

CAVES AS BIOLOGICAL SPACES

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Abstract

Caves are defined as natural underground or underwater hollow places with an opening. Depending upon their geologic origin, caves can be classified as limestone (karstic), sandstone, hydrothermal, lava, glacier, or tectonic. The total number of caves of all types around the world has been estimated in several hundred of thousands. Given that number it is not surprising that tens of thousands of biological species have been described in such environments. There is little doubt that caves and other hypogean (subterranean) environments represent unique spaces in the phenomenon of life. The aim of this article is to discuss caves as biological spaces.

Introduction

Caves are defined as natural underground or underwater hollow places with an opening¹. For cavers, a cave is any natural hole, vertical (also known as potholes), horizontal, or a combination of both, which can be penetrated by humans. Although this definition is arbitrary and anthropocentric, it is a practical one since only those caves that can be penetrated by humans can be studied directly ([Romero 2009, p. 218](#)). This definition does not include mines or tunnels or any other cavity of anthropogenic origin. Depending upon their geologic origin, caves can be classified as limestone² (karstic³), sandstone, hydrothermal, lava, glacier, or tectonic.

Although we do not know the total number of caves in the world, according to Juberthie ([2000, p. 19](#)) there are about 130,000 karstic caves in Europe alone. Therefore, the total number of caves of all types around the world must be in the hundred of thousands. Given that number it is not surprising that tens of thousands of biological species have been described in such environments. These organisms have also been the subject of many studies on evolution, physiology, and ecology ([Romero 2009](#)).

Thus, there is little doubt that caves and other hypogean⁴ (subterranean) environments represent unique spaces in the phenomenon of life. The aim of this article is to discuss caves as biological spaces.

Diversity and Distribution

Given the large number and vast distribution of caves worldwide it is not surprising to find great varieties of them from a geological viewpoint. Most caves are formed in limestone areas characterized by carbonate rocks. Their process of formation (speleogenesis⁵) is the result of rock dissolution by acidic waters (most rainfall is acidic) and from CO₂ from microbial respiration in the overlying soil – strongly influenced by temperature- generating faster rates of speleogenesis in the tropics (Klimchok et al. 2000, Palmer 2007). The landscape formed by these types of rocks constitutes about 15% of the Earth's surface,

¹ **cave:** It is a natural underground or underwater hollow place with an opening that is more or less horizontal. For cavers, a cave is any natural hole, vertical (also known as potholes), horizontal, or a combination of both, which can be penetrated by humans. This definition does not include mines or tunnels or any other cavity of anthropogenic origin.

² **limestone caves:** Caves that occur in sedimentary rock containing at least 50% calcium carbonate. Non-pure (almost 100% calcium carbonate) limestone caves have muddy limestone. Many limestone caves are porous and, therefore, permeable and can be modified by water.

³ **karst:** A soluble-rock landscape product with a combination of high rock solubility and well-developed secondary solubility in well-drained areas. Karst areas are characterized by usually having sinking streams, caves, closed depressions, flute rock outcrops, and large springs.

⁴ **hypogean:** The subsurface or subterranean environment as opposed to the **epigean** one. It also applies to organisms living there.

⁵ **speleogenesis:** The origin and development of caves.

hence their ubiquity. Additionally we find other more unique types of caves such as lava tubes, ice caves, and underground lakes and rivers without direct access by humans (phreatic⁶, artesian⁷).

We can also find variation in terms of size, from small crevices to extraordinarily long ones as is the case of Mammoth Cave in Kentucky, the world's largest cave, whose mapped passages account now for about 580 kilometers.

In terms of structure caves can be horizontal, vertical, multilayered or a combination of these. They can be found in the form of a single cavity or an extensive underground network with multiple connections to the epigean⁸ environment.

Regarding how their spaces are filled they can be air-filled, water-filled, and mixed. The amounts of water can vary greatly, particularly in tropical areas due to extreme variations of precipitation. For those that are aquatic in nature we find freshwater, marine, and anchialine⁹. The latter refers to those with restricted exposure to open air, one or more connections to the sea, and influenced by both the marine and terrestrial ecosystems with which they interface. Anchialine habitats are common in volcanic or limestone bedrocks (Sket 1996a) and are found in a wide range of latitudes around the world.

Given their diversity on all of the above-mentioned accounts, caves also contain a great variety of biodiversity of which we do not know its full extent (see Culver and Sket 2000). This is the result of lack of exploration of many of them, particularly those in tropical environments where biodiversity and biomass is higher, and the other is the lack of accessibility of many of them. Case in point is The Edwards Aquifer in Texas and northeastern Mexico. This aquifer¹⁰ resides in the Edwards limestone and is about 282 km long and from 8 to 64 km wide. It consists of a recharge area and an artesian area (Longley 1981). More than 40 hypogean species have been described for those waters, from crustaceans to fishes. Because we cannot access this environment through direct human penetration, what we know about its biodiversity is based only on what can be collected from springs¹¹ or pumped out from wells. If one considers that hypogean waters represent 97% of the world's freshwater, the potential for underground life in this type of environment is enormous (Marmonier *et al.* 1993).

