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ORIGINAL RESEARCH

Out of sight and out of mind? The conservation status of subterranean biodiversity in the United States and Canada

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Abstract
Subterranean ecosystems harbor globally important yet highly threatened biodiversity. Unfortunately, subterranean biodiversity is often neglected in regional and global conservation initiatives, including conservation assessments. We reviewed the conservation status and threats to subterranean species based on the two most popular conservation assessment protocols in North America, NatureServe and International Union for Conservation of Nature (IUCN) Red List, as well as federal and state/provincial protection status of the 1,460 described cave-obligate species occurring in the United States and Canada. Only 9.3% of species have been assessed under IUCN Red List criteria compared to 77.9% of species assessed under NatureServe criteria; notably, 1,065 and 116 of species are assessed at an elevated risk of extinction by NatureServe and IUCN Red List, respectively. Just 41 species are listed or proposed to be listed under the U.S. Endangered Species Act and none of the 10 species that occur in Canada are federally listed. Vertebrates (fishes and salamanders), decapods (crayfishes and shrimps), and U.S. federally listed species are overrepresented on the list of species with IUCN Red List assessments compared to other taxonomic groups, particularly arachnids, millipedes, and insects. Most species assessed under IUCN Red List criteria as well as federally listed species occur in the Edwards Plateau and Balcones Escarpment karst region of Texas. Major threats frequently reported in conservation assessments include habitat degradation, pollution/contamination, recreational activities, climate change, and groundwater exploitation; however, information on threats was lacking for most species for nearly all major taxonomic groups, except decapods, fishes, and salamanders. The intrinsic vulnerability of subterranean biodiversity coupled with the many potential threats facing species and extensive biodiversity knowledge gaps makes assessing their conservation status and ultimately their protection a challenging endeavor. We highlight several limitations of implementing current conservation assessment approaches while offering recommendations to improve our ability to assess the conservation status of subterranean biodiversity to better inform sound local to global conservation policies and actions.

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Introduction

Much of the world's biodiversity is at risk of extinction due to alarming environmental trends over the last 25+ years, such as deforestation, declines in freshwater resources, and global climate change, all of which are driven by continued increase in human population (Pereira et al. 2012; Ripple et al. 2017). Although often neglected in regional and global conservation assessments and efforts (Sutherland et al. 2018; Niemiller et al. 2018; Mammola et al. 2019), subterranean biodiversity is no less threatened by anthropogenic stressors than surface terrestrial and aquatic biodiversity. Many subterranean species, particularly permanent subterranean inhabitants (i.e., troglobionts and stygobionts), are intrinsically vulnerable to a plethora of threats and, consequently, are at an elevated risk of extinction (e.g., Niemiller et al. 2018; Mammola et al. 2019). Most species have extremely restricted distributions (Christman and Culver 2002; Zagmajster et al. 2008; Trontelj et al. 2009; Eme et al. 2018), with many restricted to a single cave system or small region, i.e., short-range endemics (Christman et al. 2005; Deharveng et al. 2009; Niemiller and Zigler 2013; Niemiller et al. 2017). Moreover, many species have convergently evolved similar life history traits due to strong selective forces associated with subterranean habitats that render them inherently vulnerable, such as low fecundity, low basal metabolism, slow growth rates, delayed sexual maturity, long lifespans, and limited dispersal ability (Poulson 1963; Poulson and White 1969; Culver et al. 1995; Culver and Pipan 2009, 2014; Venarsky et al. 2012, 2023). Consequently, population rescue is slow, which can lead to increased population instability from catastrophic or stochastic events (Mammola et al. 2019). Finally, subterranean species often exhibit low tolerance for perturbations in abiotic factors, as even small shifts in environmental conditions can have dramatic effects on populations (Novak et al. 2014; Raschmanová et al. 2018).

In their warning on the global conservation and importance of subterranean fauna, Mammola et al. (2019) proposed several measures to aid in the preservation of subterranean fauna, including addressing significant knowledge gaps that impede conservation of subterranean biodiversity. In particular, Mammola and colleagues identified the need for renewed efforts for conservation assessments of subterranean biodiversity using the International Union for Conservation of Nature (IUCN) Red List criteria. Very few subterranean species (estimated 850 taxa) have been assessed under IUCN Red List criteria globally (Mammola et al. 2019), with clear biases toward particular taxonomic groups (i.e., bats, salamanders, fishes, and crayfishes) and geographic regions (Niemiller et al. 2018), and subjectivity in the application of criteria for assessing the broad taxonomic diversity of subterranean taxa (Mammola et al. 2019). In addition to the IUCN Red List, conservation and threat assessments of subterranean taxa in the United States and Canada have been conducted using NatureServe criteria. NatureServe maintains biodiversity data for over 95,000 species in the United States and Canada that can be accessed through a web-based product, NatureServe Explorer (http://explorer.natureserve.org) (as of 31 August 2024). Using NatureServe, Hutchins (2018) assessed the conservation status of 69 described groundwater-obligate (i.e., stygobiotic) invertebrate species from Texas, with 55% of species ranked as critically imperiled or imperiled. While 88% of > 1,250 troglobiotic and stygobiotic taxa in the United

States and Canada had been evaluated, with the exception of Hutchins (2018), assessments for most species had not been reviewed or reassessed in > 10 years (Niemiller et al. 2018).

Because of these clear knowledge gaps, we leveraged the NatureServe and IUCN databases to expand upon the work of Hutchins (2018) and Niemiller et al. (2018) to more comprehensively summarize the conservation status (i.e., extinction risk) and threats of troglobiotic and stygobiotic species currently described in the United States and Canada, which now includes more than 1,400 species (Niemiller et al. 2019). We identify trends and gaps with respect to taxonomic coverage, and geography, as well as state/province and federal protection. In addition, we highlight limitations in approaches for assessing, including, or omitting subterranean species from the IUCN Red List, NatureServe's list of at-risk species, and federal and state/provincial lists of protected species. Finally, we offer recommendations to improve our ability to assess the conservation status of subterranean taxa to better inform conservation policies and actions for this unique but highly vulnerable biodiversity.

Methods

Compiling the species list of subterranean taxa

We began with the cave- and subterranean-obligate species in the Niemiller et al. (2019) review of cave biodiversity of the United States and Canada. This list of 1,353 species is the most comprehensive listing of troglobionts and stygobionts for this region. Several classifications of cave-associated organisms have been proposed. Herein we follow the definitions by Barr (1968) with later clarifications from Sket (2008) and Culver and Pipan (2009) to indicate species found in terrestrial (troglo-) versus aquatic (stygo-) subterranean habitats. We define a troglobiont/stygobiont (synonym: troglobite/stygobite) as a species obligately bound to subterranean habitats (including caves) at all life stages, which exhibits at least some morphological, physiological, and behavioral adaptations for living in subterranean habitats, and has few to no occurrence records from surface habitats (e.g., there may be a record suggestive of being washed out of a cave spring but no evidence of maintaining a population in a surface habitat).

Our updated species list included newly described species since publication of Niemiller et al. (2019), as well as a few species that were not included in Niemiller et al.'s (2019) species list but herein deemed to be a troglobiont or stygobiont after reviewing new information. In total, our species list includes 1,460 described species (Appendix S1). For this review, we did not include subspecies or the numerous undescribed taxa that have been referenced in the literature.

In a few cases, the scientific name for a species on our species list did not match the species name in the NatureServe or IUCN databases. This typically was due to taxonomic revision that was not reflected in NatureServe or in the Niemiller et al. (2019) species list. To maximize the information we could gather from both databases, we searched for synonyms in the NatureServe or IUCN databases. Additionally, geographic location data for some taxa were missing from NatureServe, and, therefore, we used available reference literature (often the published species description) or occurrence records maintained in the Cave Bio Database in the Cave Bio Lab at The University of Alabama in Huntsville to determine species location to the best of our ability.

NatureServe conservation assessments

NatureServe global conservation status ranks are based on a one to five scale, from most to least at risk of extinction: G1 (Critically Imperiled), G2 (Imperiled), G3 (Vulnerable), G4 (Apparently Secure), and G5 (Secure). Species can also be ranked H (Possibly Extinct), X (Presumed Extinct), NR (Unranked), or U (Unrankable; Faber-Langendoen et al. 2012). Some species on our species list were not present in NatureServe and thus did not receive a ranking. Conservation ranks are based on 10 primary factors grouped into three main categories: rarity, trends, and threats. Rarity factors include range extent of occurrence, area of occupancy, number of occurrences, number of occurrences with good viability or ecological integrity, population size, and environmental specificity. Trend factors include both short-term and long-term trends in population size, extent of occurrence, area of occupancy, number of occurrences, and viability or ecological integrity of occurrences. Threat factors include threat impact and intrinsic vulnerability to threats. Threat impacts are calculated using a rule-based approach that accounts for the number, scope (% of populations affected), and severity (% population decline) of individual threats.

We focused on the range-wide Global (G) ranks, so we report all conservation status ranks as one of G1–G5, GH, GX, GNR, or GU. In cases where a species rank incorporated uncertainty (e.g., G1G2), we used the Rounded rank, a single value that is easier to summarize (http://explorer.natureserve.org*)*. Range ranks that span adjacent ranks (e.g., G1G2 or G4G5) were rounded to the more imperiled rank (e.g., G1G2 was rounded to G1). Range ranks that span three ranks (e.g., G2G4) were rounded to the rank in the middle of the range (e.g., G2G4 was rounded to G3). Species not present in NatureServe were recorded as Not Assessed (na).

We developed a python script that queried the NatureServe database for each species on the species list. The script gathered information on common name, taxonomy, range extent, global status, federal status (if listed or proposed to be listed under the U.S. Endangered Species Act), regions (states or provinces) each species occurs, and any regional status rankings, if available. We imported the output from the python script into R for analysis of global, regional, and taxonomic patterns (Appendix S2).

We worked with troglobiont data collected from NatureServe on 31 January 2025. To place the NatureServe troglobiont data in context, we used the NatureServe Explorer (https://explorer.natureserve.org/search*)* to determine how many animal species were prese nt in the database and their global status rankings.

