

Assessing the threat of bat-associated fungal pathogens

Samantha C. Karunaratna^a, Danny Haelewaters^{b,c,*}, Michail S. Lionakis^d,
Saowaluck Tibpromma^a, Xu Jianchu^a, Alice C. Hughes^{e,*}, Peter E. Mortimer^{a,*}

^a Center for Mountain Futures, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 65201, PR China

^b Faculty of Science, University of South Bohemia, 370 05 České Budejovice, Czech Republic

^c Research Group Mycology, Department of Biology, Ghent University, 9000 Ghent, Belgium

^d Fungal Pathogenesis Section, Laboratory of Clinical Immunology & Microbiology, National Institute of Allergy & Infectious Diseases, National Institutes of Health, USA

^e School of Biological Sciences, University of Hong Kong, Hong Kong SAR, PR China

ARTICLE INFO

Keywords:

Bat-associated fungi
Bat roosts
Chiroptera
Community ecology
Emerging infectious diseases
Hibernacula
Landscape management
Microbiome–pathogen interactions
White-nose syndrome

ABSTRACT

Fungal pathogens have become an increasingly important topic in recent decades. Yet whilst various cankers and blights have gained attention in temperate woodlands and crops, the scope for fungal pathogens of animals and their potential threat has received far less attention. With a shifting climate, the threat from fungal pathogens is predicted to increase in the future, thus understanding the spread of fungi over landscapes as well as taxa that may be at risk is of particular importance. Cave ecosystems provide potential refugia for various fungi, and roosts for bats. With their well vascularized wings and wide-ranging distributions, bats present potential fungal vectors. Furthermore, whilst bat immune systems are generally robust to bacterial and viral pathogens, they can be susceptible to fungal pathogens, particularly during periods of stress such as hibernation. Here we explore why bats are important and interesting vectors for fungi across landscapes and discuss knowledge gaps that require further research.

1. Bats and fungi: scoping a knowledge gap

Bats, the only mammals capable of powered flight, have evolved a suite of adaptations to cope with the related increases in body temperature and ecophysiological stress. These adaptations have also strengthened bat immune systems and provided resistance to viruses and bacteria, enabling them to function as reservoirs for zoonoses. These diseases include recent emerging infectious diseases (EIDs), some of which have contributed toward pandemics, for example Ebola and SARS-CoV-2 [1–3]. While most research into bat-related EIDs has focused on viral pathogens [1–3], the potential threat of fungal pathogens cannot be overlooked. Fungi are responsible for a variety of EIDs, including diseases that pose a threat to a wide range of organisms, including humans, animals, and plants. Given the concern about bats as vectors of EIDs and outbreaks associated with fungal pathogens that are on the rise, we aim to assess the direct and indirect threats posed by bat-associated fungi.

Over 290 known species of fungi are directly associated with bats, and an additional 2000 species with bat habitats such as caves and roosting areas [4]. These include a sizeable percentage of novel

species—232 species were newly described in the last decade—and a high number of genera (173) that contain pathogenic taxa. To effectively assess the threat of bat-associated fungi, we will briefly outline key aspects of fungi and bats, their interactions, and how these factors contribute to risk assessment.

2. Fungal pathogens

The Kingdom Fungi is poorly studied, with only 154,000 species described [5] out of an estimated 2.2–3.8 million [6]. Although the vast majority of fungi are benign, fungal pathogens can be highly lethal [7]. For example, severe chytridiomycosis, caused by *Batrachochytrium dendrobatidis*, has decimated amphibian populations worldwide, resulting in the extinction of at least 90 species and a 90% population decline in 124 other species [8]. In total, an estimated 500 species of amphibians across 54 countries have been infected and many others are threatened with extinction. This chytridiomycosis alone has contributed to the decline of nearly half of all amphibian species worldwide [9]. Recently, the multidrug-resistant *Candida auris* has been reported in human populations in Asia, Europe, and North and South America, notably

* Corresponding authors.

E-mail addresses: danny.haelewaters@gmail.com (D. Haelewaters), ach_conservation2@hotmail.com (A.C. Hughes), peter@mail.kib.ac.cn (P.E. Mortimer).

<https://doi.org/10.1016/j.onehlt.2023.100553>

Received 13 January 2023; Received in revised form 24 April 2023; Accepted 24 April 2023

Available online 28 April 2023

2352-7714/© 2023 Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

infecting COVID-19 patients [10], with death rates of 50–80% [11]. Another example, *Pseudogymnoascus destructans*, is the fungal pathogen responsible for white-nose syndrome (WNS) in bats [12], having resulted in the death of over 7 million bats in the US and severely impacting the ecosystem services they provide. While no other bat-associated fungus equally catastrophic in scope has been recorded, potentially similar pathogenic bat-associated fungi have been recorded in China [13].

