

Biosphere Reserves and conservation of subterranean aquatic ecosystems in Brazil

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Abstract

Subterranean systems and aquifers are functional units of karst, constituting habitat units for the aquatic fauna. These are open systems, under the influence of external factors controlling the internal processes. Major well-studied Brazilian karst areas, situated in diverse biosphere reserves, are briefly described with focus on total diversity (troglobites + trogloniles + troglonenes) and diversity of troglonites, encompassing taxonomic, phylogenetic and genetic/morphological diversity. Different combinations of evolutionary and ecological processes are observed, producing unique diversity patterns. Consequently, the recognition of the importance of karst areas and their priority for conservation and management must be based on multiple criteria applied in a case-by-case analysis. Good practices for conservation and management of subterranean waters start with studies based on robust, scientifically sound criteria. The focus must be the subterranean systems, not caves per se, including the influence areas (recharge areas, the areas receiving their output, etc.), and results must be tested for sampling sufficiency. Biosphere reserves are a first step to ensure protection of subterranean waters and their ecosystems. At regional/local scale, their insertion in Conservation Units is an efficient tool for preservation if properly designed and managed.

Keywords

subterranean fauna; karst systems; conservation; good practices; Reserves of Biosphere

1. Introduction

Subterranean habitats are networks of interconnected heterogeneous spaces in the subsurface, filled with water and/or air, forming a continuum available for colonization by diverse organisms. Caves are the components of such habitats accessible to human.

In karst areas, the habitat unit for subterranean aquatic organism is the system. Karst systems are functional units, involving organized flow pathways forming a drainage unit with input-output zones and finite configurations (Gibert et al., 1994). A karst aquifer is an open system with a boundary defined by the catchment limits and input, throughput and output flows, and mechanisms and controls (Ford & Williams, 2007).

Recharge may be autogenic, when only karst rocks are found within the catchment and recharge is derived from precipitation falling directly on them, or allogenic, when waters from neighboring or overlaying non-karst rocks run into the karst aquifer. Karst systems encompass not only subterranean spaces (including caves in the human sense), but also recharge areas (fast and delayed infiltration zones and sinkholes) and catchment points along the system. Water may flow as fast-moving streams (lotic habitats, either permanent or temporary) to slow moving waters (lentic habitats). These conditions create quite diverse chemical and ecological scenarios.

External factors that control internal processes in karst systems constitute the system environment. When it is possible to recognize geographical boundaries to this environment, areas of influence are configured, which are physical spaces bringing together factors with a direct or indirect relevant influence to the system.

Energy and matter that enter the system leave it in a condition different from the original one. The geographic environment that receives and is stimulated by a given system output is also part of its area of influence (Berbert-Born, 2018). Areas of influence on caves and karst systems include not only recharge areas (delayed and fast infiltration zones, such as sinkholes) and the area receiving its output (that may include other karst systems downstream), but also foraging areas of troglomenes (see below) such as bats. Matter and energy are exchanged between terrestrial and aquatic subterranean environment, therefore influence areas on aquatic systems include terrestrial elements and vice-versa.

An important feature of the karst is vertical zonation. From the subsurface to the deepest zones, one may distinguish the epikarst, open-channel stream passages including vadose tributaries and base-level streams, the zone of seasonal oscillations of the water table, the shallow (upper) phreatic zone (connected to the surface through inaccessible fissures, resurgences, regional sinkholes, wells, and caves), and the deep phreatic zone (Trajano, 2001a). There are aquatic organisms living in all of these zones, many of them showing specific adaptations to their habitats.

The epikarst (or subcutaneous zone) is a heterogeneous interface between unconsolidated material and altered carbonate bedrock, capable of delaying or storing and locally rerouting vertical infiltration to the deeper regional phreatic zone (Jones et al., 2004). Under certain circumstances, water is permanently stored in the epikarst, forming suspended aquifers, wherein aquatic populations may evolve.

2. Diversity of Subterranean Organisms

Subterranean organisms (cavernicoles *sensu lato*) are defined as evolutionary units responding to subterranean selective regimens; subterranean habitats provide resources (food, shelter, substrate, climate etc.) which affect survival/reproductive rates. In contrast, organisms introduced into caves by mishap, but which are unable to properly orient themselves and find food in this environment, eventually vanishing, are considered “accidentals” (Trajano & Carvalho, 2017).

