

DarkCideS 1.0, a global database for bats in karsts and caves

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Abstract

Understanding biodiversity patterns as well as drivers of population declines, and range losses provides crucial baselines for monitoring and conservation. However, the information needed to evaluate such trends remains unstandardised and sparsely available for many taxonomic groups and habitats, including the cave-dwelling bats and cave ecosystems. Here, we present the DarkCideS 1.0, a global database of bat caves and bat species based on curated data from the literature, personal collections, and existing datasets. The database contains information for geographical distribution, ecological status, species traits, and parasites and hyperparasites for 679 bat species known to occur in caves or use caves in their life-histories. The database contains 6746 georeferenced occurrences for 402 cave-dwelling bat species from 2002 cave sites in 46 countries and 12 terrestrial biomes. The database has been developed to be a collaborative, open-access, and user-friendly platform, allowing continuous data-sharing among the community of bat researchers and conservation biologists. The database has a range of potential applications in bat research and enables comparative monitoring and prioritisation for conservation.

Background and Summary

Human civilization has left its footprint on every part of the planet, in the process driving what is frequently referred to as the sixth mass extinction^{1,2}. Conservation prioritisation requires a rigorous assessment of vulnerable species as well as their habitats to develop effective priorities for conservation.

However, the data needed to develop such priorities with rigour are often lacking. Biodiversity integration and synthesis is an important empirical step to identify priorities in maximising the already limited funds allocated to conservation³. The diversity and distribution of a subset of terrestrial vertebrates have become an umbrella for taxonomic and spatial conservation, despite the known biases present in popular open datasets^{4,5}. Efforts to mitigate extinction risks or protect key habitats often disproportionately focus on particular taxa, ecosystems, or regions^{6,7}. This approach neglects many other equally important species and their habitats and compromising the maintenance of ecosystem services provided by diverse functional groups^{8,9}.

There are more than 1400 known extant bat species distributed across almost all terrestrial habitats around the globe^{10,11}. Many of these species occur in biodiversity hotspots that are threatened by both anthropogenic and natural threats⁶. Caves are key habitats for bats¹² but are nonetheless threatened and in need of conservation; despite hosting high endemism, cave ecosystems receive little attention in terms of fund allocation for scientific studies and conservation compared to their surface counterparts such as agricultural and forest ecosystems^{11–14}. Cave taxa are adapted to light-limited underground environments and most of them are dependent on mobile species such as bats to transport organic nutrients into these environments^{15,16}. Bats are keystone species in karst ecosystems and ideal cave conservation surrogates, delivering vital energy sources into caves as they regularly forage from outside ecosystems. Cave ecosystems are critical for bats, with around half of all bat species reliant on caves, with a high rate of endemism and proportion of threatened species facing high risks from varying threats¹⁷. Nevertheless, conservation attention towards cave-dwelling bats remains limited compared to other mammalian taxa. Thus, there is an urgent need for better data to develop effective priorities for bats¹¹.