There is also a great deal of variation in terms of biodiversity indexes across hypogean environments in the world. Table 1 (see following page) summarizes the information of hypogean faunal surveys in selected regions of the world.

Several conclusions can be drawn from this information: one is that there is an increasing proportion of troglomorphic species as the region is located closer to the equator; the exception is Slovenia, which can be explained by the fact that almost the entire country is karstic in nature and that such a system is probably the most studied in the world, explored much longer than Mammoth Cave itself. Another conclusion is that as we start to survey more in full caves in tropical environments, we can expect to find higher biodiversity indexes latitudes. It is not uncommon to find tropical caves with ceilings literally covered by bats, the soil covered by myriads of invertebrates, and water teeming with aquatic life, including hundreds if not thousands of fish in a single pool. One confounding variable that may affect the notion that biodiversity in caves is inversely proportional to latitude is that most karstic areas in the world are in temperate regions (see the frontispiece of Wilkens *et al.* 2000). Despite that, data summarized in Table 1 supports the notion that cave biodiversity is higher in the tropics.

Despite the facts that: (1) cave biodiversity in the tropics has yet to be surveyed for the most part; (2) phreatic environments are inaccessible to direct human exploration; and (3) most cave biological studies concentrate on species that show some level of troglomorphisms (mostly blindness and depigmentation)

⁶ **phreatic:** Underground natural source of water. The phreatic zone is also the zone of saturated rock below the water table.

⁷ **artesian:** It is applied to water obtainable by artesian boring. This term is frequently used interchangeably with phreatic.

⁸ **epigean:** The surface environment as opposed to the hypogean one. It also applies to organisms living there.

⁹ **anchi(h)aline:** This term refers to aquatic habitats with a restricted exposure to open air, with one or more non-surface connections to the sea; they are thus influenced by both the marine and terrestrial ecosystems with which they interface.

¹⁰ **aquifer:** A body of permeable rock (e.g. unconsolidated gravel or a sand stratum) that is capable of storing significant quantities of water that is underlain by impermeable material and through which groundwater moves. Aquifers are permeable enough to transmit groundwater yielding such waters to wells and springs (see **artesian**).

¹¹ **spring:** The natural point of emergence of underground water.

and/or on species easily visible because of their size, the number of cave species is in the tens of thousands ([Romero 2009, Chapter 2](#)).

TABLE 1 Summary information of hypogean faunal surveys in selected regions of the world. Latitude is represented by the average for the region in question. Troglomorphic¹² refers to species showing some phenotypic adaptation to the cave environment.

Area/Cave Surveyed	Number of Non-troglomorphic Species	Number of Troglomorphic Species and % of Total	Average Latitude	Source
Southern Ontario, Canada	301	0 (0%)	50°	Peck 1988
Slovenia	1,066	190 (15.13%)	46°	Sket 1996b
France	4218	218 (4.91%)	46°	Juberthie and Ginet 1994
Pennsylvania, USA	131	15 (10.27%)	41°	Mohr 1953 , Holsinger 1976
New South Wales, Australia	422	83 (16.5%)	33°	Thurgate et al. 2001b
Northern Mexico	143	32 (18.29%)	25°	Reddell 1982
Eastern Australia	148	82 (35.65%)	20°	Thurgate et al. 2001a

Cave Ecosystem Structure

When dealing with proposing a structure for ecosystems in caves the first thing we need to remember is that in nature all is in flux which renders all compartmentalization artificial despite the fact that it can help us understand such ecosystems. This is not a new problem in ecology. Since the beginning of the twentieth century ecologists stopped looking at natural associations as static components of nature and viewed them rather as dynamic systems in both time and space. That is when the concept of succession was developed ([Tansley 1935](#)). Hence, the term ecosystem became universally accepted as one in four dimensions, i.e., the three spatial ones plus time.

Therefore, we have to see the hypogean environment as a system rather than a collection of units that need to be classified based only on external, superficial characters and without taking into consideration the temporal dimension of those objects.

Recently [Campbell et al. \(2007\)](#) proposed to view caves as an example of an ecological dendritic network. They define dendritic networks as those spatial environments in which both the branches and the nodes serve as habitat and where the specific spatial arrangement and hierarchical organization of these elements interacts with a species' way of moving and distributing which, in turn, will affect their abundance and community interactions. Since most caves do show certain geometric similarity with this type of structure, their approach seems reasonable. Furthermore, they propose that one of the reasons for high rate of endemism in cave biota is precisely the spatial organization of these habitats. Therefore, to better understand how caves work as ecosystems, we need to see them from a systemic viewpoint, interpreting its organization and the relationships among its components. The same thing happens with caves and their elements: as mentioned earlier, there is a great diversity of caves based on size and shape,

¹² **troglomorphic:** An organism having characters typical of hypogean organisms such as blindness and depigmentation.

geographical distribution, a geological nature. Additionally, caves represent but one of the many available niches for the surrounding biota.

