Why the delay in recognizing terrestrial obligate cave species in the tropics?

Francis G. Howarth

Abstract: “Nothing could possibly live there!” They believed. Indeed, until recently, few specialized cave-adapted animals were known from volcanic, tropical, or oceanic island caves, and plausible theories had been put forward to explain their absence. But assume nothing in science! One must illuminate, explore, and survey habitats before declaring them barren. Our understanding of cave biology changed dramatically about 50 years ago following the serendipitous discovery of cave-adapted terrestrial arthropods in Brazil and on the young oceanic islands of the Galápagos and Hawai‘i. These discoveries and subsequent studies on the evolutionary ecology of cave animals have revealed a remarkable hidden fauna and created new sub-disciplines within biospeleology. Biological surveys of caves in other regions have continued to expand our understanding of the evolution, adaptation, and ecology of the subterranean biome. We now predict that, rather than relicts trapped in caves by changing climate, many animals actively colonized caves and adapted to exploit food resources wherever there were suitable subterranean voids. The physical environment in caves can be determined with great precision because the habitat is buffered by rock. Furthermore, the bizarre adaptations displayed by obligatory cave animals are similar across many taxonomic groups. These two characteristics make caves nearly ideal natural laboratories for studying evolution and ecology. However, to the untrained researcher, caves can appear hostile and dangerous, and in fact, fieldwork in caves requires a unique marriage of athletic ability and science. In other words, cave research is exciting! In this contribution, I describe the exploration, discovery, and research in tropical caves and describe the factors that delayed the recognition of a significant tropical cave fauna.

Keywords: arthropods, cave environment, conservation, evolution, troglobionts


INTRODUCTION

In 1920, Emil Racovitza established the Emil Racovita Institute of Speleology, which marks a milestone in the history of the science of speleology (Tabacaru et al., 2018). To commemorate the 100-year anniversary of the founding of the institute, a symposium on biospeleology was planned for 2020 in Cluj, Romania, but the Covid-19 pandemic disrupted travel and public gatherings. The symposium and celebration were postponed to 18-22 July 2022. This contribution is an expansion of my presentation at the symposium. Herein, I briefly review the history of early biological surveys of tropical caves; describe the factors that delayed the discovery of significant cave-adapted terrestrial animals (i.e., troglobionts) in the tropics; and explain how these discoveries have expanded our understanding of evolutionary ecology and conservation biology of subterranean habitats. Many of my explanations result from my more than one-half century of research in Hawaiian and Australasian caves.

The science of biospeleology has exploded in recent decades as indicated by the spate of books and reviews published since the 1980s (e.g., Culver, 1982; Chapman, 1993; Juberthie & Decu, 1994-2001; Wilkens et al., 2000; Gunn, 2004; Romero, 2009; Culver & Pipan, 2014; Moldovan et al., 2018; Wynne, 2022). Review of this recent literature is beyond the scope of this contribution.

The tropics are traditionally defined as the geographical zone between the Tropic of Cancer in the Northern Hemisphere at 23.43631° N and the Tropic of Capricorn in the Southern Hemisphere at 23.43631° S. This equatorial band closely corresponds to the region where the nighttime temperature falls below the average annual temperature on most nights, i.e., the tropical winter effect. This phenomenon influences
the distribution of terrestrial animals within caves (Howarth, 1980); and therefore, it is appropriate to restrict the designation of tropical caves to the area within the Tropics. Nevertheless, biologists often do not distinguish subtropical caves from tropical caves, and therefore, early records from subtropical caves are included.

Until the early 1970s, the known distribution of terrestrial troglobionts was believed to be almost entirely restricted to limestone caves in temperate regions outside the limits of Pleistocene glaciation but inside the line of normal frost (Vandel, 1965; Barr, 1968; Mitchell, 1969; Poulson & White, 1969). This perceived distributional anomaly provided the foundation for the theory that obligate cavernicoles evolved in isolation after their surface populations were extinguished by the extreme warming and cooling periods generated by Pleistocene glaciations. That is, the animals sought refuge and became stranded in underground habitats and therefore were relicual.

Even though Racovitza and other early cave biologists were prescient in predicting the existence of cave-adapted species in tropical caves (Flower et al., 1898; Racovitza, 1907), the early expeditions to survey tropical caves were largely unsuccessful in finding terrestrial cave-adapted species. More than 75 years transpired before the presence of a diverse terrestrial cave fauna in the tropics was recognized by the discovery of cave-adapted arthropods in lava tubes on the young oceanic islands of Galápagos and Hawai’i (Leleup, 1967, 1968; Howarth, 1972) and in subtropical Brazil (Strinati, 1971; Souza et al., 2019). These discoveries expanded the field of biospeleology, and subsequent research has increased our understanding of the evolution, ecology, and natural history of caves and cave-life. This research has also answered the mystery of why it took so long to recognize the abundant diversity of terrestrial troglobionts in tropical caves.

Early surveys of tropical caves

Although a few cave animals were known since ancient times, the science of biospeleology began in Europe in the early to mid-19th century, following the discovery of subterranean communities inhabited by remarkable cave-adapted species. Subsequently, biological surveys of caves were conducted in other regions. Initially, tropical caves were expected to house an exceptional fauna, especially since tropical habitats are considerably older than those in temperate regions and since they support an extraordinary number of species including many apparent ancient taxa (Flower et al., 1898; Racovitza, 1907). Tropical caves were also promising because the animals sought refuge and became stranded in underground habitats and therefore were relicual. Recognizing the potential to discover remarkable cave-adapted species in tropical caves, the British Association for the Advancement of Science established a committee to organize a survey (Flower et al., 1898). The committee appointed H.N. Ridley, Director of Gardens and Forests, Straits Settlements, Malaya, to

Results of the early surveys

Surprisingly, the initial biological surveys of tropical caves in the late 19th and early 20th centuries were disappointing, as few truly cave-adapted species were found or recognized (Annandale & Gravely, 1914). Their apparent absence reinforced the glacial relict hypothesis (Jeannel & Racovitza, 1914), as well as suggested another cause. Since cave and surface environments in the humid tropics are similar and lack the extreme seasonality characteristic of the temperate zone, tropical cave animals might freely move between cave and surface environments; whereas animals in temperate caves were forced to remain underground and become cave-adapted (Flower et al., 1898; Annandale & Gravely, 1914; Wycherley, 1972).

Following the disappointing results of the early surveys, enthusiasm for further studies in tropical caves waned (Moseley, 2014). Nevertheless, evidence of diverse troglobiotic faunas in tropical caves has been accumulating during the past century. For example, in his monographic review of cave biology, Vandel (1965) emphasized that tropical caves were depauperate of troglobionts compared to the fauna of caves in the Mediterranean region. Nevertheless, he listed 14 species of highly cave-adapted animals, including a pseudoscorpion, two spiders, two springtails, two raphidophorid crickets, two cockroaches, and five isopods from tropical caves in Africa, Asia, and the Neotropics. He also listed several partly cave-adapted species that might be troglobionts from the tropics, including crickets, oligochaetes, millipedes, and springtails.

