Community Ecology and Diversity of Bats in Mountains

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Four and a half years ago I embarked on a journey that took place in four cities/villages where I was met by the warmth, kindness, and support of people who have shaped the course of this PhD, and my life at large. This section, the only part of the thesis that is written with the heart and not the mind, is dedicated to them.

I'd like to begin by thanking my supervisor, Christian Voigt. I first joined Christian's lab as an intern in 2016. It has been an honour to work with someone who is highly regarded in the bat research community. Christian has always been supportive and has looked out for me. Apart from some solid academic training, through him, I got exposed to techniques of bat research that I had little scope of learning in India, and learnt a lot about the natural history of bats. Aside from the academic life, I will miss devouring his Christmas turkeys and his special pan-fried, lime-infused, banana split sundaes! I look forward to seeing him periodically at bat conferences and relive the PhD days.

I couldn't have asked for a better co-supervisor than Viktoriia Radchuk. I first met Viktoriia over Skype when we discussed my potential PhD proposal. It wasn't even guaranteed whether the proposal would be funded or not, but her commitment, interest, and investment in the idea made me carry hope. For the next four years, every meeting with her was to be like that. I always left the meeting with hope and feeling energised. The rarest combination in academia is of a person who is empathetic, kind, friendly, supportive, while also being intellectually smart. Even rarer it is to find someone who lightens up your R script with comments like (paraphrasing): "#OK, I will now beautify the graphs. My mom thinks as a woman I should put more make up. I don't do that so might as well make the graphs beautiful". Viktoriia belongs to both the above categories! It was an absolute delight and privilege to work with her.

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Germany; a gesture that I will never forget. Apart from checking in, he would (and continues to do so) shower genuine encouragement that would make me feel more worthy of myself than anything else. It is safe to say that Anand has played a crucial role in building my character capable of finishing this thesis.

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In November 2022, with the end of my scholarship, life came full circle because I ended up writing my thesis in the same place where I wrote my master's thesis: the National Centre for Biological Sciences. NCBS is easily the best place to write a thesis. Thanks to the productive work environment that NCBS has created, a job that would have taken 10 months in Berlin, got done in 6 months here. My thanks go to Alissa Barnes who got me access to the campus, and to the librarians for always welcoming me with a smile to my writing desk.

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Lastly, this thesis is dedicated to my mother who isn't here to witness a moment that would've made her excessively proud. Starting from my first geography books that got me interested in maps to my first tiger sighting that got me interested in wildlife – everything revolves around her. She fought blindly and furiously for my career choices despite both of us being clueless about what comes after a Bachelor's in Zoology and a Master's in Wildlife Biology. Our relationship was built on banter and it would be gross injustice if I didn't end by mocking her. Apart from my thesis examiners, had my mother been alive, she would've been the only person to read this thesis word by word. The only difference – she wouldn't understand a word of it. She would've called me to ask, "What does niche partitioning mean?" and upon listening to my explanation, she'd have casually passed it off as "Ah! Yes, that's what I thought. Just wanted to check." I've missed her presence throughout my PhD, and I miss her the most as I write this.

DECLARATION OF INDEPENDENCE

Herewith I certify that I have prepared and written my thesis independently and that I have not used any sources and aids other than those indicated by me. Intellectual property of other authors has been marked accordingly. I also declare that I have not applied for an examination procedure at any other institution and that I have not submitted the dissertation in this or any other form to any other faculty as a dissertation.

Rohit Chakravarty

Bangalore, India; 12.04.2023

THIS THESIS IS BASED ON THE FOLLOWING MANUSCRIPTS

1. **Chakravarty, R**.[1,2], Mohan, R.[3], Voigt, C. C.[1,2], Krishnan, A.[3,4]*, & Radchuk, V.[1]* (2021). Functional diversity of Himalayan bat communities declines at high elevation without the loss of phylogenetic diversity. *Scientific Reports*, *11*(22556), 1–13. https://doi.org/10.1038/s41598-021-01939-3

2. **Chakravarty, R.**[1,2], Radchuk, V.[1], Managave, S.[3], & Voigt, C. C.[1,2] (2023). Increasing species richness along elevational gradients is associated with niche packing in bat assemblages. *Journal of Animal Ecology*, 1–12. https://doi.org/10.1111/1365-2656.13897

3. **Chakravarty, R.**[1,2], Radchuk, V.[1] & Voigt, C.C.[1,2] Mountains host a significantly higher proportion of data deficient bat species than lowlands (In preparation)

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CONTENTS

SUMMARY

Species distributions and the diversity of animal and plant communities are shaped by a complex interplay of geological, abiotic, and biotic factors. Species that inhabit a biome or a wider biogeographic realm are not found throughout its extent but occur within relatively smaller spatial scales. This is because species are limited, firstly, by how far and wide they can disperse, and secondly, by their tolerance to the abiotic environment, the presence/absence of resources, the abundance of their predators and parasites, and by other competing species. Of all these factors, the abiotic environment and competition have received considerable support based on empirical evidence. Linking changes in diversity across communities to proxies of ecological niches and evolutionary histories allow community ecologists and biogeographers to decipher the drivers of community assembly.

Mountains are excellent sites for studying the drivers of species distributions and the diversity of communities. Temperature decreases consistently with increasing elevation. Correspondingly, species diversity changes idiosyncratically across taxa with elevation. Different species occupy different elevational zones and some species are often restricted to very narrow elevational ranges. As a result, adjacent elevational zones may contain a mix of species with similar/dissimilar ecological niches or evolutionary histories. Therefore, an elevational gradient inherently comprises an abiotic gradient and a gradient of changing species interactions – a phenomenon that has fascinated biologists since the time of Alexander von Humboldt. However, studies on the patterns of species distributions along mountains are biased towards easily observable taxa such as birds and plants. Additionally, many mountain ranges, especially in the Global South, remain unsampled despite supporting high biodiversity.

Alarmingly, mountains are also under immense threat from anthropogenic stressors. Most notable among the stressors is climate change which is causing species to shift their elevational distributions. Without knowing about the current state of biodiversity on mountains, it is hard to predict how different taxa will respond to future climate change. Therefore, taxon-specific syntheses of the state of mountain biodiversity may help in identifying species and regions that need prioritisation in research and/or conservation.

This thesis is an exploration of the patterns of the diversity of bats and the conservation status of bats on mountains at local and global scales, using a combination of data collected in the field (**first and second chapters)** and those gathered from the public domain **(third chapter)**. In the **first chapter**, I investigated the change in taxonomic, functional, and phylogenetic diversity across an elevational gradient in the Himalaya. I found that species richness decreases with elevation, functional diversity decreases significantly only at the highest elevation, and phylogenetic diversity remained unchanged across the elevational gradient. In the **second chapter**, in order to understand the mechanisms that sustain the diversity, I investigated trophic niche partitioning among bat species in areas of high *vs*. low diversity using stable carbon and nitrogen isotopes. My results demonstrated that species in low elevation assemblage with the highest species richness show high niche overlap, whereas, those at the high elevation assemblage showed low niche overlap perhaps to avoid competition in a harsh, resource-poor landscape. In the **third chapter**, I reviewed the global distribution and conservation status of bats on mountains using data available via the International Union for Conservation of Nature (IUCN). My analyses identified 148 mountain specialists and eight high elevation specialists, a majority of which are found in the Oriental biogeographic realm. These mountain specialist and high elevation specialist species are proportionally more data deficient than lowland bat species.

Overall, the thesis fills some important knowledge gaps by adding a taxonomic and a geographical perspective to the knowledge on community ecology and biogeography. It also highlights crucial knowledge gaps in our understanding of bats found in mountains and helps identify species of conservation and research interest.

ZUSAMMENFASSUNG

Die Verbreitung von Arten und die Vielfalt von Tier- und Pflanzengemeinschaften werden durch ein komplexes Zusammenspiel von geologischen, abiotischen und biotischen Faktoren bestimmt. Arten, die ein Biom oder einen größeren biogeografischen Bereich bewohnen, sind in der Regel nicht in dessen gesamter Ausdehnung zu finden, sondern kommen in relativ kleinen räumlichen Bereichen vor. Dies liegt zum einen daran, dass die Arten durch ihre Ausbreitungsfähigkeit und zum anderen durch ihre Toleranz gegenüber der abiotischen Umwelt, dem Vorhandensein bzw. Fehlen von Ressourcen, der Häufigkeit ihrer Fressfeinde und Parasiten sowie durch ihre Toleranz gegenüber konkurrierenden Arten eingeschränkt sind. Von all diesen Faktoren haben die abiotische Umwelt und der Wettbewerb mit konkurrierenden Artenerhebliche Unterstützung durch empirische Belege erhalten. Die Verknüpfung von Veränderungen der Diversität von Gemeinschaften mit Proxies für ökologische Nischen und Evolutionsgeschichte ermöglicht es Ökologen und Biogeographen, die Gründe für den Aufbau von Artengemeinschaften zu entschlüsseln.

Gebirge eignen sich hervorragend für die Untersuchung der Faktoren, die die Verteilung der Arten und die Vielfalt der Lebensgemeinschaften beeinflussen. Ein zentraler abiotischer Faktor ist beispielsweise die Temperatur, die mit zunehmender Höhe stetig abnimmt. Dementsprechend verändert sich auch die Artenvielfalt mit steigender Höhe . Verschiedene Arten besiedeln unterschiedliche Höhenzonen und einige Arten sind oft auf sehr enge Höhenbereiche beschränkt. Infolgedessen können benachbarte Höhenzonen eine Mischung von Arten mit ähnlichen und verschiedenen ökologischen Nischen oder evolutionäre Abstammungslinien enthalten. Daher umfasst ein Höhengradient von Natur aus einen abiotischen Gradienten und einen Gradienten wechselnder Arteninteraktionen - ein Phänomen, das Biologen seit Alexander von Humboldt fasziniert. Studien über die Muster der Artenverteilung entlang von Gebirgen konzentrieren sich jedoch vor allem auf leicht zu beobachtende Taxa wie Vögel und Pflanzen. Hinzu kommt, dass viele Gebirgszüge, vor allem im globalen Süden, trotz ihrer hohen Artenvielfalt noch nicht untersucht wurden.

Alarmierenderweise sind die Berge auch durch anthropogene Stressfaktoren stark bedroht. Zu diesen Stressfaktoren gehört vor allem der Klimawandel, der dazu führt, dass sich die Verbreitung von Arten in den Höhenlagen verschiebt. Ohne den aktuellen Zustand der

biologischen Vielfalt in den Bergen zu kennen, ist es schwer vorherzusagen, wie die verschiedenen Taxa in Zukunft auf den Klimawandel reagieren werden. Daher können taxonspezifische Erfassungen des Zustands der biologischen Vielfalt in Gebirgen dazu beitragen, Arten und Regionen zu identifizieren, die in der Forschung und/oder im Naturschutz priorisiert werden müssen.

In dieser Dissertation werden die Muster der Fledermausvielfalt und der Erhaltungszustand von Fledermäusen in Gebirgen auf lokaler und globaler Ebene untersucht, wobei eine Kombination von im Feld erhobenen Daten **(erstes und zweites Kapitel)** und von Daten aus öffentlichen Berichten **(drittes Kapitel)** verwendet wird. Im **ersten Kapitel** untersuchte ich die Veränderung der taxonomischen, funktionalen und phylogenetischen Vielfalt über einen Höhengradienten im Himalaya Gebirge. Dabei stellte ich fest, dass (1) der Artenreichtum mit der Höhe abnimmt, (2) die funktionelle Vielfalt nur in der höchsten Höhenlage signifikant abnimmt und (3) die phylogenetische Vielfalt über den Höhengradienten hinweg unverändert bleibt. Um die Mechanismen zu verstehen, die die funktionelle Vielfalt aufrechterhalten, untersuchte ich im **zweiten Kapitel** die trophische Nischenverteilung zwischen Fledermausarten in Gebieten mit hoher und niedriger Vielfalt anhand stabiler Kohlenstoff- und Stickstoffisotope. Meine Ergebnisse zeigten, dass die Arten in den niedrig gelegenen Gebieten und dem höchsten Artenreichtum eine große Nischenüberschneidung aufweisen, während die Arten in den hoch gelegenen Gebieten eine geringe Nischenüberschneidung aufweisen. Dies hängt vermutlich damit zusammen, dass in niedrig gelegenen Gebieten ausreichend Ressourcen vorhanden sind, was zu einem geringeren Konkurrenzdruck zwischen den Arten führt, während in rauen, ressourcenarmen Gebieten der höheren Lagen Konkurrenz eher vermieden wird. Im **dritten Kapitel** habe ich die weltweite Verbreitung und den Erhaltungszustand von Fledermäusen in Gebirgen anhand von Daten der International Union for Conservation of Nature (IUCN) untersucht. Meine Analysen identifizierten 148 Gebirgsspezialisten und acht Hochgebirgsspezialisten, von denen die meisten im orientalischen biogeografischen Raum vorkommen. Für diese Berg- und Hochgebirgsspezialisten liegen verhältnismäßig mehr Daten vor als für Fledermausarten aus dem Tiefland.

Insgesamt füllt die Arbeit einige wichtige Wissenslücken, indem sie die Kenntnisse über die Ökologie und Biogeografie von Gemeinschaften um eine taxonomische und geografische

Perspektive erweitert. Sie schließt auch entscheidende Wissenslücken in unserem Verständnis von Fledermäusen in Gebirgen und hilft Arten zu identifizieren, die für den Biodiversitätsschutz und die Forschung von Interesse sind.

1. GENERAL INTRODUCTION

1.1. Why is life linked to geography?

I first asked this question to myself when, as a 14-year-old birdwatcher with keen interest in geography, I picked up a field guide on Indian birds. I was astounded by the rich bird diversity of my country but also intrigued by the idea that some species are found all over the country while others are restricted to some pockets. The specific case in hand was of the Grey and Red Junglefowl. The Red Junglefowl occurs in northern India, while the Grey Junglefowl occurs in southern India. My hometown, Nagpur, is situated in their zone of overlap which added to my curiosity. I had not imagined that two sister species that are seemingly adaptable and widespread would show such a marked north-south divide in their distributions. In subsequent years, I came across several exciting maps depicting species distributions, and underwent formal training in ecology and evolution, which eventually prompted me to ask research questions related to biodiversity and species distributions for my doctoral research.

Species distributions are governed by a complex interplay of past geological events, evolutionary forces, and contemporary habitat modification. Geological events, such as plate tectonics, combined with an organism’s propensity to disperse are usually a fundamental determinant of whether a species exists in a given location or not (Christenhusz & Chase, 2013; Keith et al., 2013; Lomolino et al., 2010; L. Pellissier et al., 2018). Apart from geology and dispersal, the abiotic environment acts as a very crucial first filter. Out of 146 studies reviewed by Sexton et al. (2009), 112 studies found that abiotic factors determine species range limits. For example, climate sets a limit on the global distributions of palm family (Arecaceae) to roughly 30 °N. This is because palms have a single growing point at the apex of their stems which gets easily damaged due to frost (Cox et al., 2016). High dissolved oxygen, pH, and water transparency limit the distribution of a freshwater clam of the genus *Sphaerium* found in Uganda (Joyner-Matos et al., 2007). In some cases, contemporary distributions are an artefact of past climate. For example, species such as the Rock Ptarmigan and Mountain Hare in Europe, that were previously widespread are now restricted to small fragments called refugia owing to historical climate fluctuations (Rehnus et al., 2018). In the case of Southeast Asian terrestrial mammals, both past and present climate and habitat suitability define contemporary distributions (Radchuk et al., 2019). To sum up, distribution patterns are spatial reflections of a species’ niche (Lomolino et al., 2010). The strong association between the abiotic environment and a species' distribution range led to the concept of *Grinellian niche* (Grinnell, 1917).

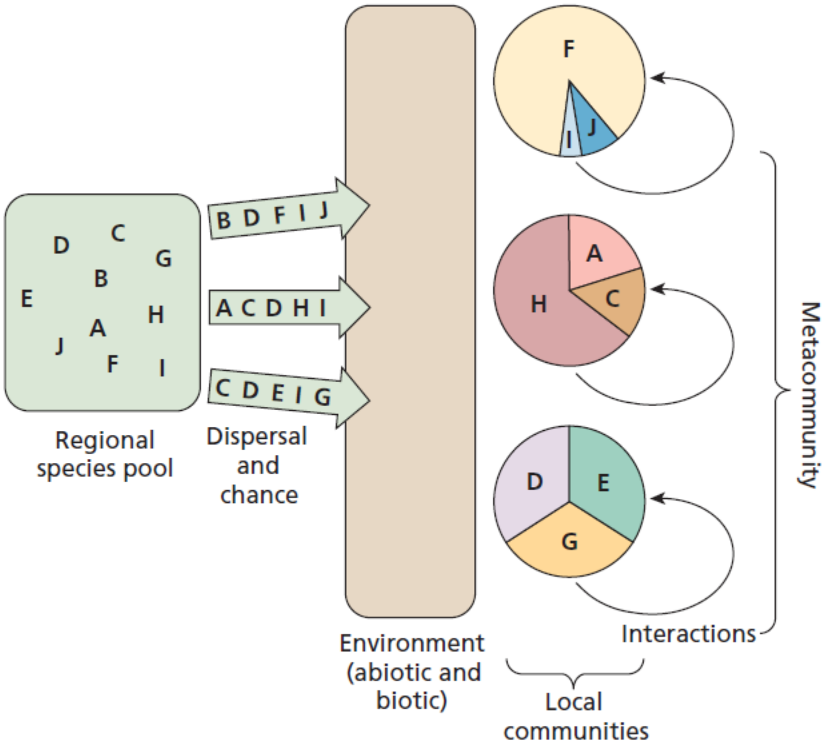


Fig. 1 A conceptual model of how species are incorporated into a local community from the regional species pool. From Mittelbach & McGill (2019).

A widely observed phenomenon is that within the limits of their abiotic tolerance, species only occupy a relatively smaller area. Sometimes this occurs due to dispersal limitation, examples of which can be seen in several transplant experiments (reviewed in Gaston, 2009) and alien/invasive species (reviewed in Pyšek et al., 2020). In both cases, species have been observed to naturalise and proliferate in environments where they did not naturally occur thereby demonstrating that they were not limited by their abiotic tolerance. However, in many other situations where a species is found in only a subset of its Grinellian niche, biotic interactions seem to have played a major role; as embodied by the *Eltonian niche* (Elton, 1927). The *Hutchinsonian niche* combines the *Grinellian* and *Eltonian niches* to define the niche as an 'n-dimensional hypervolume' of the abiotic and biotic requirements (Hutchinson, 1957)

Among all biotic interactions such as predation, parasitism, mutualism, and competition, the latter as a driver of distribution has received considerable attention and support from empirical data. Sexton et al. (2009) reported that 23 out of 26 studies that studied competitive interactions, found support for competition limiting species' ranges. The support for the role of other biotic interactions was more limited in their review. A textbook example of interspecific competition at the microhabitat scale is Joseph Connell's experiment on the Scottish coast where he experimentally removed a species of barnacle to observe its effect on a syntopic species (Connell, 1961). However, for practical reasons, such experimental studies are rare in nature. Scientists have largely relied on observing patterns of species distributions across varying spatial scales to elucidate the effects of interspecific competition. For example, Bullock et al. (2000) showed that the ranges of the shrubs *Ulex minor* and *Ulex gallii* do not overlap at three spatial scales ranging from individual heaths to 400 km^2 grids. Sometimes, 'natural experiments' are available where scientists can compare the ranges of two potentially interacting species in sympatry *vs.* allopatry. A recent study incorporating over 4.4 million citizen science records on birds from tropical mountains showed that 50% of the studied species showed an expansion in elevational range in the absence of a competing sister species. When sister species or ecologically similar species do co-occur—coexistence theory postulates that—they coexist by partitioning niches themselves by diet, space, or time (Begon & Townsend, 2021). Spatial and temporal segregation happen at much finer spatial scales and may be classified as behavioural adaptations rather than evolutionary adaptations. A textbook example of such niche partitioning comes from MacArthur's study on American warblers (MacArthur, 1958) .

The mechanisms explained above result in communities of varying diversities at different spatial scales. The study of community assembly predominantly focusses on elucidating patterns on how subsets of species from a regional community are admitted to a local community, and then tries to deduce which processes were involved (Fig. 1; Mittelbach & McGill, 2019). As will be expounded in the coming sections, this thesis mainly uses this approach to investigate patterns of diversity across gradients and to identify the mechanisms through which this diversity has arisen, or is sustained.

1.2. Measuring biodiversity and moving from patterns to processes

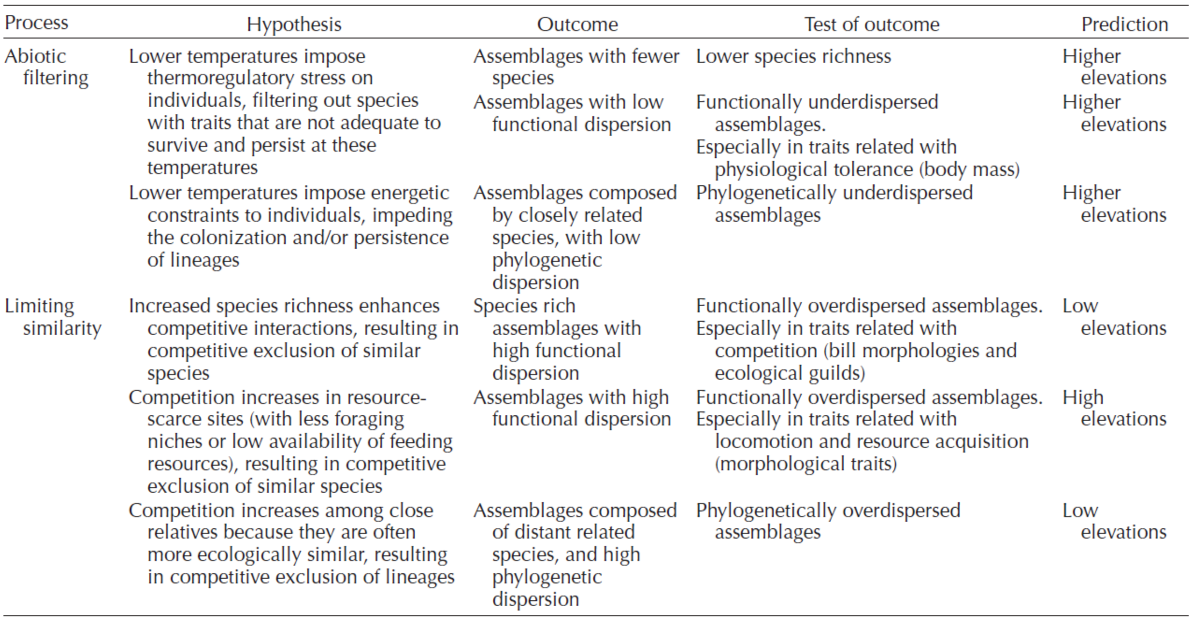
The primary descriptor of any ecological community or assemblage is the number of species *i.e., 'species richness'*. Species richness is rather easy to measure and its variation over time can be tracked easily through repeated sampling (Chao & Chiu, 2006). Species richness also has a predictable association with variables such as area (see *'species area relationship'* reviewed in Rosenzweig, 1995)) and isolation (see *'theory of island biogeography'*; Wilson & MacArthur, 2016). Plotting species richness against any of these variables thus enables us to examine the deviation of an observed pattern from the expected one. However, quantifying the total number of species disregards the (relative) abundance of species belonging to a community. In any community, some species may be inherently rare while others are more abundant. Hence, the distribution of abundance across species, called *'evenness'*, assumes equal importance as a community characteristic. The concept of evenness leads us to two other important indices of taxonomic diversity: '*Shannon-Wiener diversity index*' and '*Simpson's diversity index*' (Hill, 1973).

While taxonomic diversity has been fundamental to our understanding of global biogeographic patterns, its biggest pitfall is that it treats all species as the same. In other words, the differences in ecological functions or evolutionary histories of species are not explicitly accounted for in taxonomic diversity measures (Violle et al., 2014). This specific reason motivated researchers to find measures of functions and evolutionary relationships among co-occurring species to advance the field of community ecology.

Functional traits are morphological, physiological, or life history traits of organisms that are correlated with their functions in the ecosystem (Nock et al., 2016). Owing to their correlation with ecological functions, functional traits can also serve as proxies for species' ecological niches (Mouillot et al., 2013). Functional diversity is a measure of the diversity of traits in a community (Nock et al., 2016). Like taxonomic diversity, functional diversity can be decomposed into richness, dispersion, and evenness components. When traits are depicted in a multivariate space, *functional richness (FRic)* is the measure of the convex hull volume of all species in the community, *functional dispersion (FDis)* is measured as the mean distance of all species to the community centroid, and *functional evenness (FEve)* measures the abundance distribution of taxa (FEve is high when all traits have similar abundances) (Laliberte & Legendre, 2010; Mason et al., 2005).

Darwin (1859) was the first to explicitly state that species that belong to the same genus are inherently similar and are expected to compete more than those from different genera. Over time, owing to this perceived correlation, phylogenetic positions grew into proxies of trait similarities (Tucker et al., 2018). Analogous to taxonomic and functional diversity, phylogenetic diversity is a measure of the diversity of evolutionary lineages in a community. 'Phylogenetic richness' is typically measured as *Faith's phylogenetic diversity* which is obtained by summing the branch lengths of the tree connecting the said species. *Mean pairwise distance (MPD)* and *mean nearest taxon distance (MNTD)* are used to measure phylogenetic dispersion as the average of phylogenetic distance among all taxa and between nearest neighbouring taxa respectively (Tucker et al., 2017). The usage of phylogenetic diversity as a proxy for trait diversity is challenged by several authors (reviewed in Gerhold et al., 2015) and empirical evidence is mixed (see Cavender-Bares et al., 2004; Tucker et al., 2018). Gerhold et al. (2015) recommended combining functional and phylogenetic diversity measures for a better understanding of community assembly.

Since the first half of the 20th Century, several concepts, hypotheses, and frameworks have been proposed to explain patterns in local and regional distributions of species. One of the first among these ideas was the Competitive Exclusion Principle which proposed that two ecologically similar species cannot coexist indefinitely; a competitively dominant species will eventually outcompete the weaker species (Mittelbach & McGill, 2019). This was followed by G.E. Hutchinson's landmark keynote address (turned into a paper) that postulated, with examples, that two similar species can only coexist if they differ from each other by a factor of two in body mass (Hutchinson, 1959). Drawing on Hutchinson's ideas, Jared M. Diamond in 1975 proposed the existence of a 'checkerboard' distribution wherein the regional distribution of potentially competing species follows a checkerboard pattern (*i.e.* they avoid fine scale overlap) to avoid competition (Gotelli & Mccabe, 2002). Since phylogenetically similar species are also ecologically similar, Fox (1987) proposed that each species that gets added to a community would belong to a different genus. Despite their criticisms (for example Connor et al., 2013), these ideas (among others) culminated into the Community Assembly Theory (Kraft et al., 2015; Weiher et al., 1998).



Process	Hypothesis	Outcome	Test of outcome	Prediction
Abiotic filtering	Lower temperatures impose thermoregulatory stress on individuals, filtering out species with traits that are not adequate to survive and persist at these temperatures	Assemblages with fewer species	Lower species richness	Higher elevations
		Assemblages with low functional dispersion	Functionally underdispersed assemblages. Especially in traits related with physiological tolerance (body mass)	Higher elevations
	Lower temperatures impose energetic constraints to individuals, impeding the colonization and/or persistence of lineages	Assemblages composed by closely related species, with low phylogenetic dispersion	Phylogenetically underdispersed assemblages	Higher elevations
Limiting similarity	Increased species richness enhances competitive interactions, resulting in competitive exclusion of similar species	Species rich assemblages with high functional dispersion	Functionally overdispersed assemblages. Especially in traits related with competition (bill morphologies and ecological guilds)	Low elevations
	Competition increases in resource-scarce sites (with less foraging niches or low availability of feeding resources), resulting in competitive exclusion of similar species	Assemblages with high functional dispersion	Functionally overdispersed assemblages. Especially in traits related with locomotion and resource acquisition (morphological traits)	High elevations
	Competition increases among close relatives because they are often more ecologically similar, resulting in competitive exclusion of lineages	Assemblages composed of distant related species, and high phylogenetic dispersion	Phylogenetically overdispersed assemblages	Low elevations

Fig. 2 Testable hypotheses derived from community assembly theory that can be applied to taxa across an elevational gradient. From Montaño-Centellas et al. (2021).

Two processes are central to the community assembly theory: *abiotic filtering* (also called *habitat or environmental filtering*) and *limiting similarity*. The former indicates that abiotic conditions act as a major filter in determining whether a species from a regional species pool establishes itself in a local community or not (HilleRisLambers et al., 2012). The outcome is a functionally and/or phylogenetically clustered community (Montaño-Centellas et al., 2021) *i.e.* a community showing lower functional/phylogenetic dispersion than expected from species richness. In contrast, limiting similarity suggests that species that establish themselves do so because they are different from each other, which is a likely outcome of interspecific competition. The outcome is a community that is functionally and/or phylogenetically diverse (Montaño-Centellas et al., 2021). Typically, abiotic filtering is expected in harsh environments while limiting similarity is expected in species-rich benign environments (Lopez et al., 2016; Montaño-Centellas et al., 2021). A framework for testing these hypotheses is presented in Fig. 2. Examples of abiotic filtering and limiting similarity acting in tandem can be best witnessed from studies across natural and anthropogenic gradients such as: plant communities along a resource gradient (Menezes et al., 2020), and ant (Machac et al., 2011), small mammals (Kohli et al., 2021) and birds (Jarzyna et al., 2020; Montaño-Centellas et al., 2020, 2021) along elevational gradients among others.

Trait-based community assembly is a rapidly growing field aided by the availability of comprehensive trait databases like AVONET (Tobias et al., 2022), Elton Traits 1.0 (Wilman et al., 2014), and PHYLACINE 1.2 (Faurby et al., 2018). Technological advances also allow quantifying specific elements of niche using methods such as DNA metabarcoding and stable isotopic analysis for trophic niches (Crawford et al., 2008), and acoustic monitoring and camera trapping to detect spatio-temporal partitioning (Frey et al., 2017; Mohan et al., 2022).

1.3. Mountains as natural laboratories for biogeography

Mountains host remarkable biodiversity in comparison to surrounding lowlands (Körner, 2004). As elevation increases, distinct climatic zones and habitats emerge. Consequently, species richness changes across elevations showing idiosyncratic patterns for different taxa and mountain ranges (reviewed in McCain & Grytnes, 2010). Much of the change in diversity across elevations is often due to near complete turnover of species (McCain, 2009; Quintero & Jetz, 2018). Despite the short geographical distances, why are some species restricted to small elevational ranges and not found across the entire mountain? This question has puzzled scientists since the time when Alexander von Humboldt described changes in vegetation along the slopes of Mount Chimborazo, Ecuador in 1802 (Wulf, 2015). Therefore, mountains provide excellent opportunities for studying the interplay of the drivers of species distributions (explained in section 1.1) in the light of community assembly theory (section 1.2).

Indeed, many tests of community structure exist along elevational gradients. As explained in section 1.2, the general patterns point towards limiting similarity structuring low elevation communities and environmental filtering operating at high elevations (Montaño-Centellas et al., 2021). However, these may change with latitude and other environmental variables. For example, bird communities in tropical mountains show stronger declines in functional and phylogenetic diversity with elevation, eventually leading to underdispersed communities at high elevations (Jarzyna et al., 2020; Montaño-Centellas et al., 2020). Rodent communities typically show a mid-elevation peak in species richness but aridity influences patterns in functional and phylogenetic diversity. A decline in functional and phylogenetic diversity with increasing elevation is observed in wet mountains, whereas in arid mountains, an increase in both diversity measures is seen.