Understanding why some fungi cause such high levels of mortality in bats whereas other pathogens can often be hosted asymptotically is important. First, fungi are eukaryotes with a cell biology more akin to animals (including humans) than plants, making treatment of fungal diseases difficult [14]. Second, fungi are able to infect organisms across the tree of life, and a single fungal pathogen can move among species with relative ease [15]. And finally, fungi can shift life modes depending on environmental conditions—a benign soil fungus could transform into a devastating human pathogen upon habitat disturbance (e.g., *Coccidioides immitis* and *C. posadasii*), complicating outbreak planning and preparation [16].

Two major challenges pose a knowledge gap in preventing fungal outbreaks. The first is the need for a more comprehensive understanding on the behavior of their bat hosts. Foraging behavior and migration routes bring bats in contact with natural ecosystems and human modified landscapes, with the potential for both spreading fungal propagules across these different land-use types, and both being exposed to and being a transmitter of fungal propagules as they navigate through these varied landscapes (Fig. 1). Further compounding this is the issue that

caves represent understudied hotspots for fungal diversity [17]. Second, a community ecology approach in understanding bat–pathogen interactions is virtually non-existent. Many impacts of fungal pathogens are challenging to predict, such as the relationship of hibernation behavior and host susceptibility to pathogens, and how these may shift under changing climates [18].

High baseline body temperatures within mammals have limited the spread and severity of fungal infections, and usually limits infections to topical cases and those with compromised immunity [19]. However, three factors have compromised this intrinsic mammalian defense against fungal pathogens. Advances in medical technologies such as the use of targeted and myeloablative treatments for malignancies, the advent of targeted immunomodulatory therapies for autoimmune disorders, and the expansion of hematopoietic stem cell or solid organ transplantation for hematological disorders and organ failure have substantially increased the number of immunocompromised individuals in human populations, increasing the risk for opportunistic fungal infections. Examples include infections by *Fusarium* spp. causing organ damage or failure, and *Candida auris* resulting in numerous ailments and infections in immunocompromised patients, but most commonly causing candidemia or infection of the bloodstream [20,21]. Drug-resistant fungi further complicate the treatment regimen. Two such examples include azole resistance in *Aspergillus fumigatus* as well as azole and echinocandin resistance in *Candida albicans* and *C. glabrata*. Finally, the overall trend of a warming global climate has expanded the geographic range of some fungal pathogens [22], seen in the northward spread of both the endemic coccidioidomycosis (*Coccidioides immitis* and

