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Climate change going deep: the effects of global climatic alterations on cave ecosystems

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Keywords: cave-dwelling species, Global Warming, hypogean habitat, cave meteorology, superficial subterranean habitats, stygobionts, troglobionts, relative humidity, temperature

INDEX

I. INTRODUCTION

II. ABIOTIC FEATURES

(1) Subterranean climate

(2) Climate change and the thermal inertia of caves

42 **(3) Potential implications of subterranean warming on abiotic features**

43 **(4) Shallow subterranean habitats**

44 **III. BIOTIC FEATURES**

45 **(1) Subterranean organisms**

46 **(2) Potential species sensitivity to climate change**

47 **(3) Eco-evolutionary response to climate change**

48 **(4) Inter-connection with other systems**

49

50 **IV. FUTURE DIRECTIONS**

51 **V. CONCLUSIONS**

52 **ABSTRACT**

53 Scientists of different disciplines have recognised the valuable role of terrestrial caves as
54 ideal natural laboratories in which to study multiple eco-evolutionary processes, from
55 genes to ecosystems. Because caves and other subterranean habitats are semi-closed
56 systems characterised by a remarkable thermal stability, they should also represent
57 insightful systems for understanding the effects of climate change on biodiversity *in situ*.
58 Whilst a number of recent advances have demonstrated how promising this fast moving
59 field of research could be, a lack of synthesis is possibly holding back the adoption of
60 caves as standard models for the study of the recent climatic alteration. By linking
61 literature focusing on physics, geology, biology, and ecology, we illustrate the rationale
62 supporting the use of subterranean habitats as laboratories for studies of global change
63 biology. We initially discuss the direct relationship between external and internal
64 temperature, the stability of the subterranean climate and the dynamics of its alteration in
65 an anthropogenic climate change perspective. Due to their evolution in a stable
66 environment, subterranean species are expected to exhibit low tolerance to climatic
67 perturbations and could theoretically cope with such changes only by shifting their
68 distributional range or by adapting to the new environmental conditions. However, they
69 should have more obstacles to overcome than surface species in such shifts, and
70 therefore could be more prone to local extinction. In the face of rapid climate change,
71 subterranean habitats can be seen as refugia for some surface species, but at the same
72 time they may turn into dead-end traps for some of their current obligate inhabitants.
73 Together with other species living in confined habitats, we argue that subterranean species
74 are particularly sensitive to climate change, and we stress the urgent need for future
75 research, monitoring programs and conservation measures.

76

77 I. INTRODUCTION

78

79 Climate change is considered to be one of the most challenging concerns for humanity
80 (Walther et al., 2002; Parmesan and Yohe, 2003; Scholze et al., 2006; Williams et al.
81 2015). The complexity of the global climate issue stretches far beyond the currently
82 observed pattern of global temperature increase (Santer et al., 2003), as it involves a
83 variety of multifaceted ecological responses to climatic variations, such as shifts in species
84 distribution ranges (Chen et al., 2011), phenological displacements (Parmesan and Yohe,
85 2003; Root et al., 2003), complex interactions among previously isolated species (Williams
86 and Jackson, 2007; Krosby et al., 2015), extinctions (Thomas et al., 2004; Cahill et al.,
87 2013) and other unpredictable cascading effects on different ecosystem components
88 (Walther et al., 2002).

89 In order to minimize confounding effects, scientists have often used isolated
90 ecosystems—and specific organisms within them—as models to unravel ecological
91 responses to recent climate alterations, upscaling results and conclusions to a wider range
92 of systems and organisms. Under this perspective, mountain summits, oceanic islands,
93 lakes and other confined habitats have offered insightful models for determining the effects
94 of climate change on biodiversity *in situ* (Hortal et al., 2014; Warren et al., 2015; Whittaker
95 et al., 2017; Itescu, 2018; Mammola, 2018). Even if the potential of subterranean habitats
96 as ideal biological laboratories has been long ago foreseen (Barr, 1968; Poulson and
97 White, 1969; Culver, 1982), little has been written about the specific contribution of cave-
98 based studies to the understanding of patterns and processes in global change biology
99 (Mammola, 2018; Sánchez-Fernández et al., 2018). As a direct consequence, most
100 syntheses focusing on the effect of climate change on ecosystems did not feature
101 terrestrial caves in the potential study systems (e.g. Walther et al., 2002; Parmesan and
102 Yohe, 2003; Scholze et al., 2006). However, there exists an emerging trend in