Spatial Organization

Little work has been done on ecosystem structure and on information and energy transfer in the hypogean environment. Most cave students have seen caves as authentic islands of much reduced dimensions, in comparative terms, and in two-dimensional terms. However, caves have spatial and temporal dimensions that attest for their complexity (despite their apparent simplicity). [Bussotti *et al.* \(2006\)](#) used a multifactorial sampling design to examine the distribution of species assemblages within three different caves in Southern Italy over a period of 11 months and found a pattern of change in the structure of the assemblages along the exterior-interior axis as well as among areas that suggested a highly complex structure of the biotic community.

From a spatial viewpoint a cave might have five spatial-conceptual axes. First the terrestrial-horizontal one on which we find many terrestrial organisms, terrestrial invertebrates being the most evident to the casual observer. The second one is defined by the length of the cave: it is well known that community structure and biodiversity distribution changes throughout the length of the cave and the lengthier the cave the more complex that structure can be. The third is vertical and is largely defined by the differences between the biodiversity found on the ground and that roosting on walls or the ceiling of the cave. This is an important dimension since roosting animals -whether they are bats or birds- usually provide large amounts of nutrients to the cave via their excrements. Also, these animals usually move daily from inside the cave to the epigeal environment, thus they represent one of the most important facilitators of the interactions between the hypogean and epigeal environments. The fourth is water: whether a cave is permanently or periodically flooded with water makes a great difference not only in its biotic composition but also in its own dynamic and community structure. The fifth axis that we need to consider is that of the outside environment that influences the cave: whether it is the terrestrial community outside the cave determining the species composition and abundance of animals that frequent the cave or that of water flowing in and out of the cave, they have a tremendous impact in cave ecology.

Of course cave diversity is just too variable as to attempt to categorize all of them with these components *sensu stricto*. One could argue that given the different biological microcosms there is no reason to apply the theory of fractals to caves as they can be applied to nature in general. However, the same way that mainstream ecologists have been able to characterize ecosystem components is not because of their nature (that is clearly structured), but because these subdivisions, when not taken to extremes, are useful to understand how nature works.

For example, the way bats are distributed in caves influences their patchiness because of the heterogeneous way in which excrements will be deposited. This phenomenon has also been observed among mysid crustaceans that deposit organic material in a patchy manner ([Coma *et al.* 1997](#)). These authors found that in a cave of the Medes Island in the northwestern Mediterranean, the species *Hemisis speluncona* forms large swarms with daily migrations from the inner part of the cave, where they remain during the day, to the exterior where they feed at night. The swarms of this species play a major role in transferring organic material into the cave in the form of fecal pellets. In many caves, even soil is carried inside from the exterior (e.g., [Foos *et al.* 2000](#)).

Another remarkable example of the complexity of ecosystem structure in caves can be conveyed by looking at the ecological role played by the mite *Coprozercon scopaeus*, which was a species used to describe a new family of mesostigmatic mites, Coprozerconidae. This species was found in the feces of the wood rat, *Neotoma floridana magister*, in Mammoth Cave, Kentucky. This is the only species of its suborder (Epicrinea) whose life cycle seems to be restricted to the cave environment. The subspecies of wood rat associated with them, spends most of its life in caves and rockslide crevasses in Appalachian areas from Pennsylvania to Tennessee. They essentially defecate in the same sites (usually about 1 m away from each other) providing, thus, not only abundant but also stable sources of nutrients. These dumps also provide a source of energy to other arthropods. The dumps can be as high as 25 cm with fecal pellets of various ages ([Moraza and Lindquist 1998](#)).

In addition to these spatial dimensions, we also need to see caves from a temporal perspective. Caves have evolved, from a geological viewpoint, in many ways depending upon their geology, location, and climate. Logically we can expect that organisms living in them have co-evolved. Unfortunately, and unlike the epigeal environment, we lack a meaningful fossil record that can give us an idea of how those changes occur beyond the most recent ice ages; caves tend to be very poor in terms of sediment preservation. Even when we find fossilized elements in caves, that fossil record refers mostly to terrestrial mammals that temporarily inhabit the cave during some portion of their life cycle. Thus, there are not real fossil records that can help us elucidate evolutionary changes from epigeal to troglobites¹³ or permanent cave residents.

