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. Bats are important contributors to ecosystems and biodiversity maintenance, so understanding their complex interaction networks, including the main drivers of and responses to ecological and environmental changes and their global implications, requires adopting a systems-based perspective. In this review, we advocate for organismal biologists to adopt an approach that takes interacting systems into account from the outset of study design by explicitly probing hypotheses that cross levels of biological organization. We first walk the reader through what is gained by using the “Bats in Habitats, Bats as Habitats” conceptual framework versus traditional single-level approaches, followed by a brief overview of how to apply systems modelling tools and data requirements for using them. We next ground the framework in a comprehensive literature review of bats in habitats, bats as habitats, and multi-scale interactions across systems. Finally, we distill knowledge gaps uncovered through the framework into actionable hypotheses and research priorities. This review provides a roadmap for bat specialists and “bat beginners” from orthogonal fields to apply systems-thinking to yield a more holistic view of ecological complexity.

Keywords: Chiroptera, community ecology, habitat, microbiome, network ecology, systems ecology

1. Introduction

Biology is becoming more interdisciplinary as our understanding of the integrative relationships between biological systems and levels of organization grows. 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 to generate both mechanistic and holistic understanding of complex biological relationships. However, the adoption of these perspectives in organismal biology and their operationalization in study design lags behind broader systems perspectives. By starting with a focal taxonomic group, we can begin to identify mechanisms linking ecological and biological processes across, in addition to within, hierarchical levels as well as knowledge gaps in the system. This allows the development and testing of hypotheses about whether these mechanistic insights are generalizable to other species or even other systems and begin to prioritize research needs within and outside the specific system of study.

Bats (order Chiroptera) are an especially useful model for this type of “systems thinking” approach to organismal biology that links habitat ecology and host-associated communities because they have relatively well-studied interactions with microbes and parasites and are key to global ecosystem function as a result of their wide geographic distribution and ecological diversity.[1] In this review, we present a framework in which we examine bats as a central node of a metacommunity spanning microbes to ecosystems, synthesizing current understanding of feedbacks and interactions across various biological levels. We advocate for increased use of systems thinking and diagramming tools to facilitate the development of study designs that consider multiple organizational scales from the outset, rather than reconstructing species’ niches and ecological interactions from cross-sectional studies. The goal is to use knowledge and methods from the fields of systems biology and systems ecology to improve the ability of organismal biologists to test hypotheses, uncover knowledge gaps, and discover emergent properties that might not otherwise be evident (e.g., Bernard et al.[2], Jackson et al.[3], and Keady et al.[4]).

We begin by defining “what is a habitat” in this framework, as there are a variety of definitions in use, with several possible ways to consider it. For the purpose of this paper, “habitat” is defined as the collection of resources an organism or a population of organisms uses to survive, including physical surroundings (e.g., caves, structures, microclimate), 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 — the multidimensional set of conditions and resources required for a population to persist.[5,6]

The scope of this review is a conceptual synthesis with methodological guidance rather than a call for exhaustive multi-level data collection across all bat species. Benefits of the "Bats in/as Habitats" framework include data prioritization and cognitive scaffolding supporting inquiry into bat interactions from a systems-level vantage point, identification of important emergent variables, and prioritization of the cross-level feedbacks that are most worth measuring to build a better understanding of the system. Systems biologists and ecologists will be familiar with these concepts, and we hope that this review may spark an interest in bats as a compelling and fruitful system for inquiry. Bat biologists and other organismal biologists may be familiar with some of the literature reviewed herein, but we hope they will benefit from the synthesis and integration into the “Bats in/as Habitats” framework and be empowered to develop and integrate systems thinking in their future research.

1.a Benefits of Systems Thinking in Understanding Bat Biology

Systems-thinking approaches treat species and their interactions as networks, allowing researchers to identify emergent properties (i.e., patterns and processes that arise from the whole that are not identifiable from any single component on its own). While this perspective is well-established in ecosystem ecology, its application in bat biology is comparatively rare, even as the tools available for collecting systems-level data — genomics, metagenomics, long-term tracking, and physiological monitoring — have become increasingly available to bat researchers.

The value of developing this framework is illustrated by reviews that have advocated for even partial systems approaches. In the field of conservation, for example, Bernard et al.[2] used influence diagrams (a network-based modeling tool) to identify key knowledge gaps and conservation priorities for bats affected by white-nose syndrome (WNS) in North America. Stochastic processes and functional relationships such as the interaction between infection timing, hibernation phenology, and immune function have historically been difficult to tease apart, and this synthetic viewpoint allowed the authors to make more informed management decisions and determine conservation and research priorities. In an effort to identify rules underpinning viral dynamics, Gentles et al.[7] synthesized mechanistic models of viral dynamics across multiple bat reservoir systems, finding that the absence of lyssavirus models for migratory and more solitary bat species "points to gaps in our complete understanding of the generalizable dynamics of the viral genus as a whole," demonstrating the utility of systems approaches for identifying the limits of current knowledge.

Empirical studies demonstrate the same principle. Speer et al.[8] found that habitat fragmentation in Brazilian forests altered the bacterial microbiomes of bat ectoparasites, a pattern only detectable when the full habitat, bat, and ectoparasite chain was examined, with network interactions shaped by factors two organizational levels removed from where they were detected. Becker et al.[9] traced an explicit habitat, host physiology, and hosted-organism causal chain in Central American bats using causal mediation analysis (a form of structural equation modeling), showing through systems tools that environmental mercury exposure suppressed host neutrophil function and subsequently elevated prevalence of intracellular bacteria. In each study, the major insights were only accessible by crossing levels of organization in a deliberately planned framework rather than focusing on a single level. Thus highlight important gaps in research and uncover missing links underlying fundamental ecological processes. While we acknowledge that there are data barriers for certain systems and questions, we will next discuss a selection of tools with a variety of data requirements, making these approaches flexible given the state of knowledge in a particular system.

1.b Operationalizing the Framework with Systems Modelling

Standard single-level statistics are insufficient for probing relationships that cut across multiple biological scales because the data are confounded at every level. Changes in the habitat may affect the microbiome or virome, but they are mediated through host physiology. To implement our framework, bat biologists should embrace tools specifically designed for detecting causality in nested, hierarchical systems. Three accessible tools are presented here: two that are used *a priori* to develop hypotheses — directed acyclic graphs (DAGs) and Bayesian belief networks (BBNs), and one that can be used to test hypotheses *a posteriori* — structural equation models (SEMs). We also discuss their minimal data requirements and best use cases, noting that this is not an exhaustive list and additional methods exist.

