

Chapter 10

Ecosystem Services from Bats: The State of Knowledge in India

Authors*: Kadambari Deshpande, Baheerathan Murugavel, and Kasturi Saha

*Authorship is alphabetical

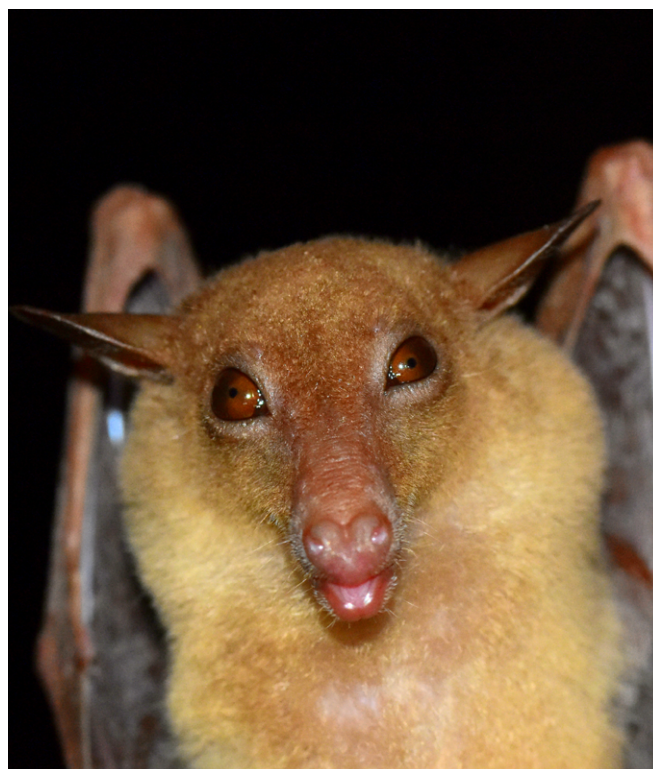
Chapter Summary

Ecosystem services to people are usually assessed at the level of entire ecosystems or of large groups of organisms. However, the direct and indirect contributions of biodiversity to ecosystem services, especially at the species level, are complex to understand. Additionally, elements of biodiversity can be both beneficial and harmful to people. This may lead to biodiversity-driven ecosystem services as well as disservices, creating both synergies and trade-offs for people. Bats are one such element of biodiversity, with the potential for simultaneous beneficial and harmful effects on human well-being.

Bats provide essential ecosystem services to people. Plant-visiting bats are important seed dispersers and pollinators of many forest trees, as well as commercial crops, but are also known to cause crop damage and loss. Insectivorous bats predate on and suppress agricultural pests, and their guano is used as an agricultural fertiliser worldwide. However, guano may negatively affect people by causing bio-fouling of property and exposing individuals who collect and handle it to potential health risks from zoonotic pathogens (e.g., histoplasmosis-causing *Histoplasma capsulatum*). Bats are known to be reservoirs of emerging viral pathogens^[1]. Growing human–bat interfaces are leading to an increase in zoonotic spillovers, which, in turn, are leading to negative outcomes for both bats and people (Chapter 8).

In this context, a conceptual understanding of ecosystem services from bats, assessment of the status of knowledge in the Indian context, and their application to bat conservation planning and prioritisation need to be imperatives for ecological research on bats and policymaking. Robust and systematic studies of ecosystem services from bats still form a nascent field in India, owing to multiple constraints. While there have been a few studies on fruit bats and seed dispersal, insectivorous bats do not feature much in Indian studies on bat ecosystem services. Additionally, most of these studies are qualitative descriptions, lacking the quantitative assessments of bat ecosystem functions that are necessary to be able to translate them into ecosystem services. Moreover, many quantitative studies for pteropodids have used methods that are mainly suitable for assessing diet or foraging behaviour rather than ecological function and, yet, have claimed to provide evidence for pollination and seed dispersal services.

In this chapter, we identify such gaps and challenges along with an overview of the existing literature on ecosystem services of bats in the Indian context. We also suggest ways forward in the form of recommendations for research and beyond, to inspire researchers and bat enthusiasts to elevate the current knowledge on the topic and to promote research on bats using these new approaches.



Greater Long-nosed Fruit Bat (*Macroglossus sobrinus*).
Photo: Rohit Chakravarty

The Concept of “Ecosystem Services”

Biodiversity and the environment constantly interact with each other. As a result, many species maintain multiple ecosystem functions, such as pollination, seed dispersal, forest regeneration, and nutrient cycling^[2]. When such ecological functions benefit people, they are termed “ecosystem services.” Ecosystem services have been formally defined as “the functions and products of ecosystems that directly or indirectly benefit humans, or yield welfare to the society” in the Ecosystem Services (ES) framework^{[3][4]}. The Millennium Ecosystem Assessment (2005)^[3] describes four types of ecosystem services: provisioning, regulating, supporting, and cultural services, which encompass both material and nonmaterial values derived from natural systems by society^[5]. Provisioning services include the contribution of ecosystems to food, resources, raw materials, products of direct use, etc., whereas supporting services may include primary productivity, nutrient cycling, microclimate maintenance, and hydrological services along with habitat availability and other enabling conditions for ecology and biodiversity^{[3][6]}. Regulating services include diverse processes, such as pollination, seed dispersal, pest regulation, natural hazard protection, etc.^[7] Cultural services relate to aesthetic, religious, or spiritual values that local people assign to biodiversity, habitats, or specific locations within ecosystems^{[8][9]}.

The direct connections between biodiversity and ecosystem services need to be investigated on two fronts: 1. identification of ecosystem services directly connected to processes maintained by biodiversity rather than by abiotic processes, and 2. quantification of these ecosystem services to evaluate actual benefits, as well as costs to human beneficiaries^[10]. With respect to bats, studying these aspects is challenging, with over 1,400 species worldwide^[11] and their remarkable diversity of life histories and functional traits.

On all continents, except Antarctica, bats are ubiquitous, occurring in forested areas, agricultural systems, peri-urban spaces, and even megacities. As a result, bats and people frequently interact with each other. This is what makes them a fascinating system through which to understand the linkages between the ecological functions they maintain and the ecosystem services they provide to people. Bats have shared spaces and interacted with people throughout human history (see Sieradzki and Mikkola 2022^[12] for a global review). While the most common perception about bats is that of cryptic, dingy animals living in dark places with mysterious lives, bats are a part of many complex ecosystem processes that are important for human food production systems. Plant-visiting bats pollinate and disperse the seeds of over 300 forest trees and commercial fruit crops^{[13][14][15][16]}. Insectivorous bats contribute to human food security and public health by controlling more than 200 species of major agricultural insect pests as well as disease-causing insect vectors such as mosquitoes and midges^{[13][17][18]}, and their droppings (guano) are used as agricultural fertiliser worldwide^{[14][19][20]}.

Table 10.1 is a summary of globally known provisioning, regulating, supporting, and cultural ecosystem services provided by bats compiled based on a review of the available literature for different regions worldwide^{[10][11][13][14][15][21][22]}. India is rich with over 100 different species of bats, and there is evidence from both Indian and international studies indicating the ecosystem services of these species (Table 10.2).

Table 10.1 Categories and examples of ecosystem services provided by fruit bats and insectivorous bat species worldwide based on a literature review ^{[10][11][13][14][15][21][22]}.

Types of Ecosystem Services	Fruit Bats	Insectivorous bats
Provisioning services	Seed aggregations and seed transfers; meat	Guano as agricultural fertiliser; meat
Regulating services	Seed dispersal; pollination; forest regeneration	Pest control for agriculture; control of disease-causing insect vectors
Supporting services	Seed germination success; nutrient cycling	Guano: nutrient recycling; phosphate mineralization; palaeo-environmental indicators in caves; a significant food source for cave systems
Cultural services	Cultural emblems; sites of worship support bat roosts; indicators of disturbance; medicinal use	Good omen; caves as sites of worship; indicators of good fortune or wealth; medicinal use

Table 10.2 The types of ecosystem services provided by Indian bat species in India and abroad based on empirical evidence.
*indicates a study conducted outside India.