The closest we have come to it is the case of *Paleozercon cavernicolous*, a species of mite known only from specimens embedded in calcium deposits of a stalagmite¹⁴ near a cave entrance ([Blaszak et al. 1995](#)); yet that does not mean that these organisms lived exclusively in caves.

Some historical populational studies have yielded interesting information about rather rapid changes over time. Studies in La Cueva Chica in Mexico and at the Cumaca Cave of Trinidad have shown the changes in rainfall regimes can have an important impact on species inhabiting caves by allowing epigeal individuals to interbreed with their related cave species and generate genetically intermediate populations (La Cueva Chica) and even ecological replacement (Cumaca Cave) in just few decades ([Romero 1983](#), [Romero et al. 2002a](#)).

Therefore, when considering temporal aspects in the evolution of populations, species and/or communities in caves one must take into consideration the temporal scale as well. However, given the lack of fossil record, how can we do that? One could be by using molecular clocks, although the results of such clocks are far from definitive given the fact that different assumptions and methodologies may yield different outcomes. The other is to use generation times. The reason is very simple: not all organisms reproduce the same number of times in fixed astronomical cycles. Furthermore, many organisms such as cave fishes have stretched life cycles when compared with their epigeal ancestors which seem to be prompted by water cycles rather than astronomical ones given the fact that the hypogean environment isolates obligatory organisms from astronomical clues.

A paradox also arises from this situation. Aided by phenotypic plasticity, the morphological evolution of many cave organisms seems to be rather fast. However, when becoming more troglomorphic many of those organisms considerably reduce the number of generation per unit of time. That means that within the same phylogenetic lines we will find different tempos of evolution, and that is why the use of molecular clocks may not be the best way to ascertain evolutionary pace for both phylogenetic lines and ecological communities. This approach is not new, though. [Ginzburg and Danuth \(2008\)](#) proposed something similar in the area of metabolic ecology.

Trophic Structure

Some (e.g. [Holsinger 2000](#)) have argued that hypogean environments are ‘harsh’ because they are poor in nutrients. Yet, available data do not support that statement as a valid generalization. Animals that colonize caves can find in those habitats food (e.g. [Ferreira and Martins 1999](#)), reproductive niches (e.g. [Rogowitz et al. 2001](#), [Briggler and Puckette 2003](#)), protection from predators (e.g. [Romero 1985a](#), [Tabuki and Hanai 1999](#)), protection against desiccation ([Jensen et al. 2002](#)), and a place for hibernation ([Zhang 1986](#), [Resetarits 1986](#); for a general discussion on this issue see [Bellés 1991](#)). These ecological opportunities of the hypogean environment allow many different species of many different taxa to undergo extensive adaptive radiations leading to many differentiated populations and/or species ([Hoch and Howarth 1999](#)). Also, contrary to generalizations based on studies of caves in temperate regions (e.g. [Poulson and White 1969](#)), many caves are very rich in nutrients, particularly in tropical regions (e.g.

¹³ **troglobite:** Organisms found in caves that display convergent phenotypes (morphological, physiological, and behavioral) such as loss of eyes and pigmentation.

¹⁴ **stalagmite:** Vertical formation of calcium carbonate on the floor of a cave.

[Deharveng and Bedos 2000](#)), and some are even chemoautotrophic¹⁵ ([Airoldi and Cinelli 1996](#), [Sarbu 2000](#), [Sarbu et al. 2000](#), [Hose et al. 2000](#)) thanks to bacteria that produce organic matter by oxidizing sulfur. Both, tropical and chemoautotrophic caves are usually very rich in species with some of those species having large population sizes.

In fact, bacteria may play a much larger role in caves than previously thought. [Engel et al. \(2004\)](#) found in Lower Kane Cave, Wyoming, U.S.A., that filamentous aquatic *Epsilonproteobacteria* and *Gammaproteobacteria* colonize the carbonate substrates so common in many caves and through their metabolism generate sulfuric acid which dissolves the substrate not only shaping the interior of the cave but also enlarging its crevices and, therefore, its size. The phenomenon known as sulfuric acid speleogenesis (SAS) was reported in the 1970s for the same cave but in the air only, where sulfuric acid oxidation replaced the aerial carbonate by gypsum¹⁶ (Fig. 4.1.). Therefore, we can say that microbes play a mayor role in subsurface karstification ([Northrup and Lavoie 2001](#)).

The fatal blow to the assumption that cave organisms in general and fishes in particular look the way they look because of lack of nutrients is provided by the troglomorphic *A. fasciatus*, which has nearly twice the routine metabolic rate than that of its epigean form ([Schlagel and Breder 1947](#)). And this is not an aberration: several cave populations of amphipods show no lower metabolism than their epigean counterparts ([Culver 1971](#), [Gilbert and Mathieu 1980](#)).

