Scientists' Warning on the Conservation of Subterranean Ecosystems

STEFANO MAMMOLA, PEDRO CARDOSO, DAVID C. CULVER, LOUIS DEHARVENG, RODRIGO L. FERREIRA, CENE FIŠER, DIANA M. P. GALASSI, CHRISTIAN GRIEBLER, STUART HALSE, WILLIAM F. HUMPHREYS, MARCO ISAIA, FLORIAN MALARD, ALEJANDRO MARTINEZ, OANA T. MOLDOVAN, MATTHEW L. NIEMILLER, MARTINA PAVLEK, ANA SOFIA P. S. REBOLEIRA, MARCONI SOUZA-SILVA, EMMA C. TEELING, J. JUDSON WYNNE, AND MAJA ZAGMAJSTER

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

BioScience 69: 641–650. © The Author(s) 2019. Published by Oxford University Press on behalf of the American Institute of Biological Sciences. All rights reserved. For Permissions, please e-mail: journals.permissions@oup.com.
doi:10.1093/biosci/biz064
Advance Access publication 19 June 2019

Downloaded from https://academic.oup.com/bioscience/article-abstract/69/8/641/5519083 by Buffalo State user on 06 August 2019

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 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 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%

Downloaded from https://academic.oup.com/bioscience/article-abstract/69/8/641/5519083 by Buffalo State user on 06 August 2019

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 Racovitzan 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 Raukiæran 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
Raunkiæran	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
Racovitzan	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, Medellin 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 (Puechmaille 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

Downloaded from https://academic.oup.com/bioscience/article-abstract/69/8/641/5519083 by Buffalo State user on 06 August 2019