The Schiner-Racovitza system (modified by Trajano, 2012 to incorporate the source-sink population model), classifies subterranean organisms into three categories: 1. Trogloniles are source populations (populations with excess production that would continue to grow if isolated; Jones et al., 2004), both in hypogean and epigeal habitats, with individuals regularly commuting between these habitats and promoting the introgression of genes selected under epigeal regimes into subterranean populations (and vice-versa). 2. Troglomenes, with source populations in epigeal habitats but using subterranean resources, for instance as shelter and food (there is no confirmed case of aquatic troglomenes in Brazil). 3. Troglobites, which are exclusively subterranean source populations, usually characterized by troglomorphisms, i.e. autapomorphies that can be directly related to the subterranean selective regime; the commonest troglomorphisms of troglobites are the reduced visual structures and dark pigmentation (Trajano & Carvalho, 2017).

In general, troglobites living in phreatic waters are the most specialized, accumulating troglomorphisms such as complete anophthalmia and melanic depigmentation, enhancement of non-visual sensory systems, delicate and frequently elongated bodies, adaptations to food-poor and hypoxic environments etc. (Trajano, 2021).

Caves are transient features within karst cycles. According to the most common speleogenetic process, which originates most karst caves, the network of small fissures formed by dissolution during the initiation phases are progressively enlarged. When the water flow changes from laminar to turbulent, with erosion also contributing to conduit enlargement, fast-flowing waters become available for colonization by preadapted populations living in epigeal lotic habitats. Eventually, in the cessation phase, large subterranean spaces disappear due to breakdowns or filling by chemical or clastic sediments. This transient characteristic of karst cycles explain why stream-dwelling troglobites in general are less troglomorphic than the phreatobitic ones - in the cessation phase, stream dwellers that have managed to adapt to the lentic conditions of the phreatic zone below may survive over a long geological period until the next cycle, frequently as relicts (Trajano, 2021).

The vast majority of researchers studying subterranean ecosystems focus primarily on the taxonomic diversity (species richness) of troglobites. However, taxonomic diversity, which only takes into account the number of species and their relative contribution, has little predictive power about the functioning of ecosystems. Phylogenetic diversity, a measure of diversity incorporating phylogenetic relationships among species, and functional diversity, which considers functional traits, are more sensitive to detecting responses of communities to environmental changes. The presence of relict taxa increases phylogenetic diversity and may overcome taxonomic diversity in terms of relevance for conservation (Cianciaruso et al., 2009; Trajano et al., 2016).

Genetic diversity expressed as diversity and disparity of phenotypes correlates with phylogenetic and functional diversities, and increases with number and degree of troglomorphisms accumulated by troglobites. Hence, the loss of one species without close relatives leads to a greater loss of genetic information than the extinction of a species with close relatives. Therefore, the best conservation strategy is to protect areas with the highest

phylogenetic diversity, preserving as much of this hierarchical variation as possible (Faith, 1992; Cianciaruso et al., 2009) and prioritizing those with the most divergent subterranean taxa.

Taxonomic diversity of troglobites is not necessarily correlated with total diversity, i.e., diversity of troglobites + troglophiles + troglaxenes. General diversity seems to be mostly a response to ecological factors, such as habitat extension and heterogeneity, and availability of organic matter. On the other hand, diversity of troglobites and their degree of differentiation is better explained by historical factors leading to genetic isolation and divergence, especially vicariance, which may not be revealed by analysis of present-day conditions (Trajano, 2001b). Troglobites, troglophiles and troglaxenes interact among themselves, therefore interspecific interactions (competition, predation etc.) are independent of the status according to the Schiner-Racovitza classification.

If we want to conserve biodiversity effectively, we need to preserve representative samples of biodiversity to ensure ecological and evolutionary processes that allow this biodiversity to persist over time, and to set targets for the conservation of biodiversity features.

3. Caves, karst areas and brazilian biosphere reserves: spots of high diversity of aquatic organisms in brazil

The UNESCO Biosphere reserves are defined as 'learning places for sustainable development'. They are sites for testing interdisciplinary approaches to understanding changes and interactions between social and ecological systems, including conflict prevention and management of biodiversity, and aiming to provide local solutions to global challenges. Biosphere reserves are nominated by national governments and remain under the sovereign jurisdiction of the states where they are located. Their status is internationally recognized (<https://en.unesco.org/biosphere>).