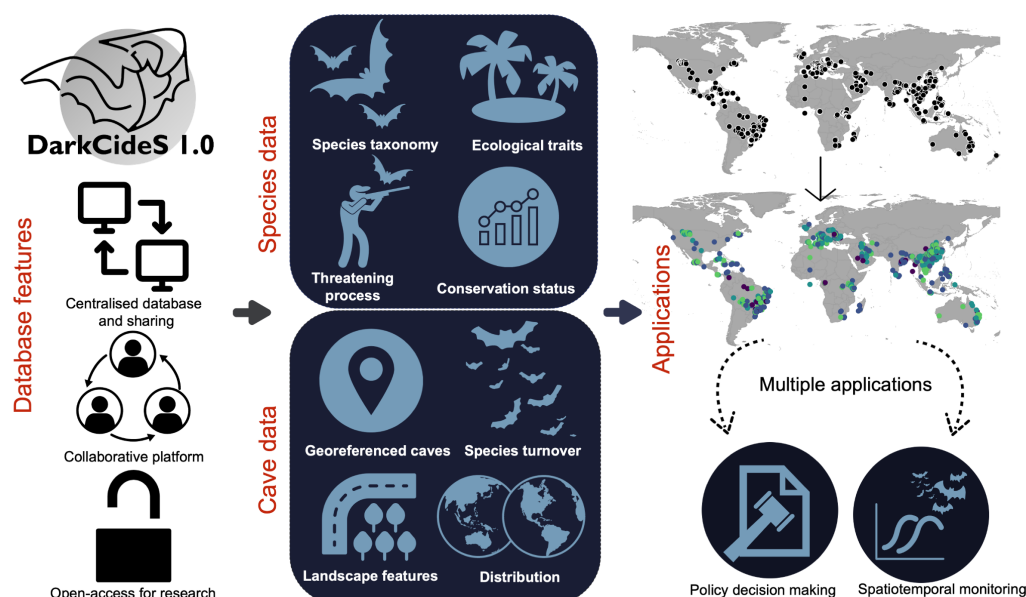


Figure 1: A schematic diagram showing the features, contents, and potential applications of the DarkCideS 1.0 database. The database is a centralised, collaborative, and open-access platform that contains information on cave-dwelling bats species and their distribution.

Effective conservation decision-making relies on the accuracy and precision of the data used to design priorities^{7,18}. Identifying priority caves for conservation requires an understanding of species diversity, endemism patterns, interactions with other organisms, and threats within and outside these systems¹⁹. Additionally, while numerous organisations and collaborative efforts aim to database bat distributions, comprehensive and specific datasets for cave-dwelling bats, including their distributions and ecological traits, are currently lacking. Large databases for species distributions such as the Global Biodiversity Information Facility (GBIF) exist and openly provide distribution data for bats. However, due to the enormous amount of information within these databases, it is challenging to selectively evaluate data for specific ecosystems such as caves, and thus more specialist datasets are needed to facilitate appropriate

habitat-based prioritisation.

To address this knowledge gap, we created *DarkCideS 1.0, A global database for bats in karsts and caves* to advance global bat cave vulnerability and conservation mapping initiatives. The creation of the dataset primarily aims to map and digitise the distribution of cave-dwelling bats to facilitate the assessment of their vulnerability to landscape threats. DarkCideS 1.0 represents a publicly available database of cave-dwelling bats across time and space including their estimated population (e.g., counts), geographical distribution (latitude and longitude), ecological traits, levels of endemism, conservation status, and threatening processes. The purpose of the DarkCideS 1.0 initiative is to centralise and develop an open-access platform for information exchange among bat researchers and conservation biologists to advance the development of targeted conservation measures and macroecological studies (Figures 1, 5). Potential applications of the database include assessing species conservation status and extinction risks; understanding drivers of extinction, cave conditions, and landscape threats; accurately developing species distribution models; and determining long-term cave conservation priorities at regional to global scales.

Methods

The DarkCideS database was initially conceptualised and developed by KCT, JAG, and ACH as part of the “Global Bat Cave Vulnerability and Conservation Mapping Initiative” in 2014, and later with the “Mapping Karst Biodiversity in Yunnan” and the “Southeast Asian Atlas of Biodiversity” projects. The initiative includes developing tools and methods (e.g., the Bat Cave Vulnerability Index²⁰) and synthesis (e.g., the global bat cave vulnerability assessment¹⁷) to identify conservation priorities and important bat caves in the tropics. Since 2019, the initiative has expanded and potential collaborators and contributors were invited through scientific conferences (Association for Tropical Biology and Conservation 2018, International Bat Research Conference 2019), social media platforms, and personal correspondences. At present, the database has 36 collaborators from twenty countries on six continents with expertise and research interests in bat conservation. Four main datasets for all known cave-dwelling bats were built for the DarkCideS database version 1.0.

Datasets and compilation for species checklist (Dataset 1)

The first dataset contains taxonomic checklists for all extant cave-dwelling bats species extracted from the expert-based International Union for the Conservation Union (IUCN) Red List database version 2020.1 (Table 1). We screened and included all bat species that were reported to use, roost in, or aggregate in “Caves”, “Underground”, and “Karsts” habitats in any part of their life histories. We also scanned major bat cave databases from expeditions such as “Bats in China” (<http://www.bio.bris.ac.uk/research/bats/China/>) and UNEP-EUROBATS (<https://www.eurobats.org/>) for European bats²¹. In addition, the first dataset contains species ecological traits, distribution range, and threatening processes.