IUCN red list conservation assessments

We used the IUCN Red List of Threatened Species (https://www.iucnredlist.org/*)* to collate similar information as done with NatureServe on the conservation status of each species on our species list as of 31 January 2025. For each species, we compiled the following information: IUCN ranking, year species was last assessed, and available information about the species' population (i.e., whether the population was severely fragmented, the number of mature individuals*)*. Seven IUCN Red List categories are recognized on a continuum of increasing extinction risk (IUCN 2012): Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CE), Extinct in the Wild (EW), and

Extinct (EX). Two additional categories are also recognized: Data Deficient (DD) in which a species has been evaluated but insufficient data are available to make a determination on conservation rank and Not Evaluated (NE) in which a species has yet to be evaluated. Critically Endangered, Endangered, and Vulnerable are considered Threatened categories. Species are classified as Threatened provided they meet one of five criteria (IUCN 2012): (1) past, present, or projected reduction in population size over three generations; (2) small geographic range in combination with fragmentation, population decline or fluctuations; (3) small population size in combination with decline or fluctuations; (4) very small population or very restricted distribution; and (5) a quantitative analysis of extinction risk. Subcriteria are detailed in IUCN (2012).

Geographic regions

Using the compiled information from NatureServe and IUCN data, we summarized the number of troglobiont species that occur in each state or territory in the United States and provinces of Canada. Additionally, we used this occurrence information to assign each species to biogeographic karst regions defined and implement in studies previously (e.g., Culver et al. 2003; Hobbs 2012; Niemiller et al. 2019): Appalachians (APP), Black Hills (BLH), Driftless Area (DLA), Edwards Plateau and Balcones Escarpment (EPB), Florida Lime Sinks (FLS), Guadalupes (GUA), Hawai‘i (HAW), Interior Low Plateau (ILP), Mother Lode (MOL), Ozarks (OZK), and other locations outside major defined karst regions (OTH). We broadened the scope of a few of these karst regions in this study more than previously considered (see Fig. 1A). For example, the Florida Lime Sinks has been delimited in the past to include only northern Florida and into the panhandle region, but we expanded this region given the vast expanse of karst in peninsular Florida.

Federal, State, and provincial protection status

We reviewed the federal protection status of each species as of 31 January 2025 by querying the U.S. Fish & Wildlife Service Environmental Conservation Online System (ECOS; https://ecos.fws.gov/ecp0/reports/ad-hoc-species-report-input*)* for listed species. For Canadian species, we searched the Canadian Species At Risk Act list; https://species-registry.canada.ca*)* and the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; https://cosewic.ca*)* candidate lists as of 31 January 2025.

To determine the level of statewide protection afforded to each troglobiont in the U.S., we searched available state lists of protected species and Species of Greatest Conservation Need (SGCN) lists and compiled information on the level of protection. States differ in how species are listed and categorized, but many states use designations that are analogous to federal designations (i.e., State Endangered or State Threatened) and/or designate Species of Greatest Conservation Need/Concern (i.e., species that are currently listed or for which future listing may be warranted and which require additional research, conservation, or management). States may also assign a tier or priority ranking (i.e., in Idaho Tier 1 = Highest priority species with critical conservation needs, Tier 2 = secondary priority species with long-term vulnerability, Tier 3 = species outside Tier 1 or 2 but have conservation needs).

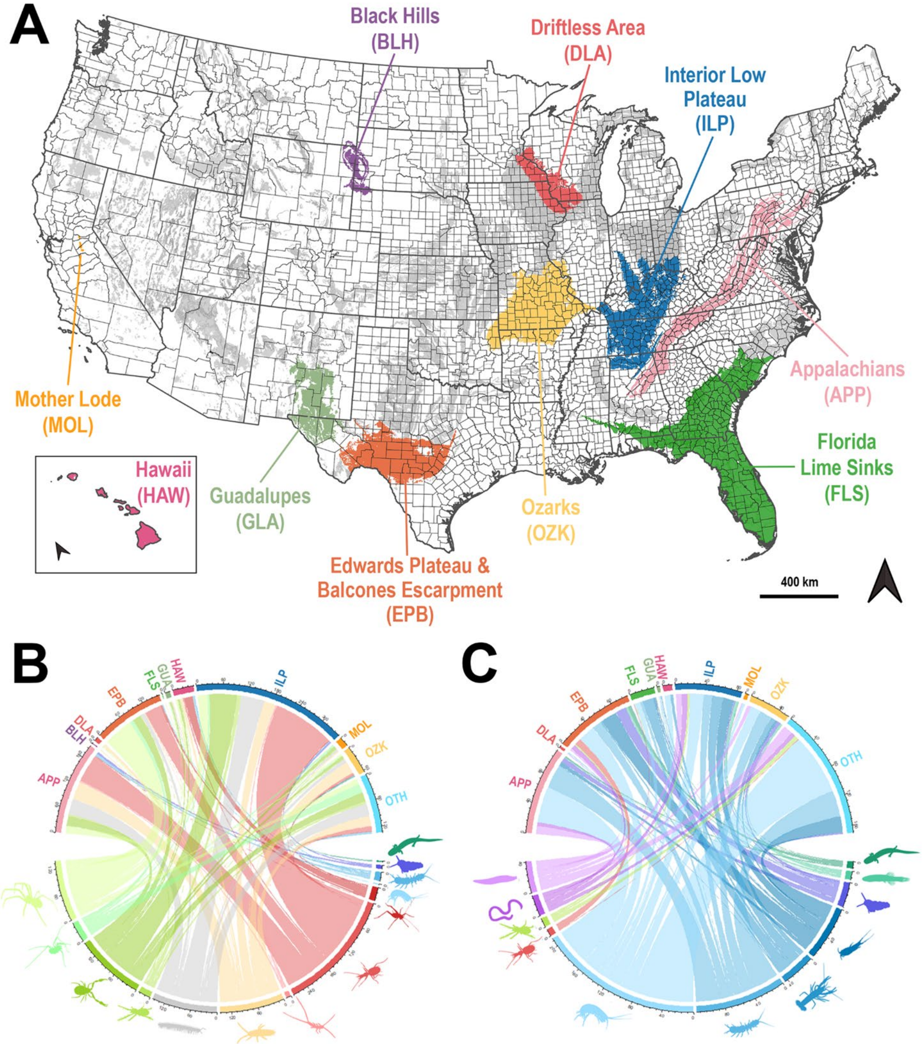

Fig. 1 Map of the United States (excluding Alaska) showing the locations of 10 primary cave biogeographic karst regions (**A**), including the Appalachians (APP), Black Hills (BLH), Driftless Area (DLA), Edwards Plateau & Balcones Escarpment (EPB), Florida Lime Sinks (FLS), Guadalupes (GUA), Hawaii (HAW), Interior Low Plateau (ILP), Mother Lode (MOL), and Ozarks (OZK). Subterranean biodiversity also occurs in other regions (OTH) outside of these biogeographic karst regions. Additional areas with karst or the potential for karst and pseudokarst development are shown in gray based on Weary and Doctor (2014). Chord diagrams show species richness by karst region for (**B**) major troglobiotic (terrestrial) taxonomic groups (L to R: spiders, harvestmen, pseudoscorpions, mites and other arachnids, millipedes and centipedes, springtails, diplurans, beetles, other insects, amphipods, isopods, snails, and salamanders) and (**C**) stygobiotic (aquatic) taxonomic groups (L to R: flatworms and allies, annelids and other worms, mites and other arachnids, beetles, amphipods, isopods, decapods, other crustaceans, snails, fishes, and salamanders). Colors for each karst region follow the map above

Similarly, for troglobiont species (N= 10) found in Canada, we searched provincial listings of species at risk in Alberta, British Columbia, Ontario, and Quebec (the four Canadian provinces with reported troglobionts and stygobionts).

Finally, we reviewed the most recent State Wildlife Action Plans (SWAP) for each U.S. state and territory where troglobiont species occur (N= 44). In 56 U.S. states and territories, SWAPs were first published in 2005 and are revised every 10 years, with the goal of investing federal funds to conserve fish and wildlife, prevent the need for endangered species listing, and restore already threatened or endangered species (U.S. Fish and Wildlife Service 2020). We assessed whether each state or territory's SWAP specifically mentioned protection of subterranean habitat and whether information about conservation threats and/or management suggestions were specifically included. We did not include states that mentioned caves as important only for bat habitat.

Threats

In addition to conservation status ranks, we also compiled a list of threats reported for individual troglobionts and stygobionts for NatureServe and IUCN Red List assessments. Major threats to subterranean fauna, derived from Hutchins (2018), Mammola et al. (2019, 2022), and Nanni et al. (2023), included habitat loss, habitat degradation, groundwater exploitation, pollution, invasive species and emergent diseases, native species interactions, overcollection, climate change and extreme weather events (i.e., severe flooding and droughts), and recreational activities. Habitat loss includes direct destruction of subterranean habitats resulting from development, mining operations, and water impoundments (dams), whereas habitat degradation includes negative impacts associated with urbanization, agricultural, and industrial activities, such as sedimentation and increased nutrient inputs. Likewise, pollution and contamination are associated with surface land use changes, including urbanization, agricultural, and industrial activities.

Statistical analyses and data visualization

Statistical analyses and visualizations of the collated datasets were conducted in R (R Core Team 2024). We used the *circulize* package (Gu et al. 2014) to generate chord diagrams depicting relationships between karst regions and species richness of 18 major taxonomic groups. Major taxonomic groups included flatworms and allies, annelids and other worms, snails, spiders, harvestmen, pseudoscorpions, mites and other arachnids, springtails, diplurans, millipedes and centipedes, beetles, other insects, amphipods, isopods, decapods, other crustaceans, fishes, and salamanders. We examined correlations between conservation ranks from IUCN Red List and NatureServe using a dataset of species assessed under both classification systems (N= 122). Species with NatureServe ranks of GNR or IUCN Red List ranks of DD were omitted. Data were coded such that 1 = least threatened (i.e., G5 or LC) and 6 = most threatened (i.e., GX or CR (PE) conservation status rank (Appendix S3) and analyzed using a Spearman rank correlation. We conducted Spearman rank correlation for this dataset and also for individual taxonomic groups and karst regions. We also calculated the ordinal rank difference (i.e., Δ in conservation rank) for each species by subtracting the ordinal NatureServe rank from the ordinal IUCN Red List rank, whereby positive values denote a more conservative NatureServe rank and negative values denote a more conservative IUCN Red List rank. We compared possible variation in the Δ in conservation rank among major taxonomic groups and karst regions using non-parametric Kruskal-Wallis tests. Following Goodenough (2012), we defined mismatches in conservation status ranks when NatureServe and IUCN Red List ranks (Appendix S3) were not equivalent, with serious mismatches defined as a rank difference of two or more (e.g., G1 by NatureServe but VU by IUCN Red List) and major mismatches as an at risk ranking in one classification system but not the other (e.g., G2 by NatureServe but LC by IUCN Red List). We used chi-square analyses of observed versus expected frequencies of total, serious, and major mismatches across taxonomic groups and karst regions to assess possible taxonomic and geographic biases.

