Scientists’ warning on the conservation of subterranean ecosystems

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Scientists' warning on the conservation of subterranean ecosystems

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ABSTRACT

In light of recent alarming trends in human population growth, climate change and other environmental disturbances, 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 non-marine environments on Earth, yet specialized subterranean organisms remain among the least documented and studied. Largely overlooked in conservation policies, subterranean habitats play a critical functional role in the functioning of the web of life and provide important ecosystem services. We highlight 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

INTRODUCTION

"*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 et al. (2017) recently published a passionately debated paper titled *"World Scientists' Warning to Humanity: a Second Notice."* This novel proclamation, which was endorsed by more than 15,000 cosignatory scientists ("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 (Ripple W.J. [Oregon State University, Corvallis, United States], personal communication, 7 September 2018). As a group of subterranean biologists with a breadth of different 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 et al. (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. While 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 (see, 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.

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 explorations (Ficetola et al. 2019). Subterranean ecosystems are likely the most widespread non-marine 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 km^2 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). In fact:

i) most subterranean voids have no entrances that are accessible to humans (Curl 1958);

ii) the small and non-accessible network of underground voids and fissures is almost limitless and this network (rather than caves) represents the elective habitat for most specialized subterranean biota (Howarth 1983);

iii) groundwater, i.e. water in the voids in consolidated and unconsolidated rocks, comprises 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);

iv) anchialine ecosystems, represented by coastal, tidally influenced, subterranean estuaries located within crevicular and cavernous terrains, represent a specialized habitat straddling the border between subterranean freshwater and marine environments and host a specialized subterranean fauna (Bishop et al. 2015);

v) a variety of superficial underground habitats, collectively termed shallow subterranean habitats, support an extensive array of subterranean biota (Culver and Pipan 2014); and

vi) if one would be 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).

Paradoxically, 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 due to their millimetre scale resolution. Consequently, specialized subterranean organisms remain among the least documented fauna on our planet. This impediment, recently termed "Racovitzan 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 practically do 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, aiming at exploring subterranean biodiversity altogether with the abiotic and biotic factors that drive its distribution patterns across space and time. Available estimates (Culver and Holsinger 1992; Zagmajster et al. 2018) suggest that most obligate subterranean species worldwide have not yet been described (i.e., the Linnean shortfall). In the epoch of 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 in particular, 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), as well as 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 emphasizing the ecosystem services that the subterranean fauna provide.

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, oftentimes serendipitous, scientific discoveries. The study of these remarkable species allows us to travel outside the limits of our own imagination, exploring unique biological adaptations (e.g., Soares and Niemiller 2013, Yoshizawa et al. 2014, 2018a), learning about fundamental ecological and evolutionary processes (Juan et al. 2010, Mammola 2018), and even gaining insights into human health (e.g., 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 functioning of the web of life. Therefore, the survival of humankind is likely to be more dependent on maintenance of healthy subterranean environments than 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% of all living mammals on earth are bats (n~ 1,300), with a huge number of species considered as 'cave-dependent' (e.g., *ca.* 46% bat species North America; 70% Europe; 45% Mexico; 77% China); bats use caves as day-roosts, maternity colonies, hibernation sites, and as swarming/mating locations (Furey and Racey 2016, Medellin et al. 2017, Teeling et al. 2018). Their heir 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, enigmatic and endangered bumble-bee bat (*Craseonycteris thonglongyai*), which is considered world's smallest mammal, is strictly restricted to the karst landscape region ~ 2,000 km^2 straddling the Thai-Myanmar border (Puechmaille et al. 2011). As major arthropod predators, bats have been shown to be keystone species ensuring optimal ecosystem functioning across multiple trophic levels (Kunz et al. 2011).