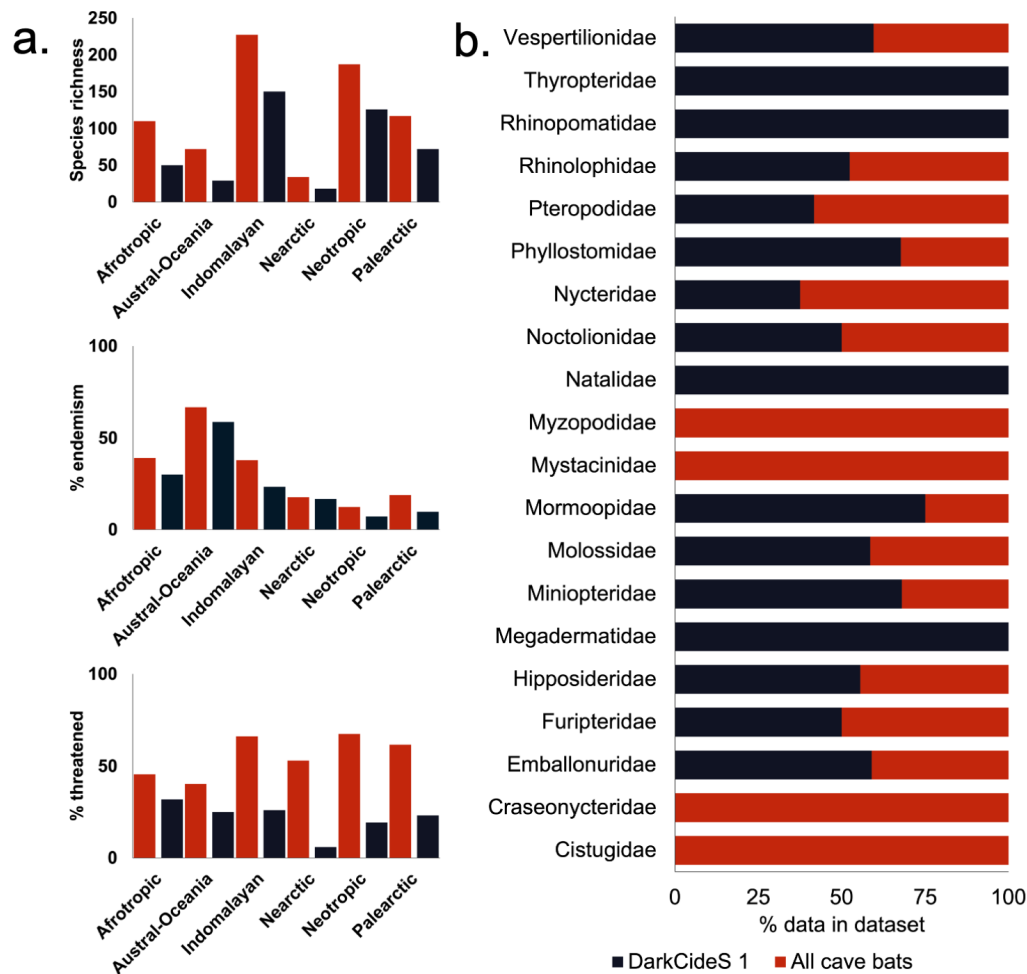


Figure 2: Biogeographic (a) and family-level (b) comparison of species turnover between IUCN estimates (red bars) and sampled caves from DarkCideS 1.0 (black bars) species richness, the proportion of endemism, and proportion of threatened species worldwide.

Habitat preference, distribution, ecological status, and traits (Dataset 1)

We classified species distribution by biogeographical realm (Indomalaya, Austral-Oceania, Afrotropical, Neotropical, Palearctic, and Nearctic) and terrestrial biomes following Olson et al.²². We described species major habitat breadth based on IUCN Level 1 classification <https://www.iucnredlist.org/resources/habitat-classification-scheme> (Caves, Forests, Savanna, Desert, Urban, Artificial, and Wetlands). Species current conservation status (Data Deficient, Least Concern, Near Threatened, Vulnerable, Endangered, and Critically Endangered) and population trends (e.g., Unknown, Decreasing, Stable, Increasing) were categorised using standard IUCN Red List assessments. Using the same criteria, we categorised species endemism as geopolitically endemic (e.g., country-endemic, and non-endemic) when a species occurs only in a single country or state territory²³, and island endemism was classified as island-restricted or predominantly mainland²⁴. The highest country endemism was in the Eastern Hemisphere with the highest in the Austral-Oceania (40%) region, followed by the Afrotropics (21%), then the Indomalayan region (16%). However, the highest proportion of threatened species, was in Indomalayan (43%) and the Neotropics (22%) (Figure 2c).