Most Brazilian caves are within Biosphere Reserves, providing a better status for conservation (Fig. 1). Herein, I focus on carbonatic caves, which harbor the most relevant aquatic faunas, situated in large and well-studied karst areas: Campo Formoso, Chapada Diamantina, Serra do Ramalho (Bahia State) - Caatinga Reserve; São Domingos (Goiás) - Cerrado Reserve; Nobres (Mato Grosso) and Serra da Bodoquena (Mato Grosso do Sul) - Pantanal Reserve; Alto Ribeira (São Paulo) - Atlantic Forest Reserve. Part of these are in protected areas: Parque Nacional da Chapada Diamantina, Parque Estadual Terra Ronca (São Domingos area), Parque Nacional da Serra da Bodoquena, and Parque Estadual Turístico do Alto Ribeira + Parque Estadual Intervalles (Alto Ribeira area).

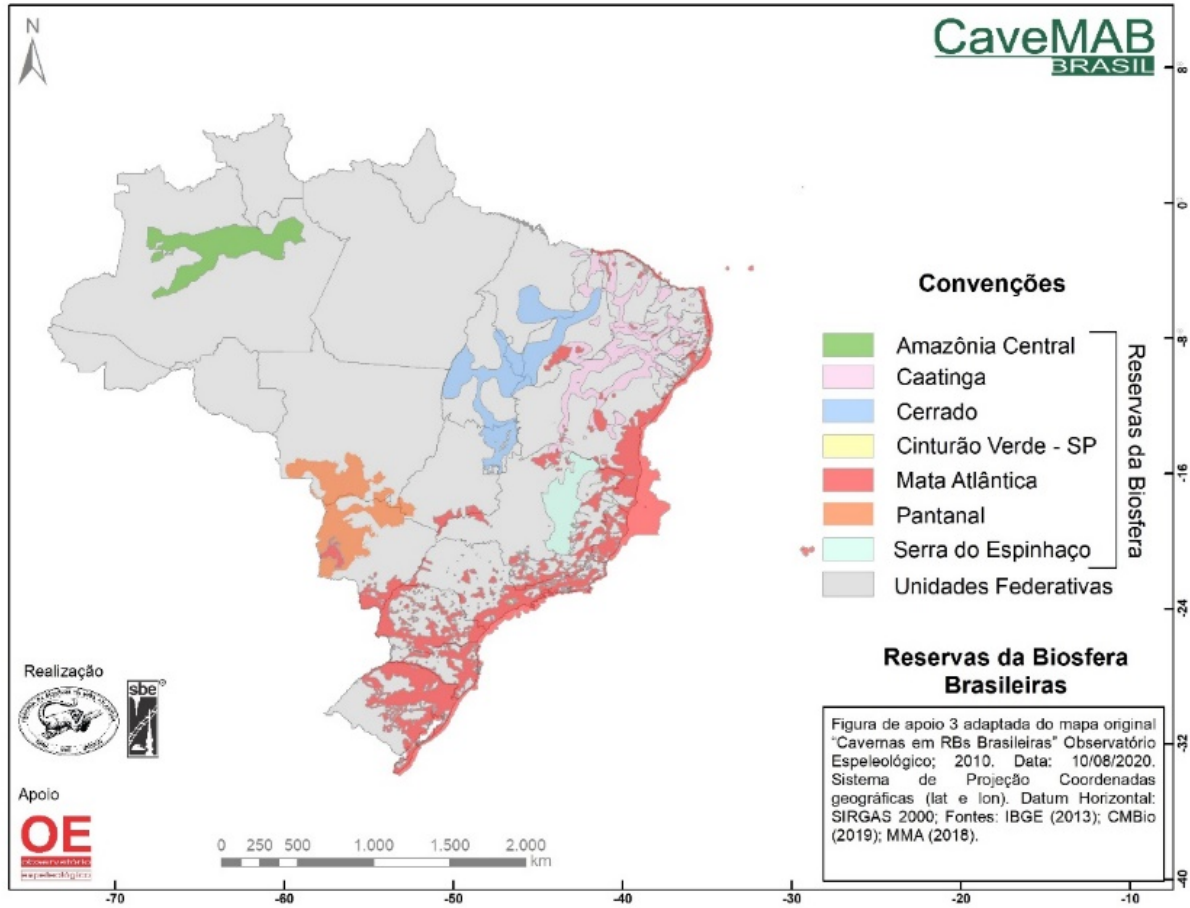


Figure 1A. Brazilian Reserves of Biosphere: Central Amazon (green), Caatinga (pink), Cerrado (blue), Atlantic Forest (red), Pantanal (orange), Serra do Espinhaço (light blue). Author: Frederico Lott, based on map from "Cavernas em RBs brasileiras", Observatório Espeleológico.