One question that could be explored further is whether water temperature may affect metabolic rate in hypogean aquatic organisms from an evolutionary viewpoint. That is difficult to answer because of the lack of data. On one hand, the example of the troglomorphic *A. fasciatus* mentioned in the previous paragraph corresponds to a tropical environment and that is one of the very few hypogean fish species for which metabolic rates has been examined. Also, water temperature is not data generally available for most hypogean fishes, much less its potential seasonal variability in temperate regions. Therefore more data on both metabolic rate and environmental temperature are needed before making any predictions.

Another by-product of the mythology of caves being very poor in nutrients is the popular misconception that troglomorphic organisms have reduced eyes and pigmentation as a response to low levels of food supplies. However, all empirical evidence indicates that the responses are physiological, not morphological, and that in those cave environments characterized by high levels of energy supply, metabolism actually increases rather than decreases and yet, reduction and/or elimination of phenotypic features still occurs.

Many hypogean organisms can and do undergo long periods of starvation. Several species of fish and salamanders, for example, can experience periods of one year or more without food ([Poulson 1964](#), [Mathieu and Gilbert 1980](#), [Hervant et al. 2001](#), [Hervant and Renault 2002](#)).

The ability to survive prolonged periods of food deprivation is not unique to hypogean organisms. Numerous epigean animal species belonging to a widespread variety of taxa undergo long periods of starvation during hibernation, aestivation, and/or spawning seasons. Yet, their responses to this kind of conditions are not reflected in the form of reduction or loss of phenotypic structures, but are physiological in nature.

Hypogean organisms subject to food deprivation respond in a fashion similar to that of epigean ones under similar conditions. [Mendez and Wieser \(1993\)](#) first proposed a set of physiological strategic responses to these conditions that now has been found to occur in a wide variety of animal species, both epigean and hypogean. This physiological strategy consists of undergoing sequential number of phases itemized as follows:

- (1) Stress: This is the start of the starvation period characterized by an increased locomotory activity associated with food finding. This phase may last up to 60 days in the cave salamander *Proteus anguinus* ([Hervant et al. 2001](#)).
- (2) Transition: This phase is characterized by a drastic reduction in activity and oxygen consumption.

¹⁵ **chemoautotrophic:** organisms that obtain energy through chemical reactions from inorganic energy sources.

¹⁶ **gypsum:** A mineral of hydrous calcium sulphate.

- (3) Adaptation: This is the longer phase, which may last a year or more. It is characterized by constant minimal rate of oxygen consumption, stable metabolic activity and highly reduced locomotory behaviors.
- (4) Recovery: This phase is characterized by exceptional hyperactivity and increase in oxygen consumption, both associated with food searching.

Birds and mammals show a similar strategy only that they add a critical phase after the adaptation phase ([Le Maho 1984](#)).

Given that this is a convergent feature among long-fasting organisms, particularly many hypogean ones, it supports [Mendez and Wieser's \(1993\)](#) initial hypothesis that natural selection is the mechanism favoring this sequential energy strategy whose overall characterization is one of a combination of 'sit and wait' behavior while no food is available, subsisting on internal energy reserves and low metabolic requirements during that period while showing high recovery abilities during re-feeding. The hypogean salamander *Proteus anguinus*, for example, can undergo periods of food deprivation for up to 96 months.

One of the byproducts of hibernation and expansion in the life cycle of animals that live in caves is also an increase in their longevity. Life span for cave fishes has been reported to be exceedingly long. The amblyopsid fish *Amblyopsis rosae* is slow growing, with a long life span (ca. 10 years) and maturation takes at least four years ([Poulson 1963](#), [Robison and Buchanan 1988](#)). A less hypogean species of this fish family, the spring cavefish *Forbesichthys agassizi*, has a life span of about three years ([Smith and Welch 1978](#), [Etnier and Starnes 1993](#)). Among bats, hibernating species live, on average, six years longer than species that do not hibernate. Also, bats that roost in caves live more than five years longer than bats that live elsewhere or do not roost ([Wilkinson and South, 2002](#)), independently of the family in which they belong. So cave roosting improves the fitness of the species associated with that environment since life span can be construed as a result of natural selection acting to maximize reproductive success.

For species that enter or use caves as temporary habitats, their relationship with those habitats is more complex than it may seem. For example, there are several species of harvestmen (opilions) that spend the daytime in caves and leave at night to predate on insects. One species of harvestmen of the genus *Goniosoma* from Brazil is found on different portions of the caves depending upon the vegetation outside, showing how external factors may influence cave organisms distribution. Interestingly enough, this species of opilion is preyed upon inside the cave by insects and spiders ([Machado et al. 2003](#)), which shows that the so-called troglonexes use caves to escape predators may be true in some cases but is not necessarily so for others.