Ecosystem Service Classification	Ecosystem Service	Species	Citation
Provisioning services	Seed aggregation	<i>Pteropus medius</i>	Deshpande & Kelkar 2015 ^[21] ; Deshpande et al. 2022 ^[22]
	Meat	<i>Eonycteris spelaea</i>	Dovih 2015 ^[23]
		<i>Hipposideros armiger</i>	Dovih 2015 ^[23]
		<i>Pteropus medius</i>	Kumar et al. 2021 ^[24] ; Low et al. 2021 ^[25]
		<i>Rousettus leschenaultii</i>	Dovih 2015 ^[23]
	Guano as fertiliser	<i>Hipposideros pomona</i>	Aye & Oo 2022* ^[26]
		<i>Hipposideros speoris</i>	Sridhar et al. 2006 ^[27]
		<i>Lyroderma lyra</i>	Misra et al. 2019 ^[28] ; Shetty et al. 2013 ^[20] ; Sakthi et al. 2023 ^[29]
		<i>Mops plicatus</i>	Furey et al. 2018* ^[30] ; Boonpha et al. 2019* ^[31]
		<i>Rhinopoma hardwickii</i>	Misra et al. 2019 ^[28] ; Yadav et al. 2017 ^[28]
		<i>Rhinopoma microphyllum</i>	Misra et al. 2019 ^[28]
		<i>Scotophilus heathii</i>	Misra et al. 2019 ^[28]
		<i>Scotophilus kuhlii</i>	Sothearen et al. 2014* ^[32] ; Misra et al. 2019 ^[28]
		<i>Taphozous nudiventris</i>	Misra et al. 2019 ^[28]
		<i>Taphozous melanopogon</i>	Palita et al. 2021 ^[33] ; Deshpande et al. 2025 ^[34]
Regulating services	Seed dispersal	<i>Cynopterus brachyotis</i>	Aul et al. 2007 ^[35]
		<i>Cynopterus sphinx</i>	Singaravelan & Marimuthu 2006 ^[36] ; Sudhakaran & Swami Doss 2012 ^[37] ; Mahandran et al. 2018 ^[38]
		<i>Latidens salimalii</i>	Vanitharani 2015 ^[39]
		<i>Pteropus faunulus</i>	Aul 2007 ^[35]
		<i>Pteropus medius</i>	Deshpande et al. 2022 ^[22] ; Goveas et al. 2006 ^[40] ; Nathan et al. 2009 ^[41] ; Raghuram et al. 2011 ^[42] ; Sudhakaran & Swami Doss 2012 ^[37]
		<i>Pteropus melanotus</i>	Aul 2007 ^[35]
		<i>Rousettus leschenaultii</i>	Singaravelan et al. 2009 ^[37] ; Sudhakaran & Swami Doss 2012 ^[37] ; Mahandran et al. 2018 ^[38]
	Pollination	<i>Cynopterus brachyotis</i>	Aul et al. 2007 ^[35]
		<i>Cynopterus sphinx</i>	Singaravelan & Marimuthu 2006 ^[36] ; Nathan et al. 2005 ^[43] ; Nathan et al. 2009 ^[41]
		<i>Eonycteris spelaea</i>	Bumrungsri et al. 2013* ^[44] ; Acharya et al. 2011* ^[45] ; Sritongchuay & Bumrungsri* ^[46] ; Bumrungsri et al. 2009* ^[47] ; Nor Zalipah et al. 2016* ^[48] ; Nuevo Diego 2018* ^[49] ; Chaiyarat et al. 2020* ^[50] ; Sheherazade et al. 2019* ^[51]
		<i>Latidens salimalii</i>	Vanitharani 2015 ^[39]
		<i>Macroglossus sobrinus</i>	Stewart & Dudash 2016* ^[52] ; Itino et al. 1991* ^[53] ; Liu et al. 2002* ^[54]
		<i>Pteropus faunulus</i>	Aul 2007 ^[35]
		<i>Pteropus hypomelanus</i>	Aziz et al. 2017* ^[55]

Table 10.2, continued

Ecosystem Service Classification	Ecosystem Service	Species	Citation
Regulating services, continued	Pollination, continued	<i>Pteropus medius</i>	Nathan et al. 2009 ^[41] ; Raghuram et al. 2011 ^[42] ; Sudhakaran & Swami Doss 2012 ^[37]
		<i>Pteropus melanotus</i>	Aul 2007 ^[35]
		<i>Rousettus leschenaultii</i>	Singaravelan et al. 2009 ^[56] ; Nathan et al. 2005 ^[43]
	Agricultural pest control	<i>Alionotula coromandra</i>	Misra & Elangovan 2016 ^[57]
		<i>Hipposideros armiger</i>	Wang et al. 2024 ^[58] ; Zhu et al. 2024 ^[59]
		<i>Hipposideros ater</i>	Sophia 2010 ^[60]
		<i>Hipposideros fulvus</i>	Misra & Elangovan 2016 ^[57]
		<i>Hipposideros larvatus</i>	Wang et al. 2024 ^[58] ; Ruadreo et al. 2018 ^[61] ; Abdullah et al. 2024 ^[62]
		<i>Hypsugo savii</i>	Baroja et al. 2021 ^[63] ; Ancillotto et al. 2023 ^[64] ; Ancillotto et al. 2024 ^[65]
		<i>Ia io</i>	Liu et al. 2023 ^[66] ; BaoYin & HongZao 2012 ^[67] ; Wang et al. 2024 ^[58]
		<i>Lyroderma lyra</i>	Misra & Elangovan 2016 ^[57] ; Jeya Praba et al. 2023 ^[68] ; Sakthi et al. 2023 ^[29]
		<i>Miniopterus fuliginosus</i>	Zhu et al. 2024 ^[59]
		<i>Mops plicatus</i>	Nguyen et al. 2019 ^[69] ; Srilopan et al. 2018 ^[70] ; Wanger et al. 2014 ^[71] ; Leelapaibul et al. 2005 ^[71] ; Thongjued et al. 2021 ^[72]
		<i>Myotis altarium</i>	Liu et al. 2023 ^[66]
		<i>Myotis laniger</i>	Wang et al. 2024 ^[58]
		<i>Myotis pilosus</i>	Wang et al. 2024 ^[58]
		<i>Pipistrellus pipistrellus</i>	Tuneu-Corral et al. 2024 ^[73]
		<i>Rhinolophus beddomei</i>	Ponmalar & Vanitharani 2014 ^[74]
		<i>Rhinolophus lepidus</i>	Ponmalar & Vanitharani 2014 ^[74]
		<i>Rhinolophus pearsonii</i>	Liu et al. 2023 ^[66] ; Wang et al. 2024 ^[58]
		<i>Rhinolophus pusillus</i>	Ponmalar & Vanitharani 2014 ^[74]
		<i>Rhinolophus sinicus</i>	Wang et al. 2024 ^[58]
		<i>Rhinopoma hardwickii</i>	Misra & Elangovan 2016 ^[57] ; Sunitha et al. 2022 ^[75]
		<i>Rhinopoma microphyllum</i>	Misra & Elangovan 2016 ^[57]
		<i>Scotophilus heathii</i>	Misra & Elangovan 2016 ^[57]
		<i>Scotophilus kuhlii</i>	Bhartiy & Elangovan 2021 ^[76] ; Misra & Elangovan 2016 ^[57]
		<i>Tadarida insignis</i>	Kahnonitch et al. 2018 ^[77] ; Baroja et al. 2021 ^[63]
		<i>Taphozous melanopogon</i>	Abdullah et al. 2024 ^[62] ; Zhu et al. 2024 ^[59]
		<i>Taphozous nudiventris</i>	Misra & Elangovan 2016 ^[57]
	Disease vector control	<i>Hypsugo savii</i>	Ancillotto et al. 2023 ^[64]
		<i>Mops plicatus</i>	Thongjued et al. 2021 ^[78]
		<i>Pipistrellus pipistrellus</i>	Puig-Montserrat et al. 2020 ^[18]
		<i>Taphozous longimanus</i>	Weterings et al. 2015 ^[79]

Table 10.2, continued

Ecosystem Service Classification	Ecosystem Service	Species	Citation
Supporting services	Seed germination success	<i>Pteropus medius</i>	Goveas et al. 2006 ^[40]
	Nutrient cycling	<i>Mops plicatus</i>	Lundberg et al. 2022 ^{*[80]}
Cultural services	Cultural symbols, roosts overlap with sites of worship and/or part of belief systems	<i>Pteropus medius</i>	Tangavelou et al. 2013 ^[81] ; Low et al. 2021 ^[82] ; Murugavel 2023 ^[83]
		<i>Rousettus leschenaultii</i>	Dovih 2015 ^[23] ; Murugan et al. 2020 ^[84] ; Jugli et al. 2020 ^[85]
	Medicinal use	<i>Alionoctula coromandra</i>	Molur et al. 2002 ^[86]
		<i>Cynopterus sphinx</i>	Molur et al. 2002 ^[86] ; Jugli et al. 2020 ^[85]
		<i>Eonycteris spelaea</i>	Dovih et al. 2015 ^[23]
		<i>Hesperoptenus tickelli</i>	Molur et al. 2002 ^[86]
		<i>Hipposideros armiger</i>	Molur et al. 2002 ^[86]
		<i>Hipposideros larvatus</i>	Supiandi et al. 2023 ^{*[87]}
		<i>Hipposideros speoris</i>	Molur et al. 2002 ^[86]
		<i>Latidens salimalii</i>	Molur et al. 2002 ^[86]
		<i>Megaderma spasma</i>	Molur et al. 2002 ^[86]
		<i>Pteropus faunulus</i>	Aul & Vijayakumar 2007 ^[35] ; Aul et al. 2014 ^[88]
		<i>Pteropus medius</i>	Molur et al. 2002 ^[86] ; Mickleburgh et al. 1992 ^[89] ; Molur et al. 2007 ^[87] ; Murugan et al. 2020 ^[84] ; Kumar et al. 2021 ^[24] ; Low et al. 2021 ^[82]
		<i>Pteropus melanotus</i>	Aul & Vijayakumar 2007 ^[35]
		<i>Rousettus leschenaultii</i>	Molur et al. 2002 ^[86] ; Dovih 2015 ^[23]

Old World Fruit Bats: Ecosystem services of relevance to India

Many commercially-important plants, such as bananas, mangoes, sapotas, figs, etc., are a part of the diet of commonly occurring fruit bat species in India (Figure 10.1). Diet has been relatively more studied in some Pteropodidae genera of India, such as *Cynopterus*, *Rousettus*, and *Pteropus*, but little is known in the other genera and species^{[37][42][90][91]}. In general, fruit bats, being highly mobile and able to travel long distances, are potential long-distance seed dispersers of many wild fruits^[15] as well as of commercial fruits^[21], with notable relevance in maintaining the forest ecosystems and for direct benefits to people. However, translation of frugivory to seed dispersal as an ecosystem service has not yet been studied in finer detail and, thus, requires attention (but see Deshpande et al. 2022^[22] for detailed study and quantification of seed dispersal services for commercial fruit crops, such as cashew and areca nut).

