

Article

Hypogean Communities as Cybernetic Systems: Implications for the Evolution of Cave Biotas

Aldemaro Romero, Jr. 

Department of Natural Sciences, Weissman School of Arts and Sciences, Baruch College,
City University of New York, One Bernard Baruch Way, Box B 8-250, New York, NY 10010-5585, USA;
aldemaro.romero@baruch.cuny.edu

Received: 30 September 2020; Accepted: 28 October 2020; Published: 29 October 2020



Abstract: Ramón Margalef proposed in 1968 that ecosystems could be better understood if they were viewed as cybernetic systems. I tested this hypothesis in the case of hypogean ecosystems using available pieces of evidence. I looked on how information on feedbacks, stability, succession, organization, diversity, and energy flows in the hypogean environment fit the cybernetics hypothesis. The results were that there are convincing arguments that the application of the concept of cybernetics in biospeleology can be beneficial to broadening our understanding of cave biota in terms of their structure. I also make the case that this approach can provide more clarity about how cave biota has evolved through time and the implications for their conservation.

Keywords: cybernetics; ecology; cave biology; biospeleology

1. Introduction to the Concept of Cybernetics in Ecology

Cybernetics can be defined as the interdisciplinary approach of exploring regulatory systems, structures, constraints, and possibilities. The term cybernetics was first introduced in the modern scientific literature by Norbert Wiener in his book “Cybernetics or Control and Communication in the Animal and Machine” [1]. He used it as a form of transfer of information. The origin of the term “cybernetics” [2] is as found in Plato’s “The study of self-governance”. There he used the word *κυβερνητικός* or *kybernetes* for helmsman, steersman, rudder, rudder-man, or skipper. The Latin form was *gubernetes* or, later, *gubernator*. Although Plato’s application of the term was to mean effective government as an art [3], Wiener’s definition concerned the scientific study of control and communication among animals and machines [4,5].

The concept of cybernetics in ecology was first formally introduced by Margalef [6], although the idea had been floating around for some time [7]. Margalef contended that cybernetics was a more holistic and elucidating way to look at ecological communities. Although this terminology might be considered by some as just a buzzword, this approach continues to be used by theoretical ecologists and system engineers [3,8–11]. For Margalef [6], the ecological approach was to look at cybernetics as a model for understanding representations of life (from cells to individuals to ecosystems) where feedbacks, stability, organization, diversity, and energy flows are interacting elements that are both the factors and the results of highly dynamic systems. How these elements interact is via information transfer. In information theory, that means quantification, storage, and communication of information. That information could be in the form of trophic energy, reproductive behavior, and evolutionary processes via molecular data, etc. [12].

I will test Margalef’s hypothesis that ecosystems can be interpreted as cybernetic mechanisms by scrutinizing his proposal using material provided by the scientific literature. Some of these data were previously published in Romero [13] but never examined under these parameters, to which I added new information generated in the last ten years. I will use the term epigean for any environment

exposed sunlight and hypogean to any environment under perpetual darkness, with one being the opposite of the other. One exception will be dealing with some caves with a portion exposed to sunlight due to their geological conditions.

2. Cybernetics in Biospeleology

2.1. Metaphysical Barriers

To fully understand how a cybernetic model can be applied to biospeleology, we need to recognize two metaphysical barriers. One is the stereotype that the hypogean ecosystems are mostly closed ecosystems or ecological islands, *sensu* [14]. The other is the artificial and rigid segregation of hypogean forms of life based on archetypes or *Baupläne*.

There are numerous arguments against the concept of caves as isolated environments. The first thing we must recognize is that unlike oceanic islands, hypogean ecosystems are not separated by long distances from other ecosystems. Therefore, they are just part of the same general ecosystem above them with the caveat that the hypogean one is under perpetual darkness. This is, therefore, the only commonality to all caves. In any case, generalizations on the concept of caves as an island would lead to stereotypes that will not fit with the diversity of caves worldwide.

Hydrogeologists have described the interactions between river waters and hypogean ones as essential to understanding the flow and biochemical nature of groundwaters [15]. Gers [16] provided evidence that there are exchanges of organic matter and living organisms between caves and the soil above them, documenting an active migration of arthropods not only from the epigeal environment to the cave but also from the cave to the epigeal environment with the food webs of both ecosystems interlinked. Similar connections have been found for the cave beetle *Speonomus hydrophilus*, which utilizes the primary producers' energy from the epigeal environment [17]. The continuous gradation of species in their distribution has also been documented. That is the case of marine caves that penetrate the ocean directly into karstic areas of 100 m or more in length. Different species of mysid crustaceans distribute themselves based on light intensity and salinity [18].

Thus, it should not be surprising that many taxa thought to be found exclusively in epigeal ecosystems are also represented in hypogean ones [13], (p. 159). The very different nature of caves further substantiates the hypogean ecosystems' nature as open ones in tropical vs. temperate ecosystems [19–21].

The other issue that creates some metaphysical barriers regarding understanding the hypogean ecosystem as cybernetics is its jargon. One of the major problems in speleology is the proliferation of terms to describe either organisms that inhabit the hypogean ecosystem based on their spatial distribution and/or different portions of the ecosystem itself. Although terms are useful to identify ideas, objects, or mechanisms, an overabundance of them leads toward confusion and, above all, the misleading interpretation of nature as a series of well-defined compartments. The reality is a different one: In nature, all is in flux. Although basic terminology such as herbivore and plankton is well understood, others can be confusing and highly artificial. Romero [13], (pp. 130–132) already mentioned how artificial the hyperclassification of cave organisms is based on their phenotype. More recently, Martínez and Mammola [22] further emphasized this point by showing statistically that these hyperclassifications were a barrier for communication among biospeleologists themselves. The hyperclassification of cave organisms induce the idea that they are instead fixed elements as continually evolving (or having the ability to evolve rather rapidly) within the system. After all, species are not members of a periodic table [13], (p. 166).

