



Mountains host significantly more data deficient and threatened bat species than lowlands

Rohit Chakravarty^{1,2,3} · Viktoriia Radchuk¹ · Kulbhushansingh Suryawanshi^{3,4,5} · Christian C. Voigt¹

Received: 9 November 2023 / Revised: 6 October 2024 / Accepted: 11 October 2024
© The Author(s) 2024

Abstract

Mountains harbour one third of the world's biodiversity and much of it is under increasing anthropogenic pressure. Yet, global assessments of the occurrence, and threat status of most mountain taxa, especially elusive ones are lacking, thereby hindering conservation and research prioritisation. 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 examined bat species richness on mountains, species that predominantly occur in mountains ('mountain dwelling species'), and those restricted to upper montane and alpine regions within mountains ('highland dwelling species'). We also used published trait datasets to investigate the traits that are associated with mountain dwelling in bats. Globally, we identified 148 mountain dwelling and 46 highland dwelling bat species. Bat diversity is highest in the Northern Andes and Guiana Highlands. The mountain dwelling nature of bat species was found to be significantly associated with biogeographic realm. Importantly, our results show that mountain dwelling species are proportionately more data deficient than species that predominantly occur in lowlands. Additionally, highland dwelling species are proportionately more threatened than lowland species. Our results highlight a significant dearth of knowledge on mountain dwelling bat species. We conclude that more research is needed for bats specialised on mountain ecosystems. Our results draw attention towards improving the knowledge and protection of bat species that occur predominantly at high elevations across the world.

Communicated by Daniel Hending.

✉ Rohit Chakravarty
rohitchakravarty@ncf-india.org

¹ Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany

² Freie Universität Berlin, 14195 Berlin, Germany

³ Nature Conservation Foundation, 1311, "Amritha", 12th Main, Vijayanagar 1st Stage, Mysore 570 017, India

⁴ CIFAR Fellow in Future Flourishing Program, MaRS Centre, West Tower, 661 University Ave., 12 Suite 505, Toronto, ON M5G 1M1, Canada

⁵ Snow Leopard Trust, 4649 Sunnyside Ave N, Suite 325, Seattle, WA 98103, USA

Keywords Bats · Mountains · Threat status · Distribution · Data deficient · High elevation

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. Among these, land use change and tourism can 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 contaminated by inorganic and organic pollutants (Schmeller et al. 2022) while invasive species are altering the habitat and resources available to native fauna (Sharma et al. 2021a). Climate change is a more severe threat to mountain species than to species from lowlands (Schmeller et al. 2022), since mountain sites are warming faster than surrounding lowlands (Pepin et al. 2022). Climatic fluctuations and increasingly longer 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, which alter the ecosystems present (Alexander et al. 2015). The difficulty in conducting research in mountains in comparison to lowlands, prevents us from comprehensively studying the impacts of anthropogenic stressors on habitats at high elevations (Beniston et al. 2018).

Elevation is a key component 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). Species that are restricted to mountain tops 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). An elevational gradient study on Amazonian bird species found that over a period of 32 years, high elevation species had lost on average 110 m of elevational range (Urban 2018). Climate change models across taxa also predict a drastic reduction in the area of suitable habitat available for many species (Dirnböck et al. 2011; Razgour et al. 2021; Brambilla et al. 2022). Therefore, identifying conservation priorities for mountains necessitates focussing on three spatial dimensions (latitude, longitude, and elevation) and identifying species that are elevationally restricted. Sadly, the current level of protection along elevational gradients worldwide needs significant improvements to meet global biodiversity conservation targets (Elsen et al. 2018).

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. According to the International Union for Conservation of Nature (IUCN) a species is Data Deficient (DD) when there is “inadequate information to make a direct, or indirect assessment of its risk of extinction based on its

distribution and/or population status” (<https://www.iucnredlist.org/>). The data deficiency is likely to be aggravated if the taxon is inherently rare or elusive. DD 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.

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 potentially allowing them to track suitable climate and expand their elevation ranges in response to climate change faster than non-volant animals (LaVal 2004). Unfortunately, their nocturnal nature makes bats harder to study. Globally, 18% of all bat species are data deficient (Frick et al. 2020) and this problem may be exacerbated on rugged and remote mountain environments where monitoring species and populations is harder.

This study provides 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 mountains and highland habitats (upper montane and alpine regions), and investigate if these bats are more threatened or data deficient; and, (c) investigate the traits that are associated with mountain dwelling, specially focussing on body size, diet, and biogeographic realm.

Materials and methods

Spatial analyses

To calculate and map 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. Over 1300 of these species were assessed after 2014 (Fig. S1). Our data, therefore, represent almost 90% of the current known global bat diversity (Simmons and Cirranello 2022). We rasterised all bat distribution polygons at a fine-scale resolution of $1/6^\circ \times 1/6^\circ$ 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 latitude. This analysis was performed using the ‘fasterize()’ function of the ‘raster’ package (Hijmans 2022) in R. 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 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). We observed that the distribution polygons of 29 species were either improperly marked or projected. Additionally, their elevational range limits reported on the IUCN website suggested that they occur only in mountains but the distribution polygons did not intersect mountain polygons. We treated them as non-mountain dwelling species in further analyses. We acknowledge that the converse is also possible with IUCN data *i.e.* that distribution polygons may encompass mountains when the species may, in fact, be found in the lowland surrounding a mountain.

Definitions of categories and statistical analyses

Species that have at least 50% of their distribution range in mountains may be defined as species that predominantly occur on mountains. For a stricter cutoff, we defined a species as 'mountain dwelling' when $\geq 75\%$ of its distribution range was on mountains. Another study (Rahbek et al. 2019) used similar cutoffs to categorise the mountain affinity of different vertebrate taxa. To test how sensitive our analysis and findings were with respect to deviations from the 75% cutoff value, we conducted a sensitivity analysis using cutoff values of 50, 60, 70, and 80%.

