

Scientists' Warning on the Conservation of Subterranean Ecosystems

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In light of recent alarming trends in human population growth, climate change, and other environmental modifications, a “Warning to humanity” manifesto was published in BioScience in 2017. This call reiterated most of the ideas originally expressed by the Union of Concerned Scientists in 1992, including the fear that we are “pushing Earth’s ecosystems beyond their capacities to support the web of life.” As subterranean biologists, we take this opportunity to emphasize the global importance and the conservation challenges associated with subterranean ecosystems. They likely represent the most widespread nonmarine environments on Earth, but specialized subterranean organisms remain among the least documented and studied. Largely overlooked in conservation policies, subterranean habitats play a critical role in the function of the web of life and provide important ecosystem services. We highlight the main threats to subterranean ecosystems and propose a set of effective actions to protect this globally important natural heritage.

Keywords: biodiversity crisis, caves, extinction risk, groundwater, nature conservation

“Human beings and the natural world are on a collision course.”

—Union of Concerned Scientists’ Manifesto, 1992

Building on the manifesto *World Scientists’ Warning to Humanity*, issued in 1992 by the Union of Concerned Scientists, Ripple and colleagues (2017) recently published a passionately debated article titled “World scientists’ warning to humanity: A second notice.” This novel proclamation, which was endorsed by more than 15,000 cosignatory scientists (the Alliance of World Scientists), reiterated most of the ideas and concerns presented in the first manifesto and, in particular, the fear that humans are “pushing Earth’s ecosystems beyond their capacities to support the web of life.” The second notice highlighted alarming trends in several environmental issues over the last 25 years (1992–2016), including global climate change, deforestation, biodiversity loss, human population increase, and a decline in freshwater resources.

Since its publication, this second notice has been extensively discussed in the scientific literature and social media, stimulating an upsurge of discipline-specific follow-up

articles focused on particular biological or social systems (William J. Ripple, Oregon State University, Corvallis, Oregon, personal communication, 7 September 2018). As a group of subterranean biologists with different areas of expertise and a strong commitment to biodiversity conservation, we take this opportunity to examine some alarming trends underscored by the Alliance of World Scientists from a subterranean perspective. We discuss the implications that this Ripple and colleagues (2017) manifesto has for the conservation of the subterranean realm, which includes some of the most unique, secluded, understudied, and difficult to study environments on our planet.

Although subterranean habitats are not at the forefront of one’s mind when thinking about global conservation issues, they support exceptional forms of life and represent critical habitats to be preserved and prioritized in conservation policies. Although some conservation efforts have been devoted to protect subterranean ecosystems at a local level, no global assessment has been conducted that explicitly takes these resources into account (e.g., Brooks et al. 2006, Sutherland et al. 2018). Even though there are common conservation concerns that affect all biological systems, many of them are

more acute and visible in the subterranean realm and are emphasized in this contribution.

The challenges of protecting the unknown

In the era of drones, satellites, and remote-sensing technology, most of the accessible places on Earth have been directly or indirectly mapped and explored. A remarkable exception to the geographic knowledge of our planet comes from the subterranean world, which is therefore recognized as one of the most important frontiers of modern exploration (Ficetola et al. 2019). Subterranean ecosystems are likely the most widespread nonmarine environments on Earth. For example, more than 50,000 caves have been documented in the United States, with nearly 10,000 known from the state of Tennessee alone (Niemiller and Zigler 2013), and some 25,000 caves are estimated solely for the Dinarides, a 60,000 square kilometers European karst region that is considered to be the world's most significant area of subterranean fauna radiation (Zagmajster et al. 2010). However, subterranean ecosystems are by no means restricted to those subterranean voids that we have mapped and listed in speleological cadasters (i.e., caves).