Most bat-visited plants have nocturnal flowering patterns and may be largely dependent on bats for pollination^[92]. Bats also visit plants that are pollinated by other pollinators. For instance, some flowering plants visited by bats open at night but also extend their flowering into the day, thus attracting both bats and diurnal pollinators, including bees, wasps, and birds^{[93][94]}. Nevertheless, many bat-pollinated plants (e.g., *Careya arborea*, *Ceiba pentandra*, *Pajanelia longifolia*) exhibit flower characteristics that attract bats, also known as “bat-flower syndromes”. Despite being pollinated by other pollinators, these plants are dependent on bats for the best or most successful pollination outcome (i.e., the highest or greater-quality seed set) (Figure 10.2a, b). Hence, many wild as well as commercial plants are potentially dependent on bats for their pollination^{[93][94]}.

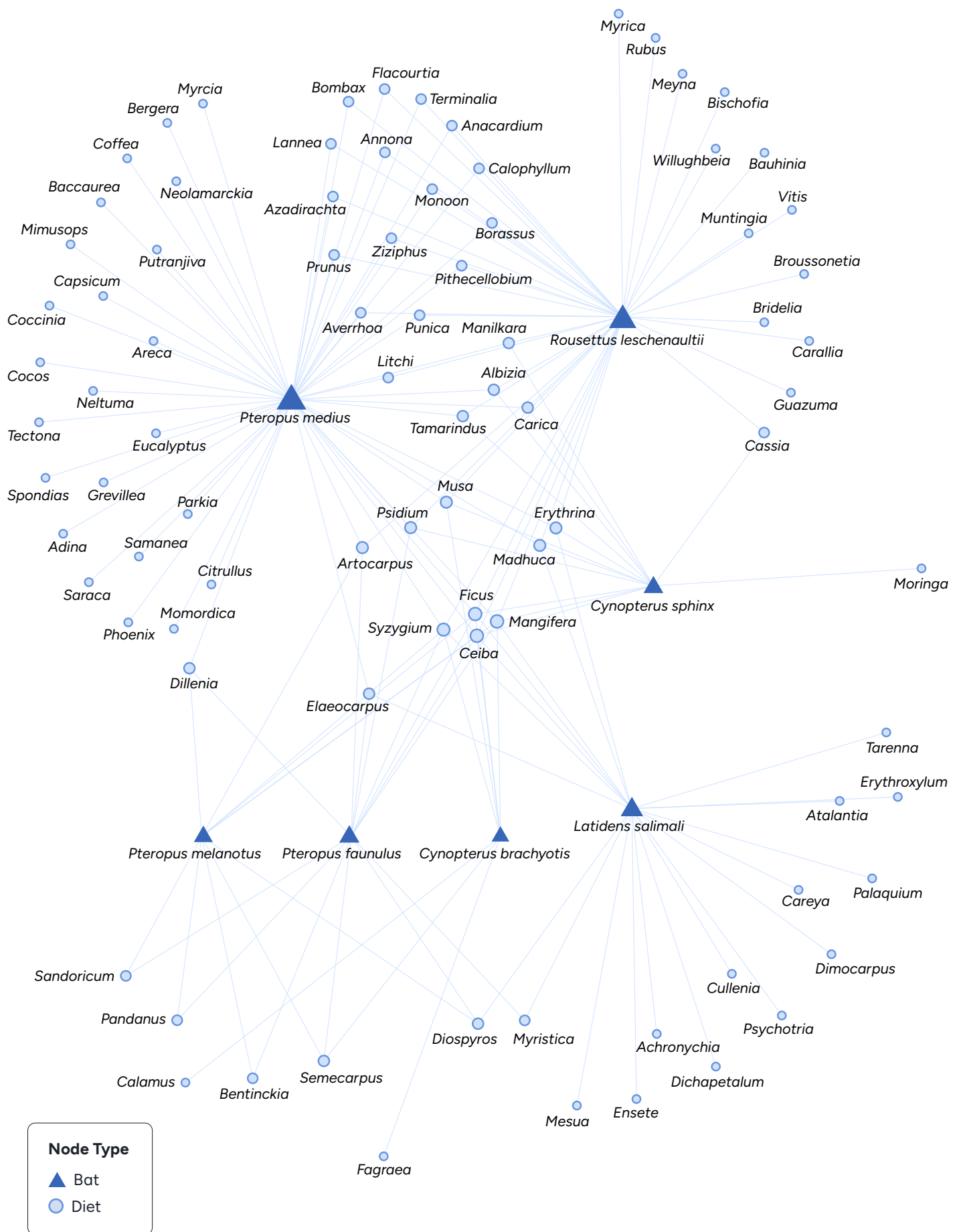


Figure 10.1 Diet network of pteropodid bats based on the available literature for India. Dark blue triangles represent bat species, and light blue circles represent plant genera. Bat visitations to and feeding on flowers and/or fruits of the plant genus constitutes inclusion as a dietary item. Larger node size represents a greater number of connections.

Fruit bats also hold a notable economic value due to their pollination service. In Southeast Asia, pteropodid bats are crucial pollinators and seed dispersers of many commercially-important plants, adding to their economic value^{[51][52][82][95]}. Some bat species, such as *Eonycteris spelaea*, *Rousettus* spp., *Pteropus* spp., and *Acerodon* spp., are key pollinators of durian plants (*Durio* spp.) in Southeast Asia and are conservatively estimated to have a direct economic value of approximately USD 117 per hectare per fruiting season^[51]. Importantly, some of these species and genera are also found in India and visit many commercial plants of India (Figure 10.1), but we still lack a proper understanding of these services from an economic point of view.

In Thailand, *Eonycteris* spp. and *Macroglossus* spp. are crucial pollinators for mangrove apple (*Sonneratia* spp.), thus playing a crucial role in mangrove conservation^[96]. Moreover, the critically endangered *Sonneratia griffithii* is dependent on bat pollinators for reproductive success and suffers from inbreeding depression due to low bat visitation rates in Thailand^{[96][97]}. These mangroves are also found in the Andaman Islands^[98], but little is known about their pollination dynamics in India. Overall, India requires detailed studies on how bat foraging and ecosystem functions can be quantified and then measured in terms of their ecological and socio-economic values. The dependence of plants, both commercial and critically endangered species such as mangroves, on bats also requires further study in terms of bats' overall economic and conservation values.



Figure 10.2 Ecosystem services provided by pteropodid bats. **Pollination:** (a) *Cynopterus* sp. visiting flowers of the night-blooming *Pajanelia longifolia* in the Western Ghats. (b) Indian Flying Fox (*Pteropus medius*) and *Cynopterus* sp. simultaneously visiting the flowers of *Ceiba pentandra*. **Seed dispersal:** (c) An Indian Flying Fox feeding on a guava fruit (*Psidium guajava*). (d) Greater Short-nosed Fruit Bat feeding on a fig fruit (*Ficus* sp.). Photo credits: a, b - Sachin Bhaskar and Sivachand MP.; c, d - Rajesh Puttaswamaiah.

