Using bats as surrogates to effectively target global hotspots for subterranean conservation and monitoring

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Research Article

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Using bats as surrogates to effectively target global hotspots for subterranean conservation and monitoring

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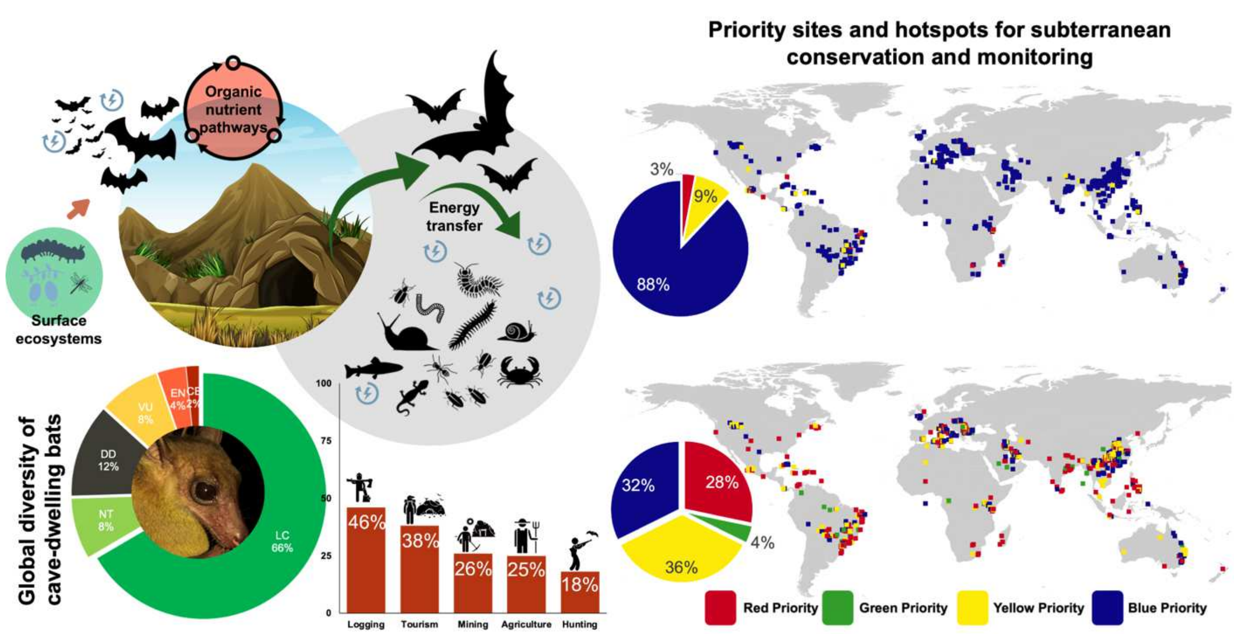
Highlights

- As the second-largest mammal taxa bats provide important ecosystem services and are keystone to cave ecosystems.
- Almost half of the global bats are dependent on caves and subterranean habitats.
- We include 679 bats species and 1930 caves from 46 countries to assay patterns of vulnerability and diversity of subterranean habitats across the world.
- Up to 28% of caves are of high priority.
- Of high priority caves 87.5% are threatened, and particularly in the tropics (15%).

Graphical Abstract



Abstract

Research and media attention is disproportionately focused on taxa and ecosystems perceived as charismatic, while other equally diverse systems such as caves and subterranean ecosystems are often neglected in biodiversity assessments and prioritisations. Yet these more challenging systems are also vulnerable, with karsts for example losing around 6% of their area each year, highlighting the urgent need for protection, especially as up to 90% of cave endemic species may be undescribed. Bats are keystone to cave ecosystems making them potential surrogates to understand cave diversity patterns and identify conservation priorities. On a global scale, almost half (48%) known bat species use caves for parts of their life histories, with 32% endemic to a single country, and 15% currently threatened. We combined global analysis of cave bats from the IUCN spatial data with site specific analysis of 1930 bat caves from 46 countries to develop global priorities for the conservation of the most vulnerable cave ecosystems. Globally, 28% of caves showed high diversity and were highly threatened and 4% had high diversity but not currently threatened. Amongst regions, the highest concentration of conservation priority caves was in the Palearctic and tropical regions (except the Afrotropics, which requires more intensive data sampling). Our results further highlight the importance of prioritising bat caves by incorporating locally collected data, and optimising parameter selection (i.e., appropriate landscape features and threats). Finally, to protect and conserve these ecosystems it is crucial that we use frameworks such as this to identify priorities in species and habitat-level, and map vulnerable habitats with the highest biodiversity and distinctiveness.

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

Introduction

We are currently facing the sixth mass extinction, with a higher rate of extinction than at any time since former mass extinctions millions of years ago (Vos et al., 2015). Global biodiversity is threatened by a variety of drivers, and understanding these is critical to determining effective conservation measures in different systems and scales (Ripple et al., 2017). Appropriate evidence-based strategies are essential to optimise the implementation and effectiveness of conservation (Ceballos et al., 2015; Pimm et al., 2014). Various methods and frameworks have been developed to prioritise taxa and their habitats for conservation such as habitat prioritisation and zoning (Conenna et al., 2017; Hernández-Quiroz et al., 2018; Wintle et al., 2019), but many countries may have limited access to such data or resources to effectively implement conservation (Chandra and Idrisova, 2011). Priorities should be matched with future targets and effort allocation to support reaching such targets and ensure that species and their ecosystems are well protected (Arponen, 2012; Groves et al., 2002; Hughes, 2017; Sutherland et al., 2019). However, many species lack the data needed for effective priorities to be developed, and even fewer receive adequate levels of attention (Dolman et al., 2012; Halpern et al., 2006). Yet, as much as conservation scientists try to address the most pressing challenges in global biodiversity conservation, many taxa and their associated habitats are overlooked (Clark and May, 2002). Whilst approaches such as the IUCN Red List of ecosystems, and the new ecosystem typology goes some-way enabling proactive targeting of ecosystems, including those with high numbers of endemic species, they may overlook certain types of habitats, particularly those which require significant expertise and may be challenging to collate data from (Keith et al., 2015).

Human activities have already transformed at least 70% of terrestrial ecosystems to support human populations (Ellis et al., 2013). Modern combined approaches and technologies are applied to understand environmental processes and threats on above-ground surface ecosystems (e.g., forest ecosystems) which can easily be mapped with remote sensing (Rose et al., 2015). Yet most subterranean habitats including caves are challenging to map, and have frequently been overlooked and neglected in prioritisation (Mammola et al., 2019a; McClure et al., 2020; Sánchez-Fernández et al., 2021). This becomes a barrier to research leaving other habitats and the species dependent on them such as bats understudied and under-protected (Cardinale et al., 2012). The lack of research necessary to understand the unique adaptations and interactions in these systems further challenged subterranean research, which not only prevents cave taxa from garnering public attention, but the special skills needed to study many cave taxa further add to the lack of existing efforts. Cave ecosystems host a variety of highly adapted and sensitive organisms, many of which are cave obligates and dependent on bat guano for nutrients (Deharveng and Bedos, 2018; Ferreira, 2019; Furey and Racey, 2016; Monro et al., 2018a; Simon, 2019), and these studies show that guano is the main source of nutrition in most of these systems. Some cave systems have relatively high endemism and up to 90% of species in a single cave may be undescribed (Monro et al., 2018b; Whitten, 2009), meaning many thousands of species remain undescribed and potentially at risk. However, most conservation projects and funds are focused on taxa or habitats generally viewed as charismatic (Ford et al., 2017), but neglect fragile ecosystems with higher endemism such as cave ecosystems (Mammola et al., 2019a).