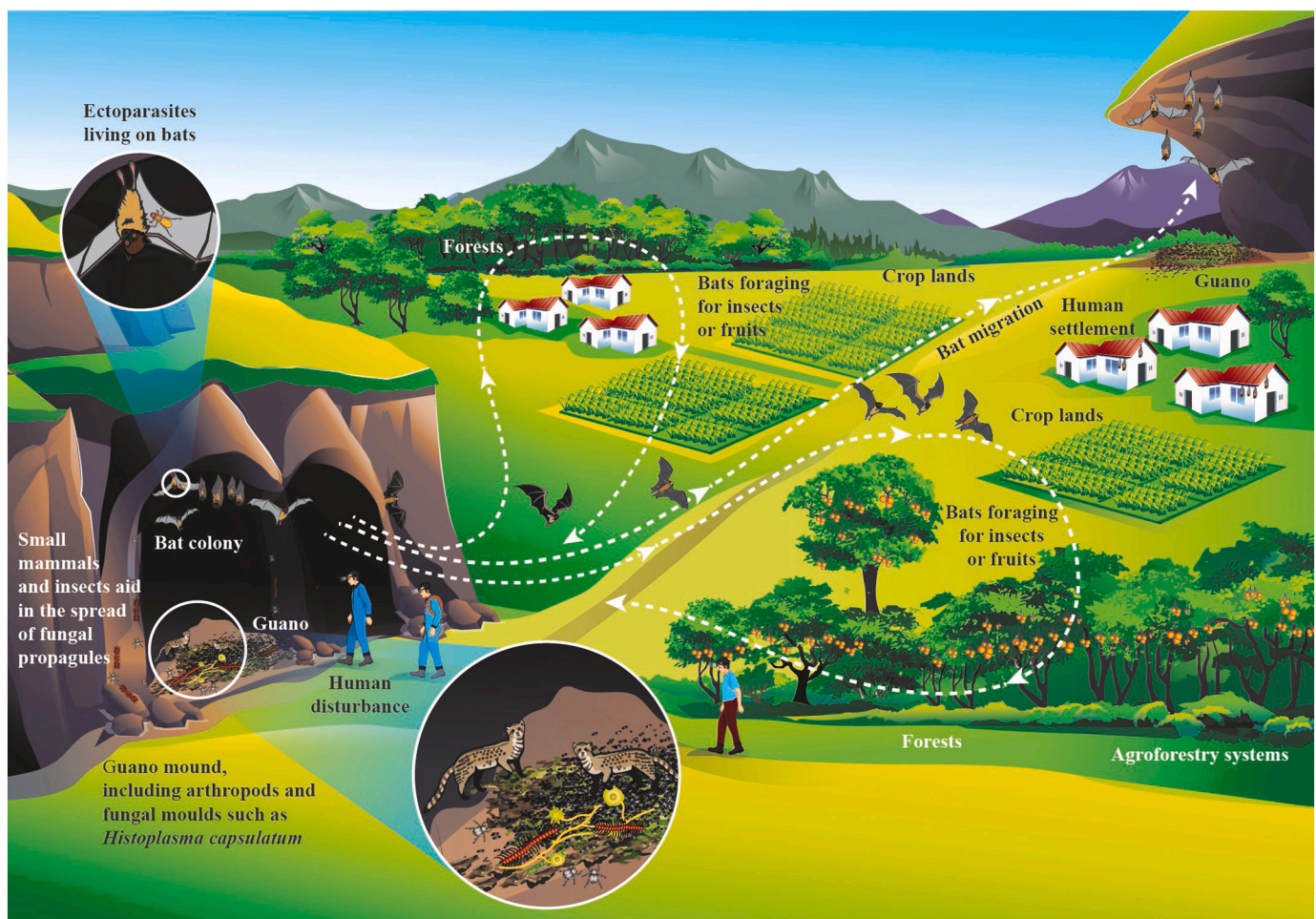


Fig. 1. Habitat and ecological interactions of bats and bat-associated fungi. Bat roosting areas facilitate interactions between fungi and bats, bat parasites, mammals, cave insects, and humans. Fungi can be found on and spread by all organisms involved.

C. posadasii) and *Pseudogymnoascus destructans* in the US. Taken together, these factors have led to a sharp increase in human infections in recent years. Yet, whilst agricultural fungi are increasingly well recognized, the impacts of fungi on wildlife populations are only just starting to become apparent, despite major fatalities associated with chytridiomycosis in amphibians, WNS in bats, and less well-known cases such as the Crayfish plague (*Aphanomyces astaci*).

3. Bats and their fungal interactions

Bats have evolved unique mechanisms for hosting and tolerating intracellular pathogens, most notably viruses, but also display tolerance against certain bacterial and protozoan infections [23]. However, bats remain sensitive to extracellular pathogens, including pathogenic fungi such as *P. destructans* [23,24].

During periods of activity, bat metabolism can reach up to 16 times the basal rate [25], dramatically changing cellular conditions and causing high levels of physiological stress. Given that flight is energetically expensive, bats must either hibernate or migrate in winter when food sources are scarce. Both responses could weaken the immune system in most mammals, though how bats respond is less well known given their unique physiology. Moreover, migration routes potentially allow for the spread of pathogens, including fungi, across broad geographic ranges (exceeding 2000 km in some cases) [26,27]. For temperate bat species that do not migrate, hibernation can last up to or even exceed six months. During hibernation, body temperatures drop, increasing susceptibility for fungal pathogenic infection, as evidenced by peak WNS infection rates during hibernation.

4. Bats as vectors of fungal pathogens

Three main factors contribute toward bats being ideal vectors for fungal pathogens. Many bats roost in caves and mines; these bat hibernacula and roosts are optimal environments for fungal growth, featuring stable mild temperatures, high humidity, and rich sources of organic matter. More than 2000 fungal species are known from caves worldwide [4], but this number is expected to be much higher. In addition, bats constantly transition between caves, forests, croplands, and human settlements in the course of their daily and seasonal activities. Thus, fungal pathogens can be transferred between land-use types with relative ease. Finally, bats host highly specialized parasites with the potential to not only spread pathogens within a bat colony, but also host their own unique fungi, including ectoparasitic ones [28–30], with some studies finding 43% of bat flies hosting fungi. Bat parasites include mites, ticks, fleas, and bat flies (streblids, nycteribiids, and ascopterans). Of the bat flies, streblids are the best adapted for moving among hosts, as, unlike the others, they have retained the ability to fly and are most likely to spread fungal propagules within a bat colony [31]. Mites, ticks, and fleas are less specialized to bats and as a result can move between bats and other mammals within a cave or roost site, providing another possible route of fungal transmission.