In the early twentieth century, ecologists confronted these problems when they stopped looking at natural associations as static components of nature and viewed them as rather dynamic systems in both time and space [6]. That is when the concept of succession [23] was fully adopted. Hence, the term ecosystem became universally accepted as one in four dimensions, i.e., the three spatial ones plus time.

Having clarified these two confounding variables in biospeleology, we can move forward in testing Margalef's hypothesis for understanding the hypogean ecosystem as a cybernetic system.

2.2. Feedbacks

Margalef [6], (pp. 4–5) wrote that “A simple example of an elementary cybernetic mechanism, in the form of a negative feedback loop, is the classical one of a predator and its prey. Organisms are the bearers of huge amounts of information. Since they can be destroyed but cannot be produced from nothing, any regulatory mechanism implies an initial overshoot”. He illustrated this point by the fact that the predators reduce excess prey and the number of predators themselves are also regulated by prey availability. The Lotka-Volterra equations can quantify this correlation [13].

This may be the most difficult of Margalef's assertions that can be tested for the hypogean ecosystem. The reasons are two-fold. First, there are not that many prey-predator relationships in the hypogean ecosystem reported in the scientific literature. Second, it is a well-established ecological principle that energy decreases as it moves up trophic levels because energy is lost as metabolic heat when organisms consume the organism from lower trophic levels. That is why a food chain can usually sustain no more than six energy transfers before all the energy is used up. Consequently, endotherms (birds and mammals) use more energy for heat and respiration than ectotherms and have to seek food outside caves. This is because of the insufficient amount of food resources present in many subterranean environments.

That is why we need to take a broader view of the transfer of energy into the hypogean ecosystem to visualize better how the transfer of information does occur in that ecosystem. The connectivity issue among the different cave ecosystem elements and how energy and information flow from one to another has been little studied. This is surprising since these ecosystems are supposed to be simplified because of the lack of primary producers' abundance. Thus, let us explore these issues in detail.

Contrary to perceptions based on caves studies in temperate regions [24], many caves are very rich in nutrients. That is particularly true in tropical regions [21], and some are even chemoautotrophic [25–29]. They are considered primary producers thanks to the bacteria that produce organic matter by oxidizing sulfur. Moreover, one of the most striking examples of the opportunistic nature of life in the hypogean ecosystem is the presence of phototrophs in caves, including algae, lichens, and plants (liverworts, mosses, ferns, and seed plants) [13] (pp. 67–69, 73–76) and [30].

Examples of animals in caves that demonstrate interesting cases of transfer of energy (i.e., information) are many. 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 (Opiliones) that spend the daytime in caves to leave at night to prey 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 that climatic factors may influence cave organisms distribution [31]. Interestingly enough, this species of opilion is preyed upon inside the cave by insects and spiders [32]. Another example is that of cave salamanders that utilize resources from both the cave and the epigeal environment [33]. According to numerous reports, snakes regularly predate on bats in tropical and subtropical caves [34–36].

Oilbirds (*Steatornis caripensis*) in South America and several species of swiftlets of the tribe Collocaliini in southern Asia, South Pacific, and northeastern Australia, are found in caves. They are permanent residents of caves during the day for resting and nesting but are the only bird species that have developed echolocation abilities to navigate the caves [37,38]. Similar to many nocturnal birds, they have very sensitive eyes, which they use mostly outside the caves to forage [39]. Yet, the development of echolocating and olfactory abilities is a major adaptation to life in caves which requires major neurological rewiring [40]. More importantly, from an ecological perspective, the droppings of these bird species and those of cave bats greatly influence the cave's ecology. Studies at Cumaca Cave in Trinidad, W.I., indicate 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 galleries

and towards the end of the cave [41–43]. The droppings of the oilbirds in that cave are prominent. Although no quantitative studies have been conducted in that regard, it is difficult to imagine that such abundant organic material does not influence that particular cave's ecology.

The best example of an organism playing a major role in cave ecology is the case of bats that roost in caves. Bat guano generates rich and complex invertebrate communities, particularly in tropical caves [44,45]. Bat guano has also been accounted for as a source of food for cavefish [46] and salamanders. Fenolio et al. [47] reported coprophagy in salamanders from an Oklahoma cave and found that their nutritional value was comparable to their invertebrate preys. They further suggested that bat guano may play an essential role as a food source among other cave vertebrates.

The effect of bat guano on microbial fauna must also be significant, but that is 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. [48] found high and relatively constant temperature levels in caves inhabited by large bat colonies. Such heat was part of the microclimate created by the bats themselves, which, in turn, generates better conditions for maternity.

The complexity of trophic structure in caves is another factor that is little studied. For example, Graening [49], while looking at six subterranean stream habitats in the Ozarks, found that there were three trophic levels in those underground streams. The first one was formed by a detrital food base of clastic sediment, bat guano, and surface inputs, a second trophic level created by detritivores, primarily crustaceans and amphibians, and a third, top-level one, of predators, mostly fishes.

Sometimes the input of energy can come from unexpected sources. That is the case of plant roots. In many karstic areas, tree roots penetrate the substrate to the phreatic levels to obtain water. Their root mats form diverse and abundant biomass. Jasinska et al. [50] 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.

