Trends in
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Opinion

Bats and ectoparasites: exploring a hidden link in zoonotic disease transmission

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Bats are increasingly in the focus of disease surveillance studies as they harbor pathogens that can cause severe human disease. In other host groups, ectoparasitic arthropods play an important role in transmitting pathogens to humans. Nevertheless, we currently know little about the role of bat-associated ectoparasites in pathogen transmission, not only between bats but also to humans and other species, even though some of these parasites occasionally feed on humans and harbor potentially zoonotic organisms. In this work, we summarize current knowledge on the zoonotic risks linked to bat-associated ectoparasites and provide novel risk assessment guidelines to improve targeted surveillance efforts. Additionally, we suggest research directions to help adjust surveillance strategies and to better understand the eco-epidemiological role of these parasites.

Highlights

Bat-associated hematophagous ectoparasites have been found harboring zoonotic and potentially zoonotic pathogens.

Some species, such as bat ticks, occasionally feed on humans and other non-chiropteran hosts.

A structured research strategy combined with risk assessment could enhance our understanding of which bat-associated parasites may act as vectors of zoonotic pathogens.

Future research needs improved guidelines, focusing on a One Health strategy to predict and prevent potential pathogen spillovers.

Recent findings on parasites associated with bats and potentially zoonotic pathogens

Bats represent great diversity worldwide, being the second most speciose group among mammals. This diversity extends to their parasites, as they frequently host a wide range of hematophagous ectoparasitic species. Common ectoparasites of bats include bat bugs (Cimicidae and Polyctenidae), bat flies (Nycteribiidae and Streblidae), fleas (Ischnopsyllidae), mites (Acari), and ticks (Argasidae and Ixodidae). With the increasing accessibility and decreasing costs of molecular pathogen screening, growing evidence supports the ubiquity of pathogenic organisms in these parasites, and their involvement in maintaining the natural transmission cycle of potentially **zoonotic pathogens** (see Glossary) in nature [1–3].

Some recent findings indicate the presence of a variety of zoonotic pathogens in bat-associated parasites, which includes bacteria, such as *Bartonella rousetti* [4,5], and *Candidatus* (*Ca.*) Mycoplasma haemohominis [6] in bat flies, *Rickettsia hoogstraalii* [7], *R. raoultii* [8] and *R. rickettsii* [8] in soft ticks, and *Anaplasma phagocytophilum* [9], *Borrelia burgdorferi* s.l. [10], *Neoehrlichia mikurensis* [11], and *Mycoplasma* spp., some of which showed high similarity to the human pathogenic *Ca.* M. haemohominis [9] in hard ticks. Furthermore, potentially human pathogenic viruses have also recently been detected in these ectoparasites, including Lloviu virus [12], and Issyk-Kul virus in soft and hard ticks [13]. These bacterial and viral pathogens are frequently detected in bats, and pathogen-positive parasites are often collected from infected hosts [12,14–17]. Infections caused by these organisms – such as *A. phagocytophilum*, *N. mikurensis*, and tick-borne rickettsioses in humans – are usually mild or asymptomatic [18–20]; however, other pathogens, which are known to cause severe disease, and even death, in some individuals include *Ca.* M. haemohominis and *R. rickettsii* [6,21].

Pathogen surveillance efforts in bats have greatly increased over the past decade due to their association with highly pathogenic viruses affecting humans, but hematophagous ectoparasites are

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often excluded from these studies. Additionally, minimal effort is usually dedicated to understanding the ecological role of these parasites in pathogen transmission between bats and other species. However, with the rise in human–wildlife interactions, there is increasing evidence that these parasites could play a significant role in the interspecies transmission of vector-borne pathogens.

Feeding behavior and vectorial capacity of bat-associated parasites, and assessing the risk of pathogen spillover

Several factors affect the transmission of vector-borne diseases between and within host populations, including ectoparasite feeding behavior, **host range**, and **vectorial capacity**. The host range and actual vectorial capacity of bat-associated ectoparasites remain unclear and difficult to study due to the technical challenges of maintaining both parasites and their hosts in the laboratory, including the stress of captivity for bats and the difficulty of obtaining permits for keeping these animals. Additionally, only a few attempts have been made to demonstrate the vector competence of bat-associated ectoparasites, such as a recent study on the Marburg virus, in which batflies were found to play no obvious role in pathogen transmission among bats [22]. Generally, the zoonotic potential of several pathogens detected in bat parasites has not been proven; therefore, their vectorial capacity requires further investigation. Soft tick species are excellent candidates for laboratory maintenance as they can live for several years, even decades (up to 25 years) and do not require the presence of their bat hosts due to their broader host range and tolerance of starvation [23]. Therefore, their feeding behavior, host range, and vectorial capacity could likely be investigated more efficiently under laboratory conditions.

