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Mapping global conservation priorities and habitat vulnerabilities for cave-dwelling bats in a changing world

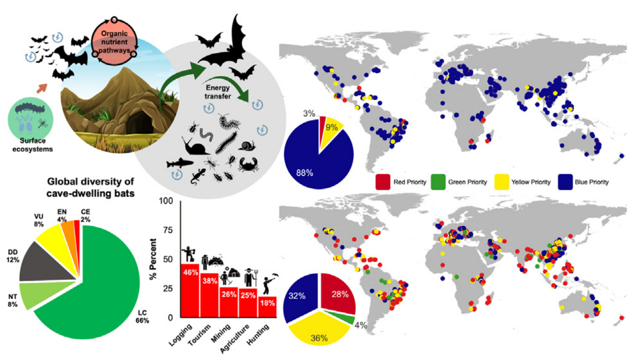
Krizler C. Tanalgo [a,b,c,d,e,*], Hernani F.M. Oliveira [f], Alice Catherine Hughes [a,b,c,g,**]

[a] Landscape Ecology Group, Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan, PR China
[b] Center for Conservation Biology, Core Botanical Gardens, Chinese Academy of Sciences, Yunnan, PR China
[c] International College of the University Chinese Academy of Sciences, Beijing, PR China
[d] Zukunftskolleg and the Centre for Advanced Study of Collective Behaviour, University of Konstanz, Universitätsstrasse 10, Baden-Württemberg, Konstanz, Germany
[e] Ecology and Conservation Research Laboratory (Eco/Con Lab), Department of Biological Sciences, College of Science and Mathematics, University of Southern Mindanao, Kabacan, North Cotabato, Philippines
[f] Department of Zoology, Federal University of Paraná, Curitiba, PR, Brazil
[g] School of Biological Sciences, The University of Hong Kong, Hong Kong Special Administrative Region

HIGHLIGHTS

- Bats provide vital ecosystem services and are keystone species to cave ecosystems.
- Almost half of the global bats are known to use caves.
- 679 species and 1930 caves from 46 countries were analysed in this study.
- Up to 28 % of caves are a high conservation priority and mostly in the tropics.
- Optimising prioritisation parameters is important for effective cave management.

GRAPHICAL ABSTRACT



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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. Highlighting the urgent need for protection, an especially large fraction of cave endemic species may be undescribed. Yet these more challenging systems are also vulnerable, with karsts for example losing a considerable proportion of their area each year. 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 %) of 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 subterranean ecosystems. Globally, 28 % of caves showed high bat diversity and were highly threatened. The highest regional concentration of conservation priority caves was in the Palearctic and tropical regions (except the Afrotropical, which requires more intensive cave 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 underground habitats with the highest biodiversity and distinctiveness.

* Correspondence to: K.C. Tanalgo, Landscape Ecology Group, Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan, PR China.
** Correspondence to: A.C. Hughes, School of Biological Sciences, The University of Hong Kong, Hong Kong Special Administrative Region
E-mail addresses: tkrizler@gmail.com (K.C. Tanalgo), ach_conservation2@hotmail.com (A.C. Hughes).

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1. 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 (Ceballos et al., 2015; Cowie et al., 2017; Vos et al., 2015). As much as conservation scientists try to address the most pressing challenges in global biodiversity conservation, many taxa and their associated habitats are consistently overlooked (Clark and May, 2002). Appropriate evidence-based strategies are essential to optimise the implementation and effectiveness of conservation efforts (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). Yet many countries may have limited access to such data or resources to effectively implement conservation efforts for understudied, yet potentially vulnerable habitats (Chandra and Idrisova, 2011). Many species lack the data needed for effective priorities to be developed (Dolman et al., 2012; Halpern et al., 2006). Whilst approaches such as the IUCN Red List of ecosystems, and the new ecosystem typology goes some way in enabling proactive targeting of ecosystems, including those with high numbers of endemic species.

Human activities have already transformed at least 70 % of terrestrial ecosystems to support human populations (Ellis et al., 2013). Using modern technologies, environmental processes and threats on above-ground surface ecosystems (e.g., forest ecosystems) can easily be mapped with remote sensing (Rose et al., 2015). Yet most subterranean ecosystems such as caves are challenging to map and have frequently been overlooked and neglected in prioritisation (Mammola et al., 2019; McClure et al., 2020; Sánchez-Fernández et al., 2021). Up to 90 % of species in a single cave may be undescribed in some countries (Manenti et al., 2018; Whitten, 2009), meaning many thousands of species remain undescribed and potentially at risk (Ficetola et al., 2019). However, most conservation projects and funds are focused on taxa generally considered to be charismatic (Ford et al., 2017), but neglect fragile ecosystems with high endemism such as cave ecosystems (Mammola et al., 2021, 2019; Manenti et al., 2018). Subterranean ecosystems are threatened by both immediate threats to the caves themselves, and modifications of the surrounding environment (Phelps et al., 2016; Tanalgo et al., 2018). 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).

The low reproductive rate in bats prevents rapid population recovery following population decreases (Barclay et al., 2004; Frick et al., 2019; Sagot and Chaverri, 2015), yet bats receive little public support and funding compared to other large mammals (Fleming and Bateman, 2016). The loss of cave bat 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). In addition to bats, cave ecosystems host a variety of highly adapted, endemic, and sensitive organisms, many of which are cave obligate and dependent on bat guano for nutrients (Deharveng and Bedos, 2018; Ferreira, 2019; Furey and Racey, 2016; Simon, 2019). 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). However, there are few large-scale and standardised approaches to identify conservation priorities for caves, hindering comparative global prioritisation to protect cave systems and their dependent diversity (Cajaiba et al., 2021; Tanalgo et al., 2018).

Because measuring cave diversity is challenging, biodiversity surrogates such as umbrella species can be used to guide targeting conservation for large cave communities (Caro, 2010; Lewandowski et al., 2010; Lindenmayer and Westgate, 2020; Margules et al., 2002). Within cave ecosystems, bats are keystone species making them ideal ecological indicators and conservation surrogates to inform ecosystem health and priorities to safeguard (Cunha et al., 2020; Ferreira, 2019; Schneider et al., 2011). 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 conservation priority setting of their habitats. Here we developed a framework to understand the species and site-specific priorities and integrate different facets of biotic importance and risks across different scales to map habitat-level priorities for cave-dwelling bats. First, we examined the priorities at the species-level by understanding the (i) patterns of diversity, distribution, and extinction risks of cave-dwelling bats, and (ii) patterns and severity of threats to species. Second, we assessed habitat-level priorities by mapping the broad-scale and fine-scale priorities of bat caves based on cave biotic potential and threat vulnerability. We aim to assess gaps in species information and to identify both priorities for research and sites most in need of conservation intervention.

2. Materials and methods

In this paper, we developed a two-step prioritisation for bat caves: species-level and habitat-level (Fig. 1). At the species-level, we used the IUCN Red list database and species traits to assess species diversity, characteristics, distribution, and extinction risk. While for habitat-level prioritisation, we used the global version of the Bat Cave Vulnerability Index ($BCVI_{global}$) to assay the conservation priorities of bat caves in different scales.