We defined a 'highland dwelling species' as one that occurs exclusively in upper montane, subalpine and alpine habitats. These habitat zones are often zones of high endemism (Fjelds  1993; Noroozi et al. 2018; Sonne et al. 2022; Mendelsohn et al. 2023) but vary in elevation in different mountains. For example, the highlands of Fiji reach up to 1300 m above sea level (a.s.l), and have an upper montane region which would not be considered the same as the upper montane region of the Himalaya. Therefore, we refrained from using an elevation cutoff to define highland species. To classify species as 'highland dwelling', we looked for phrases/words such as "highland forest dependent", "endemic to highland areas", "montane or cloud forest", or "coniferous forest dwelling" (for tropical species) in the geographic range description in the IUCN species pages. We acknowledge that this approach depends on textual accuracy. Additionally, the improper distribution projections of 29 species mentioned above meant that some of those species were not classified as mountain dwelling (based on spatial overlap between the species distribution and mountains) but were classified as highland dwelling (based on textual descriptions). This is a caveat of our approach but we believe that going by textual descriptions of mountain habitats would perform better at identifying highland species at a global scale than a uniform global elevational cutoff.

Following the definition of IUCN, we considered a species as 'threatened' when it belonged to Vulnerable (VU), Endangered (EN) or Critically Endangered (CR) Red List categories (<https://www.iucnredlist.org/documents/RedListGuidelines.pdf>). Species categorised as Least Concern (LC) and Near-Threatened (NT) were considered as non-threatened. Using univariate generalised linear models (GLM), we assessed if the probability of being data deficient or threatened is higher for mountain dwelling vs. other species; and whether the probability of being data deficient or threatened is higher for highland dwelling species vs. other species. The GLMs included

a binary response variable (whether a species was data deficient/threatened or not”) and a binary explanatory variable (whether a species was mountain dwelling/highland dwelling or not).

We tested if body mass (as a proxy of body size), diet, and biogeographic realm are associated with a bat being mountain dwelling. For this, we performed a phylogenetic generalised linear model with binomial distribution based on a pruned phylogenetic supertree (Upham et al. 2019). Whether a bat species is mountain dwelling or not was considered a binary response variable and body mass (continuous variable), diet, and biogeographic realm (categorical variables) were used as explanatory variables. We performed the regression using the ‘*phylglm*’ function of ‘*phylolm*’ package (Tung Ho and Ané 2014).

Body mass and diet were obtained from COalesced Mammal dataBase of INtrinsic and Extrinsic traits (COMBINE) (Soria et al. 2021). COMBINE also presents data on forearm length which is a standard measure of body size in bats. However, body mass had fewer missing values and was correlated with forearm (Pearson’s $r = 0.9$, $p < 0.001$), so we chose body mass as our proxy for body size. Body mass is also correlated to wing loading (Norberg and Rayner 1987) which is an important trait determining dispersal ability and colonisation potential (Norberg and Rayner 1987; Furey and Racey 2016; Chakravarty et al. 2018). Additionally, larger bats are believed to be better adapted to cool mountain environments (de Carvalho et al. 2019). Wingspan would have been a better predictor for dispersal ability and colonisation but those data are absent from COMBINE. The diet data presented in COMBINE come 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 ‘main diet’ for each bat species (plant, vertebrate or invertebrate) using the category with the highest proportion. Diet is an important predictor of a species’ niche which includes its geographic range (Rodríguez-Castañeda et al. 2010; Slatyer et al. 2013), therefore diet may be associated with a species being mountain dwelling or not. After removing extinct species and matching the taxonomies in IUCN 2022 and COMBINE databases (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 *Mormoops* 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 removed *Hipposideros gentilis* and *Nyctimene wrightae* as they were not recognised in the COMBINE dataset. 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 subsequent analyses (as keeping them would increase the number of degrees of freedom in the respective model). We assigned species to biogeographic realms following Udvardy (1975). A hundred and eight species (8.5%) spanned multiple biogeographic realms and were assigned to the realm in which majority of their distribution polygon lay based on visual assessment. After cleaning up the data, the final model included 1165 species that were represented on the phylogeny and had no missing trait values.

Results

Globally, species richness was highest (>80 species) in Panama Mountains, the northern Andes and the Guiana Highlands (Fig. 1). 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) (Fig. 1). In the Afrotropical realm, the northern Albertine Rift hosted the highest species richness (40–70 species) (Fig. 1). 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 (Fig. 1).

Out of 1329 species, 1152 (87.6%) have <75% of their distribution range in mountains. Excluding these, and those with incorrect map projections, only 148 species (11.13%) were found to be mountain dwelling. Mountain dwelling species were found in all biogeographic realms and belonged to 67 genera (Online Appendix Table S1). We found 46 highland species *i.e.* those restricted to upper montane, subalpine, and alpine habitats. Highland dwelling bats were found in all biogeographic realms except for the Palaearctic and belonged to 28 genera (Fig. 2). A consolidated list of mountain dwelling and highland bat species is provided in online Appendix Table S1.

The probability of being data deficient was significantly higher for mountain dwelling species than species that predominantly occur in the plains (Fig. 3a) (GLM, $p < 0.001$). However, the probability of being threatened was not significantly different between mountain dwelling and non-mountain dwelling species (Fig. 3a) (GLM, $p = 0.325$). Since the 75% cut off used to define species as mountain dwelling was somewhat arbitrary, we performed a sensitivity analysis by redefining mountain dwelling species using cut off values of 50%, 60%, 70%, and 80%. Under all cutoffs, the probability of being data deficient was significantly higher for mountain dwelling species ($p < 0.001$) (Fig. S3). In contrast, the probability of being data deficient was not significantly higher for highland dwelling species than lowland species (GLM, $p = 0.06$), but they were significantly more threatened (Fig. 3b) (GLM, $p < 0.05$).