103 environmental, physical, and ecological studies alike to use caves and other subterranean
104 habitats as models for unraveling current climate change dynamics. Recent relevant
105 studies focused on the role of climatic alterations on the geophysical components of the
106 cave environment (Domínguez-Villar et al., 2015; Colucci et al., 2016; Pipan et al. 2018),
107 the potential of caves as methane-sinks (Fernandez-Cortes et al., 2015) and the general
108 effects of global temperature increase on different subterranean animals (Colson-Proch et
109 al., 2010, Lencioni et al., 2010; Brandmayr et al., 2013; Mermillod-Blondin et al., 2013;
110 Rizzo et al., 2015; Sánchez-Fernández et al., 2016; Mammola and Isaia, 2017; Di Lorenzo
111 and Galassi, 2017; Mammola et al., 2018), and microorganisms (Brielmann et al., 2009,
112 2011; Gribler et al., 2016).

113 We hypothesize here that caves represent one of the most informative systems
114 for the study of climate change across its biotic and abiotic components, for multiple
115 reasons:

116 i) they are semi-closed systems that are extensively replicated across the Earth (Culver
117 and Pipan, 2009);

118 ii) they are buffered from external variations and generally characterised by a remarkable
119 thermal stability, especially in temperate areas (Badino, 2004, 2010);

120 iii) temperature inside caves highly correlate with mean annual temperatures on the
121 surface (Moore and Nicholas, 1964), at least in temperate areas (Sánchez-Fernández et
122 al., 2018); and

123 iv) subterranean organisms have evolved a suite of morphological and physiological
124 adaptations to thrive under the peculiar environmental conditions found in caves, which
125 are often convergent even across phylogenetically distant groups (Culver and Pipan, 2009;
126 Juan et al., 2010; Protas and Jeffrey, 2012).

127 However, a lack of synthesis on this topic is possibly holding back the
128 establishment of caves as standard models for the study of the effects of climate change in
129 the field. By bringing together literature focusing on cave biology, ecology, and physics that
130 were previously disconnected, we illustrate the rationale supporting the use of
131 subterranean habitats as ideal model for studies of global change biology. We describe the
132 potential effects of the anthropogenic climate alterations on the abiotic and the biotic
133 components of the cave ecosystem, giving special reference to the cave climate,
134 subterranean organisms and the interconnection between caves and other ecosystems
135 (surface and soil). We focused here mostly on terrestrial subterranean habitats and only
136 partly on groundwater systems (see Green et al., 2011; Taylor et al., 2013 for more
137 arguments on groundwaters). We did not considered marine caves. A definition of the
138 jargon used in the text is presented in Box 1. Throughout the text, the term “cave” is used
139 to refer to the extended network of fissures and cracks that permeate most substrates,
140 even if their size is not commensurable to the human-scale (Romero, 2012).

141 142 **II. ABIOTIC FEATURES**

143 **(1) Subterranean climate**

144 A wealth of literature documents the ecological peculiarity of the subterranean realm, and
145 how distinct it is from surface habitats. Whilst the absence of solar radiation is possibly the
146 most crucial factor conditioning the ecology of subsurface habitats (Culver and Pipan,
147 2015), the most important feature that corroborates the idea that caves are ideal
148 laboratories for the study of climate change in natural environment is their unique climatic
149 stability. Indeed, deep subterranean habitats have, in most cases, an almost constant
150 temperature over the year and a relative humidity often close to saturation (Cigna, 2002;
151 Badino, 2010).