Insectivorous Bats: Ecosystem services of relevance to India

Insectivorous bats feed on a plethora of insects (Figure 10.3) and also vertebrates, many of which are potential agricultural pests, predating, for example, coleopteran beetles and rodents (Figures 10.3, 10.4a, b). Empirical studies in Indian agricultural areas provide evidence of pest control services by bats such as *Rhinolophus* spp., *Hipposideros* spp., *Lyroderma lyra*, *Rhinopoma* spp., *Taphozous nudiventris*, *Scotophilus heathii*, and *Alionoctula coromandra*^{[29][57][60][68][99]}. In addition, many bat species that are known to control common insect pests in the rice fields of our neighbouring countries, such as *Hipposideros larvatus* and *Taphozous melanopogon* in Malaysia^[62], *Mops plicatus* in Thailand^[69], and *la io* in China^[67], are also found in India, potentially performing similar services. Several studies in India on insectivorous bats foraging over rice fields^{[10][100]} have found bats significantly contributing to insect predation in rice-paddies^[10]. In Spain, the pest control services by bats like *Pipistrellus pipistrel-*

lus, a species which is also present in India, prevents the loss of 70 kg of rice per hectare every year^[73]. Similarly, an exclusion experiment in apple orchards in Italy shows that *Hypsugo savii*, which is also distributed in India, along with other bats, contributes to a 50% reduction in the weight of damaged apples per tree, which translates to saving 551 euros per hectare per year that would have been spent on insecticides^[65]. Moreover, a study in China shows the possibility of invasive pest surveillance through bats, which also mentions Indian bat species, such as *Rhinolophus pearsonii*, *la io*, *Myotis pilosus*, and *Myotis altarium*^[66].

Bats from the family Megadermatidae are carnivorous and feed on large insects, beetles, rodents, birds, and even other bats^[101]. In addition to controlling insect pests, these species are potential controllers of rodent pests, which are also largely nocturnal (Figure 10.4b). From an agricultural point of view, the relevance of carnivorous bats in pest control is potentially highly valuable and needs to be quantified.

In addition to insect pest control, insectivorous bat guano is used as fertiliser by many farmer communities all over the world. Using experimental and laboratory analyses, several studies in India have examined bat guano’s potential as an organic fertiliser^{[20][26][28][34]}. These studies demonstrate that bat guano can act as an effective alternative to chemical fertilisers used by farms, thus adding more value to the Indian agricultural ecosystem. The accessibility and uptake of bat guano by larger populations in the context of its potential zoonotic disease risks (Chapter 8) and potential for disturbance to cave ecosystems during its collection needs to be examined in detail to address sustainability concerns^[34] (Figure 10.4c).

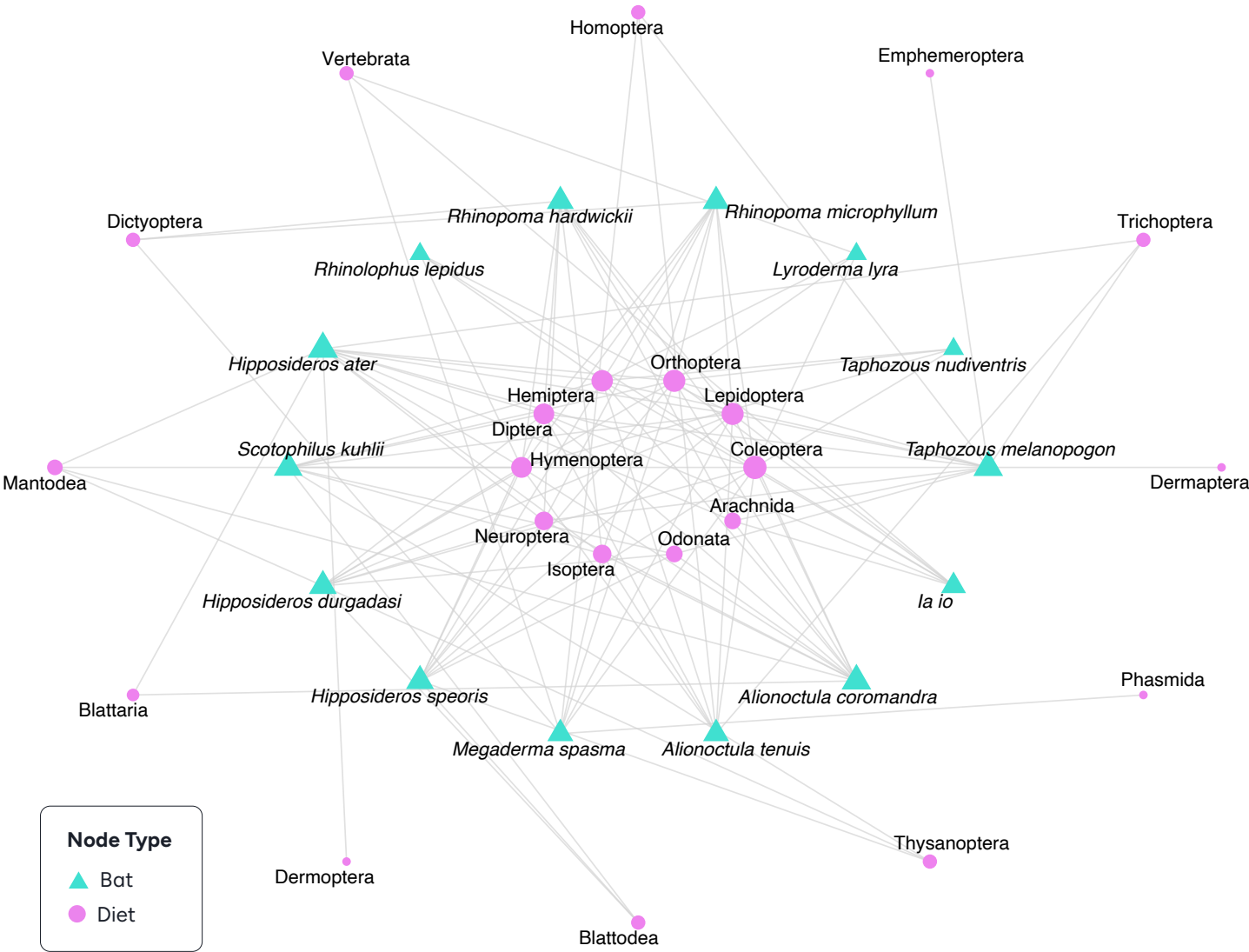


Figure 10.3 Diet network of insectivorous bats based on the available literature for India. Triangles represent bat species, and circles represent orders of insects. Larger node size represents a greater number of connections.

Apart from benefits to agriculture, some insectivorous bats can be important for direct health benefits to humans by being potential controllers of animal and human disease vectors; however, the finer details and the wide-ranging evidence for this service remain less explored. Some Indian species such as *Taphozous longimanus*, *Mops plicatus*, *Pipistrellus pipistrellus*, and *Hypsugo savii* have been reported to control disease vector insects (e.g., mosquitoes) in other countries^{[18][28][66][102]}. It is unfortunate that these species are still understudied in India, but these examples from other countries indicate the potential significance of their health-related ecosystem services that needs to be further explored in the future.

Hence, the agricultural sector as well as the public health sector can potentially benefit from both economic and environmental gains if effective management strategies are implemented to support the ecosystem services provided by bats.



Figure 10.4 Ecosystem services provided by insectivorous and carnivorous bats. **Pest control:** (a) Lesser Mouse-tailed Bat (*Rhinopoma hardwickii*) in predatory position near a cockroach. (b) Remains of Little Indian Field Mouse (*Mus booduga*) below a roost of Greater False Vampire Bats (*Lyroderma lyra*). **Guano:** (c) Guano extracted from a bat cave in the Western Ghats and left for drying in the open before being packed. Photo credits: a - Ram Mohan; b, c - Rajesh Puttaswamiah.

Cultural Services of Bats of Relevance to India

Known for its rich cultural heritage, India has had a positive cultural association with bats for centuries (Chapter 14). Recent systematic documentation in the southern Western Ghats of India highlighted more positive than negative perceptions about bats^[103]. The mention of bats as symbols of love, cues for time, and proxies for a kingdom's prosperity are found in poetry dating back to the 1st century BCE^[82] (pers.obs, author B.M.). In present-day India, bats are associated with cultural belief systems that aid co-existence and add conservation value to many species. For instance, Indian Flying Foxes (*Pteropus medius*) are considered sacred in many parts of southern India, and communities in Tamil Nadu have been conserving Indian Flying Fox roosting trees largely because those trees are associated with local deities^{[81][104][105]}. Cave temples are also places of conservation where bats can coexist with places of worship^[106]. At the same time, pilgrimage activities in Hindu and Buddhist cave temples have also displaced bat colonies, so negative impacts may attenuate positive cultural perceptions of bats and their habitat^{[107][108]}. Culture-driven belief systems also extend to the consumption of bat meat in different parts of India^{[23][82][109]}. While such consumption is largely considered to have medicinal value, systematic documentation and scientific studies of the purported medicinal benefits of bat meat are lacking^[110]. In addition, meat consumption directly exposes bat handlers to higher risks of zoonotic disease transmission, highlighting the need for exploring these trade-offs in benefits and risks in further detail.

Challenges

Conceptual challenges

Bat conservation based on arguments related to their ecosystem services alone can be challenging due to the complex nature of bats' functions in the ecosystems. For example, while fruit bats are highly important seed dispersers, they are also responsible for fruit crop damage in orchards. Hence, along with seed dispersal and pollination benefits, there can also be costs from bats as perceived by people (i.e., ecosystem "disservices" from bats^{[10][22]}). Similarly, the diet of insectivorous bats might be constituted from insect pests as well as beneficial insect species. The resulting trade-offs in ecosystem services and the so-called ecosystem disservices are therefore important to address^[22]. However, it is quite challenging to factor such nuances into empirical studies^[58].