Furthermore, species current geographical ranges were compiled from the Phylacine 1.2 database²⁴ based on species IUCN ranges. Three species traits were included: the adult body mass (in grams) per species were derived from Phylacine 1.2²⁴ and generation length from Pacifici et al.²⁵. For trophic groups, we derived diet information from EltonTraits 1.0²⁶. We grouped species as frugi-nectarivorous for

all species that forage on plant-based resources (e.g., frugivores and nectarivores). As species foraging smaller vertebrates (i.e., fish and rodents) are very few, we classified them as carnivores along with insectivorous bats. Species that forage on both resources were grouped into omnivores (Table 1).

Species threatening process (Dataset 1)

We identified potential threats for each bat species listed in the checklist using the information from the IUCN Red List assessments (version 2020.1) in addition to threats highlighted in the literature. The IUCN Red List standardised its classification based on Salafsky et al.²⁷, but we reclassified the threatening process into three key categories: Direct, Indirect, and Natural (Table 1) based on the drivers of threat^{12,20,28}. Direct threats (T_{dir}) refer to the threats or risks that are direct to or in cave systems with immediate and perceivable impacts on populations or behaviour of species. This category includes direct human impacts (e.g., persecution, eviction, and cave closures) and the use of caves for harvesting bats, tourism, religious visits, and mining (minerals or guano). Indirect threats (T_{ind}) refer to the threats outside cave systems or within cave proximity, of which the impacts to populations are secondary or non-immediate but otherwise detrimental. Examples include deforestation, agriculture, and urbanisation. Lastly, Natural threats (T_{nat}) refer to threats that are natural in origin, though their frequency may be impacted by human activities, and that may directly or indirectly impact populations, such as diseases and climate-driven risks (e.g., drought, extreme cold) (Table 1).