All of these examples indicate two things. One is that cave ecosystems cannot be considered as closed ecosystems. They take considerable input from external sources. Although their output is not comparable even when many organisms that exit the caves reproduce in those niches as it is the case of bats or cave birds, we can conclude that it is asymmetric. The other one is that there is much more that we can learn by conducting more ecological studies in tropical and subtropical regions where the presence of large populations of cave animals such as bats, play a significant role in those ecosystems. Since the vast majority of biospeleologists who have historically conducted fieldwork do so in temperate regions, the scientific literature is biased towards colder parts of the planet. That is what accounts for the apparent—but false—generalization that caves lack both primary producers and prey-predator relationships.

2.3. Stability and Succession

It has long been assumed that the hypogean ecosystem is very stable, a perception based mainly on a historical circumstance. That circumstance is that most ecological observations in caves have been drawn from studies conducted in temperate areas when diversity and biomass tend to be low. Therefore, significant variations in caves' ecological conditions located in those latitudes are difficult to ascertain, mainly when conducting short-term studies. The standard concept of stability in ecology is derived from MacArthur [51], which, in the interpretation by Margalef [6], (p. 11), presupposes the existence of alternative pathways for energy flow, chosen according to the imposition of external circumstances.

When it comes to the cybernetic model, Margalef suggested that there were two types of stability. The first one is when the system achieves a steady state under stable conditions; in the second, the system is much more robust because of its ability to display a more considerable resistance to external changes to the system in their origin. The latter is characterized by higher energy flow and a smaller number of interacting elements. In cybernetic terms, the first system, its next state is

predictable from within the system because that system contains much information, and new events add small amounts of information. Margalef argued that the future is less predictable for the second type because the system has less information, and each event represents a relatively important source of information [6], (pp. 11–12).

As Margalef himself proposed, instead of stability, we should be talking about the “frequency of fluctuations” [52]. This makes sense in the case of biospeleological studies since the long-term ecological research in caves is rare and, if so, is based on historical data. Take, for example, changes in the morphology of the cave catfish *Rhamdia quelen* of Trinidad’s island. Romero et al. [43] were able to document extraordinary morphological changes in this fish’s cave population in less than 50 years. They used museum specimens and meteorological data to map those changes through time. Those changes were most likely the result of changes in the rainfall regime in the area over time.

There is an essential distinction between caves in temperate vs. tropical and subtropical areas. In the tropics, although there are no significant changes in temperature throughout the year, periodic (yearly) floods are not only common but also predictable as part of the external factors affecting the hypogean biota, particularly the aquatic one. Although water regimes’ changes do occur in temperate areas, they are more spaced in time and smaller in intensity [13], (p. 161). The ability to withstand those fluctuations have a particular impact on whether or not they can respond to those variations rapidly and why the concept of phenotypic plasticity is so crucial for survival and evolution.

Due to the apparent lack of primary producers, it has long been believed that caves lack any expression of meaningful ecological succession (a phenomenon first and mostly studied for vegetation transformations). This 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 [53], (p. 135) characterized caves as “an environment that is relatively stable in its climatic characteristics”, and Boutin and Coineau [54], (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”.

Still, those blanket generalizations are not supported by data. Perhaps because of the apparent lack of primary producers, cave biologists think there is no succession, and therefore, the system is a ‘stable’ one. Moreover, succession tends to be slower in temperate ecosystems than in tropical, humid ones. That is why life spans of animals tend to be longer in ecosystems with slow succession instead of those with rapid ones. Subsequently, we find very long-life spans among some troglomorphic organisms in temperate caves as is the case for amblyopsid fishes [55,56]. Moreover, tropical ecosystems, because they have higher levels of energy, allow for more fluctuations and more rapid succession, which in turn accelerate the pace of evolution, both at the individual (species/population) level and at the ecosystem one [57].

Yet, you do not need primary producers for succession to happen. Milanovich et al. [58] documented succession in an abandoned mine in Arkansas that had been recently invaded by the slimy salamander (*Plethodon albagula*) for nesting. Ashmole et al. [59] described faunal succession in the lava caves of the Canary Islands. This phenomenon has also been reported for relatively short periods in marine caves [60]. Mammola and Isaia [61] provided an elegant description of how this phenomenon occurs among cave arachnids.

It is too bad that caves are terrible places for fossilization; otherwise, they could provide us with interesting ecological succession clues. Since bats are such an important source of energy for many caves, one can only wonder how their explosive radiation in the Eocene [62] may have changed the caves’ ecological landscapes.

2.4. Organization

From an information theory viewpoint, which is essential to understand ecosystems from a cybernetic standpoint, the hypogean ecosystem defies an intuitive understanding that we may have from other ecosystems about their structures. For example, in aquatic ecosystems, it is relatively easy to

separate plankton from the benthos, or in terrestrial ones, plant from animal communities despite their interconnectivity. Several factors complicate blanket generalizations for the hypogean environment: One is the limited space available in caves in comparison, for example, with oceans. That is true even for large caves. The other is that except for the hypogean ecosystems with chemoautotrophic bacteria as primary producers or tropical caves with some plants at the entrances, it is always more challenging to differentiate boundaries. Things get even more complicated when we consider that most of the energetic input in tropical and subtropical caves come from outside sources such as bat droppings. All this further emphasizes the concept discussed earlier that the hypogean ecosystem is not a closed one. Thus, we need to examine what is the evidence of any ecosystem structure in the hypogean ecosystem.