Because measuring the entire cave biota is challenging and costly, biodiversity surrogates such as umbrella species can be used to guide targeting of conservation for large cave communities (Lewandowski et al., 2010; Mammola et al., 2019b; Margules et al., 2002). Bats make up the second-largest group of mammals with over 1400 described species distributed across almost all biomes (Burgin et al., 2018; Furey and Racey, 2016). Within subterranean ecosystems, bats are keystone species by bringing nutrients within the cave in the form of their guano and excreta after foraging in surrounding areas, thus providing the basic source of nutrients in these largely lightless zones where the inability for photosynthesis within the system makes this form of nutrient-transfer critical (Cunha et al., 2020; Ferreira, 2019). This function makes bats the ideal ecological indicators and conservation surrogates to inform ecosystem health and priorities to safeguard these systems (Furey and Racey, 2016; Medellin et al., 2017; Tanalgo et al., 2018). Threats to cave-bat populations from habitat loss and degradation, hunting and other factors highlight the need for better methods to develop effective conservation priorities (De Oliveira et al., 2018; Frick et al., 2019; Furey and Racey, 2016) but a standardised approach 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 ecosystems are pervasively threatened by both immediate threats to the caves themselves, and modifications of the surrounding environment (Phelps et al., 2016; Tanalgo et al., 2018). Bats are conspicuous in caves, yet large colony sizes mean that single site impacts can have major consequences on populations especially for locally endemic species (Frick et al., 2019; Sagot and Chaverri, 2015). In addition to the relatively low reproductive rate in bats that jeopardizes rapid population recovery from loss and declines (Barclay et al., 2004), bats receive little public support and funding compared to other large mammals (Fleming and Bateman, 2016). Many caves and karst habitats are under-protected, for example, only around 13% of the approximately 800,000 km^2 of tropical Southeast Asian karsts are within protected areas (Day and Urich, 2000). Unprotected karst is especially susceptible to human activities and destruction, for example in Southeast Asia the average loss is around 5.7% of the area annually due to mineral mining (Clements et al., 2006; Hughes, 2017; Liew et al., 2016). This loss of bat cave habitats is coupled with unregulated hunting and tourism, and loss of foraging habitat; therefore understanding the impacts of these factors on the population status of bats and biotically important caves are urgently needed (Furey and Racey, 2016; Sedlock et al., 2014; Tanalgo et al., 2018; Torres-Flores and Santos-Mreno, 2017). It is estimated that at least 50% of global bat species rely at least partially upon caves (Furey and Racey, 2016) but the degree of threat to bat cave communities and prioritisation has never been analysed on a global scale (Tanalgo et al., 2018). Understanding only species distributions, and their extinction risks cannot ensure the protection of all species. The identification of key spatial areas (e.g., a high number of threatened species and endemism levels) that require protection will enable conservation biologists to develop balanced priorities to inform appropriate protection measures. This study 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 developed a framework to understand the species-specific and habitat priorities for cave-dwelling bats to identify hotspots for subterranean conservation by integrating different facets of biotic importance and risks across different scales. First, we examined the global (i) patterns of diversity, distribution, and extinction risks of cave-dwelling bats, and (ii) distribution of species threats. Second, we mapped the broad-scale and fine-scale priorities of bat caves based on cave biotic potential and vulnerability to threat. We assess gaps in species information, which is especially important for targeting appropriate conservation measures in karst environments, which represent one of the most challenging ecosystems for assessment.

Materials and methods

Data source and bat species assessment

We sampled global cave-dwelling bats from two databases, the IUCN Red list (v. 2020.1) and the DarkCideS (v 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 (Data S1-3). All species names were curated and updated using the Bats of the World: A taxonomic and geographic database (Simmons and Cirranello, 2020). 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 occurs (Etard et al., 2020). We used the weighted habitat breadth (%) values in the final analyses. Species were then classified based on island endemism and country endemism. Whilst country endemism is not strictly an ecological indicator, it is nonetheless useful as if a species is only present in a single country, then the survival of that species is also subject to strictures of a single country, which increases vulnerability if protection measures are not in place. We then compared the species recorded between the IUCN Red list and the DarkCideS 1.0 to determine gaps in species assessed and cave locality data.

Species diversity and distributions

Using IUCN data, we calculated geopolitical (e.g., country or continental) species richness based on where the species occurs (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 country (Ceballos and Ehrlich, 2002), and island endemism was classified as island-restricted or predominantly mainland (Faurby et al., 2018). Species conservation status was assessed according to the IUCN Red list criteria and were then simplified to obtained binary extinction risk: “Threatened” (e.g., Vulnerable, Endangered, and Critically Endangered) and “Nonthreatened” (e.g., Least Concern, Near Threatened). While Data Deficient (DD) species were treated as threatened as they may face higher or similar threats, hence a lack of data for formal classification (Bland et al., 2015; Tanalgo et al., 2018; Welch and Beaulieu, 2018). We compared patterns of species diversity across biogeographical realms (Olson et al., 2001; Olson and Dinerstein, 1998) (e.g., Indomalayan, 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 defined country species richness and endemism using simple coherent metrics which are comprehensible for national or regional level conservation and policymaking

(Amori et al., 2011). Using Kendall's τ B, we explored the relationships between (1) country estimated species richness, (ii) % endemic species, and (iii) % threatened to country land area (km^2).

IUCN-based species extinction risk

The IUCN bat data are imperfect, and many species lack updated assessments, using the available data we estimated the extinction risks for different groups and species attributes. Following (Hoffmann et al., 2010; Richman et al., 2015) we estimated the proportion of threatened species across biogeographical realms, species endemism (e.g., geopolitical and island), population trends, trophic levels, and families. We calculated the proportion of species vulnerable to extinction ($\hat{p}_{\text{extinction}}$) based on the proportion of threatened species as

$$\hat{p}_{\text{extinction}} = (N^o_{\text{threatened}}) \,/\, (N^o_{\text{species}} - DD_{\text{species}})$$

where $N^o_{\text{threatened}}$ is the number of threatened species assessed as Vulnerable (VU), Endangered (EN), and Critically Endangered (CE), N^o_{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 that are non-Data Deficient species (Richman et al., 2015; Tanalgo et al., 2018). We then calculated the lower estimate ($\hat{p}_{\text{extinction\_lower}} = N^o_{\text{threatened}} / N^o_{\text{species}}$) with an assumption that *DD* species are categorised as non-threatened and upper estimates ($\hat{p}_{\text{extinction\_upper}} = N^o_{\text{threatened}} + DD / N^o_{\text{species}}$) with the assumption that *DD* is threatened.

Using a Generalized Linear Model (GLM) we determined the predictors of species extinction risk (threatened vs. nonthreatened) for global species and within each suborder, Yinpterochiroptera and Yangochiroptera. We used a total of ten explanatory variables which included geographical variables (geographical range, island endemism, and geopolitical endemism), biological variables (adult body mass (kg, $\log_{10}$) (Faurby et al., 2018), generation length (Pacifici et al., 2013), forest dependency (yes or no based on the IUCN database), weighted habitat breadth (%), and trophic group). We used the Level-2 habitat data classification from IUCN (2020) that is based on suitable or important habitats for species (Etard et al., 2020). Weighted habitat breadth was calculated based on the number of habitat species used divided by all other habitats. For the trophic groups, we grouped species as frugi-nectarivorous for all species that forage on plant-based resources (e.g., frugivores and nectarivores). Species that forage on animal resources (e.g., insectivorous, sanguivorous, species feeding on vertebrates) were grouped as carnivores, while species that forage on both plant and animal resources were grouped into omnivores. Our last group of explanatory variables includes the species threat index.

Mapping and quantifying threats

We analysed threats in three different levels: species, cave-site, and country-level. First, we analysed threats per species based on the simplified expert-based IUCN Red list. We modified the threat nomenclature by Salafsky et al. (2008) as it does not completely reflect all threats in bat cave habitats. The Direct threats (T_{dir}) refer to the threats or risks that are directly within or occurring in the cave systems that have immediate and perceivable impacts on population change or species behaviour. This threat includes direct human impacts and the use of caves such as harvesting bats, tourism, and mining activities. The Indirect threats (T_{ind}) refer to the threats outside or within cave proximity, which impacts to population is secondary or non-immediate but detrimental such as deforestation, agriculture, and urbanisation. Lastly, Natural threats (T_{nat}) refers to threats that are natural in origin that may occur and impact directly or indirectly in the population such as disease and stochastic in nature. We developed the Species Threat Index (*STI*), which is calculated from the quotient of the sum of species absolute threat ($T_{\text{dir, ind, nat}}$) and the number of threats assessed (N^o 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.

$$(STI_{\text{species}} = \sum T \,/\, N^o\ T)$$

We constructed a separate generalized linear model (GLMs) with a binomial distribution (logit link function) in JAMOVI version 2, using GAMLj module (Gallucci, 2019) to understand the link between species traits to a certain threatening process. We used adult body mass (g, $\log_{10}$), geographical range ($\log_{10}$) and trophic levels as the predictor variable and threat status (threatened or not threatened) as response variable (Atwood et al., 2020). We only modelled threatening processes that impacted at least 10% of the cave-dwelling bats.

Second, we used remotely sensed data to measure cave vulnerability to threats. For landscape features, we included canopy cover height (Simard et al., 2011), tree density (Crowther et al., 2015), distance to bodies of water (Yamazaki et al., 2015), bare ground cover change (Song et al., 2018), short vegetation cover change (Song et al., 2018), tall tree cover change (Song et al., 2018) and for vulnerabilities we include distance to urban areas (Song et al., 2018), distance to roads (Meijer et al., 2018), mine density

(Labay et al., 2017), night light (Earth at Night, 2019), relative pesticide exposure (Maggi et al., 2019), and population density (Hughes, 2019; SEDAC, 2020). We then assessed the correlation between landscape variables to cave species biotic scores and the extent was compared across biogeographical realms.

Third, we ranked each country based on total species richness, the proportion of both threatened and endemic species and its concordance to sociodemographic and environmental indicators as rudimentary indicators of a country's resources to representing its capacity to monitor and protect its species and environment (e.g., Convention of Biological Diversity) (Amori et al., 2011; McGeoch et al., 2010). In our analyses, we used percent forest cover (The World Bank, 2020) 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 (Cajaiba et al., 2021; Phelps et al., 2018; Tanalgo et al., 2018). While we used country cement production (TTM*1000) (Index Mundi, 2020) 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 (Liew et al., 2016; Tanalgo et al., 2018). 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.