5. Bat-associated fungi

Of the 290 known species of fungi directly associated with bats, 50 are known pathogens and bats play known roles in transferring fungi from caves into other ecosystems, and possibly to other taxa [29,32]. *Histoplasma capsulatum*, a well-known dimorphic fungus usually found in soils or growing on piles of bat guano, causes pulmonary infections (histoplasmosis) in humans and other mammals, often with lethal consequences. Other examples of bat-associated fungal pathogens known to infect and kill humans are *Cryptococcus gattii* and *C. neoformans*, the causal agents of cryptococcosis, and *Paracoccidioides brasiliensis*, which causes paracoccidioidomycosis. At least a dozen additional species of fungi are known to live on bats and are exclusively associated with diseases in animals and humans, many of which have resulted in

fatalities among immunocompromised patients.

Karunaratna and colleagues [13] reported potential new EIDs associated with bats, from bat carcasses in a cave in southwestern China. Of the seven fungal species that were isolated during this study, two pathogens were of interest. *Neocosmospora pallidimors* was a novel species belonging to a genus of highly prevalent pathogenic fungi that have the potential to cause diseases in plants and mammals, including humans [13]. It remains unclear whether *N. pallidimors* caused the death of the bats in this study or grew on the carcasses as a saprotroph. The second pathogen was *Fusarium incarnatum*, which is found on agricultural crops and produces mycotoxins, affecting food production and human health. Examples of infections with *F. incarnatum* include fusariosis in humans, primarily infecting the skin or lungs; and the infection of the gills of black tiger shrimp [33,34].

The feeding behavior and migratory routes of bats bring them into contact with a range of fungi, including numerous plant pathogens, indirectly threatening human health. Studies have found hundreds of plant pathogenic species on bats and in bat-associated environments. These pathogens are easily transported across different land-use systems frequented by bats, transmitting pathogens between natural landscapes and agricultural environments. For example, the plant pathogens *Aspergillus flavus*, *Fusarium incarnatum*, and *Neocosmospora* spp. can devastate certain crops, and become a threat to animals, including humans [35–37]. The impact of fungal pathogens on agriculture will only intensify as human-disturbed landscapes multiply.

Thus far, bat microbiome studies have focused primarily on investigating the diversity and abundance of microbes associated with bat skin and guts [38–40]. Bat microbiome–pathogen interactions are poorly studied. Microbiota, both those on the skin and in the gastrointestinal tract, are vital for mammalian health and govern susceptibility to infection by pathogens, including fungal ones [41]. Recent work has indicated that the bat skin mycobiome is dynamic and strongly affected by geography and bat species [42]. In addition, various skin bacteria have anti-fungal properties, and these interacting factors need further work to better understand determinants of the potential of fungal growth on bats to become problematic [43].

In coming years, we will likely observe increasing rates of fungal infections in humans owing to the higher numbers of immunocompromised individuals in the general population, enhanced drug resistance, changing climatic conditions, and increased degrees of exposure [20]. As humans continue to disturb natural landscapes, the occurrence of new fungal EIDs resulting from interactions between bats and humans will likely increase, with worsening consequences. Concerted efforts are needed to advance our knowledge of fungal life cycles, especially for newly discovered and endemic dimorphic fungi. Despite this, the most critical threat posed by bat-associated fungi remains an indirect one. Evidence shows that bats host and transport plant pathogens across their natural ranges [13]. This has potential implications for global food security as fungal pathogens are responsible for the loss of approximately 30% of crops and food annually [44]. We must decrease our agricultural footprint and increase the net productivity of agricultural lands to meet sustainability goals, efforts that are being hampered by fungal pathogens.

6. Moving forward

Bats are known hosts for a diverse selection of pathogens, though there are major differences in the types of pathogens carried with different species. For example, Pteropidae fruit bats carry Hendra, Marburg, Nipah, and possibly Ebola viruses, whereas insectivorous bats host Swine acute diarrhea syndrome coronavirus (SADS-CoV) and Porcine epidemic diarrhea virus, among others [45–47]. Bats irrefutably harbor and transport fungal pathogens including *Histoplasma capsulatum* [48,49]. Fungal EIDs from bats and bat habitats could be potential sources for future infections in human and companion animal populations. Currently, the spread of plant pathogens represents the most

pressing threat from bat-associated fungi, which should be considered in future landscape management strategies, especially with the expansion of agricultural lands into natural habitats, fragmented forest environments, and increased probability of bats acting as vectors. These all constitute genuine threats to human health [50]. Understanding how bats use landscapes will be necessary to assess their vulnerability to fungal infection, and where there is the potential for bats to act as fungal vectors. Reducing habitat fragmentation and increasing habitat connectivity through the maintenance of natural habitats, and hedges in agricultural and urban landscapes will be crucial to minimizing potential exposure of bats to plant pathogens that they may inadvertently transport. Furthermore, analysis shows that ectoparasites on male bats of some species have a higher incidence of fungal infection, than those of female bats, highlighting the need for nuanced ecological analysis if we are to understand the dimensions of transmission of fungal pathogens among individuals [29].