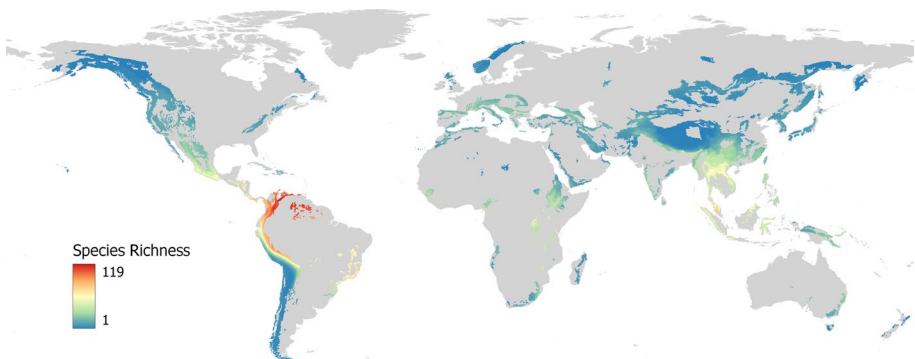


Fig. 1 Species richness of bats on all mountain ranges of the world. Mountains were defined following Körner et al. (2017) and clipped to the polygons used in that paper (available from: https://ilias.unibe.ch/goto_ilias3_unibe_cat_1000515.html)

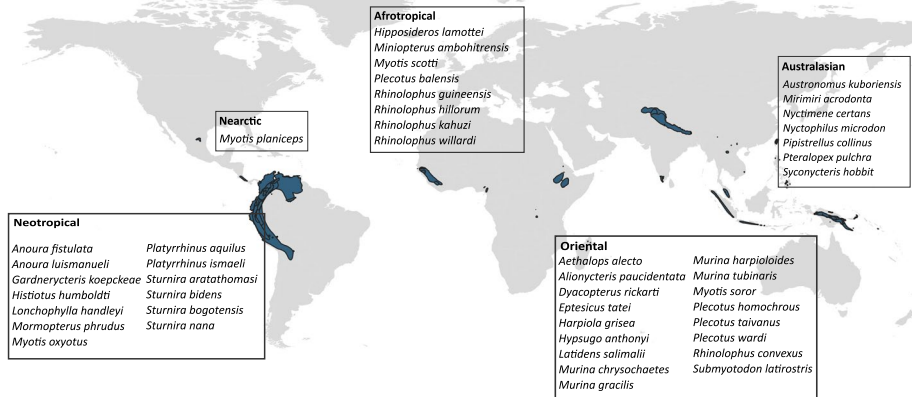


Fig. 2 The distribution all 46 highland bat species of the world. Species names are listed by biogeographic zone in the boxes

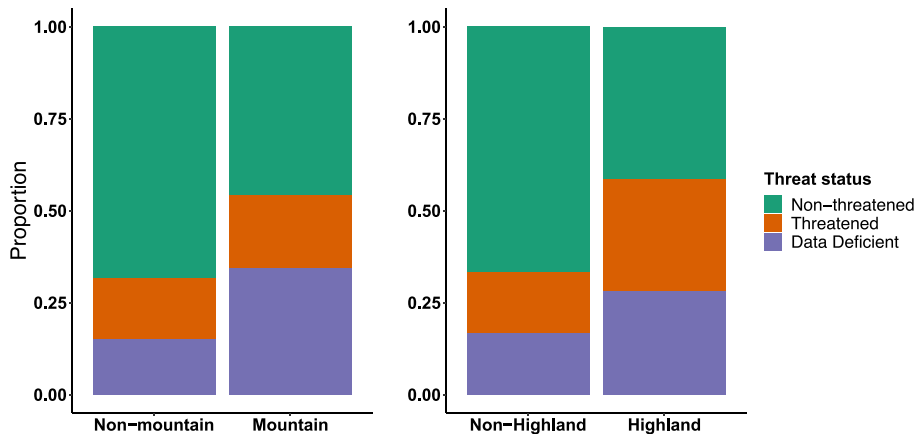


Fig. 3 Proportion of species in different threat categories in **a.** Non-mountain vs. mountain dwelling species, and **b** Non-highland vs. highland species

After controlling for phylogenetic relationships among species, only biogeographic realm had a significant association with a species being mountain dwelling (Fig. 4). Specifically, species in the Neotropical, Australasian, and Oriental realms (in ascending order) were significantly more likely to be mountain dwelling. Body mass and diet were not significantly associated with mountain dwelling. However, due to the low proportion of mountain dwelling species in the dataset, increasing the tolerance bound ('btol') of the phylogenetic generalised linear model did not overcome the issue of the boundary of the linear predictor being reached, indicating a model convergence issue.

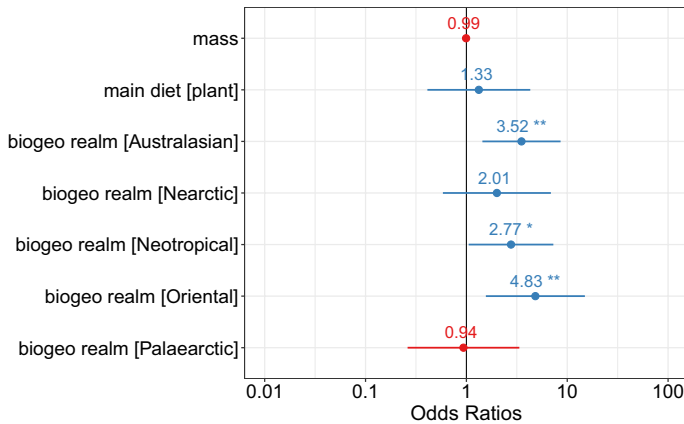


Fig. 4 Odds ratios of phylogenetic generalised linear model with mountain dwelling as a binary response variable and body mass, biogeographic realm, and diet as explanatory variables. The reference level used is insect for diet and Afrotropical realm for the biogeographic realm. Levels of the categorical explanatory variables whose confidence intervals do not overlap 1 are considered significant. Blue indicates a positive association with the explanatory variables whereas red indicates a negative association. *indicates p-value < 0.05 and **indicates p-value < 0.01