First, most subterranean voids have no entrances that are accessible to humans (Curl 1958). The small and inaccessible network of underground voids and fissures is almost limitless, and this network (rather than caves) represents the elective habitat for most subterranean species (Howarth 1983). Second, groundwater (i.e., water in the voids in consolidated and unconsolidated rocks) represents 95% of global unfrozen fresh water and hosts organisms specialized to survive at limits of life (Fišer et al. 2014), as well as more numerous species that are important to maintaining groundwater quality (Griebler et al. 2014). Furthermore, anchialine ecosystems, represented by coastal, tidally influenced, subterranean estuaries located within crevicular and cavernous terrains, are a specialized habitat straddling the border between subterranean freshwater and marine environments and host a specialized subterranean fauna (Bishop et al. 2015). Also, a variety of superficial underground habitats, collectively termed *shallow subterranean habitats*, supports an extensive array of subterranean biota (Culver and Pipan 2014). Finally, if one is keen to account also for microbial life, a large amount of continental prokaryotic biomass and, as yet, an unknown prokaryote diversity is hidden within these systems (Magnabosco et al. 2018).

Although habitats beneath the Earth's surface are more widespread and diversified than is usually perceived, most of them cannot be mapped and directly studied, either because they are too deep or because they are hardly accessible to humans because they are inaccessible to humans given the infinitesimal size of many of these 'pore space' habitats. Consequently, specialized subterranean organisms remain among the least documented fauna on our planet. This impediment, recently termed the Racovitza shortfall (Ficetola et al. 2019), poses a thorny question: If the real extension of the subterranean domain is unknown, and the

biota we observe in a cave are just the tip of the subterranean biodiversity iceberg, what can we do practically to protect the full extent of subterranean habitats and their inhabitants?

To make sound decisions for the conservation of the subterranean world, there is first an urgent need to accelerate scientific research, aimed at exploring subterranean biodiversity together with the abiotic and biotic factors that drive its distribution patterns across space and time. Available estimates (Zagmajster et al. 2018) suggest that most obligate subterranean species worldwide have not yet been described (i.e., a Linnean shortfall). In the epoch of the sixth mass extinction crisis, many of these species may face extinction before they are discovered and formally described—a phenomenon described by Wilson (1992) as “centinelan extinctions.” Moreover, several other knowledge gaps impede our ability to protect and conserve subterranean biodiversity (table 1). The distribution (i.e., the Wallacean shortfall) and the life history of most described subterranean species are virtually unknown. Acquiring basic knowledge about biological and functional diversity of subterranean organisms (i.e., the Raunkiæran shortfall), their phylogenetic relationships (i.e., the Darwinian shortfall), their interactions within different subterranean communities (i.e., the Eltonian shortfall), and their sensitivity to environmental perturbations (i.e., the Hutchinsonian shortfall), represent pivotal steps toward consolidating scientific knowledge to support conservation planning (Cardoso et al. 2011A, Diniz-Filho et al. 2013, Hortal et al. 2015) and further understanding the ecosystem services that the subterranean fauna provide.

The importance of safeguarding subterranean biodiversity

The first argument emphasizing the importance of protecting subsurface ecosystems emerges when considering the fascinating evolutionary changes many animals have undergone to become adapted to underground life. Subterranean species are astonishing and bizarre outcomes of evolution (figure 1), and subterranean habitats represent sources of unexpected—often serendipitous—scientific discoveries. The study of these remarkable species allows us to travel outside the limits of our own imagination, exploring unique biological adaptations (Soares and Niemiller 2013, Yoshizawa et al. 2014, 2018a), learning about fundamental ecoevolutionary processes (Juan et al. 2010, Mammola 2018), and even gaining insights into human health (Riddle et al. 2018, Yoshizawa et al. 2018b).

Furthermore, being intimately interconnected with both the soil and surface systems, subterranean systems play a critical role in the regulation and provision of ecosystem services and in the function of the web of life. Therefore, the survival of humankind is likely to be more dependent on the maintenance of healthy subterranean environments than is generally recognized. For example, the riparian surface communities and the life cycles of cave-dwelling organisms, such as bats, critically depend on intact connections with the underlying subterranean compartments. Over 20%

Table 1. The eight knowledge shortfalls of subterranean biodiversity (Hortal et al. 2015, Ficetola et al. 2019) and specific problems related to subterranean biology and the conservation of subterranean species.

