

Developing global vulnerabilities and conservation priorities for cave-dwelling bats

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Article

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Research and conservation interventions are disproportionately focused on taxa perceived as charismatic, while other systems with high levels of endemism, and often under-protected such as caves and subterranean ecosystems remain neglected. Bats are keystone to cave ecosystems making them ideal surrogates to understand diversity patterns and assay conservation priorities. Using a novel framework, we assessed and mapped the global bat cave vulnerabilities and priorities at the biome and site level. Almost half ($N = 678$, 48%) of bat species across the world regularly use caves, with 32% endemic to a single country, and 15% currently threatened with extinction. Tropical realms and small-ranged species faced the highest levels of risk. Our analyses consistently showed that most caves with lower threat levels show higher cave biotic potential (i.e., evolutionary distinctiveness and endemism), though this may be due to the loss of species from more disturbed caves. We estimate that 3% to 28% are high-priority caves for conservation in broad-scale (biome level) and fine-scale (site-dependent) analyses respectively. Amongst regions, the highest concentration of conservation priority areas are in the Palearctic and tropical regions (except Afrotropical), which requires more intensive data sampling. Our results further highlight the importance of prioritising bat caves at local scales but show that broader scale analysis is possible if robust cave data is present and effective parameters are included (i.e., appropriate landscape features and threats). Developing priorities for these systems requires more systematic approaches as a standard measure to develop the priorities needed to maintain cave diversity.

Keywords: Biomes, Evolutionary Distinctiveness, Extinction risks, Island endemism, Subterranean habitats, Threats.

Introductory

Global biodiversity is threatened by a variety of drivers, and understanding these is critical to determining effective conservation measures in different systems and scales¹. Appropriate evidence-based strategies are essential to optimise the effectiveness of conservation^{2,3}. Various strategies have been developed to prioritise taxa and their ecosystems for conservation such as habitat prioritisation and zoning⁴⁻⁶, but many countries may lack access to such data or resources to effectively implement conservation. Priorities should be matched with future targets and effort allocation to support reaching such targets and ensure that species and ecosystems are well protected⁷⁻¹⁰. However, many species lack data for effective priorities to be developed, and even fewer receive adequate levels of attention^{11,12}. Yet, as much as conservation scientists try to address the most pressing challenges in global biodiversity conservation, many taxa and their associated habitats are overlooked¹³.

In terrestrial ecosystems, megafaunal species (> 15 kg, terrestrial mammals) are often used as flagship or indicator species to provide an umbrella in developing priorities for other taxa and ecosystems, yet they are known to be poor indicators for small-bodied species or the ecosystems they frequently depend on^{14,15}. These measures do not ensure effective conservation and often lead to biases in funding allocation, decisions on conservation and management priorities^{16,17} thus compromising effective conservation of other taxa with possible ramifications for ecological function^{18,19}. Moreover, modern technologies are applied to understand environmental processes on above-ground surface ecosystems (e.g., forest ecosystems) which can easily be mapped with remote sensing. Yet most subterranean ecosystems including caves are challenging to map, and have frequently been overlooked and

neglected²⁰. This barrier to research risks leaving other ecosystems and the species dependent on them such as bats under-studied and under-protected²¹.

A further barrier to research, understanding and even engagement is the special adaptations which not only prevent cave taxa garnering public attention, but the special skills needed to study many cave taxa further adds to the lack of research on cave taxa. Bats are often keystone species in cave ecosystems, and make up the second-largest group of mammals with over 1400 described species distributed across almost all biomes^{22,23}. Cave ecosystems host a variety of highly adapted and sensitive organisms, the majority of which are cave obligates and depend on bat guano for nutrients²³⁻²⁶. Some cave systems have relatively high endemism and even a single cave could hold up to 90% undescribed species^{27,28}, meaning many thousands of species remain undescribed and potentially at risk. However, most conservation projects and funds are focused on charismatic megafauna, but neglect ecosystems with higher endemism and without megafauna, such as cave ecosystems.

Bats function as keystone species within cave systems by bringing nutrition from foraging in the surrounding areas into the caves and providing the basic source of nutrition in these largely lightless zones, where the inability for photosynthesis within the system makes this form of nutrition critical. This function makes bats the ideal surrogate taxa to inform priorities and safeguarding these systems^{23,29,30}. Yet the reduction of bat populations and habitat alterations is increasingly concerning global conservation biologists and threats to cave-bat populations have been widely discussed^{23,31,32} but a standardised index to identify priorities for action to safeguard these systems does not yet exist, hindering larger-scale prioritisation to protect cave systems and their dependant diversity.

Subterranean habitats are systematically threatened by combined direct and surface threats. Bats are conspicuous in subterranean ecosystems but they are vulnerable, as large

colony sizes mean that single site impacts can have major consequences on populations especially for locally endemic species^{20,32}. The relatively low reproductive rate in bats jeopardizes rapid population recovery from loss and declines³³. Cave and karst habitats are under-protected, for example, only around 13% of the approximately 800,000 km² of tropical Southeast Asia to South China's karst are within protected areas³⁴. Unprotected karst is especially susceptible to destruction, with an average loss of around 5.7% of area annually due to mining and other uses³⁵⁻³⁷. This loss of cave habitat is coupled with unregulated hunting and tourism, and foraging habitat loss; therefore understanding the impacts of these factors on the population status of bats and biotically important caves are urgently needed^{23,30,38,39}. It is estimated that at least 50% of global bat species are dependent on caves²³ but the degree of threat to bat cave communities and prioritisation has never been analysed across large scales³⁰. Understanding species distribution cannot ensure the protection of all species but identifying key areas in need of protection enable conservation biologists to develop balanced priorities to inform appropriate protection measures. This is the first extensive study to explore the global diversity patterns and extinction risk of cave-dwelling bats and using this information to create an index to guide effective priority making.

Here we develop a mechanism to integrate different facets of biotic importance and risks across different dimensions and scales using our database to develop global priorities for bat cave protection based on both vulnerability and biotic potential. First, we examine the (i) global distribution and conservation status of cave-dwelling bats, and (ii) patterns of threatening process. Second, we mapped the biotic potential and vulnerability of caves to identify broad- and fine-scale priorities for global bat caves. Our findings pinpoint gaps as a basis for prioritisation schemes, policies relevant to regional and global levels of cave and karst ecosystem conservation and improve Redlist assessments, especially in prioritising karst

environments, which represent one of the most challenging ecosystems for redlist assessments.

Results

Distribution and status of cave-dwelling bats

The IUCN lists a total of 679 ($N_{cave} = 679$ spp./1400) cave-dwelling species constituting the 48.5 % of described global bat species belonging to all bat families. Vespertilionidae comprised the largest proportion of all cave-dwelling species with 215 species ($\%_{cave} = 32$, $\%_{global} = 43$), followed by Phyllostomatidae ($N = 96$, $\%_{cave} = 14$, $\%_{global} = 45$), Rhinolophidae ($N = 84$, $\%_{cave} = 12$, $\%_{global} = 82$), and Hipposideridae ($N = 81$, $\%_{cave} = 11.92$, $\%_{global} = 92$) (**Supplementary Data 1**). The 80% ($N = 544$ spp.) of the 679 species are carnivorous (i.e., insectivores, sanguivores, and piscivores), 10% ($N = 66$ spp.) omnivorous, and 10% herbivorous (i.e., frugivorous and nectarivores) ($N = 58$ spp.). Most species are concentrated in tropical regions ($\chi^2 = 205.83$, $df = 5$, $P < 0.0001$) with 30% ($N = 227$ spp.) of global cave-dwelling bats are found in the Indomalayan region (**Fig. 1**). At a country level, Indonesia has the highest number of species ($N = 104$ spp.), followed by China ($N = 98$ spp.), and India ($N = 82$ spp.) (**Supplementary Fig. 1 and Supplementary Data 2**).

Globally, 32% ($N = 220$ of 679 spp.) of cave-dwelling bat species were endemic to a single country (**Fig. 1**). The proportion of country endemic species differed regionally ($\chi^2 = 93.49$, $df = 5$, $P < 0.0001$) and is highest in the Indomalayan region (38%, $N = 86$ spp.). The highest number of nationally endemic species was recorded in Madagascar ($N = 23$ spp., $\%_{endemism} = 82\%$), Indonesia ($N = 21$ spp., $\%_{endemism} = 20\%$), and Australia ($N = 18$ spp., $\%_{endemism} = 55\%$). The majority of nationally endemic species are classified as threatened (Vulnerable: 63%, $N = 34$ spp.; Endangered: 72%, $N = 18$ spp.; Critically Endangered:

100%, $N = 11$ spp.) compared to less threatened (Least concern: 20%, $N = 89$ spp.; Near threatened: 39%, $N = 21$ spp.) ($\chi^2 = 120.50$, $df = 5$, $P < 0.0001$). The majority of data deficient species (57%, $N = 47$ spp.) are country endemic. Moreover, the distribution of species based on island endemism significantly differed across conservation statuses ($\chi^2 = 192$, $df = 2$, $P < 0.001$). The majority of the species are mainly found on mainland and near-shore islands (77%, $N = 520$ spp.) and 23% ($N = 159$ spp.) are restricted to islands. Unsurprisingly, 75% of island species are country endemic versus 81% of the non-endemic occur in mainland areas ($\chi^2 = 171$, $df = 1$, $P < 0.001$). Moreover, the proportion of species in threatened categories within island endemism is higher for island restricted species (40%; $N = 43$ spp.) compared to mainland species (21%; $N = 173$ spp.) ($\chi^2 = 35.4$, $df = 2$, $P < 0.001$).

We compared our cave inventories to that of IUCN-sampled species richness and diversity (**Fig. 1**). A total of 1930 cave sites were included in the analyses from the current bat cave distribution (Tanalgo et al. submitted in *Scientific Data*). When compared between IUCN Redlist, our current data for spatial prioritisation included 402 species representing a dataset for 59% of all cave-dwelling species and an equivalent to 29% of global bat species (**Fig. 1**). We did find a marginally significant relationship between the proportion of species richness and threatened species between the IUCN-based global cave-dwelling bat and DarkCideS dataset (Kendall's $\tau B = 0.60$, $P = 0.07$). The highest completeness of sampled species is in the Neotropics (67.38%) and Indomalayan region (66.08%), where the highest gaps are in Austral-Oceania (40.28%) (**Fig. 1**). Highest endemism was recorded in Austral-Oceania (58.62%) ($\chi^2 = 227.32$, $df = 5$, $P < 0.001$). The proportion of threatened species is highest in the Indomalayan (16%) realm ($\chi^2 = 281.18$, $df = 5$, $P < 0.01$) (**Fig. 1**). The degree of evolutionary distinctiveness based on bat-cave data significantly differed regionally (Kruskal-Wallis, $\chi^2 = 1615.65$, $df = 5$, $P < 0.001$), and the highest ED was in the Neotropical

region ($ED_{\text{mean}} = 11.92$) with the lowest in the Palearctic ($ED_{\text{mean}} = 5.54$). Cave weighted endemism is highest in the Austral-Oceania ($CWE_{\text{mean}} = 6.32$) consistent with the proportion of species endemism observed in the region (Kruskal-Wallis, $\chi^2 = 1584.84$, $df = 5$, $P < 0.01$) (Fig. 2).