For efficient pathogen **spillover** to occur from bats to humans and other animals via ectoparasites, several factors must align, including a suitable environment for both hosts and parasites, as well as immunological, ecological, and behavioral compatibility [24]. For instance, bat flies are not yet known to feed on humans or other species besides bats, likely due to their highly specialized morphology, digestive system, and microbial composition, which are adapted exclusively to feeding on their bat hosts [25]. Therefore, they are less likely to act as vectors during interspecies pathogen spillover events.

To be considered a potential vector, parasites must also have a broader host preference that extends beyond a single bat species or closely related hosts. So far, only a number of bat-associated parasites have been observed to feed on non-chiropteran hosts; some of these species include various soft ticks – such as *Argas boueti*, *A. transgariepinus*, *Carios kelleyi*, *C. vespertilionis*, and *Reticulinasus salahi* – which often parasitize bats occupying human dwellings and can be found inside homes occasionally seeking out human hosts [2,26]. Additionally, ixodid bat ticks, such as *Ixodes simplex* and *I. vespertilionis* can also be found feeding on humans due to shared working or recreational spaces [27]. Also, human-associated parasites can occasionally be found on bats, like the common bedbug *C. lectularius* [28], and bat-associated cimicids – such as *Stricticimex parvus* and *C. insuetus* – sometimes attack humans [29]. Other mammal-associated ticks, which are known to harbor several pathogens with high medical and veterinary importance – such as *I. ricinus* and *Haemaphysalis concinna* – can be found on bats [30,31].

The above evidence suggests that some bat-associated ectoparasites play, or could play, a yet-to-be-confirmed role in the transmission of zoonotic pathogens between bats and humans. However, our understanding of the frequency of these interactions and pathogen-sharing events, the number of bat-associated parasite species capable of doing so, and the spatial occurrence of these events, remain significantly limited.

Developing **risk assessment** strategies could help to identify parasite species or groups that potentially contribute to zoonotic transmission between bats, humans, and other animals, based on

Glossary

Citizen science: the practice of engaging (non-professional) volunteers in scientific research, allowing them to contribute data, and observations.
Ecotone: a transitional zone between two distinct ecological communities or ecosystems, where species from both areas often interact.
Host range: the variety of different species that a particular pathogen, parasite, or organism can infect or live on.
Machine learning: a field of artificial intelligence (AI) that involves training algorithms to recognize patterns in data and make predictions.
Reservoir: one or multiple species in which a pathogen normally multiplies, and can transmit the infection to other individuals, serving as a source of infection.
Risk assessment: involves evaluating the likelihood and impact of pathogen-related hazards to guide protective measures and control strategies.
Spillover: the movement of disease-causing agents from one certain species (often a reservoir) to another one, which occasionally leads to a new infection.
Vectorial capacity: a measure of a vector's ability to transmit a pathogen.
Xenomonitoring: the use of different species (e.g., ticks or mosquitoes) to detect and monitor the presence of pathogens in the environment.
Zoonotic pathogen: disease-causing agents that can be transmitted from animals to humans.

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their host range (e.g., less specialized on bats), feeding behavior (e.g., occasionally feeding on humans), habitat preference (i.e., associated with hosts occupying human-made structures or habitats), and the pathogens they harbor (e.g., presence of zoonotic pathogens) (Figure 1, and see Table S1 the supplemental information online). Consequently, these species, particularly some of the hard and soft ticks, should be given particular focus due to the presence of known zoonotic pathogens, and due to their host preference, which includes not only bats, but also humans and other mammals, making them an already recognized link for zoonotic transmission towards humans.