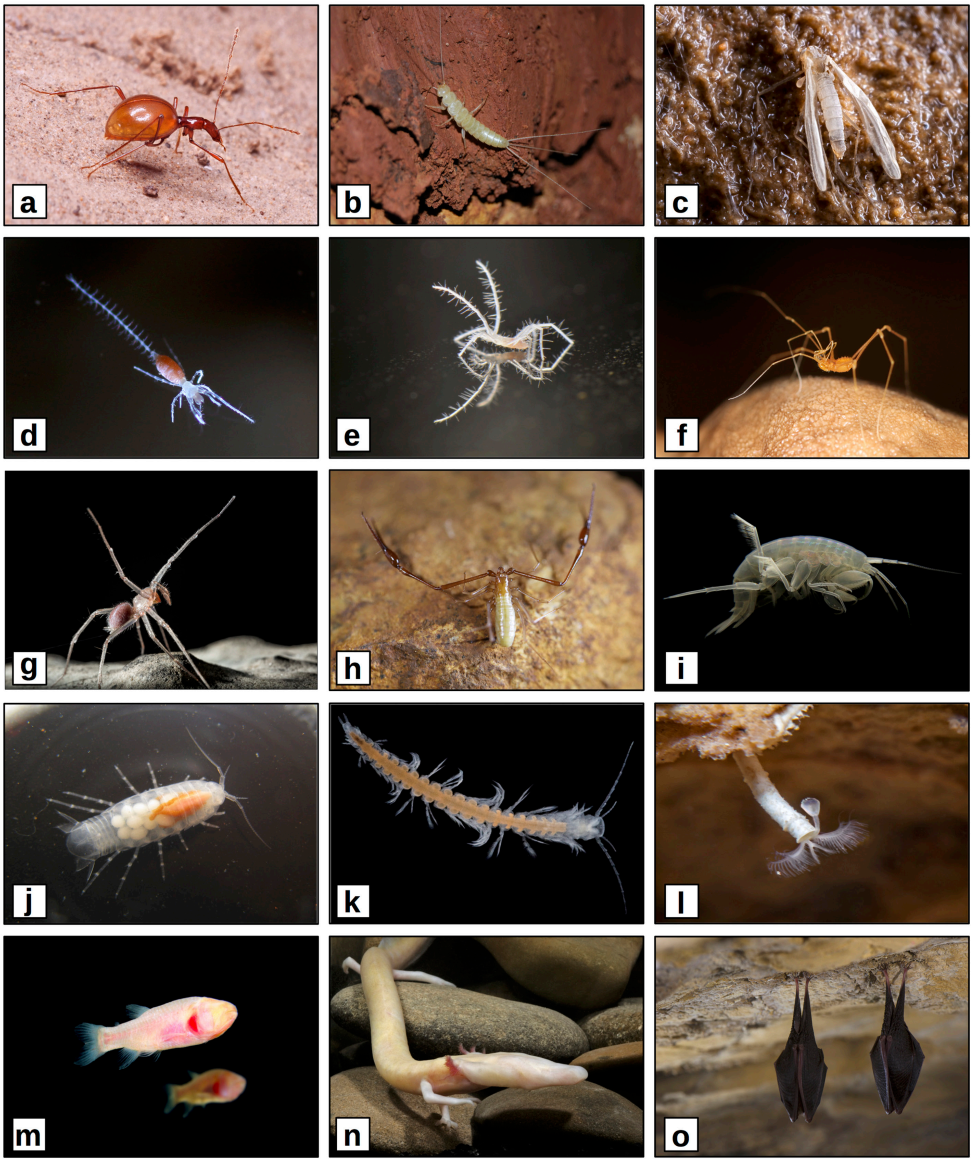

Figure 1. Examples of the diversity of life in subterranean habitats. (a) Leptodirus hochenwartii *(Schmidt 1832; Coleoptera), the first obligate subterranean invertebrate ever described. (b) The subterranean specialized silverfish* Squamatinia algharbica *(Mendes and Reboleira 2012; Zygentoma). (c)* 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* Eukoenenia *(Börner 1901; Palpigradi); Palpigradi is the most enigmatic and understudied orders of arachnids in the world. (e) A specialized* Troglocheles *(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 Hrabe 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) Lessser 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.*

Downloaded from https://academic.oup.com/bioscience/article-abstract/69/8/641/5519083 by Buffalo State user on 06 August 2019

(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 (Grünewald 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

Downloaded from https://academic.oup.com/bioscience/article-abstract/69/8/641/5519083 by Buffalo State user on 06 August 2019

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,

Downloaded from https://academic.oup.com/bioscience/article-abstract/69/8/641/5519083 by Buffalo State user on 06 August 2019

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.

Acknowledgments

We are grateful to the photographers for sharing their photos of subterranean species; see figure 1. Special thanks are due to William J. Ripple for stimulating the writing of the manuscript and for useful suggestions. Ana Komerički provided useful information on the IUCN SSC Cave Invertebrate Specialist Group. SM is supported by Bando per l'Internazionalizzazione della Ricerca—Anno 2018 (Compagnia di San Paolo). SM

Downloaded from https://academic.oup.com/bioscience/article-abstract/69/8/641/5519083 by Buffalo State user on 06 August 2019

and MI are supported by the Dark Side of Climate Change project, funded by the University of Turin and Compagnia di San Paolo (grant no. CSTO162355). RLF is supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (grant no. 304,682/2014–4). MP is supported by the HiddenLife project, funded by the European Commission through Horizon 2020 Marie Skłodowska-Curie Actions (MSCA) individual fellowships (grant no. 749,867). AM is supported by the Ancave project, funded by the European Commission through Horizon 2020 MSCA individual fellowships (grant no. 745,530). DMPG is supported by European Commission grant no. AQUALIFE LIFE12 BIO/IT/000231 for the "development of an innovative and user-friendly indicator system for biodiversity in groundwater dependent ecosystems." FM is supported by the Ecole Universitaire de Recherche's H2O'Lyon program (grant no. ANR-17-EURE-0018). MZ and CF are supported by the Slovenian Research Agency's Integrative Zoology and Speleobiology program (project no. P1–0184). PC was supported by the Ecology and Conservation of the Critically Endangered Frade Cave Spider (*Anapistula ataecina*) project, funded by the Mohamed bin Zayed Species Conservation Fund and the Towards a Sampled Red List Index for Arachnids at a Global Level project, funded by the Chicago Zoological Society's Chicago Board of Trade Endangered Species Fund. ASPSR is supported by research grant no. 15,471 from the Villum Foundation. OTM received support through a grant from the Romanian Ministry of Research and Innovation's National Research Council Executive Agency for Higher Education, Research, Development and Innovation Funding (grant no. PN-III-P4-ID-PCCF-2016–0016 within project no. PNCDI III).