Little work has been done on the structure and information and energy transfer in the hypogean ecosystem. Most cave studies have seen caves as authentic islands of much reduced dimensions, in comparative terms, and one-dimensional representations [63]. However, caves have spatial and temporal dimensions that attest to their complexity (despite their apparent simplicity). Bussotti et al. [64] used a multifactorial sampling to examine the distribution of species assemblages within three different caves in Southern Italy over 11 months. They found a pattern of change in the structure of the assemblages along the exterior-interior axis and areas that suggested a highly complex structure of the biotic community.

From a spatial viewpoint, the typical cave (if there is such a thing) has five spatial-conceptual axes. First, the terrestrial-horizontal one on which we find many terrestrial invertebrates being the most evident to the casual observer. The length of the cave defines the second one. It is well known that community structure and biodiversity distribution changes throughout the cave's length, and the lengthier the cave, the more complex that structure can be [13], (p. 166). Even for relatively small caves, we see a spatial segregation between competing species [12]. That is the case of the Cumaca cave in Trinidad or the Guácharo cave in Venezuela that was discussed earlier. The oilbirds occupy areas closer to the entrance in detriment of bat colonies that occupy deeper areas [41]. The third is vertical and is mostly defined by the differences between the biodiversity found on the ground and roosting on walls or the ceiling of a cave. This is an important dimension since roosting animals, whether they are bats or birds, usually provide large amounts of nutrients to the cave generating ample grounds for increased biodiversity [65]. Moreover, these animals typically move daily from inside the cave to the epigeal ecosystem. They represent one of the most important facilitators of the interactions between the hypogean and epigeal ecosystems. The fourth is water: Whether a cave is permanently or periodically flooded with water makes a significant difference not only in its biotic composition but also in its dynamic and community structure. The fifth dimension that we need to consider is that of the outside ecosystem that influences the cave. Whether it is the terrestrial community outside the cave determining the species composition and abundance of animals that are frequent on both sides of the equation or water flowing in and out of the cave (including marine caves), they have a tremendous impact in cave ecology [5], (p. 166).

More recently, Hutchins et al. [66] have also questioned the old paradigm that food webs in hypogean ecosystems are simple, limited to one or two trophic levels, and composed of generalist species spatiotemporally patchy food resources and pervasive energy limitation. Their fieldwork generated data that chemolithoautotrophy "has been fundamental for the long-term maintenance of species diversity, trophic complexity, and community stability in this subterranean ecosystem, especially during periods of decreased photosynthetic production and groundwater recharge that have occurred over geologic time scales".

The way bats are distributed in a cave influences patchiness in that cave because of the heterogeneous way their droppings are deposited. This phenomenon has also been observed among mysid crustaceans, which deposit organic material in a patchy manner [67]. 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*. This species was found in the feces of the wood rat

(*Neotoma floridana magister*) in Mammoth Cave, Kentucky. This is a remarkable example of a species whose life cycle seems to be restricted to the hypogean ecosystem. Individuals of this subspecies defecate in the same sites (usually about 1 m away from each other), providing a patchy source of nutrients [68].

In addition to these spatial dimensions, we also need to see caves from a temporal perspective. From a geological viewpoint, caves have evolved 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. 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 stalagmite near a cave entrance [69]; yet that does not mean that these organisms lived exclusively in caves.

However, there is more than the eye of a casual observer can see when it comes to structures associated with caves. Campbell et al. [70] proposed to view caves as an example of an ecological dendritic network. They defined 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 interact with a species way of moving and distributing, which, in turn, will affect their abundance and community interactions. Since most caves do show a certain geometric similarity with this type of structure, their approach seems reasonable. Furthermore, they proposed that one of the reasons for the high rate of endemism in cave biota is precisely these habitats' spatial organization.

This further supports the argument that there is structure in the hypogean ecosystem.

2.5. Diversity and Energy Flows

As defined by the number of species per locality/area, the concept of diversity is related to the notion of ecosystem structure. Yet, it is not the same thing. In avoiding typological thinking, we need to look closer at the idea of ecotypes since several studies have shown that when using the biological species concept, some cave populations show a high level of genetic similarities to their epigeal ancestor despite drastic phenotypic differences [13], (pp. 132–139).

The other important consideration is that since a portion of the energy is lost every time one organism passes its energy (information in cybernetic terms) to another, the more complex the ecosystem, the less efficient it is in preserving it. That is particularly important in the hypogean ecosystem, usually described in temperate areas as energetically poor [24].

This brings us to the Ashby's Law of Requisite Variety. This law was initially devised by the English psychiatrist and cybernetic pioneer W. Ross Ashby [71]. He postulated that the more variable the operating environment, the more variable a system must be. In other words, a system will fail unless its variability matches or surpasses that of its environment. Imagine that you are trying to keep in balance a broom from its top on the tip of one of your fingers. You know that you have to move your hand regularly to keep up with the highly unpredictable movement of the broom to keep it in equilibrium. Otherwise, the broom would fall.

An ecosystem has to have the ability to respond to fluctuations if it is to maintain its essential characteristics in the long term. For ecosystems such as hypogean ones, this is a complicated issue because, in general, particularly in temperate climates, they tend to be less complex and, therefore, less plastic when it comes to the system's adaptive nature. That also means that the ecosystem elements must show enough plasticity to make the system itself more plastic if it were to survive fluctuations. That brings us to the evolutionary consequences of adapting to the conditions of the hypogean ecosystem.

Romero [13], (pp. 150–156) provided empirical data and reasoning to support the idea that the phenotypic characters among many hypogean organisms are achieved via phenotypic plasticity. Moreover, that genetic rearrangement that carries such changes is triggered by parameters in the

hypogean ecosystem's physical environment, such as lack of light and flood events. This, in turn, supports the idea that the characters (or lack thereof) that we usually associate with the hypogean environment result from natural selection. Thus, phenotypic plasticity often provides a reproductive advantage over a genetically fixed phenotype because environmentally induced phenotypes have a higher probability of conforming to prevailing environmental conditions than genetically fixed ones [72].