Pioneering cave surveys in tropical Asia and Australasia

The survey for cave fauna of Southeast Asia began circa 1866 by the well-known botanist Odoardo Beccari, who reported searching in vain “for blind Coleoptera and any other special cave creatures” in Wind Cave, Sarawak (Beccari, 1904). However, Leonardo Fea was the first zoologist to scientifically collect cave animals in Southeast Asia. From 1885 to 1889, Fea led expeditions to Myanmar and vicinity and collected about 60,000 specimens of animals from caves and surface habitats (Capocaccia & Poggi, 1982). Letters and notes describing Fea’s travels were published in the Bollettino della Società geografica Italiana (Fea, 1885–1888). Fea (1897) summarized his collections of cave-associated bats, rodents, orthopterans, myriapods, and arachnids and listed the taxonomic articles by specialists that had been published by 1897. Shortly thereafter in 1890, the prominent French arachnologist Eugène Louis Simon collected arthropods in two caves in the Philippines (Raffray et al., 1892; Simon, 1896). Fea and Simon believed that they found no highly specialized cave animals.

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conduct a biological survey of certain caves on the Malay Peninsula and to collect their living and extinct fauna. After their discovery in 1878 by Hornaday (1885) and Daly (1879), Batu Caves became the most visited and best-known cave system in Malaya (Price, 2002). Ridley led a team to Batu Caves in Selangor in 1896 to collect plants and animals from both cave and surface habitats. He also recorded important notes on the natural history of the caves and tower karst (Ridley, 1898; Wycherley, 1972).

Table 1. Early biological surveys of tropical caves from 1860–1928.

<table>
<thead>
<tr>
<th>Name</th>
<th>Dates</th>
<th>Region</th>
<th>Results</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Odoarado Becarri</td>
<td>1866</td>
<td>Sarawak</td>
<td>Cultural survey with notes on biology</td>
<td>Beccari, 1904</td>
</tr>
<tr>
<td>A. Hart Everett</td>
<td>1878–1879</td>
<td>Sarawak</td>
<td>Cultural survey with notes on biology</td>
<td>Everett et al., 1880</td>
</tr>
<tr>
<td>Leonardo Fea</td>
<td>1885–1889</td>
<td>Myanmar</td>
<td>Extensive biological collections; a few troglobionts</td>
<td>Fea, 1897</td>
</tr>
<tr>
<td>Eugène Simon</td>
<td>1890</td>
<td>Philippines</td>
<td>Visited 2 caves, a few troglobionts</td>
<td>Simon, 1896</td>
</tr>
<tr>
<td>R. C. Temple</td>
<td>1892</td>
<td>Myanmar</td>
<td>Cultural survey with notes on biology</td>
<td>Temple, 1893</td>
</tr>
<tr>
<td>H. N. Ridley</td>
<td>1896</td>
<td>Batu Caves, Malaya</td>
<td>Extensive biological collections; few troglobionts</td>
<td>Ridley, 1898</td>
</tr>
<tr>
<td>William Walter Skeat</td>
<td>1899–1900</td>
<td>Malay Peninsula, S. Thailand</td>
<td>Cultural survey; extensive biological collections; a few troglobionts</td>
<td>Skeat &amp; Laidlaw, 1953</td>
</tr>
<tr>
<td>K. Rechinger</td>
<td>1905</td>
<td>Samoa</td>
<td>One troglobiont, <em>Rhaphidophora rechingeri</em></td>
<td>Holdhaus, 1909</td>
</tr>
<tr>
<td>Dr. E. Mjoberg’s Swedish Scientific Expedition to Australia</td>
<td>1910–1913</td>
<td>Chillagoe N. Queensland</td>
<td>One troglobiont, <em>Troglaridulo cavernae</em></td>
<td>Wahrberg, 1922</td>
</tr>
<tr>
<td>R. Friel</td>
<td>1918, 1921</td>
<td>Lakadong Cave, &amp; Rupmath Cave, Meghalaya, India</td>
<td>2 troglobionts: <em>Typhloblatta caeca</em> Chopard, 1921; <em>Euchytomis caecus</em> (Chopard, 1924)</td>
<td>Chopard, 1921, 1924</td>
</tr>
<tr>
<td>Stanley Kemp et al.</td>
<td>1922</td>
<td>Siju Cave, Meghalaya, India</td>
<td>Extensive biological collections; &gt;100 species, no troglobionts</td>
<td>Kemp &amp; Chopra, 1924; Harries et al., 2008</td>
</tr>
<tr>
<td>Patrick Buxton</td>
<td>1924</td>
<td>Samoa</td>
<td><em>Haploclernes buxtoni</em> (Kástner 1927)</td>
<td>Kástner, 1927</td>
</tr>
<tr>
<td>Cedric Dover</td>
<td>1926</td>
<td>Batu Caves, Mayasia</td>
<td>One troglobiont, <em>Pseudoparonella doveri</em> Carpenter 1933</td>
<td>Dover, 1929</td>
</tr>
<tr>
<td>Various explorers</td>
<td>1885–1927</td>
<td>East Africa</td>
<td>Human and vertebrates in caves</td>
<td>Sutcliffe, 1973</td>
</tr>
<tr>
<td>Eugène Simon</td>
<td>1893</td>
<td>Transvaal</td>
<td>Three caves, no troglobionts?</td>
<td>Simon, 1894</td>
</tr>
<tr>
<td>Bror Yngve Sjöstedt</td>
<td>1905–1906</td>
<td>Kilimanjaro, and surrounding area, E. Africa</td>
<td>Several caves; no troglobionts?</td>
<td>Sjöstedt, 1910</td>
</tr>
<tr>
<td>Charles Aluaud and René Jeannel</td>
<td>1911–1912</td>
<td>several countries</td>
<td>Extensive biological collections; few troglobionts</td>
<td>Jeannel, 1913—1919</td>
</tr>
<tr>
<td>Alexander von Humboldt</td>
<td>1799</td>
<td>Venezuela</td>
<td>Discovered the Oil Bird</td>
<td>von Humboldt, 1817</td>
</tr>
<tr>
<td>Dominik Bilimek</td>
<td>1866</td>
<td>México</td>
<td>One troglobiont, <em>Anelpistina anopthalma</em> (Bilimek, 1867)</td>
<td>Bilimek 1867</td>
</tr>
<tr>
<td>D. A. L Herrera</td>
<td>1891</td>
<td>México</td>
<td>Recollected <em>Anelpistina anopthalma</em></td>
<td>Herrera, 1893</td>
</tr>
<tr>
<td>F. Silvestri</td>
<td>1928</td>
<td>Cuba</td>
<td>Collected three troglobionts</td>
<td>Vandel, 1965</td>
</tr>
</tbody>
</table>

Table 1. Early biological surveys of tropical caves from 1860–1928. Additional expeditions traveled to tropical Asian caves in hopes of finding evidence of early humans, as well as document the geology, flora, and fauna (Price, 2002; Moseley, 2014). In 1878 and 1879, A. Hart Everett led an expedition to Sarawak with a goal of finding evidence of human use of caves. They described the geology, vertebrate use and remains in 32 caves. Except for brief mention of crustaceans, spiders, crickets, and millipedes, invertebrates were not studied (Everett et al., 1880). In 1892, R.C. Temple visited several caves near Maulmain and Thaton in Burma (now Myanmar). He provided detailed accounts and sketches of many caves and described their archaeological significance (Temple, 1893). In 1899 and 1900, William Walter Skeat led the Cambridge University Expedition to gather ethnographic and cultural information on the native peoples living on the Malay Peninsula and southern Thailand.
The expedition included zoologists and botanists, who collected in cave and surface habitats (e.g., Simon, 1901; Annandale & Robinson, 1903). Skeat and Frank Laidlaw published their trip report and listed the publications resulting from their fieldwork (Skeat & Laidlaw, 1953).