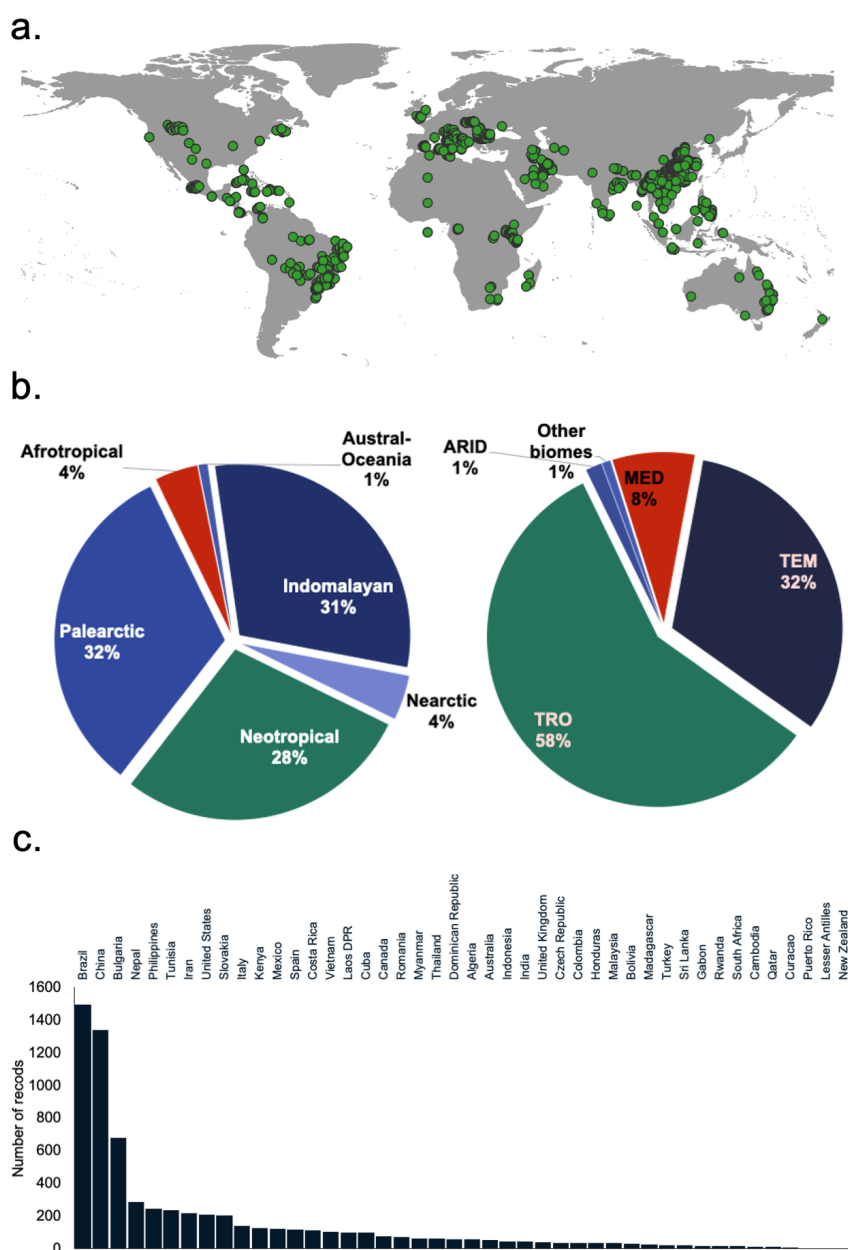


Figure 3: The geographical data turnover of the current database version: (a) geographical locations of all bat caves included in the database, (b) percent distribution of species occurrence in terms of the biogeographical realm (left) and terrestrial biome (right), (c) country-level turnover.

Bat cave georeferencing (Dataset 2)

The second dataset contains the bat cave geographical location (latitude/longitude) and recorded species (Table 2, Figure 3A). We used the Web of Science and Google Scholar to search online literature, databases, and repositories for published information on cave-dwelling bats from 1990 to 2021. We used the following combination of keywords: (*Bat** OR *Chiroptera* OR *Chiroptera fauna**) AND (*Diversity* OR *Species richness* OR *abundance* OR *distribution* OR *conservation* OR *ecology*) AND (*Cave** OR *Cave-dwelling* OR *Cave-roosting* OR *underground** OR *subterranean* OR *karst** OR *Limestone*). We also set a “create alert” in Google Scholar whenever new related papers were published. The data mining process for version 1.0 ended in June 2021. Our search returned 753 papers. We also searched using the

Baidu Research engine for Chinese literature and self-archived ResearchGate to maximise search results. To ensure the precision of the datasets included in DarkCideS 1.0, we filtered all published literature to only include those papers or reports with complete species names and geographical records. We contacted corresponding authors with requests to provide us with geographical data when these were missing from their papers or supplementary materials. In the circumstance that we were unable to find the data, and the corresponding author did not respond to our request, that “cave site” was excluded from the database. We converted all species and cave latitude and longitude into WG84 decimal degrees with five significant figures. The second dataset of DarkCideS 1.0 contains 6746 georeferenced occurrences for 402 species¹⁷ from 2002 cave sites (Figures 3). Cave sites occur in all continents except Antarctica, with most of the data originating from tropical and temperate biomes (Figure 3B). We have cave records from 46 countries of which China and Brazil have the highest number of caves recorded (Figure 3C).

Cave landscape features and vulnerabilities (Dataset 3)

The condition of surface ecosystems and the extent of threats are significant determinants of cave-dwelling bat diversity. Yet, standardising the vulnerability of caves and underground ecosystems from threats on a global scale is challenging. To address this, the surface ecosystem was mapped as a proxy to assay cave vulnerability to threats using remotely-sensed landscape features. The third dataset included in the database contains the measured land-use and landscape features of the cave surroundings using the georeferenced data from the second dataset (Table 3, Figure 4). The selected landscape features measurements of the 2002 cave sites were selected based on Tanalgo et al.¹⁷. We included the estimated distance and measures of twelve ($N = 12$) landscape variables in the database including canopy cover height²⁹, tree density³⁰, distance to bodies of water³¹, bare ground cover change³², short vegetation cover change³², tall tree cover change³²; for vulnerabilities we included distance to urban areas³², distance to roads³³, mine density³⁴, night light³⁵, relative pesticide exposure³⁶, and population density^{37,38}. For distance variables, the “distance to feature” tool was used in ArcMap 10.3 and distances were mapped at a 1-km resolution.

Cave bat parasites and hyperparasites (Dataset 4).