152 The cave temperature is coupled with surface atmosphere temperature. The
153 surface ground thermal signal is transferred by conduction through the bedrock, eventually
154 reaching the depth of the cave (Domínguez-Villar et al., 2013). External air penetrating
155 caves rapidly reaches a nearly constant temperature along the entrance sectors due to the
156 buffering effect associated to the increase of relative humidity, and the progressive
157 equilibration with the temperature of the rock (Wigley and Brown, 1971; Wigley and Brown,
158 1976). As a result of this process, mean air temperature in cave interiors correspond
159 almost exactly to the average annual value of the outside temperature (Moore, 1964,
160 Moore and Nicholas, 1964; Figure 1).

161 It is worth noting that, depending on the geophysical characteristics of the
162 ground layers above the cave, thermal differences between the cave and the external
163 mean annual temperature may occur. The main factor affecting diversion of cave
164 temperature from the mean annual atmosphere one in temperate climates is related to the
165 type of vegetation cover of the area above the cave, since different levels of shading may
166 affect ground temperature (Domínguez-Villar et al., 2013). In addition, variations in solar
167 radiation, the presence of long lasting snow cover and the evaporative cooling in soils
168 caused by evaporation, are other factors which may contribute to explain small thermal
169 disequilibria between cave and mean annual atmosphere temperatures (Beltrami and
170 Kellman, 2003; Yzaki et al., 2013). Finally, strong air circulation or significant water
171 streams can impact the cave temperature by the advection or radiation of heat from the
172 fluids (De Freitas and Littlejohn, 1987; Covington et al., 2011), although in those cases the
173 internal temperature is also linked to the external one (Smithson, 1991; Kranjc and Opara,
174 2002).

175 One may argue about the possible effect of the geothermal gradient, as
176 temperature below the surface slowly increases with the vertical distance under the

177 surface (ca. 30 °C/km away from tectonic plates). However, the geothermal gradient is
178 generally so small that tens to hundreds of meters are required to notice a shift in the
179 thermal equilibrium between the external air temperature and the cave one (Luetscher and
180 Jeannin, 2004). Moreover, in karst regions the geothermal gradient is further buffered by
181 the advection of groundwater (Bögli, 1980), limiting the sources of heat variability affecting
182 caves (Badino, 2010).

183 In light of the intimate relationship of cave temperature with the surface
184 atmosphere temperature, it is no surprise that changes in surface atmosphere temperature
185 results in shifts in the temperature recorded underground (Perrier et al., 2005; Figure 1).

186

187 **(2) Climate change and the thermal inertia of caves**

188 Theoretical models have predicted that climate warming will impact temperature in caves
189 (Badino, 2004; Covington and Perne, 2015), and model-data comparisons have confirmed
190 such scenario (Domínguez-Villar et al., 2015; Šebela et al., 2015; Pipan et al., 2018),
191 indicating that anthropogenic climate alterations are currently modifying the subterranean
192 microclimate. Most caves show fairly stable air temperature in their interiors, as a result of
193 the slow mechanism conveying underground the outer thermal signals by conduction.
194 Consequently, there is lag-time between the air temperature increase recorded at the
195 surface and its record in cave interiors. The delay depends on the cave depth (that is, the
196 thickness of the rock above the cave) and on the duration of the anomaly (Domínguez-
197 Villar, 2012). In the pioneer synthesis of Moore and Nicholas (1964), the authors
198 speculated with delay times in the order of hundreds to thousands of years for climate
199 anomalies at the surface to reach the deeper sectors of karst massifs. In a study set in a
200 Slovenian cave located 37 m under the surface, the signal of the onset of global warming

201 was recorded 20 years later (Domínguez-Villar et al., 2015). However, it should be noticed
202 that at the same site, cave conduits located closer to the surface were expected to record
203 thermal anomalies earlier, whereas cave conduits located deeper into the karst massif are
204 unlikely to have registered the thermal impact of climate warming yet.

205

206 **(3) Potential implications of subterranean warming on abiotic features**

207 In the past, caves have suffered climate changes that affected their temperature. Those
208 changes were recorded in cave deposits (e.g., Mangini et al., 2005, Fairchild and Frisia,
209 2014), although during last millennia they had limited impact on the geophysical
210 environment of most caves. An increase in cave temperature is associated to a higher
211 relative content of water vapour required to reach saturation (i.e., 100% relative humidity).
212 However, in most cases this has no environmental implication, since dripping water
213 provides enough moisture to reach saturation.