Discussion

Our global review of bat distributions revealed hotspots of bat diversity in different biogeographic realms, and retrieved 148 mountain dwelling and 46 highland dwelling species. We also found that species that predominantly occur in mountains are proportionately more data deficient than species occurring largely in the lowlands. Additionally, the species of bats that occur exclusively in highlands (upper montane, subalpine, and alpine regions) are more threatened. Our analysis revealed a significant association of the mountain dwelling nature of bats with biogeographic realm.

Variation in species richness across mountains

The most species-rich hotspots for bat diversity in mountains were found to be in parts of the 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 in northern South America (Jetz et al. 2012; Jenkins et al. 2013). In the Palearctic 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 (Jetz et al.

2012, accessed from <https://mol.org/patterns/richnessrarity?taxa=mammals>; Chakravarty et al. 2020). However, it must be noted that the high species richness in mountains in comparison to surrounding lowlands could be an artefact of mapping inaccuracies causing lowlands and mountains to fall within the same grid.

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 dwelling bat species are more data deficient

An important result of our study is that mountain dwelling species are more likely to be data deficient than species that are predominantly found in the lowlands. 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 makes our findings even more worthy of attention. Moreover, 28 of the 148 mountain dwelling species have been identified as 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).

There are eight main reasons 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 highland dwelling species (next subsection) 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) (Frick et al. 2020). Additionally, over 270 bat species have been described since 2005 (Frick et al. 2020), a statistic that continues to grow year on year (Saikia et al. 2022; Garbino et al. 2024; Fonseca et al. 2024; Patterson et al. 2024). Of the 1482 currently recognised bat species (Simmons and Cirranello 2022), over 150 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 more 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 land use change and climate change intensifies, data deficient species could go extinct without notice (Howard and Bickford 2014; Borgelt et al. 2022).

Highland dwelling bat species are more threatened

We found 46 bat species across biogeographic realms that occur close to mountain tops, with the Oriental realm hosting the highest diversity. Alarming, we also found that these highland dwelling species have a higher probability of being threatened than those that are found in lowlands or across elevations. Irrespective of geography and taxon, species dwelling in high elevations are under severe threat. For instance, long-term demographic data linked with local climate data have identified a consistent annual population decline in the Haleakalā silversword—a plant endemic to a single volcano summit in Hawaii (Krushelnicky et al. 2013). Another example using simulation models projected range contractions for range-restricted highland dwelling aquatic invertebrates and vertebrates under future climate change scenarios in North America and the Himalaya (Muhlfeld et al. 2011; Sharma et al. 2021b). The impacts of climate change on alpine regions are also a major factor driving population declines of many taxa, including mountain breeding birds in Europe (Lehikoinen et al. 2014, 2019).

Many of the highland species in our dataset are categorised as threatened on account of their small distribution areas, as population trends for bat species are largely unknown (Frick et al. 2020). Most of these species are known from single locations or a few disjunct locations. The impact of disjunct distributions across valleys has already been shown to be drastic in a long-eared bat species *Plecotus balensis*. Specifically, *Plecotus balensis* occurs on sky islands in a few summits of the Ethiopian Highlands. Local populations show marked genetic differentiation across valleys and the species' range has been progressively shrinking since the last glaciation period. The problem is likely to be accentuated by the effects of climate and land-use change (Razgour et al. 2021). Three other bat species (*Alionycteris paucidentata*, *Mirimiri acrodonta*, and *Pteralopex pulchra*) are restricted to mountain tops within isolated small-sized islands. Both *Mirimiri acrodonta* and *Pteralopex pulchra* are already critically endangered. Additionally, five highland dwelling species (*Anoura fistulata*, *Nyctophilus microdon*, *Pipistrellus collinus*, *Sturnira aratathomasi*, and *Sturnira bidens*) are strictly associated with cloud forests (Karger et al. 2021). Although these species are data deficient or least concern, their restricted elevational range warrants additional surveys and periodic monitoring. It must be noted that these species are found in regions that have not been extensively surveyed and their actual geographical distributions may be larger than currently known.

In terms of the biogeographic relevance of our results, we found that four out of the six mountain dwelling species of the genus *Plecotus* are highland dwelling (Fig. 3; Online Appendix Table S1). It appears 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 above sea level in Hoang Lien National Park in northern Vietnam (Fukui et al. 2020). This record was published following the IUCN update of this species in 2019 (Srinivasulu and Srinivasulu

2019). This is the first record of this erstwhile Himalayan endemic 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 Palearctic distribution, the tropical species of the genus are likely to be cold-adapted. Species occurring in subtropical and tropical mountains may therefore occupy higher elevations, as is also seen in some Palearctic birds, mammals, and arthropods in the Himalaya (Martens 1984; Päckert et al. 2012). These observations, however, should be treated as preliminary. IUCN distribution maps are not ideal for macroecological research as they adopt a conservative approach in depicting the complete geographical range of species and are replete with sampling biases (Herkt et al. 2017). A global phylogeny of the genus and research on phylogeography will be helpful in examining the reasons behind the mountain and highland affinity.

Variables associated with the mountain dwelling nature of bats

In total, 1829 species of mammals have > 75% of their distribution range in mountains (Rahbek et al. 2019), so mountain dwelling bats (148, based on our results) only make up 8% of this diversity. Our analysis revealed a significant association between biogeographic realm with the mountain dwelling nature of bat species. Specifically, our analysis suggests that species belonging to the Neotropical, Australasian, and Oriental realms (in ascending order) are more likely to be mountain dwelling.