Global Bat Cave Vulnerability Index (BCVI-G)

Using the global ‘Bat Cave Vulnerability Index’(Tanalgo et al., 2018) (hereafter ‘BCVI-G’), we assessed habitat-level priorities of pooled bat caves (Data S3). The prioritisation index is based on two integrated sub-indices representing cave biotic potential and vulnerability. The first component of the index is the cave Biotic Potential (BP), which analyse, and measure bat cave biological values based on bat species richness and attribute status. The second component is the cave Biotic Vulnerability (BV) measures the cave landscape feature and vulnerability to threats. Using the index, we mapped and constructed broad-scale and fine-scale cave priorities representing biome and site-level analyses respectively. We modified the first version of BCVI to address some of its limitations for incomplete or unstandardised data and make it relevant for a comparative global-scale prioritisation scheme for the new BCVI-G.

$$BCVI\text{-}G = BP \times BV$$

Cave Biotic Potential (BP)

We excluded data from population estimates to minimise bias from the missing and unstandardised assessments in caves datasets, and which is a component of the first BCVI and can be used at more local scales. Second, in addition to species attribute status scoring (conservation status, population trends, country endemism, and island endemism (Table 1), we incorporated evolutionary units including evolutionary distinctiveness (ED, based on EDGE score (Isaac et al., 2007)) and corrected weighted endemism (CWE) to factor the cave biotic potential (BP). We calculated corrected weighted endemism (CWE) (Crisp et al., 2001; Laffan and Crisp, 2003) 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

$$BP_{cave\ x} = \sum S_{cave\ x} / Max. \sum S_{cave\ y}$$

where cave BP is the calculated quotient of the sum of cave species attributes scores ($\sum S_{cave\ x}$) and the highest maximum ($\sum S_{cave\ y}$) sum of species attribute scores from all sampled caves ($_{cave\ y}$) within the single site or the entire biome. Where $S_{cave\ x}$ is the sum score of nth bat cave species evolutionary distinctiveness (ED), corrected weighted endemism (× 100) (CWE), conservation status (Cons), population trends (Pops), country endemism (E), and island endemism (Isl).

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

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 (Table 2).

Table 1. Scoring of species attributes for calculation of cave Biotic Potential (Bp) based on species Population trends (pops), Conservation status (cons), Country endemism (E), and Island endemism (Isl).

pops	score	cons	score	E	score	Isl	score
Increasing	2.5	Least concern	2	Non-endemic	5	Non-islandic	5
Stable	5	Near Threatened	4	Endemic	10	Islandic	10
Unknown	7.5	Vulnerable	6				
Decreasing	10	Endangered	8				
		Critically endangered/Data deficient	10				

Table 2. Cave Biotic Potential (Bp) priority status and description of the probable scenario. The interpretation of the probable scenario was based on Tanalgo et al. 2018.

Bp cave $_x$/BP cave $_{max}$	**BP status**	**Probable relative scenario**
0.00 – 0.24	Level 4	Contain the *lowest* species richness, *lowest* sum of species attributes, with the absence of threatened and endemic species. Probably no rare species in the cave.
0.25 – 0.49	Level 3	Species richness and the sum of species attributes may be lower. Threatened and endemic species may be present. Probably no rare species in the cave.
0.50 – 0.74	Level 2	Cave may be high in species richness and sum species attributes, with the presence of few endemic and threatened species. Rare species may potentially present.
0.75 – 1.00	Level 1	Highly species richness, with *highest* sum of species attributes. Several threatened and endemic species is present. Cave contains the rarest species.

Mapping landscape features and Cave Vulnerability (BV)

The computed cave BP is then complimented with the cave Biotic Vulnerability (BV) to derive the final cave alphanumeric priority based on vulnerability. First, we mapped and measured the extent of geophysical features represented landscape features and threats in a single cave following (Hughes, 2019) using ArcGIS version 10.3 (see reference for detailed methods for every landscape feature). Because of the relatedness of landscape features to represent cave vulnerability to threats, we selected representative features to enter in BV calculations: (i) distance to urban area, (ii) distance to roads, (iii) tree density, (iv) canopy cover, (v) mining density, and (vi) distance to bodies of water (for arid biomes). We calculated cave Biotic Vulnerability (BV_{cave}) as the quotient of summed scores of *NT* and the total number of geophysical features assessed (N^o, $N^o = 5$).

$$BV = \Sigma NT/N^{o}$$

where NT ($NT = T\,x / T_{max}\,y$) is the score of geophysical or landscape 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 is scaled in four-level range scoring representing cave relative probable scenario (Table 3).

Table 3. Scoring system for Biotic Vulnerability (BV) index based on the extend of the landscape features and cave probable relative scenario.

Threat or landscape features	$T\,x / T_{max}\,y$	BV score	Probable relative scenario (worst to best)
Distance to city/urbanisation	0.00 - 0.24	1	Cave site is within or surrounded by heavy urbanisation; highly vulnerable to visitation and unregulated tourism.
	0.25 - 0.49	2	
	0.50 - 0.74	3	
	0.75 - 1.00	4	Cave is not surrounded by urbanisation, or very far any urbanisation. Cave is probably located in a pristine area.
Distance to roads	0.00 - 0.24	1	Cave site is accessible by roads or human trails. Highly accessible and vulnerable to visitation and intrusion. Cave sites with hyper-population may be vulnerable to hunting.
	0.25 - 0.49	2	
	0.50 - 0.74	3	
	0.75 - 1.00	4	Cave site is inaccessible by roads or human trails. Roads may be absent. Difficult to access by human visitation.
Mine density	0.75 - 1.00	1	Cave site is in a high mining density area.

			Extensive mineral extraction occurs within the cave site.
	0.50 - 0.74	2	
	0.25 - 0.49	3	
	0.00 - 0.24	4	Mining is low or probably absent.
Canopy cover	0.00 - 0.24	1	Cave site is in a more open area. The occurrence of deforestation is probably high. The cave is potentially in an arid environment with low tall tree vegetation. The cave is very exposed and highly vulnerable to human intrusion and other disturbances.
	0.25 - 0.49	2	
	0.50 - 0.74	3	
	0.75 - 1.00	4	Cave is probably in a pristine or robust forested area. Tall tree vegetation is probably high. Foraging grounds for bats are highly available. The cave is probably located in a protected area.
Tree density	0.00 - 0.24	1	Cave site is in a heavily disturbed area. Deforestation and other surface threats (e.g., mining and urbanisation) may be highly present. The cave site is very exposed and highly vulnerable to population loss.
	0.25 - 0.49	2	
	0.50 - 0.74	3	
	0.75 - 1.00	4	Cave site occurs in a very pristine and intact forested area. Surface threats may be low or absent. Foraging grounds for bats are highly available. The cave is

probably covered by protected areas.

Mapping conservation priorities

We aimed to assess the vulnerability of global bat caves based on community level bat data and mappable landscape features and threats (Figure 7). We performed BCVI-G prioritisation at a number of spatial scales. First, the broad-scale priorities represent biome-dependent analyses. Secondly, we measured at the site-level diversity and vulnerability to encompass the fine-scale prioritisation. Here we set cave priorities at a national scale, with the assumption that priorities should be comparable to guide decision making at any scale. The alphanumeric index derived from BCVI-G is divided into four priority categories (Table 4). We then compared the mean biotic vulnerability (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 biomes using a chi-squared test (χ^2). We used Pielou's index in PAST - to assess evenness in BCVI-G and priorities between scales.

Table 4. Priority scales of caves based on Bat Cave Vulnerability Index-Global (BCVI-G).

BCVI-G	Priority-level	Condition	Potential action
1A, 1B, 2A	Red Priority caves	High diversity and high threat exposure	Cave needs immediate action
1D, 1C	Green Priority caves	High diversity, but threat exposure is absent	Cave needs monitoring
2B, 2C, 2D, 3A, 3B, 3C, 3D	Yellow Priority caves	Under high threat, and moderate diversity. May have already lost species.	Cave needs intervention or may no longer be worthwhile

4A, 4B, 4C, 4D	Blue Priority caves	High to low threat, with very low diversity. May have already lost species.	Cave not worth attention

Results

Global diversity and distribution 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), and followed by Phyllostomatidae (N = 96, $\%_{cave}$ = 14, $\%_{global}$ = 45) (Table S1). Most species are concentrated in the tropical regions (χ^2 = 205.83, df = 5, P < 0.0001) with 30% (N = 227 spp.) of global cave-dwelling bats in the Indomalayan region (Figure 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.) (Figure S1; Data S2). In addition, Indonesia (N = 18 spp., $\%_{threatened}$ = 17%), and India (N = 10 spp., $\%_{threatened}$ = 12%), were the countries with highest number of threatened species. Unsurprisingly, we found congruence between country land area (km^2) and estimated species richness (τ = 0.40, P < 0.001), % threatened (τ = 0.41, P < 0.001) and % endemism (τ = 0.19, P < 0.001).