DAGs are graphical models constructed before data collection that are used to visualize the interacting variables and their assumed effects on each other within a system.[10,11] DAGs can help researchers decide which covariates to include or exclude to isolate a causal pathway, avoiding overcontrol, collider bias, and confounding. DAGs can also help identify which variables to include to better estimate a causal relationship (i.e., precision covariates) and whether a set of variables is better modeled as an interaction (i.e., effect modifiers) to characterize directional relationships. Application of DAGs to identify causal chains in zoonotic infectious disease by Jackson et al.[3] demonstrated the utility of this approach in the West Nile virus (WNV) system: some variables included in the DAG (e.g., infected horses) are never a

source of human WNV infection, so they are ultimately removed from the model, allowing researchers to prioritize interactions that affect the outcome of interest (human WNV infection). DAGs are most useful when there is sufficient expert knowledge or data available to construct logical connections, while primary data are needed to test specific paths. Furthermore, DAGs are strictly qualitative, allowing for the selection of covariates for statistical modelling of relationships rather than describing quantitative dynamics.[3] They may not be suitable for application to emerging infectious diseases, data-deficient bat species, or systems whose constituents are poorly documented.

BBNs are a related approach that offer greater flexibility with lower data requirements than DAGs. BBNs are used to quantify uncertainty through a network and make predictions under incomplete information, which is useful in directing management actions in situations where species ecology or causal links are poorly described.[12] This tool is more flexible than DAGs or SEMs because expert knowledge can substitute for primary data at poorly characterized nodes via expert elicitation (e.g., Gao et al.[13]; Adams et al.[14]). Despite Bernard et al.[2] successfully implementing this approach for directing management decisions and prioritizing future WNS research, the application of BBNs to bat conservation issues remains relatively rare. While the flexible construction allows BBNs to be updated as data accumulate, expert influence in creating them introduces subjectivity which needs to be documented transparently.

While DAGs and BBNs are primarily *a priori* modelling tools, SEMs are more powerful statistical tools used to model complex relationships between directly observed and indirectly observed (latent) variables.[15] Like DAGs, SEMs also require a pre-specified model structure but can use statistical inference to detect causality, magnitude, and directionality of relationships as well as partition direct and indirect effects. In bat biology, SEMs have been successfully implemented by Perez-Torres et al.[16] to understand threats to bats in the high Andes following habitat fragmentation. Perez-Torres et al.'s model showed that foraging height was the mediating variable linking reduction in frugivorous bat species richness with habitat fragmentation. With a traditional correlative approach, the inferences would be limited to an association between forest fragmentation and species richness; with the SEM, forest height is identified as a mechanistic driver, offering more tangible conservation priorities (i.e., prioritizing preservation of tall, mature forest rather than focusing on total forest area preservation). In other SEM-based studies such as Bovendorp et al.[17], lowland forest area and structure were found to have a more direct impact on bat species richness, suggesting that communities at different elevations face different pressures. While powerful, SEMs have certain limitations: as a rule of thumb, at least 10 observations per estimated parameter must be collected, and all variables in

the hypothesized chain must be measured. Consequently, incompletely sampled or unmeasured confounders can limit the utility and power of this approach.

Practical implementation of any of the above approaches hinges on prior knowledge of the system and data availability. One possible workflow using the methods described here would be to map the system using a DAG or BBN approach, prioritize data collection based on the connections elucidated by those methods, and then test the predicted network structure using SEM. The “Bats in/as Habitats” framework prioritizes conceptualizing research questions in the context of a system of interactions, and DAGs, BBNs, SEMs, and other network-based approaches facilitate the conversion of a systems diagram into testable hypotheses. We therefore encourage bat biologists to adopt these and other systems modeling tools to investigate cross-level feedbacks and mechanisms. Organismal biologists should not use these tools when single-level characterization is sufficient to address the question, or when the system is too poorly characterized for even expert elicitation.

Knowing when and where to apply these tools requires first knowing what has already been established at each level of organization in bat systems. The review that follows maps the current state of the literature: we synthesize current understanding of feedbacks between bats and their habitats (Section 2), the biology of bat-hosted organisms and how bat traits structure their communities (Section 3), and the cross-level synthesis that emerges from this review alongside the knowledge gaps it uncovers (Section 4). Together, these sections provide the empirical foundation for applying the network modelling methods introduced above, as the causal chains mapped out by these tools are only as strong as the literature that undergirds them.

2. Bats in Habitats

2.a. Habitat determines bat community composition and dispersal

To understand the broadest level of organization, that 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 effects at smaller scales[18,19] Both are impacted by the evolutionary history of the clade, for example through the opening of new feeding niches in Phyllostomidae[20,21] or hybridization (e.g., *Myotis*[22]). 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 (**Figure 1)**. Generally, bat species richness increases toward the equator, where temperature and primary productivity are higher and more consistent.[23] However, physiological limits on bat distributions vary significantly among species, making it difficult to establish definitive distribution rules.[24–27] 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.[28] 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[28], temperature[29], water availability[30], 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.[31–34] Vegetation complexity and habitat/resource diversity locally enhance bat species richness, as spatially heterogeneous conditions provide a greater diversity of suitable niches.[35–38] Feedback between adaptations in wing morphology, echolocation, and vegetation affects foraging success.[39–41] Moreover, roost availability is crucial to determining bat occurrences, sometimes even more so than availability of prey.[42–44] 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.[45,46] Simultaneously, bats are also important influencers of local resource availability for other organisms.