Ironically, a few terrestrial cave-adapted species were discovered by these early surveys, but they were not recognized as troglobionts at the time. For example, Simon (1896) described two possible troglobiontic spiders, *Speocera microphthalmal* and *Accola caeca* from the Philippines; and Bolivar (1892; 1897) described three cave cockroaches: two from the Philippines *Noticola simoni* and *Noticola caeca* and one from the Fea expedition *Spelaebolatta gestroi*. Budde-Lund (1895) described the isopod *Philoscia coeca* (now *Burmoniscus coecus* from the Fea expedition, but the original description was too brief to determine its status (Taiti & Ferrara, 1986). Later, Carpenter (1933) described the collembolan, *Pseudoparonella doveri*, collected by C. Dover in 1926 in Dark Cave at Batu Caves (Dover, 1929).

The first troglobiont described from tropical Australia is an isopod crustacean, *Troglarmadillo cavernae* (Wahrberg, 1922), which was collected in a limestone tower in Chillagoe, North Queensland. Since its description, the tropical cave fauna of Australia remained largely unstudied until the Explorers Club, NY, in collaboration with the Chillagoe Caving Club, initiated biological surveys of caves at Chillagoe in the 1980s (Sullivan, 1988). These surveys discovered a diverse troglobiontic fauna, including Undara Lava Tube, which is a subterranean biodiversity hotspot (Howarth, 1988; Eberhard & Howarth, 2021).

The first troglobiont described from the Pacific islands is a cave cricket, *Rhaphidophora rechingeri* Holdhaus 1909 from a lava tube in Samoa. However, Holdhaus had few specimens, and its status was not clarified until Chopard's (1929) redescription using additional material. Later, Kästner (1927) described an eyeless pseudoscorpion, *Chelifer buxtoni* (now in *Haplochernes*) from the same lava tube in Samoa.

**Pioneering cave surveys in tropical Africa**

Explorers also visited caves in tropical Sub-Saharan Africa, with early reports first appearing circa 1885. These early accounts mostly reported on human and vertebrate use of the caves (reviewed by Sutcliffe (1973). The earliest collections of cavernicoles were made in 1893 by Eugène Simon (Simon, 1894), who collected arthropods in three caves in the Transvaal area of southern Africa. However, the former region of Transvaal lies mostly south of the Tropic of Capricorn and therefore subtropical. In 1905 and 1906, Bror Yngve Sjöstedt visited caves near Kilimanjaro, Meru and surrounding Massaisteppen, Merim, in East Africa (Sjöstedt, 1910). From 1911 to 1912, French zoologists Charles Alluaud and René Jeannel collected a large number of animals in caves in several African countries (Jeannel, 1913-1919). The latter zoologists discovered the first African stygobionts and troglobionts (Jeannel & Racovitza, 1914). Curiously, however, their discovery of troglobionts was overlooked by most subsequent workers (Deharveng & Bedos, 2000).

Preliminary cave surveys on Madagascar and Reunion Island recorded two troglobionts. Synave (1953) described the first troglobiontic caddis (*Typhlobrixia namorokensis*) from Madagascar; however, Vandel (1965) considered it to be a surface animal accidentally in the cave. Jarrige (1957) described the cave-adapted staphylinid beetle, *Lathrobium pauliani* (now in *Pseudolathra*) from Reunion Island. Subsequently, Paulian (1961) suggested that this troglobiont derived directly from *P. hamoni* (Jarrige, 1957), which is an epigean species living in the vicinity of the cave.

**Pioneering cave surveys in the Neotropics**

Except for Alexander von Humboldt’s famous discovery of the Oil Bird in Venezuela in 1799 (von Humboldt, 1817), and subsequent scattered reports, troglobionts occurring in the Neotropics remained largely in darkness until recent decades (Vandel, 1965). The first troglobiont known from the Neotropics is a silverfish, *Anelpisstina anophthalma* (Bilimek, 1867), who visited Grutas de Cacahuamilpa in southern Mexico in 1866. More than 60 years later in 1928, Filippo Silvestri collected three troglobionts in Bellamar Cave, Cuba: a spider (*Troglothele caeca* Fage, 1929), and an isopod (*Troglophiloscia silvestrii* Brian, 1929), and a collembolan (*Metasinella acrobates* Denis, 1929).

Initial reports of tropical troglobionts in South America were principally taxonomic and include the millipede, *Obirodesmus rupestris* Schubart 1946, from Lapinha and Lapa Vermelha caves, Minas Gerais, Brazil, and the harvestman, *Spaeleoleptes spaeleus* Soares 1966, from Cordisburgo region also in Minas Gerais. A few early records of troglobionts from Brazil are from the subtropics (e.g., cave millipedes *Alocodesmus yporangae* Schubart 1946, and *Yporangiella stiggius* Schubart 1946 both in São Paulo State). Subsequently, the science of speleology and biological surveys in South America were initiated in Venezuela in the 1950s (Chapman, 1980; Galán & Herrera, 2006) and in Brazil in 1968 (Strinati, 1971; Dessen et al., 1980; Trajano & Bichuette, 2010; Souza, 2019).