References cited

Bishop RE, Humphreys WF, Cukrov N, Žic V, Boxshall GA, Cukrov M, Iliffe TM, Kršinic F, Moore WS, Pohlman JW, Sket B. 2015. "Anchialine" redefined as a subterranean estuary in a crevicular or cavernous geological setting. Journal of Crustacean Biology 35: 511–514.

Boyles JG, Cryan PM, McCracken GF, Kunz TH. 2011. Economic importance of bats in agriculture. Science 332: 41–42.

Brooks TM, Mittermeier RA, da Fonseca GA, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues AS. 2006. Global biodiversity conservation priorities. Science 313: 58–61.

Caraballo H, King K. 2014. Emergency department management of mosquito-borne illness: Malaria, dengue, and West Nile virus. Emergency Medicine Practice 16: 1–23.

Cardoso P, Erwin TL, Borges PA, New TR. 2011a. The seven impediments in invertebrate conservation and how to overcome them. Biological Conservation 144: 2647–2655.

Cardoso P, Borges PA, Triantis KA, Ferrández MA, Martín JL. 2011b. Adapting the IUCN Red List criteria for invertebrates. Biological Conservation 144: 2432–2440.

Culver DC, Pipan T. 2014. Shallow Subterranean Habitats: Ecology, Evolution, and Conservation. Oxford University Press.

Curl RL. 1958. A statistical theory of cave entrance evolution. National Speleological Society Bullettin 20: 9–22.

Danielopol DL, Gibert J, Griebler C, Gunatilaka A, Hahn HJ, Messana G, Notenboom G, Sket B. 2004. Incorporating ecological perspectives in European groundwater management policy. Environmental Conservation 31: 185–189.

Delić T, Trontelj P, Rendoš M, Fišer C. 2017. The importance of naming cryptic species and the conservation of endemic subterranean amphipods. Scientific Reports 7: 3391.

Di Lorenzo T, Di Marzio WD, Spigoli D, Baratti M, Messana G, Cannicci S, Galassi DMP. 2015. Metabolic rates of a hypogean and an epigean species of copepod in an alluvial aquifer. Freshwater Biology 60: 426–435.

Di Lorenzo T, Cifoni M, Fiasca B, Di Cioccio A, Galassi DMP. 2018. Ecological risk assessment of pesticide mixtures in the alluvial aquifers of central Italy: Toward more realistic scenarios for risk mitigation. Science of the Total Environment 644: 161–172.

Diniz-Filho JAF, Loyola RD, Raia P, Mooers AO, Bini LM. 2013. Darwinian shortfalls in biodiversity conservation. Trends in Ecology and Evolution 28: 689–695.

Dole-Olivier MJ, Castellarini F, Coineau N, Galassi DMP, Martin P, Mori N, Valdecasas A, Gibert J. 2009. Towards an optimal sampling strategy to assess groundwater biodiversity: Comparison across six European regions. Freshwater Biology 54: 777–796.

Dror Y. 2018. Warnings without power are futile. BioScience 68: 239.

Eme D et al. 2018. Do cryptic species matter in macroecology? Sequencing European groundwater crustaceans yields small ranges but does not challenge biodiversity deteminants. Ecography 41: 424–436.

Ficetola GF, Canedoli C, Stoch F. 2019. The Racovitzan impediment and the hidden biodiversity of unexplored environments. Conservation Biology 33: 214–216.