Globally, 32% of cave-dwelling bat species were endemic to a single country and 23% to small islands. Most of the geopolitically endemic species are classified as threatened (63.58%, N = 110 spp.) compared to less threatened (21.74%, N = 63 spp.) (χ^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 island endemic species significantly differed across conservation statuses (χ^2 = 192, *df* = 2, *P* < 0.001). The 77% (*N* = 520 spp.) of the species are found on mainland and near-shore islands and 23% (*N* = 159 spp.) are restricted to islands (Figure 1). Unsurprisingly, 75% of island species are country endemic versus 81% of the non-endemic occur in mainland areas (χ^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.) (χ^2 = 35.4, *df* = 2, *P* < 0.001).

Patterns of threat and extinction risks

Using the IUCN data, the estimated extinction risks of cave-dwelling bat species ($\hat{p}_{\text{extinction}}$ = 15%, 13-25%) is lower than that of all bat species ($\hat{p}_{\text{extinction}}$ = 20%, 16-35%), of which 37% are in a threatened category and 12% are data deficient (Figure 2A, Table S2). Extinction risk is relatively higher when compared across sub-orders, families, and trophic groups compared to all species. Moreover, country endemic species ($\hat{p}_{\text{extinction}}$ = 36%, 29-50%) and species occurring on islands (islandic: $\hat{p}_{\text{extinction}}$ = 40%, 35-48%) are facing exceedingly high extinction risk (Figure 2A, Table S2). Additionally, a strong link between narrow geographic range and species extinction risk can be attributed in all cave-dwelling species (β = -1.94, *P* < 0.001) and for both suborder models (Yin: β = -2.34, *P* < 0.001; Yang: β = -2.02, *P* < 0.001). Country endemism (β = -0.67, *P* = 0.013) and island endemism (β = 1.00, *P* < 0.001) are also linked to extinction risk globally. But varies within suborders, island endemism could only predict species with a high extinction risk from Yangochiroptera (β = 1.17, *P* < 0.001) and geopolitical only for Yinpterochiroptera (β = -1.19, *P* = 0.028) (Figure 2B, Table S3). 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 (β = 2.221, P = 0.008) and between suborders (Yin: β = 2.84, P = 0.043; Yang: β = 2.50, P = 0.031) (Figure 2B).

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: χ^2 = 13.02 df = 5, P = 0.02) and indirect (Kruskal-Wallis test: χ^2 = 30.10, df = 5, P < 0.01) threats differed regionally. However, there is a large disparity in the species threatened by natural threats with only 10% (N = 70 spp.) (STI_{nat} = 1.40) of the species assessed facing geo-climatic induced threats. (Figure S1, Table S4). Species risks to dominant threats such as agricultural conversion (β = -0.214, P = 0.017) and deforestation (β = -0.154, P = 0.05) were significantly linked to small geographic range. Conversely, species with large geographic ranges were more at risk from pollution (β = 0.498, P = 0.003). Species adult body mass is a strong predictor of species vulnerability for hunting and bushmeat for large species (β = 0.845, P < 0.001). Within trophic levels, omnivores have a significantly higher risk from mining and quarrying compared to frugi-nectarivores (β = -1.029, P = 0.023) and carnivores (β = -0.636, P = 0.026). Frugi-nectarivores are more vulnerable to hunting and harvesting (β = 2.256, P = 0.001), and insectivores to pollution (β = 1.483, P = 0.044) compared to other trophic levels (Figure S2 and Table S5).

On a global scale, seven out of twelve variables showed a significant relationship with summed species biotic scores ($\Sigma\ S_{cave\ x}$) but none of the landscape features and threat variables showed a strong correlation to diversity (Figure 4A). Tree density, bare ground cover change, and short vegetation cover change showed a positive correlation with bat cave diversity. Conversely, distance to bodies of water, tall tree loss, nightlight, and population density showed a significant negative correlation 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. Furthermore, socioecological variables, GDP per capita, % forest cover, and cement production as a proxy to assess the vulnerability of geopolitically endemic species showed consistent correlations amongst species diversity attributes (Figure 3C, Data S2).

Habitat priorities for cave-dwelling bats

The degree of evolutionary distinctiveness (ED) constructed on bat cave data significantly differed regionally (Kruskal-Wallis, χ^2 = 1615.65, *df* = 5, *P* < 0.001). The highest ED was in the Neotropical region (ED_{mean} = 11.92) with the lowest in the Palearctic (ED_{mean} = 5.54). Cave weighted endemism is highest in the Austral-Oceania (CWE_{mean} = 6.32) consistent with the proportion of species endemism observed in the region (Kruskal-Wallis, χ^2 = 1584.84, *df* = 5, *P* < 0.01) (Figure 4). Prioritisation at broad and fine scales showed that the majority of cave sites are highly vulnerable to threats (Figure 5A-D). In fine-scale analysis, we found a significant relationship in biotic potential and biotic vulnerability score (Kruskal-Wallis test: χ^2 = 14, *df* = 3, *P* = 0.003). Caves with higher biotic potential are linked to lower vulnerability caves (i.e., cave systems located in relatively pristine ecosystems), while there is a lower biotic potential in caves with higher threats and vulnerability (Kruskal-Wallis test: χ^2 = 6.45, *df* = 3, *P* = 0.092). This pattern is consistent at broad scales, but the relationship was not significant (Kruskal-Wallis test: χ^2

= 6.45, *df* = 3, *P* = 0.092) (Figure 5E-F), likely relating to the lack of site-specific data needed.

Indices derived from the site-level and biome-level BCVI-G were used to construct a comparative prioritisation across the biogeographical realm and climate regions (Data S3, Table S6). On a broad scale, 95% of the caves show high biotic vulnerability (Status A) but 88% of the caves have a lower biotic potential level (Level 4) in contrast to only 1% with high biotic values (Level 1) (Figure 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) (Figure 6A). Conversely, fine-scaled BCVI-G 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 at 45% in the proportion of caves with high biotic potential (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-G, 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 occur in tropical realms (Figure 6A). We found a significant difference in the cave vulnerability index in both scales (Broad: χ^2 = 8977.87, *df* = 7, *P* < 0.001; Fine: χ^2 = 1303.09, *df* = 15, *P* < 0.001).

Table 5. Comparison of achieved per cent priorities between broad-scale and fine-scale analyses using the Bat Cave Vulnerability Index- Global (BCVI-G). Full data of BCVI-G results and priorities in two scales are in Supplementary Data 3 and Supplementary Table 6.

Priority-level	Broad-scale	Fine-scale	Global average	Priority difference
Red	3%	28%	15%	+25%
Green	0%	4%	2%	+4%
Yellow	9%	36%	23%	+27%
Blue	88%	32%	60%	-56%

Our analysis of the sampled caves showed that the priority levels of caves are scale-dependent and varied significantly across spatial scales (χ^2 = 1281.43, *df* = 3, *P* < 0.001) (Figure 6B; Table S6). 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 in need of intervention, and “green caves” which are also diverse but not currently at risk, whilst “yellow caves” are at an intermediate level in terms of diversity 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 Indomalayan (16%) regions (χ^2 = 204.20, *df* = 10, *P* < 0.001) (Figure 6B, Table S6). While on a fine scale, there is 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”, 36% are “Yellow Priority”, and 4% are “Green Priority” caves that host high biotic potential but low vulnerability (Figure 6B, Table 5). The concentration of high priority caves is highest in the Palearctic (30%) closely followed by Neotropical (29%) and Indomalayan (28%) (χ^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 ($\chi^2 = 56.76$, $df = 12$, $P < 0.001$) (Figure 6B).

Discussion

Bats and caves in the changing world

This is the first study to present the integrative taxonomic and habitat-level conservation priorities for cave-dwelling bats on a global scale. In our previous work (Tanalgo et al., 2018), we developed BVCI for local and community-level applications, including local factors such as population and other site-specific factors. However, whilst such an approach is ideal for a region or country, especially where a single team can inventory all sites, priorities across a broader region require more data that can be collated remotely and can be sourced from multiple teams. Thus the new approach provides an index that can be applied across wide regions, or as here globally, and like the Essential Biodiversity Variables (EBV's) (Jetz et al., 2019) allows remotely sensed data to be integrated with on the ground data to provide a more robust index for prioritisation. Caves and underground habitats are used by almost half (48.5%, N = 679 spp.) of all bat species, with a large fraction restricted to small ranging islands (23%) and considered endemic (32%) or threatened (25%). We observed higher extinction risk in species with a narrow geographical range distribution (e.g. island and nationally endemic species), consistent with other studies(Jones et al., 2003; Welch and Beaulieu, 2018). The association of endemism level to extinction risk varies phylogenetically showing that closely related species have a similar association (Jones et al., 2003), island and geopolitical endemism is respectively correlated to suborders Yangochiroptera and Yinpterochiroptera. Whilst cave-dwelling bats are not the sole biological indicators in subterranean ecosystems, their diversity may offer a relatively cost-effective conservation surrogate for systematic monitoring to protect the vast diversity of cave-dependent species. The patterns of cave bat diversity and distribution are consistent with the patterns observed for global bats, peaking in the tropics and particularly in the Indomalayan, Afrotropical, southern Palearctic, and Neotropical regions (Burgin et al., 2018; Frick et al., 2019). However estimates of diversity and proportion of threatened species are likely to be underestimated due to current taxonomic gaps, large numbers of undescribed cryptic species, and lack of accurate species distributions assessments for global bats (Francis et al., 2010; Murray et al., 2012; Welch and Beaulieu, 2018).