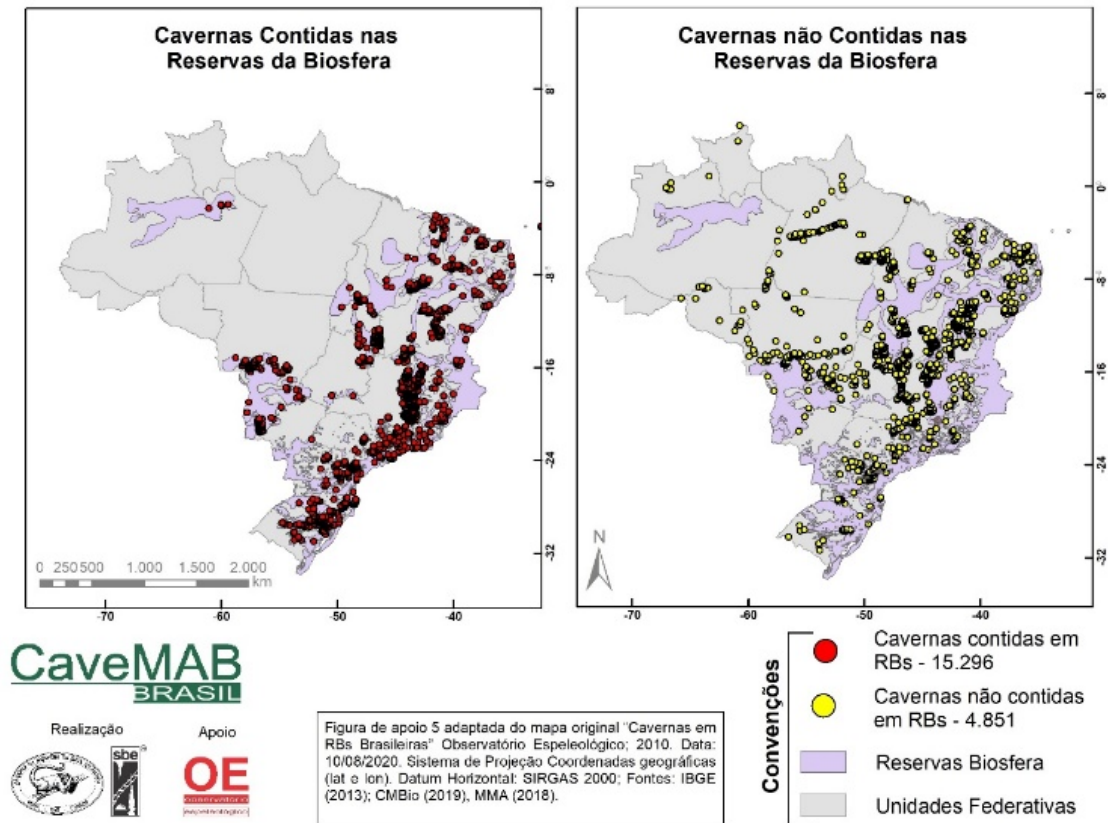


Figure 1B. Left: Brazilian caves (red dots) situated in Biosphere Reserve. Right: Brazilian caves (yellow dots) not in Biosphere Reserves. Author: Fredeico Lott, based on based on map from “Cavernas em RBs brasileiras”, Observatório Espeleológico.

These areas differ in total diversity and in taxonomic, phylogenetic and genetic diversity of troglobites, mostly due to the presence of highly specialized relicts in subterranean waters in the Caatinga Reserve. Such disparity is a consequence of historical events and of present-day geomorphology, hydrology and ecological circumstances.

The majority of subterranean habitats in the interior of Brazilian northeastern states are situated in the currently semiarid Caatinga. The Paleoclimate Model (Barr, 1968), based on the notion that wet phases of glacial cycles are times of colonization of subterranean habitats by epigeal populations, which become isolated and differentiate in subsequent dry phases, explains the high diversity of troglobites, both aquatic and terrestrial, in the Caatinga (Trajano, 1995, 2001). Studies based on speleothem dating revealed relatively frequent, dramatic and abrupt changes in the available moisture during the Pleistocene (on average, one wet event every 20,000 yr for the past 210 kyr) (Wang et al., 2004).