Finlayson CM, Davies GT, Moomaw WR, Chmura GL, Natali SM, Perry JE, Roulet N, Sutton-Grier AE. 2019. The second warning to humanity: Providing a context for wetland management and policy. Wetlands 39: 1–5.

Fišer C, Zagmajster M, Zakšek V. 2013. Coevolution of life history traits and morphology in female subterranean amphipods. Oikos 122: 770–778.

Fišer C, Pipan T, Culver DC. 2014. The vertical extent of groundwater metazoans: An ecological and evolutionary perspective. BioScience 64: 971–979.

Ford DC, Williams PW. 2007. Karst Hydrogeology and Geomorphology. Wiley.

Furey NM, Racey PA. 2016. Conservation ecology of cave bats. Pages 463–500 in Voigt C, Kingston T, eds. Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer.

Gibert J, Deharveng L. 2002. Subterranean ecosystems: A truncated functional biodiversity. BioScience 52: 473–481.

Gleeson T, Wada Y, Bierkens MFP, van Beek LPH. 2012. Water balance of global aquifers revealed by groundwater footprint. Nature 488: 197–200.

Gonzalez BC, Martínez A, Borda E, Iliffe TM, Fontaneto D, Worsaae K. 2017. Genetic spatial structure of an anchialine cave annelid indicates connectivity within—but not between—islands of the Great Bahama bank. Molecular Phylogenetics and Evolution 109: 259–270.

Griebler C, Avramov M. 2015. Groundwater ecosystem services: A review. Freshwater Science 34: 355–367.

Griebler C, Malard F, Lefébure T. 2014. Current developments in groundwater ecology: From biodiversity to ecosystem function and services. Current Opinion in Biotechnology 27: 159–167.

Grünewald U. 2001. Water resources management in river catchments influenced by lignite mining. Ecological Engineering 17: 143–152.

Foster SSD, Chilton, PJ. 2003. Groundwater: The processes and global significance of aquifer degradation. Philosophical Transactions of the Royal Society B 358: 1957–1972.

Hortal J, de Bello F, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle RJ. 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. Annual Review of Ecology, Evolution, and Systematics 46: 523–549.

Howarth FG. 1983. Ecology of cave arthropods. Annual Review of Entomology 28: 365–389.

Howarth FG, James SA, McDowell W, Preston DJ, Imada CT. 2007. Identification of roots in lava tube caves using molecular techniques: Implications for conservation of cave arthropod faunas. Journal of Insect Conservation 11: 251–261.

Downloaded from https://academic.oup.com/bioscience/article-abstract/69/8/641/5519083 by Buffalo State user on 06 August 2019

Humphreys E, Kukal SS, Christen EW, Hira GS, Singh B, Yadav S, Sharma RK. 2010. Halting the groundwater decline in north-west India: Which crop technologies will be winners? Advances in Agronomy 109: 155–216.

Jiang ZC, Lian YQ, Qin XQ. 2014. Rocky desertification in Southwest China: Impacts, causes, and restoration. Earth-Science Reviews 132: 1–12.

Juan C, Guzik MT, Jaume D, Cooper SJ. 2010. Evolution in caves: Darwin's "wrecks of ancient life" in the molecular era. Molecular Ecology 19: 3865–3880.

Kano Y, Kase T. 2004. Genetic exchange between anchialine cave populations by means of larval dispersal: The case of a new gastropod species *Neritilia cavernicola*. Zoologica Scripta 33: 423–437.

Knez M, Slabe T. 2016. Cave exploration in Slovenia. Pages 1–312 in LaMoreaux JW, eds. Cave and Karst Systems of the World. Springer.

Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH. 2011. Ecosystem services provided by bats. Annals of the New York Academy of Sciences 1223: 1–38.

Lapworth DJ, Baran N, Stuart ME, Warda RS. 2012. Emerging organic contaminants in groundwater: A review of sources, fate and occurrence. Environmental Pollution 163: 287–303.

Liu C, Yu J. 2001. Groundwater exploitation and its impact on the environment in the North China Plain. Water International 26: 265–272.