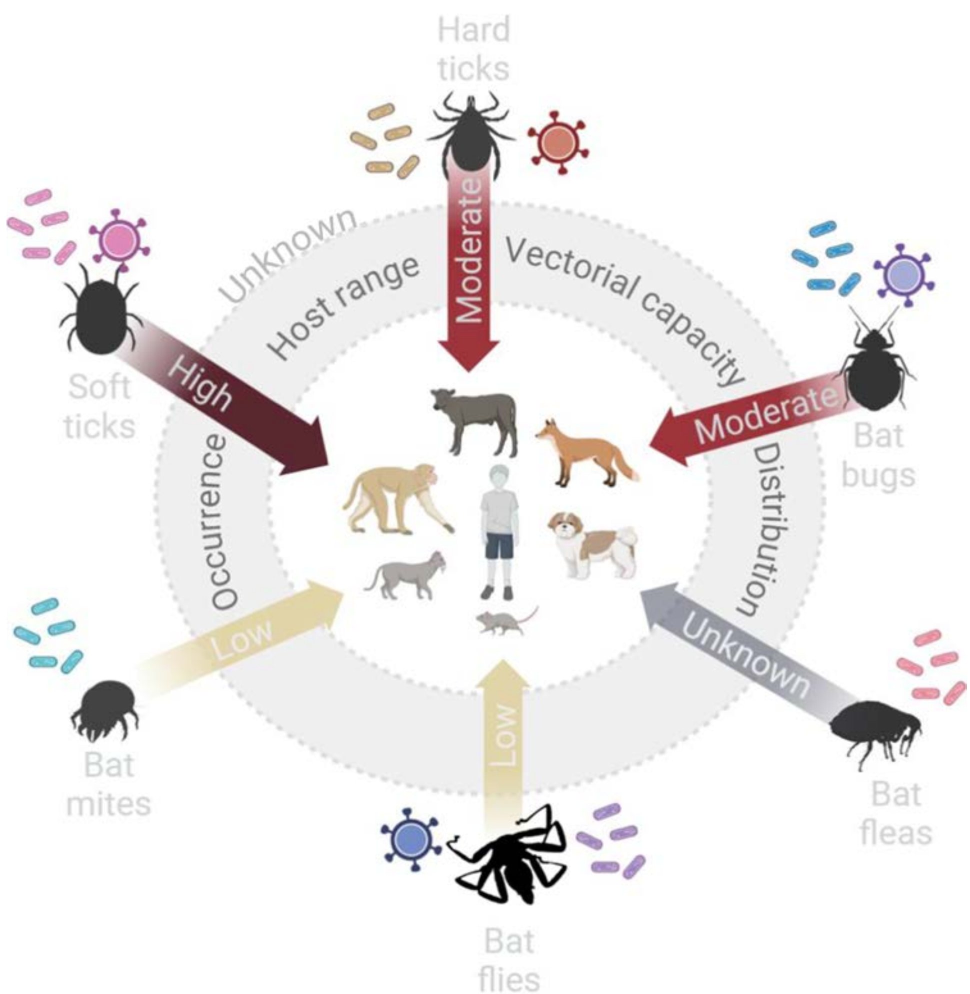

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Figure 1. Risk assessment strategy is based on data already available. Risk of possible transmission of infectious agents via bat-associated ectoparasitic groups: high, known human biting behavior, common occurrence in and around human settlements, known infection by (potentially) zoonotic pathogens; moderate, occasional known human biting behavior, rare occurrence in and around human settlements, known infection by (potentially) zoonotic pathogens; low, rare/extremely rare known human biting behavior, rare occurrence in and around human settlements, known infection by (potentially) zoonotic pathogens; unknown, unknown human biting behavior, unknown occurrence in and around human settlements, known infection by (potentially) zoonotic pathogens. Future research focuses are indicated in the gray circle, that is, vector occurrence, host range, vectorial capacity, distribution. Main known potentially zoonotic pathogenic groups are indicated, (i.e., viruses and/or bacteria), and detailed in supplementary Table S1.