2.1. Species-level prioritisation

We sampled global cave-dwelling bats from two open databases, the IUCN Red list (v. 2020.1) and the DarkCideS (v 1.0) (https://darkcides.org/database/), which contains a consolidated global dataset for cave-dwelling bats (Tanalgo et al., 2022), including all known species that occur, use, roost, or hibernate in caves and subterranean habitats for any part of their life histories (Data S1-S3). 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 in (Etard et al., 2020), and used the weighted habitat breadth (%) values in the final analyses.

Species were then classified based on island endemism and country (geopolitical) 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 the policies of a single country, which increases vulnerability if protection measures are not in place (Ceballos and Ehrlich, 2002).

Species conservation status was assessed according to the IUCN Red list criteria, whilst Data Deficient (DD) species were counted as threatened in estimating country-level species richness, 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 and Dinerstein, 1998; Olson et al., 2001). Chi-square test (χ^2) of association was then used to assess the relationship in species geopolitical endemism, island endemism, conservation status, and population status. Additionally, using Kendall's τ B, we explored the relationships between (i) country estimated species richness, (ii) % endemic species, and (iii) % threatened to country land area (km^2) (Supplementary methods).

2.1.1. IUCN-based species extinction risk

We estimated the extinction risks for different groups and species ecological status by updating their IUCN status to reflect their current status.

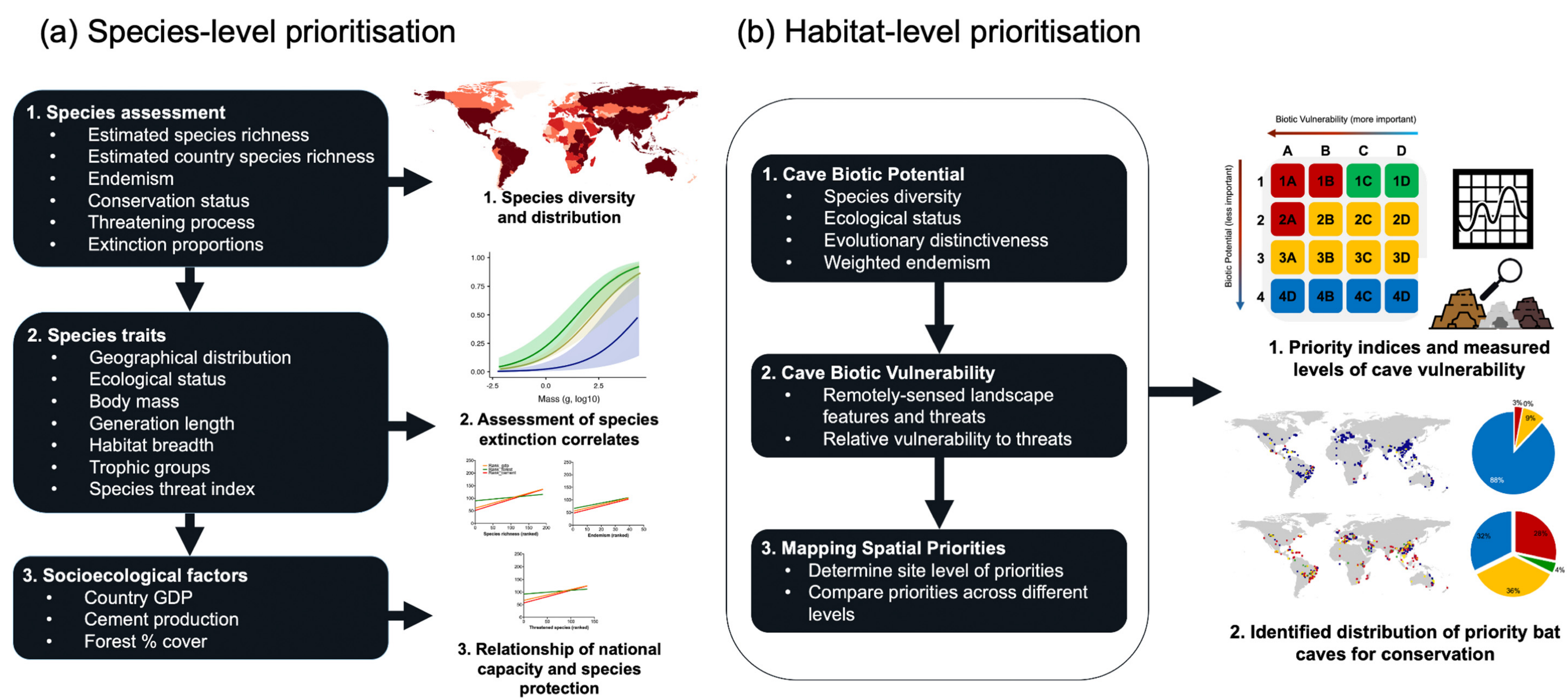

Fig. 1. Schematic diagram showing the framework of (a) species-level and (b) habitat-level prioritisation for cave-dwelling bats. At the species-level analysis, we used the information from the IUCN Red list database and combined this to other database of species traits to assess species diversity, distribution, and extinction risks. We also assessed country's capacity to protect species by combining information from estimated species richness and socioecological factors. While for habitat-level prioritisation, we assessed and compared (in broad- and fine-scales) the conservation priority of bat caves using the Global Bat Cave Vulnerability Index (BCVIglobal).

The proportion of threatened species was estimated across biogeographical realms, species endemism (e.g., geopolitical and island), population trends, trophic levels, and families (Hoffmann et al., 2010; Richman et al., 2015). The proportion of vulnerable species ($\hat{p}_{\text{extinction}}$) was calculated 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 total richness, and *DD* is the number of Data Deficient species, assuming that *DD* species will have a similar extinction risk as of other threatened categories (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 the upper estimates ($\hat{p}_{\text{extinction\_upper}} = N^{o}_{\text{threatened}} + DD / N^{o}_{\text{species}}$) with the assumption that *DD* is threatened.

A binomial generalised linear model (GLM) was used to determine the predictors of species extinction risk (threatened vs. non-threatened) for global species and within each suborder, Yinpterochiroptera and Yangochiroptera. We tested ten explanatory variables previously identified as important extinction correlates for bats (e.g., (Jones et al., 2003; Welch and Beaulieu, 2018)), which included (i) geographical variables (geographical range, island endemism, and geopolitical endemism), (ii) 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)), and the number of threats per species (Supplementary methods).

2.1.2. Comparing species threats

Threats per species were based on IUCN Red List assessments. We modified the threat nomenclature by Salafsky et al. (2008) to better reflect threats to bat caves. We reclassified threats as Direct, Indirect, and Natural (Supplementary methods). The Species Threat Index (*STI*) is calculated from the quotient of the sum of species absolute threat ($T_{\text{dir, ind, nat}}$) and the number of threats ($N^{o}\ T$) ($STI_{\text{species}} = \Sigma\ T / N^{o}\ T$). We compared *STI* across biogeographical realms, endemicity, conservation status, and population trend using a non-parametric Kruskal-Wallis test.