The association between mountain dwelling and biogeographic realm is complex. The probability of a bat being mountain dwelling was highest in the Oriental realm. In the Oriental realm, the genus *Murina* has a disproportionately high number of mountain dwelling species (16 out of 32 species). In fact, new species are constantly discovered in this genus from mountainous regions (for example, Ruedi et al. 2012; Son et al. 2015; Soisook et al. 2017) perhaps further exaggerating the data deficiency of mountain dwelling bat species (see above). *Murina* may be an interesting genus for a phylogeographic study targeted at understanding its affinity to mountains. However, in this realm the high likelihood of being mountain dwelling is possibly because a major part of the realm, especially in the biodiverse Southeast Asia, is covered in mountainous terrain (Fig. 1). The converse is true for the Palearctic and Afrotropical realms which—in proportion to its area—are excessively devoid of mountainous terrain. Neotropical mountains, such as the Andes and Guiana Highlands are among the most biodiverse mountain ranges including for bats (see above). In this realm, species of the genera *Sturnira* and *Anoura* especially have a disproportionately high proportion of mountain dwelling species. It has been phylogenetically shown that *Anoura* has a montane origin (Calderón-Acevedo et al. 2022). The mountain dwelling species of the Australasian realm are spread across different genera and predominantly occur on Sulawesi and New Guinea. However, as explained above, this analysis must be considered a preliminary exploration which hopes to generate questions and motivates future research.

Conservation implications and future directions

Our study highlights that bat species found in mountains are more data deficient and threatened than lowland species. We therefore call for targeted surveys of bats on mountains (and more funding for them), especially in the Global South which is generally understudied

and where most of the data deficient or threatened mountain and highland dwelling bat species occur. 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 monitoring schemes must be initiated to improve our knowledge of the elevational distributions and population trends of mountain and highland dwelling bat species. It is also 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). 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". Lastly, we hope that our study would draw attention to mountain biodiversity in general (and mountain dwelling bats in particular) in the same vein as island biodiversity given the absence of sufficient data and the looming threats posed by climate change.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-024-02958-y>.

Acknowledgements RC acknowledges funding support from the German Academic Exchange Service (DAAD) doctoral fellowship. Mr Arvind Datar is acknowledged for providing additional funding support which included RC's stipend. RC thanks Chintan Sheth for helpful discussions and troubleshooting with respect to spatial analyses.

Author contributions Rohit Chakravarty, Viktoriia Radchuk, and Christian C. Voigt conceptualised the study. Rohit Chakravarty and Viktoriia Radchuk conducted the formal analysis. Kulbhushansingh Suryawanshi and Christian C. Voigt acquired the funds. Viktoriia Radchuk, Kulbhushansingh Suryawanshi, and Christian C. Voigt supervised the research. Rohit Chakravarty wrote the first draft of the manuscript and all authors read, edited, and approved the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. This work was supported by Deutscher Akademischer Austauschdienst, Germany, Grant No. (91650142).

Declarations

Conflict of interest The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Alexander JM, Diez JM, Levine JM (2015) Novel competitors shape species' responses to climate change. *Nature* 525:515–518. <https://doi.org/10.1038/NATURE14952>
- Alves DMCC, Diniz-Filho JAF, da Silva e Souza K et al (2018) Geographic variation in the relationship between large-scale environmental determinants and bat species richness. *Basic Appl Ecol* 27:1–8. <https://doi.org/10.1016/j.baee.2017.12.002>

