Scientists' warning on the conservation of subterranean ecosystems

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46   **ABSTRACT**

47   In light of recent alarming trends in human population growth, climate change and other
48   environmental disturbances, a 'Warning to Humanity' manifesto was published in BioScience in
49   2017. This call reiterated most of the ideas originally expressed by the Union of Concerned
50   Scientists in 1992, including the fear that we are "[...] *pushing Earth's ecosystems beyond their*
51   *capacities to support the web of life.*" As subterranean biologists, we take this opportunity to
52   emphasize the global importance and the conservation challenges associated with subterranean
53   ecosystems. They likely represent the most widespread non-marine environments on Earth, yet
54   specialized subterranean organisms remain among the least documented and studied. Largely
55   overlooked in conservation policies, subterranean habitats play a critical functional role in the
56   functioning of the web of life and provide important ecosystem services. We highlight main threats
57   to subterranean ecosystems and propose a set of effective actions to protect this globally important
58   natural heritage.

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60   **Keywords**

61   Biodiversity crisis, Caves, Extinction risk, Groundwater, Nature conservation

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78 **INTRODUCTION**

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80   "*Human beings and the natural world are on a collision course.*"

81   Union of Concerned Scientists' Manifesto – 1992

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83 Building on the manifesto "*World Scientists' Warning to Humanity*" issued in 1992 by the Union of

84 Concerned Scientists, Ripple et al. (2017) recently published a passionately debated paper titled

85 *"World Scientists' Warning to Humanity: a Second Notice."* This novel proclamation, which was

86 endorsed by more than 15,000 cosignatory scientists ("Alliance of World Scientists"), reiterated

87 most of the ideas and concerns presented in the first manifesto, and in particular the fear that

88 humans are "[...] *pushing Earth's ecosystems beyond their capacities to support the web of life.*"

89 The second notice highlighted alarming trends in several environmental issues over the last 25 years

90 (1992–2016), including global climate change, deforestation, biodiversity loss, human population

91 increase, and a decline in freshwater resources.

92   Since its publication, this second notice has been extensively discussed in the scientific

93 literature and social media, stimulating an upsurge of discipline-specific follow-up articles focused

94 on particular biological or social systems (Ripple W.J. [Oregon State University, Corvallis, United

95 States], personal communication, 7 September 2018). As a group of subterranean biologists with a

96 breadth of different expertise and a strong commitment to biodiversity conservation, we take this

97 opportunity to examine some alarming trends underscored by the Alliance of World Scientists from

98 a "subterranean" perspective. We discuss the implications that this Ripple et al. (2017)' manifesto

99 has for the conservation of the subterranean realm, which includes some of the most unique,

100 secluded, understudied, and difficult-to-study environments on our planet. Although subterranean

101 habitats are not at the forefront of one's mind when thinking about global conservation issues, they

102 support exceptional forms of life and represent critical habitats to be preserved and prioritized in

103 conservation policies. While some conservation efforts have been devoted to protect subterranean

104 ecosystems at a local level, no global assessment has been conducted that explicitly takes these

105 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);

137 v) a variety of superficial underground habitats, collectively termed shallow subterranean habitats,

138 support an extensive array of subterranean biota (Culver and Pipan 2014); and

139 vi) if one would be keen to account also for microbial life, a large amount of continental prokaryotic

140 biomass and as yet an unknown prokaryote diversity is hidden within these systems (Magnabosco et

141 al. 2018).

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143 Paradoxically, although habitats beneath the Earth's surface are more widespread and

144 diversified than is usually perceived, most of them cannot be mapped and directly studied, either

145 because they are too deep or because they are hardly accessible to humans due to their millimetre

146 scale resolution. Consequently, specialized subterranean organisms remain among the least

147 documented fauna on our planet. This impediment, recently termed "Racovitzan shortfall" (Ficetola

148 et al. 2019), poses a thorny question: if the real extension of the subterranean domain is unknown,

149 and the biota we observe in a cave are just the "tip of the subterranean biodiversity iceberg", what

150 can we practically do to protect the full extent of subterranean habitats and their inhabitants?

151 To make sound decisions for the conservation of the subterranean world, there is first an

152 urgent need to accelerate scientific research, aiming at exploring subterranean biodiversity

153 altogether with the abiotic and biotic factors that drive its distribution patterns across space and

154 time. Available estimates (Culver and Holsinger 1992; Zagmajster et al. 2018) suggest that most

155 obligate subterranean species worldwide have not yet been described (i.e., the Linnean shortfall). In

156 the epoch of sixth mass extinction crisis, many of these species may face extinction before they are

157 discovered and formally described—a phenomenon described by Wilson (1992) as 'Centinelan

158 extinctions'. Moreover, several other knowledge gaps impede our ability to protect and conserve

159 subterranean biodiversity (Table 1). The distribution (i.e., the Wallacean shortfall) and the life