Extinctions risks and potential drivers

Using the IUCN data, the estimated proportion for the cave-bat species threatened with extinction ($\hat{p}_{\text{extinction}} = 15\%$, 13-25%) is lower than that of all bat species ($\hat{p}_{\text{extinction}} = 20\%$, 16-35%), of which 25% are threatened and 12% data deficient (Fig. 3a, Supplementary Table 1). Between sub-orders, Yinpterochiroptera ($\hat{p}_{\text{extinction}} = 24\%$; 21-32%) has higher extinction risk than Yangochiroptera ($\hat{p}_{\text{extinction}} = 10\%$; 9-22%). Taxon-rich families, Hipposideridae ($\hat{p}_{\text{extinction}} = 25\%$, 22-25%), Rhinolophidae ($\hat{p}_{\text{extinction}} = 21\%$, (18-32%)), and large-bodied Pteropodids represents an even smaller subset of cave dwelling species that have fairly similar threshold of estimated extinction risk ($\hat{p}_{\text{extinction}} = 27\%$; (25-31%)), which are higher than the global extinction proportion values. The highest extinction risk is estimated among herbivorous species ($\hat{p}_{\text{extinction}} = 23\%$, 22-27%). Extinction risk is highest for country endemic species ($\hat{p}_{\text{extinction}} = 36\%$, 29-50%) and those species occurring on islands (islandic: $\hat{p}_{\text{extinction}} = 40\%$, 35-48%) (Fig. 3a, Supplementary Table 1). Indonesia ($N = 18$ spp., % threatened = 17%), and India ($N = 10$ spp., % threatened = 12%), topped the countries with highest number of threatened species (Supplementary Data 2).

The binary extinction risk (non-threatened vs. threatened) of species was examined for all species and across sub-orders. A strong link between narrow geographic range and species extinction risk can be attributed in all cave-dwelling species ($\beta = -1.94$, $P < 0.001$) and for both suborder models (Yin: $\beta = -2.34$, $P < 0.001$; Yang: $\beta = -2.02$, $P < 0.001$). Country endemism ($\beta = -0.67$, $P = 0.013$) and island endemism ($\beta = 1.00$, $P < 0.001$) are

also linked to extinction risk globally. But varies within suborders, island endemism could only predict extinction risk species from Yangochiroptera ($\beta = 1.17, P < 0.001$) and geopolitical only for Yinpterochiroptera ($\beta = -1.19, P = 0.028$) (**Fig. 3b, Supplementary Table 2**). Moreover, none of the biotic variables (trophic level, generation length, and adult body mass) included in the model could predict extinction risk globally and within suborders. Among threat variables, only direct threats showed significant association globally ($\beta = 2.221, P = 0.008$) and between suborders (Yin: $\beta = 2.84, P = 0.043$; Yang: $\beta = 2.50, P = 0.031$) (**Fig. 3b**).

Patterns of threats

Nearly three-quarters (69%, $N = 466$ spp.) of the cave-dwelling bat species are exposed to various threats according to the IUCN. The proportion of direct (Kruskal-Wallis test: $\chi^2 = 13.02, df = 5, P = 0.02$) and indirect (Kruskal-Wallis test: $\chi^2 = 30.10, df = 5, P < 0.01$) threats differed regionally. Direct threat is dominant in the Indomalayan region and the greatest threat to 47% ($N = 321$ spp.; $STI_{dir} = 2.15$) of the global species predominantly by unregulated tourism (33%, $N = 226$ spp.), Mining and quarrying (23%, $N = 155$ spp.), and bushmeat hunting (16%, $N = 106$ spp.) (**Supplementary Fig. 2 and Supplementary Table 3**). Indirect threats occurring on the surface threatened 49% ($N = 335$ spp.; $STI_{ind} = 1.60$) of the global species primarily from deforestation (42%, $N = 284$ spp.) and agricultural conversions (23%, $N = 155$ spp.). There is a large disparity in the species threatened by natural threats (e.g., geoclimatic induced) with only 10% ($N = 70$ spp.) ($STI_{nat} = 1.40$) of the species are threatened by natural and climate-driven threats. The degree of natural threat index only differed between island endemism ($\chi^2 = 10.88, df = 2, P = 0.004$) (**Supplementary Fig. 2 and Supplementary Table 3**).

Small geographic range is a key independent predictor of species risks to direct threats agricultural conversion ($\beta = -0.214$, $P = 0.017$), deforestation ($\beta = -0.154$, $P = 0.05$). Conversely, species with large geographic ranges were more impacted by pollution ($\beta = 0.498$, $P = 0.003$). In large species adult body mass is a strong predictor of species vulnerability to hunting and bushmeat ($\beta = 0.845$, $P < 0.001$). Within trophic levels, omnivores have a significantly higher risk from mining and quarrying compared to frugivores ($\beta = -1.029$, $P = 0.023$) and insectivores ($\beta = -0.636$, $P = 0.026$). Frugivores are more vulnerable to hunting and harvesting ($\beta = 2.256$, $P = 0.001$), and carnivores to pollution ($\beta = 1.483$, $P = 0.044$) compared to other trophic levels (**Supplementary Fig. 3 and Supplementary Table 4**). None of the explanatory variables included in the analysis could determine species sensitivity to tourism and urbanisation (**Supplementary Table 4**).

Globally based on cave community data, seven out of twelve variables showed a significant relationship with species biotic scores but none of the landscape features and threat variables showed a strong correlation to diversity (**Fig. 4a**). Tree density, bare ground cover change, and short vegetation cover change showed a positive correlation with species biotic scores. Conversely, distance to river, tall tree loss, nightlight, and population density showed a significant negative correlation (**Fig. 4a**) though this may in part reflect the challenges of sampling caves in tall forested areas, but also highlights that recently disturbed areas may be threatened. When regionally compared, the mean intensity of landscape features and threat variables differed significantly except for pesticide use (**Fig. 4b**). Bat caves in the Afrotropical, Austral-Oceania, and Nearctic showed the highest vulnerability to cities and urbanisation. While Nearctic caves showed the nearest distance to roads and the highest mapped mine density. The mean proportion of bare ground cover change is low in arid regions of Afrotropical and Austral-Oceania. Whereas population density and pesticide

exposure are exceedingly high in Indomalayan caves (**Fig. 4b**). Further, socioecological variables (GDP per capita and % forest cover) and cement production as a proxy to assess the vulnerability of geopolitically endemic species showed consistent correlations amongst species diversity attributes (**Fig. 4c**).

Synthesising Priorities for bat cave conservation

We constructed broad- and fine-scale priorities then compared them across biogeographical realms and climatic regions (i.e., simplified biomes classifications). First, in both scales, there is a higher threshold of cave biotic potential and high vulnerability primarily in the tropics and across most of the world (**Fig. 5a-d**). Then, we examined the congruences in the relationship between biotic vulnerabilities (BV, status transformed scores) and cave biotic potential thresholds. Primarily, the relationship patterns between cave biological diversity and vulnerability to threats indicate that caves with high biotic potential occur in caves with the lowest threat levels (i.e., cave systems located in relatively pristine ecosystems). In fine-scale analysis, we found a significant relationship in biotic potential and biotic vulnerability score (Kruskal-Wallis test: $\chi^2 = 14$, $df = 3$, $P = 0.003$). Within fine-scale, caves with higher biotic potential are linked to lower vulnerability caves, while there is a lower biotic potential in caves with higher threats and vulnerability (Kruskal-Wallis test: $\chi^2 = 6.45$, $df = 3$, $P = 0.092$). Whilst this pattern is consistent at broad-scales, albeit the relationship was not significant (Kruskal-Wallis test: $\chi^2 = 6.45$, $df = 3$, $P = 0.092$) (**Fig. 5e-f**).

Indices derived from the site-level and biome-level Bat Cave Vulnerability Index (BCVI) were used to construct a regionally comparative prioritisation (**Supplementary Table 5**). On a broad scale, 95% of the caves show high biotic vulnerability (Status A) but 88% of the caves are in lower biotic potential level (Level 4) in contrast to only 1% with high

biotic values (Level 1) (**Fig. 6a**). The integration of two sub-indices within the broad-scale equates to the uneven and high proportion (83%) of “4A” lower vulnerability index values for overall sampled caves ($J' = 0.378$) (**Fig. 6a**). On the other hand, fine-scaled BCVI analyses showed a more even distribution of indices values ($J' = 0.917$) compared to the broad-scale analyses. At a fine scale, there is an increase of 45% of caves with high biotic potential caves (Level 1), 14% at a mid-high level (Level 2), and 41% of caves had a lower biotic potential (Level 4). Subsequently, an even distribution of biotic vulnerability was also observed with fine-scale BCVI, 45% and 41% of the caves are in high (Status A) to mid-high (Status B) vulnerability, respectively. Moreover, 10% of the caves are in the “1A” high vulnerability index. A high proportion of high vulnerability caves occurs in most of the tropical realm (**Fig. 6a**). We found a significant difference in cave vulnerability index in both scales (Broad: $\chi^2 = 8977.87$, $df = 7$, $P < 0.001$; Fine: $\chi^2 = 1303.09$, $df = 15$, $P < 0.001$).

Our analysis of the sampled caves showed that the priority levels of caves are scale-dependent and significantly varied across spatial scales ($\chi^2 = 1281.43$, $df = 3$, $P < 0.001$) (Table 4; Data S7). Caves were classified on the basis of the need for different types of intervention or management based on threat and biotic characteristics, most importantly these include “red caves”, which whilst diverse are threatened and at need of intervention, and “green caves” which are also diverse but not currently at risk, whilst “yellow caves” are at an intermediate level and may need intervention to prevent species loss and allow recovery. On a broad scale, only 3% of the sampled caves are at “Red Priority”, 9% at “Yellow Priority”, and 88% at “Blue Priority” levels. The low proportion of high priority caves are significantly concentrated in the Neotropical (45%), Afrotropical (18%) and Indo-Malayan (16%) regions ($\chi^2 = 204.20$, $df = 10$, $P < 0.001$) (**Fig. 6b and Supplementary Table 5**). While on a fine scale, we did find a significant increase in the proportion and evenness ($J' = 0.395$) of high priority caves compared to broad-scale. Of the sampled caves, 28% are “Red Priority” and

4% “Green Priority” caves or sites that contain high biotic potential but low vulnerabilities (Fig. 6b and Table 1). The patterns of concentration of high priority caves based on realms is highest in the Palearctic (30%) closely followed by Neotropical (29%) and Indo-Malayan (28%) ($\chi^2 = 73.93$, $df = 15$, $P < 0.001$). When compared by biomes and climatic regions, the 58% and 25% of high priority caves are concentrated in the tropics and temperate regions respectively ($\chi^2 = 56.76$, $df = 12$, $P < 0.001$) (Fig. 6b).