Mitigation strategies should include restricting and regulating public access to caves and culverts (home to large bat populations), as well as ensuring that caving equipment, footwear, and clothing meet biosafety standards, such as frequent washing to limit transfer of fungal propagules [51]. In addition, mining activities should proceed with stricter environmental oversight, as disturbance and resettlement of bats could spread potential pathogens. Limiting human activities in natural landscapes that harbor large bat roosting or breeding populations will reduce disturbances. This may help to minimize exposure to potential vectors, and may prove an effective mitigation strategy, as it is with viral pathogens.

An interdisciplinary effort will be needed to develop strategies to ameliorate and prevent the emergence or spread of bat-associated fungal diseases. We are only just starting to understand the potential role of microbial interactions in inhibiting the growth of pathogenic fungi [52,53]. Zoologists, mycologists, and medical scientists must collaborate to bolster our understanding of the complex interplay among bats, their habitats, and the fungal species found in these systems. In parallel, land use management strategies that limit disturbances in roosting areas, halt landscape fragmentation, and preserve key foraging sites will be crucial to reducing bat exposure to human environments, mitigating the spread of fungal pathogens. Such an integrated approach would be most effective if implemented in a preventative manner to reduce future EID risks in crops, human, and animal populations.

Funding

This work was supported in part by the Chinese Academy of Sciences President's International Fellowship Initiative (PIFI) young staff (2020FYC0002 to S.C.K.), National Science Foundation of China (31851110759 to S.C.K., Y71L481211 to P.E.M.), Research Foundation – Flanders (junior postdoctoral fellowship 1206620N to D.H.), and the Division of Intramural Research of the National Institute of Allergy and Infectious Diseases, National Institutes of Health.

CRediT authorship contribution statement

Samantha C. Karunaratna: Conceptualization, Investigation, Writing – original draft. **Danny Haelewaters:** Investigation, Writing – original draft, Writing – review & editing. **Michail S. Lionakis:** Writing – original draft. **Saowaluck Tibpromma:** Writing – original draft. **Xu Jianchu:** Writing – original draft. **Alice C. Hughes:** Conceptualization, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Peter E. Mortimer:** Conceptualization, Investigation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that the review was conducted in the absence of any commercial or financial relationships that could be construed as a

potential conflict of interest.

Data availability

No data was used for the research described in the article.