160 history of most described subterranean species in particular, are virtually unknown. Acquiring basic

161 knowledge about biological and functional diversity of subterranean organisms (i.e., the

162 Raunkiæran shortfall), their phylogenetic relationships (i.e., the Darwinian shortfall), their

163 interactions within different subterranean communities (i.e., the Eltonian shortfall), as well as their

164 sensitivity to environmental perturbations (i.e., the Hutchinsonian shortfall), represent pivotal steps

165 toward consolidating scientific knowledge to support conservation planning (Cardoso et al. 2011a;

166 Diniz-Filho et al. 2013; Hortal et al. 2015) and further emphasizing the ecosystem services that the

167 subterranean fauna provide.

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169 **IMPORTANCE OF SAFEGUARDING SUBTERRANEAN BIODIVERSITY**

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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
205 pollinators and seed dispersers in forests, mangroves and deserts (e.g., Valiente-Banuet et al. 1996,
206 Medellín and Gaona 1999, Azuma et al. 2002, Kunz et al. 2011). Cave-roosting nectar-feeding bats
207 in the southwestern U.S. and northern Mexico are primary pollinators for columnar cacti, including
208 the iconic Saguaro cacti (*Carnegiea gigantea*), which are considered keystone species of the
209 Sonoran Desert (Valiente-Banuet et al. 1996). Additionally, cave roosting nectar-feeding bats have
210 coevolved to pollinate agave, also a keystone species in Mexican deserts and scrub forests and a key
211 ingredient in tequila – production of this beverage employs 70,000 people and garners 1.2 billion
212 dollar/ year in exports alone (Trejo-Salazar et al. 2016). Another lucrative multimillion dollar
213 industry, the durian fruit of southeast Asia is primarily pollinated by a cave roosting bat species
214 (Bumrungsri et al. 2009, Stewart and Dudash 2017). Therefore, bats' role in maintaining the quality
215 of recreational outdoor areas, limiting disease transmission to humans, livestock and agricultural
216 crops, as well as ultimately enhancing human well-being through maintaining ecosystems and
217 agribusiness, is immense. Cave-roosting bat populations and their habitats must be protected to
218 ensure these key ecological services to humans continue (Medellín et al. 2017).

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

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226 **MAIN GLOBAL THREATS TO SUBTERRANEAN BIODIVERSITY**

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228 Subterranean environments and their biota are only superficially known (pun intended). Yet, we do
229 know that most of the threats highlighted by Ripple et al. (2017) in their manifesto are directly
230 affecting the subterranean domain *tout court*, because subterranean ecosystems are inextricably
231 linked to surface processes. For example, they depend on allochthonous energy supplies, which may
232 consist of flood detritus, guano deposition from bats, birds and crickets, or dissolved organic
233 materials in waters percolating from the surface. Thus, when humans adversely change the surface
234 environment, subterranean ecosystems will respond to those changes. Most notably, deforestation
235 (Trajano 2000, Souza-Silva et al. 2015), urbanization, agricultural, industrial, and mining activities
236 (Trajano 2000; Reboleira et al. 2011, Souza-Silva et al. 2015, Sugai et al. 2015), heavy metals and

237 agrochemicals pollution (Reboleira et al. 2013, Di Lorenzo et al. 2015, 2018), non-native species
238 introductions (Howarth et al. 2007, Wynne et al. 2014), tourism (Moldovan et al. 2013), and global
239 climate change (Mammola et al. 2018) negatively affect both biodiversity and subterranean
240 ecological processes. In the following sections, we briefly discuss what we consider the most
241 challenging global threats affecting subterranean ecosystems.
242
243 Habitat loss
244 Subterranean habitat loss and degradation are occurring in many regions. In several cases, the
245 disturbance of subterranean habitats is direct, although often spatially localized. For instance,
246 quarrying and mining activities often result in removal of the karst substratum, sometimes leading
247 to removal of whole karst hills (Whitten 2009). In this respect, the open pit mining for lignite
248 provides a striking example. Worldwide about 1 billion tons of lignite are produced each year. Only
249 in Germany, one of the largest lignite producers worldwide (170 million tons/year), opencast
250 mining has altered about 200,000 hectares of land including the removal of the aquifer. Moreover,
251 as a prerequisite of opencast mining, the groundwater table in the region needs to be lowered by
252 hundreds of meters to below the mining level and consequently groundwater ecosystems are
253 systematically dewatered for entire districts or even federal states accounting for billions of m^3 of
254 groundwater pumped and thousands of km^2 (Grünewald 2001); a destruction of groundwater
255 habitats at an incomparable dimension. Last but not least, subsequent to mining activities,
256 dewatered zones that re-saturate characteristically bear highly acidic groundwater as a consequence
257 of long-term pyrite oxidation (Wisotzky and Obermann 2001). The impact of mining activities is
258 also evident in ferruginous landscapes in Brazil, one of the largest extractive areas in the world,
259 where hundreds of caves have been destroyed by quarrying and mine excavation and groundwater
260 has been polluted by mineral waste, heavy metals, and other contaminants (Souza-Silva et al. 2015,
261 Sugai et al. 2015).
262   Furthermore, construction activities can directly threaten subterranean ecosystems.
263 Construction of infrastructure and tunnel drilling can entirely or partially destroy subterranean
264 habitats. For example, road construction within karst areas of Slovenia has resulted in the discovery
265 of more than 350 caves, with many being completely destroyed (Knez and Slabe 2016).
266 Development along rivers and streams, such as channelizing, regulating, and damming, can result in
267 major hydrological changes and loss of habitat, especially in the hyporheic zone and the subjacent
268 aquifers (e.g., Piegay et al. 2009). Modified river flow channels interrupt the connectivity between
269 surface and subterranean water and can lower the water table; similarly, diverting river flow may