Most permanent habitats currently available for aquatic organisms in the Caatinga subterranean habitats are represented by phreatic waters, connected to the surface through inaccessible fissures, resurgences, sink-holes, wells, caves etc., where highly specialized troglobites live. Many of these organisms are relicts, belonging to exclusively subterranean genera such as *Spelaeogammarus* (Amphipoda), *Xangoniscus* (Oniscoidea isopods, that may form amphibious populations) and *Spiripockia* (Gastropoda), or higher taxa (Calabozoa isopods) (Trajano et al., 2016). At least two species of highly modified catfishes of the genus *Rhamdiopsis* (Heptapteridae) live in this Reserve.

In addition, two highly specialized amphipods have been found in the Apodi area, Caatinga region, Rio Grande do Norte State: *Potiberaba porakuara* (Mesogammaridae) and *Seborgia potiguar* (the first Brazilian Seborgiidae) (Fiser et al., 2013).

Semi-aridity implies reduced superficial drainage, with mostly intermittent surface and underground streams, that may leave permanent pools and lakes where subterranean populations can survive and differentiate in isolation. As result of disruption of the epigeal drainage, the input of nutrients into subterranean habits is generally highly limited and seasonal, resulting in low total diversity.

In contrast, allochthonous high-energy epigeal streams presently crossing the São Domingos karst area, in Central Brazil, carry large amounts of organic matter into subterranean habitats. As consequence, these caves are characterized by high taxonomic diversity and population abundance. Regarding taxonomic diversity of troglobites, there is an apparent discordance between invertebrates, which are rare, and fishes, with seven nominal species encompassing several differentiated lineages. São Domingos harbors the richest subterranean ichthyofauna in South America, including species adapted to life in the epikarst. Nevertheless, degrees of troglomorphy are medium to low, with intra and interpopulation variation, unlike that observed for Caatinga troglobites.

The São Domingos karst area is situated in a relatively stable region - according to a reconstruction of phytogeographic domains during the last glacial (18,000 to 13,000 yr ago - Ab'Saber, 1981), this area was in the Cerrado core area as it is today. Paucity of opportunities for isolation due to extinction of epigeal congeners might explain the scarcity of troglobitic invertebrates in this area. However, the Paleoclimate Model does not explain the high taxonomic diversity of troglobitic fishes. In this case, the topographic model may apply: the high-energy streams crossing the area causes intense alluvial down-cutting lowering the regional water table and creating waterfalls inside and outside caves, which could isolate aquatic populations (Bichuette & Trajano, 2004; Reis et al., 2006, Trajano, 2021). Therefore, the São Domingos karst area represents a special situation, because different processes seem to explain the origin of troglobitic fishes and of invertebrates, respectively.

The Alto Ribeira karst area, southeastern Brazil, is a spot of high taxonomic diversity of troglobites in general, including aquatic species, such as *Potamolithus* gastropods, *Hyaella* amphipods and the catfish, *Pimelodella kronei*, the first described Brazilian troglobite (Trajano et al., 2016; Trajano, 2021). However, degrees of troglomorphy are in general medium, with population variability in most cases and, with few exceptions, belonging to genera also recorded in epigeal streams. Dating of speleothems (Cruz-Jr et al., 2005) pointed to less abrupt and dramatic climatic paleo-oscillations, not as dominant as in the Caatinga. Thus, the Paleoclimate Model also applies, but shorter and less dramatic oscillations would result in less specialized troglobites.

The Bodoquena karst area in southwest Brazil, is distinguished by the presence of flooded caves, especially in the southern plateau. Many relictual aquatic invertebrates and fishes are found in this area, including *Girardia planarians*, *oligochaetes* (unidentified), *Megagidiella* amphipods, *spelaeogriphaceans*, and siluriform fishes (at least three *Trichomycterus* species, besides a *Pimelodella* catfish and an *Ancistrus* armored catfish), typically living in the upper phreatic zone (Cordeiro et al., 2014; Trajano, 2021). The Paleoclimatic model would explain the origin of troglobites such as the *Trichomycterus* species, without congeners recorded in epigeal drainages. Adaptations to phreatic waters is explained by the progressive cave flooding from south to north, as consequence of the development of the Pantanal basin. Tectonic subsidence would be a major contributor to the relative uprising of the water table in the Bodoquena karst area due to the lowering of the regional base-level (Trajano, 2021).