In addition to the changes in multiple dimensions of diversity (and their corresponding inferences based on community assembly theory), one other model is integral to environmental gradients like elevation. MacArthur (1965) postulated two geometric constraints to explain changes in species richness along environmental gradients. Under MacArthur's first model called ‘niche expansion’, an increase in species richness is associated with species occupying novel regions of the niche space of the assemblage. In contrast, the ‘niche packing’ model suggests that an increase in species richness leads to denser packing of the assemblage niche space due to finer specialisation or increased overlap. A schematic representation is provided in Fig. 3. The general trends point towards niche packing occurring in productive environments (such as low elevations) that can support both increased specialisation and overlapping species’ niches. In contrast, niche expansion seems to be more common in high elevations and latitudes (Lamanna et al., 2014; V. Pellissier et al., 2018; Pigot et al., 2016). However, all patterns described above come from studies with a strong taxonomic bias towards plants or birds, and are largely restricted to certain regions of the world.

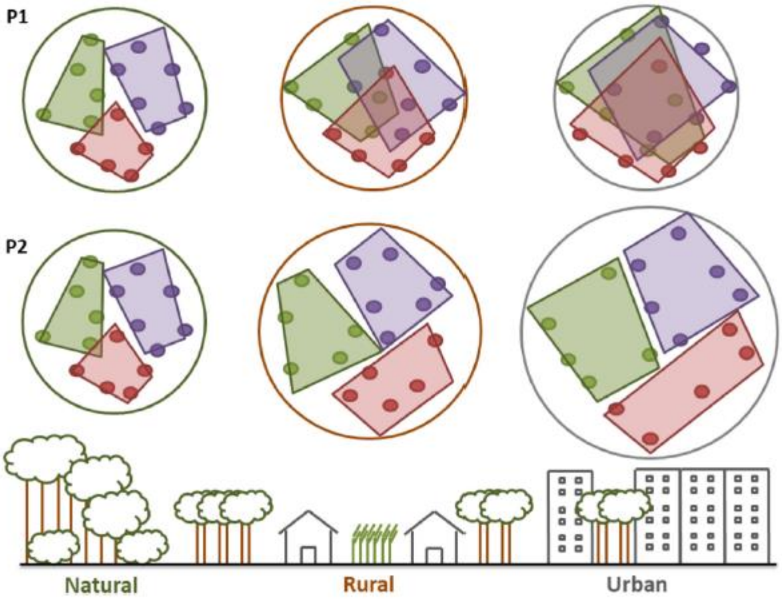


Fig. 3 A schematic representation of niche packing (above) and niche expansion (below) across a gradient of increasing bird species richness from natural to urban sites. The same framework can be applied to study any taxa along natural or anthropogenic gradients. From Pagani-Núñez et al. (2019).

1.4. Bats as model organisms

Bats are the second most diverse order of mammals in the world (Burgin et al., 2018) and are, therefore, are an excellent choice in studying community ecology. Bat assemblages contain exceptionally high diversity in comparison to other mammals (Kingston et al., 2003; Rex et al., 2008; Tanshi et al., 2022). In addition to the high diversity, species within an assemblage also show a wide range of functional traits (Denzinger & Schnitzler, 2013). Functional traits of bats such as wing morphology and echolocation call structure are linked to foraging strategies, potentially making them useful proxies of their niches (Norberg & Rayner, 1987). Wing morphology and echolocation call structure have for long been used to study niche partitioning in bat assemblages. Studies from an Australian mangrove and an African savanna show clear segregation in wing morphology and echolocation in bat assemblages that the authors link to vertical stratification and prey size selection (Aldridge & Rautenbach, 1987; McKenzie & Rolfe, 1986). Lately, there has been a surge of quantifying trophic/dietary niches of bats using stable isotopes and DNA metabarcoding. Using these approaches, bat biologists have unravelled niche partitioning in entire assemblages (Emrich et al., 2014) or between sister species (Andriollo et al., 2021; Arrizabalaga-Escudero et al., 2018; Novella-Fernandez et al., 2020; Siemers et al., 2011) or the lack of any partitioning despite trait divergence (Gordon et al., 2019). However, studies comparing niche partitioning across natural or anthropogenic gradients are uncommon. Doing so can shed light on the evolutionary drivers of diversity of assemblages (**second chapter** of this thesis), and the ecological mechanisms that sustain this diversity in the face of land-use change (for examples, see Hemprich-Bennett et al., 2021; Kemp et al., 2023).

Bats have also been sampled along several elevational gradients in various parts of the world, for example Andes (Cisneros et al., 2014; Patterson et al., 1996; Rex et al., 2008 among others), Atlantic Forest of southeastern Brazil (Coelho et al., 2018; de Carvalho et al., 2019; Mancini et al., 2019), Mount Nimba in West Africa (Reardon & Schoeman, 2017), Mount Cameroon (Manga Mongombe et al., 2019), Mount Kilimanjaro (Byamungu et al., 2021; Peters et al., 2016), Crocker Range in Malaysian Borneo (Lok et al., 2021), and Papua New Guinea (Sivault et al., 2023) among others. Most studies unanimously report a decrease in species richness with increasing elevation (McCain, 2007). However, very few studies explore the functional and phylogenetic dimensions of diversity thereby precluding inferences on community assembly.

Those that do, seem to highlight the idiosyncrasies of different mountain ranges. For example, in Mount Nimba in West Africa, Reardon & Schoeman (2017) found a decline in functional diversity only at the highest elevation; whereas in the Peruvian Andes, dispersion in phylogeny and foraging strategy traits increased at the highest elevation (Cisneros et al., 2014). In the Atlantic Forest of Brazil, Mancini et al. (2019) found different patterns of functional diversity for open and understorey bat guilds. However, most of these studies reported an effect of trait filtering at high elevations (Byamungu et al., 2021; Cisneros et al., 2014; Coelho et al., 2018; Mancini et al., 2019; Reardon & Schoeman, 2017). As is evident, there are glaring gaps in the geographical coverage of elevation gradients. The studies presented in this thesis are the first to investigate the diversity patterns of bats and niche partitioning in bat assemblages (or any mammalian taxa) along elevational gradients in the Himalaya.

1.5. Mountain biodiversity under threat

Many species found in mountains are under threat. Some keys threats to mountain biodiversity include agriculture and pisciculture in the Andes, pollutants in Canada, alien fish introductions and tourism in European mountains, water abstraction and glacial loss in Africa, road and hydropower projects in the Himalaya, and fires in Australia (Schmeller et al., 2022). The impacts of these anthropogenic stressors on biodiversity are manifold. For example, land use change and tourism have caused reduction in species diversity and gene flow (Robin et al., 2015; Rolando et al., 2007; Shahabuddin et al., 2021). Yet, perhaps the most catastrophic impacts on mountain biodiversity are being observed due to climate change. Briefly, some of these impacts include shifts in plant phenology, timing of migration, and hibernation and changing habitat structure like shifting treelines (Grabherr et al., 2010; Mccain & Colwell, 2011; Parmesan & Yohe, 2003; Wells et al., 2022).

For many high elevation species, the effects are even more pronounced as these species are often intimately adapted for life in harsh environments or fragmented sky island habitats (Razgour et al., 2021; Robin et al., 2015). Long-term monitoring trends of alpine bird species in Europe indeed show drastic population reductions (Lehikoinen et al., 2014, 2019). For most species, especially elusive taxa like bats, we lack comprehensive data on montane species richness let alone data on population trends. The inaccessibility of montane habitats in comparison to lowlands makes long-term studies challenging. In fact, a global analysis of sampling biases in ecological studies confirmed that montane environments remain poorly sampled for most taxa (Hughes et al., 2021). The lack of thorough sampling in montane forests perhaps implies that there are more species yet to be discovered in these habitats. Additionally, the ones that are known are proportionally likely to be more data deficient. However, to my knowledge, these possibilities have not been empirically tested in any taxon. Several studies have highlighted that a large proportion of data deficient species are likely to be threatened (Bland et al., 2015, 2017; Borgelt et al., 2022), hence, the lack of knowledge on montane species should also be considered a potential threat. In the absence of sufficient resources to effectively sample all the world's biodiversity on all mountains, there is need to identify range-restricted species to prioritise mountain regions for research and conservation.

The understanding of community structure along elevational gradients for any taxon holds immense value not only in knowing how assemblages were shaped due to evolutionary forces but also in predicting the fate of assemblages under future climate change (Soudzilovskaia et al., 2013). Climate-induced range shifts along elevations are becoming increasingly common (Chen et al., 2011) leading to new interactions among species. Novel interactions caused by incoming species can affect the fitness of autochthonous species as they do not have a shared history of co-evolution (Alexander et al., 2015; Gilman et al., 2010) – a phenomenon that some scientists have called an 'escalator to extinction' (Freeman et al., 2018; Urban, 2018; Watts et al., 2022). There are several well-known methodological challenges in incorporating the effects of species interactions in species distribution models under future climate change scenarios (Araújo & Guisan, 2006; Wisz et al., 2013). Functional trait similarities indicate potential differences in species' niches and can be used as proxies of ecological interactions (specifically, competition) among co-occurring species (McGill et al., 2006; Weiher et al., 2011). Functional traits can also predict dispersal ability (Mayfield et al., 2006; Norberg & Rayner, 1987). Therefore, knowing the functional diversity of elevational assemblages can help improve predictions on the fate of future communities under climate change-driven range shifts.

1.6. Thesis outline

This thesis is broadly aimed at investigating the patterns of bat diversity on mountains at local and global scales, using a combination of data collected in the field and those gathered from the public domain. I conducted fieldwork in the Indian Himalayas in the summers of 2018, 2019, and 2021 to investigate the patterns of bat diversity along an elevational gradient from 1500 to 3000 m asl. I then compared niche partitioning among bat species in assemblages of varying diversity to gather insights on the mechanisms driving the observed patterns of diversity. Subsequently, I reviewed the global diversity, distribution, and the threat status of bats on mountains to identify mountainous regions of high bat diversity and species of conservation or research interest. The results are presented as two peer-reviewed papers and a third that is in preparation for submission.

Specifically, in the **first chapter**, I investigated how taxonomic, functional, and phylogenetic diversity change across the abovementioned elevational gradient in the Himalaya. Although analysing changes in species richness along elevational gradients is a common approach, incorporating all three measures of biodiversity are rare. The variation in taxonomic, functional, and phylogenetic diversity also allows community ecologists to derive patterns from processes based on niche theory (as described in section 1.2). We found that species richness (a measure of taxonomic diversity) decreases with elevation while measures of functional diversity decrease significantly at the highest elevation. Interestingly, phylogenetic diversity remained unchanged across the elevational gradient. Our results are consistent with the idea that the harsh high elevation environment filters traits and lineages that are possibly adapted to high elevations.

Once we established the patterns in diversity along the elevational gradient, I was curious about understanding the differences in niche partitioning among bat species in areas of high *vs*. low diversity. MacArthur (1965) postulated two models integrating changes in species richness with the variation in niche occupancy of species in the assemblages, investigated across gradients. In the **second chapter**, I investigated the differences in niche partitioning in bat assemblages in the light of MacArthur's models (section 1.2). We tested these hypotheses using stable carbon and nitrogen isotopes (obtained by analysing wing tissue samples from bats caught in the field) as proxies of species' trophic niches. Our results demonstrated that the low elevation assemblage which has the highest species richness is shaped by niche packing *i.e.* the total niche width of the assemblage was small with high niche overlap among the constituent species. On the contrary, the high elevation assemblage showed large niche width and low overlap. When considered together with the findings of the first chapter, our results here suggest that although the high elevation species are functionally similar (and hence expected to compete), they perhaps coexist by means of trophic niche partitioning.

After studying local scale patterns along an elevational gradient in the Himalaya, I was deeply interested in knowing if there are general guiding principles driving the community structure of bats in mountains across the world. Unfortunately, occurrence data and trait data on bats from different elevational assemblages are too scanty to address this question. However, data publicly available via the International Union for Conservation of Nature (IUCN) are effective in comprehensively assessing the distribution and threat status of bats in mountains. Hence, in the **third chapter**, I performed spatial analyses on IUCN distribution polygons of 1331 bat species to (a) identify mountain ranges that are hotspots of bat diversity all over the world, (b) identify species that are found exclusively on mountains (‘mountain specialists’) and in high elevations (‘high elevation specialists’) and where they are found, and (c) determine differences, if any, between the threat status of mountain and high elevation specialists in comparison to lowland bat species. Our analyses returned 148 mountain specialists and eight high elevation specialists, a majority of which are found in the Oriental biogeographic realm. We found that mountain specialist and high elevation specialist bats are proportionally more data deficient than lowland bat species.

Overall, the thesis fills some important knowledge gaps. The **first two chapters** improve the understanding of how biodiversity changes and is structured along steep elevational gradients. This field of research has globally been dominated by studies on plants and birds. By studying an elusive taxon in an understudied mountain range, my data contribute both a taxonomic and a geographical perspective to the knowledge on community ecology and biogeography. The **third chapter** highlights that mountain and high elevation specialist bat species are significantly poorly studied and we, therefore, need to direct more efforts toward studying and conserving them.

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Chapter 1

Functional diversity of Himalayan bat communities declines at high elevation without the loss of phylogenetic diversity

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Functional diversity of Himalayan bat communities declines at high elevation without the loss of phylogenetic diversity

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Species richness exhibits well-known patterns across elevational gradients in various taxa, but represents only one aspect of quantifying biodiversity patterns. Functional and phylogenetic diversity have received much less attention, particularly for vertebrate taxa. There is still a limited understanding of how functional, phylogenetic and taxonomic diversity change in concert across large gradients of elevation. Here, we focused on the Himalaya—representing the largest elevational gradients in the world—to investigate the patterns of taxonomic, functional and phylogenetic diversity in a bat assemblage. Combining field data on species occurrence, relative abundance, and functional traits with measures of phylogenetic diversity, we found that bat species richness and functional diversity declined at high elevation but phylogenetic diversity remained unchanged. At the lowest elevation, we observed low functional dispersion despite high species and functional richness, suggesting a niche packing mechanism. The decline in functional richness, dispersion, and divergence at the highest elevation is consistent with patterns observed due to environmental filtering. These patterns are driven by the absence of rhinolophid bats, four congeners with extreme trait values. Our data, some of the first on mammals from the Himalayan region, suggest that in bat assemblages with relatively high species diversity, phylogenetic diversity may not be a substitute to measure functional diversity.

Elevational gradients are characterized by stark changes in climate and vegetation over short spatial scales, which, in turn, dramatically shape biodiversity[1,2]. For example, species richness (SR) exhibits well-described patterns across elevations: SR either declines linearly with elevation, or exhibits a mid-elevation peak[3]. However, studies have increasingly recognized that focusing only on SR provides a coarse quantification of biodiversity[4–6], because knowing how many species a location supports, does not provide ecological information about each species, or the traits enabling them to inhabit that location. Therefore, in addition to SR, macroecological studies are increasingly measuring two other aspects of biodiversity: functional diversity (FD) and phylogenetic diversity (PD). FD deals with traits that allow organisms to perform their range of functions in the ecosystem[7], whereas PD assesses the diversity of evolutionary relationships among species in a community[8]. Such complementary consideration of different aspects of biodiversity enables a comprehensive understanding of community assembly, which can help to better predict the impact of climate change on these communities[9].

Biodiversity is structured along natural environmental gradients by the interplay of abiotic and biotic factors, resulting in certain observable patterns in FD and PD[10]. Community assembly theory[11,12] predicts that harsh environmental conditions (typically higher elevations in mountains) support fewer species because the abiotic environment may select for certain traits that allow species to cope with harsh environmental conditions[13]. This so-called abiotic or environmental filtering[11,14] reduces the dispersion of functional traits within a community. On the contrary, competitive interactions often result in increased trait dispersion, usually in regions with

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benign environmental conditions and high diversity (typically low elevations in mountains), because each species specializes to its specific ecological niche[10,13]. If traits are phylogenetically conserved, PD varies congruently with FD[13]. Dispersal and colonization may also influence PD. For example, high rates of in situ diversification or immigration of multiple taxonomic lineages may increase PD[15]. Thus, observing the patterns of taxonomic, functional and phylogenetic diversity in concert allows us to infer the mechanisms behind community structuring[13,16].

Most of our knowledge of community structure along elevational gradients comes from studies on birds and plants. Recent meta-analyses of global functional and phylogenetic data of birds, independently found no evidence of uniform patterns of FD and PD across elevations[17,18]. Tropical lowlands and temperate highlands are functionally overdispersed whereas tropical highlands and temperate lowlands exhibit functional clustering and redundancy. Interestingly, in tropical lowlands, closely-related bird species have similar traits, and this pattern is less evident as elevation increases[18]. Despite the immense value of these studies in understanding how community composition varies with elevation, two key limitations emerge. The first is that most findings are based on published occurrence data or museum specimens that lack information on species' relative abundance or co-occurrence[10]. Such use of occurrence data may lead to biased biodiversity estimates, because they usually do not correct for detection probability, which may differ among species with different traits[19]. The second limitation is that studies of community structure have primarily focused on a few taxa, and not on those that are elusive and hard to sample, such as bats. Studying a wider range of taxa may shed light on the generality of observed elevational patterns in biodiversity.

Bats form the second most speciose mammalian order[20] and are therefore an excellent system to investigate community structure along environmental gradients. Furthermore, bats are bioindicators of climate change[21,22] and their capability of powered flight may enable them to shift their elevational ranges within short time periods[23,24]. Field studies along the Andean slopes indicate that species richness decreases with increasing elevation[25]. A global model based on regional and local climatic factors predicts that the SR of bats decreases linearly with elevation in mountains with warm and wet bases, whereas mid-elevation peaks are predicted in mountains with dry and arid bases[3]. However, the relationship of FD and PD to changes in SR remain poorly explored. Previous trait-based and phylogenetic studies of bats along elevational gradients have returned inconsistent results. FD has been observed to decrease[26] or increase[4] only at the highest elevations. Similarly, different studies found that environmental filtering leads to different traits dominating assemblages at high elevations: wing manoeuvrability[27] vs smaller body sizes[4]. The variation in PD with elevation is very poorly understood in bats. The only study that investigated this aspect of diversity found an increase in phylogenetic dispersion above 2500 m[4]. These inconsistencies highlight the differences among mountains and regional species pools necessitating more studies across the world if we are to obtain a general coherent picture of how bat diversity changes with elevational gradients.

In this study, we investigated the variation of taxonomic, functional and phylogenetic diversity of bats across a 2000 m elevational gradient in the Himalaya. Although the Himalaya have the highest mountain peaks in the world, their elevational floral and faunal biodiversity patterns, and the potential mechanisms behind these patterns have received little attention. With the exception of a few studies on birds[17,18], plants[28,29] and insects[30,31], most other taxa, including bats, remain poorly studied. The Himalaya are warming considerably faster than the global average[32] leading to range shifts in species[33], and thus a comprehensive understanding of biodiversity patterns is particularly relevant. Specifically, assuming phylogenetic conservatism of traits, we predict that (a) measures of functional and phylogenetic richness decrease with elevation; (b) the high elevational community is functionally and phylogenetically underdispersed due to extreme environmental conditions that select for certain traits, and (c) the lower elevation community exhibits greater functional and phylogenetic dispersion, as a result of more available niches, and, potentially, stronger competitive interactions. Alternatively in the absence of phylogenetic conservatism, we expect that high elevation communities are phylogenetically overdispersed if distantly-related species are characterised by similar physiological tolerance. By incorporating field data on species abundances from mistnetting and acoustic sampling methods, we additionally investigated functional evenness and divergence, in contrast to previous studies that lacked primary field data. To our knowledge, with the exception of birds, no study has hitherto been conducted on functional and phylogenetic diversity of any vertebrate taxon in the Himalaya. Our study thus provides valuable insight on community composition across a Himalayan elevational gradient.

Methods

Study area and sampling locations. We conducted this study in Kedarnath Wildlife Sanctuary (30° 25′–30° 41′ N, 78° 55′–79° 22′ E), located in Uttarakhand state in the western Himalayas of India. This sanctuary covers a broad elevational gradient from 1400 to 4000 m above sea level (asl) (Fig. 1), with corresponding changes in habitat types: from Himalayan moist temperate forests dominated by *Quercus* spp. at low elevations, to sub-alpine forests dominated by *Rhododendron* spp. and alpine meadows at high elevations[34]. This sanctuary is known to harbour 26 species of bats[35].

We sampled at four locations spanning an elevational gradient of 2200 m. Sampling points within each location were spread across the elevations mentioned in parentheses: Mandal (1500–1800 m), Ansuya (2000–2200 m), Chopta (2700–3000 m) and Tungnath (3300–3700 m) (Fig. 1). Sampling was conducted between late-March and mid-May in 2018 and 2019, starting at lower elevations and then moving to higher elevations. This sampling duration coincides with summer in the Himalaya. To comprehensively sample the bat diversity, we employed a combination of automated ultrasonic recorders and capture sampling using mist-netting. Fieldwork was approved by the Internal Committee for Ethics and Animal Welfare, Institute for Zoo and Wildlife Research (approval no. 2018-06-01), and conducted under a permit issued by the Uttarakhand State Forest Department, Government of India (permit no. 2261/5-6).

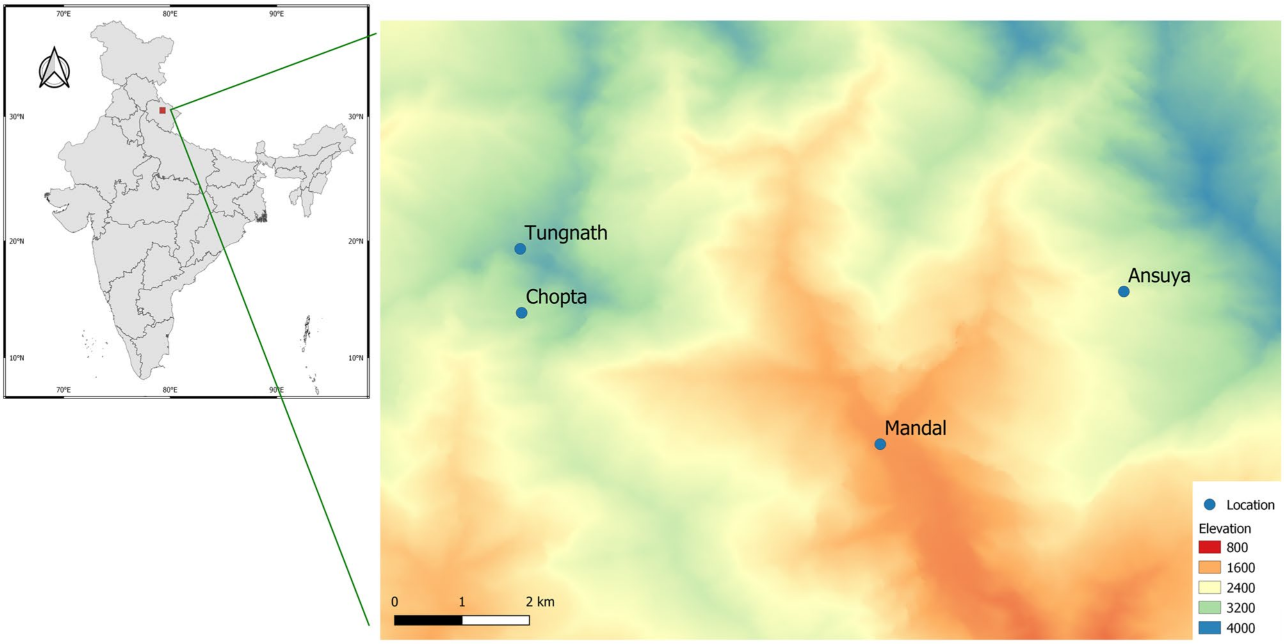

Figure 1. Map of India showing the location of the study area, Kedarnath Wildlife Sanctuary, and the sampling locations within the study area. Elevation is in m asl. The map was created using QGIS (v 3.6.3-Noosa) (QGIS Geographical Information System, www.qgis.org). Please note that the geographical boundaries represented in the map may contain areas considered disputed.

Sampling strategy. For acoustic sampling, we placed full spectrum passive ultrasonic recorders (SongMeter SM4BAT, Wildlife Acoustics, Maynard, MA, USA) in different habitat types (open, forest edge, and forest) at each elevation (hereafter, "passive recordings"). The recorders were programmed to record bat calls for two consecutive nights at each sampling point, from dusk to dawn (9–10 h/night), using a sample rate of 500 kHz/s, an amplitude threshold of 16 dB and a frequency threshold of 5 kHz. The dominant habitats at Ansuya and Tungnath are montane evergreen forests and alpine meadows respectively, therefore only these habitats were sampled at these elevations. The exact number of sampling points per habitat for each elevation is given in Table S1. On separate days after completing acoustic sampling at a site, we set up nylon and monofilament mist nets of 4, 6 or 9 m length, 16 × 16 and 19 × 19 mesh sizes (Ecotone GOC, Sopot, Poland) for four hours following dusk (starting between 18.30 h in early summer and 19.30 h in late summer). The captured bats were handled and measured following the guidelines of the American Society of Mammalogists[36]. To further refine identification in light of the paucity of taxonomic knowledge in the region, we collected only one specimen each of taxonomically-challenging species in accordance with our field research permit. We measured body mass (accuracy 0.1 g) using a spring balance (Pesola, Schindellegi, Switzerland), and forearm length (accuracy 0.01 mm) with vernier calipers (Swiss Precision Instruments SPI Inc., Melville, NY, USA). Next, we gently stretched the left wing and placed the live animal perpendicular to the background of a graph sheet of 1 × 1 cm grids. We photographed the outstretched wing using a Nikon D3400 DSLR camera at 55 mm zoom from a distance of about 90 cm. Subsequently, we released the bats and recorded their echolocation calls at a distance of 5 to 10 m using a handheld ultrasonic detector (Anabat Walkabout, Titley Scientific, Brendale, QLD, Australia) and saved them as audio files of .wav format. These recordings (henceforth referred to as "reference recordings") formed the dataset used to develop a call library for identification.

Call classifier and analysis of passive recordings. Reference recordings from 2018 and 2019 were labelled using Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA) to generate a dataset of acoustic parameters for identification. We visualized calls using a spectrogram with Hanning window, size 1024 samples with 95% overlap. From each recording, we selected 10 clear pulses and measured the following parameters: average peak frequency, maximum peak frequency, centre frequency, minimum peak frequency, peak frequency at the start and end of the call, bandwidth at 90% peak amplitude, average entropy, and call duration. All frequency variables were measured in Hz and time variables in ms. We used the peak frequency contour to determine start and end frequencies and also used bandwidth at 90% peak amplitude because higher frequencies attenuate quickly with distance from the emitting bat (causing changes to the bandwidth), and these measures are therefore more reliable in field circumstances. Using this labelled call library as a training dataset, we trained a fine K-nearest neighbours classifier using supervised learning within the 'Classification Learner' app in MATLAB (Mathworks, Inc., Natick, MA, USA). We further employed fivefold cross-validation to obtain estimates of the accuracy of each classifier in assigning calls to species. Using these pairwise values of relative accuracy (%), we generated confusion matrices for these classifiers where the species identities were represented in the columns and rows as 'True' and 'Predicted' classes, respectively. Any species with classification accuracy below 85%

Sonotype	FA	AR	WL	I	fmaxe	pfc.min	pfc.max	Duration
Arielulus circumdatus-Mirostrellus joffrei-Nyctalus leisleri (AMN)	39.06	7.77	11.86	0.93	35.56	31.31	67.65	7.13
Barbastella darjelingensis (Bdar)	39.49	5.72	8.55	0.7	34.83	24.74	41.34	5
Eptesicus-Hypsugo (EH)	49.52	7.14	9.48	1.17	29.19	22.81	47.57	8.02
Miniopterus fuliginosus (Mful)	49.15	6.89	9.4	0.82	49.31	48.09	86.91	7
Myotis muricola (Mmur)	36.38	6.79	5.43	1.19	53.06	46.32	96.19	3.92
Myotis sicarius-Pipistrellus cf. *ceylonicus* (MP)	34.71	7.03	6.84	1.1	40.03	36.98	70.39	5.69
Myotis longipes-Submyotodon caliginosus (MS)	34.85	6.95	5.84	1.34	62.93	57.6	102.08	4.27
Murina aurata-M. huttoni (Murina)	30.29	6.22	6.51	1.5	83.2	70.8	122.24	2.62
Plecotus homochrous-P. wardi (Plecotus)	40.03	6.6	6.1	1.68	36.72	28.95	43.85	2.7
Rhinolophus lepidus (Rlep)	37.47	6.78	6.51	2.52	97.93	81.93	98.7	27.3
Rhinolophus luctus (Rluc)	71.06	6.29	11.26	2.35	31.25	27.78	31.25	49.46
Rhinolophus pearsonii (Rpea)	53.77	6.12	8.27	2.2	59.51	50.5	59.81	31.68
Rhinolophus sinicus (Rsin)	48.81	6.14	10.87	1.79	84.06	73.7	84.34	32.4

Table 1. Trait matrix of the sonotypes in our assemblage (FA in mm; fmaxe, pfc.min, and pfc.max in kHz; Duration in ms). Species means of all traits were used to run a PCA and the first four PCs were used to calculated FD indices.

was clubbed with possible confusion species into a "sonotype", to improve accuracy of the classifier in the most conservative way possible (Fig. S4). The complete list of sonotypes and their mean echolocation call parameters is presented in Table 1. The classifier identified these sonotypes with > 80% accuracy, with the exception of *Miniopterus* and the *Plecotus* type B call (which, however, we could manually identify because of their call structures and frequencies). For all subsequent analyses on functional diversity and phylogenetic diversity, we used these sonotypes to ensure accurate identification.

Next, we analysed the passive recordings manually in Raven Pro. We labelled calls in subsets of 15 min per hour of the passive recordings. For each hour, the 15-min subsets were in the time windows 0–5 min, 20–25 min and 40–45 min, so as to spread out our sampling window across the hour. Following labelling, we obtained sonotype IDs using the classifier, and then verified them manually by visual comparison to the call library to improve discrimination. For every 5-min interval, we made a presence-absence matrix where 1 indicated the presence of a sonotype and 0 indicated its absence. The number of 5-min intervals in which a sonotype was detected (hereby "acoustic detections") was summed up for each sampling point. We measured the relative abundance of sonotypes as the proportion of its total number of acoustic detections relative to the total number of acoustic detections of all sonotypes in a given elevational location. The use of such a presence-absence framework is akin to 'Acoustic Activity Index'[37] which represents a relatively less biased index of activity that is less affected by differences in vocal behaviour and echolocation frequencies of different species of bats.

Assessing detectability. To assess the completeness of our species inventory, we estimated the species richness of each sampling point using the first-order Jackknife Estimator (Jack 1)[38]. Jack 1 is a nonparametric procedure for estimating species richness using presence or absence of a species in a given plot rather than its abundance[39]. Mean species detectability was calculated as the ratio of the observed to estimated species richness for different sampling point-year combinations[40,41]. We then assessed whether this mean species detectability depended on the habitat type, year, and location by fitting a linear model with the above-mentioned variables as fixed factor predictors and the mean detectability as a response. We also determined species-level detectability by following the approach of Kéry and Plattner[42]. If a sonotype was detected by mistnetting or acoustic sampling in sampling event i, we modelled its probability to be detected in sampling event $i+1$. For each sonotype, we fitted a generalized linear mixed-effects model (logit link and binomial error distribution) with detection/non-detection as the response variable, and habitat type, location, and year as the fixed factor predictors. Site and species were included as random intercepts. The significance of the fixed effects was assessed with the Likelihood Ratio Test. This test allows one to choose the best of two nested models by assessing the ratio of their likelihoods. The significance of the random effect (species) was assessed by applying a parametric bootstrap (number simulations = 100) to the model with and without the random effect, using the function bootMer of 'lme4' package. In short, a parametric bootstrap consists of fitting the model to the data and bootstrapping the obtained residuals. For these and other statistical analyses we used R version 4.0.2 (R Core Team 2020).