A separate generalised linear model (GLM) with a binomial distribution (logit link function) in JAMOVI version 2, using GAMLj module (Gallucci, 2019) was used to assess species risk to a certain threatening process based on their traits e.g., Atwood et al. (2020) and Fritz et al. (2009). 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 the response variables (Atwood et al., 2020). We only incorporated threatening processes that threaten >10 % of global cave-dwelling bats (Table S7). Lastly, we ranked and correlate country species richness, the proportion of threatened and endemic species to sociodemographic and environmental indicators as rudimentary indicators of a country's resources 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).

2.2. Habitat-level prioritisation

We modified the first version of BCVI (Tanalgo et al., 2018) to enable comparative global-scale prioritisation in the new $\text{BCVI}_{\text{global}}$. This prioritisation index integrates cave biotic potential and vulnerability. The first component of the index is the cave Biotic Potential (BP), which analyses bat diversity and endemism. The second component is the cave Biotic Vulnerability (BV) which measures the cave landscape features and vulnerability to threats. Using the index, we mapped and constructed broad-scale (from IUCN) and fine-scale (from site-specific data) cave priorities.

2.2.1. Cave biotic potential (BP)

Biotic Potential (BP) represents bat biodiversity (Tanalgo et al., 2018). For global analysis population estimates (e.g., bat counts in caves) were excluded to remove the bias from the missing and unstandardised assessments but can be used at local scales (see Tanalgo et al., 2022). In addition to species attribute scoring (conservation status, population trends, country endemism, and island endemism) (Table S1), we incorporated evolutionary units using calculated evolutionary distinctiveness (ED, from the EDGE score (Isaac et al., 2007)) and corrected weighted endemism (CWE) to determine the cave biotic potential (BP). Corrected weighted endemism (CWE) was calculated by dividing weighted endemism (WE) by richness (e.g., absolute counts of species) (Crisp et al., 2001; Laffan and Crisp, 2003). We then calculated BP using the equation: $\text{BP}_{\text{cave x}} = \Sigma\ S_{\text{cave x}} / \max \Sigma\ S_{\text{cave y}}$, where cave BP is the calculated quotient of the sum of cave species attributes scores ($\Sigma\ S_{\text{cave x}}$) and the highest maximum ($\Sigma\ S_{\text{cave y}}$) sum of species attribute scores from all sampled caves ($_{\text{cave y}}$) within the single site or the entire biome: $S_{\text{cave x}} = \Sigma\ \text{Species n}^{\text{th}}\ (\text{ED} + \text{CWE}\ (\times 100) + Cons + Pops + E + Isl) + \text{Species n}^{\text{th}}\ (\text{ED} + \text{CWE}\ (\times 100) + Cons + Pops + E + Isla) + \ldots \text{Species n}^{\text{th}}\ (\text{ED} + \text{CWE}\ (\times 100) + Cons + Pops + E + Isl)$, where $S_{\text{cave x}}$ is the sum score of n^{th} bat cave species evolutionary distinctiveness (ED), corrected weighted endemism (× 100) (CWE), conservation status (Cons), population trends (Pops), country endemism (E), and island endemism (Isl) (Table S1).

The BP_{cave} index score ranges from 0.00 to 1.00, where values near 1.00 indicate higher cave biotic potential and are scaled to four levels of priority (Table S2).

2.2.2. Mapping landscape features and cave vulnerability (BV)

Cave BP is synergised with cave Biotic Vulnerability (BV) to derive the final cave alphanumeric priority. We mapped and measured the extent of geophysical features and threats in a single cave following Hughes (2019) using ArcGIS version 10.3 (see Tanalgo et al., 2022 for detailed GIS variable methods). We assessed the correlation between landscape variables, cave species biotic scores and the extent was compared across biogeographical realms using Kendall's τ B correlation. We selected representative features for the BV calculations: (i) distance to urban area, (ii) distance to roads, (iii) tree density, (iv) canopy cover, (v) mining density, and (vi) distance to water bodies (for arid biomes). We calculated cave Biotic Vulnerability (BV_{cave}) as the quotient of summed scores of all the geophysical features or landscape (*NT*) and the total number of geophysical features assessed (N^{o}, $N^{o} = 5$): $\text{BV} = \Sigma\ NT/N^{o}$, where *NT* ($NT = T\,x / T_{\max}\,y$) is the score of geophysical or landscape features (*T*) in a specific cave (*T* x) divided by the maximum value in all sampled caves ($T_{\max}$ y). The *N* score ranges from 0.00 to 1.00 and is scaled by a four-level range score (Table S3).

2.2.3. Mapping cave conservation priorities

We performed $\text{BCVI}_{\text{global}}$ prioritisation at two spatial scales. First, the broad-scale priorities represent biome-dependent analyses. Secondly, we measured the site-level diversity and vulnerability to encompass the fine-scale prioritisation.

Cave priorities were set at a national scale, with the assumption that priorities should be comparable to guide decision-making at any scale. The alphanumeric index derived from $\text{BCVI}_{\text{global}}$ was divided into four priority scales (Table 1). Mean biotic vulnerability (i.e., values of 1-high threat to 4-low threat) was compared to cave biotic potential status. Priorities from both scales were assessed across biogeographical realms and biomes using a chi-square test (χ^2). We used Pielou's index in PAST (Hammer et al., 2001) to assess evenness in $\text{BCVI}_{\text{global}}$ and priorities between scales.

3. Results

3.1. Species-level priorities

3.1.1. Global diversity and distribution of cave-dwelling bats

The IUCN lists a total of 679 ($N_{cave} = 679$ spp./1400) cave-dwelling species constituting 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 Phyllostomidae ($N = 96$, $\%_{cave} = 14$, $\%_{global} = 45$) (Table S4). Most species are concentrated in the tropical regions ($\chi^2 = 205.83$, $df = 5$, $P < 0.0001$) with 30 % ($N = 227$ spp.) of global cave-

Table 1
Four-level priority scales for bat caves using the Global Bat Cave Vulnerability Index ($BCVI_{global}$).

$BCVI_{global}$	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 least concern for conservation.
4A, 4B, 4C, 4D	Blue Priority caves	High to low threat, with very low diversity. May have already lost species.	Cave that is least concern.

dwelling bats in the Indomalayan region (Fig. 2). 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.) (Fig. 2; 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, $P < 0.0001$). Most 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 (Fig. 2). 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, $P < 0.001$).

3.1.2. Patterns of threat and extinction risks

Using the IUCN data, the estimated extinction risks of cave-dwelling bat species ($\hat{p}_{extinction}$ = 15 %, 13–25 %) are lower than that of all bat species ($\hat{p}_{extinction}$ = 20 %, 16–35 %), of which 37 % are in a threatened category and 12 % are data deficient (Fig. 3a, Table S5). Overall extinction risk of global cave-dwelling bats is relatively lower but higher when compared across sub-orders, families, and trophic groups (Fig. 3a). Moreover, country endemic species ($\hat{p}_{extinction}$ = 36 %, 29–50 %) and species occurring on islands (islandic: $\hat{p}_{extinction}$ = 40 %, 35–48 %) are facing exceedingly high extinction risk (Fig. 3a, Table S5). 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 (Yinchiroptera: β = −2.34, $P < 0.001$; Yangochiroptera: β = −2.02, $P < 0.001$). Country endemic (β = −0.67, P = 0.013) and island endemic (β = 1.00, $P < 0.001$) species are also linked to higher extinction risk globally (Fig. 3a). But varies within suborders, Yangochiroptera that are island endemic (β = 1.17, $P < 0.001$) are at higher risk, while only geopolitically endemic Yinchiroptera (β = −1.19, P = 0.028) are at higher risk compared to more widespread species (Fig. 3b, Table S6). Furthermore, 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 (Yinchiroptera: β = 2.84, P = 0.043; Yangochiroptera: β = 2.50, P = 0.031) (Fig. 3b).