References

- [1] W. Li, Z. Shi, M. Yu, W. Ren, C. Smith, J.H. Epstein, et al., Bats are natural reservoirs of SARS-like coronaviruses, *Science*. 310 (2005) 676–679, <https://doi.org/10.1126/science.1118391>.
- [2] D.G. Bausch, L. Schwarz, Outbreak of Ebola virus disease in Guinea: where ecology meets economy, *PLoS Negl. Trop. Dis.* 8 (2014), e3056, <https://doi.org/10.1371/journal.pntd.0003056>.
- [3] D.K. Bonilla-Aldana, S.D. Jimenez-Diaz, J.S. Arango-Duque, M. Aguirre-Florez, G. J. Balbin-Ramon, A. Paniz-Mondolfi, Bats in ecosystems and their wide spectrum of viral infectious potential threats: SARS-CoV-2 and other emerging viruses, *Int. J. Infect. Dis.* 102 (2021) 87–96, <https://doi.org/10.1016/j.ijid.2020.08.050>.
- [4] A.O.B. Cunha, J.D.P. Bezerra, T.G.L. Oliveira, E. Barbier, E. Bernard, A. R. Machado, C.M. Souza-Motta, Living in the dark: bat caves as hotspots of fungal diversity, *PLoS One* 15 (2020), e0243494, <https://doi.org/10.1371/journal.pone.0243494>.
- [5] D.L. Hawksworth, R. Lücking, Fungal diversity revisited: 2.2 to 3.8 million species, *Microbiol. Spectr.* 5 (2017), <https://doi.org/10.1128/9781555819583.ch4>. FUNK-0052–2016.
- [6] P. Kirk, Species Fungorum Plus, in: O. Bánki, Y. Roskov, M. Döring, G. Ower, L. Vandeputte, D. Hobern, et al. (Eds.), *Catalogue of Life Checklist*, 2023, <https://doi.org/10.48580/dftr-4hj>.
- [7] J. Xu, Assessing global fungal threats to humans, *mLife* 1 (2022) 223–240, <https://doi.org/10.1002/mlf2.12036>.
- [8] L.F. Skerratt, L. Berger, R. Speare, S. Cashins, K.R. McDonald, A.D. Phillott, et al., Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs, *EcoHealth*. 4 (2007) 125–134, <https://doi.org/10.1007/s10393-007-0093-5>.
- [9] B.C. Scheele, F. Pasmans, L.F. Skerratt, L. Berger, A. Martel, W. Beukema, et al., Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity, *Science*. 363 (2019) 1459–1463, <https://doi.org/10.1126/science.aav0379>.
- [10] H. Prakash, A. Chakrabarti, Epidemiology of mucormycosis in India, *Microorganisms* 9 (2021) 523, <https://doi.org/10.3390/microorganisms9030523>.
- [11] H. Villanueva-Lozano, R.J. Treviño-Rangel, G.M. González, M.T. Ramírez-Elizondo, R. Lara-Medrano, M.C. Aleman-Bocanegra, et al., Outbreak of *Candida auris* infection in a COVID-19 hospital in Mexico, *Clin. Microbiol. Infect.* 27 (2021) 813–816, <https://doi.org/10.1016/j.cmi.2020.12.030>.
- [12] J.R. Hoyt, A.M. Kilpatrick, K.E. Langwig, Ecology and impacts of white-nose syndrome on bats, *Nat. Rev. Microbiol.* 19 (2021) 196–210, <https://doi.org/10.1038/s41579-020-00493-5>.
- [13] S.C. Karunaratna, Y. Dong, S. Karasaki, S. Tibpromma, K.D. Hyde, S. Lumyong, et al., Discovery of novel fungal species and pathogens on bat carcasses in a cave in Yunnan Province, China, *Emerg. Microbes Infect.* 9 (2020) 1554–1566, <https://doi.org/10.1080/22221751.2020.1785333>.
- [14] S.L. Baldauf, J.D. Palmer, Animals and fungi are each other's closest relatives: congruent evidence from multiple proteins, *Proc. Natl. Acad. Sci.* 90 (1993) 11558–11562, <https://doi.org/10.1073/pnas.90.24.11558>.
- [15] P. Chaverri, G.J. Samuels, Evolution of habitat preference and nutrition mode in a cosmopolitan fungal genus with evidence of interkingdom host jumps and major shifts in ecology, *Evolution*. 67 (2013) 2823–2837, <https://doi.org/10.1111/evo.12169>.
- [16] N.F. Crum, Coccidiomycosis: a contemporary review, *Infect. Dis. Ther.* 11 (2022) 713–742, <https://doi.org/10.1007/s40121-022-00606-y>.
- [17] V.C.S. Alves, R.A. Lira, J.M.S. Lima, R.N. Barbosa, D.M. Bento, E. Barbier, et al., Unravelling the fungal darkness in a tropical cave: richness and the description of one new genus and six new species, *Fungal Syst. Evol.* 10 (2022) 139–167, <https://doi.org/10.3114/fuse.2022.10.06>.
- [18] R.T. Jackson, E.V. Willcox, R.F. Bernard, Winter torpor expression varies in four bat species with differential susceptibility to white-nose syndrome, *Sci. Rep.* 12 (2022) 5688, <https://doi.org/10.1038/s41598-022-09692-x>.
- [19] A. Bergman, A. Casadevall, Mammalian endothermy optimally restricts fungi and metabolic costs, *mBio*. 1 (2010), <https://doi.org/10.1128/mBio.00212-10> e00212-10.
- [20] S.R. Lockhart, J. Guarner, Emerging and reemerging fungal infections, *Semin. Diagn. Pathol.* 36 (2019) 177–181, <https://doi.org/10.1053/j.semdp.2019.04.010>.
- [21] C.Y. Low, C. Rotstein, Emerging fungal infections in immunocompromised patients, *F1000 Med. Rep.* 3 (2011) 14, <https://doi.org/10.3410/m3-14>.
- [22] M.A. Garcia-Solache, A. Casadevall, Global warming will bring new fungal diseases for mammals, *Mbio*. 1 (2010), <https://doi.org/10.1128/mBio.00061-10> e00061-10.
- [23] C.E. Brook, A.P. Dobson, Bats as 'special' reservoirs for emerging zoonotic, *Trends Microbiol.* 23 (2015) 172–180, <https://doi.org/10.1016/j.tim.2014.12.004>.
- [24] J.B. Konopka, A. Casadevall, J.W. Taylor, J. Heitman, L. Cowen, One Health: Fungal Pathogens of Humans, Animals, and Plants. Colloquium Report, American Society for Microbiology, Washington, DC, 2019, <https://doi.org/10.1128/AAMCol.18Oct.2017>.
- [25] Z. Huang, C.V. Whelan, N.M. Foley, D. Jebb, F. Touzalin, E.J. Petit, et al., Longitudinal comparative transcriptomics reveals unique mechanisms underlying

