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

Contents:

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, Hedenâs & Elmqvist, 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* *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 asymptomatically 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 (Buettner *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; Víquez-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 Paleotropical 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 (Alpízar *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. guanophilic 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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Table 1. A non-exhaustive list of studies highlighted in the text describing the positive or negative impact on the bats and habitats involved in the described interaction.

	Species	Family	Geography	Key Point	For bats	For habitat	Ref
Bats in Habitats	*Pteropus niger*	Pteropodidae	Mauritius (East Africa)	63% of native woody plants come from seeds dispersed by this bat species.	+	+	Florens et al. 2017
	Chiroderma spp.	Phyllostomidae	Brazil (South America)	Bats act as pre-dispersal predators of small fig seeds, limiting seed dispersal.	+	–	Nogueira & Peracchi 2003
	Carollia sowelli	Phyllostomidae	Costa Rica (Central America)	Artificial light at night deters some frugivorous bat foraging behavior.	–	–	Lewanzik and Voigt 2014
	Tadarida brasiliensis	Molossidae	Texas, USA (North America)	Bats heavily feed on insects whose larvae are known pests in the cotton industry.	+	+	Cleveland et al. 2006
	Rhinolophus sedulus	Rhinolophidae	Malaysia (Southeast Asia)	Bats in logging areas had fewer leukocytes than bats in recovered forests.	-	-	Seltmann et al. 2017
	Desmodus rotundus	Phyllostomidae	Argentina (South America)	Abundant livestock allows blood-feeding bat population size to nearly double.	+	-	Delpietro et al. 1992
	Micronycteris microtis and other insectivores	Phyllostomidae and Vespertilionidae	Panama (Central America)	Excluding bat access to insects on plants increased insect herbivory by 209%	+	+	Kalka et al. 2008
Bats as Habitats	*Lasionycteris noctivagans*	Vespertilionidae	USA (North America)	Body temperatures in hibernation allow rabies virus to overwinter until the spring.	-	-	Davis et al. 2016
	Pteropus conspicillatus	Pteropodidae	Australia (Oceania)	*Ixodes holocyclus* ticks cause paralysis and contribute to bat population declines.	-	-	Buettner et al. 2013

	Miniopterus schreibersii	Miniopteridae	Hungary (Europe)	Bat infections with Laboulbeniales fungi shorten lifespan of nycteribiid bat flies.	+	+	Szentiványi et al. 2020
	Myotis lucifugus	Vespertilionidae	Canada (North America)	Certain skin bacteria can inhibit growth of the white-nose syndrome fungus (*Pd*).	+	+	Lemieux-Labonté et al. 2017
	Hipposideros diadema	Hipposideridae	Philippines (Southeast Asia)	Cave disturbance did not affect ectoparasite intensity, but intensity was associated with lower bat abundance.	-	-	Phelps and Kingston 2018
	Dermanura spp. and *Sturnira parvidens*	Phyllostomidae	Belize (Central America)	Mercury levels were correlated with increased risk of infection with *Bartonella* bacteria owing to immunosuppression	-	-	Becker et al. 2020
	Artibeus lituratus, Carollia perspicillata, Desmodus rotundus, Sturnira lilium, Myotis nigricans, and *Myotis riparius*	Phyllostomidae and Vespertilionidae	Brazil (South America)	Habitat fragmentation was associated with perturbance of bacterial communities of obligate bat flies (Streblidae and Nycteribiidae) found on bat hosts.	-	-	Speer et al. 2022