It is noteworthy that, at the system level, fine-grained factors may be of influence, such as fragmentation at a local scale due to geological, geographic and/or hydrological barriers, topographic isolation caused by alluvial down-cutting, and ecological singularities (Trajano et al., 2016).

Best practices in protecting and managing cave and karst waters

Conservation aims to preserve representative samples of geo- and biodiversity, including patterns and processes that produced such diversity. As exemplified by the most intensively studied Brazilian areas, combinations of different evolutionary and ecological processes produce unique diversity patterns observed in different karst areas. Therefore, the recognition of the importance and priority for conservation, and management of karst areas and systems (and other cave areas as well, such as the siliclastic and ferruginous ones, widespread in Brazil), must be based on multiple criteria applied in a case-by-case analysis.

The current Brazilian legislation regulating the use of subterranean resources for economic purposes, based on a classification of caves according to their degree of relevance, is intertwined with conceptual, logical and procedural flaws that compromise an effective conservation of these habitats (Trajano, 2020, 2022). A major problem is the focus limited to caves, not on karst systems, or equivalent in non-karst areas. Other serious problems are a consequence of deficient minimum requirements for environmental studies aiming to support the classification of caves. There is no demand for sampling sufficiency, thus the objective of preserving representative samples of diversity cannot be ensured. Likewise, case-by-case studies in areas of influence are not required. Moreover, the conservation and management of phreatic waters are hampered by the difficulty to perform hydrogeological studies aiming to uncover deep connections of slow-moving waters.

Good practices in protecting and managing subterranean waters and ecosystems, establishing priorities for conservation, begin with environmental studies based on non-negotiable, scientifically sound criteria:

- Caves are not isolated from their surroundings, therefore the study unit must be the karst system and associated aquifers, or the equivalent in other lithologies, as well as their areas of influence.

- Sampling sufficiency that is properly tested (in the case of biological studies using, for instance, accumulating curves) must be required; temporal sufficiency requires at least three annual cycles to describe seasonality, and more for infra-annual cycles (cycles with a period superior to one year) (Trajano, 2018).

- Areas of influence on systems and aquifers, including suspended aquifers, must be studied on a case-by-case basis, with focus on areas of recharge (as in Gethner et al., 2003; i.e. the area receiving the system output), foraging areas of troglomenes such as bats, etc.

- All kinds of diversity must be considered: total (troglomenes + troglomenes + troglomenes) and diversity of troglomenes; taxonomic (species richness), phylogenetic, genetic, functional diversity.

Biosphere reserves are a first step to ensure protection of subterranean waters and their ecosystems at the regional/local scale. Insertion in Conservation Units (“Unidades de Conservação - Ucs”) is an efficient tool for preservation, if properly designed and managed (which is frequently not the case).

Among the karst areas herein described, Campo Formoso and Serra do Ramalho (Bahia State), Apodi (Rio Grande do Norte State), and Nobres (Mato Grosso State) are not in protected areas. These areas are threatened by anthropic impacts, such as water exploitation, mining projects, pollution due to land use (agriculture, cattle farming), and uncontrolled cave visitation. The importance of these areas justifies the creation of Conservation Units with utmost urgency.

Even in the case of areas already in Conservation Units, protection is not completely assured because part of the influence areas are external to these Units. This is the case with PETER (São Domingos karst area), crossed by rivers coming from farming areas in Bahia State, with monocultures using pesticides and fertilizers. Land use is also a matter of concern for the PARNA Chapada Diamantina. Sedimentation due to deforestation for cattle raising at recharge areas of important karst systems is a major problem in the PARNA Serra da Bodoquena. In PETAR, pollution due to agriculture and mining in recharge areas have led to local extinction, or nearly, of populations of blind catfishes and *Aegla* decapods. In some cases, there are no licensed Management Plans and, when such Plans do exist, they have not been fully implemented. As a consequence, speleotourism is poorly controlled.

In conclusion, priority areas for conservation and management, recognized after reliable scientific studies and using multiple criteria, should be inserted in Conservation Units encompassing karst systems (or equivalent for non-karst areas) and their entire areas of influence.

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