Results

Troglobiont and stygobiont diversity

Our species list of described troglobionts and stygobionts in the United States and Canada includes 1,460 species: 930 troglobionts and 530 stygobionts (Fig. 1B, C; Appendix S1). This diversity represents seven phyla, 19 classes, 56 orders, 141 families, and 328 genera. Terrestrial invertebrate diversity is dominated by arthropods (922 species), particularly beetles (Order Coleoptera; 274 species), pseudoscorpions (Order Pseudoscorpiones; 153 species), millipedes (Class Diplopoda; 140 species), and spiders (Order Araneae; 121 species). Aquatic invertebrate diversity is dominated by crustaceans (397 species), particularly amphipods (Order Amphipoda; 190 species), isopods (Order Isopoda; 99 species), and decapods (Order Decapoda; 44 species). Vertebrate diversity includes ray-finned fishes (Class Actinopterygii; 10 species), and salamanders (Order Caudata; 12 species).

NatureServe conservation status ranks

Of the 1,460 troglobiotic and stygobiotic species in the United States and Canada, 83.0% (N= 1,212) were included in the NatureServe database (Appendix S1). Of these 1,212 species, 75 were ranked GNR (N= 74) or GU (N= 1), while 1,137 species had Global Status rankings of G1–G5, GH, or GX (Appendix S1). Overall, 77.9% of all cave-obligate species were ranked with an informative global ranking in NatureServe: three were ranked GX, nine were ranked GH, 740 were ranked G1, 176 were ranked G2, and 136 were ranked G3, placing 93.6% of species with informative ranks in one of NatureServe's at-risk categories. The conservation status ranks of only 153 species have been assessed/reviewed within the last 10 years (since 2015), with 696 species (57.4% of species in the NatureServe database) last assessed/reviewed prior to 2004. The high prevalence of at-risk cave-obligate taxa contrasts with non-troglobiotic animals with informative NatureServe rankings, where only 31.3% (5,585 of 17,859 species) are considered at-risk. Troglobionts and stygobionts with G1 status are particularly prevalent: they comprise only 6.0% of all animals with NatureServe rankings, but represent 29.9% of animals with G1 rankings.

All taxonomic groups exhibit high levels of extinction threat (Fig. 2A). Arachnids exhibit the highest threat levels of any taxonomic group, with 85.4% of species ranked G1 (238 of

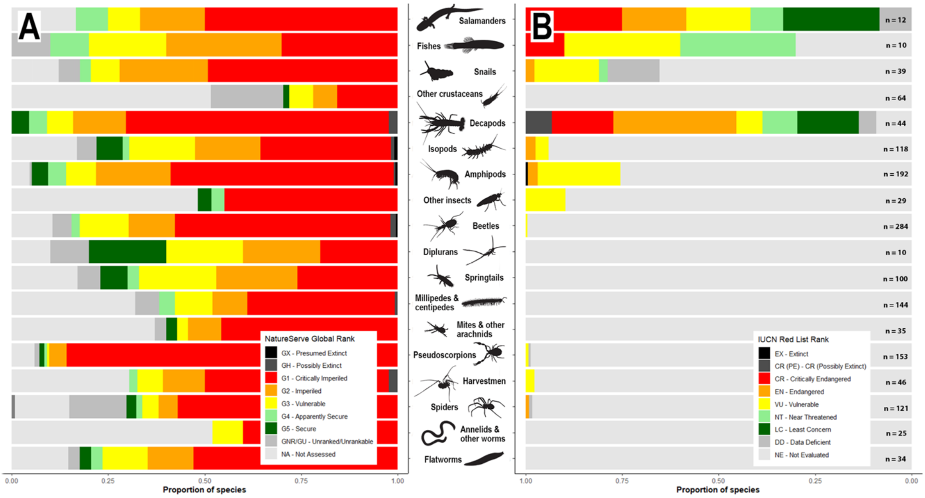

Fig. 2 NatureServe conservation status ranks (**A**) and IUCN Red List conservation ranks (**B**) for major taxonomic groups of troglobionts and stygobionts in the U.S. and Canada. Species richness for each taxonomic group is shown in B

281 assessed species) and 96.4% ranked at an elevated risk of extinction (GX, GH, or G1–G3). Other taxonomic groups with a large proportion of assessed species at an elevated risk of extinction include beetles (97.5%), snails (96.9%), millipedes and centipedes (93.3%), flatworms (92.3%), decapods (90.9%), and amphipods (90.7%).

IUCN conservation status ranks

Just 9.3% (135 of 1,460 species) of cave-obligate species in the U.S. and Canada have been assessed on the IUCN Red List (Appendix S1): 10 were assessed as Least Concern, nine as Near Threatened, 65 as Vulnerable, 26 as Endangered, 11 as Critically Endangered, three as Critically Endangered Possibly Extinct, one as Extinct, and 10 as Data Deficient (Fig. 2B). Moreover, 23.0% of stygobionts (121 of 527 species) and just 1.5% of troglobionts (14 of 930 species) have been assessed. Of the species assessed under IUCN Red List criteria, 76.3% are arthropods, 14.1% are vertebrates (salamanders and fishes), and 9.6% are gastropods (Fig. 2B). The conservation status ranks of only 13 species have been assessed/reviewed within the last 10 years (since 2015), with 48.9% (66 species) last assessed/reviewed in 1996. Fishes and salamanders were the only taxonomic groups with species assessed/reviewed in the last 10 years (Appendix S1).

Threats

At least one threat was reported for 254 species across both NatureServe and IUCN Red List assessments, which accounts for just 20.1% (N= 244) of species with a NatureServe conservation rank and 48.9% (N= 66) of species with an IUCN Red List conservation rank. Threat information was lacking for most species of nearly all major taxonomic groups (Fig. 3), except for decapods, fishes, and salamanders. The most frequently reported threats across all

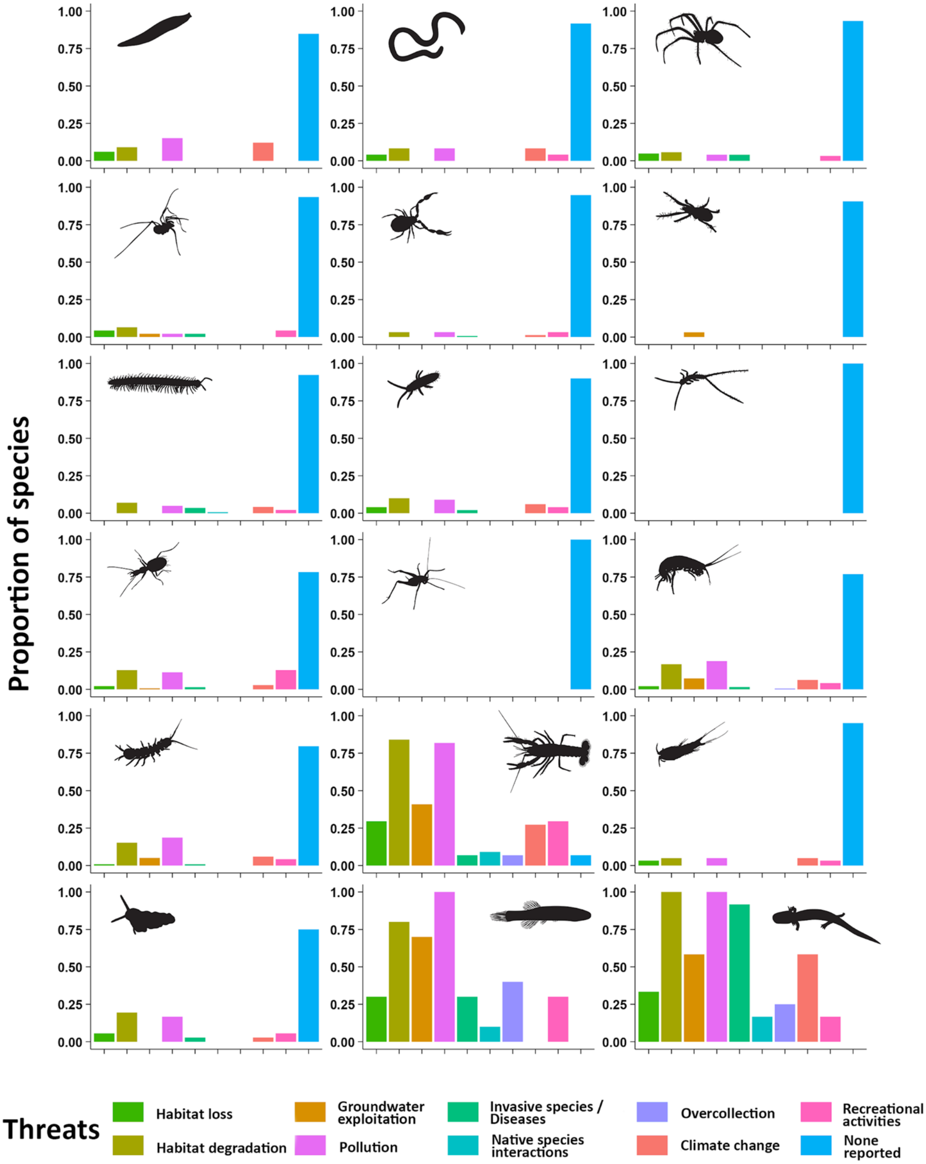

Fig. 3 Summary of threats reported for NatureServe and IUCN Red List conservation assessments combined for major taxonomic groups of troglobionts and stygobionts in the U.S. and Canada. Taxonomic groups include (in order from upper left to lower right) flatworms and allies, annelids and other worms, spiders, harvestmen, pseudoscorpions, mites and other arachnids, millipedes and centipedes, springtails, diplurans, beetles, other insects, amphipods, isopods, decapods, other crustaceans, snails, fishes, and salamanders

taxonomic groups were habitat degradation (*N*= 193), pollution/contamination (*N*= 191), recreational activities (*N*= 90), climate change (*N*= 70), and groundwater exploitation (*N*= 56).

