balloux, F. (2020) The phylogenetic range of bacterial and viral pathogens of vertebrates. *Molecular Ecology* **29**, 3361–3379.
- Sheherazade, Ober, H.K. & Tsang, S.M. (2019) Contributions of bats to the local economy through durian pollination in Sulawesi, Indonesia. *Biotropica* **51**, 913–922.
- Simonis, M.C. & Becker, D.J. (2023) A general framework for modeling pathogen transmission in co-roosting host communities. bioRxiv. <https://www.biorxiv.org/content/10.1101/2023.11.21.568148v1> [accessed 22 November 2024].
- Sivault, E., Amick, P.K., Armstrong, K.N., Novotny, V. & Sam, K. (2023) Species richness and assemblages of bats along a forest elevational transect in Papua New Guinea. *Biotropica* **55**, 81–94.
- Song, S.J., Sanders, J.G., Baldassarre, D.T., Chaves, J.A., Johnson, N.S., Piaggio, A.J., Stuckey, M.J., Nováková, E., Metcalf, J.L., Chomel, B.B., Aguilar-Setién, A., Knight, R. & McKenzie, V.J. (2019) Is there convergence of gut microbes in blood-feeding vertebrates? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **374**, 20180249.
- Sorensen, D.W., Butkus, C., Cooper, L.N., Cretokos, C.J., Rasweiler, J.J. & Sears, K.E. (2014) Palate Variation and Evolution in New World Leaf-Nosed and Old World Fruit Bats (Order Chiroptera). *Evolutionary Biology* **41**, 595–605.
- Speer, K., Rodríguez, L.V., Frick, W., Ibarra, A., Simmons, N., Dittmar, K., Calderón, R.S., Preciado, R., Medellín, R., Tschapka, M., Sommer, S. & Perkins, S. (2024) Comparative community ecology reveals conserved ectoparasite microbiomes amidst variable host and environment microbiomes. Authorea. <https://www.authorea.com/doi/full/10.22541/au.172717410.06705128?commit=507808c4adb6021d87d176bbe73cae5b24c1f4fb> [accessed 25 November 2024].
- Speer, K.A. (2022) Microbiomes mediate host–parasite interactions. *Molecular Ecology* **31**, 1925–1927.
- Speer, K.A., Dheilly, N.M. & Perkins, S.L. (2020) Microbiomes are integral to conservation of parasitic arthropods. *Biological Conservation* **250**, 108695.
- Speer, K.A., Luetke, E., Bush, E., Sheth, B., Gerace, A., Quicksall, Z., Miyamoto, M., Dick, C.W., Dittmar, K., Albury, N. & Reed, D.L. (2019) A Fly on the Cave Wall: Parasite Genetics Reveal Fine-scale Dispersal Patterns of Bats. *Journal of Parasitology* **105**, 555–566.
- Speer, K.A., Teixeira, T.S.M., Brown, A.M., Perkins, S.L., Dittmar, K., Ingala, M.R., Wulsch, C., Krampis, K., Dick, C.W., Galen, S.C., Simmons, N.B. & Clare, E.L. (2022) Cascading effects of habitat loss on ectoparasite-associated bacterial microbiomes. *ISME*

- Communications* **2**, 67.
- Stevens, R.D. (2004) Untangling latitudinal richness gradients at higher taxonomic levels: familial perspectives on the diversity of New World bat communities. *Journal of Biogeography* **31**, 665–674.
- Stothart, M.R., Palme, R. & Newman, A.E.M. (2019) It's what's on the inside that counts: stress physiology and the bacterial microbiome of a wild urban mammal. *Proceedings of the Royal Society B: Biological Sciences* **286**, 20192111.
- Streicker, D.G., Recuenco, S., Valderrama, W., Gomez Benavides, J., Vargas, I., Pacheco, V., Condori Condori, R.E., Montgomery, J., Rupprecht, C.E., Rohani, P. & Altizer, S. (2012) Ecological and anthropogenic drivers of rabies exposure in vampire bats: implications for transmission and control. *Proceedings of the Royal Society B: Biological Sciences* **279**, 3384–3392. Royal Society.