Discussion

Caves and bats in the changing world

Caves and underground habitats are used by almost half (47%, $N = 679$ spp.) global bat species, with a large fraction showing small ranges and considered as endemic and threatened. Whilst cave-dwelling bats are not the sole biological indicators in subterranean ecosystems, their diversity offers a relatively cost-effective conservation surrogate for systematic monitoring to protecting the vast diversity of cave-dependent species. Patterns of cave bat richness and endemism are parallel with the global bat patterns, peaking in the tropics and particularly in the Indomalayan, Afrotropical, southern Palearctic, and Neotropical regions^{22,32}. Although we suspect these estimates of diversity and proportion of threatened species are underestimated values because of the current taxonomic gaps, large numbers of undescribed cryptic species and lack of accurate species distributions assessments for global bats⁴⁰⁻⁴². We observed a higher risk of extinction in species with a narrow geographical range distribution (e.g island and nationally endemic species), consistent with other studies^{40,43}. Except for the association of endemism to extinction risk varies phylogenetically showing that closely related species have a similar association⁴³, island and geopolitical endemism is respectively correlated to sub-orders Yangochiroptera and Yinpterochiroptera.

Understanding threats

Direct threats were directly linked to species extinction risks in all our models. This may be explained by bat traits and behaviour, for example, the individual aggregation behaviour in colonies of most cave-dwelling bat species makes them more susceptible to introduced direct and immediate anthropogenic disturbances such as hunting, harvesting, and unregulated tourism. Large-bodied insectivorous, frugivorous and nectarivorous are likely susceptible to hunting and harvesting. The 18% of global cave-dwelling bats are threatened by hunting largely in the Afrotropical and Indomalayan regions. This represents a large proportion of 62% of the estimated number of bat species (167 spp.) hunted globally⁴⁴. The high level of hunting and harvesting in the old-world tropics is primarily driven by subsistence and primarily localised particularly in areas with high levels of poverty and driven by the demand for protein sources, food, and traditional medicine⁴⁵⁻⁴⁷. The most frequently hunted species are those common and hyper-abundant cave species (e.g., *Rousettus amplexicaudatus*, *Eonycteris spelaea*, *Eidolon helvum*), which are usually underprotected because of their widespread and globally non-threatened status⁴⁸. However, as a consequence of the absence of statutory protection for many common species intensifies unscheduled hunting and human use can cause even common and abundant species to become extinct (i.e., locally or regionally)⁴⁹. Separately, unregulated tourism is a threat to 38% of the cave-dwelling species and unregulated activities may alter cave microclimate and affect sensitive species.

Cave-dwelling bats are also at risk from loss and degradation of foraging areas^{50,51}, and up to 49% face loss of these habitats by deforestation and agricultural conversion. Disturbed caves in deforested and agricultural lands drive the loss of specialist bats, whereas less disturbed caves support higher species richness and abundance⁵⁰. Furthermore, increased deforestation and vegetation removal around cave sites increase the exposure of caves to

human intrusion and hunting. Additionally, extractive industries of mining and quarrying threaten more than a quarter of cave-dwelling bats, through degradation and destruction of caves and alterations of surface vegetation, which creates barriers that limit species movements and foraging⁵². Although our analyses showed that average mining density is higher in the Nearctic region, this may be caused by a lack of rigorous mapping of mined areas in other regions, and also largely omits quarrying for limestone (as such maps are rarely available)⁵³. However, cement export is significantly higher in countries with high cave-bat species richness and threatened species (e.g., in China and Indonesia), in part because of the extensive limestone karsts in these regions.

Conservation and prioritising vulnerable sites

Funding and resources are limited and often focus on a subset of taxa which may not be representative^{17,54}, it is imperative to set realistic priorities based on areas with higher risks, vulnerabilities and could protect larger communities^{55,56}. The integration of vulnerability to effective conservation planning is often challenging due to vague or inconsistent approaches⁵⁷. Cave ecosystems host a high diversity and endemism yet are rarely included in global priorities²⁰. The persistence of high biodiversity in caves is linked to more pristine cave environments with less anthropogenic pressure. Consequently, we observed that large spatial coverage (e.g., biome-dependent) decreases the evenness in priority distribution in a site-level comparison, thus its conservation application to protect caves is scale dependant (e.g., national-level or biome-wide protection).

Conservation decision making depends on the clear delineation between what is important to develop priorities, as frequently priorities fail to represent what is genuinely important or do not represent communities effectively^{14,58}. In particular, species deemed as “charismatic” may monopolise funding whilst failing to provide significant benefits to the

wider ecological community^{14,15}. Whilst various taxa have been used as indicators for diversity in subterranean habitats⁵⁹, bats represent better surrogates for cave conservation because they not only provide the main source of energy for cave-ecosystems but are also easier to assess and reflect changes from both internal and surfaces^{50,51}. Most conservation decision making for habitat protection centres on taxonomic diversity (e.g., counts, abundance, and rarity)^{60,61}. Common species can provide ecological services (e.g., nectarivorous cave bats as pollinators) and the reduction of population counts may indicate habitat health due to changes in service provision. Whereas, rare species are often prioritised based on their combined distinct ecological function, high sensitivity and vulnerability to declines⁶².

For cave-ecosystems maintaining the functioning of the subterranean ecosystems requires maintaining both diversity and abundance^{30,63,64}, thus a holistic tool that incorporates diversity, rarity and function is needed as a basis for conservation-decision making.

Numerous indices based on different dimensions and attributes of cave biodiversity have been developed but few integrate landscape features, and greater standardisation is needed. Our vulnerability index includes not only species diversity measures^{65,66} but also encompasses evolutionary distinctiveness and threat exposure^{30,50,63}. The inclusion of these measures enables prioritisation of cave ecosystems with rare and higher functional diversity attributes^{67,68} complimenting the metrics based on geopolitical endemism and conservation status from IUCN⁶⁸⁻⁷⁰ which are commonly used within prioritisation schemes. While the expert-based Redlist developed by the IUCN is the most comprehensive basis for conservation and species protection, it is not free from biases⁷¹⁻⁷³, especially for bats, in which a large proportion of species are either taxonomically and spatially under-sampled or disproportionately studied particularly in most megadiverse and developing countries⁷⁴.

Overall, our observed patterns are consistent with previous global studies comparing the value of broad- and fine-scale analyses in identifying priorities. Broad-scale provides an overview of patterns to guide where further focus and fine-scale prioritisation is needed. There is a slight overlap in priorities between scales such as some high priority caves from the broad-scale analysis are the same in the fine-scale prioritisation, but not all. However, we found broad-scale measures underestimated the priorities of highly vulnerable bat caves (i.e., less even distribution of priorities). Broad-scale prioritisation such as regional or biome levels may facilitate the identification of priority caves. Whereas fine-scale prioritisation (e.g., national-level priorities) enables community-level interactions and responses to be encompassed and also accounts for rare species and the impacts of threats on local populations^{30,50}, highlighting the need for good monitoring and assessment data as a basis for priority setting. Furthermore, context-specific threats (e.g., vulnerability to religious activities in Buddhist regions, where an increased proportion of caves may become temples or religious sites) need to be accounted for explicitly for indices to be effective.

For an index to be effective, a clear understanding of diversity patterns and priorities at national levels is an essential first step to implementable policy targets^{55,75}. Additionally, few countries have any policy related to the protection of caves and their biota²⁷. For example, in the Philippines, the National Cave Conservation Committee aims to identify caves for protection has very broad criteria and focused on archaeological and touristic values rather than ecological components which hamper effective protection or priority setting. National Biodiversity Action Plans (NBSAPS) should include standard provisions for priority identification and monitoring⁷⁰, thus frameworks such as this can provide information that is both consistent between countries and can be usefully applied at national levels.

Caveats and opportunities for Bat cave conservation in the Anthropocene

The uneven distribution of threats and a lack of understanding of their impacts remains a challenge for global bat conservation. Developing any index requires pragmatism in finding indicators that are reliable enough, but for which there is sufficient data available. For example, the interpretation of extinction risk requires caution as factors may act in synergy and we could not fully account for the intensity of human-induced threats⁷⁶. This is particularly challenging to pinpoint in the context of cave biota, in which even a single disturbance may alter the entire sensitive biota and ecosystems, and as such events cannot be identified vulnerability (e.g accessibility) must be used as an indicator^{31,50,77}. Furthermore, the degree of expertise required for bat and cave studies means less data is available compared to other taxonomic groups^{74,78}. For instance, in our cave prioritisation, we only accounted the 59% of the global cave-dwelling species, and species coverage varied by region, for example, Indonesia has some of the highest estimated bat cave species richness yet its contribution to the dataset based on surveys and assessments is among the lowest. Furthermore, accurate systematic and taxonomic studies for bats are vital to appropriate conservation as caves host high endemism and many cave bats (e.g., Rhinolophids) have high numbers of as yet undescribed cryptic species⁷⁹. The lack of distribution data may be explicitly linked to the lack of funding in most biodiverse countries⁸⁰, hindering effective assessment in the countries most in need. Conversely within Europe, the UNEP-EUROBATS provides guidance and regulation which comprehensively includes the protection and monitoring of bats and caves in its territory and member states making parallel and equitable policies for large scale protection⁸¹. Policies and targets that accurately account for and include monitoring in threatened systems such as caves and karsts are urgently needed and highlight a need for ecosystem-based conservation targets, as species-specific targets risk missing key habitats for neglected taxa⁸².

Synthesis

In conclusion, to protect and conserve a large fraction of species possible it is crucial, we identify highly vulnerable caves with the highest biotic potential and distinctiveness. We develop a comprehensive index to integrate facets of diversity and risk to provide a simple and scalable approach to prioritising caves for protection and delineating between those in need of urgent intervention (high diversity but high threat) and those which whilst not yet threatened require monitoring to ensure they remain protected. Whilst further data is needed, especially for data-poor, species-rich regions, relying on IUCN data alone may not provide balanced National-scale priorities^{71,83}. The IUCN Redlist must be utilised alongside other tools and measures of decision making, thus we advocate an integrative conservation approach that synthesises various dimensions of conservation. Here we integrate information from two scales, broad-scale and fine-scale represented by biome-dependent and site-level prioritisation to explore how priorities vary across scales, and how to usefully integrate information to obtain a clearer understanding of sensible priorities.