Taxonomic diversity. We calculated rarefied incidence-based species richness (SR) and Simpson diversity extrapolated to 50 sampling events (the number of sampling events in Mandal) using the 'iNEXT' R package[43]. The calculations were performed on a sonotype-by-sampling point presence-absence matrix with detections from both acoustic sampling and mistnetting pooled together. In the matrix, columns represented sampling units (Night 1, Night 2 and so on) and rows represented sonotype. By using sonotypes instead of species, we likely underestimated the SR, but this underestimation was uniform across elevations and is unlikely to change the pattern of SR with elevation.

Functional diversity. Our functional trait matrix (Table 1) comprised seven morphological and acoustic traits involved in guild classification, foraging and micro-habitat preferences (abbreviation followed by units): forearm length (FA, mm), aspect ratio (AR), wing loading (WL, N/m^2), tip-shape index (I), echolocation peak frequency/frequency of maximum energy (FmaxE, kHz), minimum and maximum frequencies of the peak frequency contour (pfc.min and pfc.max, kHz) and call duration (D, ms). FA was measured in the field using vernier calipers. We used ImageJ (National Institutes of Health, Bethesda, MD, USA)[44] to measure total wing area, areas of hand and arm wings and the wingspan from the standardised wing photos that were taken in the field. We calculated AR, WL, and I from these measurements following the equations given in Norberg and Rayner[45]. AR and WL both represent parameters that are correlated with flight aerodynamics and behaviour. I is influenced by the shape of the wing tip where values of 1 and above indicate broad, triangular tips, while those below 1 indicate acute wing tips. The four acoustic traits represent the shape of the echolocation call and they were measured from the reference recordings using Raven Pro, as described above.

We first calculated the means for each of the seven traits across all species within a sonotype (thus obtaining one average trait value for each sonotype) (Table 1) and then used those to compute four multivariate functional diversity (FD) indices: functional richness (FRic), divergence (FDiv), evenness (FEve)[46], and dispersion (FDis)[47], using the function dbFD() in the 'FD' R package[47]. Our FD measures are unlikely to be underestimated due to the pooling of species into sonotypes because these species were similar in acoustic and morphological traits. FRic is the convex hull volume of the traits of species present in a community, measured in the multidimensional trait space. This measurement is not weighted by abundance, relative abundance or biomass of the species in the community, but, it is standardised such that it ranges from 0 to 1. FDiv reflects the distribution of abundance across taxa (sonotypes in our case) in the functional space. High FDiv means the taxa with extreme trait values are more abundant in a community whereas low FDiv means that those with the trait values close to the centre of the functional space are more abundant[48]. FEve, on the other hand, measures the evenness in the abundance distribution of taxa in the functional space. FEve is high when all taxa have similar abundances, and it is low when some functional groups are abundant while others are rare[48]. Lastly, FDis is measured as the mean distance of all taxa to the abundance-weighted trait community centroid. We performed two sets of analyses: one using the number of mistnet captures as a proxy for relative abundance, and another using the number of detections of different sonotypes in 5-min intervals in the passive recordings as a proxy of relative abundance. We did not pool acoustic detections and mistnet captures as they have inherently different detection probabilities and measure different entities (relative number of detections vs. number of captured individuals). Owing to rhinolophid bats at lower elevations being taxonomically and functionally different from the remaining species pool, we performed another set of FD calculations, excluding the four rhinolophid species and using acoustic detections as relative abundance. One species, *Tadarida teniotis* was commonly detected at all elevations on acoustic recorders, but we were unable to capture it as it foraged high above the ground, and thus were unable to collect morphological trait data. Additionally, in using acoustic detections as a measure of relative abundance, we had to exclude the non-echolocating pteropodid bat *Sphaerias blanfordi* which was caught only once at Chopta. Therefore, our FD values are likely systematically underestimated across all elevational communities, which does not affect the comparison of community composition across elevations.

Phylogenetic diversity. Using the nexus file of a published phylogeny[49], we pruned the tree to represent species in the 14 sonotypes. For each of these types, we chose the species most commonly mist-netted as representative of its group. Published DNA sequences are lacking for some of the species in this region, so we chose their closest relatives from the phylogeny instead. Thus, we made the following replacements: (a) *Nyctalus leisleri* represented the AMN sonotype, (b) *Eptesicus serotinus* represented the EH sonotype, (c) *Murina aurata* for Murina sonotype, (d) *Myotis longipes* for MS sonotype, (e) *Pipistrellus javanicus* for MP sonotype, and (f) *Plecotus turkmenicus* for Plecotus sonotype. After pruning the tree, we calculated three indices of phylogenetic diversity using the 'picante' R package[50]: Faith's phylogenetic diversity (PD), Mean pairwise distance (MPD) and Mean nearest-taxon distance (MNTD). Faith's PD is a measure of phylogenetic richness which is obtained by summing the branch lengths of the tree connecting the species in the community. MPD and MNTD measure phylogenetic dispersion of communities; whereas MPD measures the average phylogenetic distance among all the taxa in a community, MNTD measures the same for the nearest neighbouring taxa[51]. We weighted MPD and MNTD by relative abundance of the sonotypes in each community (like FD, the number of detections in five-minute intervals in the passive recordings was used as a proxy of relative abundance).

Null model testing. As FD and PD are strongly correlated to species richness[52], we used a null model to assess whether the observed was significantly different than expected due to chance alone. We produced the null distribution of each FD and PD index by randomizing the community matrix 999 times using the 'independent swap' method[53,54], so as to preserve the species richness at each site and the number of sites in which each species can be found. Our randomization was further constrained by elevation, so that the abundances were randomized among the sampling points within each elevation. The null model allows for calculation of an effect size (difference between the observed value and mean of the null distribution). Given the range of FD and PD values, the effect sizes are not comparable across communities with vastly different species richness[55]. Therefore, standardized effect sizes (SES) of each index were calculated at each site as the difference between the observed value and the mean of the null distribution, divided by the standard deviation of the null distribution. $SES > 1$ and $SES < -1$ indicate that a given index is significantly higher and lower (respectively) than the null model. Tungnath was excluded from the FD analyses due to inadequate number of sampling points (only two) for randomizations. We used a generalised linear model (GLM) to assess the change in each index with elevation. Tukey's Honest Significant Difference (HSD) test was subsequently used to compare the means.

Figure 2. Portraits of some bat species found in Kedarnath Wildlife Sanctuary that represent different functional and phylogenetic groups. (**a**) *Sphaerias blanfordi*, (**b**) *Rhinolophus pearsonii*, (**c**) *Pipistrellus* cf. *ceylonicus*, (**d**) *Plecotus wardi*, (**e**) *Arielulus circumdatus* and (**f**) *Mirostrellus joffrei*. All photos by the first author.

Ethics declaration. Fieldwork was approved by the Internal Committee for Ethics and Animal Welfare, Institute for Zoo and Wildlife Research (approval no. 2018-06-01), and conducted under a permit issued by the Uttarakhand State Forest Department, Government of India (permit no. 2261/5-6).

Results

We recorded a total of 23 bat species in 15 genera and five families (Pteropodidae, Rhinolophidae, Molossidae, Vespertilionidae and Miniopteridae) across the elevational gradient in Kedarnath Wildlife Sanctuary. Of these, *Tadarida teniotis* was only recorded through acoustic sampling whereas *Sphaerias blanfordi*, a non-echolocating fruit bat of the family Pteropodidae, was only caught in a mist net. Three species: *Hypsugo affinis*, *Myotis sicarius* and *Miniopterus fuliginosus* were not recorded in a recent survey[35]. Select bat species from the study area that belong to different functional groups are depicted in Fig. 2.

Detectability. The median detection probability across species, combined across all sampling sites was 0.8 (Fig. S1). We found no significant effect of location (F = 0.44, df = 3, p = 0.73), year (F = 0.95, df = 1, p = 0.34) and habitat type (F = 1.47, df = 2, p = 0.25) on the mean species detection probability. We did not find a significant effect of species on species-level detection probability. However, habitat type affected species-level detection

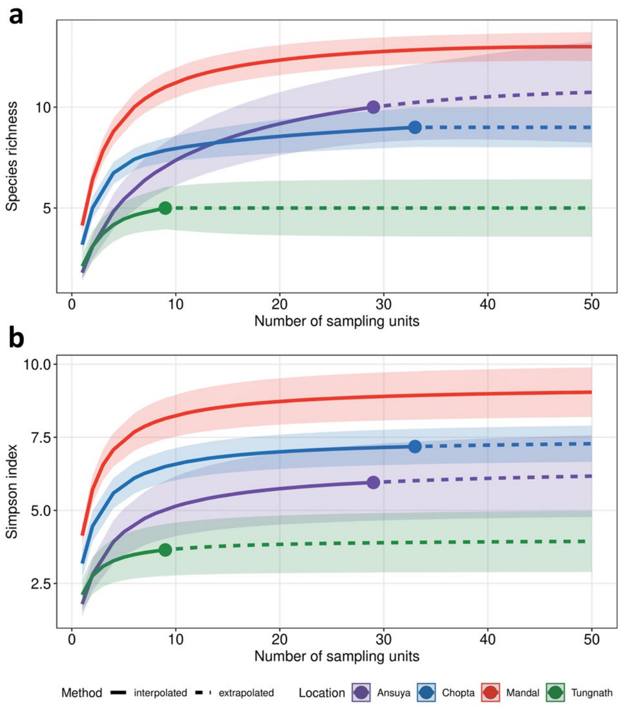

Figure 3. Rarefaction curves of (**a**) cumulative species richness and (**b**) Simpson diversity across all elevational communities plotted against the number of sampling nights. Each location is represented by a different colour. The symbols represent the number of sampling nights at each location. Species richness of all locations is extrapolated to the number of sampling nights at Mandal (shown by the dotted lines).

probability ($\chi^2 = 7.4$, df = 2, p = 0.025), being lowest in the forest habitat and high in both open habitat and at forest edges (Fig. S2). In other words, any given species was less easily detected in forest habitats.

Effect of elevation on taxonomic, functional and phylogenetic diversity. Species (sonotype) richness (SR) decreased with increasing elevation. Simpson's diversity was highest at Mandal, followed by Chopta, Ansuya and finally, Tungnath (Fig. 3). FD decreased significantly only at Chopta (Fig. 4), the highest elevation considered in the analysis. When calculating FD indices using acoustic detections as a measure of relative abundance, all FD indices at Chopta were significantly lower than expected under a random null community (SES < 1; Fig. 4a). FDis and FDiv at Chopta were also significantly lower than in Mandal and Ansuya (FDis Tukey's HSD, $p < 0.001$; FDiv Tukey's HSD, $p < 0.05$) (Fig. 4a). FRic at Mandal was significantly greater than expected under the null model (SES > 1). However, when we repeated the analysis by excluding the rhinolophids, the differences in FD indices across elevations were insignificant (Fig. 4b). Mean and median of FRic dipped at the mid-elevation and both Mandal and Chopta showed higher values than expected under a null model. Only FDis at Chopta was significantly lower than the null model and was also significantly lower than that in Mandal and Ansuya (Tukey's HSD: $p < 0.01$). We found no effect of elevation on FD when measuring FD indices using mistnet captures as relative abundance (Fig. 4c).

In contrast to FD indices, PD indices were not significantly affected by elevation irrespective of whether rhinolophid bats were considered in the analysis or not (Fig. 5). Faith's PD, MPD and MNTD of all communities were not different from the random expectation (SES between − 1 and 1).

Discussion

Our study combined field data on species occurrence, abundance, and functional traits with analyses of phylogenetic diversity in the first comprehensive study of elevational diversity patterns in Himalayan bats. We predicted that SR, FD and PD would decline with elevation, based on biogeographic studies in diverse taxa[3,17,18,26]. Assuming phylogenetic conservatism of traits, we expected FD (specifically FRic and FDis) and PD to be underdispersed (lower than the null expectation) at the highest elevational location, Chopta, and overdispersed (higher than the null) at the lowest elevational location, Mandal[10]. Contrary to our initial predictions, we uncover divergent trends in species (sonotype) richness (SR), functional diversity (FD), and phylogenetic diversity (PD) across this 2000 m gradient, with only FD being significantly lower than expected under random expectation at Chopta. Additionally, we found higher than expected FRic but not FDis at Mandal, the lowest elevation community. At the same time, PD did not change strongly across elevations. The observed patterns in FD and PD arise due to the absence of rhinolophid bats at higher elevations. Our results are consistent with environmental filtering being a driver of community assembly, as discussed below.

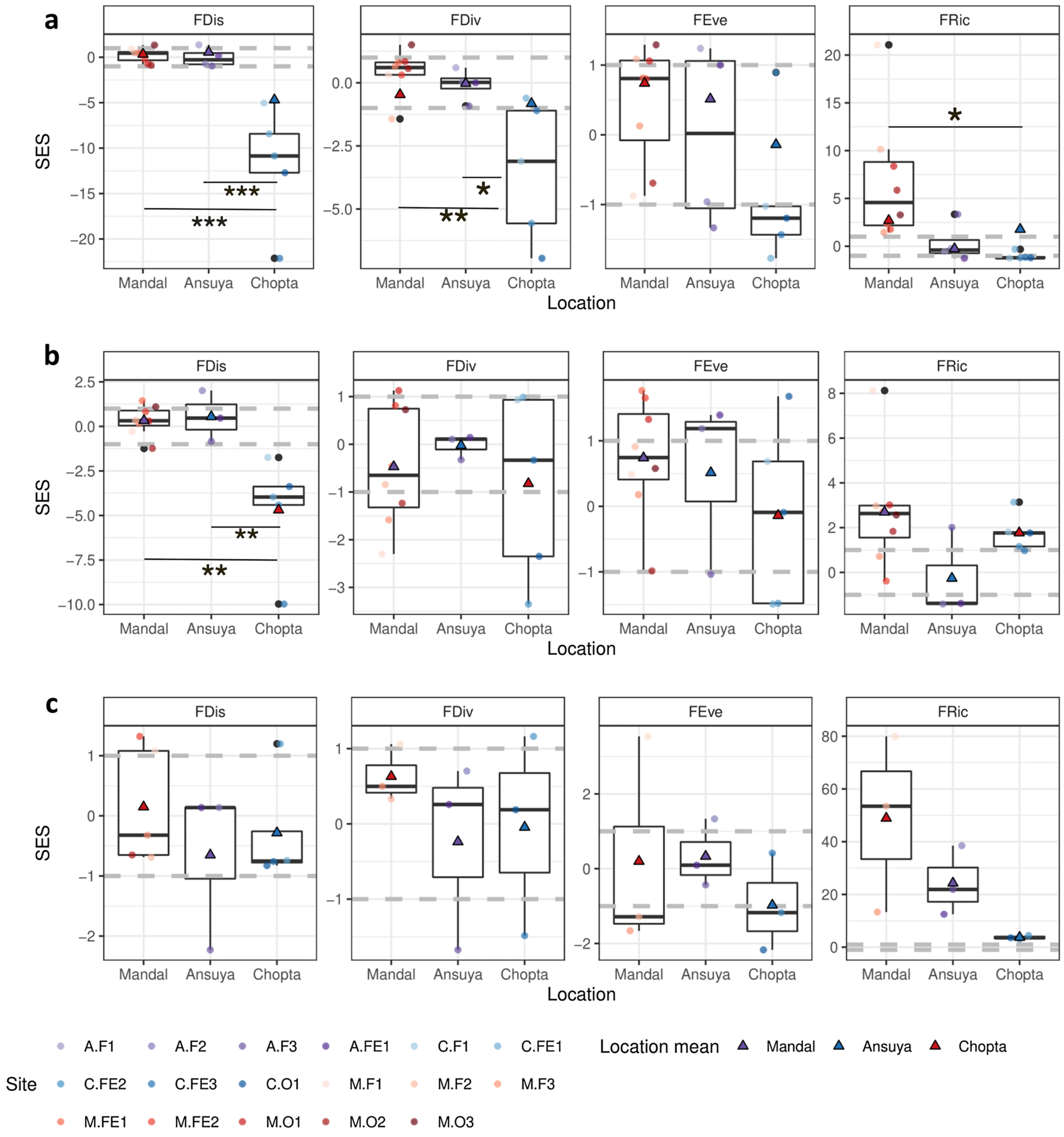

Figure 4. SES values of different elevational communities for corresponding FD indices obtained from constrained randomizations with 999 iterations; measured using (**a**) acoustic detections as relative abundance for all species/sonotypes, (**b**) acoustic detections as relative abundance excluding rhinolophid bats, and (**c**) mistnet captures as relative abundance for all species/sonotypes. |SES| = 1 and above are significantly different from the null model (for more details please see "Methods" section). Sampling points are denoted by dots and mean FD values by triangles within the boxplots. Lines connecting different elevations and *represent elevations with significantly different means as assessed from Tukey's HSD test. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

A global meta-analysis of the elevational distribution of bats (that did not include data from the Himalaya) predicted that water availability and temperature drive elevational species richness patterns of bats[3]. Therefore, species richness declines linearly in mountains with wet and warm bases[3]. We uncover a trend consistent with this prediction (Fig. 3a), paralleling other tropical elevational gradients e.g.: Manu National Park in Peru[4], Mount Kilimanjaro in Tanzania[56], Mount Nimba in tropical West Africa[26] and eastern Brazilian gradients[27,57]. However, it must be noted that our gradient starts from 1500 m asl instead of the foothills. Due to the complex topology of the Himalaya, it is hard to locate a single contiguous gradient from the foothills to above 3000 m.

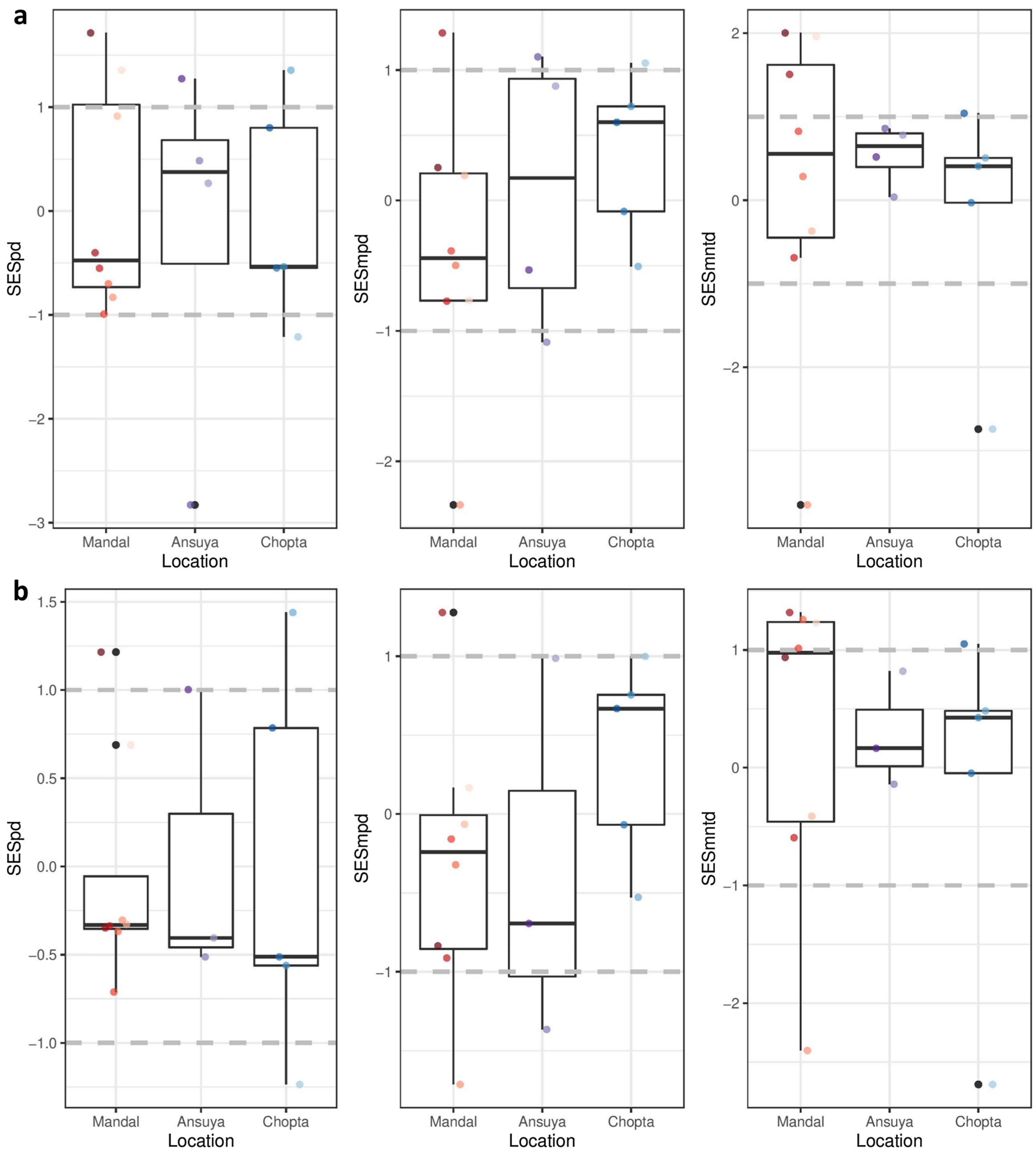

Figure 5. SES values of different elevational communities for corresponding PD indices obtained from constrained randomizations with 999 iterations; measured using acoustic detections as relative abundance for all species/sonotypes. (**a**) For all species, (**b**) for species excluding rhinolophids. |SES| = 1 and above are significantly different from the null model (for more details on SES see "Methods" section).

Therefore, our data do not adequately resolve whether SR declines monotonically across the full elevational range or exhibits a decline from a mid-elevation peak at 1500 m. The decline in Simpson's Diversity Index was non-linear (Fig. 3b) with elevation, such that it did not differ significantly between Chopta and Ansuya. This finding indicates that the community at Mandal had a few dominant species, whereas at higher elevations the dominance was less pronounced.

The observed decrease in species richness with elevation is likely due to the synergistic effect of temperature on habitat and prey availability. Indeed, the elevational gradient is characterized by a strong temperature gradient with the average minimum summer temperature at Mandal (1500 m asl) being 15 °C, whereas that at Tungnath (3500 m asl) being ~ 1 °C, with frequent sleet and hailstorms. The dominant forest types and the density of vegetation also change gradually across the gradient, ultimately transforming into alpine meadows at Tungnath. This change in habitat structure potentially influences bat roost availability[58], as well as prey density and diversity.

We observed functional underdispersion at Chopta, which is in line with our initial prediction for high-elevation communities (Fig. 4a). Functional underdispersion in high elevation communities is observed in bats in West Africa[26] and in the Atlantic Forest of Brazil[27], tropical bird communities[17,18] and plants in the western Himalaya[29]. This suggests that environmental filtering may be a driving force in structuring high elevation communities of diverse taxa in mountains, at least, in the tropical and subtropical belt. By contrast, at the lowest elevation in Mandal, we observed greater than expected FRic but FDis did not deviate from the null expectation. This pattern is consistent with the idea of niche packing, wherein an increase in species richness leads to crowding of the niche space, either due to greater specialisation, or greater overlap among the niches of community members. Niche packing is a dominant mechanism in structuring bird communities of high diversity[59,60].

The variation of PD with elevation was not significantly different from the null expectation. Recent research on tropical montane bird communities also indicates that phylogenetic structure is a poor proxy for functional diversity[18]. Studies on Himalayan birds show that much of the contemporary diversity is a result of dispersal of Southeast Asian lineages into the Himalaya since the Miocene[61,62]. During the Pliocene to Pleistocene periods, congeneric lineages organised themselves in parapatry along elevational gradients[62]. Such a colonization pattern may result in phylogenetic nestedness, and our findings may thus be reflective of past colonization processes and the resultant nestedness. Future research may focus on investigating the colonization patterns of Himalayan bats and how these affect beta diversity of FD and PD across elevations.

Previous studies that relied solely on presence data report only functional and phylogenetic dispersion measures that do not take relative abundances into account. Because we collected abundance data, we measured abundance-weighted functional dispersion, divergence and evenness (in addition to richness). Chopta has lower FDiv and FDis than expected under the null model. Its FDiv and FDis are also significantly lower than at other locations. Lower FEve implies that the abundance distribution across sonotypes is not uniform. Sonotypes such as MS, AHN and EH are more common than others at Chopta. Additionally, these common sonotypes have intermediate trait values leading to low FDiv (Fig. S3). Mandal and Ansuya have a sizeable diversity of forest-dwelling bats. The large variation in FEve at these locations is perhaps an artefact of low detection probability in forests in comparison to edge and open habitats (Fig. S2). Although FDis is most widely used to test hypotheses related to community assembly processes, data on FDiv and FEve are important in understanding alpha functional diversity which may inform local conservation measures.

Rhinolophid bats are absent at high elevations, but diverse at low elevations, with four species detected at Mandal. FD indices are calculated using distances in the standardised multidimensional trait space of the global community (i.e. across all elevations). Hence, the removal of species inevitably changes the indices for each elevational community. By removing rhinolophids from the analysis (Fig. 4b), the global trait space became smaller in its volume (richness) leading to significantly higher FRic at Chopta. The shrinking of the global trait space also altered the relative abundance distribution across all species (*cf.* FEve) and the intermediate trait values (*cf.* FDiv). Conversely, the trends in PD indices remained statistically similar to the null expectation even after excluding rhinolophids (Fig. 5b). This implies that, in terms of phylogenetic position, species are lost randomly across the elevational gradient such that phylogenetic dispersion is maintained even at high elevations. We thereby infer that the decline in FD is strongly governed by the absence of four rhinolophid bats at high elevations, which occupy peripheral regions of the trait space (Fig. S3), in addition to belonging to the same genus. This high variation in trait space is usually driven by large differences in call frequencies of sympatric rhinolophids[63] which also exist in the four species in our dataset (Table 1, Fig. S3). The non-rhinolophid bats in the community (of the families Vespertilionidae and Miniopteridae), although more diverse in terms of species, do not exert major effects on elevational patterns owing to their similarity in functional trait space, as well as their presence across the elevational gradient.

A limitation of our FD and PD results that requires highlighting is the potential recounting of individuals across sampling sites and locations. The relative abundances of sonotypes in our calculation were based on acoustic detections and it is highly probable that the same individuals were re-recorded across sites. While this bias cannot be eliminated, we employed a conservative measure of relative abundance using the 'Acoustic Activity Index' framework[37] (as described in the "Methods" section). The FD and PD calculations employ trait values and phylogenetic composition, which do not change with relative abundance when measured unweighted. The abundance-weighted group centroids may shift, but are unlikely to drastically affect the observed patterns.

Our study—a first on any mammalian taxon from the Himalaya—joins a growing body of literature quantifying community structure in montane ecosystems. Our findings are consistent with previous work on diverse taxa, with an elevational decline in species richness, and functional under dispersion in high elevation communities. These results suggest that environmental filtering likely plays a role in structuring high elevation communities. We attribute the loss of functional diversity at high elevations to the absence of four closely-related bat species with very divergent trait values belonging to the family Rhinolophidae. These changes in functional diversity across elevations are independent of phylogenetic diversity, thereby suggesting that phylogenetic diversity cannot always be used as a substitute for functional diversity. Taken together, our data provide a comprehensive understanding of the establishment of understudied tropical and montane bat communities, based on first-hand data collected in the field. This study also opens up avenues for future research on exploring (a) the role of colonization patterns in shaping community dynamics, and (b) the mechanisms of niche partitioning in communities with high functional richness. Most importantly, these data hold relevance in understanding the impacts of range-shifts of vertebrate communities, driven by climate change. Studies on the speciation of tropical montane vertebrates show that many species are adapted to live within a narrow range of temperatures[64]. Not surprisingly, tropical species are shifting their elevational ranges faster than temperate species. As the Himalaya is warming faster than the global average[32], our results serve as an important baseline in assessing changes in bat diversity with time and in predicting potential interspecific competition in the future.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

R.C., C.C.V., A.K. and V.R. conceived the ideas and generated funds. R.C. and R.M. conducted fieldwork and generated the data. R.C., R.M., A.K. and V.R. analysed the data. R.M. and A.K. prepared Fig. S4, and V.R. prepared Figs. 3, 4 and 5 and Supplementary Figs. S1 and S2. C.C.V., A.K. and V.R. supervised the research. R.C. led the writing with inputs from all co-authors. All authors reviewed the manuscript.

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Competing interests

The authors declare no competing interests.

Additional information

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Chapter 2

Increasing species richness along elevational gradients is associated with niche packing in bat assemblages

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RESEARCH ARTICLE

Increasing species richness along elevational gradients is associated with niche packing in bat assemblages

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Abstract

1. The change in species richness along elevational gradients is a well-known pattern in nature. Niche theory predicts that increasing species richness in assemblages can either lead to denser packing of niche space ('niche packing') or an expansion into its novel regions ('niche expansion'). Traditionally, these scenarios have been studied using functional traits but stable isotopes provide advantages such as identifying the degree of resource specialisation, or niche partitioning among functionally similar species.
2. In this study, we evaluate the relevance of niche packing versus niche expansion by investigating stable carbon and nitrogen isotopic niche width and overlap among 23 bat species from six functional groups across a 1500 m elevational gradient in the Himalaya.
3. Our results suggest that an increase in species richness in the low elevation is accompanied by small niche width with high overlap, whereas the high elevation assemblage shows large niche width with low overlap among functional group members. At the functional group level, edge-space foraging, trawling, and active gleaning bats have the highest niche width while passive gleaning bats that are only found in high elevations are isotopic specialists showing low overlap with other groups. Edge and open-space foraging bats showed idiosyncratic changes in niche width across elevations. We also find that the niches of rhinolophid bats overlap with edge-space and open-space foraging bats despite their unique functional traits.
4. These results support the idea that at low elevations high species richness is associated with niche packing while at high elevations strong niche partitioning prevails in dynamic and resource-poor environments. We conclude that although high elevation animal assemblages are often 'functionally underdispersed', that is show homogenous functional traits, our approach based on stable isotopes demonstrates niche partitioning among such functionally similar species.

KEYWORDS
bats, elevational gradients, Himalaya, niche expansion, niche packing, stable isotopes

1 | INTRODUCTION

Latitudinal and elevational gradients in diversity are widespread patterns across taxa and geographical regions. Typically, species richness is highest at low latitudes and elevations (McCain & Grytnes, 2010). Macarthur (1965) argued that two contrasting patterns of niche occupancy may help explain these changes in species richness (Pellissier et al., 2018; Pigot et al., 2016), wherein 'niche' is defined as an *n*-dimensional hypervolume comprising all abiotic and biotic elements that allow a species to exist (Hutchinson, 1957). Under Macarthur's first model called 'niche expansion', an increase in species richness is associated with species occupying novel regions of the niche space of the assemblage. In contrast, the 'niche packing' model suggests that an increase in species richness leads to denser packing of the assemblage niche space due to finer specialisation or increased overlap (Macarthur, 1965; Pagani-Núñez et al., 2019; Pellissier et al., 2018; Pigot et al., 2016). There is poor understanding of which of these two mechanisms structures assemblages of various taxa across latitudinal and elevational gradients.