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

Bats wield considerable influence on their own and other species' realized niches — the set of conditions actually used by an organism (Table 1).[47] For example, certain species of communally roosting bats produce significant amounts of nitrogen, phosphorus, and potassium in guano deposits beneath roosts.[48,49] The largest aggregations of living vertebrates in the world are found in caves[50], with bat colonies functioning as a sink for up to 39% of the total forest nitrogen budget in some regions.[51] 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.[48,52,53] Caves that are home to large colonies of bats typically harbor greater diversity and abundance of cave-dwelling organisms, including some entirely dependent on guano, known as guanophiles.[48] Furthermore, the heat produced during guano fermentation, combined with the body heat of resident animals, influences the cave microclimate.[54] Bats' influence on nutrient cycling in caves can lead to positive and negative feedback cycles; for example, there is some evidence that the presence of bats in caves can lead to microclimatic changes that impact their suitability as roosts for other bats.[52,55]

Apart from altering their physical and chemical habitats, bats also take part in biotic interactions that can play out on local, ecosystem, and evolutionary scales. Plant-visiting bats provide important ecological services by facilitating reproductive success and recruitment of new seedlings.[56,57] 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 species *Pteropus niger*.[58] Indeed, pteropodids are key to the persistence of Pacific island flora due to long-range dispersal of large-seeded plants; however, this relationship collapse at low population sizes.[59] Bats provide pollination services to more than 500 angiosperm species worldwide[60], which is key to reproductive success and genetic exchange between plants and can drive plant evolution.[61] Columnar cacti and agaves are dominant plant elements in arid and semi-arid habitats of the Americas, and rely heavily on bats for pollination and sexual reproduction.[57,62] In Sulawesi, fruit bats are the main pollinators of durian and are estimated to contribute US$117/ha in economic value.[63]

Ecosystem functions provided by bats are of particular importance in island systems, in which bats may constitute a majority of the mammalian assemblage, in some cases being the only native mammals.[64–66] The high vagility of bats allows them to reach islands, including remote oceanic systems that do not have pre-existing mammalian fauna. These ecosystem functions are strongly related to the maintenance and stability of their ecosystems.[66] The plants brought by bats to islands include many pioneering plant species (e.g., figs [67–69]) important to both primary and secondary succession as well as forest regeneration after significant loss due to natural disasters. Some plants become wholly dependent on flying foxes (subfamily Pteropodinae[70]) for dispersal in island systems despite these species being common in continental landscapes.[71] Additionally, while doves and pigeons contribute to seed dispersal in Pacific island systems, flying foxes provide the main avenue of large seed dispersal.[72] In Tonga, the species diversity of plants consumed by pigeons is 40% less than that of bats, while on

other islands, both contribute equally to seed dispersal but consume a different set of plant species.[73,74]

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 to trees used consistently as roosts.[75] Other bats such as *Centurio senex* are seed predators that do not increase germination success.[76,77] 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.*[78] Trees that host bats are known to benefit from the nutrients in their excrement.[79,80] 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 are useful starting points.[56,81,82]

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 (**Figure 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.[83] Across the tropics, ~80% of seed dispersal in general is performed by birds and bats.[84] Bats produce dense and diverse seed shadows, and it appears that more diverse communities of frugivorous bats are linked to more diverse forests.[85,86] 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 fruit bats[87], but Afrotropical fruit bats exert enormous influence on forests, forming seasonal aggregations of millions of individuals not seen in the Neotropics.[46] While it is clear that bats influence their habitats by changing vegetation, less certain are the impacts that these aggregates of seemingly specific bat–plant interactions have 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 by helping to make connections explicit and illuminate knowledge gaps.

Of the over 1500 bat species recorded, about 70% are insectivorous.[88,89] This highlights the role of bat assemblages in arthropod regulation and their importance in food web dynamics,

both in natural and 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.[90–92] In North America, aerial insectivores were shown to consume at least 160 known agricultural pests and pathogen vectors, with similar results reported in Europe.[93,94] For example, it is estimated that bats provide between $3.7–53 billion USD of direct insect pest control across the United States[95] and have been shown to reduce crop damage resulting from pests and their associated microbes.[96–98]

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.[99] 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.[91,100,101] Interestingly, the presence of bats alone, regardless of the number of mosquitoes they actually consume, may be sufficient to alter mosquito oviposition, thereby decreasing vector populations.[102] Bats could also regulate populations of insect vectors other than mosquitoes[103], 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 can nonetheless vary substantially not only by species but also temporally and spatially, including in response to pulses in insect abundance and emergence events. Disentangling the role of these factors in regulating insect populations is therefore imperative.[104,105] The consumption of insects has been hypothesized as a mechanism by which new parasites and microorganisms can colonize bats.[106–109] Some efforts to document bat diets globally have been initiated and could help address important knowledge gaps concerning the relationships between diet and parasitism (see Tuneu-Corral et al.[92]), but require further research effort. Without having detailed information about bat habitats and diets, we lack an important window into the relative importance of diet in structuring interactions. For example, the impacts of declining insect populations globally[110] may remove interactions in some cases via loss of a food source while establishing new ones in others if bats begin consuming new prey or insects become more accessible year-round. To predict downstream consequences of changing interaction networks and the mechanisms underpinning them, we need to understand how shifts in bat communities can cascade through trophic, parasitic, and mutualistic interactions to reshape entire ecosystems.

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 human activity (**Table 1**, **Figure 1**). Humans have altered ecosystems quickly and extensively, leaving many species unable to adapt. Some examples of how humans are altering bat habitats 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 roost sites, and in some cases contribute to bat mortality directly or indirectly (e.g., via stress).[111] Anthropogenic changes to bat habitat may force bats to alter their ecology and contribute to the spillover of viruses to humans.[112] 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 (for a full review of the effects of anthropogenic change on bats, see Voigt and Kingston[113]).

Habitat transformation can lead to fewer resources and contribute to a reduction in reproductive and survival rates of individual species, thus altering the ecosystem dynamics in which bats participate.[114–116] Human alteration of landscapes can have profound impacts on roost availability, and increasing rates of land-use change have the capacity to reduce habitat availability overall.[117] In the Neotropics, roost specialists appear to be particularly vulnerable to habitat fragmentation compared to more generalist roosting species.[44,118] Similarly, in the Paleotropics, species that roost in forest structures (i.e., standing and fallen trees, under leaves) are more vulnerable to forest loss than cave-dwelling species.[119,120] Despite this, disturbance at caves (e.g., limestone and phosphate mining, tourism) means many cave-dependent species may be living on borrowed time.[120–122]

Humans can also directly influence the availability and quality of bat food resources. Application of broad-spectrum pesticides can reduce overall prey biodiversity, but targeted pesticides applied to nuisance species may also restore prey biodiversity by changing competitive dynamics in the insect community.[123,124] However, organic farming on its own is insufficient to support bat biodiversity, with landscape features such as hedges and rivers playing a more important role.[125] Similarly, Australian nectar-feeding bats have shifted from large nomadic groups to smaller sedentary groups in agricultural areas in response to changing climate and conversion of native trees to ornamental plants (Box 1).[112] 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.[126] 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.[127] Counterintuitively, some fruit-eating bats show higher body condition and reproduction *outside* of protected areas, likely due to the increase in pioneer plants in disturbed habitats.[128] Bats therefore appear to respond variably and in potentially location-, diet-, and species-specific ways to habitat loss and urbanization.