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

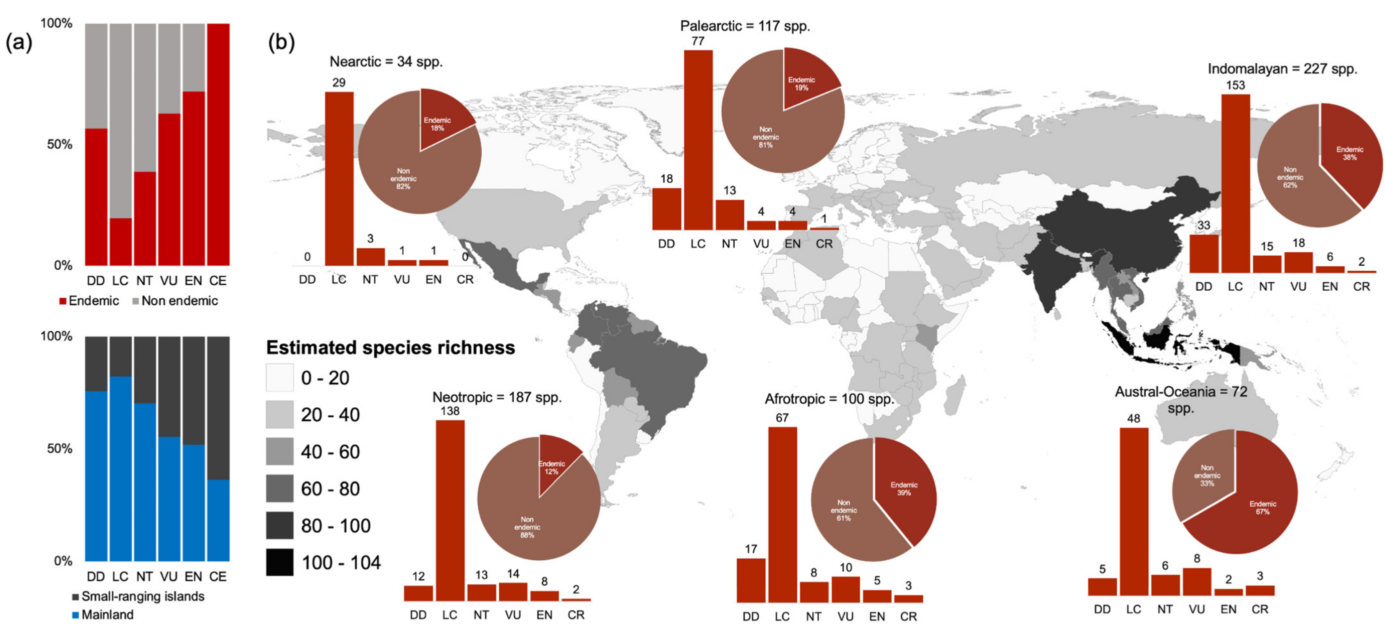

Fig. 2. Species diversity and distribution of cave-dwelling bats. IUCN-based conservation status according to (a) country and island endemism, and (b) taxonomic distribution of estimated species richness of cave bats per country, and proportion of endemic species (in pie graph) and threatened (in the bar graph) of compared by biogeographical realm. The proportion of country endemic species differed regionally (χ^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 S1-S3).

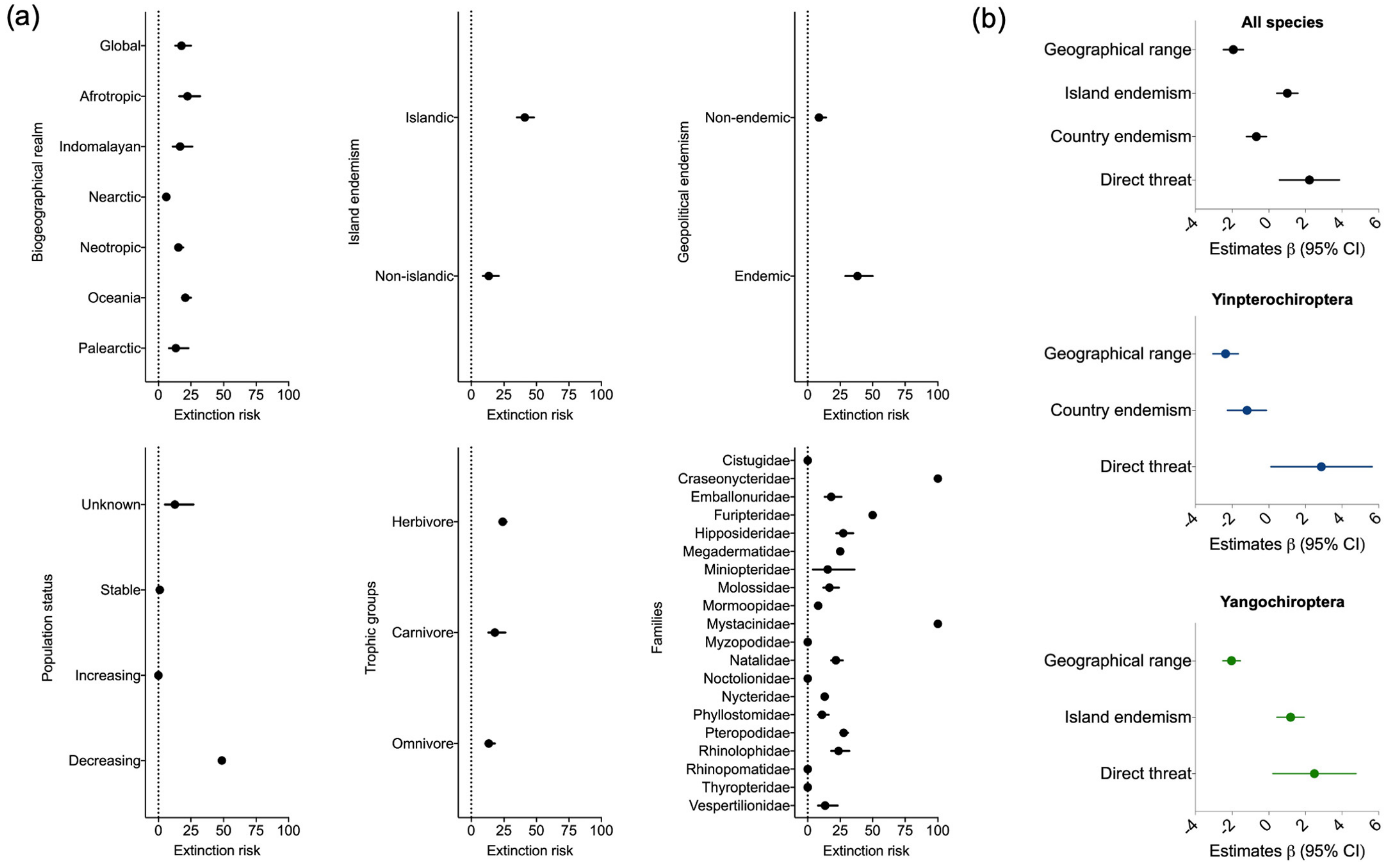

Fig. 3. IUCN-based extinction risk. (a) Estimated extinction risks ($\hat{p}_{extinction}$) of global cave-dwelling bat species compared by biogeographical realm, island endemism, geopolitical endemism, population trends, trophic groups, sub-orders and families. Estimated extinction proportion ($\hat{p}_{extinction}$) 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 among suborders Yinpterochiroptera and Yangochiroptera. Summary of binomial generalised linear mixed (GLMs) explaining species extinction risks is provided in Table S3.