Understanding threats to species and habitats

Direct threats showed a strong link to species extinction risks in all our models. Large colonies in many cave-dwelling bat species make them more vulnerable to direct anthropogenic disturbances such as hunting, harvesting, and unregulated tourism (Sagot and Chaverri, 2015). Large-bodied species are likely vulnerable to hunting and harvesting. The 18% of cave-dwelling bats are threatened by hunting, largely in parts of the Afrotropical and Indomalayan regions. This represents a large proportion (62%) of bat species (167 spp.) hunted globally (Mildenstein et al., 2016), and is likely to be an underestimate as hunting in many regions is poorly documented. 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 medicine (Cardiff et al., 2009; Goodman, 2006; Mickleburgh et al., 2009). The most frequently hunted species are common and hyper-abundant cave species (e.g., *Rousettus amplexicaudatus, Eonycteris spelaea, Eidolon* *helvum*), which have a smaller portion of their range protected because of their widespread, non-threatened status (Aziz et al., 2021). However, as a consequence of the absence of statuary protection for many common species intensifies hunting and can cause even common and abundant species to become locally or regionally extinct (Tanalgo and Hughes, 2019). Separately, unregulated tourism is a direct 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 land degradation as a result of deforestation and agricultural conversions (Cajaiba et al., 2021; Jones et al., 2009). Over 50% of the species are already losing habitat in close proximity to their roost sites but this may be underestimated as at least 12% of the species are data deficient and even more species lack updated red list assessments. Disturbed caves in deforested and agricultural lands drive the loss of specialist bats, whereas fewer disturbed caves support high species richness and abundance (Cajaiba et al., 2021). Furthermore, increased deforestation and vegetation removal around cave sites increases the exposure of caves to human intrusion and potentially increases vulnerability to direct threats e.g., hunting and tourism. 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 foraging (Theobald et al., 2020). Although our analyses showed that average mining density is higher in the Nearctic region, this largely omits quarrying for limestone (as such maps are rarely available)(Sonter et al., 2018). However, cement export is significantly higher in countries with high cave-bat species richness and high numbers of threatened species (e.g., in Southern China and throughout mainland Southeast Asia), in part because of the extensive limestone karsts in these regions.

Habitat conservation and priorities

Globally, 3% to 28% of bat caves need immediate conservation interventions, while 9% to 35% require monitoring due to high diversity, but low risk at present. Overall, the patterns of habitat level priorities are consistent with previous global studies comparing the value of broad- and fine-scale analyses in identifying priorities. The broad-scale analysis 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. Broad-scale prioritisation if applied at regional or biome levels man may facilitate the identification of priority caves. However, we found broad-scale measures underestimated the priorities of highly vulnerable bat caves (i.e., less even distribution of priorities) with a 25% difference with fine-scale prioritisation (Figure 6, Table 5). In addition, 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 (Cajaiba et al., 2021; Tanalgo et al., 2018), 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 caves often become temples or religious sites) need to be accounted for explicitly for indices to be effective.

The integration of vulnerability to effective conservation planning is often challenging due to vague or inconsistent approaches and definition (Sarkar et al., 2006).

While most habitat protection centres on taxonomic diversity (e.g., counts, abundance, and rarity) (Brum et al., 2017; Hartley and Kunin, 2003). Common species can provide ecological services (e.g., nectarivorous cave bats as pollinators, insectivores for pest control) and the reduction of population counts may indicate habitat health due to changes in service provision. Whereas, species are often prioritised based on their combined distinct ecological function, high sensitivity and vulnerability to declines (Mouillot et al., 2013). Within cave ecosystems maintaining the functioning of the subterranean ecosystems requires maintaining both diversity and abundance (Bregović et al., 2019; Phelps et al., 2016; Tanalgo et al., 2018), 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. Whilst various taxa have been used as indicators for diversity in subterranean habitats (Souza Silva et al., 2015), bats represent holistic 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 (Cajaiba et al., 2021; Jones et al., 2009). Our vulnerability index includes not only species diversity measures (Furman and Özgül, 2004; Niu et al., 2007) but also encompasses evolutionary distinctiveness and threat exposure of both species and its habitat (Cajaiba et al., 2021; Phelps et al., 2016; Tanalgo et al., 2018). The inclusion of these measures enables prioritisation of cave habitats with rare and higher functional diversity attributes (Jetz et al., 2014; Srivastava et al., 2012) complimenting the metrics based on geopolitical endemism and conservation status from IUCN (Isaac et al., 2007; Jetz et al., 2014;

Martín-López et al., 2009) which are commonly used within prioritisation schemes. While the expert-based Red list developed by the IUCN is the most comprehensive basis for conservation and species protection, it is not free from biases (Hughes et al., 2021; Martín-López et al., 2011; Trimble and Aarde, 2010), especially for bats, in which a large proportion of species are either taxonomically and spatially under-sampled particularly in most megadiverse and developing countries (Zamora-Gutierrez et al., 2019).

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 (Doi and Takahara, 2016; Rudd et al., 2011) (Figure 7). Additionally, few countries have any policy related to the protection of caves and their biota (Whitten, 2009). 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 monitoring which include all habitats (Martín-López et al., 2009), 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 threats (Howard et al., 2019). This assessing vulnerability is particularly challenging to identify in the context of cave biota, in which even a single disturbance may alter the entire sensitive biota and ecosystem, yet causal drivers are challenging, and other proximal indicators (e.g. accessibility) must be used as indicators (Cajaiba et al., 2021; De Oliveira et al., 2018; Phelps et al., 2018). Furthermore, the degree of expertise required for bat and cave studies means less data is available compared to other taxonomic groups (Herkt et al., 2017; Zamora-Gutierrez et al., 2019). 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. In addition, cave community data is lacking for biodiverse regions such as from the Afrotropical and Indomalayan regions. 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 species (Mayer et al., 2007). The lack of distribution data may be explicitly linked to the lack of funding in most biodiverse countries (McClanahan and Rankin, 2016), hindering effective assessment in countries most in need. Conversely within Europe, the UNEP-EUROBATS and EU habitats directive provides guidance and regulations, which comprehensively include the protection and monitoring of bats and caves in its territory and member states making parallel and equitable policies for large scale protection (European Commission, 2021; UNEP/EUROBATS, 2020). 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 taxa (Hughes et al., 2021).

Synthesis

Finally, to protect and conserve these ecosystems it is crucial that we identify priorities in species and habitat-level, and map vulnerable cave habitats with the highest biodiversity and distinctiveness. We illustrate 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 (Figure 7). Whilst further data is needed, especially for data-poor, species-rich regions, relying on IUCN data alone risks misleading effective priorities (e.g., spatial mismatches in the Indomalayan region) (Martín-López et al., 2011; Milner-Gulland et al., 2006). The IUCN Red list must be utilised alongside other tools and measures of decision making; thus, we advocate an integrative conservation approach that synthesises various dimensions of conservation. Furthermore, habitat focused indices complement other recent initiatives such as the IUCN Red List of ecosystems, and new IUCN ecosystem typology, but also includes high-resolution data which can be challenging to include in broader scale indices.

Cave ecosystems host both high diversity and site-specific endemism, and are used by up to 30% of all bat species, yet are rarely included in global priorities (Mammola et al., 2019a; Sánchez-Fernández et al., 2021). The persistence of high levels of biodiversity in caves is linked to more pristine cave environments with less anthropogenic pressure. Large spatial coverage (e.g., biome-dependent) analysis decreases the evenness in priority distribution in comparison to site-level, thus its conservation application to protect caves is scale dependant (e.g., national-level or biome-wide protection), and scalability in indices is also important. Conservation decision making depends on the clear delineation between what is important and urgent to develop priorities, as funding and resources are limited and often focus on a subset of taxa which may not be representative (Gordon et al., 2019; Joseph et al., 2009; Wilson et al., 2007). Ideally, priority-setting should encompass not only the aspects of biological diversity and threats but should also include the country's socio-economic capacity, the implementation cost, and political attributes. Thus, it is imperative to set realistic and cost-effective priorities based on areas with higher risks, vulnerabilities and could protect larger communities (Joseph et al., 2009; Rudd et al., 2011).