Federal, state, and provincial protected status

Although 1,064 troglobionts and stygobionts are assigned an at-risk conservation status rank by NatureServe and 116 species by IUCN, comparatively few species have been or are currently listed under the U.S. Endangered Species Act. At present, just 36 species are listed or proposed for listing as Endangered and five as Threatened (Table 1). Twenty-three species are under review for listing currently, while 324 species have been reviewed previously and are not listed. Species status assessments (SSA) have been completed for 30 troglobionts and stygobionts since 2017, including one harvestman, nine beetles, two isopods, three crayfishes, six amphipods, one aquatic snail, five salamanders, and three fishes (Table 2). Vertebrates (fishes and salamanders) and decapods (crayfishes and shrimp) are overrepresented, accounting for 39.5% (15 of 38) of species with any federal status and 36.7% (11 of 30) assessed under the SSA framework, despite accounting for just 4.6% of all troglobionts and stygobionts.

None of the troglobionts and stygobionts (*N*= 10) in Canada are listed under Canada's Species At Risk Act, and only one species is on the COSEWIC Candidate List (Group 2: Mid-priority candidate; *Stygobromus quatsinensis*). However, all four Canadian *Stygobromus* species are listed as "at-risk" species in the COSEWIC List of Prioritized Crustaceans and Related Groups at Risk in Canada, and both spider species were recognized by the Canadian Endangered Species Conservation Council as imperiled and vulnerable (*Porrhomma cavernicola* as critically imperiled and *Bathyphantes weyeri* as imperiled; Canadian Endangered Species Conservation Council 2022).

Of the 43 U.S. states and one district (Washington D.C.) with described troglobiotic taxa, 28 (63.6%) afford some level of state protection or conservation status to troglobionts. Nearly 48.5% of troglobiont species (701 out of 1445) were listed as state endangered, state threatened, or as SGCN (Appendix S1): 76 species were listed as state endangered, 17 as state threatened, 4 as state protected (only in MO and AL), and 148 species listed as Species of Greatest Conservation Need: Priority/Tier 1 species. Additionally, 193 species are classified as Priority/Tier 2 species, 9 as Priority/Tier 3 species, and 338 as State Rare, Watch list, or other Species of Greatest Need designation (Appendix S1). A few species occur in multiple states and are listed differently in each. Further, of the ten troglobionts found in the four Canadian provinces, only one (*Stygobromus quatsinensis*) was provincially listed in British Columbia (BC: Provincial List Blue, Species of Concern).

Thirty of the 44 (~ 68.2%) states/districts with troglobiotic species specifically include information about subterranean habitats in their respective SWAPs. In contrast, the other 14 states (31.8%) with troglobiotic species do not mention cave or subterranean habitats other than their presence or that bats and/or bears can inhabit caves.

Geographic patterns

Troglobionts and stygobionts are concentrated in relatively few states. Only Texas has more than 250 known troglobionts and stygobionts (*N*= 274), with Tennessee (*N*= 215), Virginia

Table 1 Troglobionts and stygobionts listed or proposed for listing as endangered or threatened under the U.S. Endangered Species Act. Karst regions include the Appalachians (APP), Edwards Plateau and Balcones Escarpment (EPB), Florida Lime Sinks (FLS), Hawaiʻi (HAW), Interior Low Plateau (ILP), Ozarks (OZK), and other areas outside major biogeographic karst regions (OTH)

Species	Common Name	Year Listed	Distribution	Karst Region
Endangered				
Cicurina baronia	Robber Baron Cave Meshweaver	2000	TX	EPB
Cicurina madla	Madla Cave Meshweaver	2000	TX	EPB
Cicurina vespera	Government Canyon Bat Cave Meshweaver	2000	TX	EPB
Tayshaneta microps	Government Canyon Bat Cave Spider	2000	TX	EPB
Tayshaneta myopica	Tooth Cave Spider	1988	TX	EPB
Adelocosa anops	Kauai Cave Wolf Spider	2000	HI	HAW
Texella cokendolpheri	Cokendolpher Cave Harvestman	2000	TX	EPB
Texella reyesi	Bone Cave Harvestman	1988	TX	EPB
Tartarocreagris texana	Tooth Cave Pseudoscorpion	1988	TX	EPB
Rhadine exilis	a ground beetle	2000	TX	EPB
Rhadine infernalis	a ground beetle	2000	TX	EPB
Rhadine persephone	Tooth Cave Ground Beetle	1988	TX	EPB
Stygoparnus comalensis	Comal Springs Dryopid Beetle	1997	TX	EPB
Batrisodes texanus	Inner Space Cavern Mold Beetle	1988	TX	EPB
Batrisodes venyivi	Helotes Mold Beetle	2000	TX	EPB
Texamaurops reddelli	Kretschmarr Cave Mold Beetle	1988	TX	EPB
Stygobromus hayi	Hay's Spring Amphipod	1982	DC	OTH
Stygobromus pecki	Peck's Cave Amphipod	1997	TX	EPB
Gammarus acherondytes	Illinois Cave Amphipod	1998	IL	OZK
Spelaeorchestia koloana	Kauai Cave Amphipod	2000	HI	HAW
Palaemonias alabamae	Alabama Cave Shrimp	1989	AL	ILP
Palaemonias ganteri	Mammoth Cave Shrimp	1983	KY	ILP
Procaris hawaiana	Hawaiian Anchialine Pool Shrimp	2016	HI	HAW
Vetericaris chaceorum	Lua o Palahemo Anchialine Pool Shrimp	2013	HI	HAW
Cambarus aculabrum	Benton County Cave Crayfish	1993	AR, MO	OZK
Cambarus zophonastes	Hell Creek Cave Crayfish	1987	AR	OZK
Lirceus usdagalun	Lee County Cave Isopod	1992	VA	APP
Antrobia culveri	Tumbling Creek Cavesnail	2002	MO	OZK
Speoplatyrhinus poulsoni	Alabama Cavefish	1987	AL	ILP
Cottus specus	Grotto Sculpin	2013	MO	OZK
Prietella phreatophila	Mexican Blindcat	1970	TX	EPB
*Satan eurystomus**	Widemouth Blindcat	2023	TX	EPB
*Trogloglanis pattersoni**	Toothless Blindcat	2023	TX	EPB
Eurycea rathbuni	Texas Blind Salamander	1967	TX	EPB
Eurycea waterlooensis	Austin Blind Salamander	2013	TX	EPB
*Gyrinophilus subterraneus**	West Virginia Spring Salamander	2024	WV	APP
Threatened				
Palaemonetes cummingi	Squirrel Chimney Cave Shrimp	1990	FL	FLS
*Procambarus milleri**	Miami Cave Crayfish	2023	FL	FLS
Antrolana lira	Madison Cave Isopod	1982	VA, WV	APP

Table 1 (continued)

Species	Common Name	Year Listed	Distribution	Karst Region
Troglichthys rosae	Ozark Cavefish	1984	AR, KS, MO, OK	OZK
Eurycea tonkawae	Jollyville Plateau Salamander	2013	TX	EPB

* - proposed to be listed

Table 2 Troglobionts and stygobionts that have been assessed under the species status assessment framework by U.S. Fish & Wildlife Service. Karst regions include the Appalachians (APP), Edwards Plateau and Balcones Escarpment (EPB), Florida Lime Sinks (FLS), Interior Low Plateau (ILP), Ozarks (OZK), and other areas outside major biogeographic karst regions (OTH)

Species	Common Name	Year Assessed	Distribution	Karst Region
Texella reyesi	Bone Cave Harvestman	2022	TX	EPB
Lirceolus smithii	Texas Troglobitic Water Slater	2023	TX	EPB
Lirceus culveri	Rye Cove Isopod	2022	VA	APP
Procambarus horsti	Big Blue Springs Cave Crayfish	2017	FL	FLS
Procambarus milleri	Miami Cave Crayfish	2023	FL	FLS
Procambarus orcinus	Woodville Karst Cave Crayfish	2017	FL	FLS
Stygobromus cooperi	Cooper's Cave Amphipod	2023	VA	APP
Stygobromus indentatus	Tidewater Amphipod	2020	MD, VA	OTH
Stygobromus morrisoni	Morrison's Cave Amphipod	2023	VA	APP
Stygobromus parvus	Minute Cave Amphipod	2023	VA	APP
Stygobromus pecki	Peck's Cave Amphipod	2024	TX	EPB
Stygobromus phreaticus	Northern Virginia Well Amphipod	2019	VA	OTH
Pseudanophthalmus cordicollis	Little Kennedy Cave Beetle	2023	VA	APP
Pseudanophthalmus holsingeri	Holsinger's Cave Beetle	2023	VA	APP
Pseudanophthalmus hubbardi	Hubbard's Cave Beetle	2023	VA	APP
Pseudanophthalmus hubrichti	Hubricht's Cave Beetle	2023	VA	APP
Pseudanophthalmus limicola	Maddens Cave Beetle	2023	VA	APP
Pseudanophthalmus parvicollis	Hupps Hill Cave Beetle	2023	VA	APP
Pseudanophthalmus praetermissus	Overlooked Cave Beetle	2023	VA	APP
Pseudanophthalmus sericus	Silken Cave Beetle	2023	VA	APP
Stygoparnus comalensis	Comal Springs Dryopid Beetle	2024	TX	EPB
Phreatodrobia imitata	Mimic Cavesnail	2022	TX	EPB
Eurycea rathbuni	Texas Blind Salamander	2024	TX	EPB
Eurycea robusta	Blanco Blind Salamander	2021	TX	EPB
Gyrinophilus gulolineatus	Berry Cave Salamander	2019	TN	APP
Gyrinophilus palleucus	Tennessee Cave Salamander	2023	AL, GA, TN	ILP
Gyrinophilus subterraneus	West Virginia Spring Salamander	2023	WV	APP
Cottus specus	Grotto Sculpin	2023	MO	OZK
Satan eurystomus	Widemouth Blindcat	2022	TX	EPB
Trogloglanis pattersoni	Toothless Blindcat	2022	TX	EPB

(*N*= 197), Alabama (*N*= 170), and Kentucky (*N*= 136) as the only other U.S. states with more than 100 species (Table 2). With respect to biogeographic karst regions, most species occur in the Interior Low Plateau (*N*= 438), Appalachians (*N*= 325), Edwards Plateau and Balcones Escarpment (*N*= 255), and Ozarks (*N*= 118) karst regions (Figs. 1 and 4). All other major karst regions have fewer than 100 species. Interestingly, 20.8% (*N*= 303) of the troglobionts and stygobionts in the U.S. and Canada occur outside of the 10 major karst regions. Most species are endemic to a single biogeographic karst region (*N*= 1,110). However, 111 species occur in more than one region (including outside of the 10 major karst regions), with 51 species occurring in both the Appalachians and Interior Low Plateau karst regions.