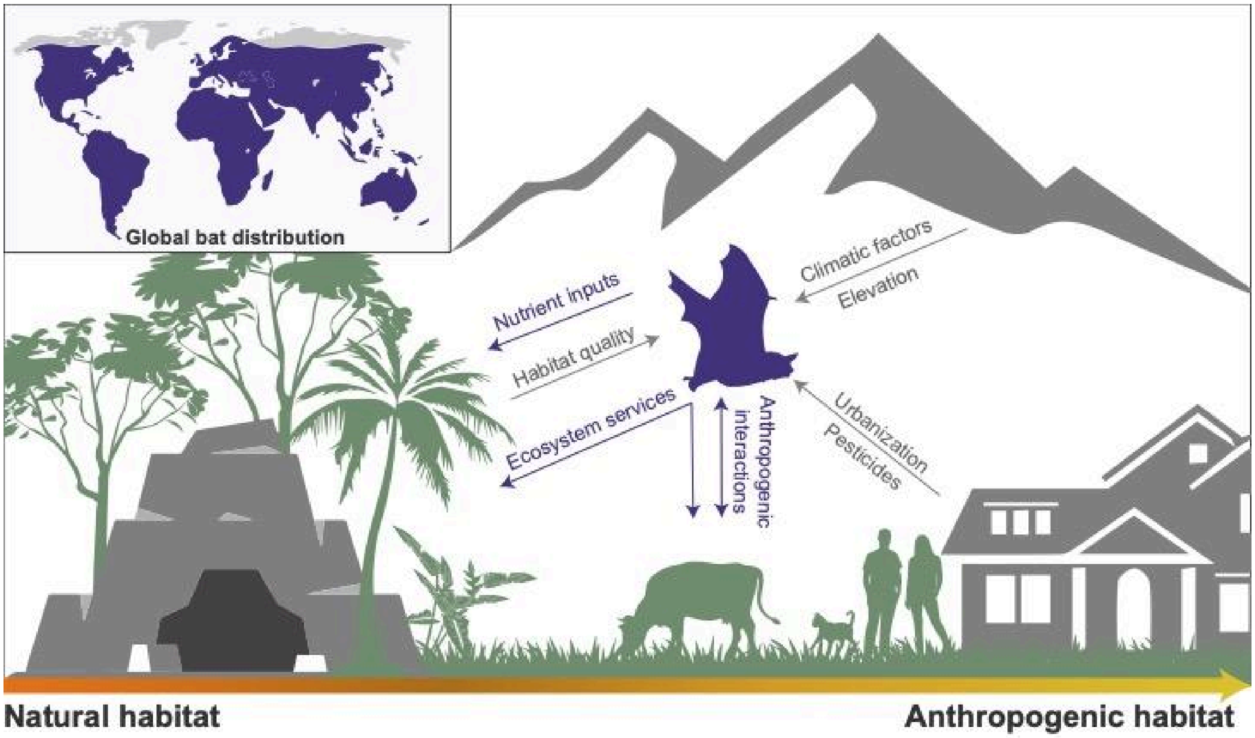

Figure 1. “Bats in Habitats”: interactions between bats (purple) and the biotic (green) and abiotic (grey) aspects of their habitats. Arrowheads point toward the recipient of each interaction, with bidirectional relationships indicated with double-headed arrows. Inset shows global bat distribution in purple, while areas of the globe where bats do not occur are shown in grey.

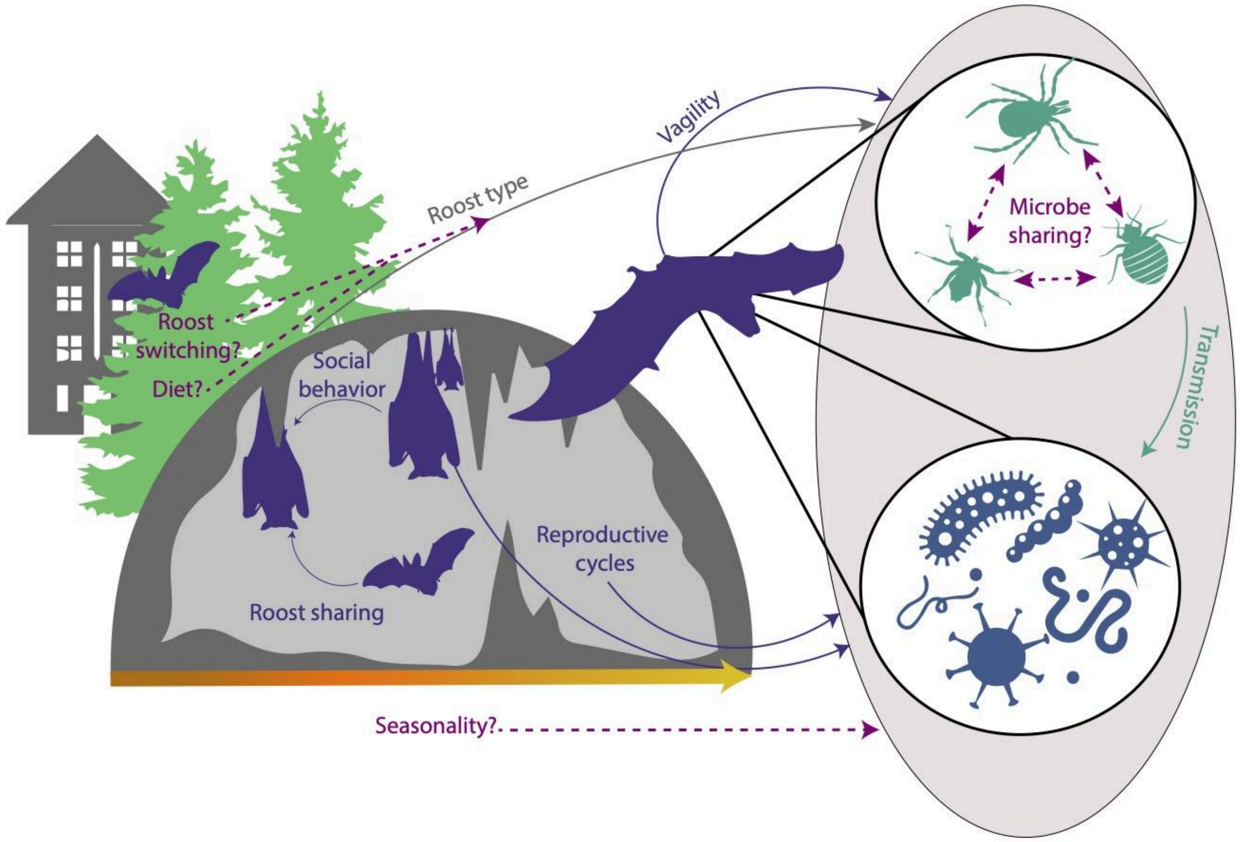

Figure 2. “Bats as Habitats”, including aspects of bat biology that influence the diversity and structure of organisms they host. Current knowledge gaps reviewed in the text are indicated as questions.