- Struebig, M.J., Kingston, T., Zubaid, A., Mohd-Adnan, A. & Rossiter, S.J. (2008) Conservation value of forest fragments to Palaeotropical bats. *Biological Conservation* **141**, 2112–2126.
- Suarez-Rubio, M., Ille, C. & Bruckner, A. (2018) Insectivorous bats respond to vegetation complexity in urban green spaces. *Ecology and Evolution* **8**, 3240–3253.
- Suominen, K.M., Vesterinen, E.J., Kivistö, I., Reiman, M., Virtanen, T., Meierhofer, M.B., Vasko, V., Sironen, T. & Lilley, T.M. (2023) Environmental features around roost sites drive species-specific roost preferences for boreal bats. *Global Ecology and Conservation* **46**, e02589.
- Syafiq, M., Nur Atiqah, A.R., Ghazali, A., Asmah, S., Yahya, M.S., Aziz, N., Puan, C.L. & Azhar, B. (2016) Responses of tropical fruit bats to monoculture and polyculture farming in oil palm smallholdings. *Acta Oecologica* **74**, 11–18.
- Szentiványi, T., Christe, P. & Glaizot, O. (2019) Bat Flies and Their Microparasites: Current Knowledge and Distribution. *Frontiers in Veterinary Science* **6**.
- Szentiványi, T., Estók, P., Pigeault, R., Christe, P. & Glaizot, O. (2020) Effects of fungal infection on the survival of parasitic bat flies. *Parasites & Vectors* **13**, 23.
- Szentiványi, T., Haelewaters, D., Pfliegler, W.P., Clément, L., Christe, P. & Glaizot, O. (2018) Laboulbeniales (Fungi: Ascomycota) infection of bat flies (Diptera: Nycteribiidae) from *Miniopterus schreibersii* across Europe. *Parasites & Vectors* **11**, 395.
- Szentiványi, T., Heintz, A.-C., Markotter, W., Wassef, J., Christe, P. & Glaizot, O. (2023) Vector-borne protozoan and bacterial pathogen occurrence and diversity in ectoparasites of the Egyptian Rousette bat. *Medical and Veterinary Entomology* **37**, 189–194.
- Szentiványi, T., Szabadi, K.L., Görföl, T., Estók, P. & Kemenesi, G. (2024) Bats and ectoparasites: exploring a hidden link in zoonotic disease transmission. *Trends in Parasitology*.
- Tait, J., Perotto-Baldivieso, H.L., McKeown, A. & Westcott, D.A. (2014) Are Flying-Foxes Coming to Town? Urbanisation of the Spectacled Flying-Fox (*Pteropus conspicillatus*) in Australia. *PLOS ONE* **9**, e109810.
- Talbot, B., Vonhof, M.J., Broders, H.G., Fenton, B. & Keyghobadi, N. (2016) Range-wide genetic structure and demographic history in the bat ectoparasite *Cimex adjunctus*. *BMC Evolutionary Biology* **16**, 268.
- Tanalgo, K.C., Sritongchuay, T., Agduma, A.R., Dela Cruz, K.C. & Hughes, A.C. (2023) Are we hunting bats to extinction? Worldwide patterns of hunting risk in bats are driven by species ecology and regional economics. *Biological Conservation* **279**, 109944.
- Tendu, A., Hughes, A.C., Berthet, N. & Wong, G. (2022) Viral Hyperparasitism in Bat Ectoparasites: Implications for Pathogen Maintenance and Transmission. *Microorganisms* **10**, 1230.
- Thaxter, C.B., Buchanan, G.M., Carr, J., Butchart, S.H.M., Newbold, T., Green, R.E., Tobias,

- J.A., Foden, W.B., O'Brien, S. & Pearce-Higgins, J.W. (2017) Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20170829.
- Thornton, I.W.B., Cook, S., Edwards, J.S., Harrison, R.D., Schipper, C., Shanahan, M., Singadan, R. & Yamuna, R. (2001) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VII. Overview and discussion. *Journal of Biogeography* **28**, 1389–1408.