Landscape ecology of vector-borne pathogen spillover from bats to humans

Changes in land use, habitat fragmentation, and climate change have been identified as significant factors influencing the dynamics of bat-associated pathogens [32,33]. Alterations in landscape structure directly affect bat populations, vectors, and other potential hosts, consequently modifying disease transmission dynamics [32]. Vector-borne disease spillovers are shaped by a complex range of ecological, environmental, and behavioral factors on the level of the reservoirs and susceptible hosts, vectors and pathogens; however, these are often difficult to monitor due to their complexity [34]. Furthermore, direct and indirect contacts determine whether human hosts are potentially exposed to these vectors and eventually to the pathogens spread by these parasites. First, it is important to determine such points of direct or indirect contact, where humans and other species may acquire such infections. **Ecotones** that are transitional zones are favored by some bat species over other habitats as these areas allow them to access a variety of environments, including forests, pastures, and human dwellings [35]. Moreover, hosts and vectors of zoonotic pathogens are often more abundant in ecotones than in other habitats [36,37]. Since ecotones are recognized as key areas where interactions between bats, humans, and domestic animals often occur, we propose that these zones are the most likely sites for potential vector-borne pathogen spillover [37–39].

Interactions between bat-associated parasites and humans are usually reported from human dwellings, such as homes, or during recreational or work activities, such as visiting caves, basements, and attics, or spending time in forested areas [27,40,41] (Figure 2). Additionally, domestic animals and livestock may be an important indirect transmission point of bat-associated pathogens through ectoparasites [11]. Exterminating bats, mostly for pest control, is common to this day worldwide [42]. Handling bats during these events provides an additional direct contact with bats, and people can be exposed to their pathogens and parasites [43]. Furthermore, spatial and behavioral changes in disturbed bat populations may amplify the spread of viruses [44] and could also increase ectoparasite abundance [45,46]. Therefore, protecting natural bat habitats, especially in or near ecotones, can help to prevent pathogen spillover from bats to other species [32]. A key focus for future research should be to understand how ecotones influence parasite ecology and to connect this knowledge with the risk of spillover for potential pathogens.

Perspectives on disease surveillance methods

To effectively monitor and identify potential pathogen spillover events between bats and other species, more effort needs to be invested in disease surveillance, as well as in understanding vector host range, distribution, and vectorial capacity. New and traditional methods to monitor wildlife diseases have been increasingly developed and improved in the past decades. In addition to conventional pathogen surveillance methods, such as microscopy, serology, molecular pathogen detection, and necropsy [47,48], modern approaches, such as **xenomonitoring**, **machine learning**, and **citizen science** are increasingly being used in disease eco-epidemiology [14,49,50]. These innovative approaches complement traditional data collection methods, offering valuable improvements in the understanding of disease spread.

Alternative and noninvasive surveillance methods, such as xenomonitoring, are useful not only for host conservation but also because they are often operationally less difficult to implement during fieldwork [14,51]. Bat flies have been used to investigate the presence of a wide range of blood-associated pathogens in their bloodmeal, including *Bartonella*, *Polychromophilus*, and *Trypanosoma* [14,51]. Additionally, bat flies have proven to be an effective alternative for monitoring the presence of viruses within bat colonies without the need for invasive sampling methods, such as blood or organ collection from bats [12]. This is particularly important in cases where bats are protected or when there are additional concerns, such as field biosafety in research