Shortfall	Knowledge gap	Specific problems in subterranean biology
Linnean	Species taxonomy	A lack of reliable estimation of subterranean diversity (Zagmajster et al. 2018) A high prevalence of cryptic species (Delić et al. 2017) A bias favoring studies on large versus subterranean microscopic animals (e.g., meiofauna), or certain taxonomic groups against others (Zagmajster et al. 2010)
Wallacean	Species distribution	A high prevalence of endemic species (Gibert and Deharveng 2002) A high prevalence of cryptic species (Eme et al. 2018) A lack of global data set of subterranean species distribution (Zagmajster et al. 2018)
Prestonian	Species abundance	A lack of reliable estimations because of habitat inaccessibility (see Racovitza shortfall) An intrinsic bias of most available methods because of low population densities Difficulties in designing capture–mark–recapture experiments because of the lack of knowledge on life cycles (see Raunkjæran shortfall)
Darwinian	Evolutionary patterns	Unknown relationships between many subterranean and surface lineages (Juan et al. 2010) A high range of variation in diversification patterns across different lineages (Juan et al. 2010) Difficulty in dating diversification events and distinguishing among diversification mechanisms (Morvan et al. 2013)
Hutchinsonian	Species abiotic tolerance	Small populations are difficult to establish and most are unavailable for field experiments Breeding species for experiment purposes is often challenging
Raunkjæran	Species traits	A lack of databases of functional traits allowing to predict effect of impacts on ecosystem level A lack of life cycles in most species because of difficulties in monitoring species' populations in their habitats A lack of biological traits predicting potential to disperse and colonize new habitats (e.g., presence of larvae) in freshwater and anchialine aquatic species (Kano and Kase 2004, Gonzalez et al. 2017)
Eltonian	Biotic interactions	A lack of knowledge on the structure of ecological networks that help unravel the mechanisms promoting and maintaining subterranean biodiversity (Mammola 2018) A lack of network analyses to calculate the resilience of subterranean environments on anthropogenic perturbations
Racovitza	Habitat extension	The majority of subterranean habitats are not accessible or explorable, unless by indirect means (Culver and Pipan 2014, Mammola 2018, Ficetola et al. 2019) Subterranean habitats accessible to humans (e.g., caves) are often challenging to explore, requiring knowledge on caving techniques and specific equipment (Zagmajster et al. 2010, Wynne et al. 2018)

of all living mammals on Earth are bats ($n \approx 1300$), with a huge number of species considered as cave dependent (e.g., 46% bat species in North America, 70% in Europe, 45% in Mexico, and 77% in China), using caves as day roosts, maternity colonies, hibernation sites, or as swarming or mating locations (Furey and Racey 2016, Medellín et al. 2017, Teeling et al. 2018). Their persistence depends on the occurrence of natural caves, which can also limit their occurrence on the landscape (Furey and Racey 2016). For example, the charismatic and endangered bumblebee bat (*Craseonycteris thonglongyai*; Hill 1974), which is considered world's smallest mammal, is totally restricted to the karst landscape region of approximately 2000 square kilometers straddling the Thai–Myanmar border (Puechmaile et al. 2011).

As major arthropod predators, bats have been shown to be keystone species ensuring optimal ecosystem function across multiple trophic levels (Kunz et al. 2011). They perform vital ecosystem services, ranging from pest arthropod

suppression to tropical plant pollination and seed dispersal. The economic loss and cost of controlling arthropod crop-pest species in the absence of bats is estimated to be \$3.7–\$53 billion per year in the United States alone (Boyles et al. 2011). Many insectivorous bat species feed on disease vector biting insects that plague humans and livestock, including mosquitoes that are vectors of life-threatening human and livestock diseases, such as malaria, Zika and West Nile virus (Caraballo and King 2014), as well as aphids that spread plant pathogens (Ng and Perry 2004) and botflies that parasitize both humans and livestock. Bats, including many cave-roosting species, are documented as both pollinators and seed dispersers in forests, mangroves, and deserts (Kunz et al. 2011). For example, cave roosting nectar-feeding bats have coevolved to pollinate agave, a keystone species in Mexican deserts and scrub forests and a key ingredient in tequila; the production of this beverage employs 70,000 people and garners \$1.2 billion per year in exports alone