Urbanization and its consequences can influence the distribution of bats across landscapes.[129] 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.[130]). The impacts of artificial light at night (ALAN) can vary with species biology, with some bat species taking advantage of the concentration of insects under lights, while light-sensitive species are pushed into increasingly concentrated areas of dark refugia.[131] Experimental and observational evidence also suggests that fruit-eating bats change foraging behaviors to avoid illuminated plants.[132] Current literature is equivocal about the extent and direction of the effect of ALAN on bat movement, including nightly foraging and migration.[133,134] 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.[135–139] Humans can also create new habitats for bats; many species aggregate in abandoned mines, buildings, or transportation structures[140,141], and this can even provide physiological advantages compared to natural roosts.[142,143] Bat species traits such as geographic range, habitat preference, and diet can impact the likelihood of anthropogenic roosting.[144] 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.[119,139,145,146] This variation in responses further emphasizes the need to address gaps in our understanding of what individual species require to survive in the Anthropocene.

Bat health and mortality, including due to 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 lead to suboptimal habitats, resulting in elevated markers of physiological stress.[147–149] Conversely, roosting in anthropogenic structures may have no physiological costs or may improve survival and thermoregulation.[142,150] While higher cortisol levels are generally assumed to be deleterious, in some cases they may have negligible effects on overall bat physiology.[148] In other cases, chronic stress may lead to poorer health outcomes for bats, including lower white blood cell counts and decreased body

mass.[151] 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[152], and periods of food scarcity are related to elevated shedding pulses of Hendra virus (Box 1).[153] Habitat fragmentation is also associated with higher bacterial microbiome variation in vampire bats, which may indicate a destabilized microbial community.[154] 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.[155] 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 Sánchez et al.[156] and Sandoval-Herrera et al.[157]).

In addition to altering the resources bats depend on, 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.[158,159] Bats are often taken as bushmeat in the Paleotropics, particularly in low socioeconomic countries with high deforestation rates, suggesting that poverty is associated with bat bushmeat harvesting.[160] In other countries, people often have negative attitudes towards bats, supporting lethal control measures to limit their populations.[161] 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.[162,163] 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.[164] Unintentional killing of bats also impacts their populations; wind energy has been identified as an increasingly important threat to migratory bat species.[165,166] 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.[167–169]

3. Bats as Habitats

The distinctive biology of bats makes them unique habitats for a variety of organisms, from macroscopic parasites to microbial organisms spanning 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 (**Figure 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.

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, ability to fly, long lifespans relative to body size, use of heterothermy, and highly gregarious social systems.[170] 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.[171–174]

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.[172] 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.[175,176] 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.[177–179] In other systems, bat ectoparasites lack genetic population structure even when host populations display structure.[180,181] The converse — where bat ectoparasites display population structure not evident among their bat hosts — can also occur.[182] 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 in vampire bats, while host genetic distances and colony size were found to have no effect.[183] 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 (**Figure 2**).

Bats have 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.[184–186] As a result, bats can 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[185,187,188]; however, even rare vagrants might introduce parasites to new regions.[189] Conceptual frameworks have been developed for understanding the relationship between migration and parasitism broadly, but our framework broadens the lens to consider habitat differences as a force potentially modulating these interactions.[190] In addition to their ability to move long distances, some bats form dense aggregations, while others roost in small groups or solitarily. This diversity in social behaviors can have a strong impact on the transmission of hosted organisms, which has been extensively reviewed elsewhere.[191] For example, co-roosting species in caves have a higher likelihood of pathogen sharing.[192,193] Ectoparasite prevalence and intensity can also 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.[194–196]

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[178], and some mites may use bats phoretically to reach new flowering plants.[197] 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.[191,198] Bat behavior and social systems can therefore influence ectoparasite dispersal and population structure, with bat species that roost in larger groups, intermix between colonies[199], 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.[200,201] 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 et al.[202]). 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.[203–207]

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[208], represent an opportunity for long-term colonization — and perhaps *in situ* evolution — not found in other small mammals.[209,210] 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, which may be further influenced by torpor.[211–213] Other explanations, including predator release, are related to the evolution of flight but not necessarily as a physiological consequence.[214] For example, *Mystacina tuberculata*, endemic to New Zealand, frequently forages on the ground[215], supporting 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 some pathogens that would cause severe symptoms or death in other mammals.[216,217] It was previously hypothesized that bats have daily metabolic patterns that mimic fever, which might allow them to better tolerate viruses[218], but current research suggests that viral tolerance is more likely a downstream effect of adaptations required for dealing with the metabolic stress of flight.[219,220] 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 endotherms, 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.[221,222] 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 remain 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.[223,224] 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.[221] As one illustrative example, hibernation of several Nearctic bat species slows rabies virus replication and allows “overwintering” of the infection.[225,226] The impact of seasonality on bat–microorganism interactions remains unclear and might have important

immunological consequences that inform questions about longevity.[227] As the multitrophic interactions of bats, their environments, and the organisms they host remain to be explored for many taxa[228,229], 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 that variably impact host bat populations (**Table 1**). Bats have a resident microbiota that supports their nutrition and health. For example, fruit-, blood-, and animal-eating bats have gut microbiota members that supplement their specialized diets with missing nutrients.[230–232] 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.[233,234] Because bat microbiomes are often strongly linked to their local environment[176,235], 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.[207,236] Important knowledge gaps remain in our understanding of the homeostatic functions of the bat microbiome; by studying these relationships, we can better understand the causes and consequences of disrupting them.