Most species that have been assessed with informative NatureServe conservation ranks are at an elevated risk of extinction in the Black Hills (*N*= 2; 100% of species), Florida Lime Sinks (*N*= 32; 97.0%), Guadalupe Mountains (*N*= 12; 80.0%), Hawaiʻi (*N*= 45; 75.0%), and Mother Lode (*N*= 24; 88.9%) (Fig. 4A). Most troglobionts and stygobionts assessed under IUCN Red List criteria are found in the Edwards Plateau and Balcones Escarpment karst region of Texas (*N*= 26), with 92.3% (*N*= 24) with an at-risk conservation rank (Fig. 4B). The Florida Lime Sinks is the only karst region with more than 50% of species assessed under IUCN Red List criteria (*N*= 18), all but two of which were assessed at an elevated risk of extinction. Florida (*N*= 18), Missouri (*N*= 17), Alabama (*N*= 16), and Arkansas (*N*= 14) are the only other U.S. states with > 10 species assessed under IUCN Red List criteria. No species that occur in Canada have been assessed under IUCN Red List criteria to date.

Geographic biases are evident in the list of taxa assessed under the SSA framework and with federal status. For example, 52.6% (20 of 38) federally listed species are found in the Edwards Plateau and Balcones Escarpment karst region of Texas, whereas only three species occur in the Interior Low Plateau despite it possessing the greatest troglobiotic species richness (Table 1). In contrast, nine of the 30 (30.0%) species assessed under the SSA framework occur in the Edwards Plateau and Balcones Escarpment karst region (Table 2), and 14 (46.7%) occur in the Appalachians karst region.

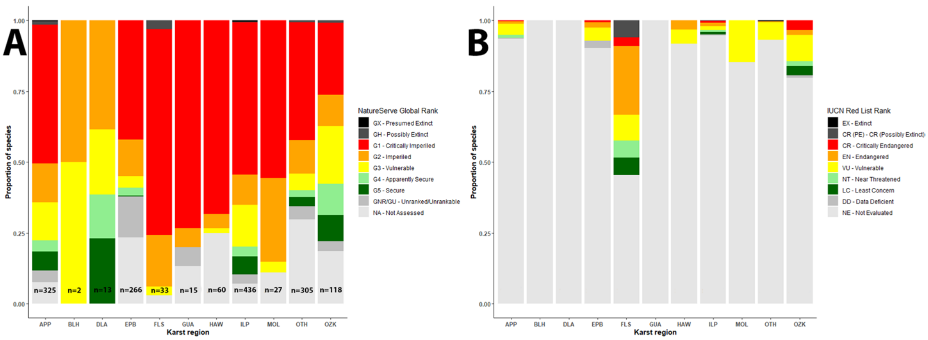

Fig. 4 NatureServe conservation status ranks (**A**) and IUCN Red List conservation ranks (**B**) of troglobionts and stygobionts for major karst regions in the U.S. and Canada. Species richness for each karst region is shown in A

Correlation between conservation status classification systems

There was a positive correlation between IUCN Red List and NatureServe conservation ranks for species (N= 122) that have been assessed under both classification systems (r_s(120) =0.44, P< 0.001), although this relationship was not particularly strong (Fig. 5A; Table 3). Among taxonomic groups, correlation coefficients were greatest for fishes, salamanders, and decapods and low and not significant for amphipods, isopods, and snails (Table 3). Among karst regions, correlation coefficients were greatest for the Interior Low Plateau, Florida Lime Sinks, and Ozarks, and low and not significant for the Appalachians, Edwards Plateau and Balcones Escarpment, and Other regions (Table 3). There were mismatches between IUCN Red List and NatureServe conservation ranks for 90 species, representing 73.8% of species with informative conservation ranks for both classification systems. Of the 90 mismatches, there were serious mismatches for 45 species (36.9%), and there were 14 (11.5%) major mismatches in which species were ranked in a threatened category for one classification system but in a non-threatened category in the other classification system. Just 26.3% of the 19 species classified as non-threatened by one classification system were also classified as non-threatened in the other classification system, while 88.0% of the 117 species classified as threatened by one system were also classified as threatened in the other classification system. Total, serious, and major mismatch frequencies did not show evidence of taxonomic bias (total mismatches: χ^2= 3.863, *d.f.*=10, P= 0.953; serious mismatches: χ^2= 12.966, *d.f.*=10, P= 0.226; major mismatches: χ^2= 9.285, *d.f.*=10, P= 0.505) or geographic bias (total mismatches: χ^2= 2.731, *d.f.*=7, P= 0.909; serious mismatches: χ^2= 9.067, *d.f.*=7, P= 0.248; major mismatches: χ^2= 6.586, *d.f.*=7, P= 0.473). NatureServe conservation ranks were one rank greater in threat level on average (mean ± 1 SD: 1.1 ± 1.0) but did not vary by taxonomic group (χ^2= 15.992, *d.f.*=10, P= 0.100; Fig. 5B) or karst region (χ^2= 12.488, *d.f.*=7, P= 0.086; Fig. 5C).

Possibly extinct species

Eighteen species have been assessed or hypothesized to be possibly extinct by recent authors (Table 4), including one harvestman, one millipede, six beetles, three amphipods, two isopods, one shrimp, three crayfishes, and one salamander. Two of these species (*Cambarus sheltae* and *C. delicatus*) were rediscovered recently (Table 4).

Discussion

Conservation status assessments are useful tools for prioritizing conservation and management efforts in the face of finite and often limited resources (de Grammont and Cuaron 2006; Rodrigues et al. 2006; Mace et al. 2008). The two most widely adopted approaches in North America—the IUCN Red List of Threatened Species, which is also a widely employed source for the conservation status of species globally (Rodriguez 2008; Hochkirch et al. 2021), and NatureServe—incorporate information about rarity, distribution, population size and trends, and threats to generate a conservation status rank that can be applied across diverse taxa and across different geographic regions (de Grammont and Curaron 2006; Schipper et al. 2008; Dietz et al. 2020). When conducted with a consistent methodology and

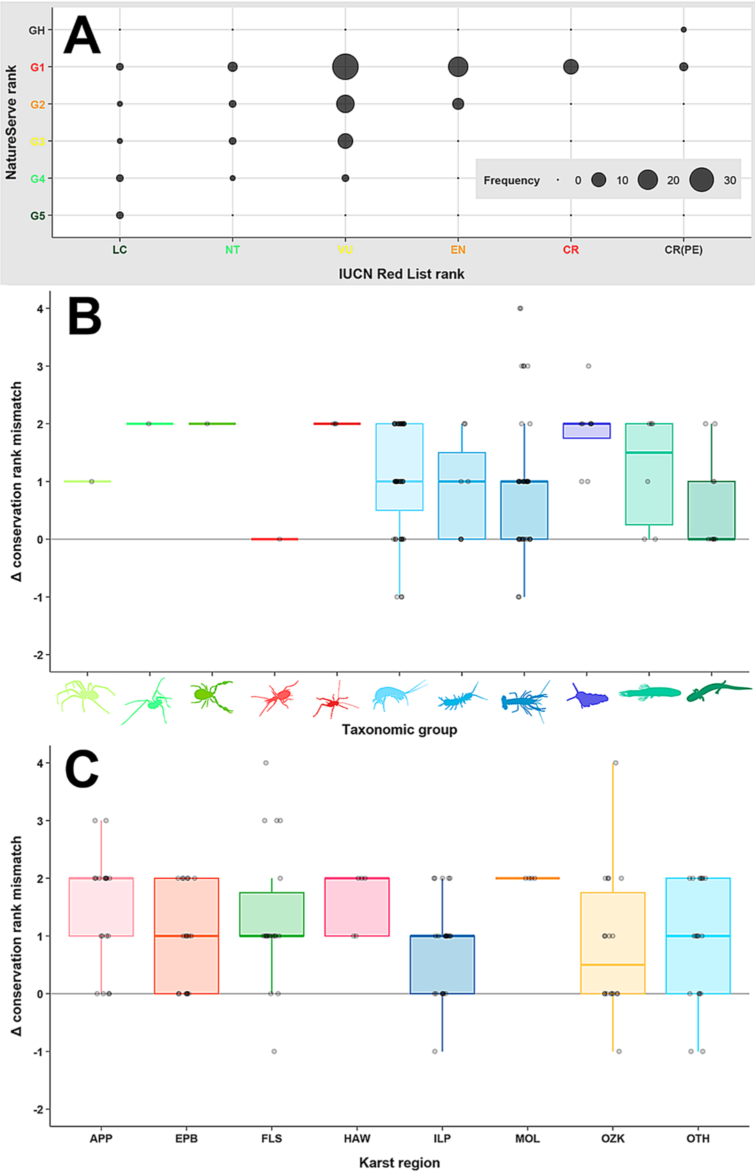

Fig. 5 Correlation between NatureServe and IUCN Red List conservation status ranks for 122 troglobionts and stygobionts with informative ranks for both classification systems. The diameter of the circle represents the frequency of species (**A**). Boxplots of the ordinal rank difference between NatureServe and IUCN Red List conservation status ranks (Δ conservation rank mismatch) by taxonomic group (**B**) and karst region (**C**). Positive values indicate NatureServe rank is more conservative (i.e., increased risk of extinction) compared to the IUCN Red List rank, while negative values indicate IUCN Red List rank is more conservative than the NatureServe rank for a species. Taxonomic groups in B from L to R are spiders, harvestmen, pseudoscorpions, beetles, other insects, amphipods, isopods, decapods, snails, fishes, and salamanders. Karst regions in C from L to R are Appalachians (APP), Edwards Plateau and Balcones Escarpment (EPB), Florida Lime Sinks (FLS), Hawai'i (HAW), Interior Low Plateau (ILP), Mother Lode (MOL), Ozarks (OZK), and other areas outside major biogeographic karst regions (OTH)