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-climatically induced threats (Fig. S1, Table S7). Species risks to dominant threats such as agricultural conversion ($\beta = -0.214, P = 0.017$) and deforestation ($\beta = -0.154, P = 0.05$) were significantly linked to small geographic range. Conversely, species with large geographic ranges were more at risk from pollution ($\beta = 0.498, P = 0.003$). Species adult body mass is a strong predictor of species vulnerability for hunting and bushmeat for large species ($\beta = 0.845, P < 0.001$). Within trophic levels, omnivores have a significantly higher risk from mining and quarrying compared to frugi-nectarivores ($\beta = -1.029, P = 0.023$) and carnivores ($\beta = -0.636, P = 0.026$). Frugi-nectarivores are more vulnerable to hunting and harvesting ($\beta = 2.256, P = 0.001$), and insectivores to pollution ($\beta = 1.483, P = 0.044$) compared to other trophic levels (Fig. S2 and Table S8).

On a global scale, seven out of twelve variables showed a significant relationship with summed species biotic scores ($\Sigma S_{\text{cave } x}$) 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 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 among species diversity attributes (Fig. 4c, Data S2).

3.2. Habitat-level priorities

3.2.1. Mapping vulnerable and priority sites for cave-dwelling bats

The degree of evolutionary distinctiveness (ED) constructed on bat cave data significantly differed regionally (Kruskal-Wallis, $\chi^2 = 1615.65$, $df = 5$, $P < 0.001$). 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, $\chi^2 = 1584.84$, $df = 5$, $P < 0.01$) (Fig. 5). Prioritisation at broad and fine scales showed that most cave sites are highly vulnerable to threats (Fig. 6a-d). In fine-scale analysis, we found a significant relationship in biotic potential and biotic vulnerability score (Kruskal-Wallis test: $\chi^2 = 14$, $df = 3$, $P = 0.003$). We observed a general pattern of diversity showing that bat 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: $\chi^2 = 6.45$, $df = 3$, $P = 0.092$). This pattern is consistent at broad scales, but the relationship was not significant (Kruskal-Wallis test: $\chi^2 = 6.45$, $df = 3$, $P = 0.092$) (Fig. 6e-f), likely relating to the lack of site-specific data needed.

Indices derived from the site-level and biome-level $BCVI_{global}$ were used to construct a comparative prioritisation across the biogeographical realm and climate regions (Data S3, Table S9). 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) (Fig. 7a, Table 2). The integration of two sub-

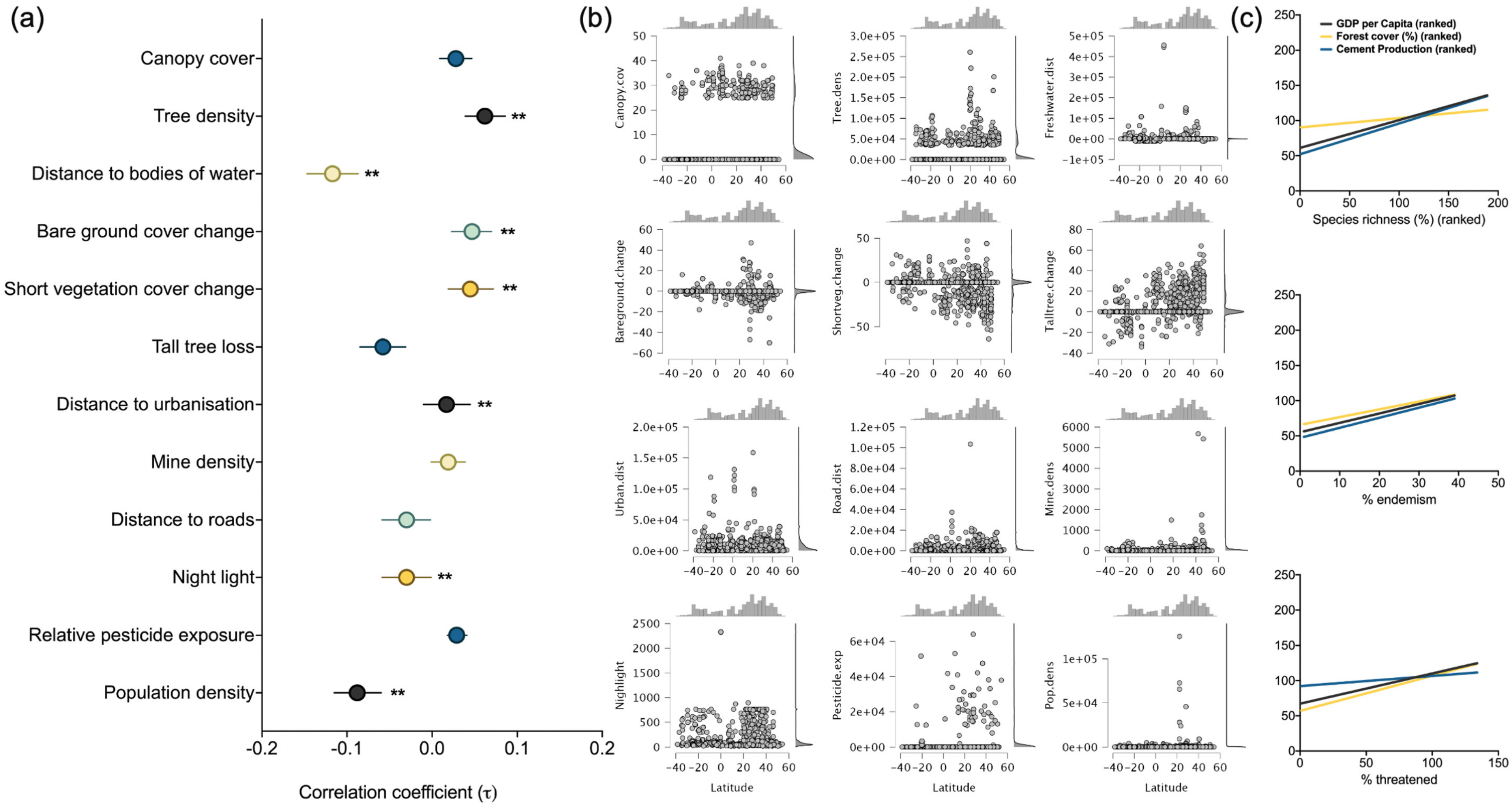

Fig. 4. Relationship, extent, and distribution of threats among assessed global cave sites. (a) Correlation coefficients (τ and 95 % CI intervals) between landscape features and threats and species cave biotic scores, (b) biogeographic comparison of mean intensity of vulnerabilities to landscape features 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 $P < 0.05$).