Parasites, while being among the most diverse modes of life, are often disregarded in conservation strategies³⁹. It is well established that parasites affect the stability of food webs and ecosystem health, but hyperparasites have thus far been severely understudied. For future studies on host associations across multiple trophic levels and on the effects of climatic conditions and land-use changes, parasites and hyperparasites are part of our DarkCideS 1.0 database. The fourth dataset lists the parasitic bat flies and their Laboulbeniales fungal hyperparasites associated with cave bats. Data were collected from several sources, including our own fieldwork³⁶, Haelewaters et al.⁴⁰, and de Groot et al.⁴¹. Bat fly taxonomy followed Dick and Gracioli⁴² and Gracioli and Dick⁴³ and fungal taxonomy followed Index Fungorum⁴⁴. In addition to the conspicuous bat flies, bats are host to several other lineages of parasites mites and ticks, lice, fleas, bugs, and earwigs^{45,46}. Consequently, the fourth dataset will be expanded on in future versions of DarkCideS with data on these parasitic organisms. A recent call for global collaborations among bat scientists and collaborations to generate multitrophic data of bats, bat flies, and fungi⁴⁵ along with the current DarkCideS 1.0 initiative will contribute to a general understanding of how ecological and life-history traits are correlated with bat parasitism and how host associations may change under changing conditions.

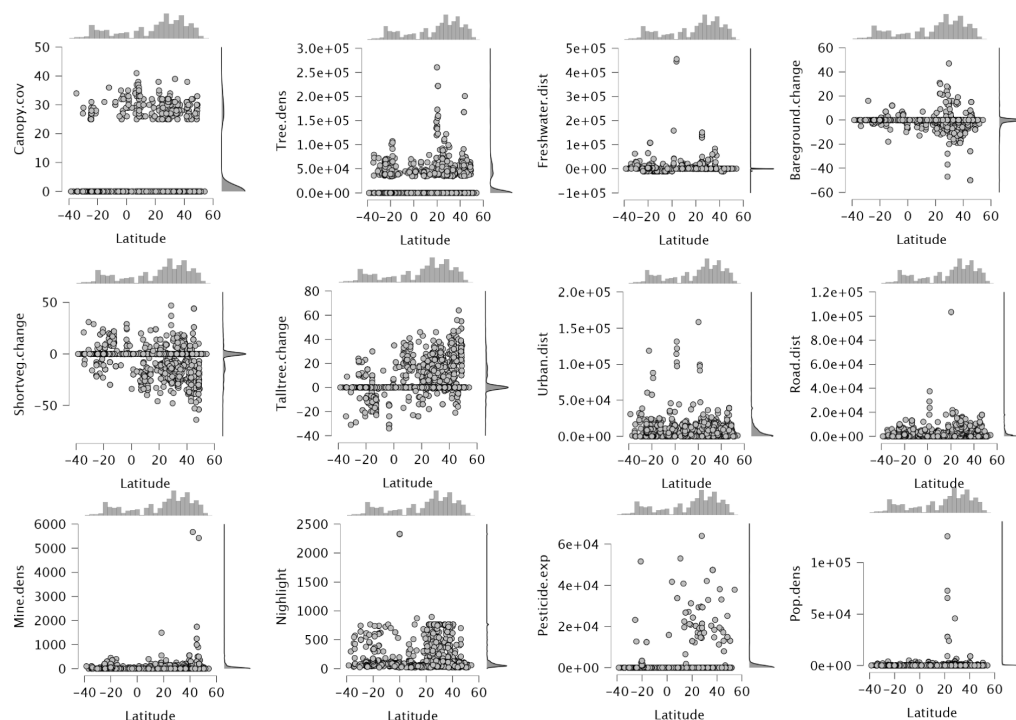


Figure 4: Density and latitudinal distribution of bat caves based on different landscape features and vulnerability (for units of each landscape feature, please refer to the original data sources, Table 3).

Data Records

The complete database for global cave-dwelling bats was organised in four main datasets stored in separate Excel workbooks (.csv file format). Each dataset contains unique sequential name IDs that correspond to metadata, variables, and references. All datasets included in the database are available and open-access on the figshare online repository (links will be included after final review) and through a public web page (<https://darkcides.org/>). The resolution of the publicly available cave and species occurrences were reduced for the protection of caves and to prevent hunting and harvesting. Database users can request high-resolution data of georeferenced species occurrence and cave sites from the corresponding authors.