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[237,238]). This resistance enables them to act as reservoirs of pathogens, such as many RNA viruses[239], rather than experiencing the population declines that these infections can precipitate in other animals. With limited exceptions, microbes may not be a major cause of mortality in bats.[158] The most notable exception is *Pseudogymnoascus destructans*, the causative fungal agent of white-nose syndrome (WNS), which has led to severe, sustained mortality of hibernating bats in the United States and Canada. Since its emergence in North

America in 2006, WNS has driven previously abundant bat species to the edge of extinction.[240,241]

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[242], but they instead act as important vectors of viruses[243], bacteria[244], and protozoa[245] to their host bat species and potentially between bats and other animals.[246] 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 .[247] 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, possibly associated with the movement of rats into agricultural areas (Box 1). 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.[248] 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 (e.g., Hasik et al.[249]).

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, partiti virus in *Pseudogymnoascus destructans*), and fungi (e.g., Laboulbeniales).[250–256] The infection of one parasite with a different parasite is a common phenomenon in nature, though still largely understudied.[228,257] Infections with Laboulbeniales fungi or *Polychromophilus* parasites negatively impact the survival and lifespan of parasitic bat flies.[258,259] 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.[250,260] Coinfections, simultaneous infections with multiple parasites in an individual host, are also common.[261,262] 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[228,262], 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).[263–267] For example, microbes may indirectly mediate host–parasite interactions[268]; correlations have been found between the composition of bacterial communities on the skin of bats and the prevalence of dipteran ectoparasites.[269] Direct interactions can also occur; bat skin bacteria have been shown to have anti-fungal effects on the WNS pathogen, *P. destructans.*[270] 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.[259] 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.[271] 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.[205,272,273] 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.[274] While tree-roosting pteropodids have also been recorded to have nycteribiid flies, they typically have a lower fly load than cave-roosting pteropodids.[275,276] 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.[277] 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 haemosporidian (malaria) parasites may be spread to new hosts during migration events.[274,278,279] The relative contributions of within-host interactions versus 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, highlights

the importance of regarding hosts as “habitats” for these communities of interacting organisms. This perspective of hosts as habitats opens the door more widely to exploring how host biology influences associated organism communities, and how environmentally mediated changes in host biology can, in turn, reshape these communities and their effects 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, 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 suppresses host innate immunity, in most cases increasing the prevalence of intracellular bacteria (i.e., *Bartonella* and hemotropic mycoplasmas) through weakened neutrophil response.[9] Despite studies showing apparent correlations between environmental toxicants and the diversity of bat-hosted organisms[280–282], *direct* impacts on parasites (i.e., not mediated by impacts on the host) are difficult to show and represent a significant knowledge gap (**Figure 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.[151,283] Anthropogenic stress can also compound normal seasonal stress due to migration, breeding, or hibernation. For example, 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[112,153]).

While direct anthropogenic disturbance can impact host stress, not all effects on hosted organisms are mediated by stress. In other cases, anthropogenic pressures alter patterns of bat dispersal or aggregation. For example, impacts on bat ectoparasite loads were found to be nuanced and context-specific, with cave complexity and population density of hosts interacting

with disturbance.[155] Intense disturbance of bats at caves (e.g., hunting, culling, or intensive guano mining) can ultimately cause bats to abandon these roosts.[50,284] In landscapes where suitable roosts are limited, this may increase aggregations at refugial roosts (i.e., those inaccessible to people), with consequences for transmission dynamics of host-associated microbes and parasites.[285]

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 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.[8] These findings suggest that network interactions may be shaped by factors *two levels* removed (i.e., 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 microbes and parasites spreading within biological communities — a phenomenon called the "dilution effect".[286] 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.[287,288] 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.[289,290] 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 (e.g., functional, spatial, genetic, etc.) can also play a role in mediating interactions among bats and bat-hosted organisms, but these are comparatively understudied.[291]

Despite promising advances in understanding these processes, the mechanistic links between habitat disturbance, stress and immunity, and interactions among bats and bat-hosted organisms remain poorly understood, with a particular need to characterize the physiological changes in bats across habitats and over time.[292,293] In addition, there is a need to understand how disturbance influences bat movements and roosting ecology, because resulting changes in inter- and intra-specific interactions, primarily at roosts, can influence transmission dynamics and parasite life cycles.[193,199,294] Even indirect or infrequent interactions (e.g., sharing roosts at different times) can modify pathogen transmission dynamics.[295] Habitat disturbance 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. Because relationships among environment, macrofauna, and hosted organisms are nested and hierarchical, feedbacks can occur among all components and may be modulated by changes at any level (**Figure 3**). 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, 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, is important to understand but not obvious unless the network is fully defined.[296,297] For example, there are developmental and physical limitations on bat skulls that prevent them from having certain shapes and might restrict their evolvability.[298] These “rules” are largely difficult to directly observe, but by using a network-level view, they may be possible to detect as latent variables. This kind of approach has been applied to other biological systems, such as the ecological interactions of predators and prey on the Serengeti[299], but it has rarely been applied to the multi-tiered system of habitats, organisms, and the organisms they host. Our framework thus provides a way to understand the mechanisms and drivers of the complex interactions that make up global biodiversity.

A key facet that differentiates this paradigm from typical predator–prey or plant–pollinator interactions is that predators and pollinators are rarely considered as “ecosystems” in their own right, but rather as part of some larger ecosystem. By considering environment–macrofauna–hosted organism(s) connections more explicitly, the top-down and bottom-up effects caused by the behaviors and physiologies of the macrofauna at the center of the network can be more fully understood (e.g., Rynkiewicz et al.[300], Johnson et al.[301], and Hassell et al.[302]). The basis of the mechanistic assembly in bat systems (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. In Box 1, we outline the application of systems thinking as applied to the system of *Pteropus* bats and Hendra virus, highlighting the benefits of a systems-based approach versus examining the issue from a single level of biological

organization. Further, we identify new research questions from conceptualizing the bat Hendra virus system under the “Bats in/as Habitats” framework, including concrete hypotheses that could be tested by gathering new and existing empirical data to support *Pteropus* conservation while balancing public health concerns.