Methodological challenges

An important methodological challenge is the quantification of ecosystem services. Many ecosystem processes and functions maintained by bats are difficult to track and to directly measure their magnitudes. Moreover, Old World fruit bats are particularly difficult to study as pollinators due to their volant, nocturnal, and elusive habits^[96]. Therefore, the link between bat functions in ecosystems and their services is usually based on correlative evidence^[10]. More specifically, for certain services of bats such as pollination, seed dispersal, and insect pest control, the conversion of bat-maintained functions to a realized service is not always possible and will require creative methodological approaches in the future.

Logistical and resource challenges

In India, studying bats at night, especially with certain methods that require tree watches and focal scans to study natural behaviours, is difficult due to safety and security concerns in different landscapes. Risks from humans as well as large animals at night pose some of the biggest challenges, especially for women scientists. This limits research not only in terms of documenting bat behaviour and natural history but also in terms of limited human resources to study these interesting creatures.

Along with a lack of human power, limited availability of advanced approaches, technology, and resources are important challenges that need to be addressed in the near future to advance our knowledge of bat ecosystem services. For instance, studying bat movement is crucial for quantifying seed dispersal and pollination services, but it is a challenge to capture large bat species (e.g., *Pteropus medius*), to tag smaller species or ones in caves, to secure funding to procure suitable equipment, and to use technologically-advanced methods for longer-term data collection, which is critical for understanding ecosystem services (Chapter 7). One possible way to address these challenges is to develop indigenous technology (e.g., tracking systems within the country to reduce the costs of movement studies). However, a potential challenge in this could be finding the right kind of collaborators (e.g., engineers or technologists).

Regulatory challenges

To delve deeper into the ecosystem services of bats would require long-term as well as large, landscape-scale studies to assess and quantify the bat-related ecosystem functions. However, securing permissions for long-term, large-scale studies in forested areas can be a difficult and time-consuming task. Securing permissions in state-owned as well as privately-owned lands has become especially challenging after the COVID-19 pandemic and recurring Nipah virus outbreaks, where bats, being potential reservoirs for zoonotic viruses, are perceived to be more harmful than useful for human well-being. Additionally, as the study of ecosystem services is a relatively new field, convincing authorities or local people (on whose lands bat studies can be conducted) with evidence is a challenge due to a lack of sufficient data or limited knowledge of the existing literature.



Leaf-nosed Bat (*Hipposideros* sp.) chasing a mosquito.
Photo: Rajesh Puttaswamaiah

Critical Knowledge Gaps and Opportunities for Future Research

Multiple research gaps remain to be addressed in the study of ecosystem services provided by frugivorous and insectivorous bats, globally and within India. These knowledge gaps can be broadly categorized into the following categories.

Conceptual understanding of ecosystem services

Ecosystem services as a framework is still an understudied topic, especially with reference to bat conservation. The understanding of ecosystem services as a concept (see above) is a major gap that makes it difficult to address bat conservation issues through an ecosystem services lens, which can be effective for on-the-ground conservation with local people and in policy-making^[10]. There have been very few systematic ecological studies, especially in India, that can potentially be related to ecosystem services from bats^{[10][100]}, their actual linkages with people's well-being^[22], and their effects on conservation action for bats.

Lack of quantification of ecosystem services by bats

In India, studying bats at night, especially with certain methods that require tree watches and focal scans to study natural behaviours, is difficult due to safety and security concerns in different landscapes. Risks from humans as well as large animals at night pose some of the biggest challenges, especially for women scientists. This limits research not only in terms of documenting bat behaviour and natural history but also in terms of limited human resources to study these interesting creatures.

Along with a lack of human power, limited availability of advanced approaches, technology, and resources are important challenges that need to be addressed in the near future to advance our knowledge of bat ecosystem services. For instance, studying bat movement is crucial for quantifying seed dispersal and pollination services, but it is a challenge to capture large bat species (e.g., *Pteropus medius*), to tag smaller species or ones in caves, to secure funding to procure suitable equipment, and to use technologically-advanced methods for longer-term



A bat exclusion experiment to measure pest insect infestation in a rice paddy field. Photo: Cárol Sierra-Durán

data collection, which is critical for understanding ecosystem services (Chapter 7). One possible way to address these challenges is to develop indigenous technology (e.g., tracking systems within the country to reduce the costs of movement studies). However, a potential challenge in this could be finding the right kind of collaborators (e.g., engineers or technologists).

Lack of interdisciplinary approaches and training to study bat ecosystem services

The limited understanding of the relevance of ecosystem services from bats is due to the lack of approaches that combine multidisciplinary perspectives, from ecological, socio-economic, and cultural angles, which would help connect bat conservation with human well-being. Bat studies from India have largely focused on systematics, anatomy, acoustics, diet, behaviour, and habitat use by bats until recently (Section II). However, there are few studies that have focused specifically on bat ecosystem services, which also suggests that many ecosystem services from bats in India have yet to be documented (e.g., the possible control of disease vectors by bats like the mosquito control documented in Australia by Gonsalves et al. 2013^[111]). Very few detailed studies from India^{[21][22]} have attempted taking an interdisciplinary approach to connect ecological responses of bats to landscape-scale and agroforestry plantation/farm-scale ecological and environmental variables, with local ecological knowledge, cultural beliefs, perceptions, and attitudes towards bats, and their effects on bat conservation (vis-à-vis human well-being) in the diverse socio-ecological settings of India.

Lack of research focus on bat ecosystem services in India

Studying ecosystem services, as elaborated above, needs an understanding of multiple perspectives beyond biology. This can only be fulfilled with an open mindset and willingness to engage with other approaches such as sociology, economics, disease vector biology, and agricultural sciences to build capacity among bat researchers to study such topics for bat conservation. However, there is a general lack of scientific engagement among bat biologists to pursue the non-biological aspects of bat conservation in order to study bat ecosystem services systematically. Collaborations between social scientists, conservationists, and bat biologists are very important to counter existing biases, as is capacity building for bat biologists to look beyond biological and ecological data alone as inputs for conservation planning and outreach. This trend is also interestingly reflected in the limited number of core authors of this chapter. Systematic, ethnographic documentation of local ecological knowledge and people's lived experiences in close proximity to bats, like near forest fringes and in agricultural settings, may provide clues to many aspects of bat ecosystem services that natural scientists may be unaware of^[21].

Due to these gaps, research on bat ecosystem services in India is still a very nascent field. Building the baseline literature on bat biology itself is going to have its own trajectory, only after which can further interesting questions be asked. Some future directions for ecosystem service research in India are related to:

- The loss of ecosystem services from insectivorous bats in increasingly pesticide-laden farms,
- Bat dispersal of native fruits as well as exotic fruits that are increasingly grown in plantations,
- The guano yield from bats in caves and its utilisation in the context of high-yielding chemical fertilisers, and
- Spatio-temporal and seasonal factors influencing the provisioning of different ecosystem services by different bat species.

To this end, we offer several recommendations for advancing the study of bat-related ecosystem services and the application of this research to bat conservation in India.

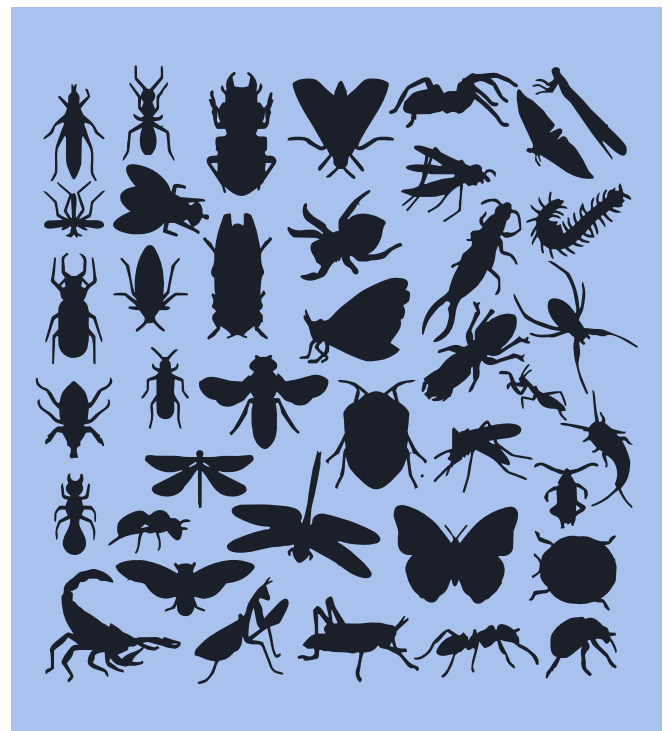


Illustration of arthropods that feature in the diet of bats.
Illustration: Adwait Pawar

Research opportunities related to pollination and seed dispersal

Systematic and species-level studies need to be undertaken with the primary objective of quantifying ecosystem services. Studies of plant–bat interactions are lacking in India, and it is high time to focus on the plant perspectives of these interactions, which occur during flowering (pollination), fruiting (seed dispersal), or both stages (double mutualisms). For prioritisation, researchers may choose ecologically or socially relevant contexts such as pollination and seed dispersal of economically important plants, including exotic species, and mangroves.