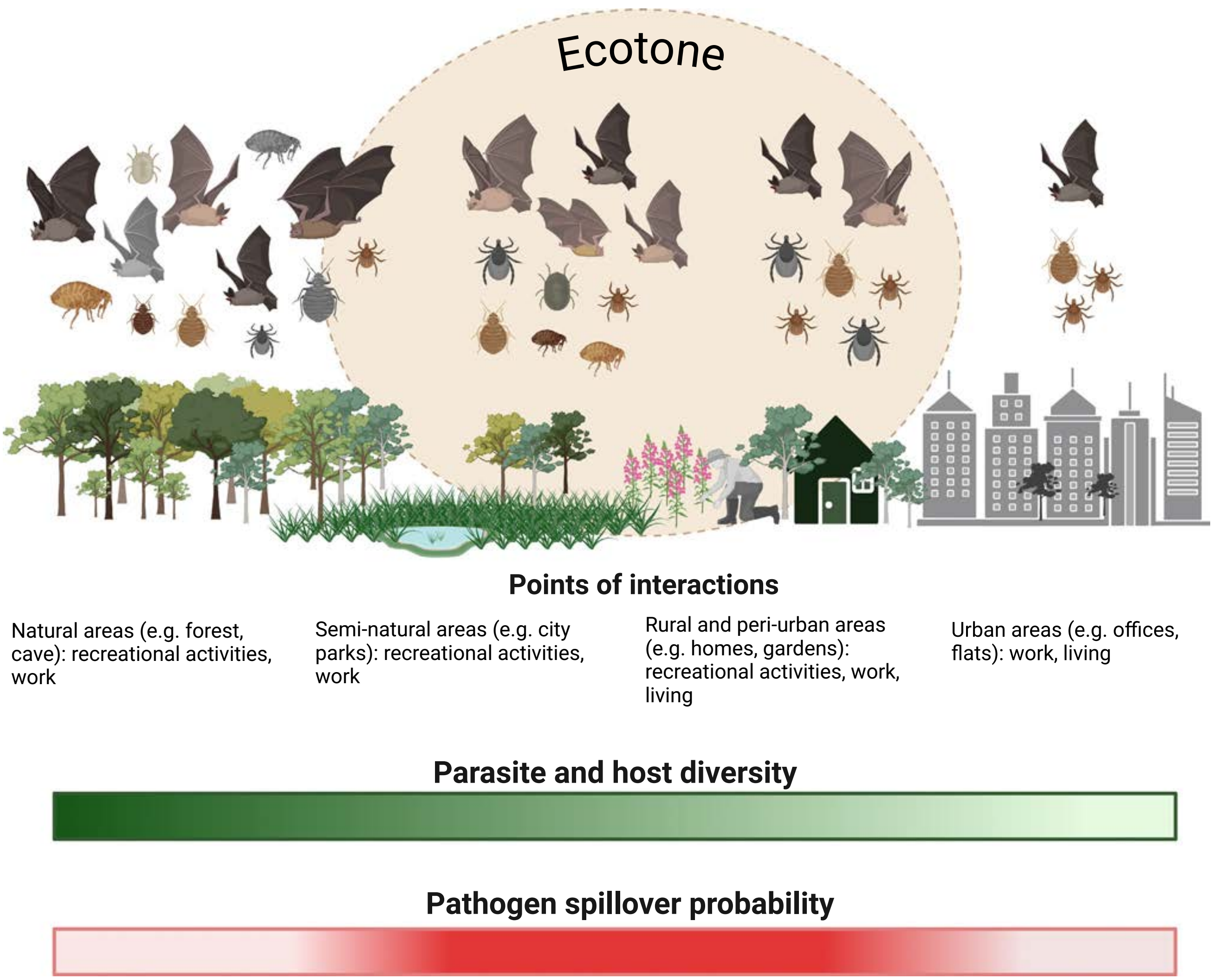

Figure 2. Points of interaction between bat-associated parasites and humans. Different habitat types affect parasite and host diversity, which leads to altered exposure to vectors and therefore affects pathogen spillover likelihood, particularly in ecotones. Host and pathogen diversity are represented by the number of bats and ectoparasites across each habitat type.

involving highly pathogenic microorganisms [12,22]. Targeting blood-sucking ectoparasites could be a potential alternative to monitoring bat-associated pathogens of host populations and could improve our understanding of the vectorial capacity of these parasites. Furthermore, since pathogen surveillance is increasingly carried out in bats, more consistently incorporating the tripartite aspect – the vector itself – could improve our understanding of its potential role in transmitting pathogens to humans.

Other rapidly developing methods, such as machine learning, have been successfully applied to explore **reservoir**s and vectors of zoonotic pathogens [52,53]. Vector status can be predicted with high accuracy in ticks using ecological, behavioral, and morphological data [53]. Applying data-driven vector prediction, the bat-associated tick, *I. vespertilionis,* is ranked high on the list of potential zoonotic vectors within *Ixodes* species [53]. Using machine learning, the vectorial capacity of other bat-associated parasites with well-known ecology and behavior could potentially be predicted; this could improve surveillance efforts and would further help to develop targeted pathogen screening. In addition, there is a strong need for collecting more ecological and behavioral data to successfully implement and extend this method to other parasitic groups (e.g., cimicids and soft ticks) with moderate or high pathogen transmission risk to humans and other species (Figure 1) as these data are currently lacking for most species. This information could help us to better understand which species have higher vectorial capacity and play a role in pathogen transmission from bats to other species.