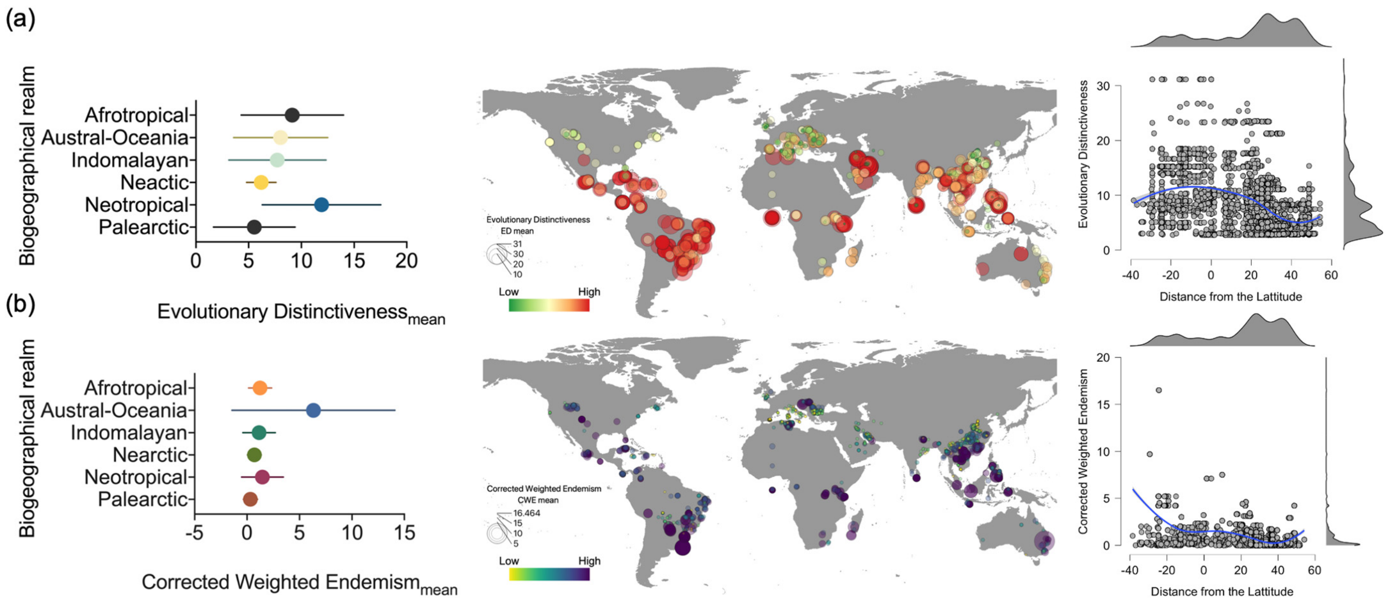

Fig. 5. Comparison of bat cave evolutionary distinctiveness and endemism. (a) Cave Evolutionary Distinctiveness and (b) corrected Weighted endemism compared across biogeographical realms (left). Map of globally-pooled showing the summed ED and CWE of individual caves (right).

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. 7a). Conversely, fine-scaled $BCVI_{global}$ 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 % 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 $BCVI_{global}$, 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 (Fig. 7a, Table 2). We found a significant difference in the 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 varied significantly across spatial scales ($\chi^2 = 1281.43$, $df = 3$, $P < 0.001$) (Fig. 7b; Table S9). Caves were classified based on 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 concentrated in the Neotropical (45 %), Afrotropical (18 %) and Indomalayan (16 %) regions ($\chi^2 = 204.20$, $df = 10$, $P < 0.001$) (Fig. 7b, Table S9). 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 (Fig. 6b, Table 3). The concentration of high priority caves is highest in the Palearctic (30 %) closely followed by Neotropical (29 %) and Indomalayan (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. 7b).

4. Discussion

4.1. Bats and caves in the changing world

This is the first study to assess and present the integrative taxonomic and habitat-level conservation priorities for cave-dwelling bats on a global scale. Whilst various taxa have been used as indicators for diversity in subterranean habitats (Souza Silva et al., 2015), bats represent an effective surrogate for cave conservation because they not only provide the main source of energy for cave ecosystems, and are also easier to assess and reflect proximal habitat changes (Cajaiba et al., 2021; Jones et al., 2009). 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 country-endemic (32 %) or threatened (25 %). We observed a 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 high diversity in caves and the dependence on vast cave-dependent species (Ferreira, 2019; Ferreira and Martins, 1999) may offer a relatively cost-effective conservation surrogate for systematic monitoring. 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 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 a lack of accurate species distributions assessments for global bats (Francis et al., 2010; Murray et al., 2012; Welch and Beaulieu, 2018).

4.2. 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-dwelling species (e.g., *Rousettus amplexicaudatus, Eonycteris spelaea, Eidolon helvum*), which have a smaller portion of their range protected because of their extensive distribution, non-threatened status and lack of statutory protection (Aziz et al., 2021; 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 conversion (Cajaiba et al., 2021; Jones et al., 2009). Over 50 % of the species are already losing habitat close 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 (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 diversity, 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.

4.3. Habitat priorities for conservation

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. There is a slight overlap in priorities

