The evolutionary dynamics of troglobionts: isolation, divergence, and speciation

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Abstract. Troglobionts, or obligate cave-dwelling organisms, exhibit remarkable evolutionary adaptations to the extreme and isolated conditions of subterranean ecosystems. These organisms, characterized by traits such as depigmentation, reduced vision, and enhanced sensory abilities, are highly specialized for life in caves and are unable to survive outside these environments. The geographical and ecological isolation of caves significantly influences the evolutionary trajectories of troglobionts, leading to genetic divergence and speciation through allopatric mechanisms. This paper examines the evolutionary implications of cave isolation, focusing on barriers to gene flow, the unique selective pressures within individual cave systems, and the resulting mosaic of evolutionary lineages. While most troglobionts are confined to single cave systems, rare cases of broader distribution reveal insights into subterranean dispersal mechanisms, such as historical connectivity, aquifer migration, and recent habitat fragmentation. The irreversible divergence of isolated populations underscores the role of caves as natural laboratories for studying speciation and adaptation. However, the high degree of endemism among troglobionts highlights their vulnerability to environmental disturbances. Conservation efforts are crucial to protect these ecosystems and preserve the evolutionary heritage of these organisms. This study emphasizes the interplay between isolation, evolution, and conservation in understanding the biodiversity of subterranean life.

Key words: allopatric speciation, cave isolation, conservation, evolutionary adaptation, subterranean ecosystems, troglobionts.

Introduction. Troglobionts, also known as obligate cave-dwelling organisms, represent some of the most fascinating examples of evolutionary specialization. These organisms have adapted to the unique and extreme conditions of subterranean ecosystems, such as perpetual darkness, limited food availability, and stable microclimates (Jureková et al 2021). However, their life histories and evolutionary trajectories are intrinsically tied to the geographical and ecological isolation imposed by their habitats. This paper explores the evolutionary implications of cave isolation, gene flow barriers, and speciation in troglobionts, alongside rare cases of broader distribution.

Permanent or temporary inhabitants of caves. Organisms inhabiting caves are classified based on their degree of adaptation to subterranean life and their dependence on the cave environment. These life forms can be categorized into three main groups (Lunghi et al 2020):

Troglobionts (or obligate troglofiles). Troglobionts are obligate cave-dwellers that live exclusively in caves and cannot survive outside this environment. They exhibit full adaptation to subterranean life, often characterized by specialized traits such as: lack of pigmentation (partial or complete albinism), reduction or absence of eyes, enhanced sensory capabilities (e.g., longer antennae, highly developed tactile or chemical sensory organs). Examples include certain species of cavefish, salamanders, and insects, such as the blind cavefish (*Astyanax mexicanus* (De Filippi, 1853), troglobiont form) or the cave beetle (*Leptodirus hochenwartii* Schmidt, 1832).

Troglophiles (or facultative troglofiles). Troglophiles are organisms capable of inhabiting both caves and surface environments, although they thrive in the subterranean setting due to favorable conditions such as food availability, humidity, and stable temperatures. While they lack the extreme adaptations of troglobionts, they may exhibit intermediate traits. Examples include certain species of spiders, beetles, and amphibians.

Trogloxenes (or accidental cave-dwellers). Trogloxenes are organisms that visit caves temporarily but cannot rely on them exclusively for survival. They typically use caves for shelter, feeding, or hibernation but depend on the external environment for reproduction and other life cycle processes. Examples include bats (which use caves as roosting sites), birds such as the cave swiftlet, and bears (for hibernation).

Geographical isolation and its evolutionary consequences. Caves, by their very nature, are isolated habitats. For most troglobionts, life outside a cave is not viable due to their specialized adaptations, such as loss of pigmentation, reduced eyesight, and heightened non-visual sensory capacities (Petrescu-Mag 2023; Bordea et al 2024). This strict dependence on cave environments severely limits their ability to migrate between distant cave systems. Consequently, populations of troglobionts inhabiting separate caves are effectively isolated from one another, preventing gene flow. This geographical isolation is a textbook example of allopatric speciation, where fragmented populations diverge genetically over time due to the lack of interbreeding.

The evolutionary divergence of troglobionts is further accelerated by the unique selective pressures within individual caves. Each cave system has its own microenvironment, including variations in temperature, humidity, and available nutrients, which impose distinct adaptive challenges. Over generations, these pressures drive genetic differentiation between populations, resulting in a mosaic of evolutionary lineages across cave networks. According to the evolutionary species concept (Simpson 1961; Wiley & Mayden 2000), each of these lineages, with its own unique evolutionary trajectory, can be considered a distinct species (Păpuc et al 2022). This approach challenges traditional notions of subspecies classification, as it elevates isolated populations to the rank of full species due to their independent evolutionary histories (Kottelat & Freyhof 2007; Kovacs & Petrescu-Mag 2022).

Mechanisms of limited distribution across multiple caves. While most troglobionts are confined to single cave systems, exceptions exist where a species is found in multiple, geographically separated caves. Such cases are rare but offer valuable insights into the mechanisms of subterranean dispersal. Next, we will see three primary explanations for these occurrences.

Historical subterranean connectivity. In some instances, the caves inhabited by a particular species were once part of a continuous subterranean network. Geological processes such as tectonic shifts, erosion, or sediment deposition may have fragmented this network, isolating populations in separate caves. This historical connectivity explains why genetically similar populations can exist in geographically distant locations.

Dispersal through aquifers. Aquatic troglobionts, such as certain crustaceans and fish, are capable of dispersing via subterranean water systems. Aquifers, which form extensive underground waterways, can act as corridors for migration between isolated caves. This mechanism is particularly relevant for species adapted to aquatic environments, where movement through water-filled passages is more feasible than over terrestrial terrain.