214 Concentration of CO₂ in caves is a major control on the dissolution and precipitation
215 of carbonates. However, at the inter-annual timescale, the CO₂ concentration does not
216 depend on the cave temperature but on the soil CO₂ production and cave ventilation
217 (Fairchild and Baker, 2012). Therefore, subtle changes in cave temperature are not
218 expected to produce large geophysical changes.

219 However, the warming rate during the last decades is unusually large compared
220 to changes recorded during previous millennia (Moberg et al., 2005), affecting the
221 magnitude of thermal change per unit of time. Due to the required time to transfer the
222 external thermal signal to caves, a thermal decoupling exists between the external
223 temperature and the cave interior temperature during a climate change period. This
224 decoupling affects the seasonal air flow in caves that, in most cases, is driven by gradients
225 in air density, depending, in turn, from temperature differences between external

226 atmosphere and the cave interior. Thus, in most caves, enhanced ventilation occurs when
227 the external temperature is below the cave temperature, whereas limited ventilation is
228 recorded during the rest of the year (e.g., Kowalczyk and Froelich, 2010). Under a scenario
229 of thermal decoupling, the thermal difference between the external and the cave
230 atmosphere increases during winters, and decreases during summers. This large thermal
231 decoupling may be affecting the duration of air flow regime in caves, causing longer
232 periods of enhanced ventilation and reducing the periods with limited ventilation. Despite
233 their potential implication for cave environments and their importance in determining
234 seasonal concentrations of CO₂ and other cave environmental parameters, changes in the
235 duration of seasonal air flows have not been studied in detail yet.

236

237 **(4) Shallow Subterranean Habitats**

238 Besides caves and the associated networks of fissures, superficial subterranean habitats
239 (SSHs; Box 1) stand out as a group of subterranean habitats which are likely to be affected
240 by the global temperature increase. As the name suggests, these habitats are restricted to
241 areas close to the surface and, compared with caves, have higher energy inputs and
242 higher intrinsic variability, including significant microclimatic variations (Gers, 1998; Pipan
243 et al., 2011; Mammola et al., 2016).

244 The increased flux of energy from the atmosphere to the subterranean
245 environment induced by climate change is expected to be primarily in the SSHs—see
246 physical models in Mammola et al. (2016)—as well as in the most superficial sectors of
247 caves (Badino, 2004). It is therefore expected that the temperature increase in these
248 habitats will parallel the external one almost synchronically. Compared to the deep
249 subterranean sectors, effects on the SSH fauna are expected to be more immediate.

250

251 **III. BIOTIC FEATURES**

252 **(1) Subterranean organisms**

253 The adaptive morphology of subterranean animals has attracted the attention of
254 evolutionary biologists since the discovery of life in caves. Subterranean obligate species,
255 either terrestrial (troglonbionts) or aquatic (stygobionts), have indeed often evolved
256 behavioral, physiological and/or morphological traits to survive the peculiar conditions of
257 the subterranean habitat (Box 1). Morphologically, they often lack eyes and pigmentation,
258 and evolved elongated appendages and an assortment of sensory organs to perceive the
259 environment by senses other than vision. Given the general low energy availability of the
260 subterranean environment, they often exhibit low metabolic rates with consequent slow
261 growth rates, high fasting performances, delayed maturation, and extended longevity when
262 compared to their surface relatives (Hervant and Renault, 2002; Mezec et al., 2010;
263 Voituron et al., 2011; Fišer et al., 2013). A charismatic example is offered by the first cave
264 species ever described, the olm *Proteus anguinus* Laurenti. This aquatic cave salamander
265 reaches sexual maturity at 16 years, lays eggs every 12 years, has an adult average
266 lifespan of nearly 70 years and a predicted maximum lifespan of over 100 years (Voituron
267 et al., 2011).