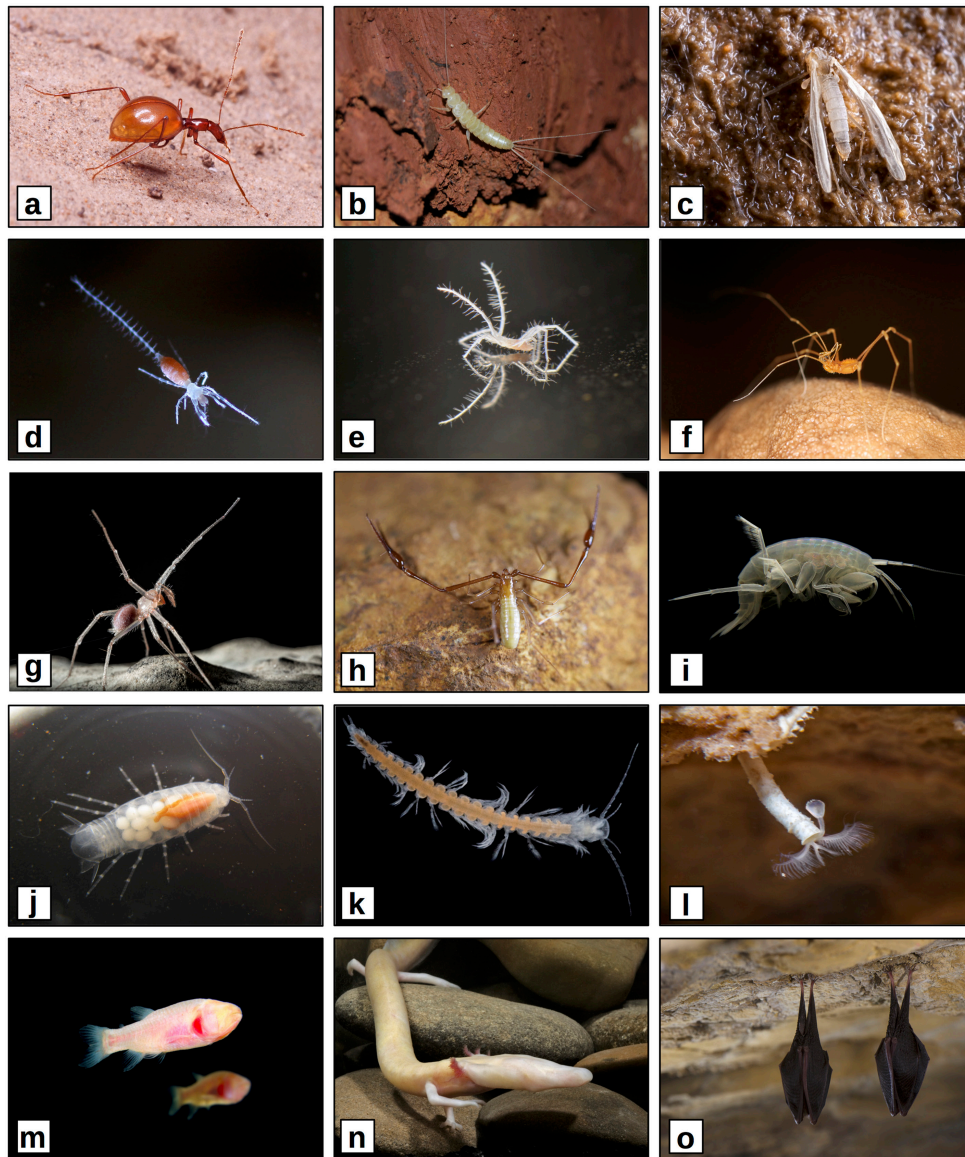


Figure 1. Examples of the diversity of life in subterranean habitats. (a) *Leptodirus hochenwartii* (Schmidt 1832; *Coleoptera*), the first obligate subterranean invertebrate ever described. (b) The subterranean specialized silverfish *Squamatinia algharbrica* (Mendes and Reboleira 2012; *Zygentoma*). (c) *Troglocladius hajdi* (Andersen et al. 2016; *Diptera*), the only specialized subterranean species known to have retained functional wings. (d) A specialized subterranean microwhip scorpion in the genus *Eukoenia* (Börner 1901; *Palpigradi*); *Palpigradi* is the most enigmatic and understudied orders of arachnids in the world. (e) A specialized *Trogloteles* (Zacharda 1980; *Acari*) hunting in a subterranean pool. (f) A specialized subterranean harvestman in the genus *Giupponia* (Pérez and Kury 2002; *Opiliones*). (g) An eyeless spider, *Hadites tegenarioides* (Keyserling 1862; *Agelenidae*). (h) The specialized subterranean giant pseudoscorpion, *Titanobochica magna* (Zaragoza and Reboleira 2010; *Pseudoscorpiones*). (i) A specialized subterranean crustacean in the genus *Spelaeogammarus* (da Silva Brum 1975; *Amphipoda*). (j) An undescribed subterranean isopod from the family *Cirolanidae*; because of the remarkable depigmentation of this species, its internal organs are clearly visible. (k) A blind crustacean belonging to the genus *Morlockia* (García-Valdecasas 1984; *Remipedia*); *Remipedia* is the latest described class of crustaceans, so far having representatives exclusively in anchialine systems. (l) *Marifugia cavatica* (Absolon and Hrabec 1930; *Annelida*), the only freshwater cave-dwelling tube worm in the world. (m) The blind tetra, *Stygichthys typhlops* (Brittan and Böhlke 1965; *Characidae*), one out of the nearly 250 cavefishes described in the world. (n) The olm, *Proteus anguinus* (Laurenti 1768; *Amphibia*), the first obligate subterranean vertebrate described. (o) Lesser horseshoe bats, *Rhinolophus hipposideros* (Bechstein 1980; *Rhinolophidae*) hibernating in a cave; bats provide critical ecological services and are keystone species in several ecosystems. Photographs: (a) Tvrtko Dražina, (b, h) Ana Sofia PS Reboleira, (c, l) Jana Bedek, (d) Alberto Chiarle, (e) Francesco Tomasinelli, (f, i, j, m) Rodrigo Lopez Ferreira, (g) Tin Rožman, (k) Ulrike Strecker, (n) Boris Krstinić, (o) Emanuele Biggi.