A global model for birds predicts that niche packing with high niche overlap occurs in areas of high net primary productivity (Pellissier et al., 2018). This observation is supported in local-scale studies along elevational gradients where niche packing is seen at low elevations (Pigot et al., 2016; Schumm et al., 2020). Old (basal) or early colonising lineages diversify and expand the community niche space while new (derived) lineages get packed within the 'boundaries' created by old lineages (Hughes et al., 2021; Tanentzap et al., 2015). The most common method of investigating niche occupancy is to measure how the diversity of functional traits in communities changes with species richness across the gradient of interest (Pellissier et al., 2018; Pigot et al., 2016). Functional traits such as morphological, physiological, and life history traits of organisms are correlated with their functions in the ecosystem (Nock et al., 2016). With the easy availability of comprehensive trait datasets like Elton Traits (Wilman et al., 2014) and AVONET (Tobias et al., 2022), the applications of trait-based ecology will undoubtedly grow. However, functional traits do not always accurately delineate feeding guilds at finer spatial scales, nor do they reliably predict specialisation on food resources (Pigot et al., 2016; Weiss & Ray, 2019). These shortcomings can be overcome by using dietary tracers like stable isotopes.

Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) in animal tissues are reliable proxies for an animal's niche breadth (Bearhop et al., 2004; Ben-David & Flaherty, 2012). δ^{13}C and δ^{15}N values vary predictably across photosynthetic pathways, habitats, and trophic levels. 'Isotopic niche' is then defined as the space that an animal occupies within the space determined by these isotopic values (Martínez Del Rio et al., 2009; Newsome et al., 2007). The isotopic niche differs from dietary niche because it is measured by the diversity of isotopically unique resources rather than taxonomically unique prey species. For example, an isotopic specialist may not necessarily be a dietary specialist because it may feed on the same mixture of isotopically distinct resources (as opposed to the same set of prey species). Also, if an animal specialises on prey items with widely divergent isotopic compositions, it will show up as an isotopic generalist (Martínez Del Rio et al., 2009; Newsome et al., 2007).

Stable isotope analysis is of great potential for assessing the niche breadth and overlap of elusive animals like bats. δ^{13}C values vary between C_3 versus C_4, aquatic versus terrestrial plants and so on (Schulting, 1998). Therefore, they indicate the basal nutrition sources of the food chain. δ^{15}N values increase with trophic level. Together, these two isotopes tell us which food chains different bats feed on and how they partition resources across food chains and trophic levels. Bat assemblages are extremely diverse (Kingston et al., 2003; Rex et al., 2008), and it is impossible to ascertain the variety of insect prey species that they consume from direct observations or conventional pellet analysis. For example, species that were conventionally thought to be solely frugivorous or insectivorous seem to be omnivorous based on isotopic data (Oelbaum et al., 2019; Rex et al., 2015). Further, stable isotope analysis includes regions of the trophic niche not covered by conventional diet analysis. For example, forest bats that forage at different vegetation strata, such as ground or canopy level, can be distinctly separated using stable isotope analysis but not based on conventional diet analysis (Voigt et al., 2015). Previous studies comparing regions of high and low bat diversity show that there is high intra- and inter-guild overlap in isotopic niches in areas of high diversity (Monadjem et al., 2018; Oelbaum et al., 2019). Bats belonging to the open-space foraging guild typically show large niches with high intra-guild overlap (Ruadreo et al., 2019; Voigt et al., 2015). However, studies also point to niche partitioning in interesting ways. For example, Neotropical fruit-eating bats show vertical stratification in foraging habitats (Rex et al., 2011) and two European congeneric species in their sympatric range feed on insects belonging to different trophic levels (Siemers et al., 2011). Only one study has compared niche partitioning between two sites of high and low diversity in Africa and observed niche packing in the high diversity site with presumably higher productivity (Monadjem et al., 2018). We do not know if these patterns hold across geographical regions, species pools, elevational or anthropogenic gradients.

In this study, we used stable carbon and nitrogen isotopes to measure the isotopic niches of bat functional groups and communities across a 1500 m elevational gradient in Kedarnath Wildlife Sanctuary (Kedarnath WLS) in western Himalaya. Previous research along this gradient has shown that species richness declines at the highest elevation, but functional dispersion is lower than expected both at the highest and the lowest elevations indicating dense packing of the functional trait space (Chakravarty et al., 2021). The bats in Kedarnath WLS can be classified into seven functional groups (Denzinger et al., 2016), as follows: (a) Edge-space aerial foragers ('edge-space foraging bats'), (b) Edge-space trawling foragers ('trawling bats'), (c) Fruit-eaters, (d) Narrow-space active gleaning foragers ('active gleaning bats'), (e) Narrow-space flutter detecting foragers ('flutter-detecting bats'), (f) Narrow-space passive gleaning foragers ('passive gleaning bats') and (g) Open space aerial foragers ('open-space foraging bats') (described in Table 1). With respect to isotopic niches of the functional groups, we predicted that (a) edge and

TABLE 1 Detailed classification of our study species into functional groups following Denzinger et al. (2016). Samples sizes of each species and their functional groups are mentioned for low, intermediate, and high elevations. Functional groups with $n < 3$ (highlighted with asterisks) were removed from the calculations of SEAb and niche overlap.

Functional group	Species	Low elevation	Intermediate elevation	High elevation
Edge-space aerial foragers (Edge-space foraging bats)	(i) *Arielulus circumdatus*	1	0	1
	(i) *Barbastella darjelingensis*	2	0	1
	(i) *Hypsugo affinis*	1	0	0
	(i) *Miniopterus fuliginosus*	2	0	0
	(i) *Mirostrellus joffrei*	19	1	0
	(i) *Myotis muricola*	3	3	3
	(i) *Myotis sicarius*	1	0	0
	(i) *Myotis siligorensis*	1	0	0
	(i) *Pipistrellus* cf. *ceylonicus*	37	3	1
	(i) *Submyotodon caliginosus*	0	0	1
		n = 67	**n = 7**	**n = 7**
Edge-space trawling foragers (Trawling bats)	(i) *Myotis longipes*	12	0	0
Fruit-eaters	(i) *Sphaerias blanfordi*	0	1	1
		n = 0	**n = 1***	**n = 1***
Narrow-space active gleaning foragers (Active-gleaning bats)	(i) *Murina aurata*	2	1	2
	(i) *Murina huttoni*	0	1	0
		n = 2*	**n = 2***	**n = 2***
Narrow-space flutter detecting foragers (Flutter-detecting bats)	(i) *Rhinolophus lepidus*	5	1	0
	(i) *Rhinolophus luctus*	2	0	0
	(i) *Rhinolophus pearsonii*	1	4	0
	(i) *Rhinolophus sinicus*	2	3	0
		n = 10	**n = 8**	**n = 0**
Narrow-space passive gleaning foragers (Passive-gleaning bats)	(i) *Plecotus homochrous*	0	2	11
	(i) *Plecotus wardi*	0	0	9
		n = 0	**n = 2***	**n = 20**
Open-space aerial foragers (Open-space foraging bats)	(i) *Eptesicus pachyomus* (formerly *E. serotinus*)	3	0	0
	(i) *Nyctalus leisleri*	12	9	2
	(i) *Nyctalus* cf. *noctula*	0	1	0
	(i) *Tadarida* cf. *teniotis*	1	0	0
		n = 16	**n = 10**	**n = 2***

open-space foraging bats would occupy the central portion of the assemblage niche space, and have the broadest, yet most overlapping isotopic niches (cf. Ruadreo et al., 2019; Voigt et al., 2015); (b) trawling, passive and active gleaning bats would occupy different peripheral portions of the assemblage niche space and have narrow niche widths in concordance with their unique feeding behaviours; (c) the extreme trait differences of flutter-detecting bats would not result in a unique isotopic niche (cf. Voigt et al., 2015). Based on previous studies (cf. Monadjem et al., 2018; Pellissier et al., 2018; Pigot et al., 2016), we predicted that (d.i) we would observe niche packing at the low elevation, species-rich site due to its presumably high productivity. However, the lowest elevation had the highest number of species of edge-space foraging bats, and trawling bats were also exclusively found there. Both of these functional groups are predicted to have large niche width, and therefore (d.ii) isotopic niche expansion could also be seen at low elevations whereas, (e) low species richness at the highest elevation would be accompanied by small niche width with or without high overlap (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted this study in Kedarnath Wildlife Sanctuary (30°25′–30°41′N, 78°55′–79°22′E) situated in the state of Uttarakhand in the western Himalaya of India (see map of study site at: https://www.nature.com/articles/s41598-021-01939-3/figures/1).

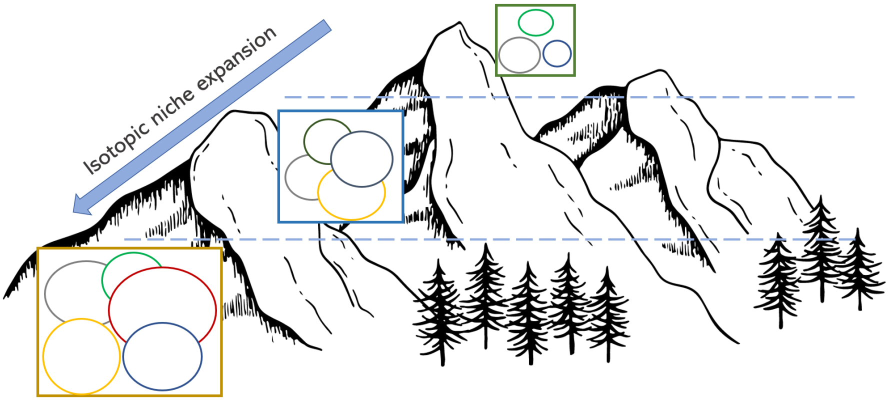

FIGURE 1 Schematic representation of our hypotheses. Each box represents an assemblage of bats and the ellipses represent the isotopic niches of its constituent bat functional groups. We predict that an expansion of isotopic niches is witnessed as species and functional group richness increase towards the lowest elevation. Vector art freely downloaded from https://www.canva.com/.

The sanctuary covers an elevational gradient from 1400 m to 4000 m above sea level (a.s.l.) with changes in the dominant vegetation. At low elevations, the forest is classified as 'Himalayan moist temperate' and is dominated by *Quercus* spp., while sub-alpine forests above 2800 m are dominated by *Rhododendron* spp. The treeline ends above 3000 m leading into alpine meadows (Champion & Seth, 1968). The sanctuary harbours 28 species of bats (Chakravarty et al., 2020, 2021).

2.2 | Field work

We sampled at the following four locations across the elevational gradient: Mandal (1500–1800 m), Ansuya (2000–2200 m), Chopta (2700–3000 m) and Tungnath (3300–3700 m) but we had to exclude Tungnath from the analysis due to low sample sizes. The former three elevations are subsequently referred to as 'low' (Mandal), 'intermediate' (Ansuya) and 'high' (Chopta). Sampling was conducted between late March and mid-May in 2018, 2019 and 2021 coinciding with summer in the Himalaya, and preceding the onset of the monsoon season (https://mausam.imd.gov.in/imd_latest/contents/monsoon.php). We caught bats using thin nylon and monofilament mistnets of 4, 6, and 9 m length, 16 × 16 and 19 × 19 mesh sizes (Ecotone GOC) for 4 h following dusk (starting between 18:30 h in early summer and 19:30 h in late summer). The captured bats were identified to species level following published studies and keys (Bates & Harrison, 1997; Chakravarty et al., 2020; Srinivasulu et al., 2010). From each bat, we collected two wing biopsies (one from each wing at roughly the same position) using a sterilised biopsy punch of 4 mm diameter. We dry stored the wing biopsies in vials containing silica gel crystals. The wing tissue samples were used for stable carbon and nitrogen isotope analysis to investigate isotopic niches of our study species. After collecting these samples, we released the bats at their site of capture.

In order to characterise the basal stable carbon and nitrogen isotope ratios at different elevations we collected plant and insect samples for stable isotope analysis. We collected one leaf each from 20 individual *Quercus* spp. and 20 individual *Rhododendron* spp. (the dominant tree species across the elevational gradient) at each elevation (low, intermediate, and high). Using a custom-made ultraviolet light-based trap, we collected 21, 21, and 17 nocturnal insects (predominantly Lepidoptera) at low, intermediate, and high elevation respectively.

We handled all live bats following the guidelines of the American Society of Mammalogists (Sikes, 2016). Fieldwork was further approved by the Internal Committee for Ethics and Animal Welfare, Institute for Zoo and Wildlife Research (approval no. 2018-06-01), and conducted under a permit issued by the Uttarakhand State Forest Department, Government of India (permit no. 2261/5-6). Wing tissue samples were exported from India to Germany following the approval of the National Biodiversity Authority, Government of India in accordance with the Nagoya Protocol (permit no. Form B/79/18/18-19/5041).

2.3 | Laboratory analysis

We analysed the wing tissue samples at the stable isotope facility of the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. We put the wing tissue samples into 1:2 methanol-trichloromethane solution for 24 h to clean surface contaminants. After 24 h, the solution was drained off and the tissue samples were dried in an oven at 50°C for more than 48 h. We then loaded the samples into tin capsules (IVA Analysentechnik) and folded them tightly. Due to the size and wing density differences of the different bat species, our sample weights ranged from 100 to 580 mg. The samples were measured using an isotope ratio mass spectrometer (IRMS, Delta V Advantage; Thermo Fisher) in continuous flow coupled to an elemental analyser (Flash EA 1112 Series; Thermo Fisher) via a Conflo III device (Thermo Fisher). Isotope ratios were expressed using the delta notation (δ^{13}C and δ^{15}N) as parts per mille deviations from the international standards Vienna Pee Dee Belemnite (V-PDB) and atmospheric nitrogen (Air N_2) respectively (given by the equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$). Samples were measured together with in-house protein standards of tyrosine (δ^{13}C = −24.0‰, δ^{15}N = 4.4‰) and leucine (δ^{13}C = −30.3‰, δ^{15}N = 11.0‰) for drift and calibration purposes.

We punched the leaf samples using a sterilised hole punch. The punches were collected in vials and powdered using a tissue homogeniser (Next Advance). We packed ~1 mg of powdered plants for carbon and nitrogen analysis. Insect samples were subjected to the same washing and drying procedure as wing tissue samples, following which they were packed into tin capsules. IRMS facility at the Indian Institute of Science Education and Research Pune was used for the $\delta^{13}C$ and $\delta^{15}N$ measurements of the leaf and insect samples. The IRMS (Isoprime 100; Isoprime, Elementar) attached to Vario Pyro cube elemental analyser (Elementar) was used for this. The repeatability and accuracy were assessed by analysing laboratory standards: sucrose I ($\delta^{13}C$ = −12.1‰), sucrose II ($\delta^{13}C$ = −26.7‰), sulfanilamide ($\delta^{13}C$ = −27.8‰, $\delta^{15}N$ = −6.3‰) and ammonium sulfate (USGS 25) ($\delta^{15}N$ = −30.41‰). Insect samples were subjected to the same washing and drying procedure as wing tissue samples, following which they were measured in the same process as described above. The accuracy of the measurements was the same as described for the other laboratory.

2.4 | Statistical analysis

We tested differences in baseline $\delta^{13}C$ and $\delta^{15}N$ values (plant and insect samples) in assemblages across elevations by performing a permutational ($n = 999$) multivariate analysis of variance (perMANOVA) using the 'adonis' function of 'VEGAN' R package (Oksanen et al., 2019). The perMANOVA was performed using Gower distances between isotopic values (continuous variable) and elevational assemblage (categorical variable).

We pooled bat species into the seven functional groups as described in Section 1 (Denzinger et al., 2016). The group membership of our study species and their sample sizes are detailed in Table 1. Fruit-eating bats had to be removed from all analyses as we only caught one individual each at intermediate and high elevations. Active gleaning bats could only be used for calculating functional group niche width across elevations.

We estimated functional group niche width, by computing Bayesian standard ellipse areas (SEAb) in two ways: (i) for each functional group within each elevation and (ii) across elevations, by pooling the data per functional group together (so as to increase the sample size). SEAb were estimated with the R package SIBER ver. 2.1.6 (Jackson et al., 2011). We tested whether elevation affects each functional group niche width differently, by fitting a linear model (normal distribution and identity link) with the functional group niche width as response and elevation, functional group identity and an interaction among them as predictors. We tested the robustness of our findings with respect to the sample size by subsampling the data to four samples per functional group at each elevation.

We calculated assemblage niche width as distance to centroid of the convex polygon using Bayesian Layman metrics (Layman et al., 2012) implemented in the SIBER package. Additionally, we measured nearest-neighbour distance as an estimate of 'packing' within the niche space. We calculated these metrics with 50 iterations and assessed the difference across elevational communities using a general linear model (GLM) and post-hoc Tukey's Honest Significance Difference (HSD) test. We chose to use 50 iterations because a higher number would have strongly inflated the sample sizes, invariably causing the differences to be significant. The bare minimum to run these analyses are three samples per functional group at any given location. Therefore, we had to exclude active gleaning bats and fruit bats from this analysis.

We assessed the statistical significance of niche overlap with elevation using a linear mixed effects model (normal distribution and identity link), with response being niche overlap per functional group, and predictors being elevation, functional group identity, and their interaction. We included a combination of functional groups for which the overlap was calculated as random intercept in the model, so as to account for variation in niche overlap among different functional groups. The model was fitted to the data generated with 40 permutations of niche overlap probabilities (calculated using the R package NICHEROVER ver. 1.10; Swanson et al., 2015) between all functional group combinations at each elevation. We chose 40 iterations so as to not inflate the significance merely due to a higher sample size. We then used likelihood ratio test (LRT) to test for the effect of elevation on niche overlap. While calculating niche overlap of functional groups at each elevation, we had to exclude active gleaning bats from the low elevation assemblage, fruit bats, active and passive gleaning bats from intermediate elevation assemblage, and fruit bats, active gleaning, and open-space foraging bats from high elevation assemblage due to low sample sizes. Since population densities of bats from these functional groups were low, we did not expect their presence or absence to strongly affect the niche packing of communities.

3 | RESULTS

When comparing the baseline $\delta^{13}C$ and $\delta^{15}N$ values from plant samples collected across the elevational gradient, we observed significant differences in the dispersion of plant isotopic values between low and high elevations (Tukey's HSD $p < 0.01$) (Figure S1, Table S1). Such differences were not seen in the samples of Lepidopteran insects collected at the three elevational communities (Tukey's HSD, $p = 0.94$) (Figure S2).

Isotopic biplots of raw $\delta^{13}C$ and $\delta^{15}N$ values (Figure 2) provide a visual estimate of niche width and niche overlap in bat communities at different elevations. The bat assemblage at high elevation had significantly higher isotopic niche width (measured as distance to centroid) and nearest-neighbour distance than at intermediate and high elevations (Figure 3; Tukey's HSD $p < 0.01$). The niche width and nearest-neighbour distance of bat assemblages at low and intermediate elevations did not differ significantly (Figure 3; Tukey's HSD $p = 0.88$). At the functional group level, edge-space foraging, trawling and active gleaning bats had the highest SEAb (calculated across elevations) and the differences among them were not significant (Figure 4; Tukey's HSD $p > 0.5$). SEAb in the other three functional groups significantly decreased in the following order: open-space foraging > flutter-detecting > passive gleaning bats (Figure 4; Tukey's HSD $p < 0.05$). We found a significant interaction between elevation and functional group

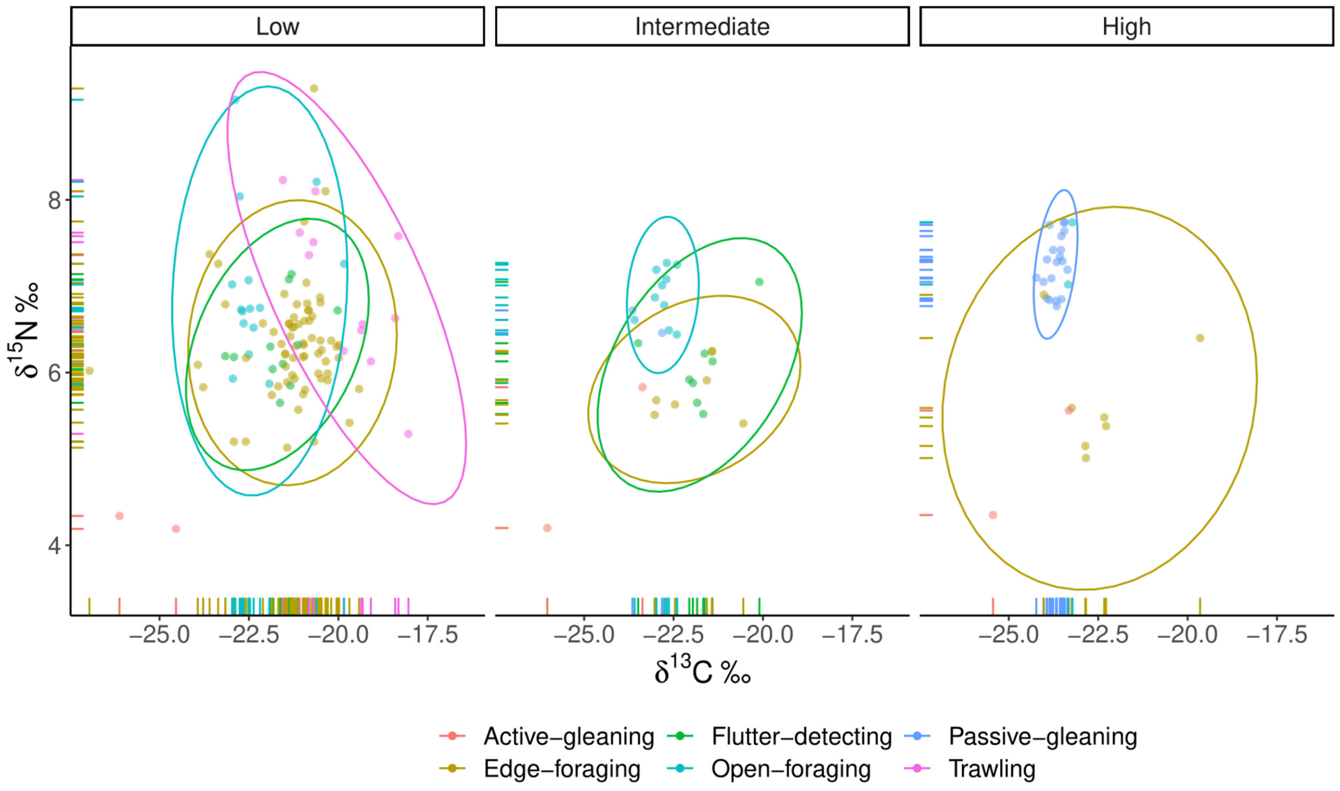

FIGURE 2 Isotopic biplots of raw $\delta^{13}C$ and $\delta^{15}N$ values (‰) plotted for bat assemblages across elevations. Ticks along the margins show the density of data points per functional group. Standard ellipse areas are plotted for different functional groups as indicated in the legend.

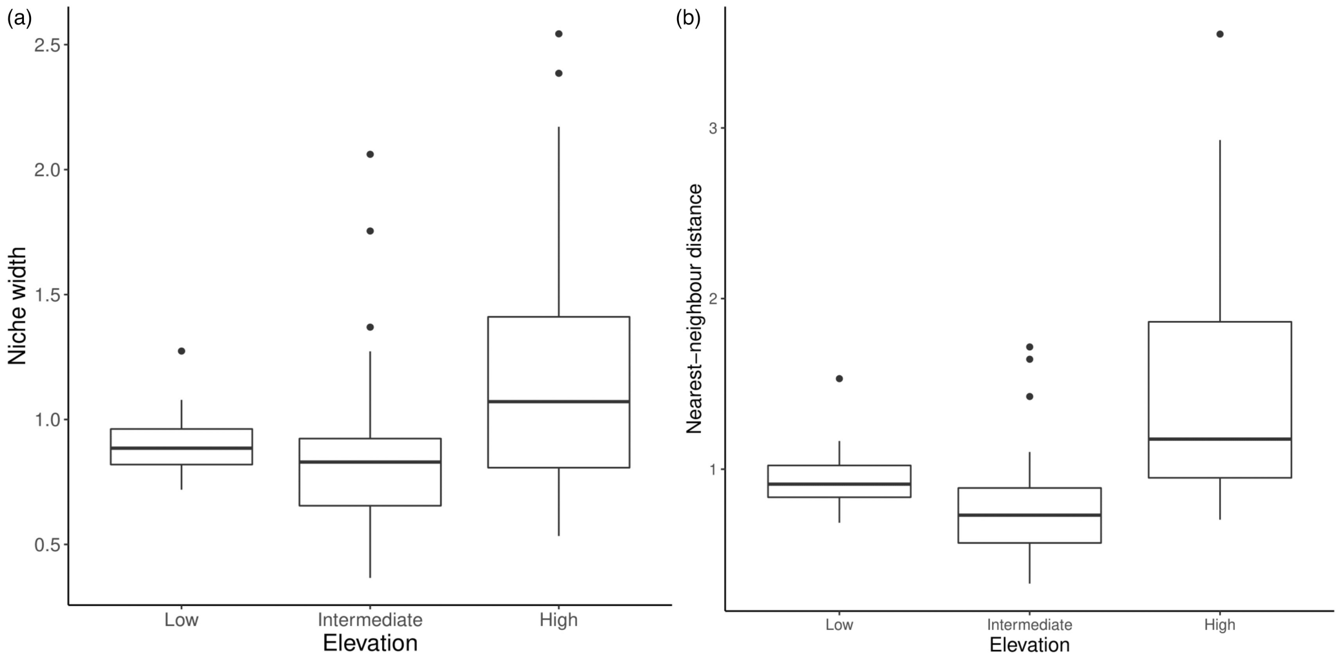

FIGURE 3 Variation in (a) isotopic niche width (measured as distance to centroid of the assemblage niche space), and (b) Nearest-neighbour distance among functional groups in bat assemblages across elevations. The bold horizontal line represents the median, the box depicts the inter-quartile range, and the whiskers show the lower and upper quartiles. Points beyond the whiskers are outliers.

niche width ($F = 8.4$, df = 2, $p < 0.001$; Figure 5), meaning that the niche width of specific functional groups changed across elevation. Our results were qualitatively similar with a reduced sample size of four individuals per functional group per elevation (Figure S3).

Isotopic niche overlap probability was high among bat species belonging to the functional groups of edge-space foraging, open-space foraging and flutter-detecting bats both across elevations and at each specific elevation (Figure 2; Figure S4). This overlap

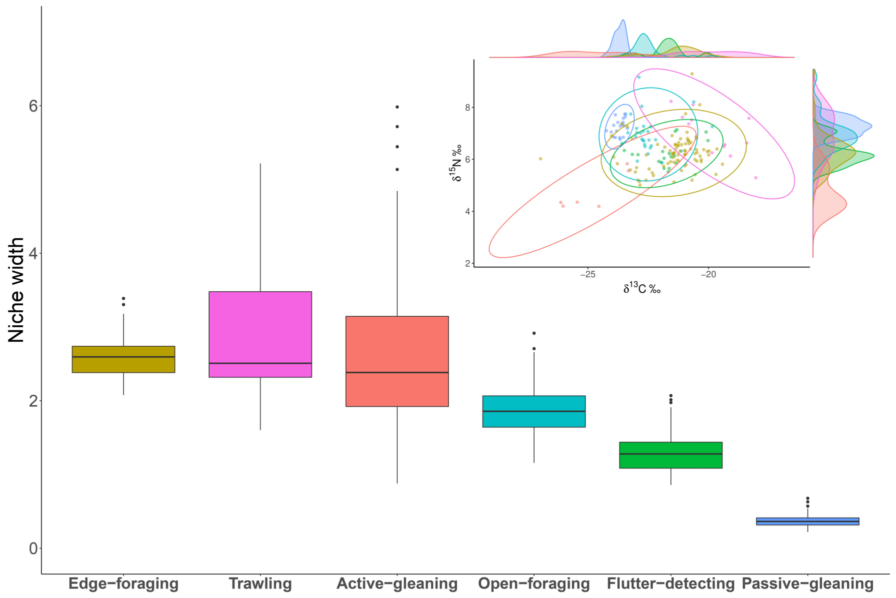

FIGURE 4 Isotopic niche width (measured as Bayesian standardised ellipse areas) of functional groups calculated across elevations and plotted from left to right according to decreasing median values. The bold horizontal line represents the median, the box depicts the inter-quartile range, and the whiskers show the lower and upper quartiles. Points beyond the whiskers are outliers. The inset shows the raw δ^{13}C and δ^{15}N values (‰) and their distributions along the δ^{13}C and δ^{15}N axes. Colours in the inset correspond to colours of functional groups in the boxplot.

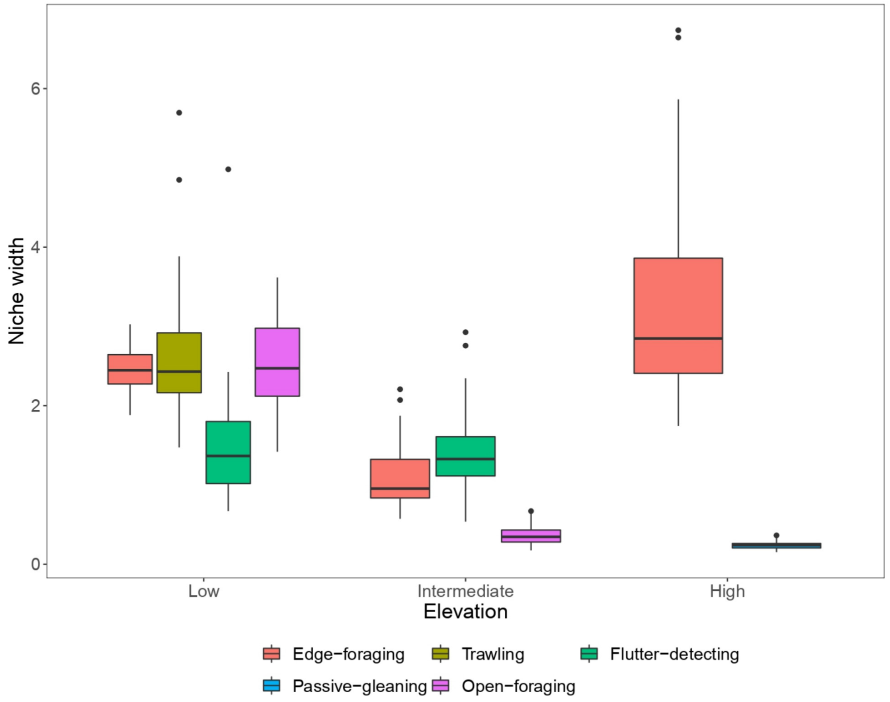

FIGURE 5 Change in niche width (measured as SEAb) of functional groups with elevation.

was predominantly along the δ^{15}N scale and not along the δ^{13}C scale (Figure 4). Trawling, passive gleaning and active gleaning bats occupied peripheral portions of the isotopic niche space of assemblages and showed low overlap with other functional groups (Figures 2 and 4; Figure S4). At low elevation, the mean overlap probability between all functional groups (except for trawling bats) was above 50% (Figure 2; Table S2). At intermediate elevation, we observed an average niche overlap probability of 68% between edge-space foraging and flutter-detecting bats, but only 30% and 8.5% between open-space foraging bats with flutter-detecting and edge-space foraging bats respectively (Figure 2; Table S3). At high elevation, we estimated an average overlap probability of 28% between passive gleaning bats and edge-space foraging bats, the two functional groups for which we had sufficient samples (Figure 2; Table S4). Our mixed effects model showed that niche overlap was significantly higher at the low elevation (mean ± SE estimate: beta = 0.39 ± 0.19) compared to the intermediate and high elevations (X^2 = 323.22, df = 2, $p < 0.01$; estimates ± SE for intermediate and high elevations are, respectively: 0.01 ± 0.19 and 0.17 ± 0.17).