- Anderson JGT (2017) Why ecology needs natural history. *Am Sci* 105:290
- Antonelli A, Kissling WD, Flantua SGA et al (2018) Geological and climatic influences on mountain biodiversity. *Nat Geosci* 11:718–725. <https://doi.org/10.1038/s41561-018-0236-z>
- Beniston M, Farinotti D, Stoffel M et al (2018) The European mountain cryosphere: a review of its current state, trends, and future challenges. *Cryosphere* 12:759–794. <https://doi.org/10.5194/tc-12-759-2018>
- Bland LM, Collen B, Orme CDL, Bielby J (2015) Predicting the conservation status of data-deficient species. *Conserv Biol* 29:250–259. <https://doi.org/10.1111/COBI.12372>
- Bland LM, Bielby J, Kearney S et al (2017) Toward reassessing data-deficient species. *Conserv Biol* 31:531–539. <https://doi.org/10.1111/COBI.12850>
- Borgelt J, Dorber M, Høiberg MA, Verones F (2022) More than half of data deficient species predicted to be threatened by extinction. *Commun Biol*. <https://doi.org/10.1038/s42003-022-03638-9>
- Brambilla M, Rubolini D, Appukuttan O et al (2022) Identifying climate refugia for high-elevation Alpine birds under current climate warming predictions. *Glob Chang Biol* 28:4276–4291. <https://doi.org/10.1111/GCB.16187>
- Calderón-Acevedo CA, Bagley JC, Muchhala N (2022) Genome-wide ultraconserved elements resolve phylogenetic relationships and biogeographic history among Neotropical leaf-nosed bats in the genus *Anoura* (Phyllostomidae). *Mol Phylogenet Evol* 167:107356. <https://doi.org/10.1016/j.ympev.2021.107356>
- Chakravarty R, Chattopadhyay B, Ramakrishnan U, Sivasundar A (2018) Comparative population structure in species of bats differing in ecology and morphology in the Andaman Islands, India. *Acta Chiropt* 20:85–98. <https://doi.org/10.3161/15081109ACC2018.20.1.006>
- Chakravarty R, Ruedi M, Ishtiaq F (2020) A recent survey of bats with descriptions of echolocation calls and new records from the western Himalayan region of Uttarakhand, India. *Acta Chiropt* 22:197–224. <https://doi.org/10.3161/15081109ACC2020.22.1.019>
- Conenna I, Rocha R, Russo D, Cabeza M (2017) Insular bats and research effort: a review of global patterns and priorities. *Mamm Rev* 47:169–182. <https://doi.org/10.1111/mam.12090>
- de Carvalho WD, Martins MA, Esbérard CEL, Palmeirim JM (2019) Traits that allow bats of tropical lowland origin to conquer mountains: bat assemblages along elevational gradients in the South American Atlantic Forest. *J Biogeogr* 46:316–331. <https://doi.org/10.1111/jbi.13506>
- Dirnböck T, Essl F, Rabitsch W (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Glob Chang Biol* 17:990–996. <https://doi.org/10.1111/J.1365-2486.2010.02266.X>
- Elsen PR, Monahan WB, Merenlender AM (2018) Global patterns of protection of elevational gradients in mountain ranges. *Proc Natl Acad Sci U S A* 115:6004–6009. <https://doi.org/10.1073/PNAS.1720141115/-DCSUPPLEMENTAL>
- Faurby S, Davis M, Pedersen RØ et al (2018) PHYLOCINE 1.2: the phylogenetic atlas of mammal macroecology. *Ecology* 99:2626. <https://doi.org/10.1002/ecy.2443/supinfo>
- Fjeldså J (1993) The avifauna of the Polylepis woodlands of the Andean highlands: the efficiency of basing conservation priorities on patterns of endemism. *Bird Conserv Int* 3:37–55. <https://doi.org/10.1017/S0959270900000770>
- Fonseca BDS, Soto-Centeno JA, Simmons NB et al (2024) A species complex in the iconic frog-eating bat *Trachops cirrhosus* (Chiroptera, Phyllostomidae) with high variation in the heart of the neotropics. *Am Museum Novit*. <https://doi.org/10.1206/4021.1>
- Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW (2018) Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proc Natl Acad Sci U S A* 115:11982–11987
- Freeman BG, Strimas-Mackey M, Miller ET (2022) Interspecific competition limits bird species' ranges in tropical mountains. *Science* 377:416–420. <https://doi.org/10.1126/science.abc17242>
- Frick WF, Kingston T, Flanders J (2020) A review of the major threats and challenges to global bat conservation. *Ann N Y Acad Sci* 1469:5–25. <https://doi.org/10.1111/nyas.14045>
- Fukui D, Tu VT, Thanh HT et al (2020) First record of the genus *Plecotus* from Southeast Asia with notes on the taxonomy, karyology and echolocation call of *P. homochrous* from Vietnam. *Acta Chiropt* 22:57–74. <https://doi.org/10.3161/15081109ACC2020.22.1.006>
- Furey NM, Racey PA (2016) Can wing morphology inform conservation priorities for Southeast Asian cave bats? *Biotropica* 48:545
- Garbino GST, Hernández-Canchola G, León-Paniagua L, Tavares VDC (2024) A new Mexican endemic species of yellow-eared bat in the genus *Vampyressa* (Phyllostomidae, Stenodermatinae). *J Mammal* 105:563–576. <https://doi.org/10.1093/JMAMMAL/GYAE001>