(Trejo-Salazar et al. 2016). Therefore, bats' role in maintaining the quality of recreational outdoor areas; limiting disease transmission to humans, domestic animals, and agricultural crops; and, ultimately, enhancing human well-being is immense. This illustrates the importance of maintaining their cave systems to ensure the provision of key ecological services (Medellin et al. 2017).

Also very important to humans is the role of subterranean systems as freshwater reservoirs. Subterranean environments store and transmit groundwater through the void spaces created by the fracturing and dissolution of (carbonate and other) rocks and unconsolidated sediments that fill river valleys and large basins. It is estimated that one quarter of the human population is completely or partially dependent on drinking water from aquifers (Ford and Williams 2007), and groundwater also largely supports agriculture and industry (Griebler and Avramov 2015).

The main global threats to subterranean biodiversity

Subterranean environments and their biota are only superficially known (pun intended). However, we do know that most of the threats highlighted by Ripple and colleagues (2017) in their manifesto are directly affecting the subterranean domain *tout court*, because subterranean ecosystems are inextricably linked to surface processes. For example, they depend on allochthonous energy supplies, which may consist of flood detritus, guano deposition from cave-dwelling bats, birds and crickets, or dissolved organic materials in waters percolating from the surface. Therefore, when humans adversely change the surface environment, subterranean ecosystems will respond to those changes. Most notably, deforestation (Trajano 2000, Souza-Silva et al. 2015), urbanization, mining, agricultural, and industrial activities (Trajano 2000, Reboleira et al. 2011, Souza-Silva et al. 2015, Sugai et al. 2015), heavy metals and agrochemicals pollution (Reboleira et al. 2013, Di Lorenzo et al. 2015, 2018), nonnative species introductions (Howarth et al. 2007, Wynne et al. 2014), tourism (Moldovan et al. 2013), and global climate change (Mammola et al. 2019) negatively affect both biodiversity and subterranean ecological processes. In the following sections, we briefly discuss what we consider the most challenging global threats affecting subterranean ecosystems.