4 | DISCUSSION

We investigated isotopic niche width of bat assemblages and niche overlap of bat functional groups across a 1500 m elevational gradient with decreasing species richness at higher elevations. According to our predictions, we observed niche packing at the species-rich low elevation with high niche overlap among functional groups. In contrast, the species-poor highest elevation assemblage showed large niche width with low overlap among functional groups. At the functional group level, we predicted large niche width for edge- and open-space foragers, and peripheral niches for all other functional groups. We obtained mixed results.

4.1 | Niche packing versus expansion

With increasing species richness at low elevation, we observed a reduction in bat assemblage niche width and a significant increase in niche overlap indicating niche packing. Niche packing in our community occurs because within assemblages the 'boundaries' of the niche space are made up of functional groups that are common to all elevations. The species that are added in the low elevation assemblage get densely packed within this boundary. This packing can largely be attributed to the wide and overlapping isotopic niches of edge-space foraging and flutter-detecting bats at low and intermediate elevations. Global and regional studies on birds using functional traits demonstrate that niche packing prevails in areas of high productivity such as low elevations and latitudes (Pellissier et al., 2018; Pigot et al., 2016). The only other study comparing isotopic niche partitioning in bat assemblages of low and high species richness found niche packing with high niche overlap in insectivorous bat assemblages across a latitudinal gradient in Africa (Monadjem et al., 2018). Our results are consistent with these observations and also align with previous research using functional traits along the same elevational gradient (Chakravarty et al., 2021). At the presumably resource-scarce high elevation, we found large isotopic niche width with low overlap among functional groups. We suggest that this low niche overlap is an indication of niche partitioning in a potentially resource-deficient, harsh, high-elevation landscape. Similar examples are found in didelphid marsupials and rodents which show low isotopic niche overlap in less productive environments (Bubadué et al., 2021) or with increased heterospecific competition (Shaner & Ke, 2022).

4.2 | Discordance between functional traits and isotopic niches

Isotopic niche width and overlap at low and high elevation differ from those predicted when using functional traits to varying extents. Chakravarty et al. (2021) found lower than expected (under a null model) functional dispersion at high elevation. Instead, we found large niche width and nearest-neighbour distances at high elevation. This is further backed by the low level of niche overlap among functional groups at this elevation. The reason behind the large nearest-neighbour distance is the dropping off of the redundant flutter-detecting group at high elevation. Rhinolophids that make up the flutter-detecting group are well-known for having large differences in morphological and echolocation traits that are frequently linked to niche partitioning in the literature (Chakravarty et al., 2021; Voigt et al., 2010). Chakravarty et al. (2021) also attributed the high functional diversity at low elevation to the presence of rhinolophid bats with extreme functional trait values that are drastically different from those of edge-space foraging bats. However, our results place them within the large central hub of the assemblage niche space, as defined by isotopes. This is not surprising as rhinolophid bats have echolocation calls that are adapted to detecting acoustic glints from fluttering insects like Lepidoptera (Tian & Schnitzler, 1997) which also feature in the diet of most aerial foraging bats (Alberdi et al., 2020). The isotopic niche redundancy of this functional group highlights a major discordance in comparison to groups classified using functional traits.

High elevation animal assemblages are often functionally underdispersed (i.e. show homogenous functional traits), a condition referred to as 'environmental filtering' (Chakravarty et al., 2021; de Carvalho et al., 2019; Jarzyna et al., 2020; Montaño-Centellas et al., 2020; Reardon & Schoeman, 2017). Our results demonstrate that niche partitioning can occur along other axes (for example, diet and habitat use) even with the homogenisation of functional traits ('environmental filtering'). Similarly, even if biotic interactions limit the similarity of functional traits ('limiting similarity') related to prey acquisition at productive low elevation sites, the actual isotopic or dietary niches may not get delimited (as shown by the high isotopic niche overlap between edge-space and fluttering detecting bats). Using stable isotopes, we detect strong evidence of niche partitioning among functionally similar species.

There is a lack of consensus between the association of species functional traits and their isotopic (or realised) niches. In temperate marine benthic consumers, traits and isotopic niches may be decoupled (Włodarska-Kowalczuk et al., 2019) but they are correlated in freshwater fish assemblages (Fitzgerald et al., 2017). Spider functional groups separate out in the isotopic niche space indicating a match between functional traits and isotopic niches (Sanders et al., 2015). However, as the diet of many rhinolophid bats is well-known, we advise caution against using their morphological and echolocation call measurements to predict trophic niche partitioning with other functional groups.

4.3 | Insights on the diets of poorly known bat species

We uncovered interesting insights on the probable diets of some bat species that have rarely been studied in the wild. As predicted, we observed that trawling bats occupy a peripheral niche space. However, contrary to our predictions, they had the largest niche width (along with edge-space foraging and active-gleaning bats). This functional group consisting of only one species, *Myotis longipes*, is exclusive to low elevation. *M. longipes* is morphologically adapted (large feet and plagiopatagium attached to the ankles instead of toes) to hunt insects by trawling the surface of water with its feet (Bates & Harrison, 1997; Chakravarty et al., 2020; Morales et al., 2019). Animals that have diets of aquatic origin typically show depleted (more negative) δ^{13}C values (Oelbaum et al., 2019; Voigt et al., 2015), but this idea is not supported by our data as *M. longipes* has the highest δ^{13}C values in our community. They also forage over a wide range of trophic levels (high range of δ^{15}N values), including at high trophic levels, and show low overlap with other functional groups. European trawling species also seem to forage at higher trophic levels than other functional groups (Voigt et al., 2015). Our data suggest that active gleaning bats forage in aquatic environments which deviates from what is known about the species in this functional group. *Murina* spp. that constitute the active foraging group have short, broadband calls that are thought to be an adaptation for navigating in dense forest and in gleaning arthropods like spiders (Kingston et al., 1999). Evidence for spider consumption is based on morphological identification of prey remains but molecular diet analysis of two sympatric *Murina* spp. from Japan suggest that they predominantly prey on lepidopterans and dipterans (Heim et al., 2021). In our study area, *Murina* spp. seem to feed on insects belonging to the lowest trophic levels.

Perhaps the most important result is the specialisation in the passive gleaning forager group that is dominated by two species of *Plecotus*, one of which (*P. wardi*) only occurs above 2700 m in our study area. *Plecotus* spp. hunt using both aerial hawking and gleaning (Dietz & Kiefer, 2014) and molecular diet analysis of two widespread European species show that they are generalists but with strong selection for noctuid moths (Andriollo et al., 2021; Razgour et al., 2011). Indeed, a study on moth diversity in western Himalayas shows that noctuid moths are more diverse and common than other moth families in the 2900–3400 m range (Sanyal, 2015). The restricted elevational distribution coupled with the isotopic specialisation of *P. wardi* make it an important conservation target. Thorough sampling of source (prey and primary producers) and subsequent use of isotopic mixing models will allow us to better identify the diets of our study species. This was beyond the scope of the present study.

4.4 | Conclusions and future directions

The association between niche expansion and packing with increasing species richness has for long fascinated ecologists and biogeographers. Our study is among the very few to employ stable isotope analysis in investigating niche partitioning in animal communities across elevational gradients. This field is conventionally dominated by a trait-based approach. We uncover niche packing in the lowest elevation site. At the highest elevation, the niche width was large, and the overlap among the constituent functional groups was low. Essentially, our results are consistent with studies on bats in Africa (Monadjem et al., 2018) and passerine birds in the Andes where increases in species richness are explained by niche packing (Pigot et al., 2016). We also detect discrepancies between inferences made using functional traits and a finer measure of niche using stable isotopes. High elevation animal assemblages are often functionally similar which is inferred as the lack of niche partitioning. However, we show that even functionally similar species/functional groups partition their niches in harsh environmental conditions. We highlight the additional insights offered by combining functional trait analyses with stable isotope information as a proxy for dietary niches. Future studies may focus on investigating niche partitioning between species within each functional group, and on investigating the role of intraspecific vs inter-specific niche partitioning in influencing patterns of niche packing and expansion.

AUTHOR CONTRIBUTIONS

Rohit Chakravarty, Viktoriia Radchuk and Christian C. Voigt conceived the ideas and generated funds; Rohit Chakravarty conducted fieldwork; Christian C. Voigt and Shreyas Managave funded the lab work, and lab data were generated by Rohit Chakravarty and Shreyas Managave; Rohit Chakravarty and Viktoriia Radchuk analysed the data; Christian C. Voigt and Viktoriia Radchuk supervised the research; Rohit Chakravarty led the writing with inputs from all co-authors. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.44j0zpcjc (Chakravarty et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Dispersion in ^{13}C and ^{15}N values of plant samples collected across the elevational gradient (Green crosses: low elevation, red triangles: intermediate elevation, and black dots: high elevation).

Figure S2: Dispersion of ^{13}C and ^{15}N values in insect samples collected across the elevational gradient (Green crosses: low elevation, red triangles: intermediate elevation, and black dots: high elevation).

Figure S3: Changes in niche width of functional groups across elevations when the sample size is reduced to four individuals per functional group per elevation.

Figure S4: Niche overlap probability of guild A (row) being in the dietary niche of guild B (column), calculated at the level of the assemblage.

Table S1: Mean values of δ^{13}C and δ^{15}N of plant samples collected across elevations.

Table S2: Niche overlap probabilities for guilds at low elevation

Table S3: Mean niche overlap probabilities for guilds at intermediate elevation.

Table S4: Mean niche overlap probabilities for guilds at high elevation.

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Chapter 3

Mountains host a significantly higher proportion of data deficient bat species than lowlands

Mountains host a significantly higher proportion of data deficient bat species than lowlands

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Abstract

1. Mountains harbour a quarter of the world's biodiversity and much of it is under increasing threat due to anthropogenic activities and climate change. Yet, global assessments of the occurrence, and threat status of most mountain taxa, especially elusive ones are lacking, and may hinder conservation and research prioritisation.
2. In this study, we synthesise the distribution and conservation status of bats; a species rich taxon on mountains. By using data on geographical and elevational distribution ranges from the International Union for Conservation of Nature (IUCN) we identified mountains with high bat diversity, species that predominantly occur in mountains ('mountain specialists') and at high elevations ('high elevation specialists'), and the drivers of mountain specialisation.
3. Bat diversity is highest in the Northern Andes and Guiana Highlands. Additionally, we identified 148 mountain specialist and eight high elevation specialist bat species. Mountain specialisation is primarily associated with biogeographic realm and diet of a species, with the Oriental realm hosting the greatest number of mountain specialists. Importantly, while mountain specialists and high elevation specialists are not proportionately more threatened than lowland species, they are proportionately more data deficient.

4. We conclude that more research is needed for bats specialized on mountain ecosystems. Specifically, we identified the Oriental realm as a crucial region for the research and conservation of mountain bats, despite its relatively lower diversity.

Keywords: bats, threat status, distribution, data deficient, mountain specialists, high elevation specialists

Introduction

Mountains host roughly one-third of the world's biodiversity (Körner 2004) and encompass half of the world's biodiversity hotspots (Myers et al. 2000). Over 1300 species of mammals, 2100 species of birds, and 3300 species of amphibians are restricted to mountain ranges (Rahbek et al. 2019), yet many mountain species are under threat from anthropogenic stressors. Land use change and tourism cause reduction in species diversity and gene flow (Rolando et al. 2007; Robin et al. 2015; Shahabuddin et al. 2021). Mountain wetlands are being increasingly polluted by inorganic and organic pollutants (Schmeller et al. 2022) while invasive species are minimizing the habitat available to native fauna (Sharma et al. 2021). Climate change is a more severe threat to mountain species than those in lowlands (Schmeller et al. 2022). Globally, mountain sites are warming faster than surrounding lowlands (Pepin et al. 2022). Climatic fluctuations and increasing warm spells have caused shifts in phenology, timing of migration, shifts in hibernation or the amount of suitable habitat (Parmesan and Yohe 2003; Mccain and Colwell 2011; Wells et al. 2022). Upslope migrations have been reported and have led to novel, and often deleterious, interactions among plant species (Alexander et al. 2015). The difficulty in accessing mountains in comparison to lowlands, prevents us from comprehensively studying the impacts of anthropogenic stressors (Beniston et al. 2018).

Elevation is a key component in mountains that creates a gradient in many abiotic factors thus shaping mountain biodiversity and facilitating the emergence of unique habitats like cloud forests, alpine meadows, and mountain wetlands (Antonelli et al. 2018). As a result, the large number of animal species that are restricted to mountains are also often endemic to narrow elevation zones (McCain 2009; Freeman et al. 2022). In many regions of the world, the proportion of endemism increases in tropical cloud forests or in the alpine zone (Noroozi et al.

2018; Karger et al. 2021). High elevation specialists are particularly vulnerable to the impacts of climate change. As the climate warms, high elevation and summit-dwelling species do not have higher elevation habitats to shift to and are, therefore – in the words of some authors – riding an “escalator to extinction” (Freeman et al. 2018; Urban 2018; Watts et al. 2022). High elevation species have lost on average 110 m of elevational range (Urban 2018) and climate change models across taxa predict a drastic reduction in the area of suitable habitat (Dirnböck et al. 2011; Razgour et al. 2021; Brambilla et al. 2022). Therefore, identifying conservation priorities for mountains necessitates focussing on three dimensions (latitude, longitude, and elevation) and identifying species that are elevation specialists. Sadly, the current level of protection along elevational gradients worldwide needs significant improvements to meet global biodiversity conservation targets (Elsen et al. 2018).

As slow-breeding, long-lived mammals that occupy high trophic levels, bats are important conservation targets (Jones et al. 2009). Their ability to fly allows them to colonise far-flung habitats like islands or high elevations on mountains, thereby influencing the diversity patterns of local ecosystems (Tsang et al. 2020; Monadjem et al. 2023). Flight also enables bats to make seasonal use of different elevations in a mountain range (Mcguire and Boyle 2013; Voigt et al. 2014), while also allowing them to expand their elevation ranges in response to climate change (LaVal 2004). Unfortunately, their nocturnal nature, makes bats harder to study especially on rugged and remote mountain environments. It is, therefore, not surprising that 18% of the world’s bat species are data deficient (Frick et al. 2020) owing to the fast rate at which new species are being described in this order (Burgin et al. 2018). Indeed, in the last two years, at least three such species were found on mountains (*cf.* Simmons et al. 2021; Saikia et al. 2022; Grunwald et al. 2023). While the elevational diversity patterns of bats are relatively well studied (see Chakravarty et al., 2021, 2023; McCain, 2007; Sivault et al., 2023 and references therein), a dataset of elevational distributions of all bat species, and the distributions of high elevation specialist species (for example see de Zwaan et al., 2022) and threatened species would help in guiding future research and conservation.

A global analysis of sampling biases in ecological studies revealed that mountains, especially the regions abutting and above the treeline, are poorly sampled for most taxa (Hughes et al. 2021). This finding implies that many species in high mountains are potentially more data deficient than lowland species. The data deficiency is likely to be aggravated if the taxon is inherently rare or elusive. Data-deficient species do not feature in conservation agendas because of their uncertain status, yet most of them are potentially threatened (Bland et al. 2017; Borgelt et al. 2022). Also, despite the relatively vast knowledge on biodiversity patterns in mountains, reports on the proportion of threatened mountain taxa and where they occur are not commonly found. Therefore, there is an urgent need to use existing biodiversity databases (like the Global Biodiversity Information Facility, the IUCN Red List of Threatened Species etc.) to assess the conservation status of mountain species and to identify priority areas and elevations for research and conservation.

This study is intended to provide a comprehensive synthesis of the status and distribution of bats on mountain ranges from all over the world. Our objectives were to (a) calculate species richness of bats on all mountain ranges to identify hotspots of diversity and conservation opportunities, (b) identify bat species that predominantly occur in mountain habitats and investigate the drivers of this ‘mountain specialisation’, (c) compile elevation ranges of all bat species and identify species that are restricted to high elevation habitats, and (d) investigate if bats that are associated with mountains and with high elevation habitats are more threatened or poorly studied. The study is based entirely on publicly available data and is envisioned to set a paradigm for reviewing the status of any taxon and biome of interest.

Materials and Methods

Spatial analyses

To calculate and project the species richness of bats on mountains, we downloaded all available distribution polygons of bat species from the IUCN Red List of Threatened Species database (IUCN 2022). As of 16th January 2023, the database contained 1331 bat species of which distribution polygons were available for 1315 species. More than 1300 species were assessed after 2014 (Fig. S1). Our data, therefore, represent 90% of the entire known global bat diversity (Simmons and Cirranello 2022). We rasterised all bat distribution polygons at a fine-scale resolution of 1/6° x 1/6° and calculated species richness in each grid as a sum of overlapping polygons. We chose this resolution as many mountains are localised areas of high relief and do not span vast degrees of latitudes. This analysis was performed using the ‘fasterize()’ function of the ‘raster’ package (Hijmans 2022). We defined mountains following Körner et al. (2017) and the polygons provided by them were accessed via: https://ilias.unibe.ch/goto_ilias3_unibe_cat_1000515.html.

We also used the bat distribution polygons and the mountain polygons to calculate the proportion of each bat species’ distribution range that falls within mountains. To do this, we first calculated the total area of the distribution range for each bat species. We then overlaid the mountain polygons over the distribution polygons of bats and calculated the areas of intersection between each species and each mountain. Many species’ distribution ranges overlapped with multiple mountain polygons, thereby generating multiple areas of intersections. Therefore, the areas of intersection of each species were summed to calculate the total area of its distribution that falls within mountains. The proportion of the total area intersecting with mountains and the total area of the distribution range and was used for further analyses. The intersections were marked using the ‘st_intersection()’ function and all areas were calculated using the ‘st_area()’ function of the ‘sf’ R package (Pebesma 2018).

Elevation ranges

IUCN website reports, for each species, the known lowest and highest elevations of occurrence. We compiled these data for all bat species. The lowest elevation was not reported for many species. In such cases, if the authors used words such as “lowland” (in the geographical range description) or they did not explicitly mention the species’ occurrence only in mountains, we assumed the lowest elevation to be ‘0’. We also entered lowest elevation values as ‘0’ if it was below sea level (for example, some insular species). After making these replacements, we had to remove 533 species with missing data. Our final dataset contained 798 species. It must be noted that the reported elevations are at the global scale, across mountains and across seasons. The species’ elevational limits may differ on specific mountain ranges. Which elevational ranges a given species is most abundant in, or seasonal usage of different elevations cannot be inferred from the data reported by IUCN.

Definitions of categories and statistical analyses

We considered a species as threatened when it belonged to Vulnerable (VU), Near-Threatened (NT), Endangered (EN) or Critically Endangered (CR) Red List categories. We categorised species with ≥ 75% of their distribution range on mountains as 'mountain specialists'. In the absence of a biologically meaningful definition of 'high elevation' that encompasses all taxa and geographies, we defined a 'high-elevation specialist' as a species that occurs in or above the elevation zones comprising deciduous forest trees and coniferous trees, and the alpine zone. Following the isotherms described in Rahbek et al. (2019) we defined these zones as being ≥ 2000 m asl in tropical mountains (between 23°N & S), ≥ 1500 m asl in the subtropics (24° to 35° N & S), and ≥ 1000 m asl in temperate mountains (>35°N & S). The reason behind not defining 'high elevation' exclusively by the alpine zone was due to the lack of trees available for roosting. Bats that feed in alpine regions are more likely to roost in trees below the treeline or in crags or cliffs below the alpine zone. We tested whether 'mountain specialists' are proportionately more threatened or Data Deficient (DD) than non-mountain species using binomial tests of proportions. To compare the proportions of threatened and data deficient species between 'high elevation specialists' and other bats (elevation generalists plus lowland species) we used Fisher's exact test because of the low number of high elevation specialists (n=8).

We tested for the effect of diet, latitudinal distribution, biogeographic realm, and whether the bat belonged to a monotypic genus or not, in predicting 'mountain specialisation'. Diet data were downloaded from PHYLACINE 1.2 database (Faurby et al. 2018). PHYLACINE 1.2 presents diet as a proportion of plant matter, vertebrate prey, and invertebrate prey consumed by a mammal species. We assigned the diet for each bat species (plant, vertebrate or invertebrate) using the category with the highest proportion. After matching the taxonomy in the IUCN and PHYLACINE 1.2 databases by making (details in Table S1), we retrieved diet data for 1141 species (*i.e.* 190 species without data) and for all but four genera. At such broad categorisation, the main diet was observed to be phylogenetically conserved within genera when visualised by plotting bar plots of diet per genus (Fig. S2). Therefore, we replaced missing data with the main diet of congeners. We assigned the monophyletic species *Dryadonycteris capixaba* to plant-feeding following Nogueira et al. (2012) whereas *Setirostris eleryi* and *Submyotodon latirostris* were assigned to insect-feeding as they split from the insectivorous genera *Mormoopterus* and *Myotis* respectively (Reardon et al. 2014; Ruedi et al. 2021). Only the recently-described *Eudiscoderma thongareeae* could not be assigned to any specific diet. The missing species and the diets that they were assigned to are listed in Table S2. We only had three sanguivorous species (0.02% of the total species) and seven carnivorous species (0.05% of the total species) and therefore removed these from our consequent analyses (as keeping them would increase the number of degrees of freedom in the respective model). Latitudinal distribution was also a categorical variable with three levels: tropical, subtropical, and temperate. Most species had their distribution polygons exclusively in one out of the three zones. Species that spanned different latitudinal zones were assigned to their main latitudinal zone by visually assessing their distribution polygon. We assigned species to biogeographic realms following Udvardy (1975). As with latitudinal zone, some species spanned biogeographic realms and were assigned to the realm in which majority of their distribution polygon lay based on visual assessment.

We performed a generalised linear mixed effects model (GLMM) with Binomial distribution (logit link) using mountain specialisation as a binary response variable (*i.e.*, 'mountain specialist': 'yes' or 'no'). 'Main diet', 'main latitudinal zone', 'main biogeographic realm', and 'monotypic genus' (binary: 'yes' or 'no') were used as fixed effects, and 'taxonomic family' was used as a random intercept. We contested for the significance of each variable by using Likelihood Ratio Test as implemented in 'drop1()' function in R. We tested differences among levels of the explanatory variables that significantly predicted mountain specialisation by comparing their estimated marginal means using a Tukey Test (implemented in the 'emmeans()' function of the 'emmeans' package in R, Lenth 2020). All the reported contrasts are marginal effects calculated while keeping factor predictors constant at their proportions of occurrence in the data.

Results

Bat species richness in most mountain ranges varied between 1 to 40 species, irrespective of the latitude (Fig. 1). Globally, species richness was highest (>80 species) in Panama, the northern Andes (Venezuela, Colombia, and Ecuador) and the Guiana Highlands (Venezuela, Guyana, Suriname, and northern Brazil). In the Palaearctic realm—and even, across temperate latitudes—the Alps, Pyrenees, Dinaric Alps (and other mountains in the Balkan region), Carpathian Mountains and Caucasus Mountains, were found to have the highest species richness with 21-40 species (comparable to mountains in South Asia and Africa). In the Afrotropical realm, the northern Albertine Rift hosted the highest species richness (40-70 species). In the Oriental biogeographic realm, the highest species richness (60-80 species) was observed in mountains in peninsular Malaysia, Malaysian Borneo, northern Thailand, and central Laos. In general, the mountains across peninsular and insular Southeast Asia were found to host >40 species.

Seventy seven percent of bat species (1014 out of 1315 species) have <50% of their distribution ranges in mountains (Fig. 2). Out of these, 732 species have <25% of their distribution range in mountains. Only 148 species (11.2%) were found to be mountain specialists *i.e.*, species with >75% of their distribution range in mountains. Mountain specialists were found in all biogeographic realms and belonged to 57 genera (Fig. 3). Out of the 798 species for which complete elevation range data were available, we found only eight species to be 'high elevation specialists' (*i.e.*, occurring > 2000 m in tropics, > 1500 in subtropics, or > 1000 m in temperate mountains). These bats were only found on three biogeographic realms (Oriental, Nearctic, and Afrotropical) and belonged to five genera. A consolidated list of mountain and high elevation specialists is provided in Appendix Table 1.

Both mountain specialists and high elevation specialists were not proportionately more threatened than non-mountain species (<75% distribution in mountains; Binomial test, p=0.62) and elevation generalist species (species occurring below the abovementioned cut-offs; Fisher's exact test, p=1), respectively. However, we found that both mountain specialists and high elevation specialists are proportionately more data-deficient (Binomial test, $p < 0.001$; Fisher's exact test, $p < 0.01$ respectively).

The GLMM indicated that biogeographic realm (LRT/Chi-square, $p < 0.001$) and diet (LRT/Chi-square, p=0.02) significantly predicted mountain specialisation. In comparison to the reference level (Neotropical realm), the odds of being a mountain specialist was significantly higher in the Oriental realm (2.08) and significantly lower in the Afrotropical realm (0.31) (Fig 4a). The mean probability of being a mountain specialist in the Oriental realm was 0.12 while that in the Afrotropical and Palaearctic realm was 0.02 (Fig 4b). Although diet significantly affected mountain specialisation, within variable comparisons did not reveal a significant difference between plant and insect-feeding species (Tukey test, p=0.06; Fig. S3)

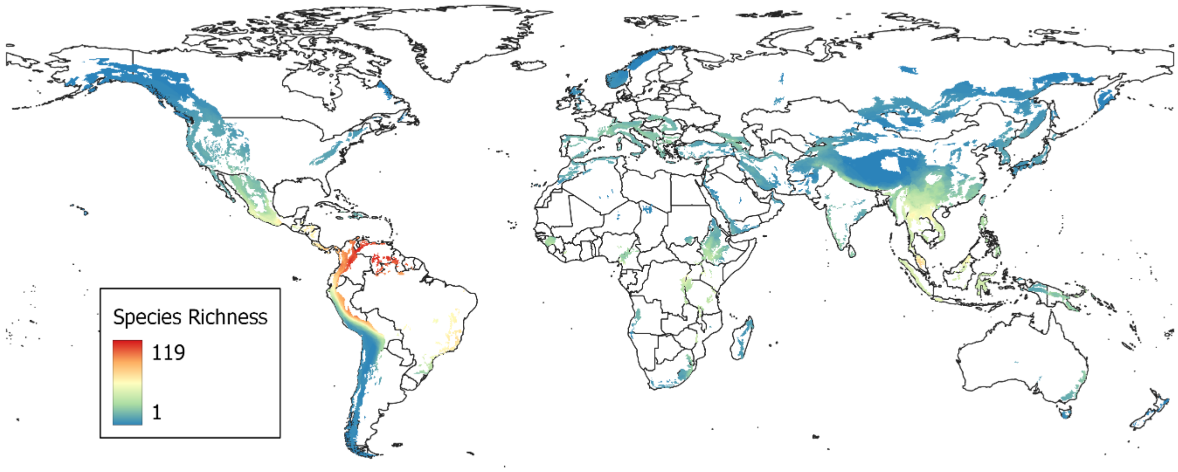

Fig. 1 Species richness of bats on all mountain ranges of the world. Mountains were defined following Körner et al. (2017) and clipped to the polygons used in that paper (available from: https://ilias.unibe.ch/goto_ilias3_unibe_cat_1000515.html).

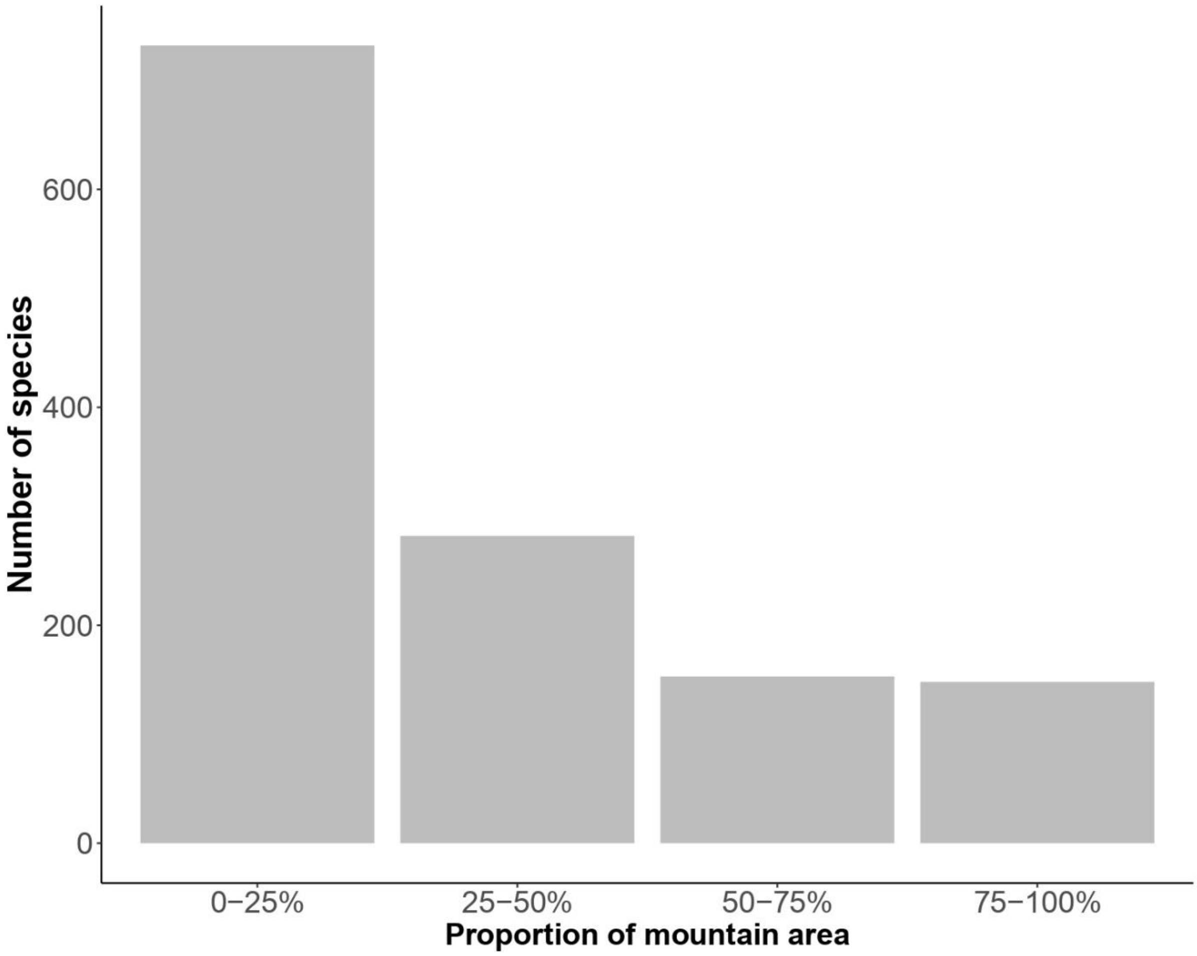

Fig. 2 Bar chart showing the number of species in each of the four categories as defined by the proportion of the area of a species' distribution range in mountains. Species having >75% of their distribution in mountains were classified as 'mountain specialists'.