Research opportunities related to pest control

India has a rich diversity of bats and insects. However, institutions studying these taxa remain separate domains, and long-term collaborations among them is lacking. Interdisciplinary collaborations among bat researchers and agricultural pest monitoring agencies to get lists of insect and rodent pests and comparing them with bat diets will aid in understanding and establishing the role of bat species as agricultural pest controllers. Specific crop-based studies focusing on the kinds of pest control provided by bat species need to be quantified. Site-specific and/or crop-specific studies on bat diet along with controlled field experiments that prevent access of bats to insects feeding on crops will help in quantifying the economic value of pest control by bats.

Research opportunities related to disease vector control

Similar to the case with pest insects, collaborations between bat researchers and disease vector control research institutions will be important to obtain lists of potential animal and human disease vectors to compare with bat diets. This will be critical, especially in the context of increasing threats from certain diseases.

Research opportunities related to guano

Systematic quantification of bat guano and their nutritional value in comparison with existing biofertilisers needs to be conducted. These data will be crucial for the recommendation of bat guano as an alternative, and likely low-cost, supplement for crops in Indian agricultural ecosystems. However, simultaneous studies on the risks of exposure to zoonotic pathogens and disturbance to cave ecosystems through long-term use of bat guano need to be conducted to assess the overall value of using bat guano in the future.

Accessing funds for research

Using this report and other publications, appeals and proposals can be submitted to various committees (government and private) requesting the promotion and support of research related to bat-provided ecosystem services with a special highlight on the potential economic value associated with these services. This can be done by estimating the direct economic value with respect to: 1. yield increase by pollination and seed dispersal of commercially important crops, and 2. decrease in cost for pesticide and fertiliser applications in agricultural fields.

Ecosystem services concept in education

The concepts of biodiversity functions, their interconnectedness, and ecosystem services can be introduced in the formal education curriculum, starting in school-level textbooks. The significance of this education goes beyond bats as this is necessary to understand the importance of other wildlife and their habitats as well.

General awareness

Different media platforms can generate awareness about the ecosystem services of bats and their economic value (Chapter 14).

Across-field collaborations

Focused multidisciplinary workshops and conferences that include medical professionals, entomologists, engineers, economists, and farmers are important to brainstorm collaborative ideas to understand and utilise the ecosystem services of bats (Chapter 12).

References

1. Guth, S. *et al.* Bats host the most virulent—but not the most dangerous—zoonotic viruses. *PNAS* **119**, e2113628119 (2022).
2. Cardinale, B. J. *et al.* Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).
3. Millenium Ecosystem Assesment. *Ecosystems and Human Well-Being: Synthesis*. (Island Press, 2005).
4. Lead, C. *et al.* *The Economics of Ecosystems and Biodiversity: The Ecological and Economic Foundation* (Earthscan, 2009).
5. Fisher, B., Turner, R. K. & Morling, P. Defining and classifying ecosystem services for decision making. *Ecol Econ* **68**, 643–653 (2009).
6. Bennett, E. M., Peterson, G. D. & Gordon, L. J. Understanding relationships among multiple ecosystem services. *Ecol Lett* **12**, 1394–1404 (2009).
7. Rodríguez, J. P. *et al.* Trade-offs across space, time, and ecosystem services. *Ecol Soc* **11**, 28 (2006).
8. Daniel, T. C. *et al.* Contributions of cultural services to the ecosystem services agenda. *Proc Natl Acad Sci U S A* **109**, 8812–8819 (2012).
9. Milcu, A. I., Hanspach, J., Abson, D. & Fischer, J. Cultural ecosystem services: A literature review and prospects for future research. *Ecol Soc* **18**, 44 (2013).
10. Deshpande, K. *Biodiversity Underpinnings of Ecosystem Services: A Study of Bats in Agroforestry Landscapes of India's Western Ghats*. (Doctoral dissertation, Ashoka Trust for Research in Ecology and Environment and Manipal Academy Of Higher Education, 2023).
11. Frick, W. F., Kingston, T. & Flanders, J. A review of the major threats and challenges to global bat conservation. *Ann N Y Acad Sci* **1469**, 5–25 (2020).
12. Sieradzki, A. & Mikkola, H. Bats in Folklore and Culture: A Review of Historical Perceptions around the World. in *Bats - Disease-prone but Beneficial* (ed Mikkola, H.) (InTech, 2022).
13. Kunz, T. H., de Torrez, E. B., Bauer, D., Lobova, T. & Fleming, T. H. Ecosystem services provided by bats. *Ann N Y Acad Sci* **1223**, 1–38 (2011).
14. Kasso, M. & Balakrishnan, M. Ecological and economic importance of bats (Order Chiroptera). *Int Sch Res Notices* **2013**, 187415 (2013).
15. Aziz, S. A. *et al.* The critical importance of Old World fruit bats for healthy ecosystems and economies. *Front Ecol Evol* **9**, 641411 (2021).
16. Fujita, M. S. & Tuttle, M. D. Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. *Cons Biol* **5**, 455–463 (1991).
17. Wanger, T. C., Darras, K., Bumrungsri, S., Tscharnkte, T. & Klein, A. M. Bat pest control contributes to food security in Thailand. *Biol Conserv* **171**, 220–223 (2014).
18. Puig-Montserrat, X. *et al.* Bats actively prey on mosquitoes and other deleterious insects in rice paddies: potential impact on human health and agriculture. *Pest Manag Sci* **76**, 3759–3769 (2020).
19. Latinne, A. *et al.* One Health surveillance highlights circulation of viruses with zoonotic potential in bats, pigs, and humans in Viet Nam. *Viruses* **15**, 790 (2023).
20. Shetty, S., Sreepada K.S. & Bhat Rama. Effect of bat guano on the growth of *Vigna radiata* L. *Int J Sci Res Pub* **3**, 1–8 (2013).
21. Deshpande, K. & Kelkar, N. How do fruit bat seed shadows benefit agroforestry? Insights from local perceptions in Kerala, India. *Biotropica* **47**, 654–659 (2015).
22. Deshpande, K., Vanak, A. T., Devy, M. S. & Krishnaswamy, J. Forbidden fruits? Ecosystem services from seed dispersal by fruit bats in the context of latent zoonotic risk. *Oikos* **2** (2022).
23. Dovih, P. Can traditional bat hunts cause disease outbreaks in India? *Econ Polit Wkly* **50**, 13–16 (2015).
24. Kumar, J., Kanaujia, A. & Verma, R. Various threats to survival of bats in district Lakhimpur-Kheri, Uttar Pradesh, India. *Asian J Conserv Biol* **10**, 337–342 (2021).
25. Low, S. Y. *et al.* Small pteropodid bats are important pollinators of durian in Terengganu, Malaysia. *Pertanika J Trop Agric Sci* **44**, 583–597 (2021).
26. Aye, K. N. & Oo, C. C. Effects of bat (*Hipposideros pomona* Andersen, 1918) guano in compare with cowdung on the growth and yield of tomato plant (*Solanum lycopersicum*(L.)) in Magway. *University of Yangoon Research Journal* **11**, 417–428 (2022).
27. Sridhar, K. R., Ashwini, K. M., Seena, S. & Sreepada, K. S. Manure qualities of guano of insectivorous cave bat *Hipposideros speoris*. *Trop Subtrop Agroecosyst* **6**, 103–110 (2006).
28. Misra, P. K., Gautam, N. K. & Elangovan, V. Bat guano: a rich source of macro and microelements essential for plant growth. *Ann Plant Soil Res* **21**, 82–86 (2019).