They provide vital ecosystem services including insect pest suppression, pollination and seed dispersal of forest plants and trees, and pollination of important food crops. As many bat species feed on crop pests, the cost of managing and controlling these arthropod pest species in the U.S. without bats, is estimated between $3.7 and $53 billion/year (Boyles et al. 2011). Many insectivorous bat species feed on disease vector biting-insects that plague humans and livestock, including mosquitoes known vectors of numerous life-threatening human and livestock diseases including Malaria, Zika and West Nile virus (e.g., Caraballo and King 2014, Boyer et al. 2018), 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 (e.g., Valiente-Banuet et al. 1996, Medellín and Gaona 1999, Azuma et al. 2002, Kunz et al. 2011). Cave-roosting nectar-feeding bats in the southwestern U.S. and northern Mexico are primary pollinators for columnar cacti, including the iconic Saguaro cacti (*Carnegiea gigantea*), which are considered keystone species of the Sonoran Desert (Valiente-Banuet et al. 1996). Additionally, cave roosting nectar-feeding bats have coevolved to pollinate agave, also a keystone species in Mexican deserts and scrub forests and a key ingredient in tequila – production of this beverage employs 70,000 people and garners 1.2 billion dollar/ year in exports alone (Trejo-Salazar et al. 2016). Another lucrative multimillion dollar industry, the durian fruit of southeast Asia is primarily pollinated by a cave roosting bat species (Bumrungsri et al. 2009, Stewart and Dudash 2017). Therefore, bats' role in maintaining the quality of recreational outdoor areas, limiting disease transmission to humans, livestock and agricultural crops, as well as ultimately enhancing human well-being through maintaining ecosystems and agribusiness, is immense. Cave-roosting bat populations and their habitats must be protected to ensure these key ecological services to humans continue (Medellín et al. 2017).

Even more important 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).

MAIN GLOBAL THREATS TO SUBTERRANEAN BIODIVERSITY

Subterranean environments and their biota are only superficially known (pun intended). Yet, we do know that most of the threats highlighted by Ripple et al. (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 bats, birds and crickets, or dissolved organic materials in waters percolating from the surface. Thus, 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, agricultural, industrial, and mining 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), non-native species introductions (Howarth et al. 2007, Wynne et al. 2014), tourism (Moldovan et al. 2013), and global climate change (Mammola et al. 2018) 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 removal of whole karst hills (Whitten 2009). In this respect, the 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/year), opencast mining has altered about 200,000 hectares of land including the removal of the aquifer. Moreover, as a prerequisite of opencast mining, the groundwater table in the region needs to be lowered by hundreds of meters to below the mining level and consequently groundwater ecosystems are systematically dewatered for entire districts or even federal states accounting for billions of m^3 of groundwater pumped and thousands of km^2 (Grünewald 2001); a destruction of groundwater habitats at an incomparable dimension. Last but not least, subsequent to mining activities, dewatered zones that re-saturate characteristically bear 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).

Furthermore, construction activities can directly threaten subterranean ecosystems. Construction of infrastructure 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 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 where deforestation, urbanization, and industrial activities are increasing—including, but 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, 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 (Finlayson et al. 2019, Ripple et al. 2017), which can be considered a clarion call to increase global efforts to halt and reverse the ongoing degradation of groundwater resources. Anthropogenic impacts in groundwater aquifers include local and diffuse sources of contamination (e.g., Schwarzenbach et al. 2010, Lapworth et al. 2012), overexploitation of groundwater resources (Wada et al. 2010, Gleeson et al. 2012), and climate change (see next section). Maintaining healthy groundwater communities appears to be a critical component of reducing anthropogenic impacts, given the potential ecosystem services provided by most of these organisms (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 while 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. 2018). 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, 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, while others may go extinct. Moreover, climate change likely will cause indirect effects underground, such as promoting colonization and establishment 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 due to global climate change, in-depth studies are needed to understand how these changes are affecting subterranean habitats.

Intrinsic vulnerability of the subterranean fauna

While 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:

i) most subterranean species are short-range endemics with extremely restricted distributions (Trontelj et al. 2009, Eme et al. 2018). Due to 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;

ii) 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). Thus, population growth is slow resulting in population instability due to catastrophic or stochastic events;

iii) 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); and

iv) it is considered that 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 et al. (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, i.e., 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 amongst the general public; this hopefully will increase political commitment (see Dror 2018). General effective measures are provided below:

i) 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, like cave-roosting bats;

ii) expanding efforts 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);

ii) renewing efforts to implement direct conservation measures, 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 priority principles and criteria for channeling conservation actions (Rabelo et al. 2018);

iv) renewing efforts 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 (*ca.* 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 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;

v) developing models 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. There is an urgent need to achieve an in-depth understanding of the global change issue from a subterranean perspective, through the analyses of empirical data (Pipan et al. 2018), experiments (Rizzo et al. 2015), modeling (Mammola & Leroy 2018), and simulation studies;

vi) promoting research into the biology and ecology of groundwater organisms so that they may act, 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);

vii) 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, i.e., 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;

viii) developing educational programs for both primary and secondary students and the lay public to heighten awareness regarding the sensitivity of subterranean organisms, as well as emphasizing 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 (like rivers) sustaining rich subterranean habitats, and other outreach activities in areas where communities both reside and are reliant upon the subterranean environments. More broadly, social media campaigns using internet, television, radio, and print media, will heighten public awareness of subterranean environments and the unique animal communities they harbour; and