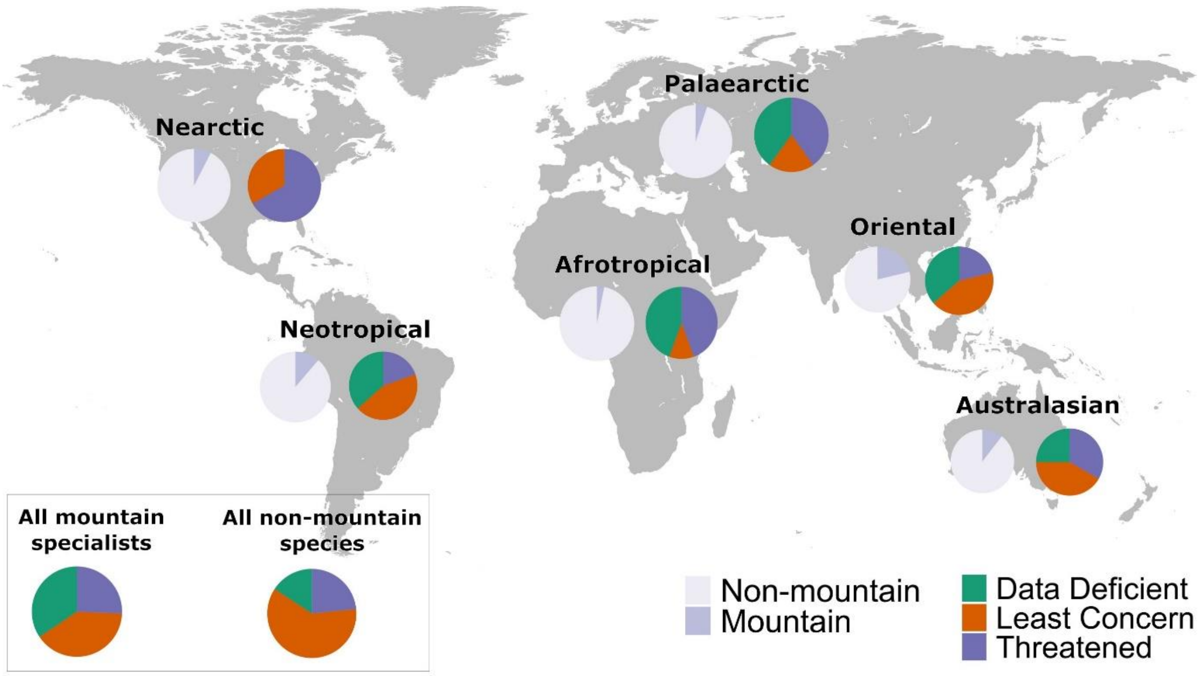

Fig. 3 Proportions of species that are: i) mountain specialists and non-mountain species, and ii) mountain specialists in threatened, Least Concern, and Data Deficient classes in different geographical realms. Threatened class comprised Near Threatened, Vulnerable, Endangered, and Critically Endangered threat categories. Inset shows a comparison of proportion of threatened, Least Concern, and Data Deficient species for all mountain specialists and all non-mountain species. Size of pie charts are not to scale. Sample sizes (mountain specialists/total): Nearctic (3/40), Neotropical (41/365), Afrotropical (9/285), Palaearctic (5/99), Oriental (66/311), Australasian (24/231).

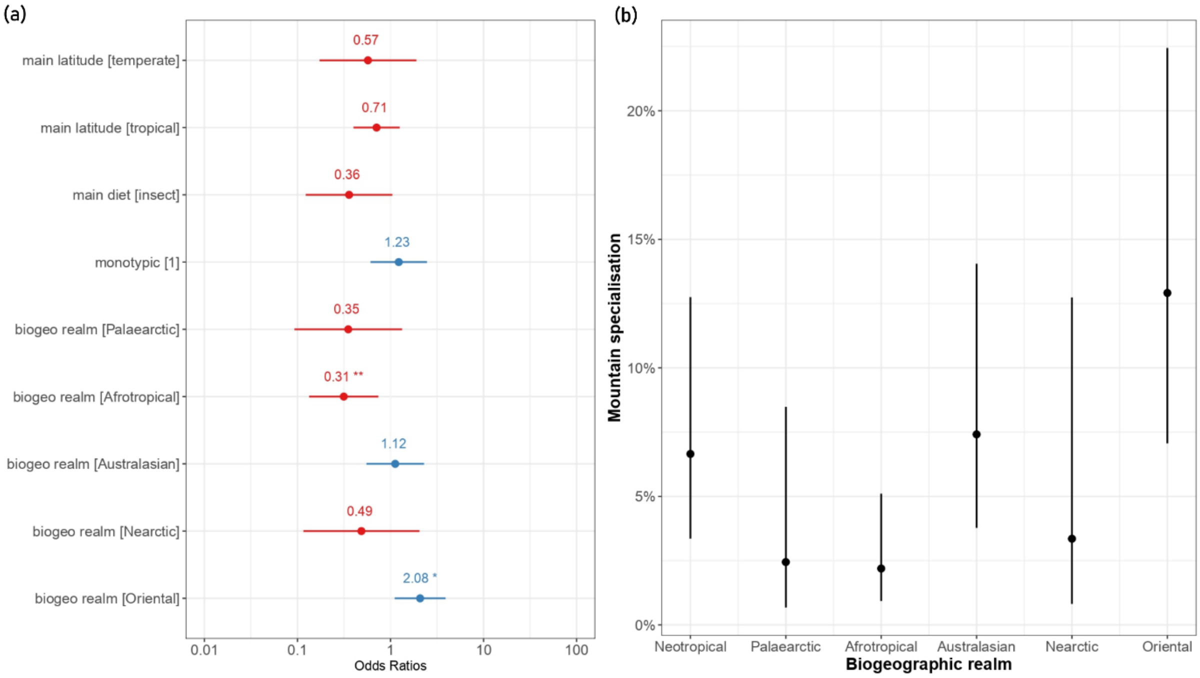

Fig. 4 a) Model estimates of generalised mixed effects model with mountain specialisation as a binary response variable and biogeographic realm, monotypic genus (yes vs no), and diet as predictor variables. Family of the bat was used as a random intercept. The reference level used is plant for diet and Neotropical realm for the biogeographic realm **b)** Probability of a bat being a mountain specialist in any given biogeographic realm. All values are shown as mean ± 95% confidence interval. Levels of the explanatory variables whose confidence intervals do not overlap (**b**) or those not overlapping 1 **(a)** are considered significant.

Discussion

Our global review of bat distributions using publicly-available datasets revealed hotspots of bat diversity in different biogeographic realms, and retrieved 148 mountain specialists and eight high elevation specialists. We also found that both mountain and high elevation specialists are proportionately more data deficient than mountain and elevation generalists. Oriental biogeographic realm is a significant predictor of being a mountain specialist.

Variation in species richness across mountains

The most species rich hotspots for bat diversity on mountains were found to be in northern Andes and the Guiana Highlands. These estimates are congruent with previous projections for mammal or bat diversities (Jetz et al. 2012; Jenkins et al. 2013; Alves et al. 2018). In fact, comparing the species richness of bats and other major mammalian orders suggests that bats have a disproportionate effect in increasing the overall mammalian diversity of this region (Jetz et al. 2012; Jenkins et al. 2013). In the Palaearctic realm, the Caucasus, Zagros, and Elburz Mountains have 10-15 more mammalian species than the surrounding lowlands (Jetz et al. 2012, accessed from https://mol.org/patterns/richnessrarity?taxa=mammals). Our species richness estimates for bats suggest that this increase is also disproportionately influenced by the region's bat diversity, especially in the Caucasus. The same effect is seen, although to a lesser extent, in mammalian species richness in the Himalaya and the lowlands to its south, and Tibetan Plateau to its north (Jetz et al. 2012, accessed from https://mol.org/patterns/richnessrarity?taxa=mammals). In the western Himalaya, roughly 40-50% of the mammalian species are bats.

Most mountain ranges, irrespective of their latitude, were found to have < 20 species. Notable among these were the Central Highlands of Madagascar. Since this region is known as a biodiversity hotspot, we had expected to find a higher species richness here. However, what Madagascar lacks in numbers, is made up by its endemism (not measured in this study), especially in the genus *Miniopterus* that have undergone a radiation in this island (Christidis et al. 2014).

Apart from highlighting areas of high diversity, our data also underscore abrupt discontinuities in species richness patterns. Two of these are worth mentioning here: the decline in species diversity as one goes from west to east in a) the Himalaya, and b) the New Guinea Highlands. For most well-studied taxa, species richness increases from west to east in the Himalaya (Srinivasan et al. 2014; Tamma and Ramakrishnan 2015; Tamma et al. 2016). Eastern Himalaya and Northeast India are also among the most species-rich biodiversity hotspots in the world (Myers et al. 2000). In the case of New Guinea, the decline in bat diversity coincides precisely with the political boundaries between Indonesia and Papua New Guinea. The same pattern is seen even when visualising species richness of the entire island (and not just mountains as in our analysis) (Jenkins et al. 2013). Both the above examples likely point towards strong sampling biases *i.e.*, the Eastern Himalaya of India and the Indonesian New Guinea are poorly sampled for bats. The strong separation at the political boundary of Indonesia and Papua New Guinea may also reflect differences in research interest or investment in sampling bat species in the respective countries.

Mountain specialisation and its drivers

Our analysis retrieved 148 mountain specialist species (those having >75% of their distribution range in mountains) (Fig. 2, Table S1). In total, 1829 species of mammals have >75% of their distribution range in mountains (Rahbek et al. 2019), so mountain specialist bats only make up 8% of this diversity. This is, perhaps, not surprising given the volant nature of bats. Nonetheless, some bat genera appear to have disproportionately high numbers of mountain specialist species. For example, we found that six out of all 17 extant *Plecotus* species (35 %), eight out of 22 *Sturnira* species (36 %), 16 out of 32 *Murina* species (50 %), and seven out of nine *Anoura* species (78 %) are mountain specialists. It has been phylogenetically shown that *Anoura* has a montane origin (Calderón-Acevedo et al. 2022), but the same is not known for the other genera listed above. These genera may therefore be interesting model organisms for studies on speciation and the building up of mountain biodiversity.

Biogeographic realm emerged as the most important predictor of mountain specialisation in our analysis. Specifically, the odds of being a mountain specialist increased if the bat belonged to the Oriental realm. Sixty six out of 311 species in this realm were mountain specialists with *Murina* spp. showing the highest proportion. One possible explanation for such high proportion of mountain specialists in Oriental realm is that a major part of the Oriental realm is covered in mountainous terrain following our definition of mountains. Therefore, the high odds of being a mountain specialist in the Oriental realm are likely solely due to the available mountain area. Similarly, the proportion of mountainous area in the Afrotropical realm is not high and this is reflected in a reduction in the odds of being a mountain specialist here. Only nine out of 284 species in this realm were mountain specialists. Surprisingly, despite hosting the highest species richness, the Neotropical realm did not significantly predict mountain specialisation in bats. Only 41 out of 365 species in this genus were mountain specialists, perhaps suggesting that most species in the Neotropics tend to have broad geographical distributions. Moreover, the most speciose family of the Neotropics, Phyllostomidae, has a tropical origin and their abundance drops drastically in montane habitats (de Carvalho et al. 2019).

Despite a relatively lower species richness, 78 to 98 % of cloud forest restricted species (plants, amphibians, birds, and mammals) in Africa are single region endemics (Karger et al. 2021). The contribution of bats to this endemism is likely to be low due to their vagile nature but it would be worthwhile measuring endemism in mountain ranges to properly assess the importance of mountains to African bat fauna. In comparison, 32 to 56 % cloud forest species in Asia-Pacific and only 12 to 26 % in the Neotropics are single region endemics (Karger et al. 2021). The Oriental realm also has the highest proportion of island endemic species that are in urgent need of research and conservation (Conenna et al. 2017). Therefore, although the Neotropics host the highest species richness of bats, the Oriental realm appears to be equally crucial when a biome/ecosystem-centric approach in conservation is adopted.

High elevation specialisation and its potential impacts

On account of our stringent elevation cut-offs, we retrieved only eight high elevation specialists (out of 798 species with elevation data) (Appendix Table 1). Five of these species belonged to the Oriental realm. Interestingly, three species belonged to the genus *Plecotus*. As mentioned above, *Plecotus* spp. show strong affinity to mountain habitats. The data presented herein suggest that Palaearctic species of this genus show relatively broader elevational distributions but tropical and subtropical species occur in narrower elevational ranges. A recent record of *Plecotus homochrous* comes from 2200 m asl in Hoang Lien National Park in northern Vietnam (Fukui et al. 2020). This record was published following IUCN update of this species in 2019 (Srinivasulu and Srinivasulu 2019). This is the first record of this erstwhile Himalayan species from Southeast Asia. Interestingly, even in Southeast Asia, it was caught in a high elevation site. Assuming that low elevation sites are better sampled, this observation suggests that *P. homochrous* has a wide geographical distribution but a restricted elevational distribution. As the genus *Plecotus* predominantly has a Palaearctic distribution, they are likely to be cold-adapted. Species occurring in subtropical and tropical mountains may therefore occupy higher elevations, as is also seen in some Palaearctic birds, mammals, and arthropods in the Himalaya (Martens 1984; Päckert et al. 2012). A global phylogeny of the genus will be helpful in examining the reasons behind the mountain affinity in *Plecotus* spp.

The impacts of this high elevation specialisation have already been demonstrated to be alarming in one species. *Plecotus balensis* that occurs on sky islands in a few summits in the

Ethiopian Highlands shows marked genetic differentiation across valleys and its range has been progressively shrinking since the last glaciation period. The problem is likely to get accentuated by the effects of climate and land-use change (Razgour et al. 2021). Similar dual effects of historical patchiness and contemporary habitat fragmentation are known in a sky island bird species in the Western Ghats of India (Robin et al. 2015). Three out of the eight high elevation specialists that we identified (*Hypsugo anthonyi*, *Myotis soror,* and *Rhinolophus kahuzi*) are known from single localities which potentially puts them at an even greater risk of extinction.

Mountain and high elevation specialists are more data deficient

The most important and alarming result of our study is that mountain specialists and high elevation specialists are proportionately more data deficient than lowland species. We did not find a significant difference in the proportion of threatened species in mountains vs lowlands, but we argue that our results are concerning. Data deficient species are normally excluded from conservation prioritisation and funding schemes because of their uncertain status (Bland et al. 2017). Yet, data deficiency is far more common in elusive taxa like bats in comparison to other mammals (Frick et al. 2020). We now demonstrate that a greater proportion of these species are found on mountains. Recent predictions unequivocally demonstrate that data deficient species are more likely to be threatened (Bland et al. 2015; Borgelt et al. 2022) which make our findings even more worthy of attention. Moreover, 28 of the 148 mountain specialist species are listed under high priority island endemic species for research and conservation, including two species (*Neopteryx frosti* and *Hesperoptenus gaskelli*) that rank in the top-10 (Conenna et al. 2017). Much like sky island species, species found on insular mountains occur on 'islands-within-islands', further increasing their extinction risk (Taylor and Kumar 2016).

There are eight main reasons as to why species are assessed as data deficient: uncertain provenance, type series, less than five records, records from before 1970, uncertain population status or distribution, uncertain threats, new species (discovered in the last 10 years), and taxonomic uncertainty (Bland et al. 2017). Each of these justifications applies to the data deficient mountain and high elevation specialists in our dataset. Fifty seven percent of all bat species—including those that are classified as ‘least concern’—have unknown population trends (compared to 39% mammals and 8% of birds). Additionally, over 270 bat species have been described since 2005 (Frick et al. 2020), and as is, around 120 species have not even been evaluated by the IUCN. The number of data deficient species, although very high, is still an underestimate.

Mountain environments pose several challenges in sampling wildlife such as lack of accessibility, inclement and uncertain weather conditions, and short breeding seasons. Consequently, even observable vertebrates like birds are much poorly known in montane and alpine habitats (Scridel et al. 2018). The lack of sufficient records and uncertain population trends are widely recognised as hampering accurate IUCN assessments, yet ironically, in the current research landscape, funding is not easily available for taxonomic inventorying and long-term monitoring (Anderson 2017). These problems make it all the more important to gather data on rare and elusive taxa. As the threat of climate change intensifies and specialised ecosystems like cloud forests are lost at unprecedented rates (Karger et al. 2021), data deficient species could go extinct without a notice.

Conservation implications and future directions

Our study highlights that bat species found on mountains are more data deficient than lowland species. We therefore call for targeted surveys of bats on mountains (and more funding for them), especially in the Global South that is generally understudied and where species inventories are often lacking. In fact, this prescription applies to all montane taxa that are known to be elusive or hard to sample. Recent bat species discoveries on Mount Nimba in West Africa boldly underscore the need for such surveys (Simmons et al. 2021; Grunwald et al. 2023). Long-term acoustic monitoring schemes along elevational gradients may be initiated wherever bat echolocation call libraries exist. Such a scheme may enable tracking changes in relative abundances, breeding phenology, and elevational range shifts. It is also highly advisable to initiate a dedicated working group on mountain bat ecology within the IUCN Bat Specialist Group or Global Union of Bat Diversity Networks (GBatNet). We acknowledge the stringency of our high elevation cut-offs. The high elevation specialists in our dataset may therefore be treated as the most vulnerable species, but there are likely to be more high elevation specialists across the globe. Future studies may define such species more accurately using high-resolution relief or vegetation data, which was beyond the scope of this study. Lastly, we call for better reporting of elevational distribution in IUCN assessments and in the Map of Life database (https://mol.org/). Elevation data were missing for 533 species and when they were reported it was not uncommon for the lowest elevation to not be reported (or to be misreported as ‘0’) even when the geographical distribution description mentioned phrases like “lowlands” or “only reported from 2600 m”. Regional assessments must be carried out so that differences in elevational distribution of different bat species can be compared across mountain ranges. It is high time that we hold this third dimension of habitat in utmost importance given the rate at which climate change is affecting our mountains and their biodiversity.

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Author contributions

Rohit Chakravarty, Viktoriia Radchuk, and Christian C. Voigt conceived the ideas. Rohit Chakravarty analysed the data, and wrote the draft. Viktoriia Radchuk and Christian C. Voigt supervised the research. All authors contributed critically to the draft.

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5. GENERAL DISCUSSION

Taken together, this thesis is an investigation of the diversity patterns, community structure, and threat status of bats found in mountains. In the **first chapter**, I investigated how taxonomic, functional, and phylogenetic diversity change across an elevational gradient in the Himalaya. Going from low to high elevation, I found a consistent decline in species richness; however, functional richness and dispersion declined significantly only at the highest elevation. Phylogenetic diversity did not differ significantly across elevations. In the **second chapter**, I compared trophic (isotopic) niche partitioning across these three elevation sites with varying species richness. At the species-rich and functionally-diverse low elevation site, I observed low assemblage niche width with high overlap—fitting a 'niche packing' model (MacArthur, 1965). At the species-poor and functionally underdispersed high elevation, I found evidence of trophic niche partitioning. In the **third chapter**, I reviewed the global distribution and threat status of bats found in mountains. I identified regions of high bat diversity and demonstrated that mountain and high elevation specialist species are more data deficient than lowland species. The main findings of each chapter are discussed in detail therein. Here, I will attempt to draw syntheses by tying the results of different chapters together.

5.1. Connecting community assembly and niche partitioning

Functional traits are commonly used as proxies for species' ecological niches, and the dispersion within trait spaces in assemblages is then equated to niche partitioning (Nock et al., 2016; Pigot et al., 2016). However, very few studies exist that link ecomorphological traits to their functionality in the animal kingdom (Mlambo, 2014; Petchey & Gaston, 2006). Although linking traits to their functions is admittedly difficult, a complementary approach combining traits with estimates of trophic niches and spatiotemporal habitat use can result in greater understanding of the diversity of animal communities—an approach that Schoener also hints at in his classic paper on resource partitioning (Schoener, 1974). For example, functional trait spaces mimic isotopic niche spaces in assemblages of spiders in Switzerland (Sanders et al., 2015), freshwater fish communities in the Amazon basin (Fitzgerald et al., 2017), and in aquatic macroinvertebrates in bromeliads (Dézerald et al., 2018). In these communities, functional traits appear to serve as reliable proxies of trophic niches. However, Włodarska-Kowalczuk et al. (2019) found decoupling of trait spaces and isotopic niche spaces in temperate marine benthic taxa, which are similar to the results of my **first and second chapters.** Tying the results of those two chapters together, we see that functionally-similar species partition their trophic niches in a potentially resource-scarce landscape. In general, there are not many tests of niche partitioning in assemblages that are (theoretically) structured by environmental filtering (like the high elevation assemblage in our study area). Likewise, there is high potential in exploring the role of niche specialisation in driving dispersion in assemblages structured by limiting similarity.

The complementary use of traits and stable isotopes to define different niche elements in this thesis also highlighted a fundamental analytical issue that bat community ecologists may need to pay more attention to in future studies. The patterns observed in my **first chapter** were strongly driven by the presence of rhinolophid bats in the low and intermediate elevations. As described in detail in both the **first and second chapters**, rhinolophid bats generally strongly influence assemblage trait spaces due to the vast spectral differences in echolocation calls among co-occurring species, and between them and bats of other families. These differences are commonly inferred as niche partitioning among them, and between them and other species. However, this assumption has rarely been empirically tested using DNA barcoding or stable isotope analysis. My data (**second chapter**) also show that rhinolophids have high trophic overlap with edge and open-space foraging bats which is expected because their echolocation calls are adapted to detecting fluttering prey like Lepidopterans (Tian & Schnitzler, 1997). As for niche partitioning within congeners, there is evidence that rhinolophid bats segregate spatially (Arrizabalaga-Escudero et al., 2018) or differ in their hunting behaviour (for example, aerial hawking *vs.* perch hunting) (Jones & Rayner, 1989). These differences are not explicitly accounted by measurements of wing morphology or echolocation calls, but need thorough natural history observations that are lacking for many species. Therefore, bat researchers should exercise caution when inferring trophic niche partitioning solely based on differences in morphological and echolocation call traits in assemblages that include rhinolophid bats (or other high duty cycle echolocators like *Hipposideros* spp. or *Pteronotus parnellii*).

5.2. Improving knowledge on mountain bats

As I highlighted in my **third chapter**, mountain and high-elevation specialist bat species are proportionately more data deficient than lowland species. Data on elevation ranges are either poorly known or are improperly reported. Some bats have vast global elevational distributions but it is not known if they occur at different elevations in different mountain ranges (**third chapter**). The lack of elevational range data from different mountains has implications in advancing knowledge on the diversification and community structure of bats on mountains. As an example, such data can allow us to investigate character displacement and competitive release by analysing changes in a species' niche when it occurs in sympatry *vs.* allopatry with another potentially competing species (see Freeman et al., 2022 for an example on birds in the Andes).

The lack of data on mountain and high-elevation specialist species also has conservation implications (as elaborated in the **third chapter**). Conservation policies cannot be made surrounding data deficient species, even though many of them are likely to be threatened (Bland et al., 2015; Borgelt et al., 2022). Many mountain and high-elevation specialist bat species are known from single locations and some have been recently discovered (Appendix, Chapter III; Grunwald et al., 2023; Saikia et al., 2022; Simmons et al., 2021). Therefore, data on their distributions are lacking and studies on their ecology/natural history are even rarer. Two such poorly known mountain and high elevation specialist species feature in my data from the Himalaya (**first and second chapters**): *Plecotus homochrous* and *Plecotus wardi*. My results show that these two species occur in restricted elevational ranges both locally (**first and second chapter**) and globally (**third chapter**) and are trophic niche specialists.

In the **third chapter**, I have recommended ways to improve knowledge (or reduce data deficiency) on mountain bats. Briefly, these include setting up dedicated mountain bat working groups, initiating long-term acoustic monitoring schemes (wherever appropriate), and improving compilation and reporting of elevational ranges for as many species as possible. Additionally, using the *Plecotus* spp. as a case study, I also suggest that researchers find ways to identify niche specialisation along a range of niche dimensions (such as diet, habitat, microhabitat, and physiological tolerance) in mountain or high elevation specialist species. Following the approaches defined by Winemiller et al. (2015) and Pianka et al. (2017) in developing a periodic table of niches can allow us to identify if mountain/high elevation specialist species show convergence in niche dimensions. This would allow us to better estimate the risk posed to a species due to climate change or anthropogenic stressors, and to develop holistic management plans for their conservation.

5.3. My results in the light of climate change

Trait-based ecology can improve predictions on the impacts of climate change on animal communities. When species shift their ranges to track favourable conditions (in response to climate change) they enter communities that are already shaped by local plants and animals and their interactions. Novel interactions caused by incoming species can affect the fitness of autochthonous species as they do not have a shared history of co-evolution (Gilman et al., 2010). Theoretically, species that are functionally similar are expected to face greater competition (McGill et al., 2006; Weiher et al., 2011). However, as my results show, functionally similar species may still partition their niches along axes such as diet.

I have not measured beta diversity in my data from the Himalaya, but anecdotal observations suggest that intermediate and high elevation assemblages are taxonomic and functional subsets of the low elevation assemblage. Species unique to the low elevation assemblage are added via niche packing, perhaps implying that the low elevation site has enough resources to allow niche overlap (**second chapter**). Therefore, if the unique species (mostly of the edge space foraging guild) were to expand their elevational ranges, one may potentially expect an increase in competition over dietary resources. However, it must be noted that these expectations rely on the assumption that range expanding species exhibit niche conservatism under future climate change, and they do not consider factors such as shifts in insect prey abundance/diversity or shifting vegetations. Such expectations, therefore, are associated with multiple uncertainties.

5.4. Future directions

In this thesis, I have used a broad spectrum of approaches to investigate bat diversity and community assembly in mountains. Trait data and tissue samples collected in the Himalaya allowed me to define the niches of bats in a complementary manner. Additionally, I used publicly-available data to review the global distribution and lack of knowledge on mountain bats. In some ways, this thesis has filled the knowledge gaps that it has itself highlighted. Out of the ‘seven shortfalls’ of biodiversity (Hortal et al., 2015), this thesis helps in addressing *Wallacean shortfall* (*i.e.* data on species distributions), *Raunkiæran shortfall* (*i.e.* data on species traits), and *Eltonian shortfall* (*i.e.* data on species’ interactions). Nonetheless, the scope of this thesis was also constrained by the difficulty of sampling bats in rugged terrain, the lack of global datasets on fine-scale bat distributions and traits, and so on. Therefore, to build upon the work presented herein, I recommend the following future directions.

i) Understanding the phylogeographic patterns of bats in the Himalaya will greatly aid in improving interpretations on community structure. This should ideally involve creating a dated phylogeny by sampling bats from east to west in the Himalaya and adjoining areas (including peninsular Southeast Asia).

ii) A common limitation of animal functional trait studies is that traits can rarely predict physiological adaptations. Incorporating physiological traits in a study along an elevational gradient can add immense value. Future studies may investigate if easily morphological traits or phylogenetic positions are correlated with metabolic rates or thermoregulatory capabilities.

iii) The temporal axis of niche partitioning is relatively poorly studied. Acoustic studies show significant fine-scale temporal partitioning between ecologically similar pairs of bat species (Lambert et al., 2018; Mohan et al., 2022) but often at the level of the community, the inferences are based on lumping bats to sonotypes (Beilke et al., 2021; first chapter). This approach may not be very informative because, as echolocating animals, bat species that are acoustically similar should have greater pressure to reduce temporal overlap. I could not explore temporal partitioning due to the high acoustic similarities among syntopic bat species in my study area. However, it would be worthwhile doing so as more data become available on reliable acoustic identification to the species level, or when it becomes cost-effective to track the movement of these bats.

iv) Given the rugged terrain of our field site, we did not have enough sample sizes to compare niche partitioning among species within guilds/functional groups. It would also be worthwhile exploring niche partitioning across seasons, perhaps by collecting tissues with differing turnover rates for stable isotope analysis. This could not be achieved in this thesis due to logistical constraints related to the export of samples. For the *Plecotus* spp. which are isotopic niche specialists found above 2500 m asl, metabarcoding of faecal pellets can tell us which prey species these bats specialise on.

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Chapter I

Chakravarty et al. 2021 *Scientific Reports*

SUPPORTING INFORMATION

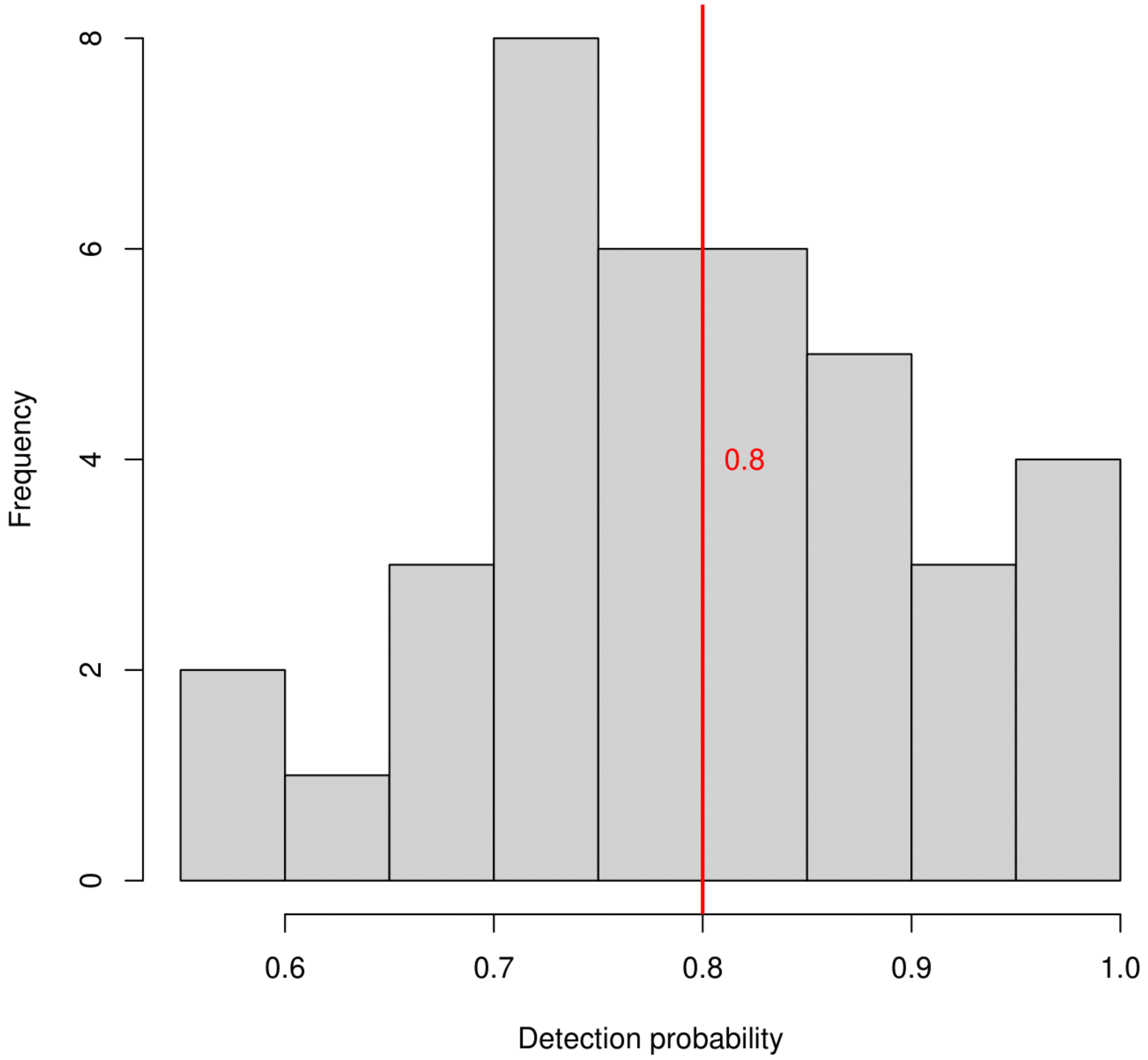


Fig S1 The median detection probability calculated across all sites using mistnet captures and acoustic detections.