**Recognition of a significant tropical troglobiontic fauna**

Ultimately, Leleup (1967; 1968) reported the discovery of a diverse hypogean fauna in lava tubes in the Galápagos Islands; Strinati (1971) found ten species of troglobionts in two subtropical caves in Brazil; Chapman (1980) listed nine troglobionts from caves in Venezuela collected in 1973; and my report of the highly diverse troglobiontic fauna in young lava tubes in the Hawaiian Islands (Howarth, 1972). The true potential for continental caves in the humid tropics to house highly diverse communities of troglobionts was finally confirmed by Chapman (1984), who reported discoveries in Mulu Caves, Sarawak. The extraordinary biodiversity of tropical troglobionts is widely recognized especially in Australasia (Howarth, 1988; Deharveng & Bedos, 2000) and in the Neotropics (Reddell, 1981; Trajano, 2000; Galán & Herrera, 2006).
There is now evidence that diverse troglobiontic and stygobiontic faunas occur in all suitable subterranean habitats from glacier caves in ice (Howarth, 2021) to the tropics (Deharveng & Bedos, 2019), and in many types of subterranean voids (Juberthie et al., 1980; Wilkens et al., 2000, Howarth & Moldovan, 2018) including limestone (Vandel, 1965) lava (Howarth, 1972), sandstone (Auler & Sauro, 2019a), calcrites (Halse, 2018), and iron ore caves (Auler et al., 2019b). Nevertheless, huge gaps in our knowledge remain including vast regions containing caves that have not yet been biologically inventoried (Ficetola et al., 2019). Significantly, tropical troglobionts have corroborated the generality that terrestrial cave-adapted species are restricted to humid passages where evaporation is negligible or absent (Howarth, 1980; Ahearn & Howarth, 1982). This observation has important implications for understanding the delay in discovering tropical troglobionts.

Factors contributing to the delay in recognizing tropical troglobionts

The initial surveys in the late 19th and early 20th centuries did not recognize any highly cave-adapted species in their collections, and several hypotheses were put forward to explain why. (1) The apparent absence corroborated the accepted paradigm that troglobionts were characteristic of temperate limestone caves. (2) The environment within tropical caves was so similar to the constantly warm, humid conditions on the surface that there was no necessity for animals living in caves to adapt. (3) The tropical caves accessible at that time were more open allowing cave and surface animals to intermingle (Annandale & Gravely, 1914). These explanations then discouraged further surveys in tropical caves (Moseley, 2014). The reasons that the early efforts failed to discover cave-adapted animals can be grouped into separate but overlapping categories.

Limited scope of the investigations

The early investigators surveyed only a tiny fraction of tropical caves, and of those, the stable deep zone was entered in only a few. In fact, most of the caves visited were shallow and did not have an accessible deep zone (e.g., Temple, 1893; Ridley, 1898; Annandale & Gravely, 1914). Only the Fea, Simon, Ridley, Skeat, and Jeannel expeditions included finding cave-adapted species as one of their primary goals.

Difficult logistics and access to tropical caves

Increased solution of limestone in the tropics results in more open caves with larger entrances (Jennings, 1971; Sweeting, 1973). The long dark passages and underground rivers found in temperate regions are also well represented in the tropics but were mostly unknown to colonial biologists working in the tropics at that time. Most known caves were large conspicuous entrances in limestone towers. However, the rugged case-hardened limestone surface characteristic of tropical tower karst deterred locating and entering caves. Case-hardened limestone is caused by alternate wetting and drying of the surface, which promotes the filling and sealing of the surface by recrystallization of calcite. Few rocky surfaces are as cruel to the human body as case-hardened limestone (Fig. 1). Hornaday (1885) and Ridley (1898) vividly describe the extreme efforts required to find and explore caves on the Malay Peninsula. Furthermore, the high temperatures and humidity were debilitating to explorers more accustomed to cooler climes.

Fig. 1. Case-hardened limestone at Chillagoe, N Queensland. Photo F.D. Stone.

The early explorers were inexperienced in exploring and collecting in caves

Tropical karsts were unfamiliar terrain for colonial explorers. In addition, most had no or little prior experience in caves (Moseley, 2014). Exploring and collecting in caves often requires unique skills and equipment (Wynne et al., 2018), some of which were not available at the time, e.g., adequate lights, safer single rope equipment and techniques, and protective clothing (White, 2019). The equipment available to cave biologists in Europe and North America at the time was often difficult or impossible to procure in remote colonial outposts. The elevated temperature, humidity, stagnant air, and guano deposits exacerbated the difficulty in working in tropical caves. Hornaday’s party explored caves using torches made with bamboo sticks. Daly’s party in Batu Caves used dammar torches, but after the flaming drops of resin ignited the guano, they switched to bamboo torches (Price, 2002).

Difficulty in collecting and preserving specimens

Collecting cave animals faces many of the same problems described under logistics and exploration of tropical caves. In addition, preserving and shipping specimens to taxonomists was especially problematic at that time. Mail service was insecure, and containers were limited to glass, metal, and wood. The high temperature and humidity, as well as the abundance of pests, rapidly destroyed unprotected specimens. For example, a large portion of Ridley’s important collection from Batu Caves arrived in London in unusable condition and was never studied (Ridley, 1898; Wycherley, 1972; Price, 2002; Moseley, 2014). The loss is especially unfortunate, as Ridley’s party collected in Dark Cave at Batu before the habitat was
badly damaged by guano extraction and limestone mining (Moseley, 2014).

The explorer’s inexperience regarding the taxa sought

Many animals that the early explorers encountered were unfamiliar and belonged to groups not found in temperate caves. Absent were taxa related to the highly cave-adapted fauna known from temperate caves, such as beetles, which were often the quest of the investigators (Everett et al., 1880; Flower, 1898). Thus, most collecting was opportunistic; that is, largely consisting of conspicuous species observed in the flickering light from torches. A few taxa, such as blind nicticolid cockroaches and cixiid planthoppers, were discarded as nymphs of epigean species.

The taxonomic and Linnean impediments wherein the animals collected belonged to taxa that were unfamiliar to the biologists who received specimens.

Many specimens sent from the tropics belonged to orphan groups; that is, there were no specialists available to study them. Also, tropical cave animals were unrelated and distinct from the cave-adapted fauna known from temperate caves. Furthermore, the ecology of tropical caves was poorly known, and therefore, the few specialized cave species that were described were not recognized as troglobionts at the time. For example, researchers occasionally dismissed the animals as exceptional and not indicative of a significant obligate cave fauna; or they were dismissed as soil and leaf litter inhabitants and not strictly cave species (Vandel, 1965; Barr, 1968; Mitchell, 1969). Reinforcing these impediments was the volume and bewildering array of biological diversity found in caves due largely to the increased amount of energy inputs by bats and birds. The diversity and abundance of unfamiliar taxa created an embarrassment of riches. Since tropical bat and swiftlet colonies supported so much life, containers were filled, and collecting was completed before deeper cave passages were reached.

The high rates of erosion, solution, and soil formation in the tropics

Temperate and tropical caves differ significantly in their physical environment, which affects the distribution of troglobionts within caves (Howarth, 1980). The main driver of the difference in the abiotic environment is the higher temperature, which governs the rate of evaporation, limestone solution, erosion, and soil formation.