Table 3 Correlations and mismatches between IUCN red list and natureserve conservation status ranks for 122 species by taxonomic groups and major biogeographic karst regions. Significant correlations ($P < 0.05$) are highlighted in bold

Taxonomic group	Correlations			Mismatches		
	r_s	*N*	*P*	*N* (%)	Serious (%)	Major (%)
All	**0.44**	**102**	**< 0.001**	90	45	14
Spiders	na	1	na	1	0	0
Harvestmen	na	1	na	1	1	0
Pseudoscorpions	na	1	na	1	1	0
Beetles	na	1	na	0	0	0
Other insects	na	3	na	3	3	0
Amphipods	0.18	47	0.233	38	19	2
Isopods	0.32	7	0.481	4	2	0
Decapods	**0.61**	**38**	**< 0.001**	26	8	8
Snails	0.00	8	1.000	8	6	1
Fishes	**0.89**	**6**	**0.019**	4	3	2
Salamanders	**0.76**	**9**	**0.018**	4	2	1
Karst region						
Appalachians	−0.05	18	0.853	14	10	2
Edwards Plateau & Balcones Escarpment	0.16	18	0.525	11	6	0
Florida Lime Sinks	**0.56**	**18**	**0.016**	16	5	4
Hawaii	na	5	na	5	3	0
Interior Low Plateau	**0.87**	**23**	**< 0.001**	16	5	4
Mother Lode	na	4	na	4	4	0
Ozarks	**0.49**	**18**	**0.041**	10	5	3
Other regions	0.33	18	0.180	14	7	1

appropriate criteria, conservation status assessments can highlight distributional and other biodiversity knowledge shortfalls (i.e., gaps), identify deficiencies in protection efforts, and serve as an objective approach for designation of protected status and prioritization of conservation actions (e.g., Croxall et al. 2012; Hutchins 2018; Dietz et al. 2020). We compiled the most complete summary of the IUCN Red List and NatureServe conservation status, as well as state and federal protected status, for cave-obligate biodiversity of the United States and Canada. We identified several trends and gaps with respect to taxonomic coverage and geography, which we discuss in more detail herein. In addition, we highlight limitations of these assessment approaches as well as other factors that may influence conservation status rankings of subterranean biodiversity. Finally, we offer recommendations to improve our ability to assess the conservation status of subterranean taxa to better inform local to global conservation policies and actions.

IUCN Red List

While some taxonomic groups are well represented on the Red List, such as mammals, birds, and amphibians, several groups, particularly plants, fungi, and invertebrates are not. Invertebrates have attracted far less attention than vertebrates and have long been recognized as being underrepresented in IUCN status assessments globally (Cardoso et al. 2011, 2012; Collier et al. 2016; Braby 2018; Karam-Gemael et al. 2020). Thus, the lack of representation of U.S. and Canadian subterranean invertebrates, which account for 98.5% of

Table 4 Troglobionts And stygobionts of the U.S. And Canada hypothesized or assessed as possibly extinct in recent years

Species	Common Name	NatureServe rank	IUCN rank	Karst Region	Last Observed	Reference
Banksula californica	Alabaster Cave Harvestman	GH		OTH	1885?	NatureServe; Briggs (1974); Ubick and Briggs (2002)
Bactrurus cellulanus	Indiana University Groundwater Amphipod	GX		ILP	1963	NatureServe; Elliott (2000, 2005); Lewis and Lewis (2015); Taylor and Niemiller (2016); Niemiller and Taylor (2019)
Caecidotea nordeni	Norden's Groundwater Isopod	GH		APP	1980	NatureServe
Caecidotea teresae	Indiana University Southeast Groundwater Isopod	GX		ILP	1995	NatureServe; Lewis (2015)
Cambarus sheltae	Shelta Cave Crayfish	G1		ILP	2020	Buhay and Crandall (2005); Elliott (2005); Niemiller and Taylor (2019)
Cambarus veitchorum	White Spring Cave Crayfish	G1	CR (PE) D2	ILP	1968	IUCN; Niemiller and Taylor (2019)
Palaemonetes cummingi	Squirrel Chimney Cave Shrimp	GH	CR (PE) B1ab(iii) +2ab(iii)	FLS	1973	NatureServe; Niemiller and Taylor (2019)
Procambarus delicatus	Bigcheek Cave Crayfish	G1	CR (PE) B1ab(iii) +2ab(iii)	FLS	2020	IUCN
Stygobromus carolinensis	Carolina Seep Amphipod	GH		OTH	1971	NatureServe
Stygobromus lucifugus	Rubious Cave Amphipod	G1G2	EX	OTH	1882	IUCN; Elliott (2005); Niemiller and Taylor (2019)
Conotyla vista	A Cave Obligate Millipede	GH		APP	1967	NatureServe
Batriasymmodes parki	Neely Farm Cave Ant Beetle	GH		APP	1969	NatureServe
Horologion speokites	Arbuckle Cave Ground Beetle	GH		APP	1931	NatureServe
Pseudanophthalmus krameri	Kramer's Cave Beetle	G1		ILP	1973	Hobbs (1997); Elliott (2000, 2005); Niemiller and Taylor (2019)
Pseudanophthalmus krekeleri	Rich Mountain Cave Beetle	GX		APP	1957	NatureServe; Niemiller and Taylor (2019)
Pseudanophthalmus parvus	Tatum Cave Beetle	GH		ILP	1965	NatureServe; Niemiller and Taylor (2019)
Rhadine ozarkensis	Ozark Cave Beetle	GH		OZK	1940	NatureServe
Eurycea robusta	Blanco Blind Salamander	G1	DD	EPB	1951	Elliott (2000, 2005)

subterranean biodiversity in these countries, on the Red List is unsurprising. Just three of the 22 troglobiotic and stygobiotic vertebrate species have not been assessed, and this is only because these species (three cavefishes) were described or elevated to full species status within the past decade. Among subterranean invertebrates, 40 of the 44 decapod (crayfishes and shrimps) species have conservation status ranks, with two species (*Orconectes barri* and *Cambarus hubrichti*) deemed Data Deficient. Among other invertebrate groups, only gastropods (13 of 36 taxa, 36.1%) have had more than 20% of species assessed; five species are ranked as Data Deficient. What is perhaps most striking is that < 2% of terrestrial subterranean species have been assessed under IUCN Red List criteria. Moreover, assessments for 122 of the 135 species assessed (90.4%) were conducted more than a decade ago and are considered out-of-date (Rondinini et al. 2014).

The proportion of taxa evaluated in the U.S. and Canada is consistent with global trends: <5% of subterranean taxa have been assessed worldwide (Mammola et al. 2019). The poor representation of subterranean fauna, particularly invertebrates, evaluated under IUCN Red List criteria is due in part to a lack of taxonomic experts, funding, and public awareness. Consequently, there have been recent calls for renewed effort in IUCN Red List assessments of subterranean biodiversity, with clear guidelines and standardized methodology needed to minimize subjectivity and reduce inconsistencies across diverse taxonomic groups (Cardoso et al. 2011; Mammola et al. 2019). We echo these calls. Shortfalls in our knowledge of the distribution, population sizes and trends, life history and ecology, and threats for many species are reflected in the number of species that remain to be assessed. While some species may never be assessed (Bland et al. 2017; Hochkirch et al. 2020), most of those that have not yet been assessed, like Data Deficient species, lack the requisite information to confidently assess their conservation status.

One might reason that subterranean invertebrates would be better represented on the IUCN Red List, given that there is an IUCN Species Survival Commission Cave Invertebrates Specialist Group (SSC) that was founded in 2014. While this small group of global experts (~ 80 members including some from North America) has been active in addressing this issue by assessing subterranean invertebrates from other continents (1,115 species from subterranean habitats assessed as of January 2023), assessments for North American fauna have lagged behind and are not listed as a priority in the most recent IUCN SSC Cave Invertebrate Specialist Group Annual Report (IUCN SSC Cave Invertebrate Specialist Group 2022).