The convergent nature of troglomorphic characters further supports this explanation. Convergent evolutionary patterns are strong evidence of adaptation via natural selection [73].

Plasticity can (and should) be maintained in fluctuating environments, especially when fluctuations in the environment are predictable to some extent as exemplified in the case of the Cumaca cave mentioned above. In another longstanding generalization about the cave environment, there is the belief that caves are so constant that no ecological fluctuations occur. However, this view has been challenged for some time. Hawes [74], for example, was the first to provide specific examples of flooding being a periodic event in caves leading toward fluctuations in their ecological conditions. He showed how, despite other factors such as temperature and lack of light being constant, periodic floods provide conditions of a fluctuating environment and play a role in colonization events.

Thus, it is not surprising that the cave organisms for which phenotypic plasticity has been demonstrated are all aquatic: Crayfish, fishes, and salamanders. Fluctuating environmental conditions are the case in tropical caves where there are constant (but predictable) fluctuations in water level due to drastic seasonal changes in rainfall regimes [13], (p. 156).

Finally, when it comes to energy flows, we must look at the concept of biomass. When dealing with the biomass concept for hypogean ecosystems, we also need to take a broader view. Biomass is usually defined in ecology textbooks as the total mass of organisms in a given area or volume. However, as we saw throughout this article, one major component of the hypogean ecosystem can be the droppings from organisms such as bats and birds that reside in caves. If we were to apply the above definition of biomass, we would be excluding the energetic contribution of those droppings to the entire ecosystem. This will be shortsighted. Therefore, for the definition of biomass, we need to include these droppings as organic material consumed and the process by living organisms that end up being utilized by other living organisms. Only then we can include them as information in cybernetic terms.

3. Conclusions

All the data and concepts presented here show a remarkable similarity between hypogean ecosystems and cybernetic systems. The question is, what do we have to gain from applying these cybernetic structures to a hypogean ecosystem?

First, a cybernetic approach can help us systematize hypogean ecosystems, which, in turn, will make us understand better how they work, especially when it comes to the interplay between different biotic and abiotic factors.

Second, this cybernetic characterization will allow us to recognize better—and even quantify—the diversity in ecosystem structures worldwide, as well as when it comes to different latitudes and the biome with which hypogean environment interacts.

Third, a cybernetic approach will help us open up more to understand the interaction between hypogean ecosystems and their surrounding environment to see them as open instead of a closed ecosystem.

Although Margalef [6], (p. 24), was ambivalent about the immediate descriptive application of cybernetic approaches to the understanding of ecosystems, and that we still have some holes to fill in our biospeleology knowledge, he reasoned that because (a) they tend to be too complex and (b) we are far from understanding all of its variables, I would argue that the hypogean ones are an excellent laboratory for such endeavor. First, they tend to be less complex than, for example, a tropical rain forest or a coral reef, and, second, the smaller the cave, the easier it would be to understand how they operate from a cybernetic viewpoint. Moreover, with the use of artificial intelligence that can generate models

of fluctuations to visualize how they operate under different circumstances, that could be an excellent tool for conservation purposes. The reason for that is that we can better represent the role that different organisms play in the cave community as an instrument to convince the proper authorities of the importance of preserving each element of that community [13], (p. 182). Tesler’s Theorem, as Douglas Hofstadter [75] puts it, goes as follows “Artificial Intelligence is whatever hasn’t been done yet”.

Funding: This research received no external funding.

Acknowledgments: Three reviewers provided very useful comments to the original manuscript. Andrea Romero, Brian O’Neill, and Enrico Lunghi read an earlier version of this MS and made valuable suggestions. I want to pay homage to the late Ramón Margalef, who inspired me to think out of the box. His teachings and writings led me to write this article.

Conflicts of Interest: The author declares no conflict of interest.