Cavernous landforms and early successional habitats (such as coarse-grained fluvial deposits and talus slopes) often contain vast systems of interconnected subterranean voids into which organic debris falls or is transported by sinking water or animals (Howarth & Wynne, 2022). Rainwater rapidly percolates to the water table or an impermeable layer, and the surface appears nearly barren. The sparse vegetation often includes plants able to send their roots deep underground to obtain water and nutrients (Howarth et al., 2007; Bleby et al., 2010; Geekiyanage et al., 2019; Carrière et al., 2020), but there are exceptions (Querejeta et al., 2007). Howarth

How deep plant roots can grow remains an important question in plant ecology (Canadell et al., 1996; Jackson et al., 1999; Maeght et al., 2013; Pierret & Lacombe, 2018). In a worldwide review of rooting depth, Canadell et al. (1996) found that plant roots grow much deeper than is assumed in most biomes and recorded a maximum depth of 68 m in unconsolidated sand by the tree Boscia albitrunca in Botswana and suggested that the potential depth might be 140 m (i.e., the depth of the local water table). Deeply rooted trees commonly grow on tropical tower karst and young basaltic lava, notably in seasonally dry tropical regions, where the high rate of evapotranspiration limits plant growth. For example, within the tower karsts of tropical north Queensland, Australia, large root mats have been found more than 60 m underground. Furthermore, these roots continue downward into cracks to an unknown depth.

During early succession, developing soil sinks or is washed into voids in the vadose zone, which delays the establishment of a surficial soil layer. The development of soil near the surface supports shallow rooted plants as their roots can usually obtain the required water and nutrients from the soil (Fan et al., 2017). Surficial soil captures water and nutrients thus desiccating and starving cave communities.

The effect of soil accumulation partly corroborates the observation that troglobionts are less common in caves in the perpetually humid tropics (Deharveng, 2004), since the water-logged soil acts as a barrier to deep root growth (Fan et al., 2017). For example, on the island of Hawai’i, lava tubes more than 20,000 years old in rainforests receiving over 700 cm of rain per year support few troglobionts; however, disturbances such as lava flows, tectonic events, and erosion can reset succession and rejuvenate subterranean habitats (Howarth, 1996; Howarth & Wynne, 2022). Also, caves that receive sufficient inputs of nutrients (e.g., harbor colonies of trogloxenes or capture streams) may not be as affected by soil formation.

Another factor influences succession on cavernous substrates that are created by water. As soil develops on the surface, excess water (often charged with CO₂ and organic acids) sinks into cracks and depressions where it dissolves or erodes the substrate to form deeper depressions and larger routes into subterranean voids. Developing soil sinks or washes into these voids while diminishing development of a surficial soil layer. The accumulations of soil in the vadose zone serve as a source of water and nutrients for deep-rooted plants (Carrière et al., 2020) Where soil formation outpaces erosion and solution because of climate, organic fallout, or substrate type, a surface soil layer can develop.

The layer of soil may seal subterranean voids from air exchange with the surface, which allows decomposition gases, especially carbon dioxide (CO₂) to accumulate. In theory, the more inaccessible mesocavernous voids would occasionally become anoxic placing strong selection on animals to adapt, which suggests that CO₂ may be a stressor in the evolution of troglobionts as has been shown in aquatic systems (Sarbu & Kane, 1995; Bishop et al., 2004).
Corroborating this theory is the observation that caves with elevated CO₂ concentrations commonly harbor highly diverse communities of troglobionts (Howarth & Stone, 1990; Deharveng & Bedos, 2000; Ginés, 2022).

Cave temperature

Temperature regimes in terrestrial habitats have been investigated in several caves in temperate regions (e.g., Williams, 1954; Sanderson & Bourne, 2012; Kambesis et al., 2013; Culver & Pipan, 2014; Rau et al., 2015; McClure et al., 2020; Saccò, Blyth, Humphreys, Cooper et al., 2021; Lipar & Ferk, 2022), but there are few data from tropical caves (McClure et al., 1967; Howarth, 1982; Ladle et al., 2012; Culver & Pipan, 2014; Mejía-Ortíz et al., 2020). Except for temperature changes caused by air or water flow, most previous cave temperature data were simply reported without identifying the source of heat or an analysis of the dynamics of heat exchange.

The temperature within caves is generally near the mean annual surface temperature (MAST) over the cave, but many factors alter local cave temperatures. For example, the temperature in the entrance, twilight, and transition zones fluctuates in response to weather and diurnal and seasonal changes. Also, dead-end passages that trend upslope may trap heat and are warmer than expected, whereas downward sloping passages trap cooler air (Williams, 1954; Cigna, 2004).

Excess heat enters caves with incoming water and air, respiration by resident organisms (including plant roots), composting of organic material, and geothermal energy. In addition, caves in iron ore deposits can be heated by exothermic reactions between the ore and incoming water (Piñol et al., 2022). Some of the excess heat leaves the cave by air flow and exiting water, especially in the more open caves and those with several entrances. Heat also escapes slowly via conduction upwards into the overlying rock. Incoming water and moist air can significantly change the deep zone temperature (Howarth, 1982; Saccò et al., 2021), but temperature change is attenuated towards MAST with increasing distance from the input (Howarth, 1982; Kambesis et al., 2013). Both liquid water and water vapor have such a high specific heat capacity compared to dry air and the substrate, that pulses of incoming water from moist air, rain, or sinking streams have a much larger effect on cave temperatures than incoming dry air.

Temperatures in the deep zone are relatively constant but may change slowly due to weather events on the surface. The deep zone is often warmer than expected. The additional heat is generated by respiration and decomposition of organic material, residual heat from the input of warm water, retention of heat by passage shape (e.g., constrictions limiting air circulation and dead-end upper-level passages), and from geothermal energy. In addition, caves with high concentrations of CO₂ are usually warmer than expected since CO₂ absorbs and stores heat.

Large colonies of roosting bats and birds can raise the temperature by 10°C or more and maintain high humidity of the roost by their body heat and respiration (Harris, 1970; Rodíguez-Duran, 1998; Tejedor, 2005; Moulds, 2006; Lundberg & McFarlane, 2009; Ladle et al., 2012; Torres-Flores, 2012; Piñol et al., 2022). Such caves are classed as “hot caves” (Tejedor, 2005; Ladle et al., 2012). The heat generated in large guano deposits explains in part the scarcity of highly cave-adapted species in these habitats. The conventional explanation for the paucity of troglobionts associated with large deposits of guano is the belief that troglobionts are adapted to exploit food-poor environments (Pouslón & White, 1969; Hüppop, 2000); however, this rationalization seems unlikely as all organisms continually evolve towards greater energy efficiency. Theory and empirical evidence reveal that organisms exploiting nutrient rich resources often display a greater reduction of characters than related organisms exploiting oligotrophic habitats (e.g., Steffan, 1975). More realistic causes for the observed avoidance of guano by troglobionts include the following:

• Competition from the huge populations of guanophiles (Deharveng & Bedos, 2000).
• The high temperature may repel stenothermal animals (Moulds, 2006).
• Large guano deposits tend to dry out as the added heat evaporates the excess water (Moulds, 2006), which makes the habitat unsuitable for troglobionts. Deposits of guano where there is sufficient moisture and stable air (i.e., the deep zone) can support troglobionts, at least on swampy deposits (Chapman, 1982) and along the margins (Deharveng & Bedos, 2000).
• Troglobionts characteristically are especially sensitive to being touched and to any nearby movement. These behaviors cause them to avoid large concentrations of antagonistic animals.
• Setting nutrient-rich baits in oligotrophic habitats often attracts large numbers of troglobionts (Howarth & Stone, 1990).