Our study identified gaps and priorities for bat cave conservation, for example, the lack of data from the Afrotropical region, which reflect what form of intervention may be needed for different sites. To address global gaps for effective conservation and develop more rigorous priorities, collaborative efforts among bat scientists is necessary to enable the development of an effective international agenda and nationally adaptable goals for cave prioritisation and assessment. We propose a framework to identify priorities based on the type of interventions needed to safeguard diversity. This framework calls for standardisation of methods of bat cave assessment and monitoring based on key indicators for diversity and threat, and for this data to be more widely shared to facilitate better conservation and policy. Furthermore, maintaining cave bat diversity relies on their inclusion into conservation agendas and priorities, and the use of science-based targets and frameworks, synthesising conservation effectiveness (e.g., Conservation Evidence Initiative⁸⁴) to ensure that

approaches such as that detailed here can be effectively applied to enable key sites to be identified, and appropriately protected on a global basis.

Methods

Dataset building

We sampled global cave-dwelling bats from the databases of IUCN redlist and the DarkCideS 1.0, a global dataset for cave-dwelling bats, including all species that occur, use, roost, or hibernate in caves and underground habitats for any part of their life histories. All species names were curated and updated using the Mammal Diversity Database²² and Bats of the World: A taxonomic and geographic database⁸⁵. We included species-specific information including species taxonomy, endemism at geopolitical and biogeographical scales, species range and distributions, conservation status, population trends, ecological traits, and threatening processes. The habitat breadth was determined according to the number of habitats a species occurs⁸⁶. We used the weighted habitat breadth (%) values in the final analyses. Species were then classified based on island endemism and country endemism. We used the data from its congeneric species for those species without trait or ecological data. We then compared the species turnover between IUCN Redlist and the DarkCideS 1.0 to determine gaps and caveats in the current data knowledge and availability.

Species diversity and distributions of global species

Using IUCN data we calculated geopolitical (e.g., country or continental) species richness based on where the species occurs as (including native, extant, resident, possibly extinct or migrant classifications by the IUCN). Second, we analysed and defined endemism in two ways: geopolitical endemism (i.e., a country endemic) if the species occurred only in a single sovereign country⁸⁷, and island endemism was classified as island-

restricted or predominantly mainland⁸⁸. Species conservation status was assessed according to the IUCN Redlist criteria and were then simplified to obtained binary extinction risk: Non-threatened (e.g., Least Concern, Near Threatened) and Threatened (e.g., Vulnerable, Endangered, and Critically Endangered). While Data Deficient species were treated as the latter as they may face higher or similar threats with threatened species, hence a lack of data for formal classification^{30,40}. We compared species diversity across the biogeographic realm^{89,90} (e.g., Indomalaya, Austral-Oceania, Afrotropical, Neotropical, Palearctic, and Nearctic). Chi-squared test (χ^2) of association was then used to assess the relationship in species geopolitical endemism, island endemism, conservation status, and population status.

We plotted the logarithm of species richness (i.e., estimated number of species per country) against the logarithm of country land areas (km²)⁹¹ to estimate the broad Species-Area Relationships (SAR) applying the equation $S = cA^z$, where S is the species richness equal to the Area (A) sampled, and z and c are fitted constants⁹². We defined endemism in a simplistic manner that is coherent for national or regional level conservation policymaking.

IUCN-based extinction proportions and risks

Following^{93,94} we estimated the species extinction proportions within bat biogeographical realms, endemism (e.g., geopolitical and island), population trends, trophic levels, and families. The IUCN bat data is imperfect and many species lack updated assessments, using the available data we generate the mean extinction risks and upper and lower bound estimates for different groups and species attributes. We calculated the proportion of extinction risk ($\hat{p}_{\text{extinction}}$) based on the proportion of threatened species as $\hat{p}_{\text{extinction}} = (N^{\circ}_{\text{threatened}}) / (N^{\circ}_{\text{species}} - DD_{\text{species}})$, where $N^{\circ}_{\text{threatened}}$ is the number of threatened species assessed as Vulnerable (VU), Endangered (EN), and Critically Endangered (CE), $N^{\circ}_{\text{species}}$ is the total number of species, and DD is the number of Data Deficient species,

assuming that *DD* species will have a similar extinction risk as of other threatened categories as they may face similar or higher threats than those non-Data Deficient species^{30,94}. We then calculated the lower estimate ($\hat{p}_{\text{extinction_lower}} = N^{\circ}_{\text{threatened}} / N^{\circ}_{\text{species}}$) with an assumption that *DD* species are categorised as non-threatened and upper estimates ($\hat{p}_{\text{extinction_upper}} = N^{\circ}_{\text{threatened}} + DD / N^{\circ}_{\text{species}}$) with the assumption that *DD* is threatened.

Using a Generalized Linear Model (GLM) we determined the predictors of species binary extinction risk (e.g., threatened vs, non-threatened) for global cave bats and within suborders, Yinpterochiroptera and Yangochiroptera. We used a total of ten ($N = 10$) explanatory variables divided into geographical variables (geographical range, island endemism, and geopolitical endemism) extracted from, biotic variables (adult body mass (kg, \log_{10})⁸⁸, generation length⁹⁵, forest dependency (yes or no based on the IUCN database), habitat breadth (%), and trophic group. For the trophic groups, we grouped species as herbivores for all species that forage on plant-based resources (e.g., frugivores and nectarivores). Species that forage on animal resources (e.g., insectivorous, sanguivorous, piscivores) were grouped as carnivores. While species that forage on both resources were grouped into omnivores. Our last group of explanatory variables includes the species threat index (*SPI*) (e.g., direct, indirect, and natural).

Patterns and turnover of threats

We analysed threats in three different levels: species, cave-site, and country-level. First, we analysed species threats based on the simplified expert-based IUCN redlist. We modified the threats assessment by Salafsky et al. (2008) as it does not completely capture other breadths of threats in caves ecosystems. We developed the Species Threat Index (*STI*) calculated from the quotient of the sum of species absolute threat ($T_{\text{dir, ind, nat}}$) and the number of threats assessed ($N^{\circ} T$) ($STI_{\text{species}} = \sum T / N^{\circ} T$). We compared *STI* ($STI_{\text{dir, ind, nat}}$) across the

biogeographical realm, endemism, conservation status, and population trend using a non-parametric Kruskal-Wallis test. We performed a separate generalized linear model (GLMs) with a binomial distribution in JAMOVI version 1.2.6, using GAMLj module ⁹⁷ to determine the influence of species traits on species vulnerability to threats. We used adult body mass (g, log 10), geographical range (log 10) and trophic levels as predictors of risks ⁹⁸ from to key threatening process that threatens at least 10% of the global cave-dwelling bats.

Second, we mapped the cave surrounding landscapes features to measure cave susceptibility to threats (full details are provided in the supplements). For landscape features, we include canopy height ⁹⁹, tree density ¹⁰⁰, distance to river ¹⁰¹, bare ground cover change ¹⁰², short vegetation cover change ¹⁰², tree canopy change ¹⁰² and for vulnerabilities we include distance to urbanisation ¹⁰², distance to roads ¹⁰³, mine density ¹⁰⁴, night light¹⁰⁵, pesticide use ¹⁰⁶, and human density ^{107,108}. We then assessed the correlation between these variables to species biotic scores (see “Cave Biotic Potential section”) and the extent was compared across biogeographical realms.

We explored country ranking in terms of species richness and species-area relationship, threatened and endemic species proportions and its concordance to sociodemographic and environmental indicators as rudimentary indicators of a country’s resources to representing its capacity to protect its species and environment. In our analyses, we used percent forest cover ¹⁰⁹ as a proxy for habitat intactness and quality per country, with the assumption that caves surrounded by intact forest are more protected and least vulnerable to intrusions ^{30,50,77}. While we used country cement production (TTM*1000) ¹¹⁰ as a proxy to species susceptibility to direct threats assuming that in areas with higher cement production species are more prone to habitat loss and direct disturbances ^{30,37}. We applied Kendall’s τ B to test for the ranked-concordance in (i) country-level species richness (log 10), (ii) %

endemism, (iii) % threatened species, (iv) percent forest cover (% , log 10) (iii) socioeconomic indicators: GDP per capita (log 10), country cement production (TTM). We mapped and visualised estimated species richness, endemism, and threatened species using QGIS version 3.14.

Cave Biotic Potential

We mapped the global bat cave priorities based on its vulnerability at site-level and biome-levels based on geographical data extracted from the DarkCideS 1. (Tanalgo et al. to be submitted in *Nature Scientific Data*) database. Following the approach of Tanalgo et al. (2018), we determined cave priorities using the Bat Cave Vulnerability Index, BCVI = (BP)(BV). Where, BP is the cave biotic potential (i.e., species diversity and attributes) and BV is the cave's landscape feature and threats. We derived a new version of BCVI using Tanalgo et al.'s (2018), which was primarily developed in community-scale prioritisation relying on IUCN Redlist's endemism and conservation and lacks components relevant for comparative global-scale prioritisation scheme. First, we exclude the data from population estimates to minimise bias from the missing and unstandardised assessment in caves datasets (See the Tanalgo et al. data paper for caveats). Second, we incorporated evolutionary units (e.g., evolutionary distinctiveness (ED) and corrected weighted endemism (CWE)) in deriving the cave biotic potential (BP). First, we used the evolutionary distinctiveness values following Isaac et al.⁶⁹. We calculated corrected weighted endemism (CWE)^{111,112} by dividing weighted endemism (WE) by the total cave species richness (e.g., absolute counts of species). This measures the proportion of bat species in a cave site.

We then calculated BP using the equation: $BP_{cave\ x} = \sum S_{cave\ x} / \mathbf{Max.} \sum S_{cave\ y}$, where cave BP is the calculated quotient of the sum of species attributes scores in a cave ($\sum S_{cave\ x}$) and the highest maximum ($\sum S_{cave\ y}$) sum of species attribute scores from all sampled caves

($S_{cave\ x}$). Where $S_{cave\ x}$ is the score of n^{th} bat cave species evolutionary distinctiveness (ED), corrected weighted endemism ($\times 100$) (CWE), conservation status (Cons), population trends (Pops), and geopolitical endemism (E). It is calculated as:

$$S_{cave\ x} = \Sigma \text{Species 1 (ED + CWE (} \times 100) + \text{Cons + Pops + E) + Species 2 (ED + CWE (} \times 100) + \text{Cons + Pops + E) + Species 3 (ED + CWE (} \times 100) + \text{Cons + Pops + E)}.$$

The BP_{cave} index score ranges from 0.00 to 1.00, with values near 1.00 indicates higher cave biotic potential and scaled to four levels of priority.