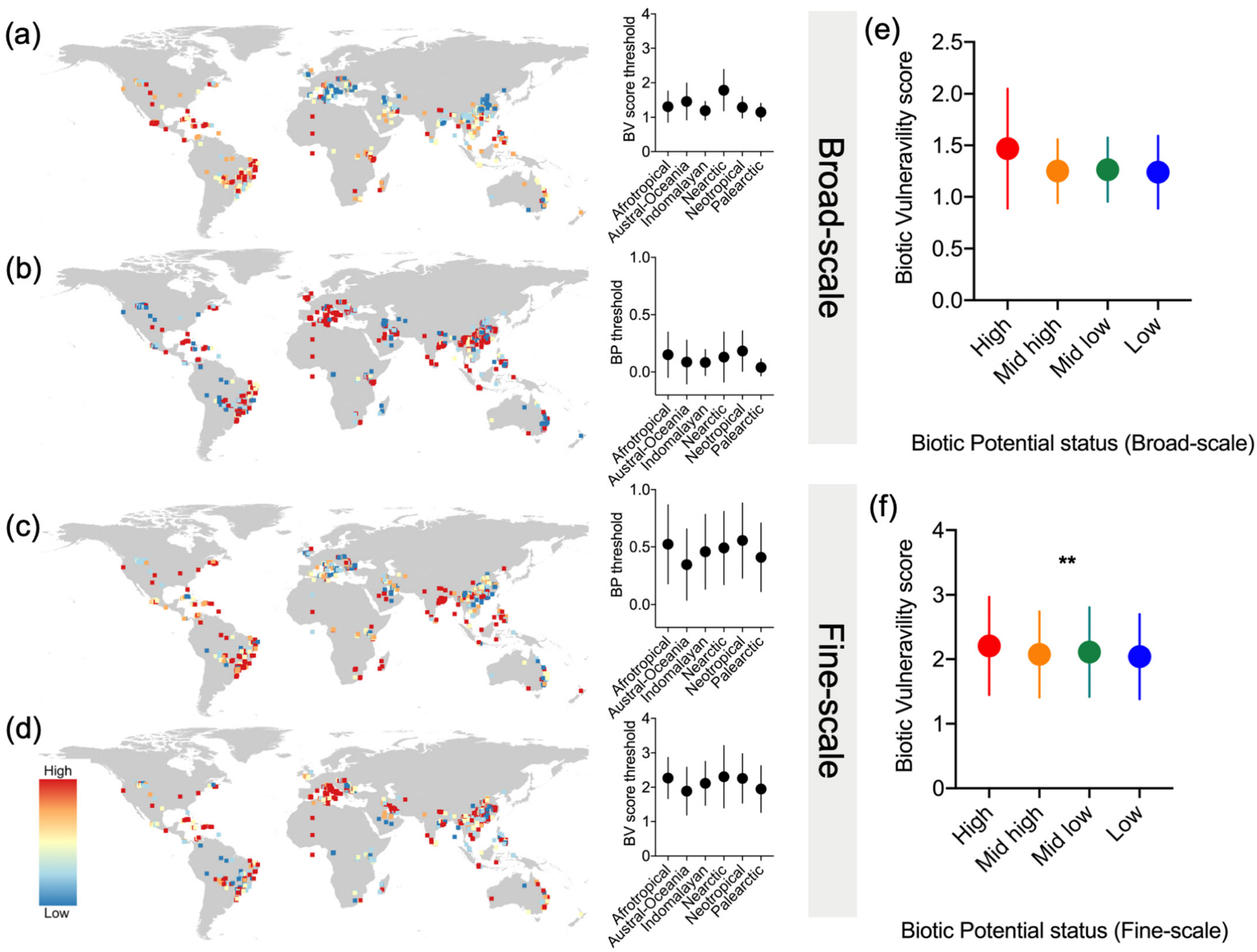

Fig. 6. Distribution and relationships of cave biotic potential and vulnerability worldwide. Site-level (left maps) and biogeographic comparison of thresholds of cave Biotic Potential (BP) and Biotic Vulnerability scores (BV) scores between Broad-scale (a) Biotic Potential (BP), (b) Biotic Vulnerability (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).

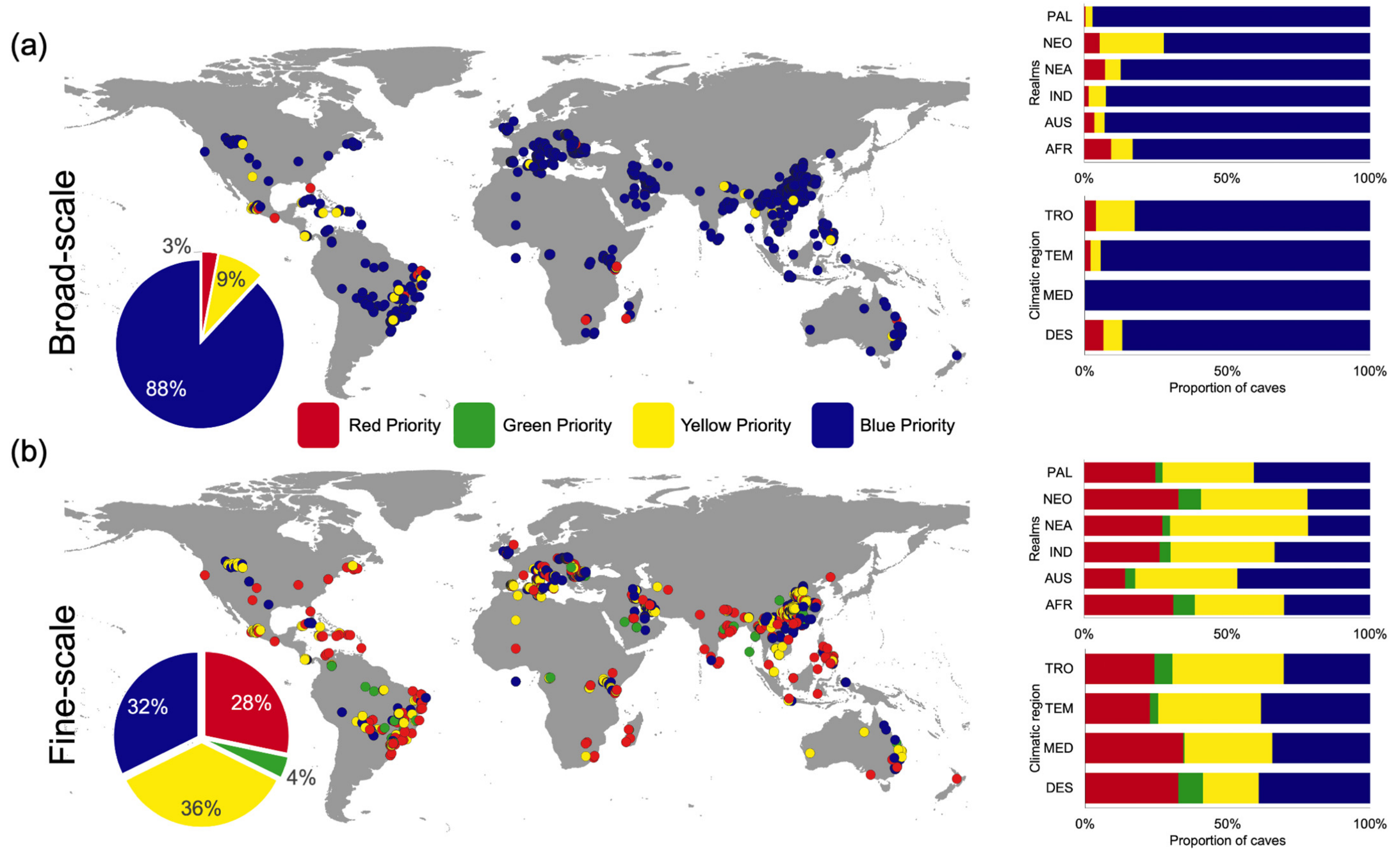

Fig. 7. Global Bat Cave Vulnerability Index and Priorities. (a) Proportion and proportion differences of cave Bat Cave Vulnerability Index- Global (BCVI-G) analysed in broad-scale and fine-scale. The number and percentage of caves according to BCVI-G scales is supplemented in Data S3. Spatial conservation 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.

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 that 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 (Fig. 7, Table 3). While 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

Table 2
Proportions differences of cave Global Bat Cave Vulnerability Index ($BCVI_{global}$) analysed in broad-scale and fine-scale. The number and percentage of caves according to $BCVI_{global}$ scales is supplemented in Data S3.

$BCVI_{global}$	Broad-scale	Fine-scale	Proportion difference
1A	0.01	0.10	0.09
1B	0	0.11	0.11
1C	0	0.03	0.03
1D	0	0.01	0.01
2A	0.02	0.06	0.04
2B	0	0.06	0.06
2C	0	0.02	0.02
2D	0	0	0
3A	0.08	0.12	0.04
3B	0	0.12	0.12
3C	0	0.04	0.04
3D	0	0	0
4A	0.83	0.17	−0.66
4B	0.05	0.12	0.07
4C	0.01	0.03	0.02
4D	0	0	0

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.