References

- Wiener, N. *Cybernetics or Control and Communication in the Animal and Machine*; Wiley: New York, NY, USA, 1948.
- Lunghi, E.; Manenti, R.; Ficetola, G.F. Seasonal variation in microhabitat of salamanders: Environmental variation or shift of habitat selection? *PeerJ* **2015**, *3*, e1122. [[CrossRef](#)] [[PubMed](#)]
- Young, C. Plato’s Concept of Liberty in the Laws. *Hist. Political Thought* **2018**, *39*, 379–398.
- Heylighen, F.; Joslyn, C. Cybernetics and Second-Order Cybernetics. In *Encyclopedia of Physical Science & Technology*, 3rd ed.; Meyers, R.A., Ed.; Academic Press: New York, NY, USA, 2001; pp. 1–24. [[CrossRef](#)]
- Piotrowski, R. Between Plato and Wiener. Philosophical cybernetics in the 17th century. *Stud. Logic Gramm. Rhetor.* **2012**, *28*, 63–71.
- Margalef, R. *Perspectives in Ecological Theory*; The University of Chicago Press: Chicago, IL, USA, 1968.
- Patten, B.C. An Introduction to the Cybernetics of the Ecosystem: The Trophic-Dynamic Aspect. *Ecology* **1959**, *40*, 221–231. [[CrossRef](#)]
- McNaughton, S.J.; Coughenour, M.B. The Cybernetic Nature of Ecosystems. *Am. Nat.* **1981**, *117*, 985–990. [[CrossRef](#)]
- Oksanen, L. Ecosystem Organization: Mutualism and Cybernetics or Plain Darwinian Struggle for Existence? *Am. Nat.* **1988**, *131*, 424–444. [[CrossRef](#)]
- Bergandi, D. Eco-cybernetics: The ecology and cybernetics of missing emergences. *Kybernetes* **2000**, *29*, 928–942. [[CrossRef](#)]
- Makarieva, A.M. Cybernetics. In *Systems Ecology*; Encyclopedia of Ecology; Jørgensen, S.E., Fath, B.D., Eds.; Elsevier: Oxford, UK, 2008; Volume 1, pp. 806–812.
- Huelsenbeck, J.P.; Ronquist, F.; Nielsen, R.; Bollback, J.P. Bayesian Inference of Phylogeny and Its Impact on Evolutionary Biology. *Science* **2001**, *294*, 2310–2314. [[CrossRef](#)] [[PubMed](#)]
- Romero, A. *Cave Biology: Life in Darkness*; Cambridge University Press: Cambridge, UK, 2009.
- Culver, D.C. Analysis of Simple Cave Communities I. Caves as Islands. *Evolution* **1970**, *24*, 463–474. [[CrossRef](#)] [[PubMed](#)]
- Hancock, P.J.; Boulton, A.J.; Humphreys, W.F. Aquifers and hyporheic zones: Towards an ecological understanding of groundwater. *Hydrogeol. J.* **2005**, *13*, 98–111. [[CrossRef](#)]
- Gers, C. Diversity of energy fluxes and interactions between arthropod communities: From soil to cave. *Acta Oecologica* **1998**, *19*, 205–213. [[CrossRef](#)]
- Crouau, Y.; Ferre, C.; Crouau-Roy, B. Dynamic and temporal structure of the troglobitic beetle *Speonomus hydrophilus* (Coleoptera: Bathysciidae). *Ecography* **1992**, *15*, 12–18. [[CrossRef](#)]
- Wittmann, K. Retromysis Nura New Genus and Species (Mysidacea, Mysidae, Heteromysini) from a Superficial Marine Cave in Minorca (Balearic Islands, Mediterranean Sea). *Crustaceana* **2004**, *77*, 769–783. [[CrossRef](#)]
- Mitchell, R.W. A Comparison of Temperate and Tropical Cave Communities. *Southwest. Nat.* **1969**, *14*, 73. [[CrossRef](#)]
- Deharveng, L. Diversity Patterns in the Tropics. In *Encyclopedia of Caves*; Culver, D.C., White, W.B., Eds.; Elsevier: Amsterdam, The Netherlands, 2005; pp. 166–170. [[CrossRef](#)]