Mapping landscape features, threats, and cave vulnerability

The computed BP is then complimented with the cave Biotic Vulnerability (BV) to derive the cave alphanumeric priority based on vulnerability. We mapped and measured the extent of geophysical features represented landscape features and threats in a single cave following (Hughes 2019) (See Supplementary Methods). Because of the relatedness of threats we only selected representative threats and landscape features in the BV analyses including (i) distance to city/urbanisation, (ii) distance to roads, (iii) tree density, (iv) canopy cover, (v) mining density, and (vi) distance to the river (for arid biomes). We calculated cave Biotic Vulnerability (BV_{cave}) as the summed scores of N divided by the total number of geophysical features assessed (N^0): $BV = \Sigma NT/N^0$, where NT ($NT = T_x / T_{max\ y}$) is the score of geophysical features (T) based on the quotient between the measured extent of geophysical features in a specific cave (T_x) divided to the maximum value of measured extent of threats and landscape features in all sampled caves ($T_{max\ y}$). The N score ranges from 0.00 to 1.00 and scaled in four-level range scoring.

Bat Cave Vulnerability Index (BCVI)

For the purpose and limitation of this work, we aimed to assess the global bat cave vulnerability based on our database and mappable landscape features and threats. We performed BCVI prioritisation in contrasting spatial scales. First, biome-dependent representing the broad-scale priorities, which assumes the priorities are compared relative to all caves surveyed based on biogeographical assessments. Secondly, country-dependent: representing the fine-scale prioritisation, based on the survey-relative priorities that represent, with assumptions that determination of priority should be comparable based on the caves surveyed within the country to guide statutory decision making. The alphanumeric index based on BCVI is then converted into four priority levels (**Table 2**). We then compared the mean biotic vulnerability threshold (i.e., values range from 1 to 4, the lower the values the higher the vulnerabilities) versus cave biotic potential status, and then the priorities from both scales across biogeographical realms and climatic biomes using a chi-squared test (χ^2) of association. We used Pielou's index to assess evenness in BCVI and priorities between scales.

References

1. Ripple, W. J. *et al.* World Scientists' Warning to Humanity: A Second Notice. *BioScience* **67**, 1026–1028 (2017).
2. Ceballos, G. *et al.* Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci. Adv.* **1**, e1400253 (2015).
3. Pimm, S. L. *et al.* The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246752–1246752 (2014).

4. Conenna, I., Rocha, R., Russo, D. & Cabeza, M. Insular bats and research effort: a review of global patterns and priorities. *Mammal Rev.* **47**, 169–182 (2017).
5. Hernández-Quiroz, N. S., Badano, E. I., Barragán-Torres, F., Flores, J. & Pinedo-Álvarez, C. Habitat suitability models to make conservation decisions based on areas of high species richness and endemism. *Biodivers. Conserv.* **27**, 3185–3200 (2018).
6. Wintle, B. A. *et al.* Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proc. Natl. Acad. Sci.* **116**, 909–914 (2019).
7. Arponen, A. Prioritizing species for conservation planning. *Biodivers. Conserv.* **21**, 875–893 (2012).
8. Groves, C. R. *et al.* Planning for Biodiversity Conservation: Putting Conservation Science into Practice. *BioScience* **52**, 499 (2002).
9. Hughes, A. C. Mapping priorities for conservation in Southeast Asia. *Biol. Conserv.* **209**, 395–405 (2017).
10. Sutherland, W. J. *et al.* A Horizon Scan of Emerging Issues for Global Conservation in 2019. *Trends Ecol. Evol.* **34**, 83–94 (2019).
11. Dolman, P. M., Panter, C. J. & Mossman, H. L. The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *J. Appl. Ecol.* **49**, 986–997 (2012).
12. Halpern, B. S. *et al.* Gaps and Mismatches between Global Conservation Priorities and Spending. *Conserv. Biol.* **20**, 56–64 (2006).
13. Clark, J. A. & May, R. M. Taxonomic Bias in Conservation Research. *Science* **297**, 191–192 (2002).
14. Wang, F. *et al.* The hidden risk of using umbrella species as conservation surrogates: A spatio-temporal approach. *Biol. Conserv.* **253**, 108913 (2021).

15. Gerber, L. R. Conservation triage or injurious neglect in endangered species recovery. *Proc. Natl. Acad. Sci.* **113**, 3563–3566 (2016).
16. Bellon, A. M. Does animal charisma influence conservation funding for vertebrate species under the US Endangered Species Act? *Environ. Econ. Policy Stud.* **21**, 399–411 (2019).
17. Gordon, E. R., Butt, N., Rosner-Katz, H., Binley, A. D. & Bennett, J. R. Relative costs of conserving threatened species across taxonomic groups. *Conserv. Biol.* **0**, (2019).
18. Macdonald, E. A. *et al.* Conservation inequality and the charismatic cat: *Felis felis*. *Glob. Ecol. Conserv.* **3**, 851–866 (2015).
19. McGowan, J. *et al.* Conservation prioritization can resolve the flagship species conundrum. *Nat. Commun.* **11**, 994 (2020).
20. Mammola, S. *et al.* Scientists' Warning on the Conservation of Subterranean Ecosystems. *BioScience* (2019) doi:10.1093/biosci/biz064.
21. Cardinale, B. J. *et al.* Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).
22. Burgin, C. J., Colella, J. P., Kahn, P. L. & Upham, N. S. How many species of mammals are there? *J. Mammal.* **99**, 1–14 (2018).
23. Furey, N. M. & Racey, P. A. Conservation Ecology of Cave Bats. in *Bats in the Anthropocene: Conservation of Bats in a Changing World* (eds. Voigt, C. C. & Kingston, T.) 463–500 (Springer International Publishing, 2016). doi:10.1007/978-3-319-25220-9_15.
24. Monro, A. K., Bystriakova, N., Fu, L., Wen, F. & Wei, Y. Discovery of a diverse cave flora in China. *PLOS ONE* **13**, e0190801 (2018).

25. Simon, K. S. Chapter 26 - Cave ecosystems. in *Encyclopedia of Caves (Third Edition)* (eds. White, W. B., Culver, D. C. & Pipan, T.) 223–226 (Academic Press, 2019). doi:10.1016/B978-0-12-814124-3.00025-X.
26. Deharveng, L. & Bedos, A. Diversity of Terrestrial Invertebrates in Subterranean Habitats. in *Cave Ecology* (eds. Moldovan, O. T., Kováč, L. & Halse, S.) 107–172 (Springer International Publishing, 2018). doi:10.1007/978-3-319-98852-8_7.
27. Whitten, T. Applying ecology for cave management in China and neighbouring countries. *J. Appl. Ecol.* **46**, 520–523 (2009).
28. Monro, A. K., Bystriakova, N., Fu, L., Wen, F. & Wei, Y. Discovery of a diverse cave flora in China. *PLOS ONE* **13**, e0190801 (2018).
29. Medellín, R. A., Wiederholt, R. & Lopez-Hoffman, L. Conservation relevance of bat caves for biodiversity and ecosystem services. *Biol. Conserv.* **211**, 45–50 (2017).
30. Tanalgo, K. C., Tabora, J. A. G. & Hughes, A. C. Bat cave vulnerability index (BCVI): A holistic rapid assessment tool to identify priorities for effective cave conservation in the tropics. *Ecol. Indic.* **89**, 852–860 (2018).
31. De Oliveira, H. F. M., Oprea, M. & Dias, R. I. Distributional Patterns and Ecological Determinants of Bat Occurrence Inside Caves: A Broad Scale Meta-Analysis. *Diversity* **10**, 49 (2018).
32. Frick, W. F., Kingston, T. & Flanders, J. A review of the major threats and challenges to global bat conservation. *Ann. N. Y. Acad. Sci.* **0**, (2019).
33. Barclay, R. M. R. *et al.* Variation in the reproductive rate of bats. *Can. J. Zool.* **82**, 688–693 (2004).
34. Day, M. & Urich, P. An assessment of protected karst landscapes in Southeast Asia. *Cave and Karst Science* <https://eurekamag.com/research/030/010/030010724.php> (2000).

35. Clements, R., Sodhi, N. S., Schilthuizen, M. & Ng, P. K. L. Limestone Karsts of Southeast Asia: Imperiled Arks of Biodiversity. *BioScience* **56**, 733–742 (2006).
36. Hughes, A. C. Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere* **8**, e01624 (2017).
37. Liew, T.-S., Price, L. & Clements, G. R. Using Google Earth to Improve the Management of Threatened Limestone Karst Ecosystems in Peninsular Malaysia. *Trop. Conserv. Sci.* **9**, 903–920 (2016).
38. Sedlock, J. L., Jose, R. P., Vogt, J. M., Paguntalan, L. M. J. & Cariño, A. B. A survey of bats in a karst landscape in the central Philippines.
<https://www.ingentaconnect.com/content/miiz/actac/2014/00000016/00000001/art00018>
(2014) doi:info:doi/10.3161/150811014X683390.
39. Torres-Flores, J. W. & Santos-Mreno, A. Inventory, features, and protection of underground roosts used by bats in Mexico.
<https://www.ingentaconnect.com/content/miiz/actac/2017/00000019/00000002/art00019>
(2017) doi:info:doi/10.3161/15081109ACC2017.19.2.019.
40. Welch, J. N. & Beaulieu, J. M. Predicting Extinction Risk for Data Deficient Bats. *Diversity* **10**, 63 (2018).
41. Francis, C. M. *et al.* The Role of DNA Barcodes in Understanding and Conservation of Mammal Diversity in Southeast Asia. *PLOS ONE* **5**, e12575 (2010).
42. Murray, S. W. *et al.* Molecular phylogeny of hipposiderid bats from Southeast Asia and evidence of cryptic diversity. *Mol. Phylogenet. Evol.* **62**, 597–611 (2012).
43. Jones, K. E., Purvis, A. & Gittleman, J. L. Biological Correlates of Extinction Risk in Bats. *Am. Nat.* **161**, 601–614 (2003).
44. Mildenstein, T., Tanshi, I. & Racey, P. A. Exploitation of Bats for Bushmeat and Medicine. in *Bats in the Anthropocene: Conservation of Bats in a Changing World* (eds.