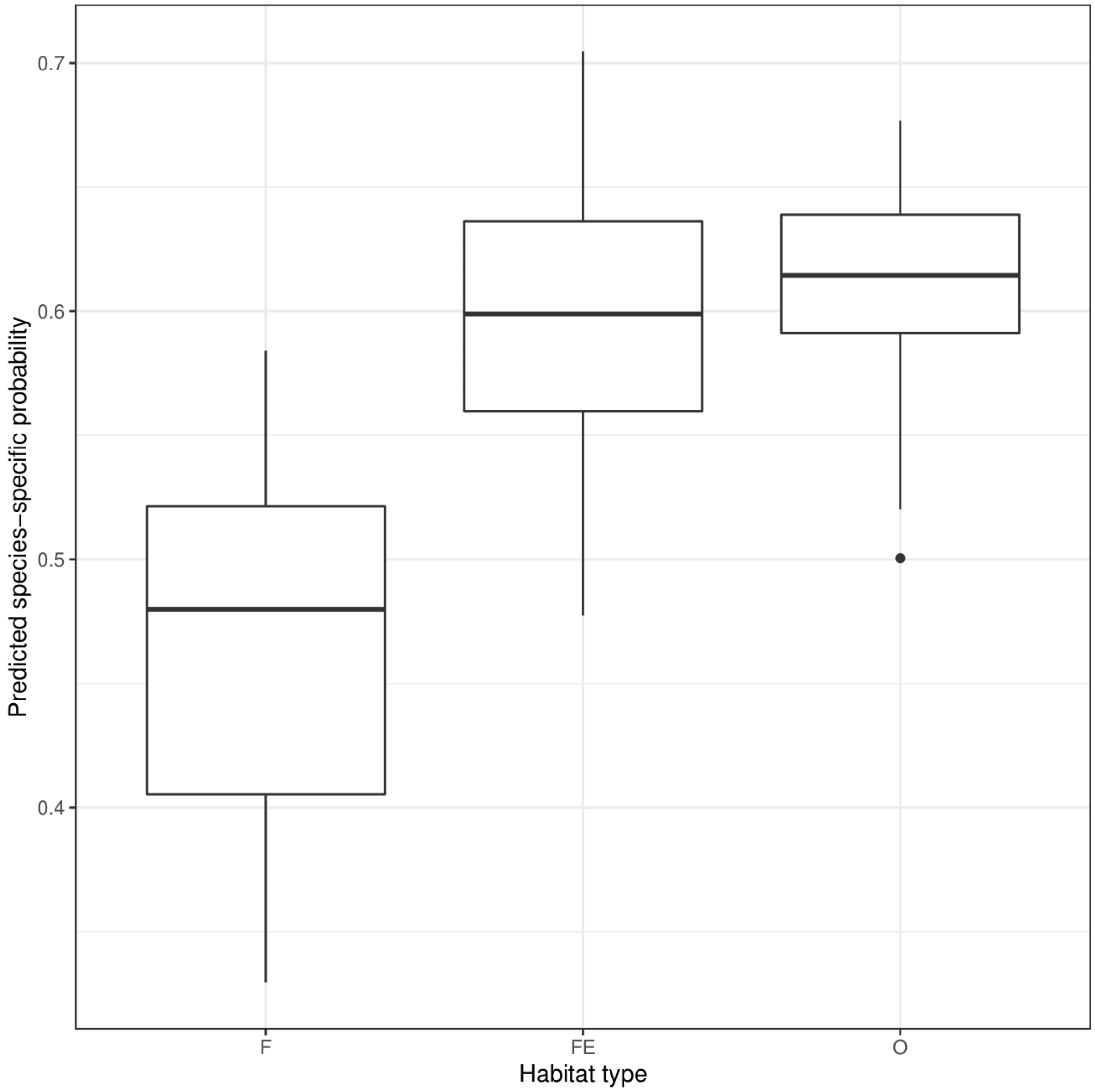


Fig. S2 The heterogenity in detection probabilities across habitat types. F = forest, FE = forest edge and O = open. Species were more likely to be detected in edge and open habitats.

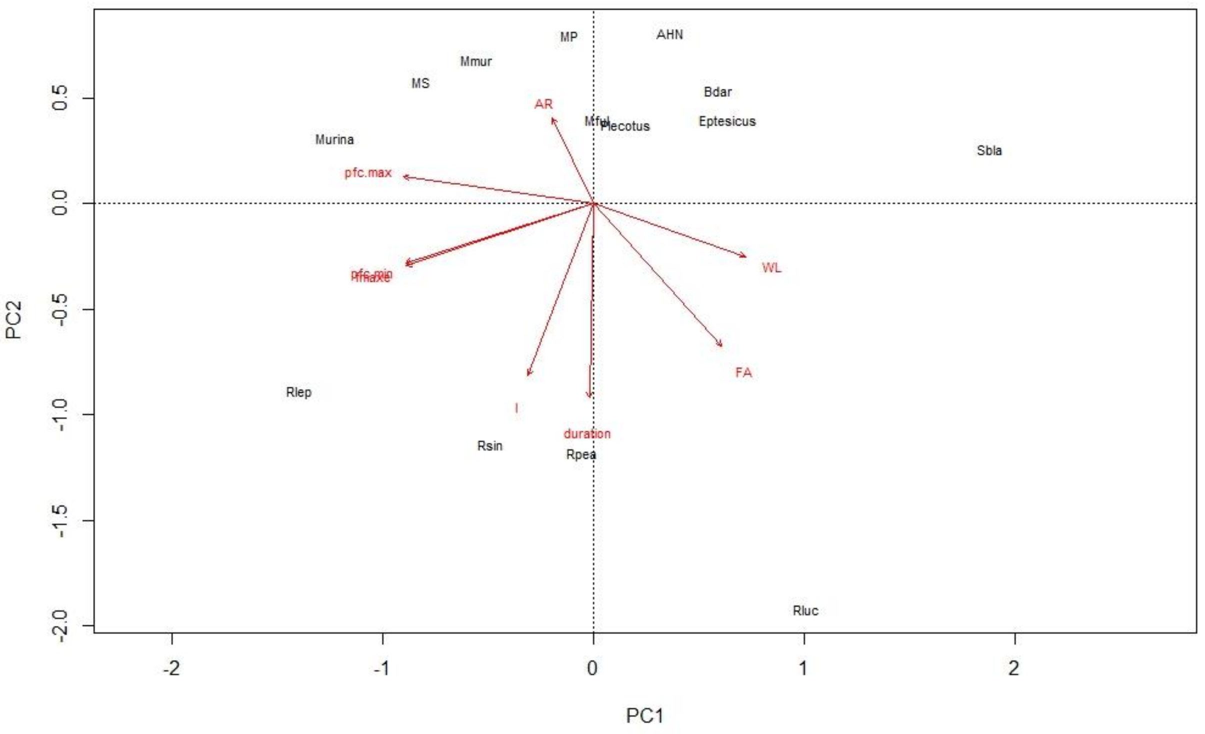
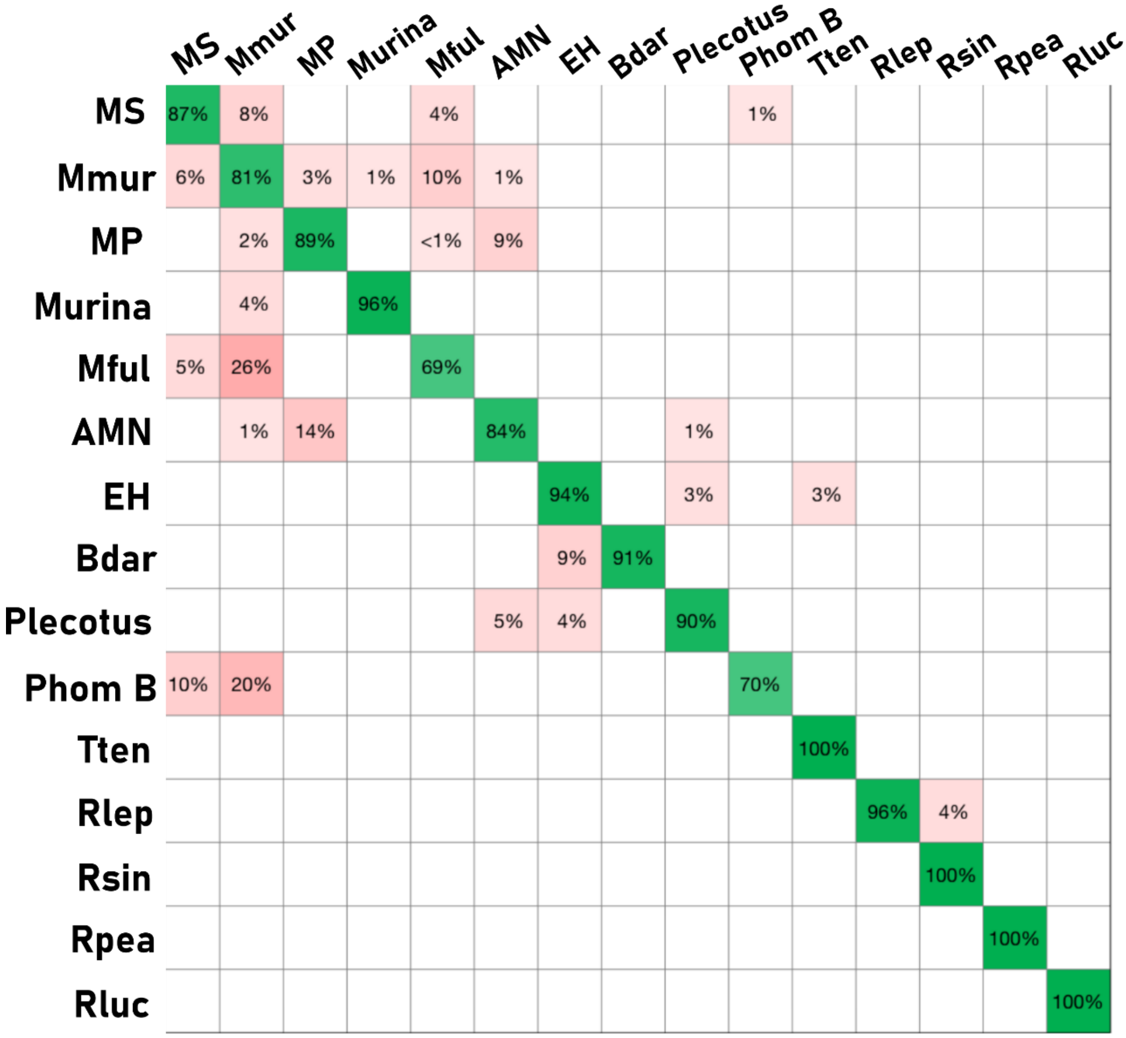


Fig. S3 PCA ordination plot of sonotypes based on their traits listed in Table 1 of the main text. Notice the distinction between the rhinolophid bats (Rlep, Rsin, Rpea and Rluc) and the remaining bats in the assemblage.



	MS	Mmur	MP	Murina	Mful	AMN	EH	Bdar	Plecotus	Phom B	Tten	Rlep	Rsin	Rpea	Rluc
MS	87%	8%			4%					1%					
Mmur	6%	81%	3%	1%	10%	1%									
MP		2%	89%		<1%	9%									
Murina		4%		96%											
Mful	5%	26%			69%										
AMN		1%	14%			84%			1%						
EH							94%		3%		3%				
Bdar							9%	91%							
Plecotus						5%	4%		90%						
Phom B	10%	20%								70%					
Tten											100%				
Rlep												96%	4%		
Rsin													100%		
Rpea														100%	
Rluc															100%

Fig. S4 Confusion matrix showing success rates in classification of different species. Values in green show the percentage of calls that were correctly identified while the ones in red were misidentified to the corresponding species. For full forms of sonotypes, refer to Table 1. '*Plecotus homochrous B'* represents a high-pitched call of *Plecotus homochrous*.

Table S1. Number of sampling points at each habitat type within each elevational location.

Sampling location	**Forest**	**Forest edge**	**Open**	**Total**
Mandal **(1400-1600 m)**	3	2	3	8
Ansuya **(2000-2200 m)**	3	1	-	4
Chopta **(2700-3000 m)**	1	3	1	5
Tungnath **(3500-3700 m)**	-	-	2	2

Chapter II

Chakravarty *et al.* 2023 *Journal of Animal Ecology*

SUPPORTING INFORMATION

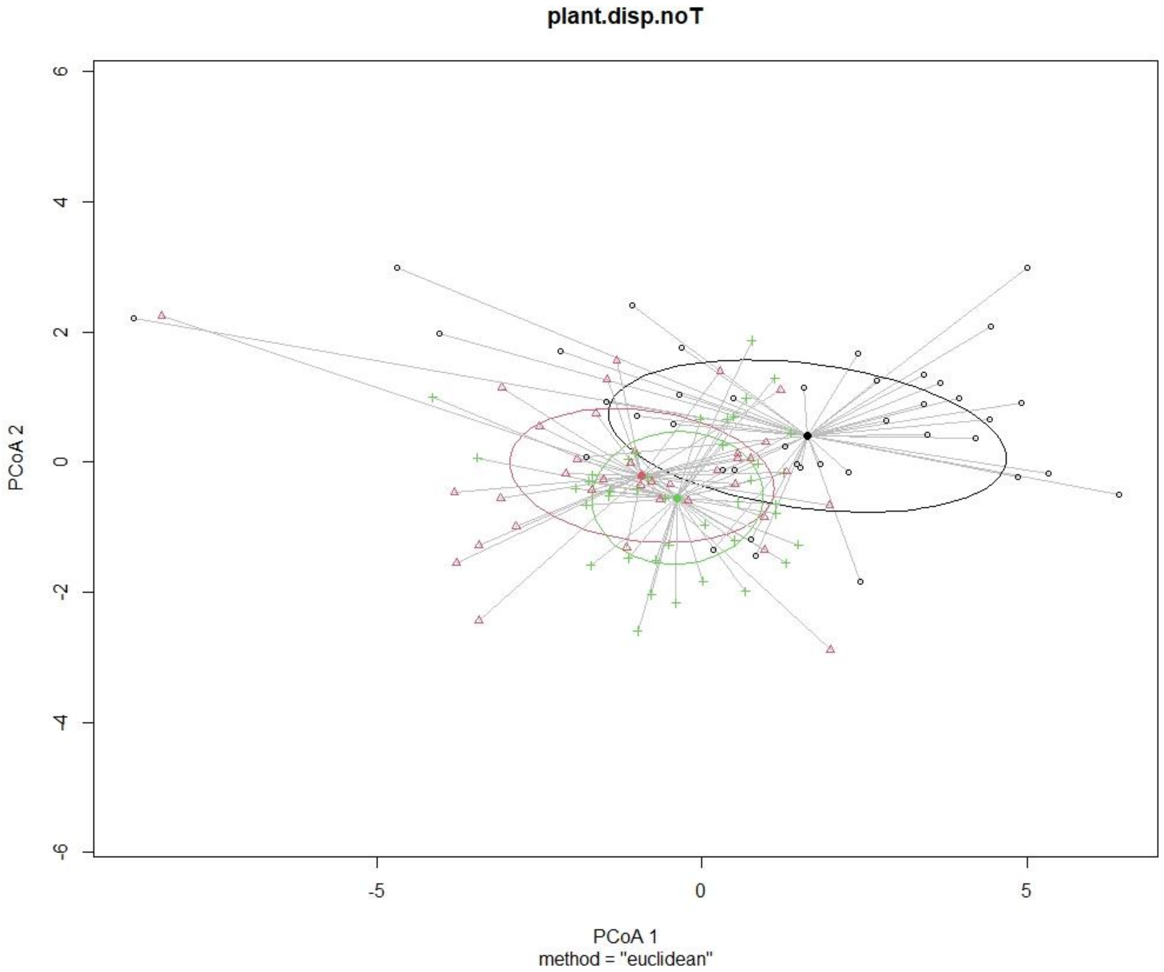


Fig. S1 Dispersion in ^{13}C and ^{15}N values of plant samples collected across the elevational gradient (Green crosses: low elevation, red triangles: intermediate elevation, and black dots: high elevation). The differences between low elevation and high elevation were significant.

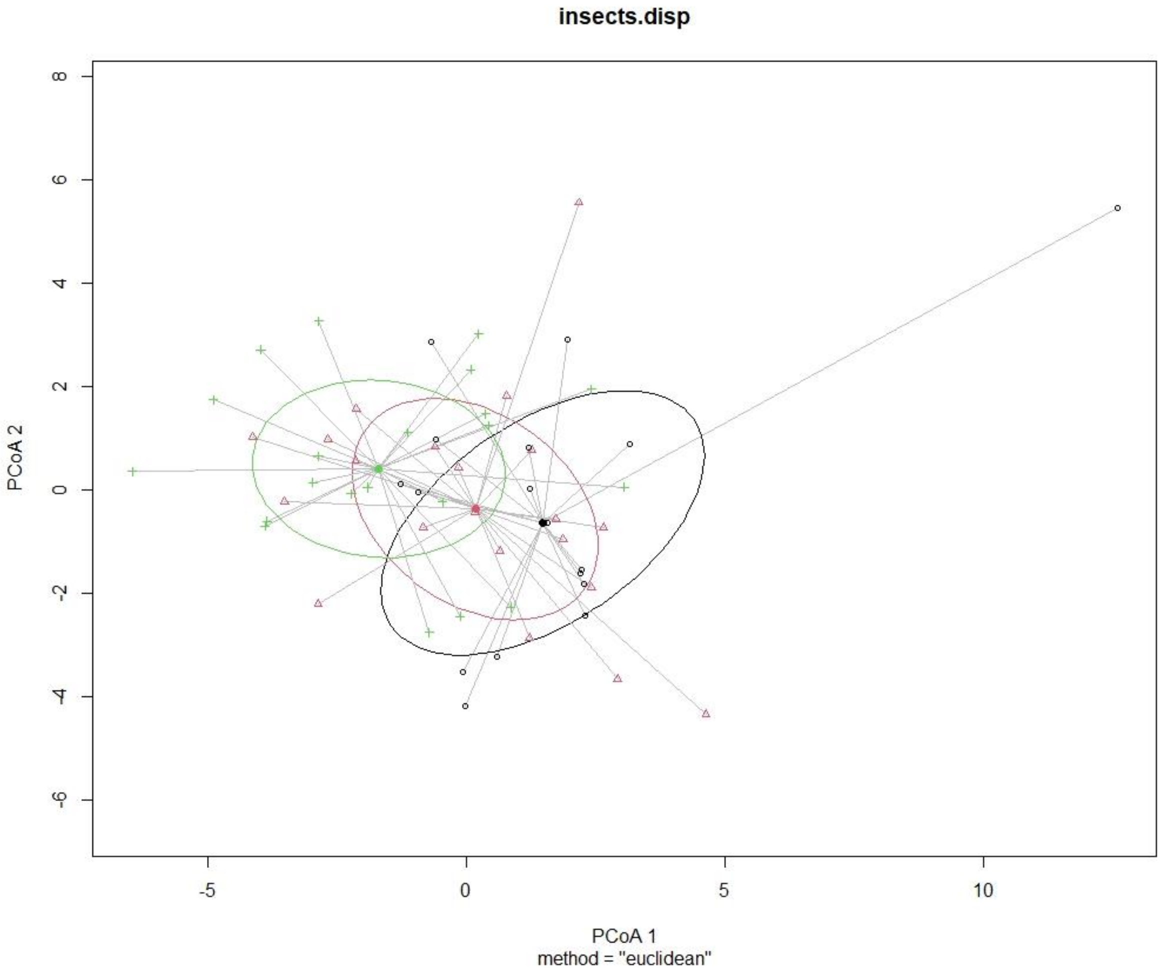


Fig. S2 Dispersion of ^{13}C and ^{15}N values in insect samples collected across the elevational gradient (Green crosses: low elevation, red triangles: intermediate elevation, and black dots: high elevation). No significant differences across elevations were obtained.

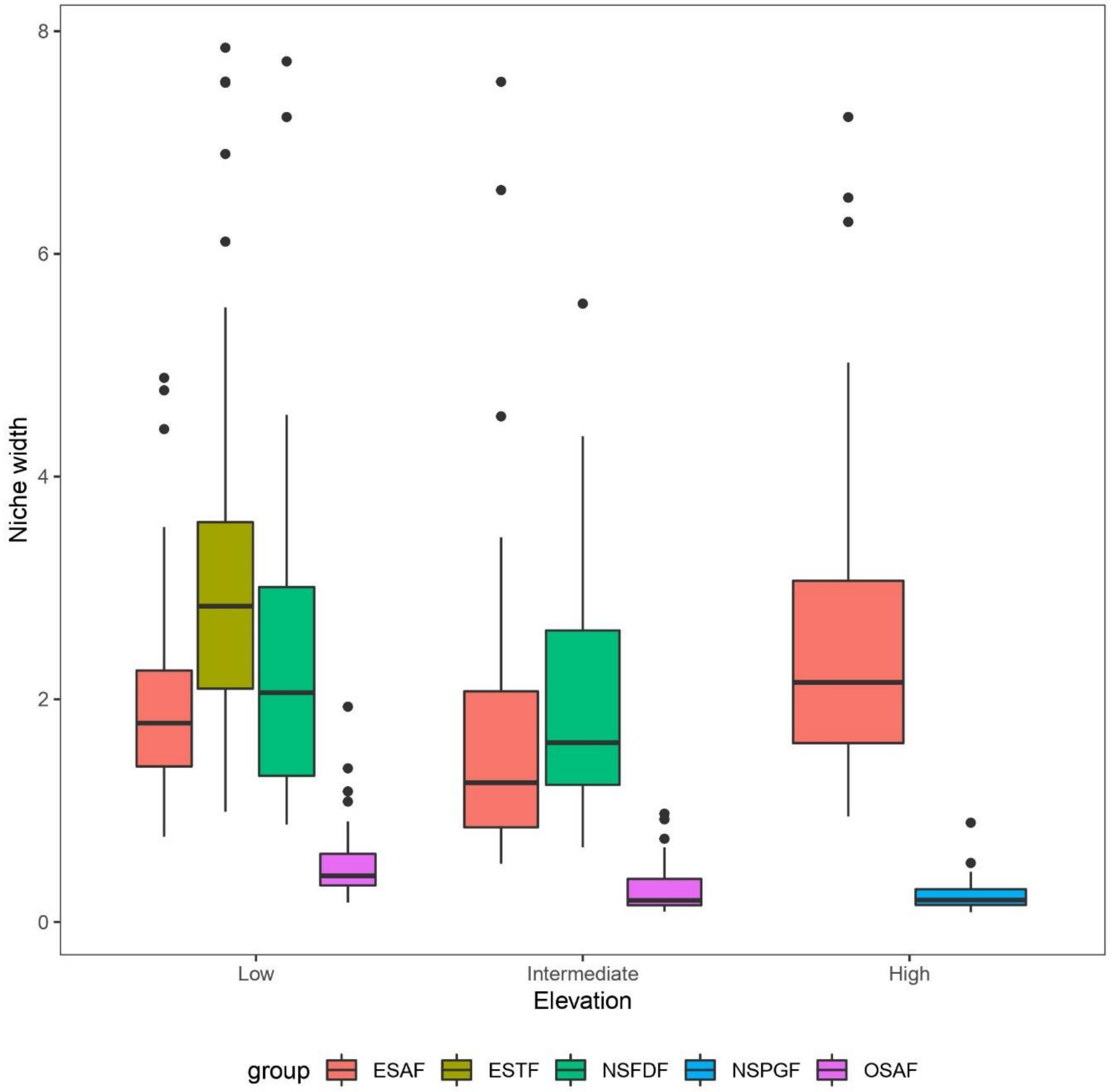


Fig. S3 Changes in niche width of functional groups across elevations when the sample size is reduced to four individuals per functional group per elevation.

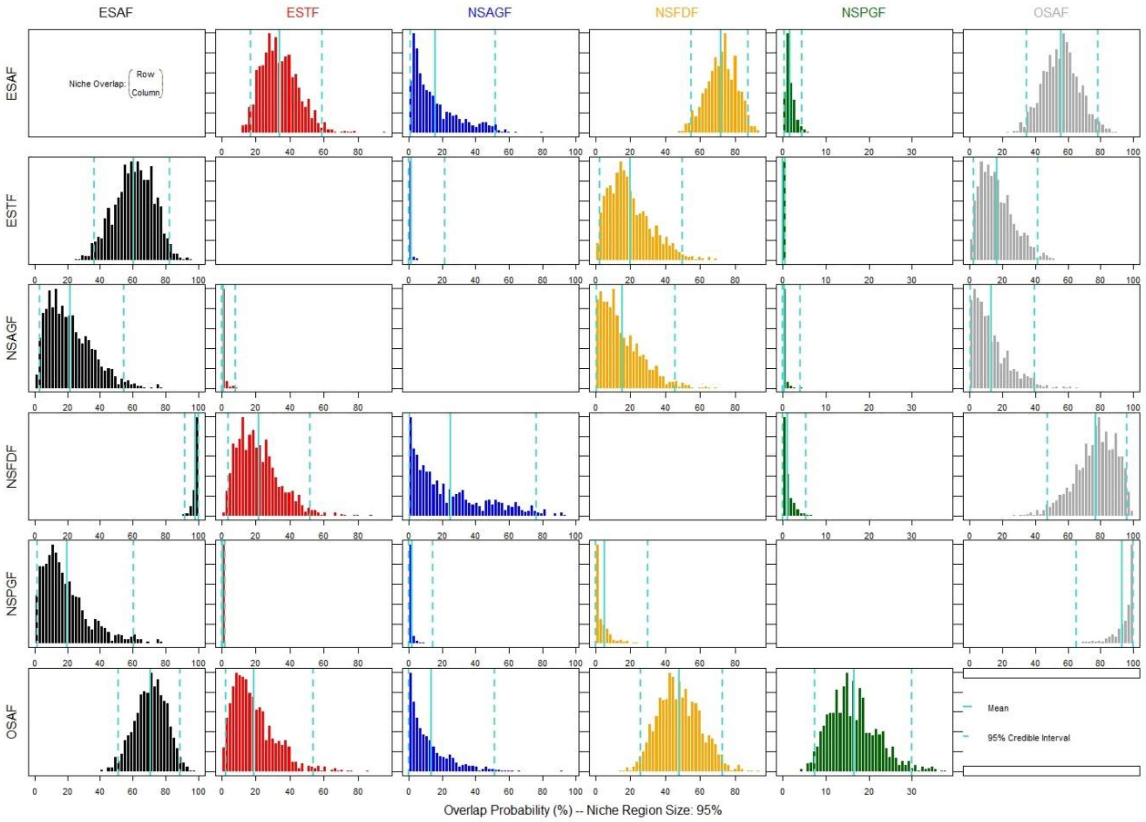


Fig. S4 Niche overlap probability of guild A (row) being in the dietary niche of guild B (column), calculated at the level of the assemblage. The solid blue line shows the mean and dotted lines represent 95% confidence intervals. ESAF = Edge-space foraging bats, ESTF = Trawling bats, NSAGF = Active gleaning bats, NSFDF = Flutter-detecting bats, NSPGF = Passive gleaning bats, OSAF = Open-space foraging bats.

Table S1 Mean values of δ 13C and δ 15N of plant samples collected across elevations.

Elevation	**Mean δ 13C**	**Mean δ 15N**
Low	-29.97	-2.56
Intermediate	-29.80	-1.78
High	-28.54	-4.05

Table S2 Niche overlap probabilities for guilds at low elevation

Guild B

Guild A	**Edge-space foraging**	**Trawling**	**Flutter-detecting**	**Open-space foraging**
Edge-space foraging	-	37.71	66.20	72.43
Trawling	64.53	-	20.87	32.70
Flutter-detecting	97.38	24.53	-	89.53
Open-space foraging	76.62	26.85	49.30	-

Table S3 Mean niche overlap probabilities for guilds at intermediate elevation

	Guild B		
Guild A	**Edge-space foraging**	**Flutter-detecting**	**Open-space foraging**
Edge-space foraging	-	84.13	2.93
Flutter-detecting	67.85	-	6.95
Open-space foraging	8.49	29.99	-

Table S4 Mean niche overlap probabilities for guilds at high elevation

	Guild B	
Guild A	**Edge-space foraging**	**Passive-gleaning**
Edge-space foraging	-	1.34
Passive-gleaning	27.58	-

Chapter III

Chakravarty et al. Mountain Bats (in prep)

SUPPLEMENTARY INFORMATION

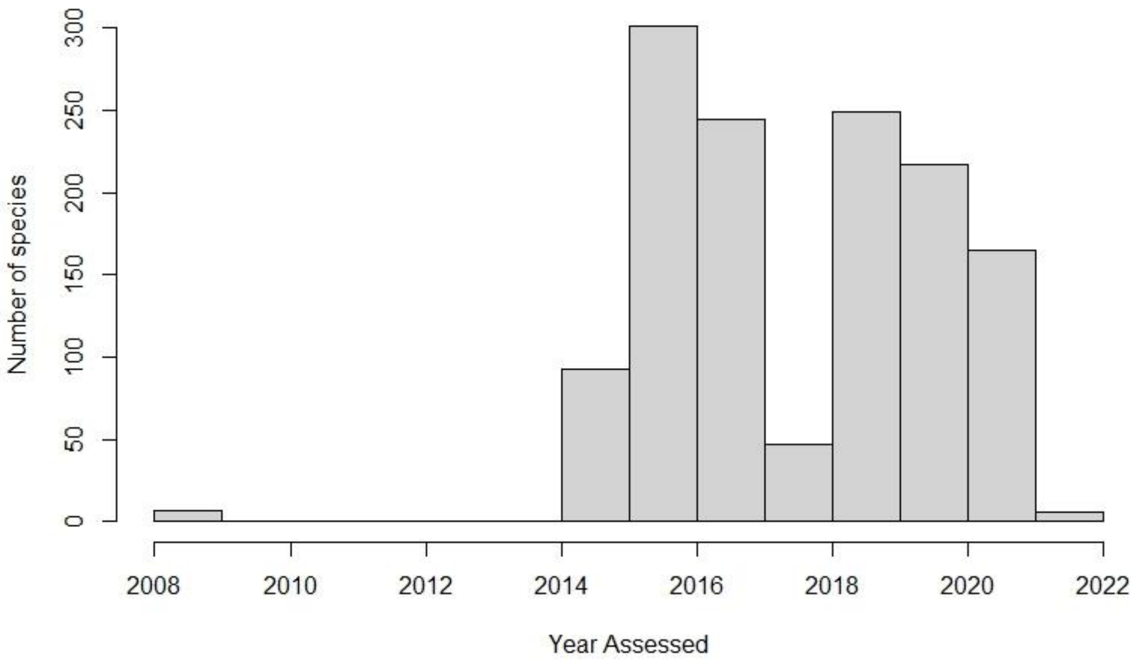


Fig S1 Number of species that were assessed by the IUCN in a given year in our dataset. Most species were assessed after 2014.