- extended healthspan in bats, *Nat. Ecol. Evol.* 3 (2019) 1110–1120, <https://doi.org/10.1038/s41559-019-0913-3>.
- [26] G.N. Pandian, J. Dhivahar, A. Parthasarathy, E. Lavanya, B.S. Kovi, Bat-associated microbes: opportunities and perils, an overview, *Heliyon* (2022), <https://doi.org/10.2139/ssrn.4265433>. Preprint. [cited 2023 Jan 11].
- [27] M.L. Taylor, M.R. Reyes-Montes, D.A. Estrada-Bárcenas, R.M. Zancopé-Oliveira, G. Rodríguez-Arellanes, J.A. Ramírez, Considerations about the geographic distribution of *Histoplasma* species, *Appl. Environ. Microbiol.* 88 (2022) e0201021, <https://doi.org/10.1128/aem.02010-21>.
- [28] D. Haelewaters, C.W. Dick, K.P. Cocherán Pittí, K. Dittmar, B.D. Patterson, Bats, Bat flies, and fungi: Exploring uncharted waters, in: B.K. Lim, M.B. Fenton, R. M. Brigham, S. Mistry, A. Kurta, E.H. Gillam, et al. (Eds.), 50 Years of Bat Research. Fascinating Life Sciences, Springer, Cham, 2021, pp. 349–371, https://doi.org/10.1007/978-3-030-54727-1_21.
- [29] Á. Péter, A.D. Mihalca, D. Haelewaters, A.D. Sándor, Focus on hyperparasites: biotic and abiotic traits affecting the prevalence of parasitic microfungi on bat ectoparasites, *Front. Ecol. Evol.* 10 (2022), 795020, <https://doi.org/10.3389/fevo.2022.795020>.
- [30] J.L.V.R. Carvalho, J.M.S. Lima, E. Barbier, E. Bernard, J.D.P. Bezerra, C.M. Souza-Motta, Ticket to ride: fungi from bat ectoparasites in a tropical cave and the description of two new species, *Braz. J. Microbiol.* 53 (2022) 2077–2091, <https://doi.org/10.1007/s42770-022-00841-y>.
- [31] M.L.S. Pereira, J.L.V.R. Carvalho, J.M.S. Lima, E. Barbier, E. Bernard, J.D. P. Bezerra, C.M. Souza-Motta, Richness of *Cladosporium* in a tropical bat cave with the description of two new species, *Mycol. Prog.* 21 (2022) 345–357, <https://doi.org/10.1007/s11557-021-01760-2>.
- [32] J.E. Carpouron, S. de Hoog, E. Gentekaki, K.D. Hyde, Emerging animal-associated fungal diseases, *J. Fungi* 8 (2022) 611, <https://doi.org/10.3390/jof8060611>.
- [33] L.V. Khao, K. Hatai, T. Aoki, *Fusarium incarnatum* isolated from black tiger shrimp, *Penaeus monodon* Fabricius, with black gill disease cultured in Vietnam, *J. Fish Dis.* 27 (2004) 507–515, <https://doi.org/10.1111/j.1365-2761.2004.00562.x>.
- [34] M. Nucci, E. Anaïs, *Fusarium* infections in immunocompromised patients, *Clin. Microbiol. Rev.* 20 (2007) 695–704, <https://doi.org/10.1128/cmr.00014-07>.
- [35] G. Perrone, A. Susca, G. Cozzi, K. Ehrlich, J. Varga, J.C. Frisvad, et al., Biodiversity of *Aspergillus* species in some important agricultural products, *Stud. Mycol.* 59 (2007) 53–66, <https://doi.org/10.3114/sim.2007.59.07>.
- [36] A. Jacobs, L. Mojela, B. Summerell, E. Venter, Characterisation of members of the *Fusarium incarnatum-equiseti* species complex from undisturbed soils in South Africa, *Antonie Leeuwenhoek* 111 (2018) 1999–2008, <https://doi.org/10.1007/s10482-018-1093-x>.
- [37] M. Sandoval-Denis, V. Guarnaccia, G. Polizzi, P.W. Crous, Symptomatic *Citrus* trees reveal a new pathogenic lineage in *Fusarium* and two new *Neocosmospora* species, *Persoonia*. 40 (2018) 1–25, <https://doi.org/10.3767/persoonia.2018.40.01>.
- [38] M.R. Ingala, N.B. Simmons, S.L. Perkins, Bats are an untapped system for understanding microbiome evolution in mammals, *mSphere*. 3 (2018), <https://doi.org/10.1128/mSphere.00397-18> e00397-18.
- [39] H.L. Lutz, E.W. Jackson, P.W. Webala, W.S. Babyesiza, J.C. Kerbis Peterhans, T. C. Demos, et al., Ecology and host identity outweigh evolutionary history in shaping the bat microbiome, *mSystems*. 4 (2019) e00511–19, <https://doi.org/10.1128/mSystems.00511-19>.