Our study identifies gaps and priorities for bat cave conservation. We highlight just how many high diversity caves are currently threatened (red caves) and those that are currently at low risk but biotically important (green caves), which reflects 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 are necessary to enable the development of an effective international agenda and nationally adaptable goals for cave prioritisation and assessment. 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, and synthesising conservation effectiveness (e.g., Conservation

Evidence Initiative (Conservation Evidence, 2021)) 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, even despite a lack of data in many regions. Ultimately, developing effective decisions requires comparable data and standardised frameworks to enable its translation into policy and practice and effectively protect threatened species and facilitate sustainable development.

Data accessibility statement

The data which are used in this study have been provided in the supplementary material accompanied with this manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

KCT and ACH contributed equally to the work. KCT and ACH conceptualised and designed the study. KCT, HFMO, and ACH collected the data. KCT and ACH analysed the data. KCT and ACH led the manuscript writing. KCT performed data visualisation. ACH supervised the project. All authors contributed to the editing, reviewing, and approved the final version of the manuscript.

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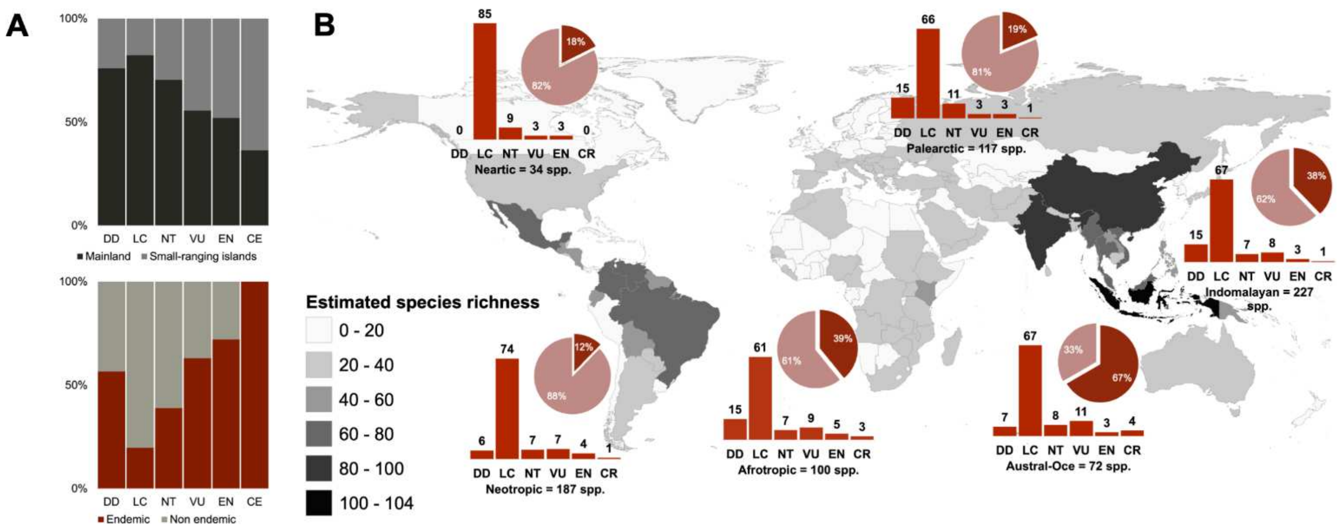

Figure 1. Species diversity and distribution of cave-dwelling bats. IUCN-based conservation status according to (a) country and island endemism, and (b) taxonomic distribution of estimated species richness of cave bats per country, and proportion of endemic species (in pie graph) and threatened (in the bar graph) of compared by biogeographical realm. 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., $\%_{endemism} = 55\%$) (See also Data S2).

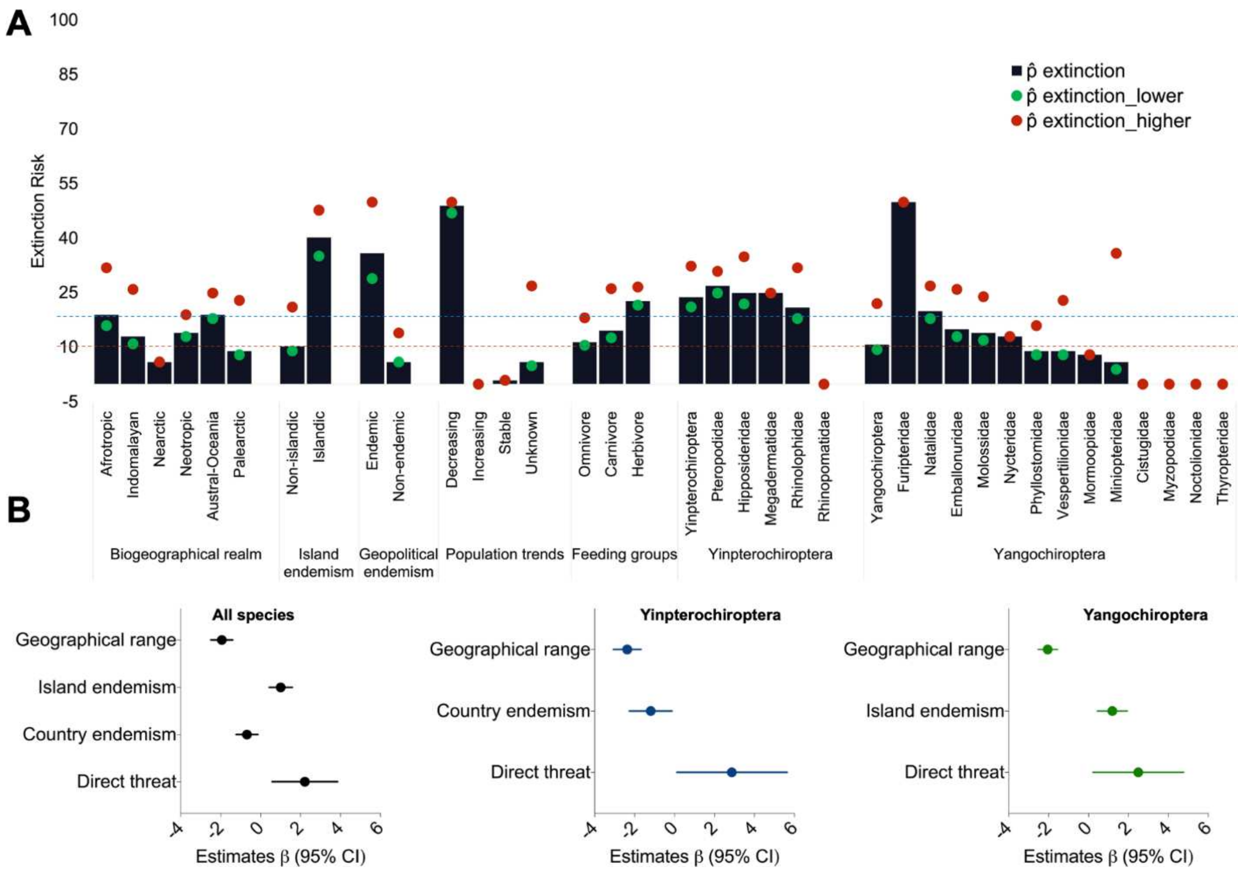

Figure 2. IUCN-based extinction risk. (a) Estimated extinction risks ($\hat{p}_{extinction}$) of global cave-dwelling bat species compared by biogeographical realm, island endemism, geopolitical endemism, population trends, trophic groups, sub-orders and families. Estimated extinction proportion ($\hat{p}_{extinction}$) for global species (blue dashed line) and all cave-dwelling bats (red dashed line) is provided. All computed values are supplemented in Table S2. (B) Estimate coefficients of significant determinants 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 Table S3.