Magnabosco C, Lin LH, Dong H, Bomberg M, Ghiorse W, Stan-Lotter H, Pedersen K, Kieft TL, van Heerden E and Onstott TC. 2018. The biomass and biodiversity of the continental subsurface. Nature Geoscience 11: 707.

Mammola S. 2018. Finding answers in the dark: Caves as models in ecology fifty years after Poulson and White. Ecography 41: 1–21.

Mammola S, Leroy B. 2018. Applying species distribution models to caves and other subterranean habitats. Ecography 41: 1194–1208.

Mammola S, Piano E, Cardoso P, Vernon P, Culver DC, Pipan T, Isaia M. 2019. Climate change going deep: the effects of global climatic alterations on cave ecosystems. The Anthropocene Review 00: 1–19. doi:10.1177/2053019619851594.

Medellín RA, Wiederholt R, Lopez-Hoffman L. 2017. Conservation relevance of bat caves for biodiversity and ecosystem services. Biological Conservation 211: 45–50.

Moldovan O., Racoviţă Gh., Rajka G. 2003. The impact of tourism in Romanian show caves: The example of the beetle populations in the Urşilor Cave of Chişcău (Transylvania, Romania). Subterranean Biology 1: 73–78.

Ng JC, Perry KL. 2004. Transmission of plant viruses by aphid vectors. Molecular Plant Pathology 5: 505–511.

Niemiller ML, Zigler KS. 2013. Patterns of cave biodiversity and endemism in the Appalachians and Interior Plateau of Tennessee, USA. PLOS ONE 8 (art. e64177).

Novak T, Šajna N, Antolinc E, Lipovšek S, Devetak D, Janžekovič F. 2014. Cold tolerance in terrestrial invertebrates inhabiting subterranean habitats. International Journal of Speleology 43: 265–272.

Piegay H, Alber A, Slater L, Bourdin L. 2009. Census and typology of braided rivers in the French Alps. Aquatic Sciences 71: 371–388.

Pipan T, Petrič M, Šebela S, Culver DC. 2018. Analyzing climate change and surface–subsurface interactions using the Postojna Planina Cave System (Slovenia) as a model system. Regional Environmental Change 19: 379–389.

Puechmaille SJ, Gouilh MA, Piyapan P, Yokubol M, Mie KM, Bates PJ, Satasook C, Nwe T, Bu SSH, Mackie JI, Petit JE, Emma C, Teeling CE. 2011. The evolution of sensory divergence in the context of limited gene flow in the bumblebee bat. Nature Communications 2: 573.

Rabelo LM, Souza-Silva M, Ferreira RL. 2018. Priority caves for biodiversity conservation in a key karst area of Brazil: Comparing the applicability of cave conservation indices. Biodiversity and Conservation 9: 1–33.

Raschmanová N, Šustr V, Kováč L, Parimuchová A, Devette. 2018. Testing the climatic variability hypothesis in edaphic and subterranean Collembola (Hexapoda). Journal of Thermal Biology 78: 391–400.

Reboleira AS, Borges PA, Gonçalves F, Serrano AR, Oromí P. 2011. The subterranean fauna of a biodiversity hotspot region—Portugal: An overview and its conservation. International Journal of Speleology 40: 23–37.

Reboleira ASPS, Abrantes NA, Oromí P, Gonçalves F. 2013. Acute toxicity of copper sulfate and potassium dichromate on stygobiont *Proasellus*: General aspects of groundwater ecotoxicology and future perspectives. Water, Air, and Soil Pollution 224: 1550.

Riddle MR, et al. 2018. Insulin resistance in cavefish as an adaptation to a nutrient-limited environment. Nature 555: 647–651.

Ripple WJ, et al. 2017. World scientists' warning to humanity: A second notice. BioScience 67: 1026–1028.

Rizzo V, Sánchez-Fernández D, Fresneda J, Cieslak A, Ribera I. 2015. Lack of evolutionary adjustment to ambient temperature in highly specialized cave beetles. BMC Evolutionary Biology 15: 10.