- Grunwald AL, Demos TC, Nguéagni Y et al (2023) A review of bats of the genus *Pseudoromicia* (Chiroptera: Vespertilionidae) with the description of a new species. Syst Biodivers. <https://doi.org/10.1080/14772000.2022.2156002>
- Herk H, Skidmore AK, Fahr J (2017) Macroecological conclusions based on IUCN expert maps: a call for caution. Glob Ecol Biogeogr 26:930–941. <https://doi.org/10.1111/GEB.12601>
- Hijmans RJ (2022) Raster: geographic data analysis and modeling.
- Howard SD, Bickford DP (2014) Amphibians over the edge: silent extinction risk of Data Deficient species. Divers Distrib 20:837–846. <https://doi.org/10.1111/DDI.12218>
- Hughes AC, Orr MC, Ma K et al (2021) Sampling biases shape our view of the natural world. Ecography 44:1259–1269. <https://doi.org/10.1111/ecog.05926>
- IUCN (2022) The IUCN red list of threatened species. Version 2022-1.
- Jenkins CN, Pimm SL, Joppa LN (2013) Global patterns of terrestrial vertebrate diversity and conservation. Proc Natl Acad Sci U S A 110:E2603–E2610. <https://doi.org/10.1073/PNAS.1302251110>
- Jetz W, McPherson JM, Guralnick RP (2012) Integrating biodiversity distribution knowledge: toward a global map of life. Trends Ecol Evol 27:151–159. <https://doi.org/10.1016/J.TREE.2011.09.007>
- Jones G, Jacobs DS, Kunz TH et al (2009) Carpe noctem: the importance of bats as bioindicators. Endanger Species Res 8:93–115. <https://doi.org/10.3354/esr00182>
- Karger DN, Kessler M, Lehnert M, Jetz W (2021) Limited protection and ongoing loss of tropical cloud forest biodiversity and ecosystems worldwide. Nat Ecol Evol 5:854–862. <https://doi.org/10.1038/s41559-021-01450-y>
- Körner C (2004) Mountain biodiversity, its causes and function. Ambio 33:11–17. <https://doi.org/10.1007/0044-7447-33.sp13.11>
- Körner C, Jetz W, Paulsen J et al (2017) A global inventory of mountains for bio-geographical applications. Alp Bot 127:1–15. <https://doi.org/10.1007/s00035-016-0182-6>
- Krushelnitsky PD, Loope LL, Giambelluca TW et al (2013) Climate-associated population declines reverse recovery and threaten future of an iconic high-elevation plant. Glob Chang Biol 19:911–922. <https://doi.org/10.1111/GCB.12111>
- LaVal RK (2004) Impact of global warming and locally changing climate on tropical cloud forest bats. J Mammal 85:237–244
- Lehikoinen A, Green M, Husby M et al (2014) Common montane birds are declining in northern Europe. J Avian Biol 45:3–14. <https://doi.org/10.1111/j.1600-048X.2013.00177.x>
- Lehikoinen A, Brotons L, Calladine J et al (2019) Declining population trends of European mountain birds. Glob Chang Biol 25:577–588. <https://doi.org/10.1111/gcb.14522>
- Martens J (1984) Vertical distribution of Palearctic and Oriental faunal components in the Nepal Himalayas. Erdwissenschaftl Forsch 18:321–336. <https://doi.org/10.2476/ASJAA.56.15>
- McCain CM (2009) Vertebrate range sizes indicate that mountains may be ‘higher’ in the tropics. Ecol Lett 12:550–560. <https://doi.org/10.1111/J.1461-0248.2009.01308.X>
- Mccain CM, Colwell RK (2011) Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. Ecol Lett 14:1236–1245. <https://doi.org/10.1111/J.1461-0248.2011.01695.X>
- McGuire LP, Boyle WA (2013) Altitudinal migration in bats: evidence, patterns, and drivers. Biol Rev 88:767–786. <https://doi.org/10.1111/brv.12024>
- Mendelsohn JM, Huntley BJ, Vaz PP (2023) Monograph on endemism in the Highlands and Escarpments of Angola and Namibia
- Monadjem A, Healy K, Guillerme T, Kane A (2023) Dispersal ability is associated with contrasting patterns of beta diversity in African small mammal communities. J Biogeogr 50:539–550. <https://doi.org/10.1111/jbi.14532>
- Muhlfeld CC, Giersch JJ, Hauer FR et al (2011) Climate change links fate of glaciers and an endemic alpine invertebrate. Clim Change 106:337–345. <https://doi.org/10.1007/S10584-011-0057-1/METRICS>
- Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. <https://doi.org/10.1038/35002501>
- Nogueira MR, Lima IP, Peracchi AL, Simmons NB (2012) New genus and species of nectar-feeding bat from the Atlantic Forest of Southeastern Brazil (Chiroptera: Phyllostomidae: Glossophaginae). pp. 3747:
- Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philoso Trans Royal Soc London B, Biol Sci 316:335–427. <https://doi.org/10.1098/rstb.1987.0030>
- Noroozi J, Talebi A, Doostmohammadi M et al (2018) Hotspots within a global biodiversity hotspot-areas of endemism are associated with high mountain ranges. Sci Rep 8:1–10. <https://doi.org/10.1038/s41598-018-28504-9>

- Päckert M, Martens J, Sun YH et al (2012) Horizontal and elevational phylogeographic patterns of Himalayan and Southeast Asian forest passerines (*Aves: Passeriformes*). *J Biogeogr* 39:556–573. <https://doi.org/10.1111/j.1365-2699.2011.02606.x>
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37. <https://doi.org/10.1038/nature01286>
- Patterson BD, Demos TC, Torrent L et al (2024) Systematics of the *Rhinolophus landeri* complex, with evidence for 3 additional Afrotropical bat species. *J Mammal*. <https://doi.org/10.1093/JMAMMAL/GYAE085>
- Pebesma E (2018) Simple features for R: standardized support for spatial vector data. *R J* 10:439–446
- Pepin NC, Arnone E, Gobiet A et al (2022) Climate changes and their elevational patterns in the mountains of the world. *Rev Geophys* 60:e2020RG000730. <https://doi.org/10.1029/2020RG000730>
- Rahbek C, Borregaard MK, Colwell RK et al (2019) Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science* 365:1108–1113. <https://doi.org/10.1126/science.aax0149>
- Razgour O, Kasso M, Santos H, Juste J (2021) Up in the air: threats to Afromontane biodiversity from climate change and habitat loss revealed by genetic monitoring of the Ethiopian Highlands bat. *Evol Appl* 14:794–806. <https://doi.org/10.1111/eva.13161>
- Reardon TB, McKenzie NL, Cooper SJB et al (2014) A molecular and morphological investigation of species boundaries and phylogenetic relationships in Australian free-tailed bats *Mormopterus* (*Chiroptera: Molossidae*). *Aust J Zool* 62:109–136. <https://doi.org/10.1071/ZO13082>
- Robin VV, Gupta P, Thatte P, Ramakrishnan U (2015) Islands within islands: two montane palaeo-endemic birds impacted by recent anthropogenic fragmentation. *Mol Ecol* 24:3572–3584. <https://doi.org/10.1111/MEC.13266>
- Rodríguez-Castañeda G, Dyer LA, Brehm G et al (2010) Tropical forests are not flat: how mountains affect herbivore diversity. *Ecol Lett* 13:1348–1357. <https://doi.org/10.1111/J.1461-0248.2010.01525.X>
- Rolando A, Caprio E, Rinaldi E, Ellena I (2007) The impact of high-altitude ski-runs on alpine grassland bird communities. *J Appl Ecol* 44:210–219. <https://doi.org/10.1111/j.1365-2664.2006.01253.x>
- Ruedi M, Biswas J, Csorba G (2012) Bats from the wet: two new species of tube-nosed bats (*Chiroptera: Vespertilionidae*) from Meghalaya, India. *Rev Suisse Zool* 119:111–135
- Ruedi M, Saikia U, Thabab A et al (2021) Molecular and morphological revision of small Myotinae from the Himalayas shed new light on the poorly known genus *Submyotodon* (*Chiroptera: Vespertilionidae*). *Mamm Biol*. <https://doi.org/10.1007/s42991-020-00081-3>
- Saikia U, Ruedi M, Csorba G (2022) Out of Southeast Asia: a new species of thick-thumbed bat (*Chiroptera: Vespertilionidae: Glischropus*) from Meghalaya, north-eastern India. *Zootaxa* 5154:355–364. <https://doi.org/10.11646/zootaxa.5154.3.8>
- Schmeller DS, Urbach D, Bates K et al (2022) Scientists' warning of threats to mountains. *Sci Total Environ* 853:158611. <https://doi.org/10.1016/J.SCITOTENV.2022.158611>
- Scridel D, Brambilla M, Martin K et al (2018) A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. *Ibis* 160:489–515
- Shahabuddin G, Goswami R, Krishnadas M, Menon T (2021) Decline in forest bird species and guilds due to land use change in the Western Himalaya. *Glob Ecol Conserv* 25:e01447. <https://doi.org/10.1016/J.GECCO.2020.E01447>
- Sharma A, Dubey VK, Johnson JA et al (2021a) Dendritic prioritization through spatial stream network modeling informs targeted management of Himalayan riverscapes under brown trout invasion. *J Appl Ecol* 58:2415–2426. <https://doi.org/10.1111/1365-2664.13997>
- Sharma A, Dubey VK, Johnson JA et al (2021b) Is there always space at the top? Ensemble modeling reveals climate-driven high-altitude squeeze for the vulnerable snow trout *Schizothorax richardsonii* in Himalaya. *Ecol Indic* 120:106900. <https://doi.org/10.1016/J.ECOLIND.2020.106900>
- Simmons NB, Flanders J, Moïse E et al (2021) A new dichromatic species of Myotis (*Chiroptera: Vespertilionidae*) from the Nimba Mountains, Guinea. *Am Mus Novit* 3963:1–37
- Simmons NB, Cirranello AL (2022) Bat species of the world: a taxonomic and geographic database. <https://batnames.org/>. Accessed 27 Jan 2023
- Slatyer RA, Hirst M, Sexton JP (2013) Niche breadth predicts geographical range size: a general ecological pattern. *Ecol Lett* 16:1104–1114. <https://doi.org/10.1111/ELE.12140>
- Soisook P, Thaw WN, Kyaw M et al (2017) A new species of *Murina* (*Chiroptera: Vespertilionidae*) from sub-Himalayan forests of northern Myanmar. *Zootaxa* 4320:159–172. <https://doi.org/10.11646/ZOOTAXA.4320.1.9>
- Son NT, Csorba G, Tu VT et al (2015) A new species of the genus *Murina* (*Chiroptera: Vespertilionidae*) from the central Highlands of Vietnam with a review of the subfamily Murinae in Vietnam. *Acta Chiropt* 17:201–232. <https://doi.org/10.3161/15081109ACC2015.17.2.001>