Geothermal heat from deep underground attenuates as it rises and is small and difficult to measure near the surface, averaging about 0.087 W/m² (Davies & Davies, 2010). In comparison, the global average from solar radiation is approximately 240 W/m². The increase in temperature by geothermal heat near the surface is influenced by heat capacity and conductivity of the substrate as well as by surface perturbations, such as climate, weather events, topography, hydrology, erosion, and sedimentation (Lucazeau, 2019). In the entrance, twilight, and transition zones of caves, the effect of this heat flow is obscured by exchange of air and water with the surface. However, in the deep zone, the small input of heat from below would increase the cave temperature. Geothermal heat increases with depth, so that deeper caves receive more heat than shallow caves. Young lava tubes and caves in active geological settings can receive additional heat from residual hot magma below the caves (e.g., Levin, 2015).

Solar radiation can increase the surface temperature, especially of exposed rock; however, this heat is not conducted directly into underlying voids, because
land surfaces are poor heat conductors and because heat is generally conducted upwards. However, this surficial heat can warm the air and water that subsequently enters caves.

Under stable, moist conditions occurring in the deep zone, the atmosphere would remain saturated unless disturbed. However, the added heat from decomposing organic matter and geothermal energy raises the temperature of the floor. The increase in temperature and evaporation rate creates a supersaturated atmosphere near the floor. Since water vapor is less dense than air and absorbs heat, the warm, supersaturated air will rise and mix with the cave atmosphere (Piló et al., 2022). The excess water vapor can condense on the walls and ceilings (Lundberg & McFarlane, 2009; Piló et al.; 2022). This cycling of water between the floor and ceiling explains in part the foggy atmosphere and the observed constant wetting of the walls and ceilings.

The effect of this heat flux is much greater in tropical caves than in temperate caves since warm air can hold more moisture and since the potential evaporation rate of water increases nearly exponentially with rising temperature. For example, at standard atmospheric pressure at sea level, saturated air at 25°C contains 23.1 g of water vapor per cubic meter, and at 25.5°C, the amount increases 0.6 g to 23.7 g. At 15°C, saturated air holds 13.3 g, and at 10°C saturated air holds 9.4 g. In the tropics, even a fraction of a degree difference between floor and ceiling temperature is sufficient to maintain the water vapor cycle.

Evaporation is proportional to saturation deficit (difference between the actual vapor pressure of air and the vapor pressure at saturation at a given temperature and barometric pressure); whereas condensation is proportional to relative humidity. Thus, evaporation and condensation of water occur simultaneously, and which process predominates depends on available moisture and the temperature differential.

**Winter effect**

The dark zone in caves sometimes can be divided into two distinct zones: transition and deep zones that are distinguishable by potential evaporation rate. That is, in the transition zone, the atmosphere is frequently desiccating, and the cave passage remains dry; whereas in the deep zone, the air remains saturated, and substrates remain wet. The boundary between these zones is often dynamic and shifts with the seasons and extreme weather events. During summer in temperate regions, warm moist outside air entering caves mixes with cooler cave air and becomes saturated or even supersaturated; and a transition zone is rarely present. But during winter when cold dry air enters caves, it warms, which increases evaporation creating a transition zone. The desiccating environment forces the more specialized cave animals to retreat further into the cave (Barr & Kuehne, 1971; Cigna, 2004; Ginés, 2022).

However, in the tropics, winter occurs nearly every night (Howarth, 1980). That is, night-time temperature usually falls below the cave temperature; and therefore, a transition zone is often present. The early cave biologists did not realize this and failed to search far enough from entrances. Also, because of the higher temperatures that result in higher potential evaporation rates, the transition zone is larger and more pronounced in tropical caves than in temperate caves. In both temperate and tropical caves, the winter effect is more pronounced in larger caves with a single or only a few well-separated entrances. In short horizontal caves with multiple entrances, the winter effect may be difficult to detect (Mejía-Ortíz et al., 2021).

The winter effect is enhanced in the tropics by the atmospheric tide, which is caused by the heating of the atmosphere by the sun and by rotation of the Earth (Oberheide et al., 2015). These tides occur twice daily, and due to the time lag in heat absorption, high pressure occurs at approximately 10:00 and 22:00 h local time, and low pressure occurs circa 4:00 and 16:00 h at the latitude of Hawai‘i. Except when disturbed by storms, the tide is often conspicuous in the tropics, whereas it becomes weaker towards the poles from the reduced insolation, slower relative rotation, changing daylength, and the episodic low- and high-pressure fronts. Even though the tide is weak, that is only a few 100 hPa between high and low, air flow in and out of large volume caves would be significant (Cigna, 2004). Surface winds can also push or pull air into and out of caves (Gomell et al., 2021).

The tropical winter effect is so conspicuous in tropical caves that I often detected the change in airflow and especially its cooling effect as the evaporation rate increased at night. I tested the phenomenon by setting three hygrothermographs, one each in the twilight, transition, and deep zone within Charcoal Cave at ~800 m elevation on Hawai‘i Island (Fig. 2, left) (Howarth, 1982). The instruments recorded data continuously for 15 days. The potential evaporation rate was measured continuously during the same period with two Piché atmometers set at each site, each with a 6 cm diameter filter paper disc (Fig. 2, right). Each atmometer was fitted with a 15 cm plastic disc, which served as an umbrella protecting the filter paper from drips. The data from the two atmometers at each site were averaged. Piché atmometers integrate airspeed, temperature, barometric pressure, and saturation deficit of the atmosphere to accurately measure relative potential evaporation rate.

The temperature and RH data during four days between 27–31 August 1979 are shown in Fig. 3. The temperature varied slightly in the twilight zone but was constant deeper in the cave. The RH, however, demonstrated a strong tropical winter effect with RH dropping precipitously each night in the twilight zone. The drop in RH was attenuated deeper into the cave with a significant time lag of one to two hours as the passage dried.

Figure 4 presents plan and profile maps of the cave, along with the locations of the study sites, and atmometer data during the same period. The potential evaporation rate decreased nearly hyperbolically in proportion to distance from the entrance and in proportion to the hygrothermograph data. The mean
potential evaporation rate at the deep zone station was only 0.15 cm³ per day. Also, both atmometers and umbrellas at the deep zone station were wet, indicating that condensation had occurred. During the study period, specialized cave animals were found only beyond 165 m from the entrance, where the interpolated evaporation rate was less than 0.16 cm³ per day.
**Discovery of tropical troglobionts**

According to conventional theory, the discovery of troglobionts in Hawaiian lava tubes was unexpected (Howarth, 1972). The islands were too young, and lava tubes too ephemeral and inhospitable (Fig. 5). Isolation between cave and surface populations was absent. Conspicuous food resources, such as cave-roosting bats and crickets and sinking rivers were absent. And finally, typical cave taxa found in continental limestone caves are poorly represented in the native fauna. The native fauna of Hawai‘i descended from vagile sun-loving taxa able to cross the 1000s of km of open ocean.