Habitat loss. Subterranean habitat loss and degradation are occurring in many regions. In several cases, the disturbance of subterranean habitats is direct, although often spatially localized. For instance, quarrying and mining activities often result in removal of the karst substratum, sometimes leading to obliteration of whole karst hills (Whitten 2009). In this respect, open-pit mining for lignite provides a striking example. Worldwide, about 1 billion tons of lignite are produced each year. Only in Germany, one of the largest lignite producers worldwide (170 million tons per year), opencast mining has altered about 200,000 hectares of land, including the removal of an entire aquifer. Moreover, as a prerequisite

of opencast mining, the groundwater table in the region is lowered by hundreds of meters to below the mining level; consequently, groundwater ecosystems are systematically dewatered for entire districts or even federal states accounting for billions of cubic meters of groundwater pumped and thousands of square kilometers affected (Grünwald 2001). A destruction of groundwater habitats at an unprecedented scale. Last but not least, subsequent to mining activities, dewatered zones that resaturate frequently develop highly acidic groundwater as a consequence of long-term pyrite oxidation (Wisotzky and Obermann 2001). The impact of mining activities is also evident in ferruginous landscapes in Brazil, one of the largest extractive areas in the world, where hundreds of caves have been destroyed by quarrying and mine excavation, and groundwater has been polluted by mineral waste, heavy metals, and other contaminants (Souza-Silva et al. 2015, Sugai et al. 2015).

Construction activities may also directly threaten subterranean ecosystems. Infrastructure development and tunnel drilling can entirely or partially destroy subterranean habitats. For example, road construction within karst areas of Slovenia has resulted in the discovery of more than 350 caves, with many being completely destroyed (Knez and Slabe 2016). Development along rivers and streams, such as channelizing, regulating, and damming, can result in major hydrological changes and loss of subterranean habitat, especially in the hyporheic zone and the subjacent aquifers (e.g., Piegay et al. 2009). Modified river flow channels interrupt the connectivity between surface and subterranean water and can lower the water table; similarly, diverting river flow may result in both flooding or desiccation within subterranean systems, which results in direct loss of habitat.

Other large-scale human activities result in a more generalized and pervasive degradation of the subterranean environment, especially in those areas in which deforestation, urbanization, and industrial activities are increasing. Areas experiencing such changes include, but are certainly not limited to, vast portions of Southeast Asia and South America. Deforestation, in particular, represents one of the major ecological threats to subterranean habitats (Jiang et al. 2014), especially in tropical areas (Trajano 2000). In fact, the loss of surface vegetation can quickly result in habitat alterations (e.g., desertification) that may alter subterranean hydrological regimes and nutrient inputs from the surface. The resultant degradation of the subterranean environment can either reduce populations of subterranean species or result in the extinction of endemic animal populations.

Groundwater overexploitation and contamination. The decline in freshwater resources was highlighted as one of the most critical negative trends that humanity is facing (Ripple et al. 2017, Finlayson et al. 2019), which can be considered a clarion call to increase global efforts to halt and reverse the ongoing degradation of groundwater resources (Gleeson et al. 2012). Overexploitation of groundwater is primarily due to agricultural irrigation (Siebert et al. 2010) and

industrial uses (Griebler and Avramov 2015). Although the way in which abstraction affects groundwater levels is often complex, especially when water is drawn from deep aquifers that have limited local connectivity to the surface, there is very widespread and substantial loss of subterranean fauna habitat associated with the global irrigation of 114 million hectares with groundwater. For example, in parts of China alone, where more than 8 million hectares of agriculture is irrigated with groundwater, shallow water tables are declining by 0.43 meters per year (Liu and Yu 2001). In India, there is nearly 27 million hectares of irrigated agriculture (Foster and Chilton 2003) and groundwater levels are declining by up to 1 meter per year (Humphreys et al. 2010). In addition to the direct loss of groundwater habitat, agriculture and other human activities frequently degrade remaining groundwater with high levels of nutrients, herbicides, pesticides, and many other contaminants (e.g., Schwarzenbach et al. 2010, Lapworth et al. 2012). Maintaining healthy groundwater invertebrate communities appears to be a critical component of reducing anthropogenic impacts (Griebler and Avramov 2015). Indeed, the eventual collapse of groundwater communities would in turn hinder the self-purifying processes provided by these organisms, thus accelerating the degradation of this precious resource.