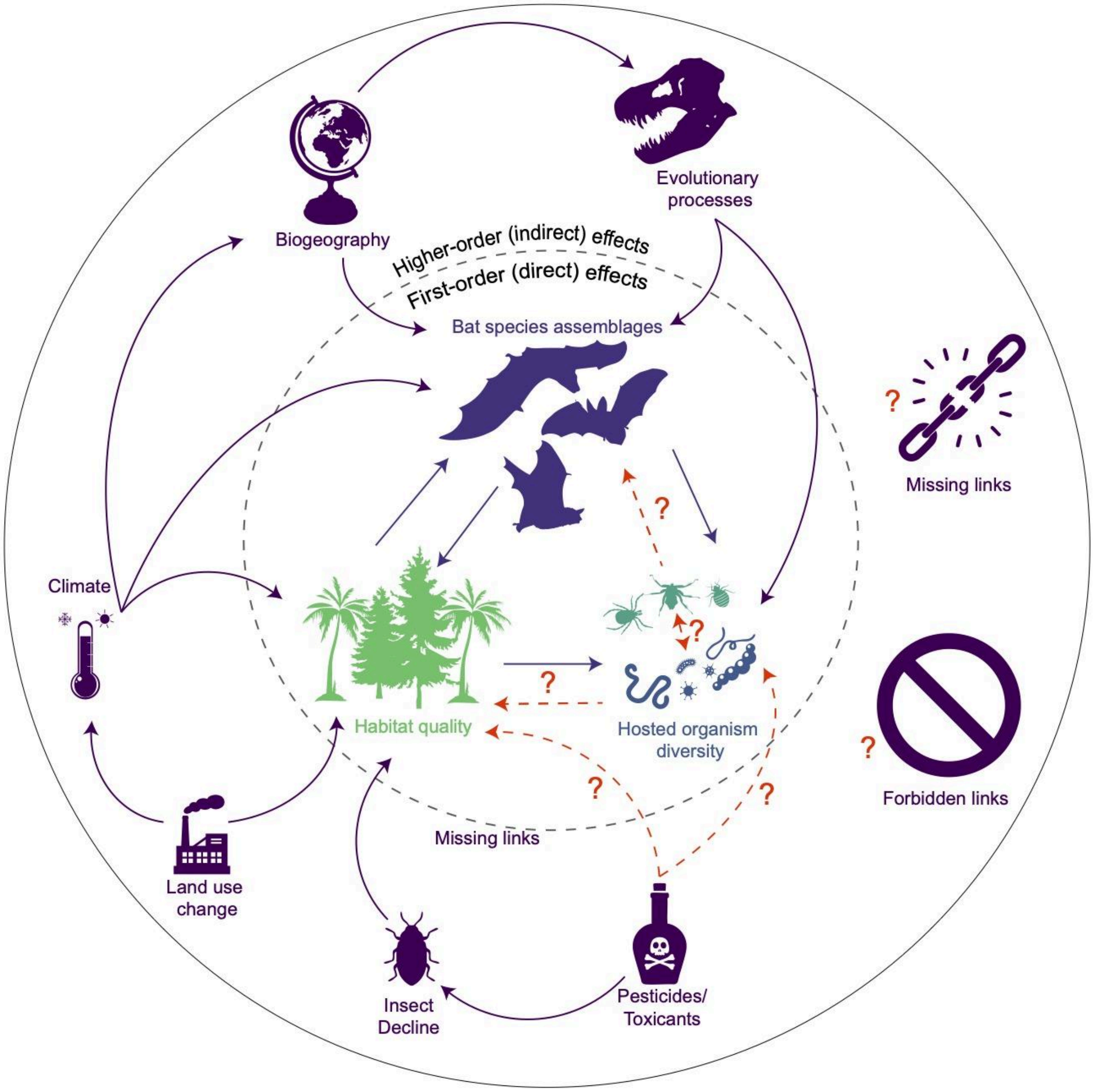

Figure 3. Hierarchical system diagram depicting direct and indirect effects structuring nested interactions among bats, their habitats, and hosted organisms. The inset circle represents direct, first-order interactions while indirect effects are listed in the outer ring. Arrows show a non-exhaustive set of possible interactions occurring throughout the network that can affect its overall structure. Some significant knowledge gaps discussed in the text are highlighted in red.

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