- Sonne J, Dalsgaard B, Borregaard MK et al (2022) Biodiversity cradles and museums segregating within hotspots of endemism. *Proc Royal Soc B*. <https://doi.org/10.1098/RSPB.2022.1102>
- Soria CD, Pacifici M, Di Marco M et al (2021) COMBINE: a coalesced mammal database of intrinsic and extrinsic traits. *Ecology* 102:e03344. <https://doi.org/10.1002/ECY.3344/SUPPINFO>
- Srinivasan U, Tamma K, Ramakrishnan U (2014) Past climate and species ecology drive nested species richness patterns along an east-west axis in the Himalaya. *Glob Ecol Biogeogr* 23:52–60. <https://doi.org/10.1111/geb.12082>
- Srinivasulu C, Srinivasulu B (2019) *Plecotus homochrous* (Hodgson's Long-eared Bat). The IUCN Red List of Threatened Species e.T85537505A85537516:
- Tamma K, Ramakrishnan U (2015) Higher speciation and lower extinction rates influence mammal diversity gradients in Asia. *BMC Evol Biol* 15:1–13. <https://doi.org/10.1186/s12862-015-0289-1>
- Tamma K, Marathe A, Ramakrishnan U (2016) Past influences present: mammalian species from different biogeographic pools sort environmentally in the Indian subcontinent. *Front Biogeogr* 8:217–220
- Tsang SM, Wiantoro S, Veluz MJ et al (2020) Dispersal out of *Wallacea* spurs diversification of *Pteropus* flying foxes, the world's largest bats (*Mammalia: Chiroptera*). *J Biogeogr* 47:527–537. <https://doi.org/10.1111/jbi.13750>
- Tung Ho LS, Ané C (2014) A linear-time algorithm for gaussian and non-gaussian trait evolution models. *Syst Biol* 63:397–408. <https://doi.org/10.1093/SYSBIO/SYU005>
- Udvardy MDF (1975) A classification of the biogeographical provinces of the world
- Upham NS, Esselstyn JA, Jetz W (2019) Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol* 17:e3000494. <https://doi.org/10.1371/JOURNAL.PBIO.3000494>
- Urban MC (2018) Escalator to extinction. *Proc Natl Acad Sci U S A* 115:11871–11873
- Voigt CC, Helbig-Bonitz M, Kramer-Schadt S, Kalko EKV (2014) The third dimension of bat migration: evidence for elevational movements of *Miniopterus natalensis* along the slopes of Mount Kilimanjaro. *Oecologia* 174:751–764. <https://doi.org/10.1007/s00442-013-2819-0>
- Watts SH, Mardon DK, Mercer C et al (2022) Riding the elevator to extinction: disjunct arctic-alpine plants of open habitats decline as their more competitive neighbours expand. *Biol Conserv* 272:109620. <https://doi.org/10.1016/J.BIOCON.2022.109620>
- Wells CP, Barbier R, Nelson S et al (2022) Life history consequences of climate change in hibernating mammals: a review. *Ecography*. <https://doi.org/10.1111/ECOG.06056>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.