Climate change. Climate change represents one of the most complex and challenging issues in the Anthropocene (Ripple et al. 2017), and although its effects are already visible on the surface, the impacts on subterranean systems are poorly understood. In the medium- to long-term, climate change is expected to modify both deep terrestrial (Pipan et al. 2018) and aquatic subterranean ecosystems (Taylor et al. 2013). Given that deep subterranean habitats are typically characterized by environmental stability, it has been proposed that most subterranean-adapted organisms have a reduced ability to cope with significant variation in temperature (Novak et al. 2014, Raschmanová et al. 2018), resulting in these species being potentially highly sensitive to climate change (Mammola et al. 2019). However, it seems there is extensive variability in thermal tolerance among species related to evolutionary history and degree of subterranean adaptation (Novak et al. 2014, Rizzo et al. 2015, Raschmanová et al. 2018). In addition to thermal stability, a relative humidity deficit is another important factor for subterranean-adapted species. High water saturation of the atmosphere is essential for the survival of most terrestrial subterranean organisms (Howarth 1983). Desiccation of terrestrial habitats due to global environmental change is expected to have severe negative impacts on subterranean communities (Shu et al. 2013); some taxa may be forced to retreat to greater depths, where energy sources are usually scarcer, whereas others may go extinct. Moreover, climate change likely will cause indirect effects underground, such as promoting colonization by alien species (Wynne et al. 2014) and variations in external trophic inputs. Strong inference-based predictions concerning the effects of climate change on organisms dwelling in

climatically stable environments represent a challenging and largely unstudied field of inquiry (Mammola 2018); because the planet is already changing because of global climate change, in-depth studies are needed to understand how these changes are affecting subterranean habitats.

Intrinsic vulnerability of the subterranean fauna. Although the global issues discussed above represent the main threats to ecosystems, their impact is more profound on subterranean organisms owing to their intrinsic vulnerability. There are several reasons why subterranean fauna is vulnerable, including that most subterranean species are short-range endemics with extremely restricted distributions (Trontelj et al. 2009, Eme et al. 2018). Because of this range restrictedness, geographically localized threats are much more likely to have a global effect on biodiversity, as a result of irreversible species loss, than is the case in surface systems. Energy-limited and stable subterranean environments have selected for long-lived species with low basic metabolisms and fecundity (Voituron et al. 2011, Fišer et al. 2013). Therefore, population growth is slow, which can result in population instability because of catastrophic or stochastic events. Moreover, subterranean species often have a low tolerance for shifts in abiotic conditions, and even small alterations in the environment may have major consequences (Novak et al. 2014, Raschmanová et al. 2018). Finally, there is little redundancy in subterranean communities (Gibert and Deharveng 2002). Simple communities with few species and often no redundancy of functional roles in turn exhibit a low ecological resilience and are more vulnerable to perturbations and disturbance.

Proposed actions to illuminate research, conservation, and educational needs

Ripple and colleagues (2017) proposed several effective steps that humanity can implement to create a transition to sustainability. Their recommendations for surface environments would also aid in the preservation of the subterranean world; that is, reversing most of the ongoing negative trends in surface ecosystems will have an immediate positive influence on the preservation of subterranean ecosystems. From a discipline-oriented perspective, subterranean biologists can identify the key requirements for the protection of subterranean habitats and also work to increase the awareness of the subterranean natural heritage among the general public; this will hopefully increase political commitment (see Dror 2018).

General effective measures include collecting the much needed information on life history, ecology, distribution, and sensitivity to environmental alterations of subterranean restricted species (see table 1), as well as external species that depend on subterranean ecosystems, such as cave-roosting bats.

Efforts will be also needed to document and monitor subterranean diversity through the use and evaluation of standardized sampling techniques (e.g., Dole-Olivier et al. 2009,

Wynne et al. 2018), as well as vulnerability assessments (with adaptive management protocols) to determine threat levels to subterranean ecosystems and sensitive species populations (e.g., Di Lorenzo et al. 2018, Tanalgo et al. 2018).