- Voigt, C. C. & Kingston, T.) 325–375 (Springer International Publishing, 2016).
doi:10.1007/978-3-319-25220-9_12.
45. Cardiff, S. G., Ratrimomanarivo, F. H., Rembert, G. & Goodman, S. M. Hunting, disturbance and roost persistence of bats in caves at Ankarana, northern Madagascar. *Afr. J. Ecol.* **47**, 640–649 (2009).
 46. Goodman, S. M. Hunting of Microchiroptera in south-western Madagascar. *Oryx* **40**, 225–228 (2006).
 47. Mickleburgh, S., Waylen, K. & Racey, P. Bats as bushmeat: a global review. *Oryx* **43**, 217–234 (2009).
 48. Aziz, S. A. *et al.* The critical importance of Old World fruit bats for healthy ecosystems and economies. *Front. Ecol. Evol.* **9**, (2021).
 49. Tanalgo, K. C. & Hughes, A. C. Priority-setting for Philippine bats using practical approach to guide effective species conservation and policy-making in the Anthropocene. *Hystrix Ital. J. Mammal.* **30**, 74–83 (2019).
 50. Cajaiba, R. L. *et al.* Are neotropical cave-bats good landscape integrity indicators? Some clues when exploring the cross-scale interactions between underground and above-ground ecosystems. *Ecol. Indic.* **122**, 107258 (2021).
 51. Jones, G., Jacobs, D. S., Kunz, T. H., Willig, M. R. & Racey, P. A. Carpe noctem: the importance of bats as bioindicators. *Endanger. Species Res.* **8**, 93–115 (2009).
 52. Theobald, E., Hosken, D. J., Foster, P. & Moyes, K. Mines and bats: the impact of open-pit mining on bat activity.
<https://www.ingentaconnect.com/contentone/miiz/actac/2020/00000022/00000001/art00014> (2020) doi:10.3161/15081109ACC2020.22.1.014.
 53. Sonter, L. J., Ali, S. H. & Watson, J. E. M. Mining and biodiversity: key issues and research needs in conservation science. *Proc. R. Soc. B Biol. Sci.* **285**, 20181926 (2018).

54. Wilson, K. A. *et al.* Conserving Biodiversity Efficiently: What to Do, Where, and When. *PLOS Biol.* **5**, e223 (2007).
55. Rudd, M. A. *et al.* Generation of Priority Research Questions to Inform Conservation Policy and Management at a National Level. *Conserv. Biol.* **25**, 476–484 (2011).
56. Joseph, L. N., Maloney, R. F. & Possingham, H. P. Optimal Allocation of Resources among Threatened Species: a Project Prioritization Protocol. *Conserv. Biol.* **23**, 328–338 (2009).
57. Sarkar, S. *et al.* Biodiversity Conservation Planning Tools: Present Status and Challenges for the Future. *Annu. Rev. Environ. Resour.* **31**, 123–159 (2006).
58. Game, E. T., Kareiva, P. & Possingham, H. P. Six Common Mistakes in Conservation Priority Setting. *Conserv. Biol.* **27**, 480–485 (2013).
59. Souza Silva, M., Martins, R. P. & Ferreira, R. L. Cave conservation priority index to adopt a rapid protection strategy: a case study in Brazilian Atlantic rain forest. *Environ. Manage.* **55**, 279–295 (2015).
60. Brum, F. T. *et al.* Global priorities for conservation across multiple dimensions of mammalian diversity. *Proc. Natl. Acad. Sci.* **114**, 7641–7646 (2017).
61. Hartley, S. & Kunin, W. E. Scale Dependency of Rarity, Extinction Risk, and Conservation Priority. *Conserv. Biol.* **17**, 1559–1570 (2003).
62. Mouillot, D. *et al.* Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. *PLOS Biol.* **11**, e1001569 (2013).
63. Phelps, K., Jose, R., Labonite, M. & Kingston, T. Correlates of cave-roosting bat diversity as an effective tool to identify priority caves. *Biol. Conserv.* **201**, 201–209 (2016).
64. Bregović, P., Fišer, C. & Zagamajster, M. Contribution of rare and common species to subterranean species richness patterns. *Ecol. Evol.* **9**, 11606–11618 (2019).

65. Niu, H., Wang, N., Zhao, L. & Liu, J. Distribution and underground habitats of cave-dwelling bats in China. *Anim. Conserv.* **10**, 470–477 (2007).
66. Furman, A. & Özgül, A. The distribution of cave-dwelling bats and conservation status of underground habitats in Northwestern Turkey. *Biol. Conserv.* **120**, 243–248 (2004).
67. Srivastava, D. S., Cadotte, M. W., MacDonald, A. A. M., Marushia, R. G. & Mirotchnick, N. Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.* **15**, 637–648 (2012).
68. Jetz, W. *et al.* Global Distribution and Conservation of Evolutionary Distinctness in Birds. *Curr. Biol.* **24**, 919–930 (2014).
69. Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C. & Baillie, J. E. M. Mammals on the EDGE: Conservation Priorities Based on Threat and Phylogeny. *PLOS ONE* **2**, e296 (2007).
70. Martín-López, B., Montes, C., Ramírez, L. & Benayas, J. What drives policy decision-making related to species conservation? *Biol. Conserv.* **142**, 1370–1380 (2009).
71. Martín-López, B., González, J. A. & Montes, C. The pitfall-trap of species conservation priority setting. *Biodivers. Conserv.* **20**, 663–682 (2011).
72. Trimble, M. J. & Aarde, R. J. V. Species Inequality in Scientific Study. *Conserv. Biol.* **24**, 886–890 (2010).
73. Hughes, A., Orr, M., Yang, Q. & Qiao, H. Effectively and accurately mapping global biodiversity patterns for different regions and taxa. *Glob. Ecol. Biogeogr.* (2020) doi:10.22541/au.159654424.40253314.
74. Zamora-Gutierrez, V., Amano, T. & Jones, K. E. Spatial and taxonomic biases in bat records: Drivers and conservation implications in a megadiverse country. *Ecol. Evol.* **9**, 14130–14141 (2019).

75. Doi, H. & Takahara, T. Global patterns of conservation research importance in different countries of the world. *PeerJ* **4**, e2173 (2016).
76. Howard, C., Flather, C. H. & Stephens, P. A. What drives at-risk species richness? Environmental factors are more influential than anthropogenic factors or biological traits. *Conserv. Lett.* **12**, e12624 (2019).
77. Phelps, K., Jose, R., Labonite, M. & Kingston, T. Assemblage and Species Threshold Responses to Environmental and Disturbance Gradients Shape Bat Diversity in Disturbed Cave Landscapes. *Diversity* **10**, 55 (2018).
78. Herkt, K. M. B., Skidmore, A. K. & Fahr, J. Macroecological conclusions based on IUCN expert maps: A call for caution. *Glob. Ecol. Biogeogr.* **26**, 930–941 (2017).
79. Mayer, F., Dietz, C. & Kiefer, A. Molecular species identification boosts bat diversity. *Front. Zool.* **4**, 4 (2007).
80. McClanahan, T. R. & Rankin, P. S. Geography of conservation spending, biodiversity, and culture. *Conserv. Biol.* **30**, 1089–1101 (2016).
81. UNEP/EUROBATS. UNEP/EUROBATS | Agreement on the Conservation of Populations of European Bats. <https://www.eurobats.org/> (2020).
82. Hughes, A. C., Qiao, H. & Orr, M. C. Extinction Targets Are Not SMART (Specific, Measurable, Ambitious, Realistic, and Time Bound). *BioScience* **71**, 115–118 (2021).
83. Milner-Gulland, E. J. *et al.* Application of IUCN Red Listing Criteria at the Regional and National Levels: A Case Study from Central Asia. *Biodivers. Conserv.* **15**, 1873–1886 (2006).
84. Conservation Evidence. Conservation Evidence: Evidence Data. [https://www.conservationevidence.com/data/index/?synopsis_id\[\]=14](https://www.conservationevidence.com/data/index/?synopsis_id[]=14) (2021).
85. Simmons, N. & Cirranello, A. Bat species of the World: A taxonomic and geographic database. <https://batnames.org/> (2020).

86. Etard, A., Morrill, S. & Newbold, T. Global gaps in trait data for terrestrial vertebrates. *Glob. Ecol. Biogeogr.* **n/a**, (2020).
87. Ceballos, G. & Ehrlich, P. R. Mammal Population Losses and the Extinction Crisis. *Science* **296**, 904–907 (2002).
88. Faurby, S. *et al.* PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology* **99**, 2626–2626 (2018).
89. Olson, D. M. *et al.* Terrestrial Ecoregions of the World: A New Map of Life on EarthA new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* **51**, 933–938 (2001).
90. Olson, D. M. & Dinerstein, E. The Global 200: A Representation Approach to Conserving the Earth’s Most Biologically Valuable Ecoregions. *Conserv. Biol.* **12**, 502–515 (1998).
91. Land area (sq. km) | Data. <https://data.worldbank.org/indicator/AG.LND.TOTL.K2>.
92. Brunet, A. K. & Medellín, R. A. The Species–Area Relationship in Bat Assemblages of Tropical Caves. *J. Mammal.* **82**, 1114–1122 (2001).
93. Hoffmann, M. *et al.* The Impact of Conservation on the Status of the World’s Vertebrates. *Science* **330**, 1503–1509 (2010).
94. Richman, N. I. *et al.* Multiple drivers of decline in the global status of freshwater crayfish (Decapoda: Astacidea). *Philos. Trans. R. Soc. B Biol. Sci.* **370**, 20140060 (2015).
95. Pacifici, M. *et al.* Generation length for mammals. *Nat. Conserv.* **5**, 89–94 (2013).
96. Salafsky, N. *et al.* A Standard Lexicon for Biodiversity Conservation: Unified Classifications of Threats and Actions. *Conserv. Biol.* **22**, 897–911 (2008).
97. Gallucci, M. *GAMLj: General analyses for linear models.[jamovi module]*. (Version, 2019).

98. Atwood, T. B. *et al.* Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Sci. Adv.* **6**, eabb8458 (2020).
99. Simard, M., Pinto, N., Fisher, J. B. & Baccini, A. Mapping forest canopy height globally with spaceborne lidar. *J. Geophys. Res. Biogeosciences* **116**, (2011).
100. Crowther, T., Glick, H. & Covey, K. Global tree density map. https://elischolar.library.yale.edu/yale_fes_data/1/ (2015).
101. Yamazaki, D., Trigg, M. A. & Ikeshima, D. Development of a global ~90m water body map using multi-temporal Landsat images. *Remote Sens. Environ.* **171**, 337–351 (2015).
102. Song, X.-P. *et al.* Global land change from 1982 to 2016. *Nature* **560**, 639–643 (2018).
103. Meijer, J. R., Huijbregts, M. A. J., Schotten, K. C. G. J. & Schipper, A. M. Global patterns of current and future road infrastructure. *Environ. Res. Lett.* **13**, 064006 (2018).
104. Labay, K. *et al.* Global Distribution of Selected Mines, Deposits, and Districts of Critical Minerals. (2017) doi:10.5066/F7GH9GQR.
105. Earth at Night (Black Marble) 2016 Color Maps. <https://www.visibleearth.nasa.gov/images/144898/earth-at-night-black-marble-2016-color-maps> (2019).
106. Maggi, F., Tang, F. H. M., Cecilia, D. la & McBratney, A. PEST-CHEMGRIDS, global gridded maps of the top 20 crop-specific pesticide application rates from 2015 to 2025. *Sci. Data* **6**, 1–20 (2019).
107. Hughes, A. C. Understanding and minimizing environmental impacts of the Belt and Road Initiative. *Conserv. Biol.* **33**, 883–894 (2019).
108. SEDAC. Population Density, v4: Gridded Population of the World (GPW), v4 | SEDAC. (2020).