268

269 **(2) Potential species sensitivity to climate change**

270 While much attention has been given to the effects of global climate change on surface
271 organisms, communities and ecosystems, studies about the influence of temperature
272 increase on subterranean biota are still at their infancy (Table 1). The contrasting response
273 obtained on different animal groups indicate that the sensitivity of subterranean species to
274 altered climatic conditions is likely to depend on phylogeny, evolutionary history and by the
275 degree of subterranean adaptations or other functional traits.

276 The most important, yet heterogeneous, evidence about the sensitivity of
277 subterranean species to the ongoing climate change derives from physiological tests. As a
278 direct result of a long evolutionary history in a thermally stable environment, it is
279 theoretically expected that most subterranean species should exhibit a stenothermal
280 profile (*sensu* Huey and Kingsolver, 1989), which maximises their physiological
281 performance over a narrow temperature range. However, in a climate change perspective,
282 adaptation to narrow ranges of temperature turns out to be a strong limitation. Indeed,
283 while most invertebrates living in the vicinity of the surface have the capacity to withstand
284 temperature variations, most deep subterranean species lack such thermoregulatory
285 mechanisms (Novak et al., 2014; Raschmanová et al., 2018). In certain species, even a
286 positive or negative variation of 2°C in respect to their habitat temperature proved to be
287 fatal (Mermillod-Blondin et al., 2013). However, the figure remains rather crude, as most
288 studies conducted so far focused on single model taxa and thus lacked a wider
289 phylogenetic perspective (but see Pallarés et al., 2019). For instance, tests carried on
290 subterranean beetles are divergent, pointing out a wide thermal niche for numerous
291 species of Cholevidae (Rizzo et al., 2015; Sánchez-Fernández et al., 2016). In addition, it
292 has been shown that two cold stenothermal cave-dwelling beetles in the genus
293 *Neobathyscia* (Coleoptera: Catopidae) have the ability to synthesise heat shock proteins,
294 which provide resistance to heat exposure (Bernabò et al., 2011). The same kind of pattern
295 (inducible HSP70 heat shock response) has been observed in subterranean amphipods in
296 the genus *Niphargus* (Crustacea: Amphipoda) (Colson-Proch et al., 2010).

297 Also, contrasting results were obtained by different authors focusing on survival
298 and performance patterns in stygobiont crustaceans living in thermally buffered
299 subterranean aquatic habitats. Physiological tests suggested that certain species have lost
300 the mechanisms for withstanding thermal variation, while certain others have not (Mathieu,

301 1968; Issartel et al., 2005; Colson-Proch et al., 2010; Mermillod-Blondin et al., 2013).
302 Moreover, an intra-specific variability in the thermal performance across different
303 populations of *Niphargus rhenorhodanensis* Schellenberg was demonstrated (Colson-
304 Proch et al., 2009). Some of this variability may be the result of different cave habitats. For
305 example, epikarst (an SSH) inhabitants face a wider range of temperatures than do deep
306 cave inhabitants (see Pipan et al., 2011). One would expect species facing this increased
307 range of temperatures to have an increased thermal tolerance, but there are no data to
308 directly bear on this point. It seems clear that thermal tolerance is necessarily species-
309 specific, and the resulting bioindicator potential should be evaluated on a case-by-case
310 basis.

311 Apart from thermal tolerance, it is worth noting that air moisture content (i.e. humidity)
312 is one of the most important limiting factors for terrestrial cave obligate species (Howarth,
313 1980, 1983; Simões et al., 2015). For example, Howarth (1980) tested in laboratory the
314 longevity of spiderlings of *Lycosa howarthi* Gertsch (Araneae: Lycosidae) at three distinct
315 values of relative humidity (100%, 95%, and 90%). At 90% the longevity dropped to one-
316 fourth of the mean value at 100% (15.4 ± 0.9 versus 61.8 ± 1.3 days), pointing toward a
317 pronounced sensitivity to saturation deficit. Accordingly, the maintenance of high humidity
318 levels appears to be essential for the survival of different troglobionts. This is generally
319 explained by the high cuticular permeability of many species, associated with a low
320 resistance to desiccation (Howarth, 1980, 1983; Hadley et al., 1981). As previously
321 explained, in caves from regions with limited water infiltration, relative humidity of cave
322 environments may be reduced as a consequence of the cave temperature increase.
323 However, the impacts associated to the alteration of relative humidity due to increased
324 temperature is rather limited when compared to role of infiltrating water in karst (Eraso,
325 1962). Nevertheless, in many regions of the planet, such as the Mediterranean, it adds on

326 top of the decrease in precipitation (Xoplaki et al., 2004) that is reducing infiltration of
327 water in karst, pushing caves towards lower relative humidity scenarios. Consequently,
328 drops in the relative humidity in some regions of the planet are likely to play a critical role
329 in the species response of subterranean species to climate change (Shu et al., 2013).