- Toshkova, N., Zhelyzkova, V., Reyes-Ruiz, A., Haerens, E., de Castro Deus, M., Lacombe, R.V., Lecerf, M., Gonzalez, G., Jouvenet, N., Planchais, C. & Dimitrov, J.D. (2024) Temperature sensitivity of bat antibodies links metabolic state of bats with antigen-recognition diversity. *Nature Communications* **15**, 5878.
- Tschapka, M. & Cunningham, S.A. (2004) Flower Mites of *Calyptrogyne ghiesbreghtiana* (Arecaceae): Evidence for Dispersal Using Pollinating Bats. *Biotropica* **36**, 377–381.
- Tuneu-Corral, C., Puig-Montserrat, X., Riba-Bertolín, D., Russo, D., Rebelo, H., Cabeza, M. & López-Baucells, A. (2023) Pest suppression by bats and management strategies to favour it: a global review. *Biological Reviews* **98**, 1564–1582.
- Vardon, M., Simpson, B., Sherwell, D. & Tidemann, C. (1997) Flying-foxes and tourists: a conservation dilemma in the Northern Territory. *Australian Zoologist* **30**, 310–315.
- Vazquez, J.M., Lauterbur, M.E., Mottaghinia, S., Bucci, M., Fraser, D., Gray-Sandoval, G., Gaucherand, L., Haidar, Z.R., Han, M., Kohler, W., Lama, T.M., Corf, A.L., Loyer, C., Maesen, S., McMillan, D., et al. (2024) Extensive longevity and DNA virus-driven adaptation in nearctic *Myotis* bats. bioRxiv. <https://www.biorxiv.org/content/10.1101/2024.10.10.617725v2> [accessed 8 January 2025].
- Vesterinen, E.J., Puisto, A.I.E., Blomberg, A.S. & Lilley, T.M. (2018) Table for five, please: Dietary partitioning in boreal bats. *Ecology and Evolution* **8**, 10914–10937.
- Viana, M., Benavides, J.A., Broos, A., Ibañez Loayza, D., Niño, R., Bone, J., da Silva Filipe, A., Orton, R., Valderrama Bazan, W., Matthiopoulos, J. & Streicker, D.G. (2023) Effects of culling vampire bats on the spatial spread and spillover of rabies virus. *Science Advances* **9**, eadd7437.
- Viquez-R, L., Speer, K., Wilhelm, K., Simmons, N., Medellín, R.A., Sommer, S. & Tschapka, M. (2021) A Faithful Gut: Core Features of Gastrointestinal Microbiota of Long-Distance Migratory Bats Remain Stable despite Dietary Shifts Driving Differences in Specific Bacterial Taxa. *Microbiology Spectrum* **9**, e01525-21.
- Voigt, C.C., Borissov, I. & Kelm, D.H. (2015) Bats Fertilize Roost Trees. *Biotropica* **47**, 403–406.
- Voigt, C.C. & Kingston, T. (2016) Bats in the Anthropocene. In *Bats in the Anthropocene: Conservation of Bats in a Changing World* (eds C.C. Voigt & T. Kingston), pp. 1–9. Springer International Publishing, Cham.
- Voigt, C.C., Rehnig, K., Lindecke, O. & Pētersons, G. (2018) Migratory bats are attracted by red light but not by warm-white light: Implications for the protection of nocturnal migrants. *Ecology and Evolution* **8**, 9353–9361.
- Voss, R.S., Fleck, D.W., Strauss, R.E., Velazco, P.M. & Simmons, N.B. (2016) Roosting Ecology of Amazonian Bats: Evidence for Guild Structure in Hyperdiverse Mammalian Communities. *American Museum Novitates* **2016**, 1–43.
- Wandrag, E.M., Dunham, A.E., Miller, R.H. & Rogers, H.S. (2015) Vertebrate seed dispersers maintain the composition of tropical forest seedbanks. *AoB PLANTS* **7**, plv130.
- Webber, Q.M.R., Czenze, Z.J. & Willis, C.K.R. (2015) Host demographic predicts ectoparasite dynamics for a colonial host during pre-hibernation mating. *Parasitology* **142**, 1260–1269.
- Webber, Q.M.R. & Willis, C.K.R. (2016) Sociality, Parasites, and Pathogens in Bats. In *Sociality in Bats* (ed J. Ortega), pp. 105–139. Springer International Publishing, Cham.