109. The World Bank. Forest area (% of land area) | Data.
<https://data.worldbank.org/indicator/AG.LND.FRST.ZS?end=2016&start=1990&view=chart> (2020).
110. Index Mundi. Hydraulic Cement Production by Country (Thousand metric tons).
<https://www.indexmundi.com/minerals/?product=cement&graph=production> (2020).
111. Laffan, S. W. & Crisp, M. D. Assessing endemism at multiple spatial scales, with an example from the Australian vascular flora. *J. Biogeogr.* **30**, 511–520 (2003).
112. Crisp, M. D., Laffan, S., Linder, H. P. & Monro, A. Endemism in the Australian flora. *J. Biogeogr.* **28**, 183–198 (2001).

Figures

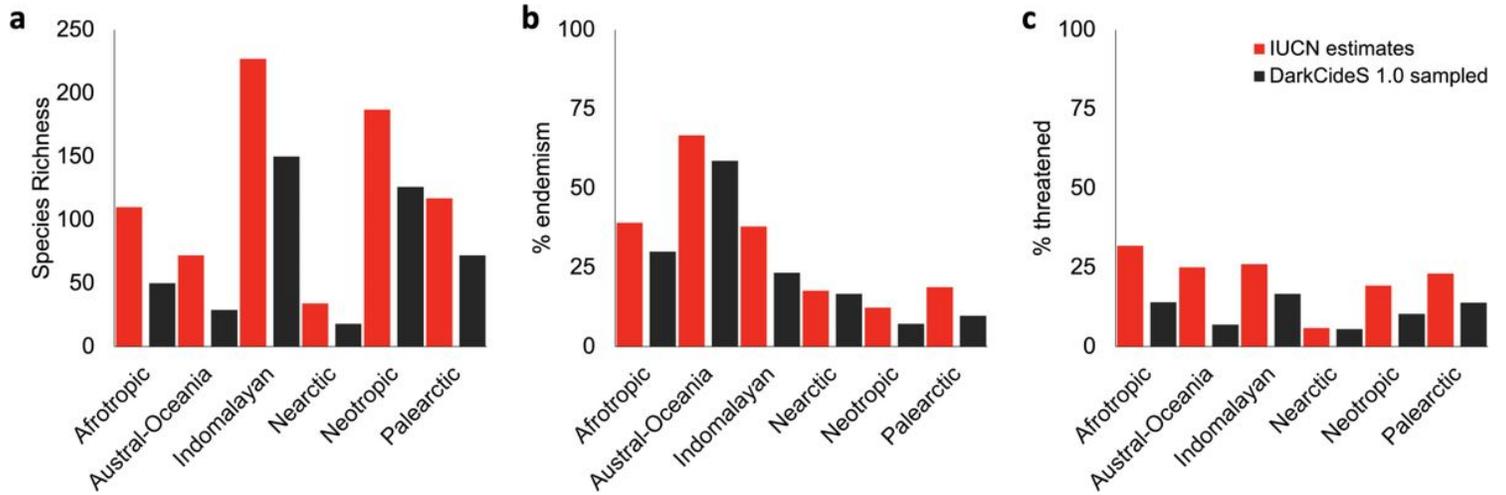


Figure 1

Biogeographic comparison of species turnover between IUCN estimates (red bars) and sampled caves from DarkCideS 1.0 (black bars) (A) species richness, (B) proportion of endemism (B), and (C) proportion of threatened species worldwide. Complete data for IUCN-based estimates is is supplemented in Supplementary Data 1 and DarkCideS 1.0 sampled data will be supplemented in the Data Paper to be co-published with this manuscript.

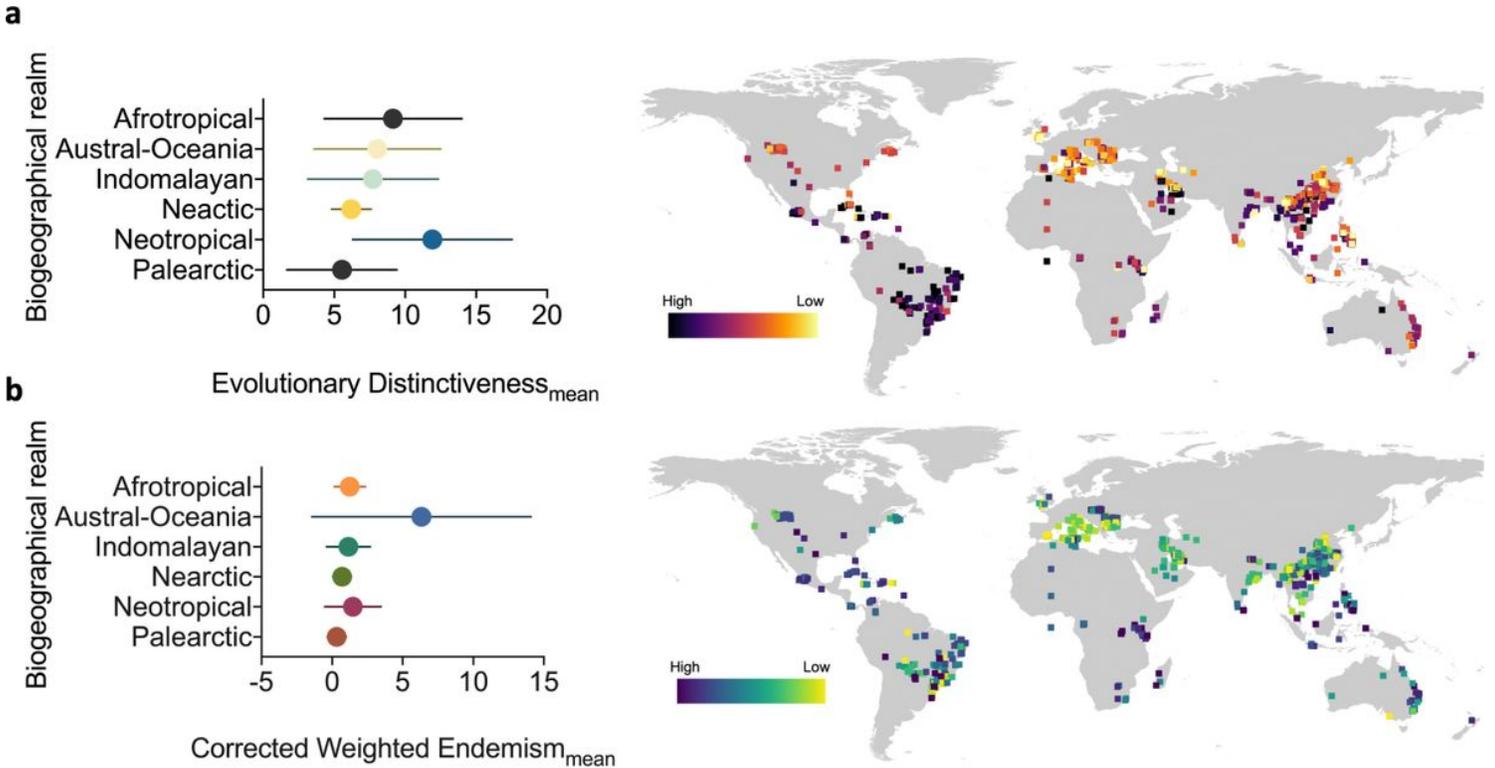


Figure 2

Comparison of bat cave evolutionary distinctiveness and endemism. (A) Cave Evolutionary Distinctiveness and (B) corrected Weighted endemism compared across biogeographical realms (left). Sum of ED and CWE of individual sampled caves (right). The ED and CWE of sampled cave is supplemented in the Data Paper co-published with this manuscript. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