Technical Validation

The data included in this database are mainly derived from expert-based databases, published material and bat researchers, therefore ensuring the accuracy of the included data. We provided the corresponding reference (when applicable) for each cave record for cross-referencing and data validation purposes. When published “cave datasets” were unclear or lacked detailed information, we contacted the corresponding authors. We encourage continued contributions to the DarkCideS database as we aim to regularly update the entries for species checklists, traits, geographical locations of caves, and species occurrence data. For species ecological status (e.g., current conservation status, population trends, geopolitical endemism), we will update entries after every IUCN Red List assessment cycle. Datasets that were originally entered as “unpublished” or “personal data” will also be updated after the respective author or contributor has published their findings. The database will be updated when new data are contributed and will be corrected when an error in the data entries are reported to any of the corresponding authors. Quality screening of new entries based on the criteria listed above will be made before adding new

records to the database (Figure 5). Once an update is made, a release note will be published on the database website. When updating new versions of DarkCideS, we will continue to make available previous releases. Contributors will be included as co-authors when the next version of the database is published. Furthermore, as each cave has a unique ID, additional surveys of other taxa at the same locality can be integrated into the database, to provide a backbone for enhancing our understanding of cave biodiversity through time.

Usage Notes

Users should cite this publication when using the DarkCideS 1.0 database and future version releases, especially when using the georeferenced data of caves and bat species. Although we aim to maximise spatial coverage with datasets from across the globe, we acknowledge that geographical biases inevitably exist⁴⁷. For example, we have multiple datasets from the Palearctic, Indomalayan, and Neotropical realms, whereas very little data originated from the Afrotropical region (Figure 3). We also encountered similar coverage bias in country-level data richness, for example, Indonesia is one of the most diverse countries for estimated cave-dwelling bat species richness¹⁷, but a very small number of species were included in the current version of the database. The database is intended as a long-term data-sharing platform, and we hope to fill these gaps in the next versions of the database. Further data and coverage will provide a better index for regional prioritisation in addition to further research on bat diversity patterns and threats.

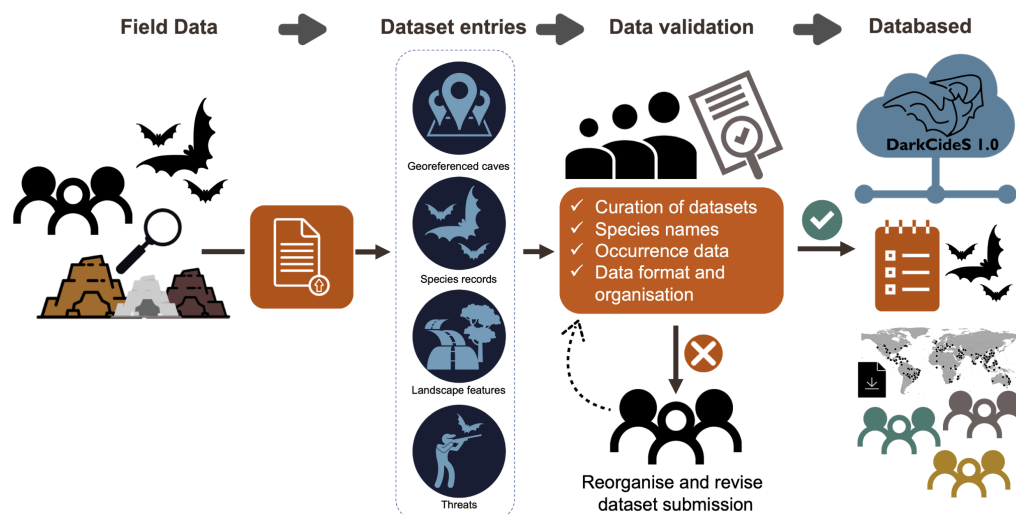


Figure 5: Schematic diagram showing the updating workflow of the database from new data entry. The DarkCideS database aims to be a long-term biodiversity data exchange platform by including new data from fieldwork and assessments. Authors can upload their dataset containing species data, geographical information, and landscape threats on the web page. The new data will be received by the corresponding authors for validation before being merged into the database.

Code Availability

No code or costume code was used to generate the data presented in this data paper.

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Authors contributions

KCT, JAG, and ACH conceived and primarily developed the database, with funding acquired by ACH. Data collection, organisation, and formatting were led by KCT and ACH. ACH performed the landscape feature mapping and analyses. Data on bat parasites and hyperparasites were compiled and curated by DH. The first draft of the manuscript was written by KCT and ACH. KCT performed data visualisation. All authors provided inputs and suggestions on the draft and approved the final manuscript. The majority of the authors provided data to at least one of the DarkCideS datasets.

Competing interests

The authors declare no competing interests.

