Cave Biology: Science and Exploration

ANA SOFIA REBOLEIRA, NATURAL HISTORY MUSEUM OF DENMARK (ZOOLOGICAL MUSEUM), UNIVERSITY OF COPENHAGEN, DENMARK.
*CORRESPONDING AUTHOR: SREBOLEIRA@SNM.KU.DK

The perpetual darkness of caves remarkably reduces the energy content and consequently the complexity of the biological processes, providing unusually simplified models for testing hypotheses.

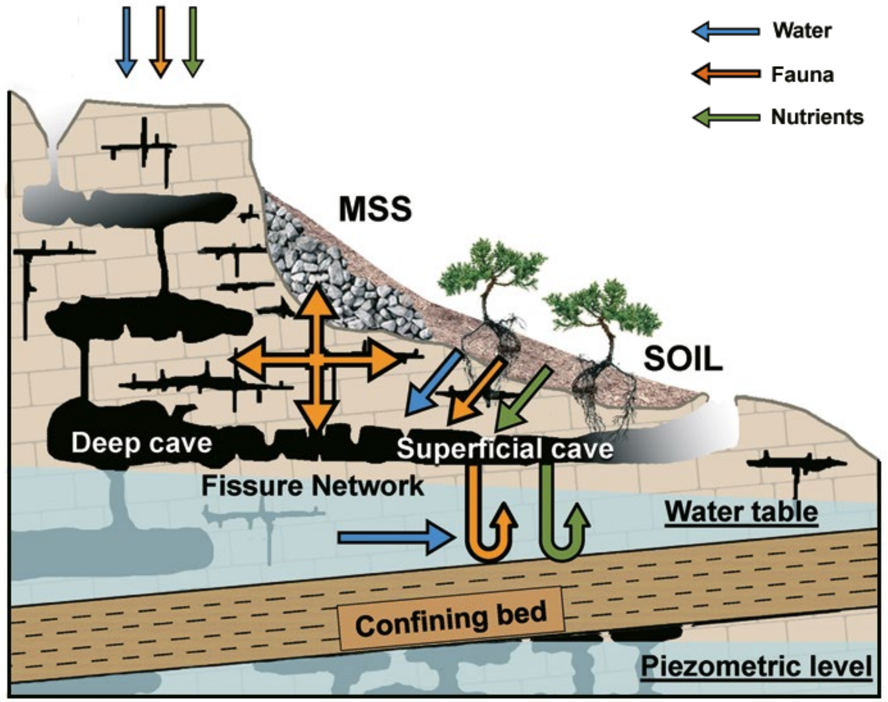

Fig. 1. Profile of the subterranean ecosystem in limestone (adapted from Sendra et al 2014).

Subterranean habitats

The genesis of subterranean habitats is driven by chemical or physical phenomena and by the action of tectonic forces in different types of rock, and they may be filled with air or water. Caves are the better-known type of subterranean ecosystems, especially the ones developed in karst landscapes. Karst lithology (= limestone where the rock has been partly dissolved by water running through it) is estimated to occupy 15% of the Earth's surface. Other types of caves are also known to be important substrates for life, such as the volcanic caves formed within the cooling lava flows or the caves in quartzite rocks.

The concept of a cave is commonly defined under an anthropometric perspective, as a natural subterranean cavity through which humans are able to move. Nevertheless, invertebrate animals living in the underground are much smaller. In fact, subterranean ecosystems are composed of wide networks of fissures and cracks inaccessible to humans along all the bedrock, but also more close to the surface in the empty spaces between unconsolidated rocks, the so-called shallow subsurface habitats (mss) (Fig. 1). The relative inaccessibility of the subterranean environment is a challenge and cave exploration provides a continuous source of new windows into these ecosystems.

Environmental parameters in caves are very stable throughout the year. The lack of light is characteristic of all subterranean habitats, as a consequence the primary production in the subterranean environment is scarce or non-existent, food resources are limited and mainly consist of material generated outside the cave. The temperature variation is low and the humidity close to saturation, increasing near the floor and varying with the surface proximity and due to air mass movement.

The temperature in caves varies with the altitude, number of entries, active circulation of water streams and the shape of subterranean galleries, factors that influence the movement of air masses inside the cave. Usually, the cave temperature approximates the annual average surface temperature of the locality. The closer to the surface, the greater is the annual temperature variation, and the thermal fluctuation is higher in the shallow subsurface habitats.

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Classification of subterranean organisms

The communities living in caves are composed of species that are adapted to the subterranean life to different degrees. Worldwide, many species evolved towards a strictly subterranean life-style, developing convergent morphological and physiological adaptations. These adaptations are called troglomorphisms and include regressive traits as the loss of eyes, pigment and circadian rhythm (i.e., day and night rhythm), but also the increase of sensorial organs and lifespan, as well as changes in their reproductive strategies.