The discovery of the Hawaiian and other tropical cave faunas called into question the paradigm that troglobionts evolved from populations that were isolated in caves after their surface populations were extirpated by a change in the surface environment. The conventional theory was corroborated by the observation that cave populations were far smaller than surface populations, and therefore, if not isolated, any adaptations to cave-life would be swamped by mating with surface relatives. Also, the extreme reductive adaptations displayed by troglobionts were assumed to require a long time (Vandel, 1965; Barr, 1968). The latter assumption has been refuted by studies demonstrating that characters can be rapidly lost during relaxed selection (Carson et al., 1982); that the loss or reduction of a complex structure can occur following a deleterious mutation of any of the loci required for its development (Culver & Wilkens 2000); and that small changes in regulatory genes can have large heritable phenotypic effects (Rice & Rebeiz, 2019).

If not extinction of local epigean populations, what was the isolating mechanism that allowed tropical cave species to adapt? Two clues provide an answer. First, the discovery that the major habitat for most troglobionts is not caves, but the vast anastomosing system of intermediate sized voids (mesocaverns). Therefore, the populations of cave animals may be many times that of surface relatives (Howarth, 1983; Howarth & Wynne, 2022). Second, subterranean habitats are stressful for most surface animals, not only by the abiotic environment (especially darkness and humidity, but also by the absence or inappropriateness of the cues used to find food, reproduce, and escape threats. For example, cracks and pools act as pitfall traps to lost surface animals. Thus, nutrients sinking or washing underground are inaccessible to most surface animals.
Mesocaverns

During the initial surveys on the island of Hawai‘i, troglobionts were found in a 90-year-old lava tube. Since it was unlikely that these species could disperse on the surface, they were believed to live in inaccessible voids within lava flows. Exposed layers of lava flows, as well as geological evidence, indicate that young cavernous basaltic lava flows enclose a vast anastomosing system of voids of variable sizes from cave-size passages to gas vesicles (Howarth, 1983; Howarth & Wynne, 2022). The intermediate size voids (i.e., mesocaverns) could serve as suitable habitat for troglobionts. We tested this by constructing a nearly airtight screen to restrict air flow into the dark passage of a short, dry cave on the island of Kaua‘i (Fig. 6). The cave was one-half kilometer from the nearest inhabited cave. We added water and monitored the cave for animals. Within two months, troglobionts had colonized the cave confirming our hypothesis. We have also found troglobionts in lava tubes as young as seven months; in fact, when the lava flow and cave were still warm. In addition, mesocavernous voids as habitat for troglobionts has been substantiated in temperate regions (Ueno, 1977; Juberthie et al., 1980; López & Oromí, 2010).

Adaptive shifts

The discovery of troglobionts with epigean relatives still extant supports an alternate theory, which posits that, rather than being relicts stranded in caves by extirpation of their surface relatives, the ancestors of troglobionts actively entered subterranean voids and adapted to exploit resources there (Howarth, 1987; Rivera et al., 2002). This scenario fits the well-supported model of evolution by adaptive shift across a steep environmental gradient (Craddock, 2000; Rane et al., 2015; Howarth et al., 2019; Hager, et al., 2022).

For example (Fig. 7), nymphs of cixiid planthoppers have piercing mouthparts and drill into tree roots to suck xylem sap. They do not feed on root exudates. Epigean adults emerge into surface environments to disperse and reproduce. In cavernous substrates, nymphs may follow roots deep underground. However, emerging adults of epigean species are unlikely to make their way to the surface. Over time, some of these waifs may survive, find mates and reproduce underground; and BINGO, a vast new habitat and new resources become available to them (Howarth et al. 2019).
Howarth

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pale and blind with flightless females living in the
depth zone of lava tubes on the islands of Hawai'i and
Maui; and a troglophilic form living in the entrance
and twilight zones in the same caves (Fig. 8). The two
forms can be distinguished even when several meters
distant as the eyes of the twilight zone morph shine
red in reflected light, whereas the eyes of the cave
morph display no eye-shine. Long complex caves often
support a kaleidoscope of intermediate morphs. DNA
analyses revealed that all populations represent a
single polymorphic species (Schrankia howarthi)
Davis & Medeiros, 2009), which hybridizes (Medeiros et al.,
2009). Thus, in contrast to the situation discovered
with cixiid planthoppers, mating behavior may not be
involved in the adaptation of the moth to live in caves.
A possible mechanism for maintaining the divergence
of the two adaptive forms is a chromosomal inversion
that prevents recombination of the genes involved
in the adaptive traits (Hager, et al., 2022). Note that
if the cave morph becomes extinct, there would be
no evidence that this cave moth ever evolved. If the
troglophilic form perished, the result would match the
relict hypothesis.

Cave and surface populations of moths in the genus
Schrankia provide another example. Two distinct
morphologies exist: a cave-adapted form, which is

As additional precise analyses comparing cave
and surface populations are completed, further
examples of parapatric speciation will be found.
For example, Schilthuizen et al. (2005) compared
mtDNA between cave and surface populations of the
terrestrial snail, Georissa saulae (van Benthem-
Jutting, 1966), and found evidence that the cave
population represented an undescribed species
that descended directly from G. saulae. Like the
Schrankia example, the two populations hybridize
across the ecotone.

Some adaptive shifts are surprising, such as the
underground tree crickets in Hawai'i, which migrated
from trees to caves where they prefer to forage on
the ceiling (Fig. 9). Even more bizarre is the noted
big-eyed hunting spider, Adelocosa anops
Gertsch, 1973, from Kaua'i. It seems inconceivable
that a lycosid, a family known for its large eyes
would become trogloorphic; yet it has happened
independently twice in Hawai'i: A. anops on Kaua'i
and Lycosa howarthi Gertsch, 1973, on Hawai'i I.

To date at least at least 18 native Hawaiian taxa
have independently invaded caves on two or more
islands, including pseudoscorpions (1), spiders (2),
crickets (2), planthoppers (3+), moths (1), millipedes
(1), springtails (2+), and isopods (2) (Gertsch, 1973;
Howarth, 1987; Christiansen & Bellinger, 1992;
These multiple invasions, along with other examples
in the Canary Islands (Oromí et al., 1991) Galápagos
(Peck, 1990), and elsewhere, indicate that the
colonization of caves and evolution of troglobionts
are general phenomena and not exceptional. In fact,
it is now recognized that caves and cave-like voids in
all regions and all types of substrates can support a
cave-adapted community if the habitat is extensive,
persists, and contains sufficient food resources
(Howarth & Wynne, 2022).
Cave-adapted species evolved from pre-adapted fauna native to each region, mostly by adaptive shifts to exploit a stressful underground niche. The isolation that allowed divergence from the ancestral surface populations was fostered by [1] parapatry across an environmental boundary; [2] erosion and tectonic events dividing the habitat; [3] dispersal to a new area; and [4] vicariance by extirpation of surface populations such as by climate change, habitat destruction, or by invading alien species. Factors that maintain the adaptive traits and facilitate divergence include [1] geographic isolation; [2] mating behaviors; [3] stressful subterranean environment; and [4] genetic factors such as chromosomal inversions.