21. Deharveng, L.; Bedos, A. The cave fauna of southeast Asia. Origin, evolution and ecology. In *Subterranean Ecosystems*; Wilkens, H., Culver, D.C., Humphries, W.F., Eds.; Elsevier: Amsterdam, The Netherlands, 2000; pp. 603–632.
22. Martínez, A.; Mammola, S. Specialized Terminology Limits the Reach of New Scientific Knowledge. *bioRxiv* **2020**. [[CrossRef](#)]
23. Trudgill, S.; Tansley, A.G. The use and abuse of vegetational concepts and terms. *Prog. Phys. Geogr. Earth Environ.* **2007**, *31*, 517–522. [[CrossRef](#)]
24. Poulson, T.L.; White, W.B. The Cave Environment. *Science* **1969**, *165*, 971–981. [[CrossRef](#)]
25. Airoidi, L.; Cinelli, F. Variability of fluxes of particulate material in a submarine cave with chemolithoautotrophic inputs or organic carbon. *Mar. Ecol. Prog. Ser.* **1996**, *139*, 205–217. [[CrossRef](#)]
26. Sarbu, S.M. Movile Cave: A chemoautotrophically based groundwater ecosystem. In *Subterranean Ecosystems*; Wilkens, H., Culver, D.C., Humphries, W.F., Eds.; Elsevier: Amsterdam, The Netherlands, 2000; pp. 319–343.
27. Sarbu, S.M.; Galdenzi, S.; Menichetti, M.; Gentile, G. Geology and biology of the Frasassi caves in central Italy: An ecological multi-disciplinary study of a hypogenic hypogean karst system. In *Subterranean Ecosystems*; Wilkens, H., Culver, D.C., Humphries, W.F., Eds.; Elsevier: Amsterdam, The Netherlands, 2000; pp. 359–378.
28. Hose, L.D.; Palmer, A.N.; Palmer, M.V.; Northup, D.E.; Boston, P.J.; DuChene, H.R. Microbiology and geochemistry in a hydrogen-sulphide-rich karst environment. *Chem. Geol.* **2000**, *69*, 399–423. [[CrossRef](#)]
29. Dattagupta, S.; Schaperdoth, I.; Montanari, A.; Mariani, S.; Kita, N.; Valley, J.W.; Macalady, J.L. A novel symbiosis between chemoautotrophic bacteria and a freshwater cave amphipod. *ISME J.* **2009**, *3*, 935–943. [[CrossRef](#)]
30. Mulec, J. Phototrophs in Caves. In *Cave Ecology. Ecological Studies (Analysis and Synthesis)*; Moldovan, O., Kováč, L., Halse, S., Eds.; Springer: Cham, Switzerland, 2018; Volume 23. [[CrossRef](#)]
31. Lunghi, E.; Manenti, R.; Mulargia, M.; Veith, M.; Corti, C.; Ficetola, G.F. Environmental suitability models predict population density, performance and body condition for microendemic salamanders. *Sci. Rep.* **2018**, *8*, 7527. [[CrossRef](#)] [[PubMed](#)]
32. Machado, S.F.; Ferreira, R.L.; Martins, R.P.; Martins, R.P. Aspects of the population ecology of *Goniosoma* sp. (Arachnida Opiliones Gonyleptidae). *Trop. Zool.* **2003**, *16*, 13–31. [[CrossRef](#)]
33. Soares, D.; Adams, R.; Hammond, S.; Slay, M.E.; Fenolio, D.B.; Niemiller, M.L. Evolution of coprophagy and nutrient absorption in a Cave Salamander. *Subterr. Biol.* **2017**, *24*, 1–9. [[CrossRef](#)]
34. Available online: <http://sciencenetlinks.com/science-news/science-updates/snakes-cave/> (accessed on 28 October 2020).
35. Esberard, C.E.L.; Vrcibradic, D. Snakes preying on bats: New records from Brazil and a review of recorded cases in the Neotropical Region. *Rev. Bras. Zool.* **2007**, *24*, 848–853. [[CrossRef](#)]
36. Toulkeridis, T.; Martin-Solano, S.; Addison, A.; Pozo-Rivera, W.E. Predation of *Desmodus rotundus* Geoffroy, 1810 (Phyllostomidae, Chiroptera) by *Epicrates cenchria* (Linnaeus, 1758) (Boidae, Reptilia) in an Ecuadorian Cave. *Subterr. Biol.* **2016**, *19*, 41–50. [[CrossRef](#)]
37. Price, J.J.; Johnson, K.P.; Clayton, D.H. The evolution of echolocation in swiftlets. *J. Avian Biol.* **2004**, *35*, 135–143. [[CrossRef](#)]
38. Holland, R.A.; Wikelski, M.; Kümmeth, F.; Bosque, C. The Secret Life of Oilbirds: New Insights into the Movement Ecology of a Unique Avian Frugivore. *PLoS ONE* **2009**, *4*, e8264. [[CrossRef](#)]
39. Martin, G.R.; Rojas, L.M.; McNeil, R. The eyes of oilbirds (*Steatornis caripensis*): Pushing at the limits of sensitivity. *Naturwissenschaften* **2004**, *91*, 26–29. [[CrossRef](#)]
40. Blin, M.; Fumey, J.; Lejeune, C.; Policarpo, M.; Leclercq, J.; Pèrè, S.; Torres-Paz, J.; Pierre, C.; Imarazene, B.; Rétaux, S. Diversity of Olfactory Responses and Skills in *Astyanax Mexicanus* Cavefish Populations Inhabiting different Caves. *Diversity* **2020**, *12*, 395. [[CrossRef](#)]
41. Romero, A.; Creswell, J.; Romero, A.; Creswell, J. In search of the elusive ‘eyeless’ cave fish of Trinidad, W.I. *Natl. Speleol. Soc. News* **2000**, *58*, 282–283.
42. Romero, A.; Singh, A.; McKie, A.; Manna, M.; Baker, R.; Paulson, K.M. Return to the Cumaca Cave, Trinidad, W.I. *Natl. Speleol. Soc. News* **2001**, *59*, 220–221.
43. Romero, A.; Singh, A.; McKie, A.; Manna, M.; Baker, R.; Paulson, K.M.; Creswell, J.E. Replacement of the Troglomorphic Population of *Rhamdia quelen* (Pisces: Pimelodidae) by an Epigeal Population of the Same Species in the Cumaca Cave, Trinidad, West Indies. *Copeia* **2002**, *2002*, 938–942. [[CrossRef](#)]