There are also species of fish that enter and exit caves playing a major role in the ecology of those environments. That is the case of the cardinal fish *Apogon imberbis*. This is a small-sized fish distributed along the eastern Atlantic coast from Morocco to the Gulf of Guinea, including the Azores. It can be found as solitary or forming schools and is common in small crevices to marine caves, where they can be found in large densities. They show no troglomorphisms whatsoever, yet they play a major role in transferring organic material to these marine caves as mysid crustaceans do. Just like bats, they tend to stay in the caves during the day and leave the caves at night, presumably for feeding ([Bussotti et al. 2003](#)). Upon reflection, caves would be greatly different places if we were not to consider these 'troglonexes' as an integral part of cave ecology just because they are not troglomorphic.

One aspect of cave ecology that has yet to be studied is how this vertical transfer of nutrients occur, particularly from bats and cave birds to the terrestrial and aquatic organisms found on the bottom of the cave. Once those studies are carried out, it would not be surprising to see that such an energy transport occurs in a similar manner than elsewhere on Earth – that is with a strong vertical polarity where a lot of the energy is concentrated at the top (e.g., bats) and at the bottom (e.g., guano¹⁷), which is an accommodation to the way life on our planet receives its main source of energy: the Sun ([Margalef 1993](#)).

¹⁷ **guano:** It is an accumulated deposit of animal excrement. Bats produce most guano in caves, but cave birds such as swifts and oilbirds also produce some.

In any case, some preliminary studies tend to confirm the complexity of the trophic structures of caves. [Graening \(2005\)](#) while studying six subterranean stream habitats in the Ozarks found that there were three trophic levels in those subterranean streams. The first one was formed by a detrital food base of clastic sediment, bat guano, and surface inputs; a second trophic level formed by detritivores, primarily crustaceans and amphibians; and a third, top level one, of predators, primarily fishes.

There are two groups of birds that use caves on a daily basis for resting and reproduction: the oilbird *Steatornis caripensis* (Steatornithidae) and several species of swifts of the genus *Collocalia* (Apodidae). Both of these not only utilize caves as a permanent habitat during the day for resting and nesting but also are the only bird species that have developed echolocation abilities to navigate inside the caves. Like many nocturnal birds they have large eyes that they use mostly outside the caves to forage. Yet, despite the fact that the development of echolocating abilities is clearly a major adaptation to life in caves which requires major neurological rewiring, they tend to be dismissed as not “true cavernicoles”¹⁸ as mentioned in the classical biospeleological literature. More importantly, from an ecological perspective, the droppings of these bird species, as well as those of cave bats, have a great influence on the ecology of the cave they inhabit. Studies at Cumaca Cave in Trinidad, W.I., indicated that oilbirds were a major component of the ecology of that cave, occupying the cliffs of most of the largest halls and displacing the bats to the smaller halls and towards the end of the cave ([Romero and Creswell 2000](#), [Romero et al. 2001](#), 2002a). The droppings of the oilbirds were prominent and, although no quantitative studies have been conducted in that regard, it is difficult to imagine that such abundant organic material has no influence on the ecology of that particular cave.

The best example of a non-troglophobic group of organisms playing a major role in cave ecology is the case of cave bats. Bat guano generates rich and complex invertebrate communities, particularly in tropical caves ([Ferreira and Martins 1999](#)). Bat guano has also been accounted as a source of food for fish ([Romero 1983](#)) and even salamanders. [Fenolio et al. \(2005\)](#) reported coprophagy in salamanders from an Oklahoma cave and found that their nutritional value was comparable to that of their invertebrate preys. They further suggested that bat guano may play an important role as a source of food among other cave vertebrates. Cave crickets have also been found to contribute significantly to the input of energy in some caves ([Lavoie et al. 2007](#)).

Needless to say, the effect of the presence of bat guano on microbial fauna must also be immense but that is an area largely unstudied. Explorers of tropical caves know very well that caves with high levels of guano deposits have higher temperatures. This anecdotal observation has been confirmed empirically. [Baudinette et al. \(1994\)](#) found high and rather constant temperature levels in caves inhabited by large bat colonies and that such heat was part of the microclimate created by the bats themselves which, in turn, generates better conditions for maternity.

Another source of food for hypogean organisms can be plant roots. In many karstic areas tree roots penetrate the substrate all the way to the phreatic levels where they can obtain water. These root mats form a diverse and abundant biomass. [Jasinska et al. \(1996\)](#) reported 41 species of aquatic hypogean organisms including annelids, arthropods, and fish from a cave in Australia that had root mats in their waters. Their study concluded that the root mats were the primary source of energy for all these organisms.

From a taxonomic viewpoint, in the case for fishes, we can say that there are about equal number of species/populations of non-troglophobic and troglophobic ones and the situation is similar for other groups of organisms normally found in caves ([Romero 2001](#), [Romero et al. 2009](#)).