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

EPILOGUE

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. Yet, 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 specialised literature, they have never been formalised 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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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	– Lack of recent estimation of subterranean diversity (see Culver and Holsinger 1992) – High prevalence of cryptic species (Delić et al. 2017) – Bias favouring studies on large versus subterranean microscopic animals (e.g., meiofauna), or certain taxonomic groups against others (Zagmajster et al. 2010)
Wallacean	Species distribution	– High prevalence of endemic species (Culver and Pipan 2009) – High prevalence of cryptic species (Eme et al. 2018) – Lack of global dataset of subterranean species distribution (Culver et al. 2013)
Prestonian	Species abundance	– Lack of reliable estimations due to habitat inaccessibility (see Racovitzan shortfall) – Intrinsic bias of most available methods due to low population densities – Difficulties on designing capture-mark-recapture experiments due to the lack of knowledge on life cycles (see Raukiæran shortfall)
Darwinian	Evolutionary patterns	– Unknown relationships between many subterranean and surface lineages (Juan et al. 2010) – High range of variation in diversification patterns across different lineages (Juan et al. 2010) – Difficulty to date diversification events and distinguish among diversification mechanisms (Morvan et al. 2013)
Hutchinsonian	Species abiotic tolerance	– Small population available for experiments – Breeding species for experiment purposes is often challenging
Raunkiæran	Species traits	– Lack of databases of functional traits allowing to predict effect of impacts on ecosystem level – Lack of life cycles in most species due to difficulties in monitoring species populations in its habitats – 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	– Lack of knowledge on the structure of ecological networks that help unravel the mechanisms promoting and maintaining subterranean biodiversity (Mammola 2018) – Lack of network analyses to calculate the resilience of subterranean environments upon anthropogenic perturbations
Racovitzan	Habitat extension	– The majority of subterranean habitats are not accessible/explorable, unless by indirect means (Culver & Pipan 2014, Ficetola et al. 2019, Mammola 2018) – 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)

FIGURE CAPTIONS

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 algharbica* Mendes & Reboleira, 2012 (Zygentoma). **c**) *Troglocladius hajdi* Andersen et al., 2016 (Diptera), the only specialized subterranean species that have retained functional wings; **d**) A specialized subterranean microwhip scorpion in the genus *Eukoenenia* Börner, 1901(Palpigradi)—palpigrads are one of the most enigmatic and understudied orders of arachnids in the world; **e**) A specialized *Troglocheles* Zacharda, 1980 (Acari) hunting on a water puddle in a cave; **f**) A specialized subterranean harvestman in the genus *Giupponia* Pérez & Kury, 2002 (Opiliones); **g**) An eyeless spider *Hadites tegenarioides* Keyserling, 1862 (Agelenidae); **h**) The specialized subterranean giant pseudoscorpion *Titanobochica magna* Zaragoza & 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—due to the remarkable depigmentation of this species, 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 & Hrabe, 1930 (Annelida)—the only freshwater cave-dwelling tube worm in the world; **m**) The blind tetra, *Stygichthys typhlops* Brittan & Böhlke, 1965 (Characidae), one out of the nearly 250 cavefishes described in the world; **n**) The olm, *Proteus anguinus* Laurenti, 1768 (Amphibia), the first subterranean animal ever described; **o**) Lessser horseshoe bats *Rhinolophus hipposideros* Bechstein, 1980 (Rhinolophidae) hibernating in a cave—bats provide critical ecological services and are keystone species in several ecosystems. Photo credits/by courtesy of: **a**) Dražina T; **b**, **h**) Reboleira ASPS; **c**,**l**) Bedek J; **d**) Chiarle A; **e**) Tomasinelli F; **f**,**i**,**j**,**m**) Ferreira RL; **g**) Rožman T; **k**) Strecker U; **n**) Krstinić B; **o**) Biggi E.