44. Ferreira, R.L.; Martins, R.P. Trophic structure and natural history of bat guano invertebrate communities, with special reference to Brazilian caves. *Trop. Zool.* **1999**, *12*, 231–252. [[CrossRef](#)]
45. Lopes Ferreira, R.; Parentoni Martins, R.; Yanega, D. Ecology of bat guano arthropod communities in a Brazilian dry cave. *Ecotropica* **2000**, *6*, 105–116.
46. Romero, A. Introgressive hybridization in a population of *Astyanax fasciatus* (Pisces: Characidae) at La Cueva Chica. *Natl. Speleol. Soc. Bull.* **1983**, *45*, 81–85.
47. Fenolio, D.B.; Graening, G.; Collier, B.A.; Stout, J.F. Coprophagy in a cave-adapted salamander; the importance of bat guano examined through nutritional and stable isotope analyses. *Proc. R. Soc. B* **2005**, *273*, 439–443.
48. Baudinette, R.V.; Wells, R.T.; Sanderson, K.J.; Clark, B. Microclimate conditions in termite caves of the bent-wing bat, *Micropterus schreibersii*—An attempted restoration of a former maternity site. *Wildl. Res.* **1994**, *12*, 607–619. [[CrossRef](#)]
49. Graening, G.O. Trophic Structure of Ozark cave streams containing endangered species. *Oceanol. Hydrobiol. Stud.* **2005**, *34*, 3–17.
50. Jasinska, E.J.; Knott, B.; McComb, A.J. Root Mats in Ground Water: A Fauna-Rich Cave Habitat. *J. N. Am. Benthol. Soc.* **1996**, *15*, 508–519. [[CrossRef](#)]
51. MacArthur, R. Fluctuations of Animal Populations and a Measure of Community Stability. *Ecology* **1955**, *36*, 533. [[CrossRef](#)]
52. Leigh, E.G. On the relation between the productivity, biomass, diversity, and stability of a community *. *Proc. Natl. Acad. Sci. USA* **1965**, *53*, 777–783. [[CrossRef](#)] [[PubMed](#)]
53. Langecker, T.G. The effects of continuous darkness on cave ecology and cavernicolous evolution. In *Subterranean Ecosystems*; Wilkens, H., Culver, D.C., Humphries, W.F., Eds.; Elsevier: Amsterdam, The Netherlands, 2000; pp. 135–157.
54. Boutin, C.; Coineau, N. Evolutionary rates and phylogenetic age in some stygobiontic species. In *Subterranean Ecosystems*; Wilkens, H., Culver, D.C., Humphries, W.F., Eds.; Elsevier: Amsterdam, The Netherlands, 2000; pp. 433–451.
55. Romero, A. Threatened fishes of the world: *Amblyopsis rosae* (Eigenmann, 1898) (Amblyopsidae). *Environ. Biol. Fishes* **1998**, *52*, 434. [[CrossRef](#)]
56. Romero, A. Threatened fishes of the world: *Speoplatyrhinus poulsoni* Cooper and Kuehne, 1974 (Amblyopsidae). *Environ. Biol. Fishes* **1998**, *53*, 293–294. [[CrossRef](#)]
57. Gibert, J.P.; Yeakel, J.D. Eco-Evolutionary Origins of Diverse Abundance, Biomass, and Trophic Structures in Food Webs. *Front. Ecol. Evol.* **2019**, *7*. [[CrossRef](#)]
58. Milanovich, J.; Trauth, S.E.; Saugey, D.A.; Jordan, R.R. Fecundity, reproductive ecology, and influence of precipitation on clutch size in the western slimy salamander (*Plethodon albagula*). *Herpetologica* **2006**, *62*, 292–301. [[CrossRef](#)]
59. Ashmole, N.P.; Oromí, P.; Ashmole, M.J.; Martín, J.L. Primary faunal succession in volcanic terrain: Lava and cave studies on the Canary Islands. *Biol. J. Linn. Soc.* **1992**, *46*, 207–234. [[CrossRef](#)]
60. Denitto, F.; Terlizzi, A.; Belmonte, G. Settlement and primary succession in a shallow submarine cave: Spatial and temporal benthic assemblage distinctness. *Mar. Ecol.* **2007**, *28*, 35–46. [[CrossRef](#)]
61. Mammola, S.; Isaia, M. Spiders in caves. *Proc. R. Soc. B* **2017**, *284*, 1–10. [[CrossRef](#)]
62. Teeling, E.C.; Springer, M.S.; Madsen, O.; Bates, P.; O'Brien, S.P.; Murphy, W.J. A Molecular Phylogeny for Bats Illuminates Biogeography and the Fossil Record. *Science* **2005**, *307*, 580–584. [[CrossRef](#)]
63. Ravn, N.R.; Michelsen, A.; Reboleira, A.S.P.S. Decomposition of Organic Matter in Caves. *Front. Ecol. Evol.* **2020**, *8*, 554651. [[CrossRef](#)]
64. Bussotti, S.; Terlizzi, A.; Frascchetti, S.; Belmonte, G.; Boero, F. Spatial and temporal variability of sessile benthos in shallow Mediterranean marine caves. *Mar. Ecol. Prog. Ser.* **2006**, *325*, 109–119. [[CrossRef](#)]
65. Peck, S.B.; Kukulova-Peck, J.; Bordón, C. Beetles (Coleoptera) of an Oil-Bird Cave: Cueva Del Guácharo, Venezuela. *Coleopt. Bull.* **1989**, *43*, 151–156.
66. Hutchins, B.T.; Engel, A.S.; Nowlin, W.H.; Schwartz, B.F. Chemolithoautotrophy supports macroinvertebrate food webs and affects diversity and stability in groundwater communities. *Ecology* **2016**, *97*, 1530–1542. [[CrossRef](#)] [[PubMed](#)]
67. Coma, R.; Carola, M.; Riera, T.; Zabala, M. Horizontal transfer of matter by a cave-dwelling mysid. *Mar. Ecol. Pubbl. Della Stn. Zool. Napoli* **1997**, *18*, 211–226.

68. Moraza, M.L.; Lindquist, E.E. Coprozerconidae, a new family of Zerconoid mites from North America (Acari: Megostigmata: Zerconoidea). *Acarologia* **1998**, *39*, 291–313.
69. Blaszak, C.; Cokendolpher, J.C.; Polyak, V.J. Paleozircon cavernicolus, n.gen., n.sp., fossil mite from a cave in the Southwestern U.S.A. (Acari, Gamasida: Zerconidae), with a key to Nearctic genera of Zerconidae. *Int. J. Acarol.* **1995**, *21*, 253–259. [[CrossRef](#)]
70. Grant, E.H.C.; Lowe, W.H.; Fagan, W.F. Living in the branches: Population dynamics and ecological processes in dendritic networks. *Ecol. Lett.* **2007**, *10*, 165–175. [[CrossRef](#)]
71. Ashby, W.R. Requisite Variety and Its Implications for the Control of Complex Systems. *Facets Syst. Sci.* **1991**, *1*, 405–417. [[CrossRef](#)]
72. Whiteman, H.H. Evolution of Facultative Paedomorphosis in Salamanders. *Q. Rev. Biol.* **1994**, *69*, 205–221. [[CrossRef](#)]
73. Endler, J.A. *Natural Selection in the Wild*; Princeton University Press: Princeton, NJ, USA, 1986.
74. Hawes, R.S. The Flood Factor in the Ecology of Caves. *J. Anim. Ecol.* **1939**, *8*, 1–5. [[CrossRef](#)]
75. Hofstadter, D. *Gödel, Escher, Bach: An Eternal Golden Braid*; Vintage Books: New York, NY, USA, 1979.

Publisher’s Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



© 2020 by the author. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).