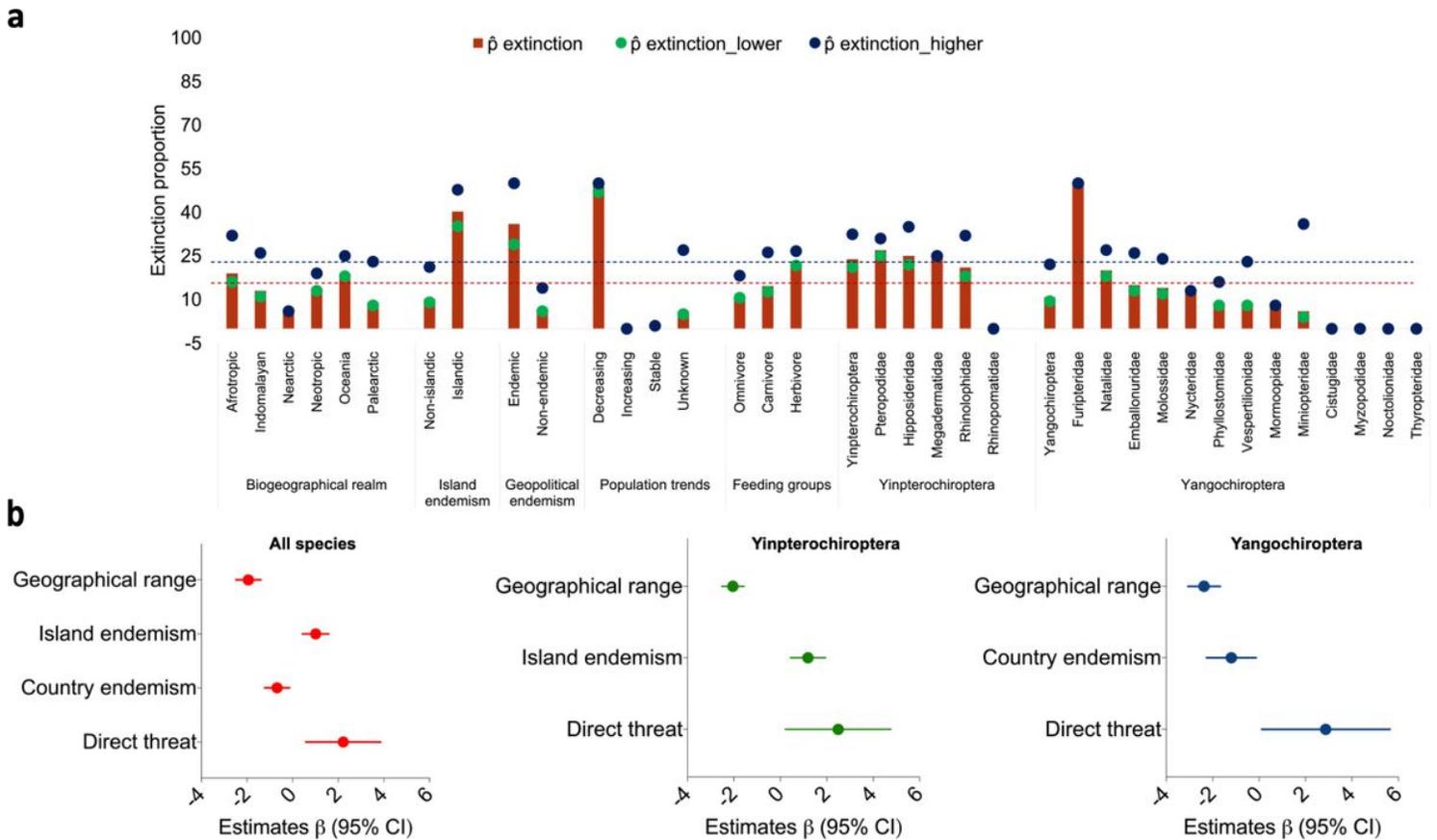


Figure 3

IUCN-based extinction risk. (A) Estimated extinction proportion (\hat{p} extinction) of global cave-dwelling bat species compared by biogeographical realm, island endemism, geopolitical endemism, population trends, trophic groups, sub-orders and families. Estimated extinction proportion (\hat{p} extinction) for global species (blue dashed-line) and all cave-dwelling bats (red dashed-line) are provided. All computed values are supplemented in Supplementary Table 1. (B) Estimate coefficients of significant determinants binary extinction risks of all global species, and amongst suborders Yinpterochiroptera and Yangochiroptera. Summary of Binomial Generalised Linear Mixed (GLMs) explaining species extinction risks is provided in Supplementary Table 2.

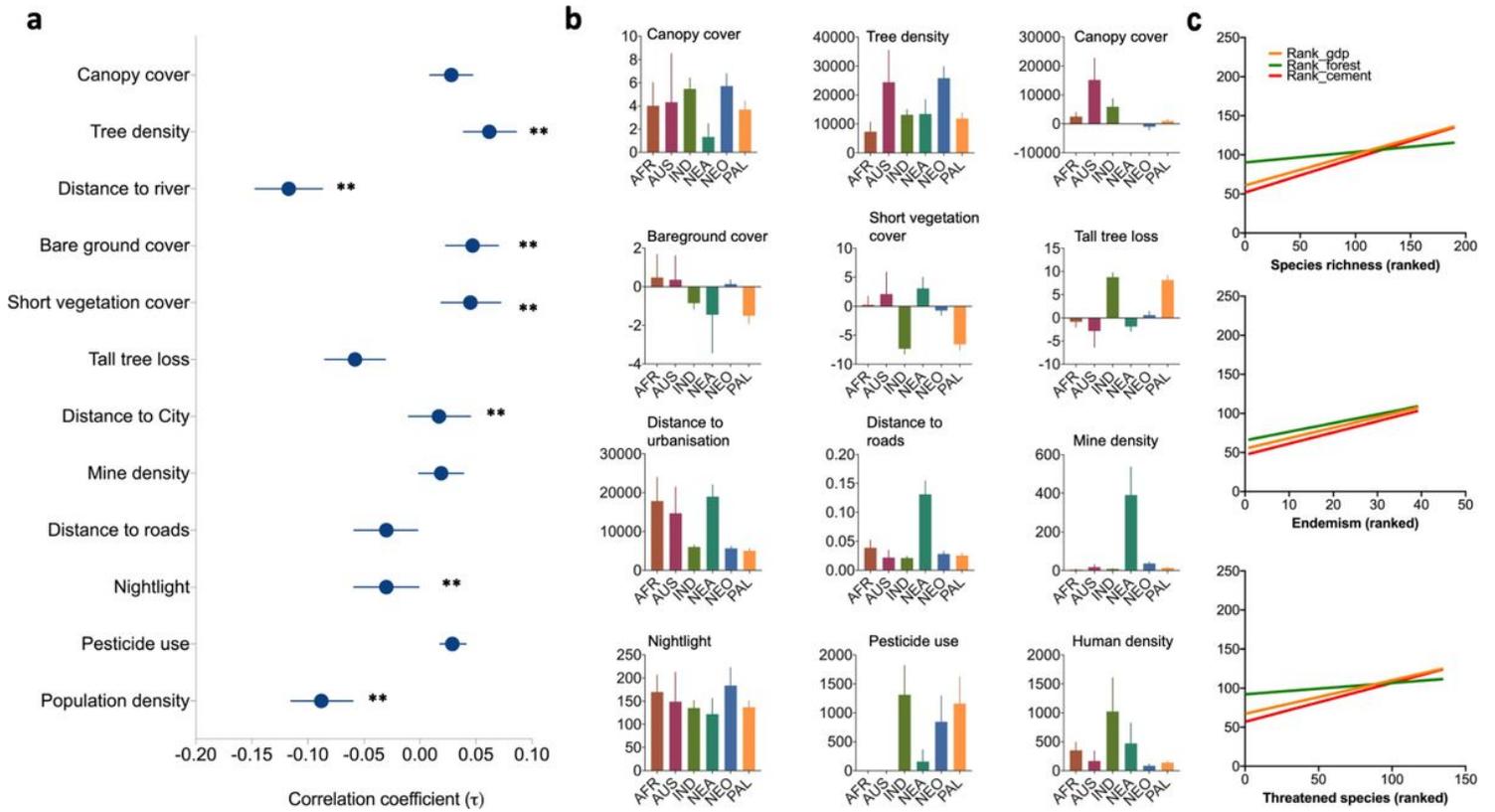


Figure 4

Relationship and turnover of threats amongst assessed global cave sites. (A) Correlation coefficients (τ and 95% CI intervals) between landscape features and threats and species cave biotic scores, (B) biogeographic comparison of mean intensity of vulnerabilities to landscape features and threats, (C) Global concordance of between country socioecological indicators (country GDP, Forest cover, cement export production) and species attributes (up to down: country species richness, endemism, and proportion of threatened species). Landscape and threat exposure of sampled cave is supplemented in the Data Paper co-published with this manuscript.

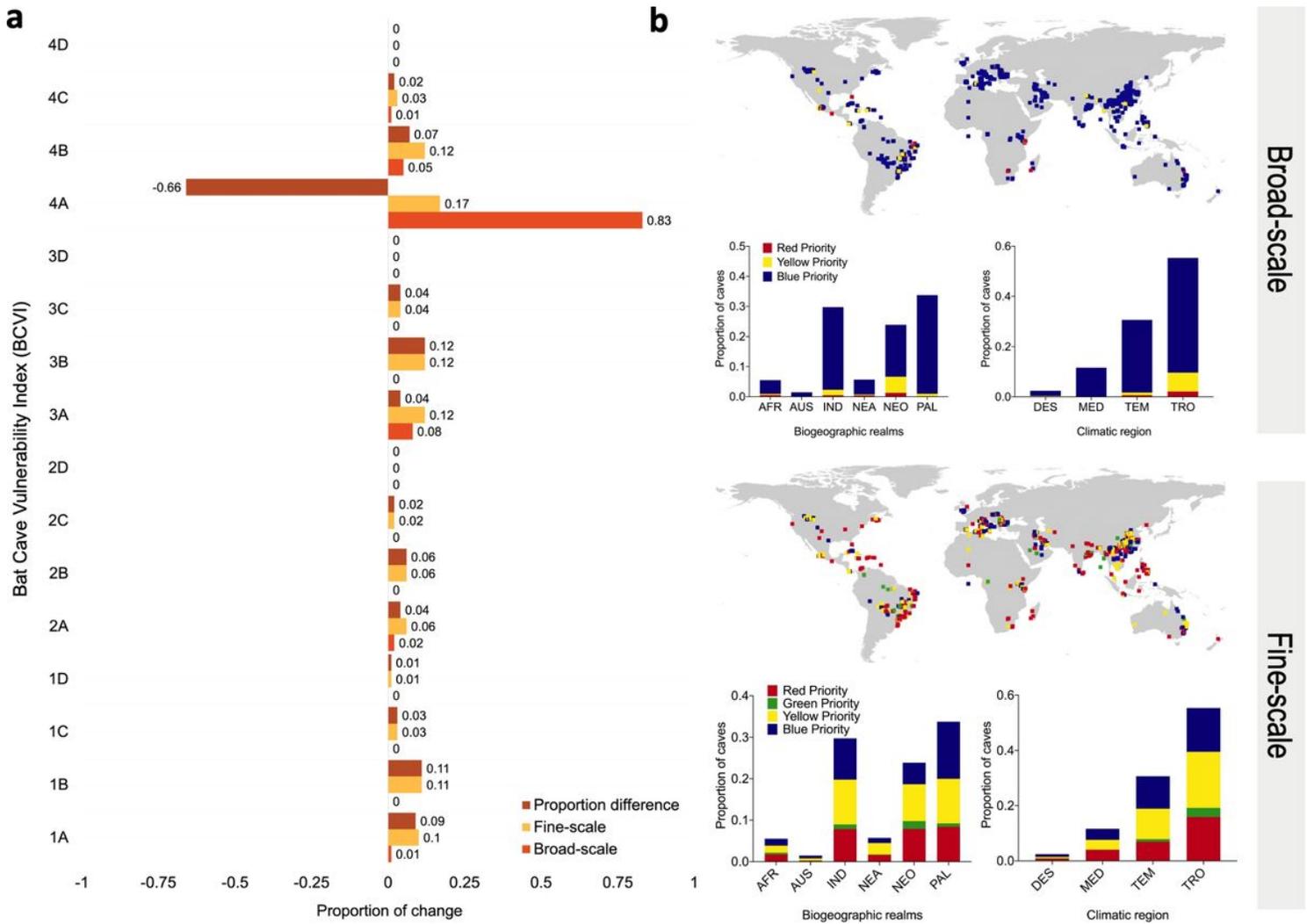


Figure 6

Global Bat Cave Vulnerability Index and Priorities. (A) Proportion and proportion differences of cave Bat Cave Vulnerability Index (BCVI) analysed in broad-scale and fine-scale. The number and percentage of caves according to BCVI scales is supplemented in Supplementary Data Sxxx. (B) Broad- (A) and fine-scale (B) spatial conservation priorities based on Global Bat Cave Vulnerability Index (BCVI). Proportions are compared across biogeographical realms and climatic regions. Summaries BCVI-based priorities are being supplemented in Supplementary Table 5 and individual cave priorities are supplemented in Data Paper co-published with this manuscript. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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