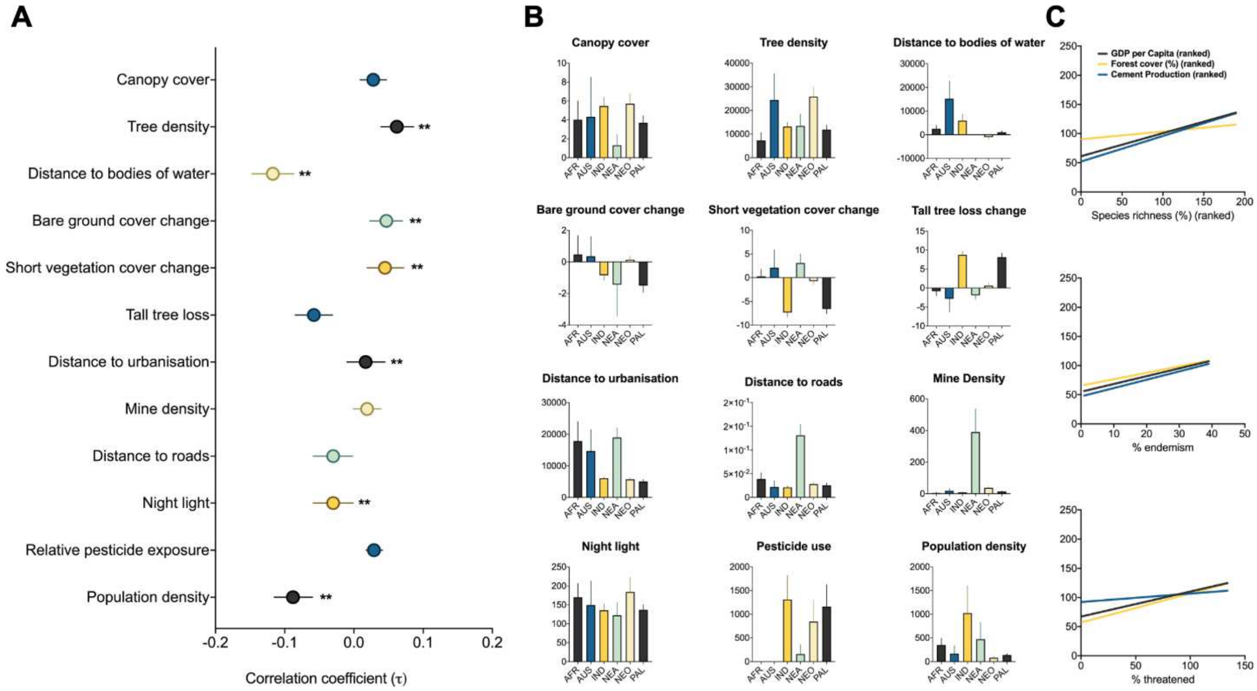

Figure 3. Relationship, extent, and distribution of threats amongst assessed global cave sites. (a) Correlation coefficients (τ and 95% CI intervals) between landscape features and threats and species cave biotic scores, (b) biogeographic comparison of mean intensity of vulnerabilities to landscape features and threats. When compared regionally, the mean intensity of landscape features and threat variables differed significantly except for relative exposure to pesticide. Bat caves in the Afrotropical, Austral-Oceania and Nearctic regions showed the highest vulnerability to distance to urban areas. 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 the Afrotropical and Austral-Oceania. Whereas population density and relative pesticide exposure are exceedingly high in Indomalayan caves, highlighting potentially high deforestation and loss of natural habitats. (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). (values with ** showed significance at $P < 0.05$).

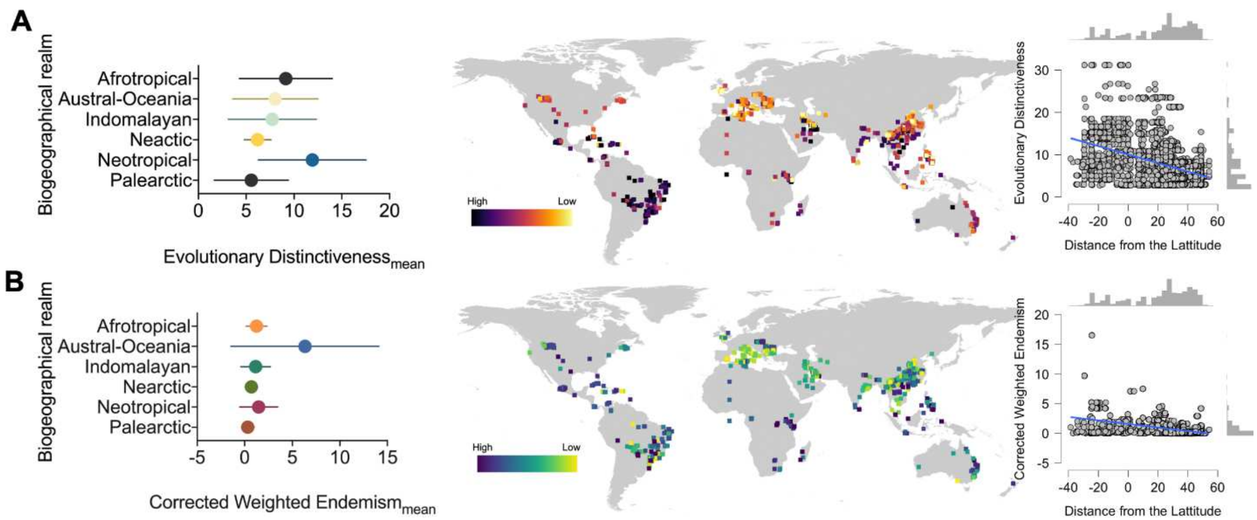

Figure 4. Comparison of bat cave evolutionary distinctiveness (A) and endemism (B) across biogeographical realm and the latitudinal relationship of ED and CWE (right).

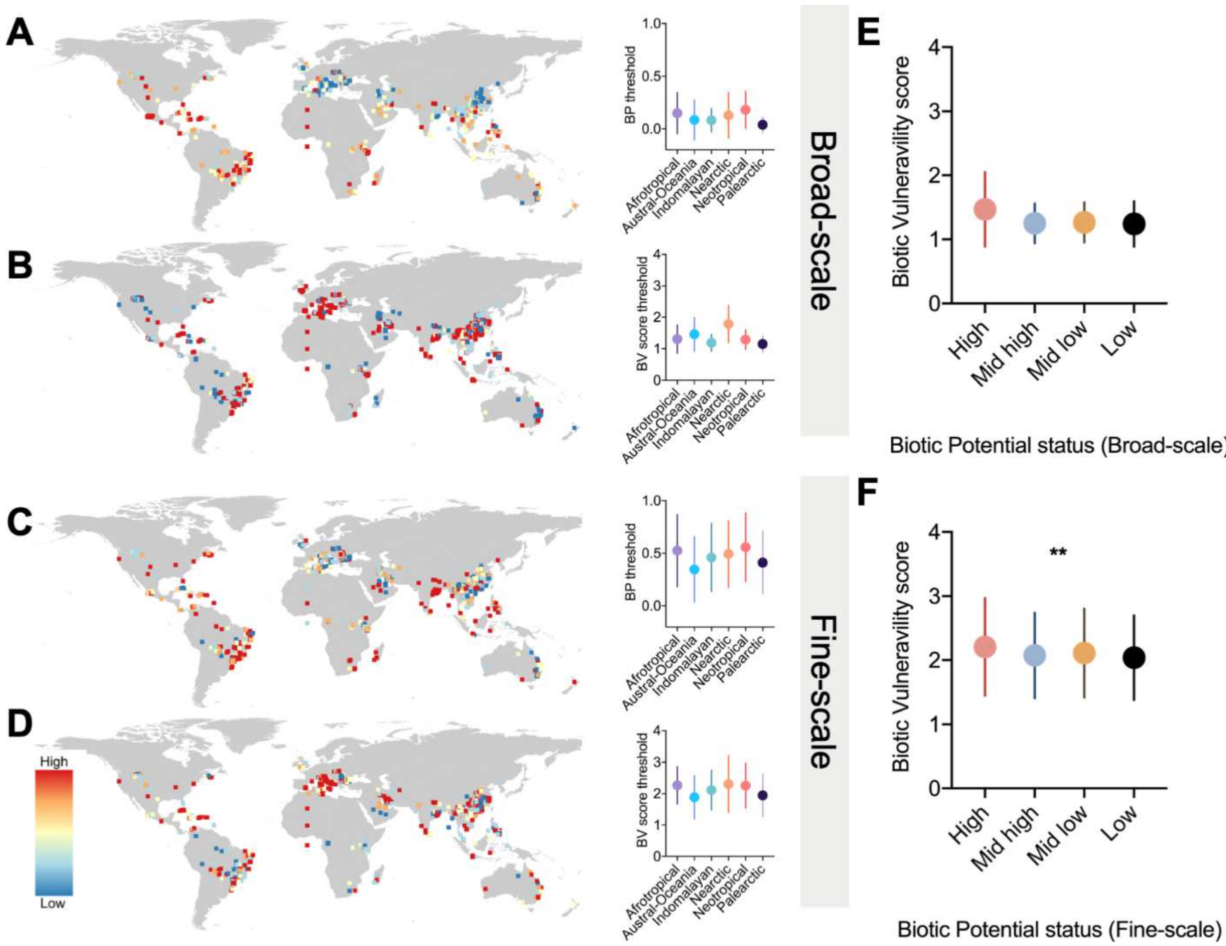

Figure 5. Distribution and relationships of cave biotic potential and vulnerability worldwide. Broad-scale (A) Biotic Potential (BP), (B) Biotic Vulnerability (BV); and Fine-scale (C) Biotic Potential (BP), and (D) Biotic Vulnerability (BV)) (All values significantly differed; error bar represents mean ± SD). (E-F) relationship of cave Biotic Potential status to Biotic Vulnerability scores compared in both broad-scale and fine-scale analyses (values with ** showed significance at *P* < 0.05; error bars represent mean ± SD).