29. Sakthi, V. S., Indhu, C., Margaret, I. V. & Jeyapraha, L. An Investigation on the vestiges of *Lyroderma lyra* and *Taphozous melanopogon* guano in Tirunelveli District of Tamil Nadu, India. *UPJZ* **44**, 244–250 (2023).
30. Furey, N. M., Racey, P. A., Ith, S., Touch, V. & Cappelle, J. Reproductive ecology of wrinkle-lipped free-tailed bats *Chaerephon plicatus* (Buchanan, 1800) in relation to guano production in Cambodia. *Diversity* **10**, 91 (2018).
31. Boonpha, N., Duengkai, P., Wacharapluesadee, S. & Kaewket, C. Seasonal variation in sexual size dimorphism in the wrinkle-lipped free-tailed bat (*Chaerephon plicatus* Buchanan, 1800) population in the Khao Chong Phran non-hunting area, Thailand. *Environ Nat Resour J* **17**, 50–57 (2019).
32. Sothearen, T., Furey, N. M. & Jurgens, A. J. View of effect of bat guano on the growth of five economically important plant species. *J Trop Agri* **52**, 169–173 (2014).
33. Palita, S. K., Panigrahi, R. & Panda, D. Potentiality of bat guano as organic manure for improvement of growth and photosynthetic response in crop plants. *Proc Natl Acad Sci India Sect B Biol Sci* **91**, 185–193 (2021).
34. Deshpande, K., Hegde, G., Deshpande, K. & Krishnaswamy, J. Bat guano as an ecosystem service: benefits, trade-offs, and effectiveness across socio-ecological contexts in southern India. Preprint at <https://papers.ssrn.com/sol3/Delivery.cfm?abstractid=5430165> (2025).
35. Aul, B. & Vijayakumar, S. *Bats of Nicobar—Distribution and Conservation Status. Final Technical Report submitted to the BP Conservation Programme* (Ecotone, 2003).
36. Singaravelan, N. & Marimuthu, G. *Muntingia calabura* (an attractive food plant of *Cynopterus sphinx*) deserves planting to lessen orchard damage. *Acta Chiropterol* **8**, 239–245 (2006).
37. Sudhakaran, M. R. & Swami Doss, P. Food and foraging preferences of three pteropodid bats in southern India. *J Threat Taxa* **4**, 2295–2303 (2012).
38. Mahandran, V., Murugan, C. M., Marimuthu, G. & Nathan, P. T. Seed dispersal of a tropical deciduous Mahua tree, *Madhuca latifolia* (Sapotaceae) exhibiting bat-fruit syndrome by pteropodid bats. *Glob Ecol Conserv* **14**, e00396 (2018).
39. Vanitharani, J. *Latidens salimalii* (endemic, endanger [sic] fruit bat) a reliable propagator of endemic trees of southern western Ghats. *Journal of Life Sciences* **9**, 423–435 (2015).
40. Goveas, S. W., Miranda, Eldrich, C., Seena, S. & Sridhar, K. R. Observations on guano and bolus of Indian flying fox, *Pteropus giganteus*. *Curr Sci* **90**, 160–162 (2006).
41. Nathan, P. T., Karuppudurai, T., Raghuram, H. & Marimuthu, G. Bat Foraging Strategies and Pollination of *Madhuca latifolia* (Sapotaceae) in Southern India. *Acta Chiropterol* **11**, 435–441 (2009).
42. Raghuram, H., Singaravelan, N., Nathan, T. P., Rajan, E. K. & Marimuthu, G. Foraging Ecology of Pteropodid Bats: Pollination and Seed Dispersal. in *Bats: Biology, Behavior, and Conservation* (eds Zupan, J.L. & Mlakar, S.L.) 177–188 (Nova Science Publishers, 2011).
43. Nathan, T. P., Raghuram, H., Elangovan, V., Karuppudurai, T. & Marimuthu, G. Bat pollination of kapok tree, *Ceiba pentandra*. *Curr Sci* **88**, 1679–1681 (2005).
44. Bumrungsri, S. et al. The dawn bat, *Eonycteris spelaea* Dobson (Chiroptera: Pteropodidae) feeds mainly on pollen of economically important food plants in Thailand. *Acta Chiropterol* **15**, 95–104 (2013).
45. Acharya, P. R., Bumrungsri, S. & Racey, P.A. Cave nectar bat (*Eonycteris spelaea*: Pteropodidae) crucial pollinator of tropical crops: issues of habitat management and conservation problems. *Proceedings of the Asian Trans-Disciplinary Karst Conference 2011* 284–288 (2011).
46. Sritongchuay, T. & Bumrungsri, S. Specialized and facultative nectar-feeding bats have different effects on pollination networks in mixed fruit orchards, in southern Thailand. *J Pollinat Ecol* **19**, 98–103 (2016).
47. Bumrungsri, S., Sripaoraya, E., Chongsiri, T., Sridith, K. & Racey, P. A. The pollination ecology of durian (*Durio zibethinus*, Bombacaceae) in southern Thailand. *J Trop Ecol* **25**, 85–92 (2009).
48. Zalipah, M. N., Anuar, M. S. S. & Jones, G. The potential significance of nectar-feeding bats as pollinators in mangrove habitats of Peninsular Malaysia. *Biotropica* **48**, 425–428 (2016).
49. Nuevo-Diego, C.E., Stewart, A.B. & Bumrungsri, S. Pollinators necessary for the reproductive success of critically endangered mangrove, *Sonneratia griffithii*. *Aquat Bot* **169**, e103340 (2021).
50. Chaiyarat, R., Boonma, W. & Koedrith, P. The role of pteropodid bats in pollination of durian (*Durio zibethinus*) in managed orchards in suburban habitat of Thailand. *Urban Ecosyst* **23**, 97–106 (2020).
51. Sheherazade, Ober, H. K. & Tsang, S. M. Contributions of bats to the local economy through durian pollination in Sulawesi, Indonesia. *Biotropica* **51**, 913–922 (2019).
52. Stewart, A. B. & Dudash, M. R. Differential pollen placement on an Old World nectar bat increases pollination efficiency. *Ann Bot* **117**,

145–152 (2016).

53. Itino, T., Kato, M. & Hotta, M. Pollination ecology of the two wild bananas, *Musa acuminata* subsp. *halabanensis* and *M. salaccensis*: chiropterophily and ornithophily. *Biotropica* **23**, 151–158 (1991).
54. Liu, A. Z., Li, D. Z., Wang, H. & Kress, W. J. Ornithophilous and chiropterophilous pollination in *Musa itinerans* (Musaceae), a pioneer species in tropical rain forests of Yunnan, Southwestern China. *Biotropica* **34**, 254–260 (2002).
55. Aziz, S. A. et al. Pollination by the locally endangered island flying fox (*Pteropus hypomelanus*) enhances fruit production of the economically important durian (*Durio zibethinus*). *Ecol Evol* **7**, 8670–8684 (2017).
56. Singaravelan, N., Marimuthu, G. & Racey, P. A. Do fruit bats deserve to be listed as vermin in the Indian Wildlife (Protection) & Amended Acts? A critical review. *Oryx* **43**, 608 (2009).
57. Misra, P. K. & Elangovan, V. Light and scanning electron microscopic studies on food habit analysis of insectivorous bats. *Adv Life Sci* **5**, 3649–3654 (2016).
58. Wang, Q., Feng, J., Wu, H. & Jiang, T. Insectivorous bats provide more pest suppression services than disservices - a case study in China. *Biol Control* **188**, 105435 (2024).
59. Zhu, D. et al. The consumption and diversity variation responses of agricultural pests and their dietary niche differentiation in insectivorous bats. *Animals* **14**, 815 (2024).
60. Sophia, E. Foraging behaviour of the microchiropteran bat, *Hipposideros ater* on chosen insect pests. *J Biopestic* **3**, 68–73 (2010).
61. Ruadreo, N., Voigt, C. C. & Bumrungsri, S. Large dietary niche overlap of sympatric open-space foraging bats revealed by carbon and nitrogen stable isotopes. *Acta Chiropterol* **20**, 329–341 (2018).
62. Abdullah, N. I., Elias, N. A., Ohte, N. & Vincenot, C. Resource partitioning among bat species in Peninsular Malaysia rice fields. *PeerJ* **12**, e16657 (2024).
63. Baroja, U. et al. Bats actively track and prey on grape pest populations. *Ecol Indic* **126**, 107718 (2021).
64. Ancillotto, L. et al. Predator-prey traits and foraging habitat shape the diet of a common insectivorous bat. *Acta Oecologica* **118**, 103890 (2023).
65. Ancillotto, L. et al. A bat a day keeps the pest away: bats provide valuable protection from pests in organic apple orchards. *J Nat Conserv* **78**, 126558 (2024).
66. Liu, Y., Si, M., Huang, Z., Feng, J. & Jiang, T. Bats are sentinels for invasive pest surveillance based on DNA metabarcoding. *Ecol Indic* **152**, 110354 (2023).
67. BaoYin H. & HongZao H. Effect of *la io* predatory behavior on pest occurrence in rice field. *Guizhou Agricultural Sciences*, 115–117 (2012).
68. Jeya Praba, L., Addline, D. & Sakthi, V. Nocturnal flying mammal act as a bio-control agent in agricultural ecosystem. *Int J Entomol Res* **8**, 42–46 (2023).
69. Nguyen, T. N., Ruangwiset, A. & Bumrungsri, S. Vertical stratification in foraging activity of *Chaerephon plicatus* (Molossidae, Chiroptera) in Central Thailand. *Mamm Biol* **96**, 1–6 (2019).
70. Srilopan, S., Bumrungsri, S. & Jantarit, S. The wrinkle-lipped free-tailed bat (*Chaerephon plicatus* Buchannan, 1800) feeds mainly on brown planthoppers in rice fields of central Thailand. *Acta Chiropterol* **20**, 207–219 (2018).
71. Leelapaibul, W., Bumrungsri, S. & Pattanawiboon, A. Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchannan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. *Acta Chiropterol* **7**, 111–119 (2005).
72. Thongjued, K., Chotigeat, W., Bumrungsri, S., Thanakiatkrai, P. & Kitpipit, T. Direct PCR-DGGE technique reveals wrinkle-lipped free-tailed bat (*Chaerephon plicatus* Buchanan, 1800) predominantly consume planthoppers and mosquitoes in central Thailand. *Acta Chiropterol* **23**, 93–106 (2021).
73. Tuneu-Corral, C. et al. Bats and rice: quantifying the role of insectivorous bats as agricultural pest suppressors in rice fields. *Ecosyst Serv* **66**, 101603 (2024).
74. Ponmalar, S. & Vanitharani, J. Insect pest management by the horse shoe bats (*Rhinolophus* species) in the forest ecosystem of Kalakad Mundanthurai Tiger Reserve, India. *SIRJ-BES* **1**, 1–19 (2014).
75. Sunitha, V. et al. The lesser mouse-tailed bat (*Rhinopoma hardwickii*) - A potential bio control agent in suppression of insect pests in rice. *Biol Forum* **14**, 482–485 (2022).
76. Bharti, S. K. & Elangovan, V. Seasonal prey availability and diet composition of lesser asiatic yellow house bat *Scotophilus kuhlii* Leach, 1821. *J Threat Taxa* **13**, 19002–19010 (2021).
77. Kahnnonitch, I., Lubin, Y. & Korine, C. Insectivorous bats in semi-arid agroecosystems - effects on foraging activity and implications

for insect pest control. *Agric Ecosyst Environ* **261**, 80–92 (2018).