270 result in both flooding or desiccation within subterranean systems, which results in direct loss of
271 habitat.

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

281

282 **Groundwater overexploitation and contamination**
283 The decline in freshwater resources was highlighted as one of the most critical negative trends that
284 humanity is facing (Finlayson et al. 2019, Ripple et al. 2017), which can be considered a clarion call
285 to increase global efforts to halt and reverse the ongoing degradation of groundwater resources.
286 Anthropogenic impacts in groundwater aquifers include local and diffuse sources of contamination
287 (e.g., Schwarzenbach et al. 2010, Lapworth et al. 2012), overexploitation of groundwater resources
288 (Wada et al. 2010, Gleeson et al. 2012), and climate change (see next section). Maintaining healthy
289 groundwater communities appears to be a critical component of reducing anthropogenic impacts,
290 given the potential ecosystem services provided by most of these organisms (Griebler and Avramov
291 2015). Indeed, the eventual collapse of groundwater communities would in turn hinder the self-
292 purifying processes provided by these organisms, thus accelerating the degradation of this precious
293 resource.

294

295 **Climate change**

296 Climate change represents one of the most complex and challenging issues in the Anthropocene
297 (Ripple et al. 2017), and while its effects are already visible on the surface, the impacts on
298 subterranean systems are poorly understood. In the medium- to long-term, climate change is
299 expected to modify both deep terrestrial (Pipan et al. 2018) and aquatic subterranean ecosystems
300 (Taylor et al. 2013). Given that deep subterranean habitats are typically characterized by
301 environmental stability, it has been proposed that most subterranean-adapted organisms have a
302 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;

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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

368   networks of protected areas for a significant proportion of the world's subterranean hotspots

369   of diversity. Insofar as funds invested in conservation will be limited, special efforts are

370   needed to define priority principles and criteria for channeling conservation actions (Rabelo

371   et al. 2018);

372

373   iv) renewing efforts in the threat assessment of subterranean species using the International

374   Union for Conservation of Nature (IUCN) Red List criteria. Currently very few subterranean

375   species have been assessed (*ca.* 850 species), and the subjectivity in applying the criteria

376   across a large diversity of taxa assessed separately by various specialists has led to

377   numerous inconsistencies. The standardization of interpretation of criteria and

378   implementation of clear guidelines applicable across taxa can greatly improve the current

379   situation (Cardoso et al. 2011b), a process in which the involvement of the IUCN SSC Cave

380   Invertebrate Specialist Group will be fundamental. Through these steps, we can improve our

381   ability to assess the conservation status of subterranean species, as a sound basis for global

382   and local conservation policy, as well as for designing efficient species and site conservation

383   plans;

384

385   v) developing models to quantify the effects of global climate change on subterranean

386   communities. Although climate change is one of the most pervasive global impacts (Ripple

387   et al., 2017), studies on the effects of climate change on cave ecosystems are few, and their

388   results are often inconclusive. There is an urgent need to achieve an in-depth understanding

389   of the global change issue from a subterranean perspective, through the analyses of

390   empirical data (Pipan et al. 2018), experiments (Rizzo et al. 2015), modeling (Mammola &

391   Leroy 2018), and simulation studies;

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393   vi) promoting research into the biology and ecology of groundwater organisms so that they

394   may act, when appropriate, as sentinel species of clean waters in water quality monitoring

395   activities. In addition, the use of most widespread contaminants that accumulate in

396   subterranean aquifers, e.g., fertilizers and pesticides in agricultural landscapes, should be

397   limited and a sustainable use of groundwater promoted (Danielopol et al. 2004);

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399   vii) in recognition of the interconnectivity of surface and subterranean compartments, it is

400   important to implement conservation measures bridging these environments. Fostering

401   interdisciplinary scientific cooperation will be critical, i.e., by designing specific studies