Renewing efforts to implement direct conservation measures is a potential approach, prioritizing communication with political powers and public institutions to develop well-funded and well-managed networks of protected areas for a significant proportion of the world's subterranean hotspots of diversity. Insofar as funds invested in conservation will be limited, special efforts are needed to define the priority principles and criteria for channeling conservation actions (Rabelo et al. 2018).

Renewed efforts will be needed in the threat assessment of subterranean species using the International Union for Conservation of Nature (IUCN) Red List criteria. Currently, very few subterranean species have been assessed (c. 850 species), and the subjectivity in applying the criteria across a large diversity of taxa assessed separately by various specialists has led to numerous inconsistencies. The standardization of interpretation of criteria and implementation of clear guidelines applicable across taxa can greatly improve the current situation (Cardoso et al. 2011b), a process in which the involvement of the IUCN's Species Survival Commission's (SSC) Cave Invertebrate Specialist Group will be fundamental. Through these steps, we can improve our ability to assess the conservation status of subterranean species, as a sound basis for global and local conservation policy, as well as for designing efficient species and site conservation plans.

Models will need to be developed to quantify the effects of global climate change on subterranean communities. Although climate change is one of the most pervasive global impacts (Ripple et al. 2017), studies on the effects of climate change on cave ecosystems are few, and their results are often inconclusive (Mammola et al. 2019). There is an urgent need to achieve an in-depth understanding of this issue from a subterranean perspective, through the analyses of empirical data (Pipan et al. 2018), experiments (Rizzo et al. 2015), modeling (Mammola and Leroy 2018), and simulation studies.

Research into the biology and ecology of groundwater organisms should be promoted, so that those organisms may serve, when appropriate, as sentinel species of clean waters in water quality monitoring activities. In addition, the use of most widespread contaminants that accumulate in subterranean aquifers (e.g., fertilizers and pesticides in agricultural landscapes) should be limited, and a sustainable use of groundwater promoted (Danielopol et al. 2004).

In recognition of the interconnectivity of surface and subterranean compartments, it is important to implement conservation measures bridging these environments. Fostering interdisciplinary scientific cooperation will be critical—that is, by designing specific studies involving broad collaborations with taxonomists, ecologists, biologists, conservation biologists, ecotoxicologists, geologists,

hydrologists, and soil scientists, who typically work in surface environments.

Educational programs should be developed for both primary and secondary students and for the lay public to heighten awareness regarding the sensitivity of subterranean organisms, as well as to emphasize the connection between surface and subsurface ecosystems. We recommend, together with local communities and caving associations, developing classroom curricula, subterranean-themed public exhibitions, guided and regulated outdoor activities to karst and other natural terrains (such as rivers) sustaining rich subterranean habitats, and other outreach activities in areas in which communities are reliant on the subterranean environments. More broadly, social media campaigns using the Internet, television, radio, and print media will heighten public awareness of subterranean environments and the unique animal communities they harbor.

Finally, empowering local and indigenous communities in decision-making and management of caves, watersheds, and geological formations that contain subterranean systems is necessary, to make them aware of the natural heritage of their territory.

Conclusions

Although we represent a small group of scientists within the large and heterogeneous community of subterranean biologists, we aimed to provide a multifaceted view of the global issues affecting the subterranean world. As we have experienced during the writing of this work, the perspective from which these issues are observed by the different authors can be quite diverse. However, we all agreed on the fact that these systems are poorly recognized as conservation priorities, that they provide vital ecosystem services to humankind, and that they represent a true research frontier. Most importantly, we reached a full consensus in highlighting the high vulnerability of the subterranean world and the seriousness of the threats affecting it, as well as the need of making this information available to stakeholders and the general public. Indeed, although the conservation issues we discuss are well understood within our community and partially covered in the specialized literature, they have never been formalized in a scientific publication written for a broader audience. As with most ecosystems important to supporting both diversity and providing ecological services, we reaffirm that it is our duty to humankind and toward sustainable stewardship of our planet to develop strategies to achieve their preservation.

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