Therefore, if we really want to have a clear picture of the true biodiversity values in caves, we cannot stop at looking only at troglophobic organisms. This typological view of life, with roots in eighteenth and nineteenth century essentialism and which is so prevalent until the introduction of the Modern Synthesis with a populational view of biology, impairs us to really view these things the way they really are ([Romero 2007](#)).

¹⁸ **cavernicole, cavernicolous:** Any organism living in caves, whether permanently or just for part of their life cycle.

Is There Succession in Caves?

Because of the lack of primary producers, it has long been believed that caves lack any expression of meaningful ecological succession (a phenomenon first and mostly studied with vegetation). This belief has led to the idea of the so-called “stability” of the cave ecosystem. Much has been written alleging that the cave ecosystem is stable. For example, [Langecker \(2000, p. 135\)](#) characterized caves as ‘an environment that is relatively stable in its climatic characteristics’ and [Boutin and Coineau \(2000, p. 434\)](#) affirmed that “the relative temporal stability of subterranean habitats, postulated for a long time by many authors, has been demonstrated in many particular cases and constitutes one of the generally accepted paradigms of biospeleology”¹⁹. We need to consider, in any case, that stability will also depend upon what part of the cave we are talking about: the closer to the entrance the less stable a cave is. Therefore there is zonation in caves.

Yet, those statements are not really backed up by data allowing such a blanket generalization. Perhaps because of the lack of primary producers, cave biologists think that there is no succession and therefore, the system is a “stable” one. Also, succession tends to be slower in temperate environments than in tropical, humid ones. That is the reason why life spans of animals tend to be longer in ecosystems with slow succession instead of those with rapid ones. Therefore, that is why we find very long life spans among some troglomorphic organisms in temperate caves (e.g., amblyopsid fishes). Also, tropical ecosystems, because they have higher levels of energy in terms of both, absolute and in flow, allow for more fluctuations and more rapid succession, which in turn accelerate the pace of evolution, both at the individual (species/population) level as well as at the ecosystem one. Yet primary producers are not needed for succession to happen and mines provide a good example of that. [Milanovich et al. \(2006\)](#) reported that an abandoned mine in Arkansas had been recently invaded by the slimy salamander (*Plethodon albagula*) for nesting. They reported not only this phenomenon as a recent one, but also one in which fecundity is influenced by precipitation.

[Ashmole et al. \(1992\)](#) described faunal succession in the lava caves of the Canary Islands. They found that the first hypogean communities were characterized by pioneering epigean species common in the surrounding areas that were, opportunistically, taking advantage of the new environment, mostly for either feeding or looking for protection from predators during the day. According to these authors, the presence of chemolithotrophic²⁰ bacteria suggested the possibility for some primary production taking place early on. They further discussed the idea that as the lava cave ages the animal community in them also changes by increasing the number of species. Therefore, succession does occur in caves. What may have happened in the past is that the typological concept of caves as static and relatively isolated ecological units created a philosophical barrier to understand the dynamics involved in this process.

As mentioned earlier, ecological replacement has been reported between two populations of the catfish *Rhamdia quelen* in Trinidad, W.I., where in less than 100 years an eyed, pigmented population has replaced one that was blind and depigmented ([Romero et al. 2001](#)), another sign of the fluctuations that can take place among cave biota.

Another major impact of bacteria is their potential role in the contribution of cave formations *per se*. [Engles et al. \(2004\)](#) found that numerous bacteria colonize carbonate surfaces generating sulfuric acid as a metabolic byproduct that in turn lowers pH, thus contributing to the dissolution of the rocks. Therefore as the cave habitat changes so does its biota.

If there is no regularity of ‘laws’ governing succession in ‘lighted’ ecosystems, should we expect to find such regularities among hypogean ones? Caves, like any other environments, particularly extreme ones, will be invaded by living organisms following the most conspicuous of all of evolution’s characteristics: opportunism. They may or may not interact with other invading organisms, but certainly there is no evidence that they will be structured in one way or another. Furthermore, nobody to my knowledge has ever expressed the idea that hypogean ecosystems reach a climax in the ecological sense.

¹⁹ **speleology:** The science that studies life in caves.

²⁰ **chemolithotrophy:** The process of extracting nutrients from the substrate carried out by some microbial organisms.

Changes in hypogean environments (and even its organisms) seem to be asymmetrical, meaning that they do not always occur in parallel through the entire cave ecosystem.

We really know very little about succession in hypogean environments. Therefore, all that we can do at this point is to speculate. One of those speculations, however, can also be a word of warning: do not expect to find regularities with universal applications. The best evidence that such statement may be true is the differential biodiversity composition that we find among caves around the world.

And what do we know about natural (non-anthropocentric) perturbations in the hypogean environments? The answer is: very little. We do know that despite the fact that many populations that have lost their circadian rhythmicity, they can adjust their breeding period to the availability of water.