Schwarzenbach R, Egli T, Hofstetter TB, von Gunten U, Wehrli B. 2010. Global water pollution and human health. Annual Review of Environment and Resources 35: 109–136.

Shu SS, Jiang WS, Whitten T, Yang JX, Chen XY. 2013. Drought and China's cave species. Science 340: 272.

Siebert S, Burke J, Faures JM, Frenken K, Döll P, Portman, FT. 2010. Groundwater use for irrigation: A global inventory. Hydrology and Earth System Sciences 14: 1863–1880.

Soares D, Niemiller ML. 2013. Sensory adaptations of fishes to subterranean environments. BioScience 63: 274–283.

Souza-Silva M, Martins RP, Ferreira RL. 2015. Cave conservation priority index to adopt a rapid protection strategy: A case study in Brazilian Atlantic rain forest. Environmental Management 55: 279–295.

Sugai LSM, Ochoa-Quintero JM, Costa-Pereira R, Roque FO. 2015. Beyond above ground. Biodiversity and Conservation 24: 2109–2112.

Sutherland WJ, et al. 2018. A 2018 horizon scan of emerging issues for global conservation and biological diversity. Trends in Ecology and Evolution 33: 47–58.

Tanalgo KC, Tabora JA, Hughes AC. 2018. Bat cave vulnerability index (BCVI): A holistic rapid assessment tool to identify priorities for effective cave conservation in the tropics. Ecological Indicators 89: 852–860.

Taylor RG et al. 2013. Ground water and climate change. Nature Climate Change 3: 322–329.

Teeling EC, Vernes SC, Dávalos LM, Ray DA, Gilbert MTP, Myers E, Bat1K Consortium. 2018. Bat biology, genomes, and the Bat1K Project: To generate chromosome-level genomes for all living bat species. Annual Review of Animal Biosciences 6: 23–46.

Trajano E. 2000. Cave faunas in the Atlantic tropical rain forest: Composition, ecology, and conservation. Biotropica 32: 882–893.

Trejo-Salazar RE, Eguiarte LE, Suro-Piñera D, Medellin RA. 2016. Save our bats, save our tequila: Industry and science join forces to help bats and agaves. Natural Areas Journal 36: 523–531.

Trontelj P, Douady C, Fišer C, Gibert J, Gorički Š, Lefébure T, Sket B, Zakšek V. 2009. A molecular test for hidden biodiversity in groundwater: How large are the ranges of macro-stygobionts? Freshwater Biology 54: 727–744.

Voituron Y, de Frapoint M, Issartel J, Guillaume O, Clobert J. 2010. Extreme lifespan of the human fish (*Proteus anguinus*): A challenge for ageing mechanisms. Biology Letters 7: 105–107.

Whitten T. 2009. Applying ecology for cave management in China and neighbouring countries. Journal of Applied Ecology 46: 520–523.

Wilson EO. 1992. The Diversity of Life. Belknap Press.

Wisotzky F, Obermann P. 2001. Acid mine groundwater in lignite overburden dumps and its prevention: The Rhineland lignite mining area (Germany). Ecological Engineering 17: 115–123.

Wynne JJ et al. 2014. Disturbance relicts in a rapidly changing world: The Rapa Nui (Easter Island) factor. BioScience 64: 711–718.

Wynne JJ, Sommer S, Howarth FG, Dickson BG, Voyles KD. 2018. Capturing arthropod diversity in complex cave systems. Diversity and Distributions 24: 1478–1491.

Downloaded from https://academic.oup.com/bioscience/article-abstract/69/8/641/5519083 by Buffalo State user on 06 August 2019

Yoshizawa K, Ferreira RL, Kamimura Y, Lienhard C. 2014. Female penis, male vagina, and their correlated evolution in a cave insect. Current Biology 24: 1–5.

Yoshizawa, K., Kamimura, Y., Lienhard, C., Ferreira, R. L., and Blanke, A. 2018a. A biological switching valve evolved in the female of a sex-role reversed cave insect to receive multiple seminal packages. eLife 7: e39563.