Furthermore, citizen science has also proved useful in the detection of pathogen vectors, such as ticks and mosquitoes [54,55], and it can also be used to reveal certain environmental and ecological factors that are associated with the occurrence of these invertebrates [55]. Bat-associated parasites have also been observed in and around human settlements, due to citizen science activity [50]. The bat-associated soft tick species, *C. kelleyi* has been reported multiple times in homes across North America on iNaturalist [50], which is the potential vector of several pathogens (Table S1). Developing citizen-science-based projects to explore the occurrence of bat-associated parasites could greatly improve our understanding of parasite species around human settlements.

In addition, unique evolutionary adaptations – such as flight, echolocation, longevity, and pathogen tolerance – can be explored using modern genomics [56,57]. Long-read sequencing is increasingly used to generate reference-quality bat genomes, which have already provided answers to key evolutionary questions related to these special traits [58]. Additionally, thanks to the application of this technique, significant insights have been gained into the role of bats as efficient viral reservoirs [57–60]. Interestingly, these developments have not been applied in bat-associated parasite research to date, even though they have proven to be effective tools for describing basic evolutionary traits related to vector roles (e.g., endogenous viral elements) [61,62]. They could also provide insights into the microbiome of these parasites [63], which is known to affect pathogen presence and transmission in other tick species [64].

Molecular techniques for sequencing and rapid, PCR-based detections are increasingly used and have been developed rapidly during the last decade, mostly in association with outbreak situations [65]. These advancements and techniques can be used for rapid monitoring of vector populations in bats. Conducting field-based surveillance may be beneficial in resource-limited setups and in regions where it is difficult to support cold chains for sample transport. In addition, mobile laboratory diagnostic techniques (e.g., PCR detection or sequencing) and on-site data generation are an important aspect to align with the Nagoya protocol and support ethical research and data sharing globally.

Outlook on present and future research directions

Several key aspects of bat-associated vector-borne pathogen eco-epidemiology are still not fully understood, particularly the role of ectoparasites in pathogen maintenance and transmission. We propose that a comprehensive approach, similar to the One Health strategy, should be used to understand this pathogen niche (including bats, vectors, the environment, and potential satellite factors) as a whole (Figure 3).

However, there are various major knowledge and research gaps, which we summarize in three categories: host–vector interactions' ecology, laboratory-based investigations, and intra-vector mechanisms (Figure 3). To optimize research capacities, we propose categorizing pathogen–