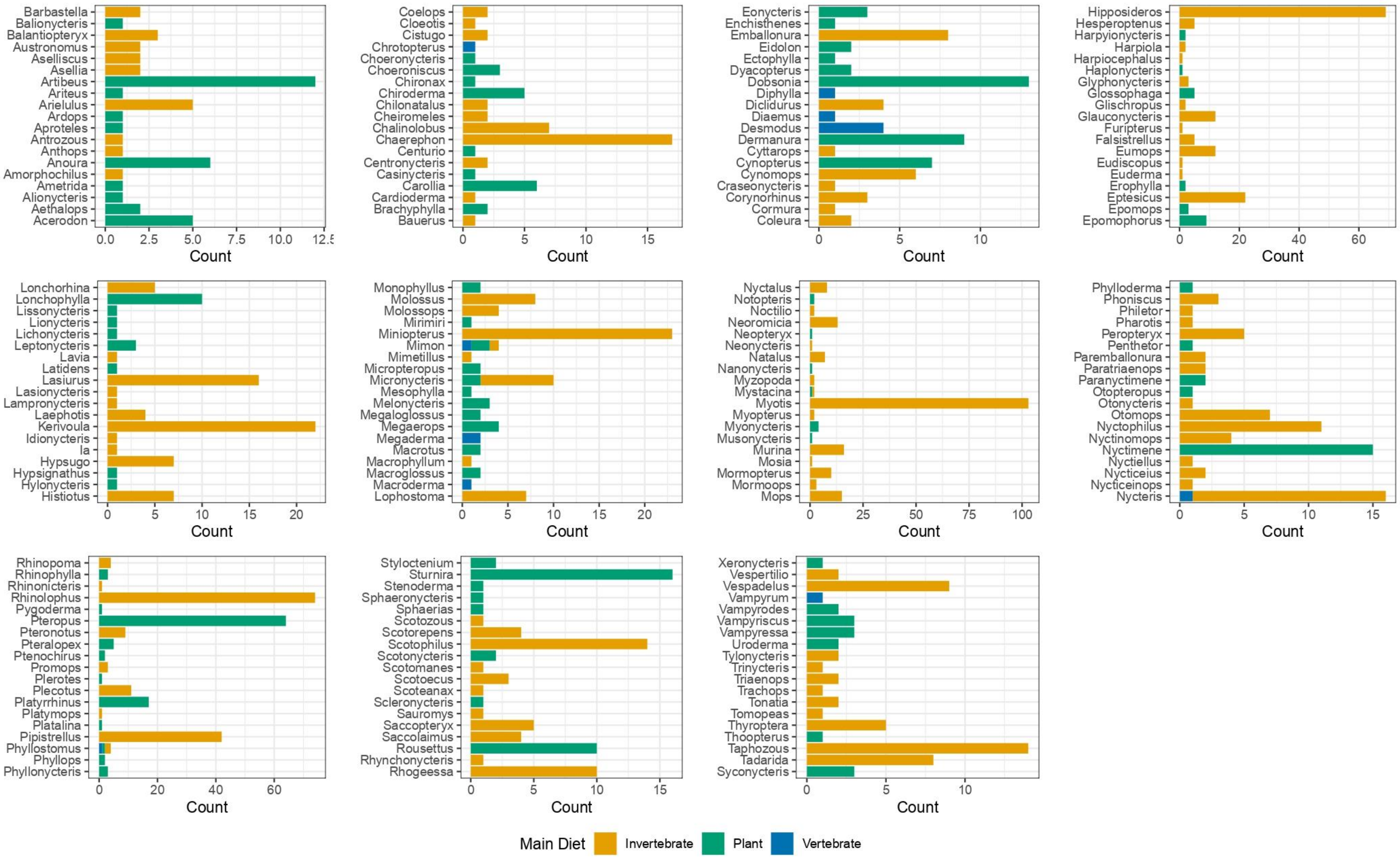


Fig. S2 Barplots showing the main diets of all bat genera in the PHYLACINE 1.2 database

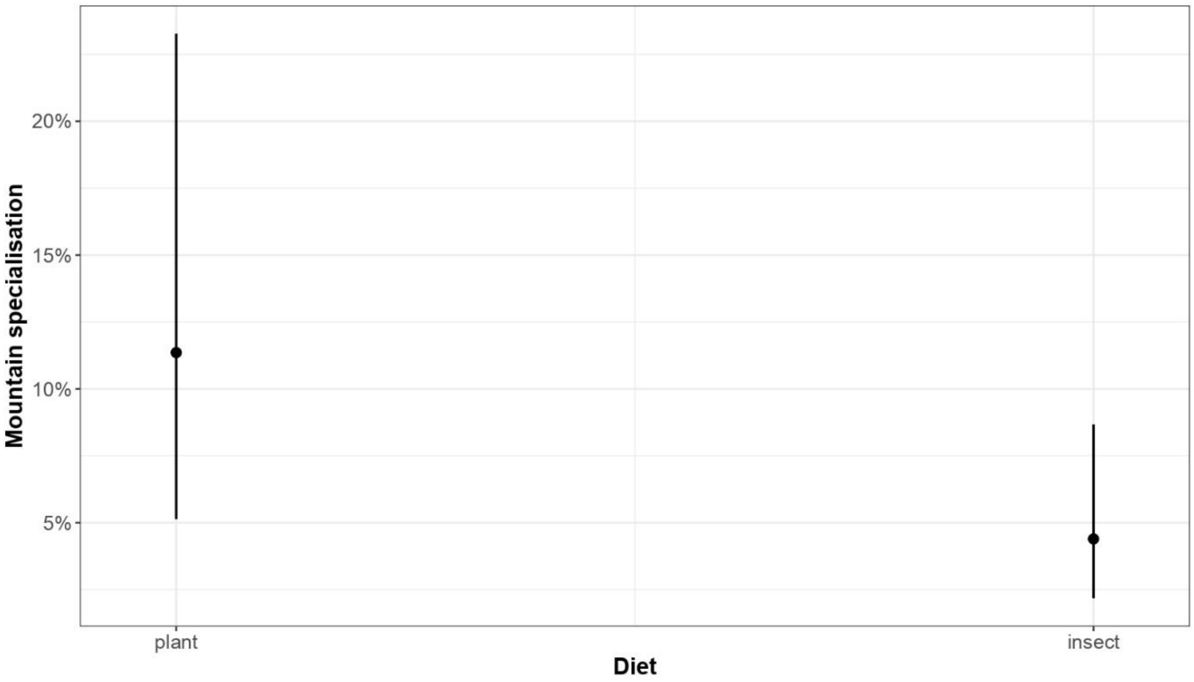


Fig. S3 Probability of a bat species (mean ± 95% confidence interval) being a mountain specialist with a plant vs insect diet.

Table S1 Names of species in the PHYLACINE 1.2 database whose names were updated to match the taxonomy used by the IUCN.

Sno.	**Scientific name in PHYLACINE**	**Scientific name in IUCN**
1	*Arielulus aureocollaris*	*Thainycteris aureocollaris*
2	*Eptesicus nasutus*	*Rhyneptesicus nasutus*
3	*Falsistrellus affinis*	*Hypsugo affinis*
4	*Hipposideros commersoni*	*Macronycteris commersoni*
5	*Hipposideros gigas*	*Macronycteris gigas*
6	*Hipposideros thomensis*	*Macronycteris thomensis*
7	*Hipposideros vittatus*	*Macronycteris vittatus*
8	*Megaderma lyra*	*Lyroderma lyra*
9	*Mimon crenulatum*	*Gardnerycteris crenulatum*
10	*Mimon koepckeae*	*Gardnerycteris koepckeae*
11	*Mormopterus beccarii*	*Ozimops beccarii*
12	*Mormopterus loriae*	*Ozimops loriae*

13	*Mormopterus norfolkensis*	*Micronomus norfolkensis*
14	*Mormopterus planiceps*	*Ozimops planiceps*
15	*Pipistrellus alaschanicus*	*Hypsugo alaschanicus*
16	*Pipistrellus arabicus*	*Hypsugo arabicus*
17	*Pipistrellus ariel*	*Hypsugo ariel*
18	*Pipistrellus cadornae*	*Hypsugo cadornae*
19	*Pipistrellus eisentrauti*	*Hypsugo eisentrauti*
20	*Pipistrellus hesperus*	*Parastrellus hesperus*
21	*Pipistrellus musciculus*	*Hypsugo musciculus*
22	*Pipistrellus pulveratus*	*Hypsugo pulveratus*
23	*Pipistrellus subflavus*	*Perimyotis subflavus*
24	*Pteropus leucopterus*	*Desmalopex leucopterus*
25	*Rhogeessa alleni*	*Baeodon alleni*
26	*Rhogeessa gracilis*	*Baeodon gracilis*
27	*Rousettus bidens*	*Boneia bidens*

Table S2 Species in the IUCN dataset that were missing from the PHYLACINE 1.2 database. The main diet was correlated with the genus in each of these genera (see Fig. S2 for details). Therefore, these species were also assigned the same diet as their congeners.

Genus	**Species**	**Main diet**
Anoura	*Anoura aequatoris* *Anoura cadenai* *Anoura peruana*	Plant
Artibeus	*Artibeus aequatorialis*	Plant
Asellia	*Asellia arabica* *Asellia italosomalica*	Insect
Balionycteris	*Balionycteris seimundi*	Plant
Barbastella	*Barbastella beijingensis* *Barbastella darjelingensis*	Insect

Carollia	*Carollia benkeithi* *Carollia monohernandezi*	Plant
Casinycteris	*Casinycteris campomaanensis*	Plant
Chaerephon	*Chaerephon atsinanana*	Insect
Chilonatalus	*Chilonatalus macer*	Insect
Chiroderma	*Chiroderma vizottoi*	Plant
Coleura	*Coleura kibomalandy*	Insect
Dermanura	*Dermanura bogotensis* *Dermanura rava*	Plant
Desmalopex	*Desmalopex microleucopterus*	Plant
Dobsonia	*Dobsonia magna*	Plant
Dryadonycteris	*Dryadonycteris capixaba*	Plant
Dyacopterus	*Dyacopterus rickarti*	Plant
Eptesicus	*Eptesicus anatolicus* *Eptesicus kobayashii* *Eptesicus ognevi* *Eptesicus pachyomus* *Eptesicus taddeii*	Insect
Eumops	*Eumops delticus* *Eumops ferox* *Eumops nanus*	Insect
Glischropus	*Glischropus bucephalus*	Insect
Hipposideros	*Hipposideros alongensis* *Hipposideros atrox* *Hipposideros einnaythu* *Hipposideros gentilis* *Hipposideros griffini* *Hipposideros khasiana*	Insect

	Hipposideros nicobarulae *Hipposideros pendleburyi* *Hipposideros tephrus*	
Hypsugo	*Hypsugo bemainty* *Hypsugo dolichodon* *Hypsugo lanzai*	Insect
Kerivoula	*Kerivoula crypta* *Kerivoula depressa* *Kerivoula dongduongana* *Kerivoula furva*	Insect
Lasiurus	*Lasiurus salinae*	Insect
Lichonycteris	*Lichonycteris degener*	Plant
Lonchophylla	*Lonchophylla cadenai* *Lonchophylla fornicata* *Lonchophylla orienticollina* *Lonchophylla pattoni* *Lonchophylla peracchii*	Plant
Micronycteris	*Micronycteris yatesi*	Insect
Miniopterus	*Miniopterus aelleni* *Miniopterus ambohitrensis* *Miniopterus brachytragos* *Miniopterus egeri* *Miniopterus griffithsi* *Miniopterus maghrebensis* *Miniopterus mahafaliensis* *Miniopterus pallidus*	Insect
Molossus	*Molossus bondae*	Insect
Mops	*Mops bakarii* *Mops leucogaster* *Mops pusillus*	Insect

Mormopterus	*Mormopterus francoismoutoui*	Insect
Murina	*Murina annamitica* *Murina balaensis* *Murina beelzebub* *Murina bicolor* *Murina chrysochaetes* *Murina eleryi* *Murina feae* *Murina fionae* *Murina gracilis* *Murina harpioloides* *Murina jaintiana* *Murina lorelieae* *Murina pluvialis* *Murina recondita* *Murina shuipuensis* *Murina walstoni*	Insect
Myotis	*Myotis annatessae* *Myotis badius* *Myotis borneoensis* *Myotis diminutus* *Myotis escalerai* *Myotis federatus* *Myotis indochinensis* *Myotis izecksohni* *Myotis lavali* *Myotis longicaudatus* *Myotis petax* *Myotis peytoni* *Myotis rufoniger*	Insect

	Myotis secundus *Myotis sibiricus* *Myotis soror* *Myotis weberi*	
Neoromicia	*Neoromicia isabella* *Neoromicia robertsi* *Neoromicia roseveari*	Insect
Nyctimene	*Nyctimene wrightae*	Plant
Nyctophilus	*Nyctophilus corbeni* *Nyctophilus daedalus* *Nyctophilus major* *Nyctophilus shirleyae*	Insect
Otomops	*Otomops harrisoni*	Insect
Otonycteris	*Otonycteris leucophaea*	Insect
Ozimops	*Ozimops cobourgianus* *Ozimops halli* *Ozimops kitcheneri* *Ozimops lumsdenae* *Ozimops petersi* *Ozimops ridei*	Insect
Paratriaenops	*Paratriaenops pauliani*	Insect
Phoniscus	*Phoniscus aerosa*	Insect
Pipistrellus	*Pipistrellus aladdin* *Pipistrellus grandidieri* *Pipistrellus sturdeei*	Insect
Platyrrhinus	*Platyrrhinus angustirostris* *Platyrrhinus fusciventris* *Platyrrhinus incarum*	Plant
Plecotus	*Plecotus ariel* *Plecotus homochrous*	Insect

	Plecotus kozlovi *Plecotus strelkovi* *Plecotus turkmenicus* *Plecotus wardi*	
Pteropus	*Pteropus ennisae* *Pteropus pelagicus*	Plant
Rhinolophus	*Rhinolophus belligerator* *Rhinolophus chiewkweeae* *Rhinolophus cohenae* *Rhinolophus damarensis* *Rhinolophus huananus* *Rhinolophus indorouxii* *Rhinolophus kahuzi* *Rhinolophus mabuensis* *Rhinolophus mcintyrei* *Rhinolophus microglobosus* *Rhinolophus mossambicus* *Rhinolophus perditus* *Rhinolophus proconsulis* *Rhinolophus schnitzleri* *Rhinolophus smithersi* *Rhinolophus tatar* *Rhinolophus thailandensis* *Rhinolophus willardi* *Rhinolophus xinanzhongguoensis*	Insect
Rhinopoma	*Rhinopoma cystops* *Rhinopoma hadramauticum*	Insect
Rhogeessa	*Rhogeessa bickhami* *Rhogeessa menchuae* *Rhogeessa velilla*	Insect

Scotonycteris	*Scotonycteris bergmansi* *Scotonycteris occidentalis*	Plant
Scotophilus	*Scotophilus andrewreborii* *Scotophilus ejetai* *Scotophilus livingstonii* *Scotophilus trujilloi*	Insect
Setirostris	*Setirostris eleryi*	Insect
Sturnira	*Sturnira angeli* *Sturnira bakeri* *Sturnira burtonlimi* *Sturnira hondurensis* *Sturnira parvidens* *Sturnira paulsoni*	Plant
Submyotodon	*Submyotodon latirostris*	Insect
Thoopterus	*Thoopterus suhaniahae*	Plant
Triaenops	*Triaenops afer* *Triaenops parvus*	Insect
Tylonycteris	*Tylonycteris pygmaeus*	Insect

Chapter III

Chakravarty et al. Mountain Bats (in prep)

Appendix

Table 1 List of all mountain specialist bat species (>75% distribution range on mountains). Species highlighted in bold within grey cells are high elevation specialists (Lowest elevation >1000 m on temperate mountains, >1500 m on subtropical mountains, and >2000 m on tropical mountains). * indicates island endemic species shortlisted for high priority in research by Conenna et al. (2017)

Species	**Family**	**% area in mountain**	**IUCN Status**	**Lowest elevation**	**Highest elevation**	**Main diet**	**Broad distribution**
Acerodon celebensis *	Pteropodidae	80.31	VU	0	1500	fruit	Sulawesi and neighbouring islands
Anoura aequatoris	Phyllostomidae	82.95	LC	600	1500	nectar	tropical Andes
Anoura cadenai	Phyllostomidae	99.07	DD	800	1600	nectar	western slope of Andes from Colombia to Ecuador
Anoura cultrata	Phyllostomidae	90.90	LC	50	2600	nectar	cloud forest species from Central America through northern Andes
Anoura fistulata	Phyllostomidae	85.08	DD	1175	2510	nectar	cloud forest species of eastern and western Andean slopes of Ecuador.
Anoura latidens	Phyllostomidae	78.68	LC	50	2100	nectar	northern Andes, Guyana highlands
Anoura luismanueli	Phyllostomidae	99.91	LC	1100	2400	nectar	northern Andes
Anoura peruana	Phyllostomidae	82.30	LC	100	3800	nectar	Ecuador, Peru, Bolivia Andes
Arielulus torquatus *	Vespertilionidae	75.08	LC	178	1840	insect	Taiwan endemic
Artibeus hirsutus	Phyllostomidae	75.20	LC	NA	NA	fruit	Pacific Mexico
Aselliscus stoliczkanus	Hipposideridae	83.32	LC	20	2100	insect	peninsular Southeast Asia
Austronomus kuboriensis *	Molossidae	91.72	LC	1900	2900	insect	New Guinea endemic

Baeodon alleni	Vespertilionidae	81.11	LC	125	1990	insect	Mexico endemic
Baeodon gracilis	Vespertilionidae	91.30	LC	600	2000	insect	Mexico endemic
Barbastella darjelingensis	Vespertilionidae	76.92	LC	0	2350	insect	Afghanistan and Himalayas.
Boneia bidens	Pteropodidae	85.99	VU	200	1060	fruit	Sulawesi and neighbouring islands
Carollia manu	Phyllostomidae	99.36	LC	1300	2250	fruit	Montane Peru
Carollia monohernandezi	Phyllostomidae	100.00	DD	1200	1200	fruit	only one location in Colombia
Dobsonia exoleta *	Pteropodidae	78.98	LC	NA	NA	fruit	Sulawesi
Dyacopterus rickarti	Pteropodidae	75.51	EN	550	1680	fruit	Philippines
Eptesicus andinus	Vespertilionidae	75.59	LC	100	3300	insect	tropical Andes
Eptesicus japonensis *	Vespertilionidae	100.00	VU	700	NA	insect	Montane Japan
Eptesicus pachyotis	Vespertilionidae	78.42	LC	NA	NA	insect	China, Myanmar and Nepal
Eptesicus tatei	Vespertilionidae	100.00	DD	NA	NA	insect	1695 and 3065 m from Himalayas
Eudiscoderma thongareeae	Megadermatidae	100.00	CR	0	0	NA	endemic to southern Thailand
Eudiscopus denticulus	Vespertilionidae	75.97	LC	NA	NA	insect	peninsular Southeast Asia
Gardnerycteris koepckeae	Phyllostomidae	100.00	DD	1600	1600	insect	Peru
Glischropus javanus *	Vespertilionidae	100.00	DD	NA	NA	insect	Java
Glossophaga morenoi	Phyllostomidae	75.38	LC	0	1500	nectar	Mexico
Harpiola grisea	Vespertilionidae	100.00	DD	1367	1692	insect	Indian Himalayas
Harpiola isodon *	Vespertilionidae	100.00	LC	400	2600	insect	Taiwan
Harpyionycteris celebensis *	Pteropodidae	83.87	NT	0	2100	fruit	Sulawesi
Hesperoptenus gaskelli *	Vespertilionidae	100.00	DD	0	500	insect	Sulawesi

Hipposideros corynophyllus *	Hipposideridae	78.81	LC	20	2700	insect	Papua New Guinea
Hipposideros einnaythu	Hipposideridae	92.15	DD	NA	NA	insect	southern Myanmar
Hipposideros inexpectatus *	Hipposideridae	93.56	DD	NA	NA	insect	Sulawesi
Hipposideros khaokhouayensis	Hipposideridae	85.79	VU	180	400	insect	Cambodia
Hipposideros pelingensis *	Hipposideridae	80.13	NT	0	1000	insect	Sulawesi
Hipposideros pomona	Hipposideridae	87.88	EN	0	1200	insect	Western Ghats endemic, India
Hipposideros rotalis	Hipposideridae	89.65	LC	NA	NA	insect	Laos
Hipposideros scutinares	Hipposideridae	91.97	VU	NA	NA	insect	Vietnam
Histiotus humboldti	Vespertilionidae	79.48	DD	1500	2600	insect	northern South America
Histiotus magellanicus	Vespertilionidae	76.08	LC	500	1200	insect	temperate Andes
Hypsugo anthonyi	**Vespertilionidae**	**100.00**	**DD**	**2134**	**2134**	**insect**	**northern Myanmar**
Hypsugo arabicus	Vespertilionidae	88.79	DD	NA	NA	insect	southern Arabian peninsula
Ia io	Vespertilionidae	87.62	NT	200	1700	insect	Himalayas, China, SE Asia
Kerivoula crypta	Vespertilionidae	78.24	LC	0	1062	insect	southern Western Ghats endemic
Kerivoula eriophora	Vespertilionidae	100.00	DD	NA	NA	insect	Ethiopia
Kerivoula kachinensis	Vespertilionidae	75.91	LC	150	800	insect	peninsular Southeast Asia
Kerivoula krauensis	Vespertilionidae	79.92	NT	0	1600	insect	Southeast Asia
Lasiurus ebenus *	Vespertilionidae	100.00	DD	NA	NA	insect	southeastern Brazil
Latidens salimalii	Pteropodidae	88.31	EN	800	1100	fruit	southern Western Ghats endemic
Lonchophylla chocoana	Phyllostomidae	100.00	DD	NA	NA	nectar	Ecuador and Colombia
Lonchophylla orcesi	Phyllostomidae	100.00	DD	1200	1200	nectar	Ecuador

Miniopterus petersoni *	Miniopteridae	83.03	DD	0	550	insect	Madagascar endemic
Mops mops	Molossidae	77.64	NT	NA	NA	insect	peninsular Malaysia
Mormopterus kalinowskii	Molossidae	89.91	LC	0	1830	insect	Pacific slope of Andes
Mormopterus phrudus	Molossidae	100.00	VU	1800	3000	insect	Peruvian Andes
Murina annamitica	Vespertilionidae	83.70	LC	500	1300	insect	peninsular Southeast Asia
Murina aurata	Vespertilionidae	83.44	DD	1154	2300	insect	China, South and SE Asia
Murina balaensis	Vespertilionidae	100.00	CR	340	340	insect	southern Thailand
Murina bicolor	Vespertilionidae	99.04	LC	400	3350	insect	Taiwan
Murina chrysochaetes	Vespertilionidae	100.00	DD	978	1950	insect	northern Vietnam, southern China
Murina eleryi	Vespertilionidae	100.00	LC	200	1140	insect	northern Vietnam
Murina feae	Vespertilionidae	75.89	LC	340	1250	insect	peninsular Southeast Asia
Murina fusca	Vespertilionidae	99.97	DD	NA	NA	insect	northeastern China
Murina gracilis	Vespertilionidae	99.99	LC	1000	3000	insect	Taiwan
Murina harpioloides	Vespertilionidae	100.00	EN	1400	1800	insect	southern Vietnam
Murina harrisoni	Vespertilionidae	77.08	LC	NA	NA	insect	peninsular Southeast Asia
Murina huttoni	Vespertilionidae	85.87	LC	1450	2500	insect	Himalayas and SE Asia
Murina lorelieae	Vespertilionidae	100.00	DD	978	1583	insect	southern China
Murina recondita	Vespertilionidae	99.08	LC	40	2200	insect	Taiwan
Murina shuipuensis	Vespertilionidae	100.00	DD	NA	NA	insect	southern China
Murina tubinaris	**Vespertilionidae**	**98.49**	**DD**	**1200**	**2650**	**insect**	**Kashmir and Pakistan**
Musonycteris harrisoni	Phyllostomidae	89.63	VU	0	1700	nectar	western Mexico
Myotis aelleni	Vespertilionidae	100.00	DD	NA	NA	insect	western Argentina
Myotis annamiticus	Vespertilionidae	100.00	DD	NA	NA	insect	Annamite Mountains, Vietnam
Myotis annatessae	Vespertilionidae	89.27	DD	200	1300	insect	Laos and Vietnam
Myotis annectans	Vespertilionidae	94.63	LC	260	1100	insect	Himalayas and SE Asia

Myotis atacamensis	Vespertilionidae	86.28	EN	0	2250	insect	Peru and northern Chile
Myotis badius	Vespertilionidae	100.01	DD	NA	NA	insect	southern China
Myotis cobanensis	Vespertilionidae	85.35	DD	1305	1305	insect	Guatemala
Myotis csorbai	Vespertilionidae	95.33	DD	1300	1700	insect	Nepal Himalayas
Myotis federatus	Vespertilionidae	75.90	DD	0	900	insect	peninsular Malaysia
Myotis hermani	Vespertilionidae	92.16	DD	0	500	insect	southern Thailand
Myotis keenii	Vespertilionidae	87.82	LC	NA	NA	insect	western British Columbia, Canada
Myotis longipes	Vespertilionidae	91.52	DD	300	2000	insect	Himalayas, China, SE Asia
Myotis montivagus	Vespertilionidae	88.60	DD	200	2000	insect	Myanmar and Laos
Myotis peninsularis	Vespertilionidae	99.14	EN	0	2200	insect	southern Baja California
Myotis planiceps	**Vespertilionidae**	**89.96**	**EN**	**2100**	**3200**	**insect**	**central Mexico**
Myotis scotti	Vespertilionidae	81.66	VU	1300	2500	insect	Ethiopia
Myotis secundus	Vespertilionidae	98.94	LC	40	2600	insect	Taiwan
Myotis soror	**Vespertilionidae**	**100.00**	**DD**	**2100**	**2600**	**insect**	**central Taiwan**
Myotis weberi	Vespertilionidae	83.90	DD	0	1609	insect	Philippines
Neopteryx frosti *	Pteropodidae	100.00	EN	NA	NA	fruit	Sulawesi
Nyctalus montanus	Vespertilionidae	82.73	LC	680	1692	insect	Himalayas, Hindu Kush
Nyctimene certans *	Pteropodidae	78.79	LC	800	2800	fruit	central Papua New Guinea
Nyctimene masalai *	Pteropodidae	91.03	DD	NA	NA	fruit	Bismarck Archipelago
Nyctophilus microdon *	Vespertilionidae	98.18	LC	1900	2200	insect	central Papua New Guinea
Pipistrellus collinus *	Vespertilionidae	80.70	LC	700	3000	insect	New Guinea
Pipistrellus minahassae *	Vespertilionidae	100.00	DD	NA	NA	insect	Sulawesi
Platalina genovensium	Phyllostomidae	83.88	NT	50	2300	nectar	western slope of Andes
Platyrrhinus nigellus	Phyllostomidae	93.83	LC	NA	NA	fruit	tropical Andes
Platyrrhinus nitelinea	Phyllostomidae	76.84	DD	36	1100	fruit	Colombia, Ecuador

Platyrrhinus umbratus	Phyllostomidae	93.47	DD	250	2000	fruit	northern South America
Plecotus ariel	Vespertilionidae	81.67	DD	NA	NA	insect	central China
Plecotus balensis	**Vespertilionidae**	**98.57**	**DD**	**2500**	**3000**	**insect**	**Ethiopia**
Plecotus homochrous	**Vespertilionidae**	**89.42**	**DD**	**2000**	**3938**	**insect**	**Hindu Kush, western Himalayas**
Plecotus taivanus *	Vespertilionidae	95.38	NT	1000	2800	insect	Taiwan
Plecotus teneriffae *	Vespertilionidae	76.06	VU	100	2300	insect	Canary Islands
Plecotus wardi	**Vespertilionidae**	**100.00**	**LC**	**1700**	**3600**	**insect**	**Hindu Kush, western Himalayas**
Pteropus ennisae	Pteropodidae	91.03	VU	0	1200	fruit	Bismarck Archipelago
Rhinolophus belligerator	Rhinolophidae	100.00	EN	0	NA	insect	Sulawesi
Rhinolophus convexus	Rhinolophidae	100.00	DD	NA	NA	insect	Laos and southern Thailand
Rhinolophus formosae *	Rhinolophidae	88.77	LC	0	2800	insect	Taiwan
Rhinolophus hilli	Rhinolophidae	100.00	CR	1750	2512	insect	southwestern Rwanda
Rhinolophus kahuzi	**Rhinolophidae**	**100.00**	**EN**	**2600**	**2600**	**insect**	**Mount Kahuzi, eastern Democratic Republic of Congo**
Rhinolophus maclaudi	Rhinolophidae	99.58	EN	NA	NA	insect	Guinea
Rhinolophus osgoodi	Rhinolophidae	90.58	LC	NA	NA	insect	southern China
Rhinolophus rex	Rhinolophidae	76.50	EN	NA	NA	insect	southern and central China
Rhinolophus schnitzleri	Rhinolophidae	100.01	DD	1550	1550	insect	southern China
Rhinolophus siamensis	Rhinolophidae	79.87	LC	NA	NA	insect	Laos, Vietnam, southern China
Rhinolophus tatar	Rhinolophidae	83.73	LC	0	NA	insect	Sulawesi
Rhinolophus thomasi	Rhinolophidae	75.08	LC	400	1100	insect	peninsular Southeast Asia

Rhinolophus xinanzhongguoensis	Rhinolophidae	100.00	NT	1500	1980	insect	southern China
Rhinolophus yunanensis	Rhinolophidae	75.96	LC	0	1231	insect	Myanmar and Thailand
Rhogeessa mira	Vespertilionidae	93.45	VU	125	340	insect	southern Mexico
Rousettus celebensis *	Pteropodidae	78.42	LC	0	1400	fruit	Sulawesi
Rousettus linduensis *	Pteropodidae	100.00	DD	NA	NA	fruit	central Sulawesi
Saccopteryx antioquensis	Emballonuridae	100.00	EN	650	1200	insect	northwestern Colombia
Scotophilus celebensis *	Vespertilionidae	83.91	DD	NA	NA	insect	Sulawesi
Scotophilus ejetai	Vespertilionidae	94.70	LC	NA	NA	insect	Ethiopia
Sphaerias blanfordi	Pteropodidae	78.97	LC	308	2710	fruit	Himalayas, southern China, SE Asia
Sturnira aratathomasi	Phyllostomidae	86.93	LC	1650	3165	fruit	Colombia, Ecuador, Peru
Sturnira bidens	Phyllostomidae	82.04	LC	1700	3000	fruit	Colombia, Ecuador, Peru
Sturnira bogotensis	Phyllostomidae	84.03	LC	1200	3100	fruit	Venezuela through Peru
Sturnira koopmanhilli	Phyllostomidae	96.36	DD	300	2000	fruit	Ecuador, Colombia
Sturnira mistratensis	Phyllostomidae	97.68	DD	0	980	fruit	northwestern Colombia
Sturnira mordax	Phyllostomidae	88.10	LC	100	3000	fruit	Costa Rica, Panama
Sturnira nana	Phyllostomidae	98.82	EN	1430	1670	fruit	Ecuador and Peru
Sturnira sorianoi	Phyllostomidae	75.21	DD	NA	NA	fruit	Venezuela, Bolivia
Styloctenium wallacei *	Pteropodidae	83.27	NT	0	1800	fruit	Sulawesi
Submyotodon latirostris	Vespertilionidae	100.00	LC	1000	3000	insect	Taiwan
Thainycteris aureocollaris	Vespertilionidae	87.90	LC	0	2000	insect	southern China, Laos, Vietnam

Thoopterus nigrescens *	Pteropodidae	77.70	LC	0	2400	fruit	Sulawesi
Thoopterus suhaniahae	Pteropodidae	83.04	LC	0	2100	fruit	Sulawesi
Tomopeas ravus	Molossidae	78.00	EN	0	2300	insect	Peru
Tylonycteris pygmaeus	Vespertilionidae	100.00	DD	NA	NA	insect	southern China