The Danish zoologist Jørgen C. Schiødte established the first ecological approach to the classification of cave inhabitants in 1849, an important work that was used by Darwin to explain how environmental conditions drive natural selection. Nowadays, we commonly refer to cave-adapted animals as troglofauna for terrestrial and stygofauna for aquatic organisms (Fig. 2). These include representatives of groups such as nematodes, molluscs, annelids and the largely dominating arthropods. The remaining animals found in caves, the non-troglobionts, are commonly called troglo (or stygo) -xenes ('strangers') or –philes ('friends'), if their occurrence in the subterranean environment is accidental or frequent, but not obligatory.

Fig. 2. Animals adapted to the subterranean habitat, from upper left to right: pseudoscorpion, spider, mollusc, millipede, centipede, crustacean, and a bristletail (a primitive, wingless insect).

Ecology and evolution

Thousands of species have been described from subterranean ecosystems over the last decades. All have in common a high degree of endemism, as a result of multiple independent colonisations of the underground environment, in different time periods. Subterranean animals are estimated to correspond to 8% of the diversity of European aquatic fauna, and there are more species of crustaceans in groundwater than in surface freshwater.

From a paleogeographic point of view the cave fauna can be seen as a »time capsule«, preserving the record of earlier climate conditions, expressed in their present distributions and in their phylogenetic relations, by representing lineages already extinct on the surface, known as the 'living fossils'.

The tradition of subterranean studies in Europe is reflected in number of cave records, making Europe the richest continent in number of subterranean species known. Of about 5,000 subterranean species currently known, 40% are in Europe, 24% in Asia, 20% in North America and 10% in Africa. To this fact contributes the large development of biodiversity studies in Europe. A complex combination of geological and climate factors, such as the Messinian crisis (the drying out of the Mediterranean more than 5 million years ago) and the inter-glacial periods of the Pleistocene during the last 2.5 million years, appear to have enhanced the colonization of the subterranean environment at different times and areas of Europe.

Nutrient resource limitation and reliance on input of organic matter from the outside inhibits the growth of subterranean populations. Besides abundance of individuals, species richness is also low. There are few caves in the world inhabited by more than 20 species of troglobionts or stygobionts, a threshold considered to define a subterranean biodiversity hotspot. Food chains are composed of a few trophic levels and in the absence of photosynthesis, cave species are detritivores or predators. The number of predators is lower, the degree of generalism is very high and cases of cannibalism are observed.

Two main theories explain the origin and evolution of cave animals. The hypothesis of the climate relict suggests that troglobiont populations derived from troglophiles who were isolated in the subterranean environment while

Fig. 3. Cave biologist squeezing through a narrow pit deep in the world's deepest cave in Western Caucasus.

their surface relatives became extinct as a result of climate change. In contrast, the adaptative shift hypothesis is used to explain the troglomorphism in species with close relatives on surface in which the colonization of subterranean habitats occurs driven by exploration of new niche resources. On the other hand, evidence of later recolonization of the surface by cave-adapted animals questions the supposed irreversibility of troglomorphism, seen previously as an evolutionary dead end towards life in the underground.

Conservation

The proportion of relicts and endemic species in caves is higher than in any other habitat. Due to low accessibility, subterranean ecosystems constitute one of the most poorly known and unprotected natural resources of our planet.

Fig. 4. Tropical cave in Maubisse district, East-Timor.

These characteristics increase the risk of extinction due to human induced disturbance, and the subterranean biota is accordingly classified as a valuable and threatened biological heritage.

Caves are always connected with the surface through the entrance or throughout a network of cracks and microfissures allowing percolation of substances to the subterranean environment. It is important to better understand the subterranean ecosystems, because we depend on them for a range of functions, especially those related to groundwater quality.

Around 97% of the global resources of unfrozen freshwater on Earth are stored in the underground, where groundwater organisms play a key role in global freshwater purification. They provide important services for human health, and ensure the ecological balance of groundwater-dependent ecosystems, such as

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Fig. 5. Cueva del Viento-Sobrado, the world's 4th largest lava tube, Tenerife, Canary Islands.

Fig. 6. Sampling cave fauna in alpine caves with extreme low temperatures.

springs, rivers and lakes. Therefore, maintaining a high quality of groundwater is dependent on the integrity of its unique biodiversity. Unfortunately, these hidden aquatic ecosystems are particularly exposed to all kinds of pollutants originating from agriculture as well as domestic and industrial activities. The water that reaches the surface quickly infiltrates into the underground carrying multicomponent chemical »cocktails«. Due to the high endemism in the underground, it is urgent to understand the impacts of human activities in subterranean biodiversity across different types of climatic, geographical and impacted areas, to generate a framework for future ecological assessment of subterranean ecosystems, ensuring their sustainability.

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