Beyond addressing conservation, 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.[303] 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, the authors know of no study that 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.[304]

An important caveat to the value of this framework is that it is not universally applicable. There are questions for which a single-level study remains the right design, for example the impacts of wind farms on migratory bat populations or the mechanism by which wind turbines cause mortality. For these, careful experimental or observational study design in a traditional organismal biology framework will be more tractable in terms of time, money, and effort, while still providing the results to draw conclusions and fill knowledge gaps. Furthermore, the predictive and inferential value of any network model may be jeopardized by the instability of extreme events arising from anthropogenic change. The most apparent of these changes are extreme weather events including extended droughts, heat events, and 100-year floods, among others. While many of the changes we review are incremental, repeated and severe climate perturbations may produce stochastic and non-linear responses that are difficult to predict based on the data we already have.[305] Even if the current data or model 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. Future Directions

The gaps embedded in the preceding sections are numerous and, considered individually, can appear disconnected from one another. Consolidating them under the "Bats in/as Habitats" framework reveals a tractable set of research priorities that map onto the hierarchical structure depicted in **Figure 3**. Below, we organize these priorities by the level of biological organization at which they primarily operate: at the bat–habitat interface (5.a), at the bat–hosted organism interface (5.b), and cross-level questions whose resolution requires integrating across the framework as a whole (5.c). We do not aim to be exhaustive; rather, we have deliberately prioritized areas in which the framework most changes the research question relative to conventional single-level designs, and in which existing partial data suggest that progress is tractable using the methods described in section 1.b.

5.a. Priorities at the bat-habitat interface

1. Resolving conflicting evidence regarding whether bats consume enough mosquitoes to meaningfully reduce vector populations, exploring how the presence of bats alters mosquito behavior, and directly linking bat predation of vectors to a measurable reduction in human infectious disease incidence.
2. Conducting fundamental natural history studies on the roughly 18% of bat species currently classified as "Data Deficient" by the IUCN. Gathering data on their species-specific traits, range, diet, and roosting preferences is required to build accurate predictive models of how bats will respond to ongoing urbanization and climate change.
3. Investigating how extreme, stochastic events (such as extended droughts, severe heatwaves, and 100-year floods) produce non-linear responses in bat systems, and identifying which specific ecological linkages are entirely severed or permanently altered under these extreme conditions.
4. Integrating multi-scale interactions to understand why different tropical regions display distinct ecological patterns; are there generalizable rules about ecosystem functions such as bat-facilitated seed dispersal, or do the data reflect idiosyncrasies within particular ecological contexts?

5.b Priorities at the bat-hosted organism interface

1. Developing unified frameworks to distinguish the relative contributions of inside-the-host interactions (e.g., direct resource competition or indirect immune pathways) from outside-the-host transmission dynamics (e.g., migration events or shared roosting preferences).

2. Studies treating individual bats explicitly as moving "habitat patches" by applying metapopulation and metacommunity dynamic models to the hosted organisms to understand how they colonize, compete, and persist across shifting host populations.

5.c. Priorities requiring integration across levels

1. Designing experiments to isolate and show the direct impacts of environmental toxicants and habitat changes on microbial and parasite communities, independent of host-mediated stress and immunity filters.
2. Designing studies that track changes in bat abundance, overall community biodiversity, and specific host competence to test if the dilution effect holds true for bats and under what conditions. This includes exploring how other understudied layers of diversity — such as spatial, functional, and genetic diversity — mediate these host–parasite networks.
3. Leveraging existing databases to perform network-level analyses, with a focus on detecting "missing links" (undetected interactions) and "forbidden links" (interactions that cannot occur due to physical, evolutionary, or developmental constraints, such as allometric limitations on foraging).
4. Moving past broad generalizations by isolating specific mechanistic drivers, i.e.:
    a. Explicitly separating the impacts of native habitat loss from human resource provisioning.
    b. Understanding precise interactions among multiple pathogens both within and between hosts to better predict infection dynamics.

None of these priorities require conceptual innovation beyond what is already present in the bat ecology literature, and several are already partially addressed by individual studies cited throughout this review. What the framework contributes is a scaffold that makes cross-level dependencies visible, because that ultimately determines whether a given question can be answered at the level at which it is typically asked, or whether a broader design is required. Progress on these priorities will depend not only on individual research efforts but on coordinated data collection, sample archiving, and cross-lab collaboration of the kind supported by consortia such as The Global Union of Bat Diversity Networks (GBatNet), including the batshare database[306], a community-curated database of samples dispersed across individual institutions and laboratories; the broader Arctos[307] museum collection database; trait databases such as EltonTraits[308], MorphoBank[309], and the BigBatDatabase (https://www.bigbatdatabase.org/); literature databases such as BatLit[310]; and efforts to curate

taxonomy and geographic ranges such as Bats of the World[311] and the Bat Taxonomic Alignment project[312]. We invite the bat research community to take up these questions under this or related integrative frameworks.

6. Conclusions

Bats, like other organisms, occupy a distinct position in ecological research: they are simultaneously nodes within diverse habitats and habitats themselves for a wide range of hosted organisms. Recognizing this duality, and treating it as an organizing principle rather than an incidental feature of bat biology, reveals cross-level dependencies that are largely invisible under conventional single-level study designs. The "Bats in/as Habitats" framework proposed here is not a fundamentally new ecological principle, but makes explicit the hierarchical structure of interactions in bat systems, points to existing tools (SEMs, BBNs, DAGs) capable of formalizing and testing hypotheses at that scale, and identifies where the payoff of cross-level design is likely to be highest. It can be used to prioritize research study design and data collection, as well as identify fruitful new avenues for study. The research priorities consolidated in Section 5 offer concrete, testable entry points for bat biologists to begin exploring some of the most pressing research questions in the field.

The demand for this kind of integrative synthesis is increasingly reflected in the broader scientific enterprise, from the U.S. National Science Foundation's former Rules of Life initiative to the One Health framework and the United Nations Quadripartite. Bats provide a particularly informative model for developing such synthesis because of their global distribution, ecological diversity, and comparatively well-studied interactions with microbes and parasites, but the framework itself is not bat-specific. The conceptual scaffolding presented here is directly translatable to any host system in which habitat, host, and hosted organisms interact across levels, and we hope it will encourage integrative study designs beyond bat biology as well.