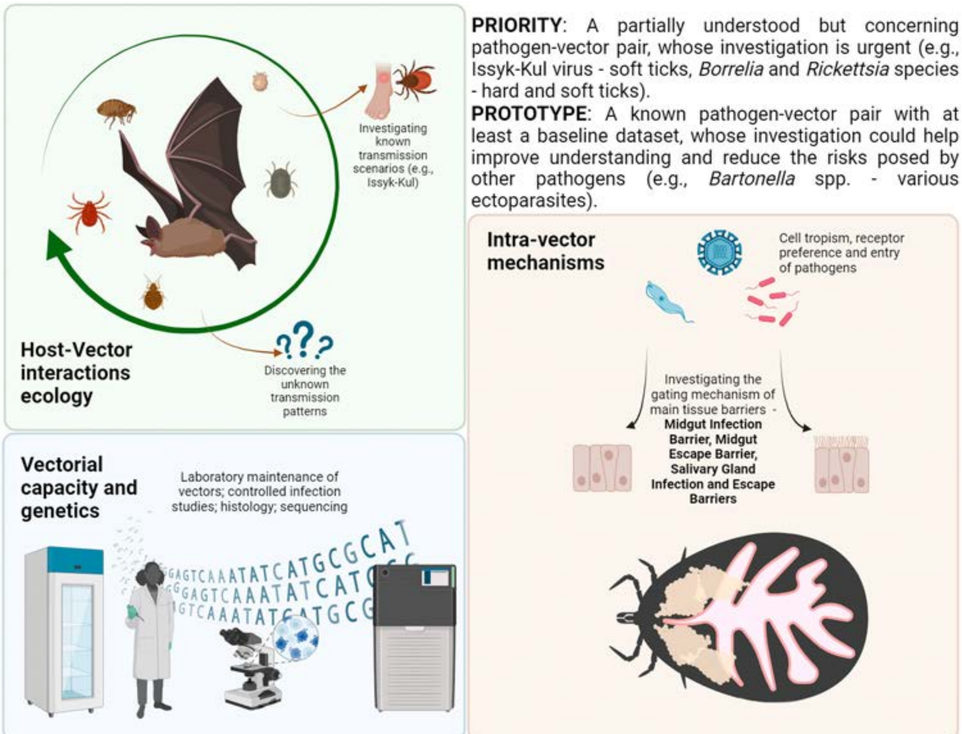

Figure 3. Knowledge gaps in different aspects of bat ectoparasite host–vector interactions, ecology, vectorial capacity and genetics, and intra-vector mechanisms. Current and future research focus on goals to get a better understanding of the role of bat-associated parasites in zoonotic disease eco-epidemiology. We highlight possible research directions and main outcomes in three categories and propose a two-category framework for pathogen–vector pairs.

vector pairs as either 'priority' or 'prototype' subjects of investigation, based on their relevance to human or animal health and their potential broader significance. Intensified surveillance activities are needed to understand the complex ecology of different ectoparasites and to identify the nodes of spillover. This is particularly important in the case of 'priority' pathogen–vector pairs in which preventing spillover events is crucial. For example, Issyk–Kul virus was recently detected and isolated from multiple countries in Europe, giving the possibility of detailed investigations [16,66,67]. The other proposed direction is to intensify the discovery of yet unidentified nodes of transmission outside of the bat–vector ecosystem (Figure 3).

Laboratory-based studies with vectors, such as ticks, are effective tools to understand vector competence to different pathogens [68,69]. Developing the technological and methodological foundation to maintain a wider diversity of ectoparasites, including bat-associated parasites, may open up possibilities for similar studies. This includes integrating host–vector ecology studies to help develop maintenance protocols for vectors in a laboratory setting and to establish feeding methods. For both wild-caught and laboratory-maintained ectoparasites, genomic studies are effective for revealing the evolutionary and functional perspectives of their potential role as vectors.

Finally, understanding the complexity of intra-vector mechanisms, particularly the entry and dissemination of pathogens, is a key component of this system [70]. While the main tissue barriers for effective pathogen dissemination from vectors have been extensively studied in ticks [70], they have largely been neglected in other ectoparasites, representing a significant knowledge gap.

This complex investigative approach may lead to the development of effective strategies for host conservation, preventing and predicting zoonotic spillovers, and a better understanding of the evolution of these pathogens. There is still much to explore when studying bat-associated parasites on a disease eco-epidemiology scale. We need improved insights into how climate change, habitat fragmentation, and increased human–wildlife interactions affect the ecology of vector-borne pathogens to prevent transmission between bats and non-chiropteran species.

Concluding remarks

Understanding the mechanisms of vector-borne pathogen transmission beyond bat colonies is essential for further exploring the role of bats as pathogen reservoirs. Bat-associated parasites may serve as an important link in disease transmission between humans and other animals. Integrating new and improved methods into monitoring efforts for bat-associated parasites and diseases, whether in the laboratory or in the field, can provide valuable insights into the dynamics of vector-borne diseases at the human–bat interface and support strategic risk assessments and preventive efforts (see Outstanding questions). Additionally, bat-associated pathogen surveillance in humans and other non-chiropteran mammals is still largely lacking and should be a focus of future research. It should be also highlighted that bats are vulnerable to anthropogenic disturbances, which likely influence disease and parasite dynamics, potentially affecting both bat and human health. Bats may be susceptible to certain human pathogens and other diseases from wildlife species; therefore, we need a better understanding of reverse spillover to bats to enable effective conservation and protect their diversity.

Outstanding questions

Which bat-associated ectoparasites represent the highest risk to human health?

What is the vectorial capacity of most bat parasites that have been associated either with humans or zoonotic pathogens?

How could climate change, landscape modifications, and other anthropogenic activities affect the eco-epidemiology of bat-associated vector-borne pathogens?

How can bat conservation efforts be improved using knowledge about pathogen vectors and reverse spillover pathways?

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Declaration of interests

The authors declare no competing interests.

Supplemental information

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