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., 2019; 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-dependent (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). Thus, it is imperative to set realistic and cost-effective priorities based on areas with

Table 3
Comparison of achieved percent priorities between broad-scale and fine-scale analyses using the Global Bat Cave Vulnerability Index ($BCVI_{global}$). Full data of $BCVI_{global}$ results and priorities in two scales are in Data S3 and Table S6.

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 %

higher risks, and vulnerabilities and could protect larger communities (Joseph et al., 2009; Rudd et al., 2011).

The integration of vulnerability into effective conservation planning is often challenging due to vague or inconsistent approaches and definitions (Sarkar et al., 2006). Most habitat prioritisation is widely based on taxonomic diversity (e.g., counts, abundance, and rarity) (Brum et al., 2017; Hartley and Kunin, 2003). Whereas species are often prioritised based on their distinct ecological function, high sensitivity and vulnerability to declines (Mouillot et al., 2013). Within cave ecosystems maintaining cave ecosystem function 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 are needed as a basis for conservation-decision making.

4.4. Developing habitat level indices for caves

In our previous work (Tanalgo et al., 2018), we developed the Bat Cave Vulnerable Index (BVCI), but this framework was limited to local and community-level applications. 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, even 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. In addition, the integration of species diversity, evolutionary distinctiveness, and threat exposure of both species and their habitat in our vulnerability index enables the prioritisation of cave habitats with rare and higher functional diversity attributes.

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) (Fig. 8). Whilst further data are needed, especially for data-poor, species-rich regions, relying on IUCN Red List data alone risks misleading effective priorities (e.g., spatial mismatches in the Indomalayan region) (Martín-López et al., 2011; Milner-Gulland et al., 2006). Thus, the IUCN Red List must be utilised alongside other tools and measures of decision-making. Furthermore, habitat-focused indices complement other recent initiatives such as the IUCN Red List of Ecosystems, and the new IUCN ecosystem typology, but also include high-resolution data which can be challenging to include in broader scale indices. Our approach complements the metrics based on geopolitical endemism and conservation status from IUCN which are commonly used within prioritisation schemes (Isaac et al., 2007; Jetz et al., 2014; Martín-López et al., 2009).

4.5. 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. 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 fewer data are 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 (Tanalgo et al., 2022). In addition, cave community data (e.g., country-level assessments) are lacking for biodiverse regions such as 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; Chornelia et al., 2022). 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

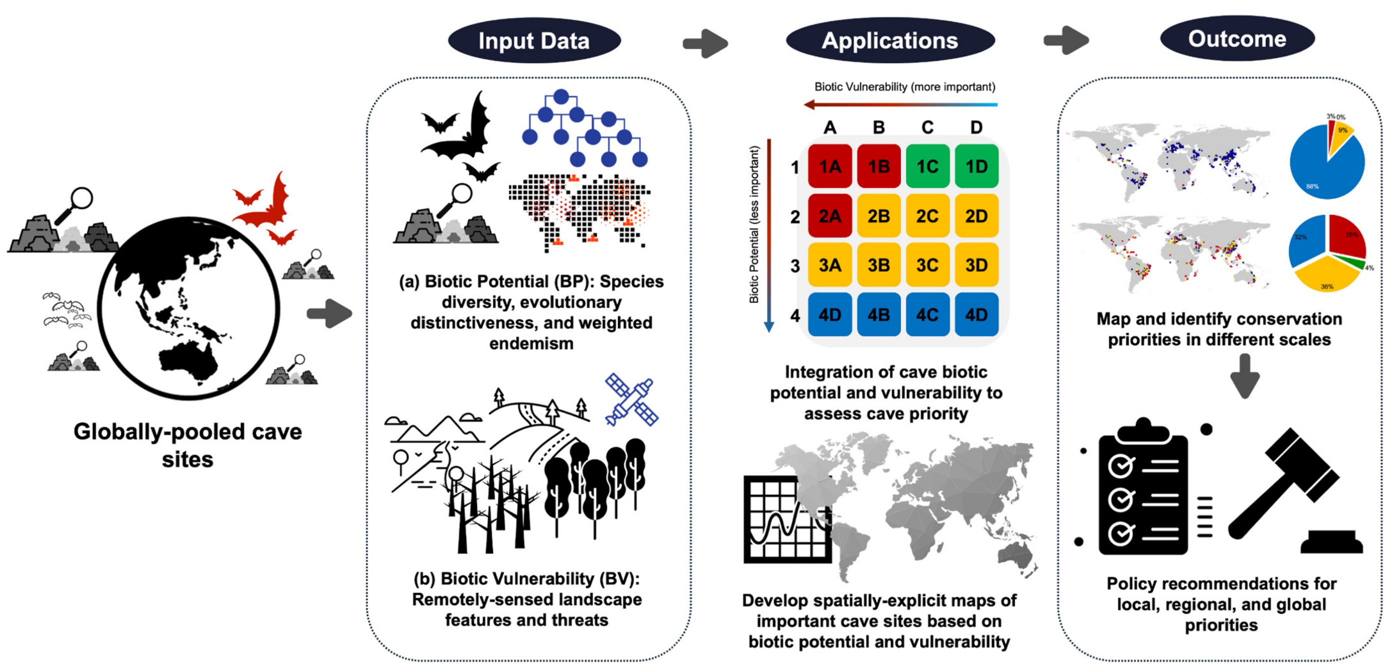

Fig. 8. Framework for prioritising bat caves for conservation. The schematic diagram showing the frame of the Bat Cave Vulnerability Index-Global (BCVI) in identifying and setting priorities for bat caves for conservation on a global scale. The process starts with the pooling of caves sites for assessment 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.

countries most in need. Conversely within Europe, the UNEP-EUROBATS and EU habitats directive provide 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., 2021a, 2021b; Tanalgo et al., 2022).

Only a few countries have any policy related to the protection of caves and their biota (Medellin et al., 2017; 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 in national levels.

5. Conclusions

To protect, sustainably manage and conserve these ecosystems it is crucial that we identify priorities and map vulnerable cave habitats with the highest biodiversity and distinctiveness, as well as those most at risk (Navarro et al., 2017). 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 (Fig. 8).

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. Maintaining cave bat diversity relies on their inclusion in conservation agendas and priorities, the use of science-based targets and frameworks, and synthesising conservation effectiveness (e.g., Conservation Evidence Initiative (Conservation Evidence, 2021). Ultimately, developing effective decisions requires comparable data and standardised frameworks to enable its translation into policy and practice, such as DarkCideS (www.darkcides.org) (Tanalgo et al., 2022). We highlight the power of good data, integration, and the potential for impacts on policy. We hope that with our analysis, and the framework developed here we can begin to use data-driven approaches to help detect and better protect bats and their habitats and that by working collaboratively we can enhance our understanding of bats across the planet.

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Data accessibility statement

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

CRediT authorship contribution statement

KCT and ACH contributed equally to the work. KCT and ACH conceptualised and designed the study. KCT, HFMO, and ACH collated the data. KCT and ACH integrated, synthesised, and 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 approving of the final version of the 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.

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