402   involving broad collaborations with taxonomists, ecologists, biologists, conservation
403   biologists, ecotoxicologists, geologists, hydrologists, and soil scientists, who typically work
404   in surface environments;

405

406   viii) developing educational programs for both primary and secondary students and the lay
407   public to heighten awareness regarding the sensitivity of subterranean organisms, as well as
408   emphasizing the connection between surface and subsurface ecosystems. We recommend,
409   together with local communities and caving associations, developing classroom curricula,
410   subterranean-themed public exhibitions, guided and regulated outdoor activities to karst and
411   other natural terrains (like rivers) sustaining rich subterranean habitats, and other outreach
412   activities in areas where communities both reside and are reliant upon the subterranean
413   environments. More broadly, social media campaigns using internet, television, radio, and
414   print media, will heighten public awareness of subterranean environments and the unique
415   animal communities they harbour; and

416

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

420

421   **EPILOGUE**

422

423 Although we represent a small group of scientists within the large and heterogeneous community of
424 subterranean biologists, we aimed to provide a multifaceted view of the global issues affecting the
425 subterranean world. As we have experienced during the writing of this work, the perspective from
426 which these issues are observed by the different authors can be quite diverse. Yet, we all agreed on
427 the fact that these systems are poorly recognized as conservation priorities, that they provide vital
428 ecosystem services to humankind, and that they represent a true research frontier. Most importantly,
429 we reached a full consensus in highlighting the high vulnerability of the subterranean world and the
430 seriousness of the threats affecting it, as well as the need of making this information available to
431 stakeholders and the general public. Indeed, although the conservation issues we discuss are well
432 understood within our community and partially covered in the specialised literature, they have never
433 been formalised in a scientific publication written for a broader audience. As with most ecosystems
434 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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759 **Table 1.** The eight knowledge shortfalls of subterranean biodiversity (Hortal et al. 2015, Ficetola et
760 al. 2019) and specific problems related to subterranean biology and the conservation of
761 subterranean species.

762

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)

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764

FIGURE CAPTIONS

766

767 **Figure 1.** Examples of the diversity of life in subterranean habitats. **a**) *Leptodirus hochenwartii*
768 Schmidt, 1832 (Coleoptera), the first obligate subterranean invertebrate ever described; **b**) The
769 subterranean specialized silverfish *Squamatinia algharbica* Mendes & Reboleira, 2012
770 (Zygentoma). **c**) *Troglocladius hajdi* Andersen et al., 2016 (Diptera), the only specialized
771 subterranean species that have retained functional wings; **d**) A specialized subterranean microwhip
772 scorpion in the genus *Eukoenenia* Börner, 1901(Palpigradi)—palpigrads are one of the most
773 enigmatic and understudied orders of arachnids in the world; **e**) A specialized *Troglocheles*
774 Zacharda, 1980 (Acari) hunting on a water puddle in a cave; **f**) A specialized subterranean
775 harvestman in the genus *Giupponia* Pérez & Kury, 2002 (Opiliones); **g**) An eyeless spider *Hadites*
776 *tegenarioides* Keyserling, 1862 (Agelenidae); **h**) The specialized subterranean giant pseudoscorpion
777 *Titanobochica magna* Zaragoza & Reboleira, 2010 (Pseudoscorpiones); **i**) A specialized
778 subterranean crustacean in the genus *Spelaeogammarus* da Silva Brum, 1975 (Amphipoda); **j**) An
779 undescribed subterranean isopod from the family Cirolanidae—due to the remarkable
780 depigmentation of this species, internal organs are clearly visible; **k**) A blind crustacean belonging
781 to the genus *Morlockia* García-Valdecasas, 1984 (Remipedia)—Remipedia is the latest described
782 class of crustaceans, so far having representatives exclusively in anchialine systems; **l**) *Marifugia*
783 *cavatica* Absolon & Hrabe, 1930 (Annelida)—the only freshwater cave-dwelling tube worm in the
784 world; **m**) The blind tetra, *Stygichthys typhlops* Brittan & Böhlke, 1965 (Characidae), one out of the
785 nearly 250 cavefishes described in the world; **n**) The olm, *Proteus anguinus* Laurenti, 1768
786 (Amphibia), the first subterranean animal ever described; **o**) Lessser horseshoe bats *Rhinolophus*
787 *hipposideros* Bechstein, 1980 (Rhinolophidae) hibernating in a cave—bats provide critical
788 ecological services and are keystone species in several ecosystems. Photo credits/by courtesy of: **a**)
789 Dražina T; **b**, **h**) Reboleira ASPS; **c,l**) Bedek J; **d**) Chiarle A; **e**) Tomasinelli F; **f,i,j,m**) Ferreira RL;
790 **g**) Rožman T; **k**) Strecker U; **n**) Krstinić B; **o**) Biggi E.