NatureServe

Unlike the IUCN Red List, most (79.0%) of the 1,445 subterranean taxa in the U.S. and Canada have been assessed under NatureServe criteria. An additional 5.1% (*N*= 74) of species are included in the NatureServe database but were ranked GNR or GU. Most of the species not present in the NatureServe database are small, understudied taxonomic groups, such as mites and microcrustaceans, or were formally described within the last 15 years. Of the species that have been assessed, 1,065 were ranked at an elevated risk of extinction (GX, GH, or G1–G3), with a high proportion of at-risk species across all taxonomic groups. In particular, the proportion of Critically Imperiled (G1) species is substantially higher in subterranean habitats than in surface ecosystems. Many subterranean species have extremely restricted distributions, and in many cases, stygobionts and troglobionts are known from a single cave system (Christman et al. 2005; Deharveng et al. 2009; Niemiller and Zigler 2013). In addition, these short-range endemics also tend to have small population sizes, limited dispersal ability (but see Jordan et al. 2020 and Faliowski et al. 2021), and low reproductive rates, among other traits that make them especially vulnerable to extinction (Culver et al. 2000; Culver and Pipan 2009, 2019). At face value, it is therefore unsurprising that such a large percentage of species were ranked at an elevated risk of extinction. However, conservation ranks for most species have been based largely on rarity factors, particularly range extent/area of occupancy and number of occurrences. Very few status assessments have incorporated information for factors in the other two primary factor categories—threats and trends. Population monitoring is challenging for subterranean taxa (Mammola et al. 2019) and rare among North American troglobiont and stygobionts. Even when population monitoring is feasible, threats are particularly challenging to quantify using the NatureServe framework, in which severity is calculated as percent population decline; multiple threats are often present, and isolating the effect of a single threat is rarely possible. In some cases, presumed high intrinsic vulnerability has been used when information on threats was unavailable. Moreover, 86.1% of troglobionts and stygobionts in the NatureServe database have not been reviewed in more than a decade, and ranks are often slow to be updated, even when revised. For example, the revision of Hutchins (2018) has not been adopted by NatureServe at the time of this writing.

NatureServe and IUCN Red List conservation status ranks were positively correlated, but there was considerable variation in correlation coefficients among taxonomic groups. The strongest correlations were for taxonomic groups that have been the best studied and for which the most data are available to inform conservation assessments (i.e., decapods, fishes, and salamanders). Past studies have revealed positive correlations in conservation ranks between the two classification systems across several taxonomic groups; however, discordance in conservation ranks is not uncommon (Mehlman et al. 2004; O'Grady et al. 2004; Goodenough 2012). Interestingly, conservation ranks were one threat category more conservative (i.e., species were assigned a greater level of imperilment), on average, for NatureServe ranks compared to IUCN Red List ranks. Differences in conservation ranks, as well as proportion of species assessed, between the two classification systems is likely related to several factors. First, conservation assessments are often conducted by different individuals; thus, there is potential for variation among assessors when interpreting data and implementing assessment protocols (Regan et al. 2005). NatureServe and IUCN Red List assessments employ many of the same concepts (e.g., geographic distribution size metrics such as area of occupancy and extent of occurrence, population size) and approaches to classifying and coding to inform conservation status assessments, and have generally analogous thresholds between different threat categories; however, the nature and processes for evaluating criteria and assigning ranks differ between the two systems (O'Grady et al. 2004). NatureServe assessments follow a weight-of-evidence and rule-based approach that prioritizes rarity in assessing extinction risk, whereas IUCN Red List assessments apply a rule-based approach to several criteria but place a greater emphasis on trends (Master et al. 2009; Frances et al. 2018; IUCN 2024). Moreover, the two classification systems were developed originally for different purposes. NatureServe, which was originally rooted in The Nature Conservancy's Natural Heritage Network, aims to assist in identifying and protecting biodiversity at regional and local scales for conservation planning and site-based prioritization (Master et al. 2009), whereas the IUCN Red List aims to identify and prioritize species at risk of extinction at a global scale to inform biodiversity policies and conservation actions (Rodrigues et al. 2006; IUCN 2024). Finally, current criteria for objectively evaluating and ranking species based on extinction risk on the IUCN Red List are difficult to apply for most invertebrate groups, particularly species with restricted distributions and low dispersal abilities, such as subterranean organisms, and may require some modifications to more comprehensively and effectively assess such taxonomic groups (Cardoso et al. 2011). Because the two classification systems are complementary but not identical, it may be useful to consider both assessments in concert when feasible for conservation and management decisions.

Federal, State, and provincial protected status

Conservation ranks based on IUCN Red List and NatureServe criteria are not well reflected in either federal listing by the U.S. Fish and Wildlife Service (USFWS) under the Endangered Species Act or, in many cases, protected status at the state level. The USFWS has listed or proposed to list just 36 and five species as endangered or threatened, respectively, representing 2.6% of troglobiotic/stygobiotic taxa. In Canada, none of the nine troglobionts and stygobionts are listed under Canada's Species At Risk Act. The proportion of taxa federally listed under the U.S. Endangered Species Act is similar to the proportion of taxa ranked as Extinct (EX), Critically Endangered Possibly Extinct (CR PE), Critically Endangered (CE), or Endangered (EN) on the IUCN Red List (2.8%), though the taxonomic composition of species is not the same. In contrast, 64.5% of species are ranked as Extinct (GX), Possibly Extinct (GH), Critically Imperiled (G1), or Imperiled (G2) by NatureServe. Directly comparing lists of at-risk species based on NatureServe and IUCN Red List criteria with species listed under the Endangered Species Act are not expected to result in perfect concordance as conservation status assessments and listing under the Endangered Species Act have different underlying objectives (O'Grady et al. 2004; Harris et al. 2012). Conservation status assessments and associated ranks are designed to approximate extinction risk, which is just one factor that is considered when identifying management priorities and listing under the ESA (Mace et al. 2008; Harris et al. 2012). The under recognition of invertebrate subterranean taxa listed under the ESA is particularly striking but mirrors trends for invertebrates in general in which >90% of IUCN-listed invertebrates are not listed in the United States under the ESA (Harris et al. 2012). Our study adds additional evidence that most United States imperiled species are not yet listed under the Endangered Species Act.

Threats and factors associated with extinction risk

Although potential anthropogenic threats to subterranean biodiversity and ecosystems, such as habitat loss and degradation, groundwater contamination, and climate change, have been qualitatively summarized (e.g., Griebler et al. 2014; Mammola et al. 2019, 2020; Kretschmer et al. 2023), few studies have quantitatively evaluated the potential impacts of and how best to mitigate such threats (Mammola et al. 2020; Wynne et al. 2021; Nanni et al. 2023). Our review of NatureServe and IUCN Red List assessments for troglobionts and stygobionts of the U.S. and Canada also highlights that information on current and potential threats are not reported (at best) or incorporated (at worst) into assessments for many cave-obligate species. Of the species for which threats are reported, habitat degradation (76.0%

of species with threats reported) and pollution (75.2%) associated with surface land use change (e.g., urbanization, agricultural activities, and deforestation) are the most frequently reported threats. Recreational activities (35.4%), such as amateur spelunking and tourism of commercial caves, and climate change (27.6%) were also frequently reported. Threats to subterranean biodiversity likely operate at varying spatial scales. For example, recreational activities are more likely to impact species at a local scale (i.e., individual cave system), whereas the impacts of climate change manifest across the range of a species. Moreover, threats to subterranean biodiversity likely do not operate alone but rather in concert with other threats producing cumulative or synergist impacts (Mammola et al. 2019; Wynne et al. 2021). Unfortunately, quantitative evidence of the biological impacts for many threats, including synergistic effects, on subterranean populations, communities, and ecosystems is limited. A recent global meta-analysis on the impacts of climate change on subterranean biodiversity and ecosystems by Vaccarelli et al. (2023) revealed that impacts occur at multiple levels of biological organization, are influenced by multiple factors, and are complex, varying in strength and direction. Their study highlighted the need for multifaceted approaches to examine the effects of not only climate change, but also other stressors on subterranean biodiversity to inform sound conservation and management strategies for threat mitigation.

Many troglobionts and stygobionts share several intrinsic traits that are correlated with increased extinction risk (Culver and Pipan 2009, 2019; Niemiller et al. 2018; Niemiller and Taylor 2019; Mammola et al. 2019). Most species appear to have small, often extremely restricted geographic ranges (; Zagmajster et al. 2008; Deharveng et al. 2009) and in many instances are endemic to a single or just a few cave systems (Christman et al. 2005; Deharveng et al. 2009; Niemiller and Zigler 2013). Robust data on population abundance/size are lacking for the overwhelming majority of species; nevertheless, species for which demographic data are available suggest most populations are small, which may increase susceptibility to demographic stochasticity and catastrophic events (Niemiller and Taylor 2019). Several troglobionts in the United States are known only from a single or few specimens (e.g., Niemiller et al. 2017). However, it is unclear whether observed rarity truly reflects actual rarity; i.e., are these species actually composed of very small populations or does rarity reflect undersampling or sampling of suboptimal habitat? For example, some species, such as *Anillinus* beetles, may be more common in epikarst and deep soil (habitats difficult to sample) but are infrequently observed in caves.

Several life history traits common to many troglobionts and stygobionts are associated with increased risk of extinction, including low reproductive rates/fecundity and limited dispersal ability (Poulson 1963; Culver and Pipan 2009, 2014; Fišer 2019; Mammola et al. 2019; Venarsky et al. 2023). Consequently, population rescue is often much slower and risk of extinction much greater relative to populations of surface species. Moreover, cave-obligate species appear to have narrow environmental tolerances and may be particularly sensitive to changes in abiotic conditions (e.g., temperature, humidity, dissolved oxygen, concentrations of heavy metals, among others) (e.g., Novak et al. 2014; Raschmanová et al. 2018; Castaño-Sánchez et al. 2020; Pallarés et al. 2021), such as those caused by threats resulting in habitat disturbance and degradation. These life history traits and factors act in concert to increase the intrinsic vulnerability of subterranean fauna and ecosystems. Moreover, there often is little redundancy in subterranean communities (Gibert and Deharveng 2002). Consequently, simple subterranean communities with few species and limited to no redundancy of functional roles exhibit low ecological resilience and are more vulnerable to perturbations and disturbance (Mammola et al. 2019). However, life history and other ecological data are lacking for most species, and generalizations of life history traits in subterranean fauna are derived from comparatively few species and studies.