It is too bad that caves are terrible places for fossilization; otherwise they could provide us with interesting clues about ecological succession. Since bats are such an important source of energy for many caves, one can only wonder how their explosive radiation in the Eocene ([Teeling et al. 2005](#)) may have changed the ecological landscapes of caves.

Interactions of Cave Habitats with the Epigeal Environment

Hypogean environments such as caves are not closed systems. Many cave creatures as well as abiotic elements such as water, air, and many chemicals constantly move in and out of this environment. Thus, to better understand how caves work from an ecological viewpoint we need to look at it in a holistic way that includes the external ecosystems with which they interact.

In addition to the obvious openings to caves, whether horizontal or vertical, they interact with their surrounding environments via either underground waters and/or the soil above them. In the case of groundwater the linkages in terms of volume and chemical components have been well documented (for a review see [Hancock et al. 2005](#)). For exchanges via the soil above them, there is ample documentation in terms of organic matter and living organisms (e.g., [Gers, 1998](#)). That kind of connections has been described as MSS²¹ (*milieu souterrain superficiel*) or superficial underground section. This section is made of weathered bedrock with heterogeneous spaces in rocky material. A great deal of biodiversity has been described for that zone ([Juberthie et al. 1981](#)). Although there is some organic material being passively transported by percolation from the soil to the caves, [Gers \(1998\)](#) found that there is also active migration of arthropods not only from the epigeal environment to the cave, but also from the cave to the epigeal environment with the MSS being the area where the food webs of both environments interlink.

The energy base for many cave organisms has been, in fact, identified as derived from primary productivity from epigeal environments being transported into the cave via the MSS (e.g., [Crouau-Roy et al. 1992](#)). That flow of energy is influenced by both the geology between the cave and the surface as well as by seasonal fluctuations.

In the case of the aquatic fauna found between the soil and the cave, one can find not only species from both environments but also unique fauna to the MSS which leads to the consideration that such ecological zone represents an ecotone or transition zone between two ecosystems ([Prous et al. 2004](#); [Pipan et al. 2006](#)).

These transitional areas tend to have high species richness for having not only its unique biodiversity but also species from the contiguous areas. The same can be said of the visible cave entrances, whether dry or wet (e.g., [Culver and Poulson 1970](#), [Prous et al. 2004](#)). In the case of marine caves that penetrate from the ocean directly into karstic areas of 100 m or more in length, the biodiversity composition seems to be directly influenced by light penetration and salinity (e.g., [Wittmann 2004](#)).

We can conclude that the differentiation between caves environments and its surroundings is not as clear-cut as many had suspected in the past. This means that the food web connectance (symbolized as C), an ecological measure of the linkage patterns between or among different food webs, ([Margalef and Gutiérrez 1983](#), [Dunne et al. 2002](#)) is relatively high.

²¹ **MSS:** Acronym for the French *milieu souterrain superficiel* or mesovoid shallow stratum. MSS refers to the interstitial spaces deep in the soil and bedrock interface; it is typical of glacially fragmented zones.

One of the consequences of this approach is that when we study caves in temperate ecosystems we find that there is a periodic interruption (or diminishing) of epigeal activities in winter that is more acute the higher the latitude. This means that activities such as colonization and competition are severely reduced in those areas that, in turn, mean that caves are poorer in terms of biodiversity in those high latitudes.

The complexity of connectivity between the epigeal and the hypogean environment also means that caves that lack primary producers (all but a few with chemosynthetic bacteria) receive relatively limited input of energy, particularly in temperate areas, since energy is reduced by one-tenth from one level from another. This concept helps to explain why there are no large predators in caves (even snakes are very rare and mostly limited to cave entrances).

Also, we need to look into even more elaborated trophic relationships as is the case of parasitic organism (where the energy is transferred from the host to the parasite) among cave species. Surprisingly, parasites are not a rarity in the hypogean environment. Until we have more studies on parasites of organisms in tropical caves, we cannot draw conclusions in this regard.

We also know little about competition among organisms in tropical caves. We do know that in locations such as the Cumaca Cave of Trinidad, there is competition for ceiling space between birds and bats (Romero et al. 2002a), but we need more data to see if there is also competition for other resources such as light and, more importantly, nutrients.

Conclusions

Despite the great number of specific adaptations shown by organisms to the cave environment, the same general ecological laws that rule the development of life on Earth govern these adaptations to caves as biological spaces. Those adaptations represent, in many instances, extraordinary case studies but always within the known parameters of ecological science, not as a special biological phenomenon as it has been attributed in some of the classical biospeleological literature (for a discussion on this see Romero 2009, pp. 1-61). Thus, despite its uniqueness, particularly when it comes to adaptations to the lack of light, cave organisms display adaptive characters within the framework of opportunism that characterizes life as a phenomenon.

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