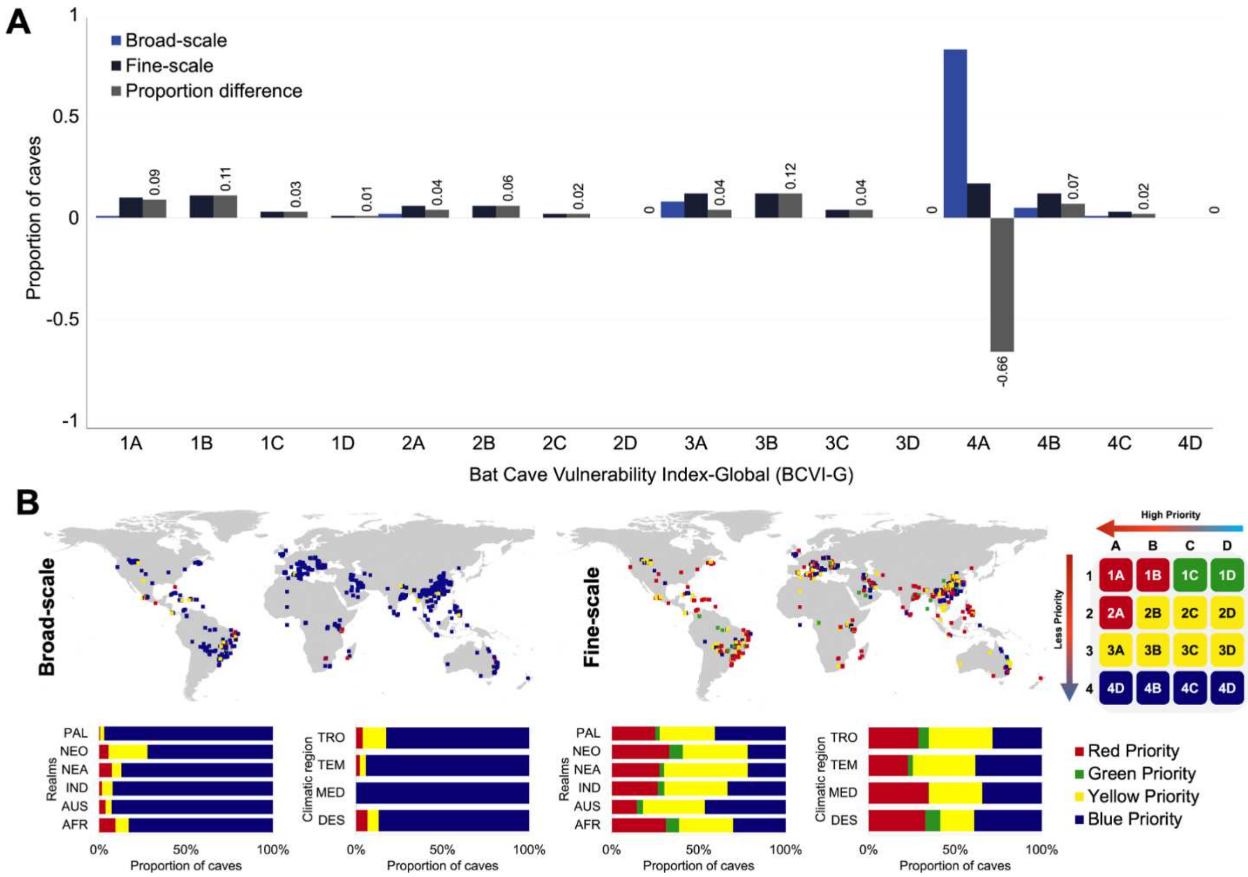

Figure 6. Global Bat Cave Vulnerability Index and Priorities. (a) Proportion and proportion differences of cave Bat Cave Vulnerability Index- Global (BCVI-G) analysed in broad-scale and fine-scale. The number and percentage of caves according to BCVI-G scales is supplemented in Data S3. Spatial conservation priorities in (b) broad-scale and fine-scale based on Bat Cave Vulnerability Index- Global (BCVI-G). Broad-scale shows poor performance in showing high priority caves compared to fine-scale prioritisation. Proportions are compared across biogeographical realms and climatic regions. Summaries BCVI-G based priorities are being supplemented in Table S6.

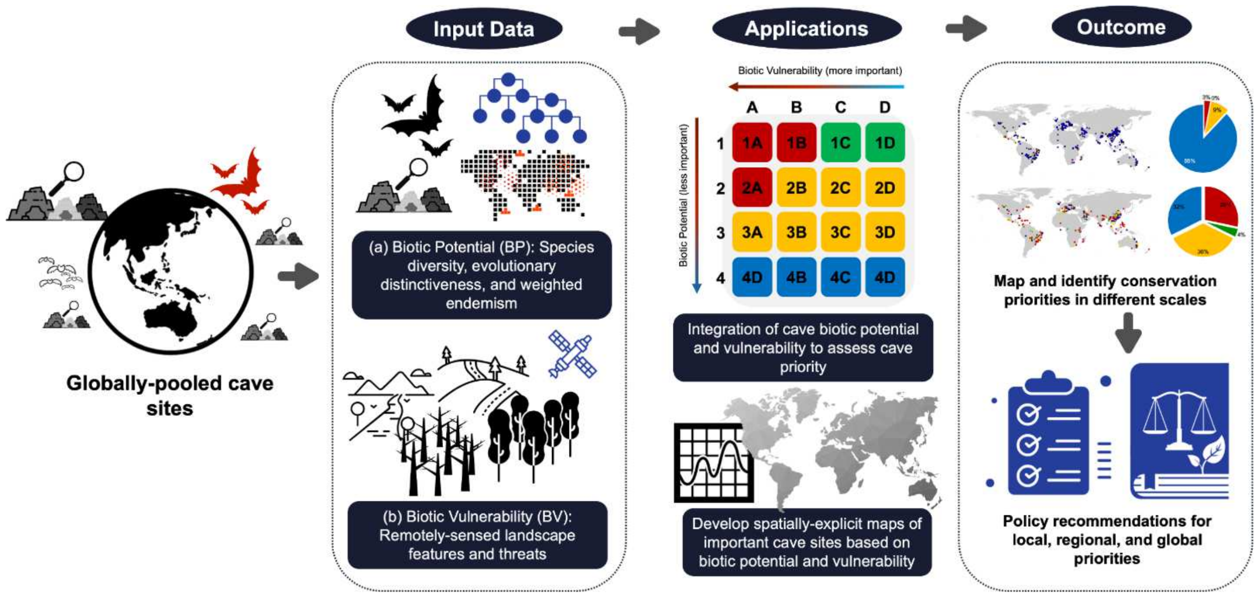

Figure 7. Framework for prioritising bat caves for conservation. The schematic diagram showing the frame of the Bat Cave Vulnerability Index-Global (BCVI) in identifying and setting priorities for bat caves for conservation on a global scale. The process starts with the pooling of caves sites for assessment assess cave priorities. The input data includes the bat cave diversity (BP) and remotely senses landscape features to assay threats (BV). The index is categorised in four (4) levels with red caves are high priority sites containing the highest diversity and threats and requires immediate conservation actions, while blue caves are the lowest priority sites with the least biodiversity and high to low threat, but no immediate conservation attention is needed.

List of Supplementary Information

Data S1. Complete list of cave-dwelling bat species pooled from the International Union for the Conservation of Nature Red List (IUCN Red List) version 2020. The supplementary dataset contains complete taxonomic information, habitat preference, biogeographical range, species distribution, conservation status, endemism, ecological traits, and threatening process.

Data S2 Country-level species diversity of cave-dwelling bats including estimated species richness, endemism, and proportion of threatened species. The supplementary data also contains the country-level socioecological status including the rate of cement production, forest cover (%), and country Gross Domestic Production (GDP).

Data S3. Complete list of cave sites and species diversity analysed for prioritisation using Bat Cave Vulnerability Index-Global (BCVI-G). The results of BCVI-G prioritisation in broad-scale and fine-scale are also provided.

Figure S1. Supplementary Figure 2. Distribution of global dominant threats (A) and biogeographical patterns (frequency) of the threatening process (B) and mean threat index (C). Complete threat distribution per species is supplemented in Supplementary Data 1.

Figure S2. Effects of geographic range, adult body mass, trophic group and island endemism on species risks to key threatening process. Complete results of the models are supplemented in Supplementary Table 4.

Table S1. Distribution of conservation status across families.

Table S2. Extinction risks of cave-dwelling bats across different taxonomic and ecological dimensions

Table S3. Summary of Binomial Generalised Linear Mixed (GLMs) explaining species extinction risk of (A) global species, and in between suborders (B) Yinpterochiroptera, and (C) Yangochiroptera.

Table S4. Summary of threatening process across the biogeographical realm and Species Threat Index (SPI) in each ecological dimension.

Table S5. Summary statistics of Generalised Linear Models (GLM) predicting the independent effects of species traits: geographical range, adult body mass, and trophic levels on the vulnerability of species to top threatening process in a global scale.

Table S6. Distribution (cave count) of BCVI in broad-scale and fine-scale across Biogeographical realm and climatic regions.

Supplementary Files

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