Yoshizawa M, Settle A, Hermosura M, Tuttle L, Centraro N, Passow CN, McGaugh SE. 2018b. The evolution of a series of behavioral traits is associated with autism-risk genes in cavefish. BMC Evolutionary Biology 18: 89.

Zagmajster M, Culver DC, Christman M, Sket B. 2010. Evaluating the sampling bias in pattern of subterranean species richness: Combining approaches. Biodiversity and Conservation 19: 3035–3048.

Zagmajster M, Malard F, Eme D, Culver DC. 2018. Subterranean biodiversity patterns from global to regional scales. Cave Ecology. Springer.

Stefano Mammola and Marco Isaia are affiliated with the Department of Life Sciences and Systems Biology at the University of Turin, in Turin, Italy. Stefano Mammola and Pedro Cardoso are affiliated with the Laboratory for Integrative Biodiversity Research, in the Finnish Museum of Natural History, at the University of Helsinki, in Helsinki, Finland. Stefano Mammola, Pedro Cardoso, and Marco Isaia are also affiliated to the IUCN SSC Spider and Scorpion Specialist Group. David C. Culver is affiliated with the Department of Environmental Science at American University, in Washington, DC. Louis Deharveng is affiliated with the Institut de Systématique, Evolution, Biodiversité, at the Museum National d'Histoire Naturelle at Sorbonne Université, in Paris, France. Louis Deharveng, Rodrigo L. Ferreira, Cene Fišer, Diana M. P. Galassi, William F. Humphreys, Oana T. Moldovan, Ana Sofia P. S. Reboleira, J. Judson Wynne, and Maja Zagmajster are affiliated with the IUCN SSC Cave Invertebrate Specialist Group. Rodrigo L. Ferreira and Marconi Souza-Silva are affiliated with the Center of Studies in Subterranean Biology, in the Biology Department at the Federal University of Lavras, in Lavras, Brazil. Cene Fišer and Maja Zagmajster are affiliated with the SubBio Lab, in the Department of Biology at the University of Ljubljana, in Ljubljana, Slovenia. Diana M. P. Galassi is affiliated with the Department of Life, Health, and Environmental Sciences at the University of L'Aquila, in L'Aquila, Italy. Christian Griebler is affiliated with the Helmholtz Zentrum München, at the Institute of Groundwater Ecology, in Neuherberg, Germany, and with the Division of Limnology at the Center of Functional Ecology, at the University of Vienna, in Vienna, Austria. Stuart Halse is affiliated with Bennelongia Environmental Consultants, in Jolimont, Australia. William F. Humphreys is affiliated with the School of Biological Sciences at the University of Western Australia, in Crawley, Australia. Florian Malard is affiliated with the Université Claude Bernard Lyon 1's Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés, in Villeurbanne, France. Alejandro Martinez is affiliated with the IRSA – Water Research Institute, at the Consiglio Nazionale delle Ricerche, in Verbania, Italy. Oana T. Moldovan is affiliated with the Emil Racovitza Institute of Speleology, in Cluj-Napoca, Romania. Matthew L. Niemiller is affiliated with the Department of Biological Sciences at The University of Alabama in Huntsville, Alabama. Martina Pavlek is affiliated with the Department of Evolutionary Biology, Ecology, and Environmental Sciences and with the Biodiversity Research Institute, at the University of Barcelona, in Barcelona, Spain, and with the Croatian Biospeleological Society, in Zagreb, Croatia. Ana Sofia P. S. Reboleira is affiliated with the Natural History Museum of Denmark, at the University of Copenhagen, in Copenhagen, Denmark. Emma C. Teeling is affiliated with the School of Biology and Environmental Science at University College Dublin, in Ireland. J. Judson Wynne is affiliated with the Department of Biological Sciences at the Merriam-Powell Center for Environmental Research, at Northern Arizona University, in Flagstaff.

Downloaded from https://academic.oup.com/bioscience/article-abstract/69/8/641/5519083 by Buffalo State user on 06 August 2019