78. Thongjued, K., Chotigeat, W., Bumrungsri, S., Thanakiatkrai, P. & Kitpipit, T. Direct PCR-DGGE technique reveals wrinkle-lipped free-tailed bat (*Chaerephon plicatus* Buchanan, 1800) predominantly consume planthoppers and mosquitoes in central Thailand. *Acta Chiropterol* **23**, 93–106 (2021).

79. Weterings, R., Wardenaar, J., Dunn, S. & Umponstira, C. Dietary analysis of five insectivorous bat species from Kamphaeng Phet, Thailand. *Raff Bull Zool* **63**, 91–96 (2015).

80. Lundberg, J., McFarlane, D. A. & Van Rentergem, G. The nitrogen dynamics of Deer Cave, Sarawak, and the role of bat caves as biogeochemical sinks in tropical moist forests. *Int J Speleol* **51**, 4 (2022).

81. Tangavelou, A. C., Jansi Rani, P. & Karthikeyan, S. Conservation of sacred Indian flying fox (bat) at sacred landscape of Pudukottai district, Tamil Nadu, India. *Asian J Conserv Biol* **2**, 178–180 (2013).

82. Low, M. R. et al. Bane or blessing? Reviewing cultural values of bats across the Asia-Pacific region. *J Ethnobiol* **41**, 18–34 (2021).

83. Murugavel, B. The sacred Indian flying foxes: A story of a spiritual ecology model for conservation from southern India. *Bat News, Bat Conservation Trust* **132**, 22–23 (2023).

84. Murugan, C. M., Saravana Bhavan, P., Nathan, P. T. & Mahandran, V. Hunting bats for bushmeat despite Nipah concerns in Idukki, Kerala, India. *Ecotropica: Int J Trop Ecol* **22**, 202006 (2020).

85. Jugli, S., Chakravorty, J. & Meyer-Rochow, V. B. Zootherapeutic uses of animals and their parts: an important element of the traditional knowledge of the Tangsa and Wancho of eastern Arunachal Pradesh, North-East India. *Environ Dev Sustain* **22**, 4699–4734 (2020).

86. Molur, S., et al. (eds) *Status of South Asian Chiroptera: Conservation Assessment and Management Plan (C.A.M.P.) Workshop Report, 2002* (Zoo Outreach Organisation, CBSG South Asia, and WILD, 2002).

87. Supiandi, I. M., Syafruddin, D., Gandasari, A., Mahanal, S. & Zubaidah, S. View of animals ethnozoology as traditional medicine in the Dayak Tamambaloh Tribe, Labian Ira'ang Village, Kapuas Hulu District, Indonesia. *Biodiversitas* **24**, 26–33 (2023).

88. Aul, B., Bates, P. J. J., Harrison, D. L. & Marimuthu, G. Diversity, distribution and status of bats on the Andaman and Nicobar Islands, India. *Oryx* **48**, 204–212 (2014).

89. Mickleburgh, S. P., Hutson, A. M. & Racey, P. A. *Old World Fruit Bats: An Action Plan for Their Conservation* (IUCN, 1992).

90. Singaravelan, N. & Marimuthu, G. Nectar feeding and pollen carrying from *Ceiba pentandra* by Pteropodid bats. *J Mammal* **85**, 1–7 (2004).

91. Singaravelan, N. & Marimuthu, G. In situ feeding tactics of short-nosed fruit bat (*Cynopterus sphinx*) on mango fruits: Evidence of extractive foraging in a flying mammal. *J Ethol* **26**, 1–7 (2008).

92. Fleming, T. H., Geiselman, C. & Kress, W. J. The evolution of bat pollination: a phylogenetic perspective. *Ann Bot* **104**, 1017–1043 (2009).

93. Raju, A. J. S., Rao, S. P. & Ezradanam, V. Pollination by bats and passerine birds in a dry season blooming tree species, *Careya arborea* in the Eastern Ghats. *Curr Sci* **86**, 509–511 (2004).

94. Baqi, A. et al. A review of durian plant-bat pollinator interactions. *J Plant Interact* **17**, 105–126 (2022).

95. Acharya, P. R., Racey, P. A., Sothibandhu, S. & Bumrungsri, S. Home-range and foraging areas of the dawn bat *Eonycteris spelaea* in Agricultural Areas of Thailand. *Acta Chiropterol* **17**, 307–319 (2015).

96. Stewart, A. B. et al. Bat pollinators: a decade of monitoring reveals declining visitation rates for some species in Thailand. *Zoological Lett* **10**, 5 (2024).

97. Nuevo-Diego, C. E., Stewart, A. B. & Bumrungsri, S. Pollinators necessary for the reproductive success of critically endangered mangrove, *Sonneratia griffithii*. *Aquat Bot* **169**, e103340 (2021).

98. Ragavan, P. et al. Critical notes on the identity and distribution of *Sonneratia griffithii* Kurz (Lythraceae) in India – a critically endangered mangrove species. *Nord J Bot* **37**, e02119 (2019).

99. Ponmalar, S. & Vanitharani, J. Insect pest management by the horse shoe bats (*Rhinolophus* species) in the forest ecosystem of Kalakad Mundanthurai Tiger Reserve, India. *SIRJ-BES* **1**, 1–19 (2014).

100. Bhalla, I. S., Aguirre-Gutiérrez, J. & Whittaker, R. J. Batting for rice: the effect of bat exclusion on rice in North-East India. *Agric Ecosyst Environ* **341**, 108196 (2023).

101. Gual-Suárez, F. & Medellín, R. A. We eat meat: a review of carnivory in bats. *Mamm Rev* **51**, 540–558 (2021).

102. Sridhar, K. R., Ashwini, K. M., Seena, S. & Sreepada, K. S. Manure qualities of guano of insectivorous cave bat *Hipposideros speoris*. *Trop Subtrop Agroecosyst* **6**, 103–110 (2006).

103. Deshpande, K. & Kelkar, N. How do fruit bat seed shadows benefit agroforestry? Insights from local perceptions in Kerala, India. *Biotropica* **47**, 654–659 (2015).

104. Balamurugan, S., Sophia, E., Swamidoss, P. D. & Isaac, S. S. Conservation of the Indian flying fox at Murappanadu Sacred Grove in Tamil Nadu. *Small Mammal Mail* **36**, 19–21 (2021).
105. Marimuthu G. The sacred flying fox of India. *Bats* **6**, 10–11 (1988).
106. Mahandran, V., Murugan, C. M. & Nathan, T. P. An unusual roosting behaviour of Schneider's leaf-nosed bat, *Hipposideros speoris* at a cave-temple roost in Tamil Nadu. *Curr Sci* **109**, 858 (2015).
107. Ganesh, T., Saravanan, A. & Mathivanan, M. Temples and bats in a homogeneous agriculture landscape: importance of microhabitat availability, disturbance and land use for bat conservation. *PLoS One* **17**, 1–20 (2022).
108. Lim, T., Cappelle, J., Hoem, T. & Furey, N. Insectivorous bat reproduction and human cave visitation in Cambodia: A perfect conservation storm? *PLoS One* **13**, e0196554 (2018).
109. Kumar, J., Kanaujia, A. & Verma, R. Various threats to survival of bats in district Lakhimpur-Kheri, Uttar Pradesh, India. *Asian J Conserv Biol* **10**, 337–342 (2021).
110. Tackett, E. S., Kingston, T., Sadeghmoghaddam, N. & Rutrough, A. L. Global medicinal use of bats: a systematic literature and social media review. *Diversity* **14**, 179 (2022).
111. Gonsalves, L., Law, B., Webb, C. & Monamy, V. Foraging ranges of insectivorous bats shift relative to changes in mosquito abundance. *PLoS One* **8**, e64081 (2013).