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Trait category	Trait	Variable type	Data Filters	N Species	Source			
Habitat preference	Forest	Binomial	Yes = 1, No = 0	586	IUCN database			
Ecological status and distribution	Savanna	Nominal	Decreasing	140	Phylacine 1.2			
	Desert			45				
	Urban			16				
	Underground			523				
	Wetlands			56				
	Population.status			150				
	Conservation.status			Stable		161		
				Increasing		6		
				Unknown		362		
				Data.Deficient		83		
				Least.Concern		452		
				Near.Threatened		54		
				Vulnerable		54		
				Endangered		25		
				Critically.Endangered		11		
				Geopolitical.endemism		Non.Endemic	459	
	Island.endemism			Endemic		220		
				Island.Endemic		159		
	Biogeographic.breadth			Mainland		520		
				Afrotropical		102		
				Indomalayan		184		
				Austral-Oceania		49		
	Feeding groups			Feeding.groups		Neotropical	173	EltonTraits 1.0
						Palaearctic	85	
						Neactic	18	
						Cosmopolitan	68	
Geographical range	Current.range	Carnivore	553	Phylacine 1.2				
		Frugi-nectarivore	60					
		Omnivore	66					
		N/A	679					
Biological traits	Natural.range	Continuous	N/A	679				
	Generation.length	Continuous	N/A	679				
Direct threats	Body.mass	Continuous	N/A	679	IUCN database			
	Mining.quarrying	Binomial	Yes = 1, No = 0	155				
Indirect threats	Sacred.activities			11				
	Tourism.caving			226				
	Guano.extraction			69				
	Vandalism			106				
	Nest.harvesting			5				
	Hunting.bushmeat			109				
	Intensional.killings			48				
	Gating			7				
	Scientific.research			7				
	Agricultural.conversion			155				
	Urbanisation			76				
	Deforestation			284				
	Pollution			65				
	Road.kills			12				
Natural threats	Disease.parasites	5						
	Invasive.species	21						
	Fires	36						
	Drought	9						
	Extreme.cold	1						
	Storm	17						

Table 1: DarkCideS 1.0 includes key traits for all living cave-dwelling bat species ($N = 679$). General metadata for traits included in the current version of the database: habitat preference, ecological status, feeding groups, geographical range, island endemism, geopolitical endemism, distribution range, biogeographical breadth, generation length, body mass, and threatening process.

Data.Column	Data Type	Data Filters	N Species
Biogeographical.realm	Nominal	Afrotropical	
		Indomalayan	
		Austral-Oceania	
		Neotropical	
		Palaearctic	
		Nearctic	
Biome.classification	Nominal	Deserts & Xeric Shrublands = DES	
		Flooded Grasslands & Savannas = FLO	
		Mangroves = MAN	
		Mediterranean Forests, Woodlands & Scrub = MFWS	
		Montane Grasslands & Shrublands = MGS	
		Temperate Broadleaf & Mixed Forests = TBMF	
		Temperate Conifer Forests = TCF	
		Temperate Grasslands, Savannas & Shrublands = TGSS	
		Tropical & Subtropical Coniferous Forests = TSCF	
		Tropical & Subtropical Dry Broadleaf Forests = TSDB	
		Tropical & Subtropical Grasslands, Savannas & Shrublands = TSGS	
		Tropical & Subtropical Moist Broadleaf Forests = TSMB	
Country.record	Nominal	All country	N/A
Latitude	Continuous (WGS 84 in DD)	N/A	N/A
Longitude	Continuous (WGS 84 in DD)	N/A	N/A

Table 2: Metadata of the georeferenced information of cave-dwelling bats and caves.

Variables	Variable type	Data Filters	References
Biogeographical.realm	Nominal	Afrotropical	N/A
		Indomalayan	
		Austral-Oceania	
		Neotropical	
		Palaearctic	
		Nearctic	
Region		All continents entered	
Country		All countries entered	
Cave_Name		All cave names entered	
Latitude	Continuous (WGS84 DD)	N/A	
Longitude	Continuous (WGS84 DD)	N/A	
Canopy cover	Continuous (see source for units)	Canopy.cov	25
Tree density		Tree.dens	26
Distance to freshwater bodies		Freshwater.dist	27
Bare ground cover change		Bareground.change	28
Short vegetation cover change		Shortveg.change	28
Tall tree cover change		Talltree.change	28
Distance to urban areas		Urban.dist	28
Distance to roads		Road.dist	29
Mine density		Mine.dens	30
Nightlight		Nightlight	31
Relative pesticide exposure		Pesticide.exp	32
Population density		Pop.dens	33, 34

Table 3: Landscape features included in the current version of the database.