Recent habitat fragmentation. In some cases, a species may have occupied a broader subterranean habitat that has only recently become fragmented due to environmental changes. For example, fluctuations in water levels, human activities such as mining, or natural cave collapses can divide previously continuous populations into isolated groups. In such scenarios, the genetic differentiation between populations may still be in its early stages, explaining the presence of the same species in multiple caves.

The irreversibility of divergence. Once populations of troglobionts become isolated, their evolutionary paths begin to diverge irreversibly. Genetic drift, mutation, and localized selection pressures ensure that the gene pools of separate populations become increasingly distinct over time. Given enough time, this divergence leads to the emergence of entirely new species. The lack of gene flow not only accelerates speciation but also ensures that the evolutionary trajectories of these populations remain unique.

Moreover, the degree of divergence is often so pronounced that even closely related populations exhibit significant morphological, physiological, or behavioral differences. For example, troglobionts from different caves may display variations in body size, appendage length, or metabolic rates, reflecting their adaptation to specific cave conditions. These differences underscore the role of caves as natural laboratories for studying the mechanisms of speciation and adaptive evolution (Bordea et al 2024).

For instance, 31 new species of aquatic and terrestrial arthropods have been described from Movile Cave, Romania (Sarbu 2000; Nitzu et al 2016; Nae et al 2018). Four endemic spiders have so far been described from this ecosystem: *Agraecina cristiani* (Georgescu, 1989), *Hahnia caeca* (Georgescu & Sarbu, 1992), *Lepthyphantes constantinescui* Georgescu, 1989, and *Kryptonesticus georgescuae* Nae, Sârbu & Weiss, 2018 (Figure 1) (Nae et al 2018). Although caves, being poor in resources, have a low number of species, they continue to impress us with the large number of endemics that we discover in these unique habitats.

Figure 1. *Kryptonesticus georgescuae*, female. The male has not been observed or described yet (Nae et al 2018).

Implications for conservation. The high degree of endemism and specialization among troglobionts highlights their vulnerability to environmental disturbances (Whynne 2022). Habitat destruction, pollution, and climate change pose significant threats to these organisms, as their entire populations are often confined to single cave systems. Conservation efforts must prioritize the protection of cave ecosystems and recognize the unique evolutionary heritage of each troglobiont population (Gavriloaie et al 2016). Furthermore, understanding the genetic and ecological diversity within and between cave populations can inform strategies for preserving these ancient lineages.

Conclusions. Troglobionts exemplify the profound impact of geographical isolation on evolutionary processes. The impossibility of gene flow between fragmented populations drives speciation, creating a remarkable diversity of species adapted to the subterranean world. While rare cases of broader distribution reveal mechanisms such as historical connectivity and aquifer dispersal, the overall pattern remains one of isolation and divergence. These organisms not only offer insights into the principles of evolutionary biology but also underscore the importance of conserving the fragile ecosystems they inhabit.

Conflict of interests. The authors declare that there is no conflict of interest.

References

Bordea D., Brasovean I., Gavriloaie C., 2024 Extremophilic cave species: evolutionary relics of a hidden world. ELBA Bioflux 16(1):7-9.

Gavriloaie C., Rusu C., Petrescu-Mag I. V., 2016 The present day status of a remarkable area: Taușoare Cave, Romania. ELBA Bioflux 8(2):56-63.

Kottelat M., Freyhof J., 2007 Handbook of European freshwater fishes. Kottelat, Cornol and Freyhof, Berlin, 646 pp.

Kovacs E., Petrescu-Mag I. V., 2022 What is the species concept most currently accepted by zoologists? AES Bioflux 14(2):57-61.

Lunghi E., Ficetola G. F., Zhao Y., Manenti R., 2020 Are the neglected Tipuloidea crane flies (Diptera) an important component for subterranean environments? Diversity 12(9): 333.

Jureková N., Raschmanová N., Miklisová D., Kováč Ľ., 2021 Mesofauna at the soil-scree interface in a deep karst environment. Diversity 13(6):242.

Nae A., Sarbu S. M., Weiss I., 2018 *Kryptonesticus georgescuae* spec. nov. from Movile Cave, Romania (Araneae: Nesticidae). Arachnologische Mitteilungen: Arachnology Letters 55(1):22-24.

Nitzu E., Giurginca A., Nae A., Popa I., Baba Ș., Meleg I. A., Vlaicu M., 2016 The catalogue of caves with endemic cavernicolous arthropod fauna of Romania. Travaux de l'Institute de Spéologie „Émile Racovitza" 55:3-62.

Păpuc T., Balint C., Petrescu-Mag R. M., 2022 Why is *Poecilia wingei* a distinct species from other species of the genus? Poec Res 12(1):29-33.

Petrescu-Mag I. V., 2023 The olm (*Proteus anguinus*) and cave life. ELBA Bioflux 15(1):8-9.

Sarbu S. M., 2000 Movile Cave, a chemoautotrophically based groundwater ecosystem. In: Ecosystems of the world - subterranean ecosystems. Wilkens H., Culver D. C., Humphreys W. F. (eds), Elsevier Science, Amsterdam, pp. 319-343.

Simpson G. G., 1961 Principles of animal taxonomy. Columbia University Press, New York, 247 pp.

Wynne J. J. (ed), 2022 Cave biodiversity: speciation and diversity of subterranean fauna. John Hopkins University Press, 352 pp.

Wiley E. O., Mayden R. L., 2000 The evolutionary species concept. In: Species concepts and phylogenetic theory. Wheeler Q. D., Meier R. (eds), Columbia University Press, New York, pp. 70-89.

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