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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	Reference
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[58]
	Chiroderma spp.	Phyllostomidae	Brazil (South America)	Bats act as pre-dispersal predators of small fig seeds, limiting seed dispersal.	+	–	Nogueira & Peracchi 2003[76]
	Carollia sowelli	Phyllostomidae	Costa Rica (Central America)	Artificial light at night deters some frugivorous bat foraging behavior.	–	–	Lewanzik and Voigt 2014[132]
	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[317]
	Rhinolophus sedulus	Rhinolophidae	Malaysia (Southeast Asia)	Bats in logging areas had fewer leukocytes than bats in recovered forests.	-	-	Seltmann et al. 2017[151]
	Desmodus rotundus	Phyllostomidae	Argentina (South America)	Abundant livestock allows blood-feeding bat population size to nearly double.	+	-	Delpietro et al. 1992[318]

	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[90]
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[225]
	*Pteropus conspicillatu*s	Pteropodidae	Australia (Oceania)	*Ixodes holocyclus* ticks cause paralysis and contribute to bat population declines.	-	-	Buettner et al. 2013[247]
	Miniopterus schreibersii	Miniopteridae	Hungary (Europe)	Bat infections with Laboulbeniales fungi shorten lifespan of nycteribiid bat flies.	+	+	Szentiványi et al. 2020[258]
	Myotis lucifugus	Vespertilionidae	Canada (North America)	Certain skin bacteria can inhibit growth of the white-nose syndrome fungus (*Pd*).	+	+	Lemieux-Labonté et al. 2017[270]
	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[122]
	Dermanura spp. and *Sturnira*	Phyllostomidae	Belize (Central America)	Mercury levels were correlated with increased risk of infection with *Bartonella* bacteria owing to immunosuppression.	-	-	Becker et al. 2021[9]

	parvidens						
	Artibeus lituratus, Carollia perspicillata, Desmodus rotundus, Sturnira lilium, Myotis nigricans, and *Myotis riparius*	Phyllostomidae and Vespertilionidae	Brazil (South America)	Habitat fragmentation was associated with perturbation of bacterial communities of obligate bat flies (Streblidae and Nycteribiidae) found on bat hosts.	-	-	Speer et al. 2022[8]

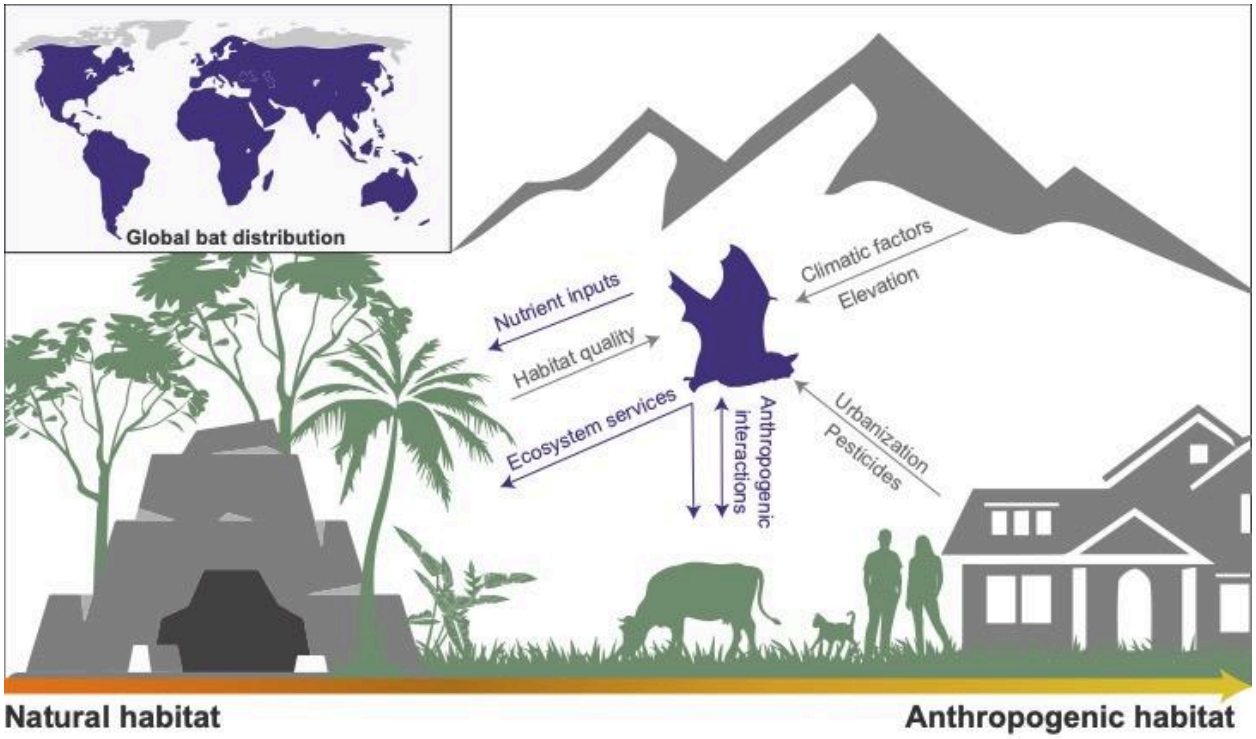

Figure 1. “Bats in Habitats”: interactions between bats (purple) and the biotic (green) and abiotic (grey) aspects of their habitats. Arrowheads point toward the recipient of each interaction, with bidirectional relationships indicated with double-headed arrows. Inset shows global bat distribution in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