- Welbergen, J.A., Meade, J., Field, H.E., Edson, D., McMichael, L., Shoo, L.P., Praszczalek, J., Smith, C. & Martin, J.M. (2020) Extreme mobility of the world's largest flying mammals creates key challenges for management and conservation. *BMC Biology* **18**, 101.
- Welch, J.N. & Beaulieu, J.M. (2018) Predicting Extinction Risk for Data Deficient Bats. *Diversity* **10**, 63.
- Whittaker, R.J. & Jones, S.H. (1994) The Role of Frugivorous Bats and Birds in the Rebuilding of a Tropical Forest Ecosystem, Krakatau, Indonesia. *Journal of Biogeography* **21**, 245–258.
- Wickramasinghe, L.P., Harris, S., Jones, G. & Vaughan Jennings, N. (2004) Abundance and Species Richness of Nocturnal Insects on Organic and Conventional Farms: Effects of Agricultural Intensification on Bat Foraging. *Conservation Biology* **18**, 1283–1292.
- Wilkinson, G.S. & Adams, D.M. (2019) Recurrent evolution of extreme longevity in bats. *Biology Letters* **15**, 20180860.
- Wilkinson, G.S. & South, J.M. (2002) Life history, ecology and longevity in bats. *Aging Cell* **1**, 124–131.
- Willoughby, A.R., Phelps, K.L., PREDICT Consortium & Olival, K.J. (2017) A Comparative Analysis of Viral Richness and Viral Sharing in Cave-Roosting Bats. *Diversity* **9**, 35.
- Winter, A.S., Hathaway, J.J.M., Kimble, J.C., Buecher, D.C., Valdez, E.W., Porras-Alfaro, A., Young, J.M., Read, K.J.H. & Northup, D.E. (2017) Skin and fur bacterial diversity and community structure on American southwestern bats: effects of habitat, geography and bat traits. *PeerJ* **5**, e3944.
- Witsenburg, F., Schneider, F. & Christe, P. (2015) Signs of a vector's adaptive choice: on the evasion of infectious hosts and parasite-induced mortality. *Oikos* **124**, 668–676.
- Wordley, C.F.R., Sankaran, M., Mudappa, D. & Altringham, J.D. (2015) Landscape scale habitat suitability modelling of bats in the Western Ghats of India: Bats like something in their tea. *Biological Conservation* **191**, 529–536.
- Wray, A.K., Jusino, M.A., Banik, M.T., Palmer, J.M., Kaarakka, H., White, J.P., Lindner, D.L., Gratton, C. & Peery, M.Z. (2018) Incidence and taxonomic richness of mosquitoes in the diets of little brown and big brown bats. *Journal of Mammalogy* **99**, 668–674.
- Xiao, G., Liu, S., Xiao, Y., Zhu, Y., Zhao, H., Li, A., Li, Z. & Feng, J. (2019) Seasonal Changes in Gut Microbiota Diversity and Composition in the Greater Horseshoe Bat. *Frontiers in Microbiology* **10**.
- Yoh, N., Azhar, I., Fitzgerald, K.V., Yu, R., Smith-Butler, T., Mahyudin, A. & Kingston, T. (2020) Bat Ensembles Differ in Response to Use Zones in a Tropical Biosphere Reserve. *Diversity* **12**, 60.
- Zacks, R. (2008) A comparison of hemoparasite loads between bats (F: Phyllostomidae) of different feeding guilds in San Luis, Costa Rica, November 2008.
- Zepeda Mendoza, M.L., Xiong, Z., Escalera-Zamudio, M., Runge, A.K., Thézé, J., Streicker, D., Frank, H.K., Loza-Rubio, E., Liu, S., Ryder, O.A., Samaniego Castruita, J.A., Katzourakis, A., Pacheco, G., Taboada, B., Löber, U., et al. (2018) Hologenomic adaptations underlying the evolution of sanguivory in the common vampire bat. *Nature Ecology & Evolution* **2**, 659–668.
- Zortéa, M. & Alho, C.J.R. (2008) Bat diversity of a Cerrado habitat in central Brazil. *Biodiversity and Conservation* **17**, 791–805.