**Conservation**

Conservation of cave species has been extensively reviewed (Elliott, 2000; Clements et al., 2006; Romero, 2009; Mammola, Cardoso, Culver, Deharveng, Ferreira, Fisser, et al., 2019; Wynne, Howarth, Mammola, Ferreira, Cardoso et al., 2021; Gillieson et al., 2022; Elliott et al., 2023), and a comprehensive review is beyond the scope of this contribution. However, I concur with the recommendation by Wynne et al. (2019) that researchers should provide relevant observations on conservation in their reports concerning caves and their fauna.

Subterranean species and ecosystems are vulnerable and threatened by novel environmental stressors. Novel perturbations are severe environmental stressors for which the ecosystem has had no or little previous experience. For example, the absence of a flood during the usual flood season may be more harmful to a cave community than would a severe flood during the normal flood season or a relatively minor flood occurring at an unusual time (Poulson & Kane, 1977; Lisowski & Poulson, 1981).

Important novel perturbations affecting subterranean communities include using entrances as refuse dumps (Fig. 10), changes in land use, mining, invading alien species, direct disturbances by visitors, and climate by change (Petty, 1976; Raedts & Smart, 2015).

Changes in land use directly and indirectly affect underground communities by altering water and nutrient inputs, as well as potentially impacting air flow. Transformations include conversions of the surface by urbanization, agriculture, forestry, and wildfire (Mammola et al., 2019; Clements et al., 2006; Geological Society of America, 2021).

Cave habitats are damaged or destroyed by mining, such as limestone for cement and marble, iron ore, and other minerals (Vermeulen & Whitten, 1999; Clements et al., 2006, Deharveng et al., 2018). Figure 11 demonstrates what happens when gold is discovered in a limestone tower.

Often overlooked in cave conservation work are the impacts of invasive alien species on cave resources, especially on vulnerable species and communities (Howarth, 1981; Howarth & Moore, 1984; Reeves, 1999; Moseley, 2009; Wynne et al., 2014; Howarth & Stone, 2020; Hoyt et al., 2021); however, interest and research on the issue is increasing (Nicolosi et al., 2023). A few troglobionts have been purposefully moved to new regions (e.g., Kocot-Zalewska et al., 2021). More attention to the issue is needed, including studies documenting impacts and monitoring cave communities to detect and, when necessary, control harmful alien species. Even epigean invasive species can impact cave communities by, for example, changing the species composition, hydrology, and reducing populations of trogloxenes on the surface (Elliott, 2000; Taylor et al., 2005; Geological Society of America, 2021; Cornwall, 2022). Alien plants can send roots deep into caves and disrupt host plant communities (Howarth et al., 2007). Alien diseases impact native tree species and trogloxenes that provide nutrients for cave communities (Asner et al., 2018; Hoyt et al., 2021).

In addition to the impacts of human activity on the surface, visitors and researchers can disturb or destroy cave resources (Elliott, 2023). Human visitors introduce foreign material and toxins, trample and break resources, and harm cave life. Loss of troglobione communities (such as bats abandoning a cave after a disturbance) can have devastating effects on cave ecosystems (Deharveng & Bedos, 2019). Importantly, researchers and visitors should be sensitive and not harm vulnerable resources in other disciplines, such as sacred cultural sites, archaeology, geology, and paleontology (Stone et al., 2007).

Direct effects of climate change on cave communities are largely unknown since cave habitats are buffered from temperature changes on the surface except for the fauna of glacier caves (Howarth, 2021) and cave systems with seasonal or perennial ice (Iepure, 2018).
for most, a few representatives of each species should be collected from each locality. This will allow future workers to confirm the presence and distribution of species. Furthermore, as taxonomy improves, the identity of the specimens may need to be revised. The latter is especially important for cave species to confirm or falsify the assumption that cavernicoles are narrowly distributed. Recent DNA analyses have shown that many cave species are suites of cryptic species listed under one name. Thus, it is critically important to protect all populations so that crucial evidence on the evolution of biodiversity is not lost.

A related issue is that past biological surveys of caves have been incomplete (Moseley, 2009; Wynne et al., 2018). All too often, taxa are omitted from surveys because of the difficulty in collecting and assumptions that the taxon is accidentally in caves, and therefore unimportant. Caves in each region harbor representatives of the local native fauna. Tropical caves have added new higher taxonomic groups (such as arachnids, moths, crickets, planthoppers, and bugs) to the list of troglobionts and other cavernicoles. What other taxa are we missing?

**Recommended actions**

Before developing management programs, conservationists and ecologists should assess how the impacts of novel stressors affect the cave community, not as researchers and managers subjectively perceive them. For instance, habitat restoration programs often use soil enhancement and increased vegetation cover. Such actions can have severe repercussions in underlying subterranean habitats (Pellegrini et al., 2016).

Evolutionary and ecological studies, and conservation programs are only as good as the taxonomy upon which they are based. Given the high taxonomic diversity in caves, well-preserved and cared for voucher specimens documenting the presence of a species are essential for the advancement of biospeleology. Well-known species may be photo- or visually documented, but...
Major gaps in the number of caves surveyed, i.e., the Recovitza impediment (Picetola et al., 2019) and the backlog of systematics research, i.e., the taxonomic or Linnean impediment (Giangrande, 2003) hinder advancing the science of biospeleology. For example, each new region surveyed has provided important new taxa and data on evolutionary ecology of caves as well as increased our understanding of cave biodiversity. Since each karst tower frequently harbors many endemic species (Hoch & Howarth 1989, Clements et al., 2006; Deharveng et al., 2018) and since there are many examples of cryptic species (Wessel et al., 2013, Mammola et al., 2019, the true biodiversity of subterranean ecosystems is grossly underestimated. The emerging DNA technology provides important tools to filling these lacunae, e.g., use of e-DNA in surveys will fill in gaps in faunal diversity of cave habitats (Lunghi et al., 2022). However, DNA analyses should complement not replace traditional morphological research.

Keep the common species common. They often are keystone species helping to maintain the health of the community (Deharveng & Bedos, 2019). They also enhance the aesthetics, research, and educational values of caves. Use whatever tools that are available for conservation. For example, a cave trap (or hazard) on a golf course on the island or Kaua‘i protects the United States endangered no-eyed, big-eyed hunting spider, the threatened terrestrial cave amphipod Spaeleorchestia koloana Bousfield & Howarth, 1976, and their associated species (Fig. 12).

Finally, assume nothing in science! One must survey habitats as thoroughly as possible before declaring any habitat barren.

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