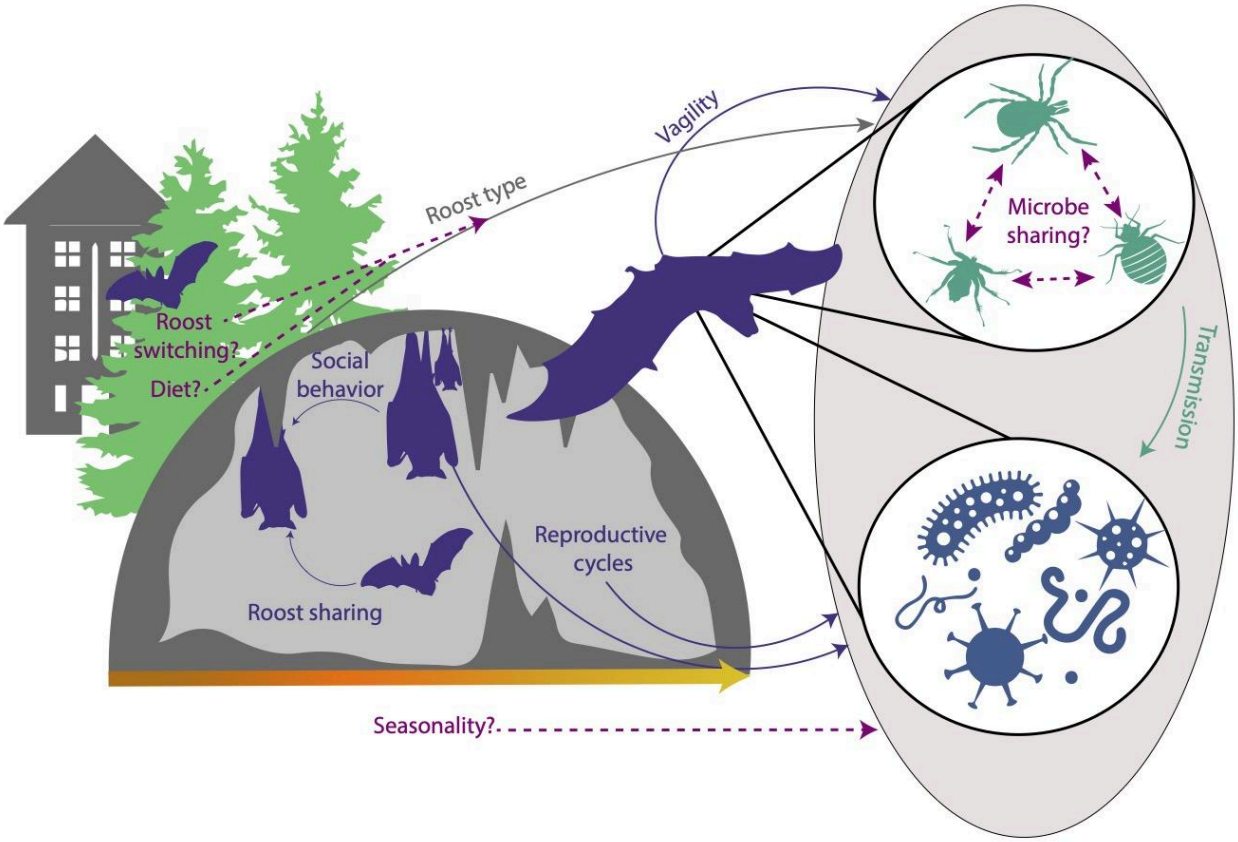

Figure 2. “Bats as Habitats”: including aspects of bat biology that influence the diversity and structure of organisms they host. Current knowledge gaps reviewed in the text are indicated as questions.

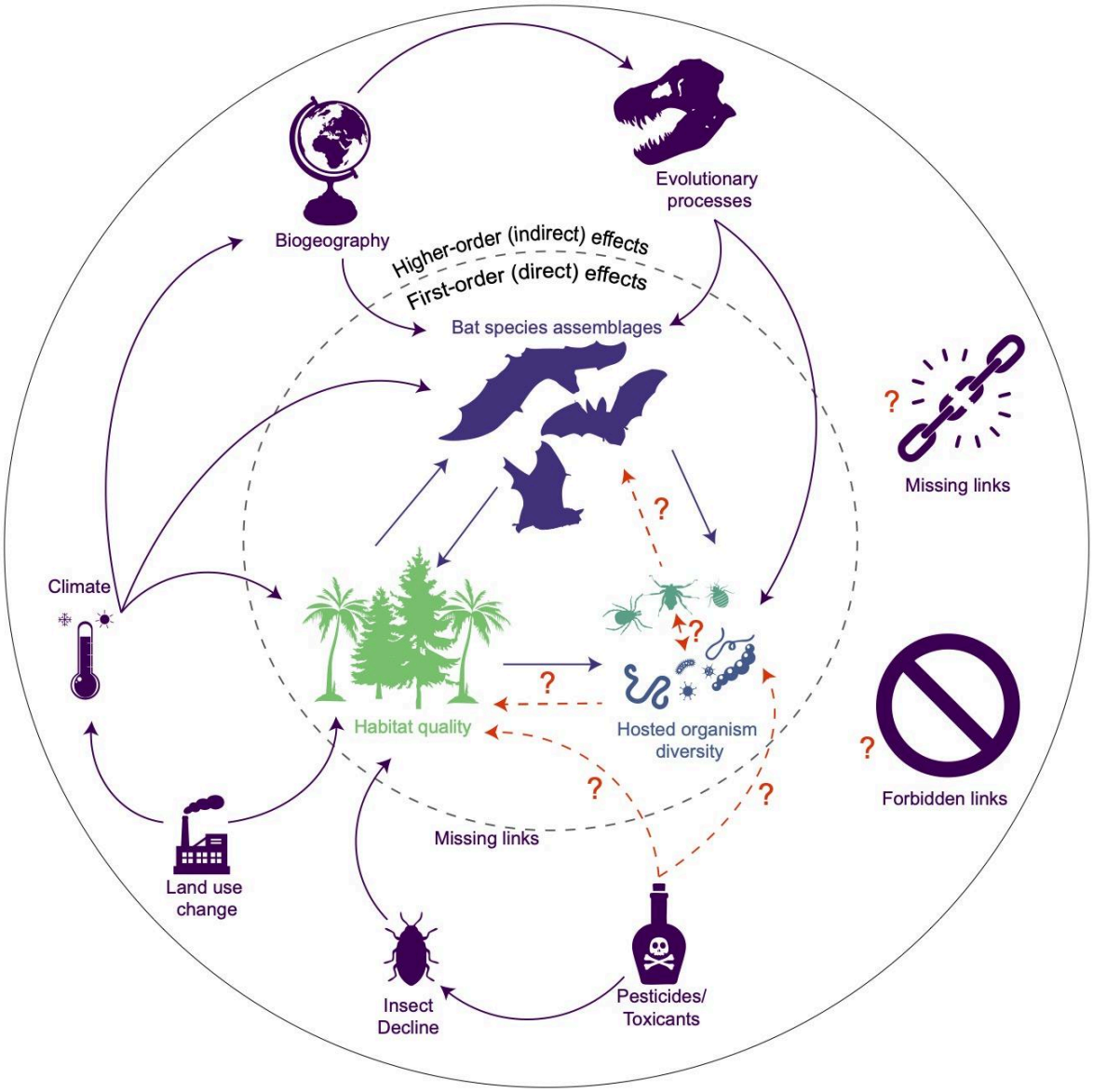

Figure 3. Hierarchical system diagram depicting direct and indirect effects structuring nested interactions among bats, their habitats, and hosted organisms. The inset circle represents direct, first-order interactions while indirect effects are listed in the outer ring. Arrows show a non-exhaustive 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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