- [40] I. Dimkić, D. Fira, T. Janakiev, J. Kabić, M. Stupar, M. Nenadić, et al., The microbiome of bat guano: for what is this knowledge important? *Appl. Microbiol. Biotechnol.* 105 (2021) 1407–1419, <https://doi.org/10.1007/s00253-021-11143-y>.
- [41] D.N. Jones, N.A.F. Ravelomanantsoa, C.J. Yeoman, R.K. Plowright, C.E. Brook, Do gastrointestinal microbiomes play a role in bats' unique viral hosting capacity? *Trends Microbiol.* 30 (2022) 632–642, <https://doi.org/10.1016/j.tim.2021.12.009>.
- [42] P.J. Kearns, A.S. Winter, D.C. Woodhams, D.E. Northup, The mycobiome of bats in the American Southwest is structured by geography, bat species, and behavior, *ResearchSquare*. (2022), <https://doi.org/10.21203/rs.3.rs-2092895/v1> [cited 2023 Jan 11].
- [43] D.E. Colley, Investigating how Bat Ectoparasites Influence the Skin Microbiome Diversity and Composition in Washington State Bats, Master Thesis, Eastern Washington University, 2022 [cited 2023 Jan 11]. Available from, <https://dc.ewu.edu/cgi/viewcontent.cgi?article=1746&context=theses> [cited 2023 Jan 11]. Available from.
- [44] M.C. Fisher, D.A. Henk, C.J. Briggs, J.S. Brownstein, L.C. Madoff, S.L. McCraw, S. J. Gurr, Emerging fungal threats to animal, plant and ecosystem health, *Nature*. 484 (2012) 186–194, <https://doi.org/10.1038/nature10947>.
- [45] G. Nabi, Y. Wang, L. Lü, C. Jiang, S. Ahmad, Y. Wu, D. Li, Bats and birds as viral reservoirs: a physiological and ecological perspective, *Sci. Total Environ.* 754 (2021), 142372, <https://doi.org/10.1016/j.scitotenv.2020.142372>.
- [46] H. Zhou, J. Ji, X. Chen, Y. Bi, J. Li, Q. Wang, et al., Identification of novel bat coronaviruses sheds light on the evolutionary origins of SARS-CoV-2 and related viruses, *Cell*. 184 (2021) 4380–4391, <https://doi.org/10.1016/j.cell.2021.06.008>.
- [47] P. Eby, A.J. Peel, A. Hoegh, W. Madden, J.R. Giles, P.J. Hudson, R.K. Plowright, Pathogen spillover driven by rapid changes in bat ecology, *Nature*. 613 (2023) 340–344, <https://doi.org/10.1038/s41586-022-05506-2>.
- [48] J. Mulec, E. Covington, J. Walochnik, Is bat guano a reservoir of *Geomyces destructans*? *Open J. Vet. Med.* 3 (2013) 161–167, <https://doi.org/10.4236/ojvm.2013.32025>.
- [49] C.E. Brook, A.P. Dobson, Bats as 'special' reservoirs for emerging zoonotic pathogens, *Trends Microbiol.* 23 (2015) 172–180, <https://doi.org/10.1016/j.tim.2014.12.004>.
- [50] R.V. Ramanantsalama, S.M. Goodman, M. Dietrich, C. Lebarbenchon, Interaction between Old World fruit bats and humans: from large scale ecosystem services to zoonotic diseases, *Acta Trop.* 231 (2022), 106462, <https://doi.org/10.1016/j.actatropica.2022.106462>.
- [51] V. Zhelyazkova, A. Hubancheva, G. Radoslavov, N. Toshkova, S.J. Puechmaille, Did you wash your caving suit? Cavers' role in the potential spread of *Pseudogymnoascus destructans*, the causal agent of White-Nose Disease, *Int. J. Speleol.* 49 (2020) 149–159, <https://doi.org/10.5038/1827-806X.49.2.2326>.
- [52] A. Li, Z. Li, W. Dai, K.L. Parise, H. Leng, L. Jin, et al., Bacterial community dynamics on bats and the implications for pathogen resistance, *Environ. Microbiol.* 24 (2022) 1484–1498, <https://doi.org/10.1111/1462-2920.15754>.
- [53] Z. Li, A. Li, J.R. Hoyt, W. Dai, H. Leng, Y. Li, et al., Activity of bacteria isolated from bats against *Pseudogymnoascus destructans* in China, *Microb. Biotechnol.* 15 (2022) 469–481, <https://doi.org/10.1111/1751-7915.13765>.