Possibly extinct species

Some troglobionts, which have not been observed in several decades, may now be extinct (Elliott 2000; Taylor and Niemiller 2016; Niemiller et al. 2018). Ten species are currently ranked as possibly (GH) or presumed extinct (GX) in the wild under NatureServe criteria, with two species ranked as Extinct (EX) or Critically Endangered but Possibly Extinct (CR (PE) under IUCN Red List criteria (Table 4). Some single-site endemic species are hypothesized to be extinct because habitat has been destroyed due to quarrying/mining operations, such as the harvestman *Banksula californica* and the beetle *Pseudanophthalmus krekeleri*. For several potentially extinct stygobionts, groundwater pollution and surface land use modification are the primary drivers of extinction. The asellid isopod *Caecidotea teresae* was known from three drain outlets and a well on and adjacent to the Indiana University Southeast campus in Floyd County, Indiana. Termiticide application on the grounds around campus buildings extirpated the population at the type locality, while on-going development has either directly destroyed or impaired the other sites. Consequently, the isopod has not been observed since 1995 (Lewis 2015). The cave crayfish *Procambarus delicatus* is currently assessed as Critically Endangered but Possibly Extinct; however, Tyler Turner (Florida Fish and Wildlife Conservation Commission) trapped a male at the mouth of a small vent at the type locality, Alexander Springs in Lake County, Florida, in 2020 (P. Moler, personal communication). In addition, he observed a female that was recently predated by a Warmouth (*Lepomis gulosus*). The cave crayfish (*Cambarus sheltae*), which is known only from Shelta Cave in Madison County, Alabama, was thought to be extinct after the aquatic community in the cave crashed, likely in response to groundwater pollution and loss of a Gray Bat (*Myotis grisescens*) colony (Buhay and Crandall 2005; Elliott 2005; Niemiller and Taylor 2019). However, Dooley et al. (2022) reported on the recent rediscovery of the species; an adult female was observed in 2019 and an adult male in 2020. Niemiller et al. (2017) reported on the rediscovery of four species of *Pseudanophthalmus* cave beetles in Tennessee, two of which were assessed previously as Possibly Extinct (GH) by NatureServe.

Addressing knowledge gaps and other recommendations

The intrinsic vulnerability of subterranean biodiversity, coupled with the plethora of potential threats, makes protection of subterranean biodiversity and ecosystems an inherently challenging endeavor (Nanni et al. 2023). Moreover, conservation and management of subterranean biodiversity is hindered by extensive biodiversity knowledge gaps (Niemiller et al. 2018; Ficetola et al. 2019; Mammola et al. 2019, 2020; Wynne et al. 2021). Although the Linnean shortfall, i.e., substantial biodiversity remains to be discovered, cataloged, and described (Brown and Lomolino 1998), is acute in subterranean ecosystems (Culver et al. 2013; Niemiller et al. 2013, 2018, 2019; Ficetola et al. 2019; Mammola et al. 2019, 2021), our review highlights a need to address other knowledge shortfalls that impede our ability to effective assess, manage, and protect described troglobionts and stygobionts. In particular, most species are data deficient with regards to distribution, abundance, population size and trends, ecology and environmental sensitivity, and habitat extent and diversity (the Wallacean, Prestonian, Hutchinsonian, and Racovitzan (Ficetola et al. 2019) shortfalls, respectively). Most caves and other subterranean habitats are not easily accessible or explorable by humans, which makes acquiring information on subterranean habitats and their biodiversity, even through indirect means, a challenging endeavor (Culver and Pipan 2014, 2019; Ficetola et al. 2019; Mammola et al. 2021). Synoptic evaluations of non-cave habitats (e.g., the hyporheic zone and milieu souterrain superficiel (MSS) (Juberthie et al. 1980) in North America are in their infancy, even though imperiled 'cave' species may also occur in these widespread habitats (Hutchins et al. 2020). As for invertebrates in general (Cardoso et al. 2011), these and other knowledge shortfalls are consequences of limited research on and funding for the study of subterranean biodiversity, particularly for taxonomic and ecological studies (Niemiller et al. 2018; Mammola et al. 2019). Increased funding for qualitative, standardized sampling is needed to address these knowledge gaps, inform conservation assessments, and ultimately prioritize species and areas for conservation (Niemiller et al. 2018; Mammola et al. 2019; Wynne et al. 2021).

Increased effort to evaluate U.S. and Canadian subterranean biodiversity under IUCN Red List criteria (and more comprehensively under NatureServe criteria) is needed for most invertebrate taxa. However, the financial costs associated with assessments may prohibit many species from being assessed in the short-term, at least using traditional assessment approaches. Rondinini et al. (2014) reported that the mean cost of a species assessment through in-person workshops was US $333 in 2013, which is $451 in 2024 adjusted for inflation. Thus, we estimate it would cost about US $460,000 to reach a target of 80% taxonomic coverage for U.S. and Canadian subterranean biodiversity. Cheaper alternatives to in-person workshops include remote, online workshops, which reduce the mean cost to US $93 per species (2024 inflation adjusted) (Rondinini et al. 2014). Additionally, automated tools and predictive models of extinction risk can be calibrated on taxa with current conservation status ranks and then applied to assess comparable taxa (e.g., Bland et al. 2015a, b, 2017; Darrah et al. 2017; Walls and Dulvy 2020; Zizka et al. 2022; Lucas et al. 2024; Cazalis et al. 2024), further reducing the time and cost of assessments.

Evaluating subterranean species under IUCN Red List and NatureServe criteria, even with predictive models, may not be a productive endeavor, however, as many species will likely be data deficient, given extremely limited distributional and population status information available. One or more of the eight justifications for assigning DD status under IUCN Red List criteria (Bland et al. 2017) apply to many subterranean species, particularly uncertainty in population status or distribution, uncertainty in threats, few (< 5) records, and old (< 1970) records. DD species, much like most subterranean fauna in general, are afforded very little consideration, protection, and funding in conservation legislation and planning due to their uncertain conservation status (Walsh et al. 2013; Bland et al. 2017), despite evidence that many DD species may, in fact, be at a higher risk of extinction (Howard and Bickford 2014; Roberts et al. 2016; Borgelt et al. 2022). Predictive models for the conservation status assessment of subterranean taxa are promising, but the lack of biological information and the paucity of species with reliable conservation assessments to inform models may limit their effectiveness, particularly for orphaned taxonomic groups, such as flatworms, microcrustaceans, arachnids, millipedes, and springtails. Nevertheless, predictive models may be useful for identifying and prioritizing species for assessments and reassessments. Finally, there are additional tools that have been developed that may accelerate assessments for subterranean taxa, such as Species Conservation Profiles (SCPs; Cardoso et al. 2016) and sRedList (Cazalis et al. 2024). SCPs represent an IUCN-approved template and vocabulary for conservation treatments of individual species to facilitate the publication of conservation-relevant information and support assessments (Cardoso et al. 2016). SCPs are becoming increasingly popular for cave-dwelling arthropods in Europe (Borges et al. 2019; Milano et al. 2022; Reboleira et al. 2022; Reboleira and Eusebio 2023) but have yet to be implement in the United States and Canada.

The continued decrease in the number of well-trained taxonomists and the lack of adequate funding for taxonomy are recognized as major impediments to addressing the Linnean shortfall and its impacts on conservation (Agnarsson and Kuntner 2007; Drew 2011; Britz et al. 2020; Engel et al. 2021). The Taxonomy Crisis is particularly prominent in biospeleology (Elliott 2005; Niemiller and Taylor 2019; Mammola et al. 2019). Our review of the conservation status of U.S. and Canadian subterranean fauna focused on described biodiversity, yet dozens of species reported in the literature await taxonomic description and likely hundreds remain to be discovered. Some of these species may even be on the brink of extinction and could be lost before they are even described (Niemiller et al. 2013). The lack of taxonomic expertise for many invertebrate taxonomic groups as well as the associated decline of the field of taxonomy also impedes our ability to address other knowledge shortfalls, particularly the Wallacean shortfall, and accurately assess the conservation status of many species. The retirements as well as passings of several prominent U.S. biospeleological taxonomists, such as Drs. Thomas Barr (beetles), Ken Christiansen (springtails), Roman Kenk (flatworms), John Holsinger (amphipods), and others, has regrettably resulted in a substantial loss of taxonomic expertise for subterranean biodiversity. As remaining taxonomists have increasing queues of specimens on shelves to work through, new species descriptions have dramatically slowed or even halted for many invertebrate groups.

To move forward, renewed efforts are needed to ascertain aspects of life history, demography, distribution, and environmental sensitivity across taxonomic groups, with the goal of leveraging information from surrogate species to better inform and evaluate the efficacy of models to predict conservation status. Efforts to detect and monitor subterranean species should ideally employ standardized quantitative approaches for sampling (e.g., the PASCALIS protocols; Malard et al. 2002) and threat vulnerability assessments, the latter of which is critically needed for all but listed species. Assuming that funding for conservation will remain or become even more limited in the future, it will be critical to prioritize species across taxonomic groups and regions to maximize return on investment. In that same vein, we will need to prioritize species and cave systems for legal protection to maximize protection of subterranean biodiversity and ecosystems (i.e., the umbrella species conservation strategy; Roberge and Angelstam 2004), as protection of all species at high extinction risk is financially intractable. Moreover, now may be the time to transition from more species-based to habitat- and ecosystem-based approaches for conserving subterranean biodiversity in North America, like the Natura 2000 network in Europe. Given the uncertainty surrounding the distribution of subterranean species and the nature and extent of their threats, protecting broader areas of subterranean habitat rather than focusing solely on individual endangered species may be the most viable way to preserve functional subterranean communities (see Mammola et al. 2024 for a broader discussion). An investment in taxonomic research, including support for (1) the training and development of a new generation of students with taxonomic expertise in understudied taxonomic groups and (2) international taxonomic collaboration is essential. Garnering support for these actions and the conservation of subterranean biodiversity, in general, will require increasing efforts to raise awareness of subterranean fauna and ecosystems, including their importance, sensitivity, and threats, through education and outreach programs aimed at students, the general public, and government officials. These recommended actions should be implemented in collaboration with local, state, and federal agencies and other conservation-minded organizations and partners, including caving organizations, to foster long-term participation of and coordination among stakeholders to conserve and protect this unique and underappreciated fauna.

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Data availability The datasets generated during and/or analyzed during the current study are available in Supplementary Information and from the corresponding author.

Declarations

Competing interests The authors declare no competing interests.

Supplementary Information Extended information on the list of U.S. and Canadian troglobionts and stygobionts, including conservation ranks, distributions, and threats (Appendix S1), python code for acquiring NatureServe conservation rank data (Appendix S2), and equivalent NatureServe and IUCN Red List conservation ranks (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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