330

331 **(3) Eco-evolutionary response to climate change**

332 Despite the predicted and observed extinction of different taxa across terrestrial and
333 aquatic biomes (Thomas et al., 2004, Cahill et al., 2013), Bellard et al. (2012) underlined
334 how species can respond to climate change by shifting their climatic niche along three
335 non-exclusive axes: time (e.g. phenology), space (e.g. range) and self (e.g. physiology).
336 However, studies observing eco-evolutionary responses mostly concern surface
337 organisms, while subterranean species may not be able to adapt in the same way. As a
338 rule of thumb, subterranean species can theoretically couple with climatic alterations only
339 by shifting their distributional range (i.e. spatial information) or by adapting to the new
340 environmental conditions (i.e. physiological information). It must be added that it is difficult
341 to integrate temporal information as phenology in caves is not directly linked to climatic
342 factors (e.g. light, temperature; Figure 2).

343 If the dispersal capacity is enough to accompany the spatial change in
344 temperatures, one of the most common response of surface organisms to climate change
345 is the altitudinal and/or latitudinal shift of distribution ranges (Parmesan and Yohe, 2003;
346 Chen et al., 2011). However, most subterranean systems are geographically isolated,
347 acting as islands for many species (e.g., Cardoso, 2012; Niemiller et al., 2013; Fattorini et
348 al., 2016; Rizzo et al., 2017). This ecological feature, together with physiological
349 constraints, caused an extreme reduction in the dispersal potential of most troglobionts
350 (Bohonak, 1999). Indeed, as discussed in Juan et al. (2010), a breadth of studies

351 uncovered pronounced genetic structuring and low gene flow between populations
352 inhabiting different caves. Thus, long range dispersal events in troglobionts are extremely
353 unlikely and, in fact, available future projections point at reductions in troglobiont ranges
354 rather than range expansions or shifts (Sánchez-Fernández et al., 2016; Mammola et al.,
355 2018). In this respect, due to the same kind of barriers inhibiting local migrations,
356 altitudinal shifts may be equally unlikely. However, it is worth noting that isolation between
357 caves should be theoretically higher for troglobionts than for stygobionts, as subterranean
358 waters present broader connections than subterranean terrestrial habitats (Christman and
359 Culver, 2001), often resulting in aquatic subterranean species having wider ranges than
360 terrestrial ones (Lamoreaux, 2004). Also, it has been recently shown that adaptation to
361 subterranean habitats is not always a one-way evolutionary path, with subterranean
362 species being occasionally able to recolonise and widely disperse in surface habitats
363 (Prendini et al., 2009, Copilas-Ciocianu et al., 2018).

364 At a smaller scale, in response to climate change cave species could
365 theoretically change their spatial distribution inside the cave system itself (Fejér and
366 Moldovan, 2013; Mammola et al., 2015, 2017; Lunghi et al., 2017). Evidence suggests that
367 a number of subterranean species are indeed able to seasonally migrate toward greater
368 depths and vice versa (e.g., Juberthie, 1969; Crouau-Roy et al., 1992; Tobin et al., 2013).
369 However, a permanent shift in the species spatial niche toward greater depths may be less
370 likely, because this would affect the general energetic needs, as the energy input far from
371 the surface is generally scarcer especially in temperate oligotrophic caves (Gers, 1998;
372 Souza-Silva et al., 2011; Venarsky et al., 2014). Moreover, most of specialised
373 subterranean arthropods are confined in caves lacking climatic heterogeneity to be
374 exploited (Figure 2).

375 If enough genetic variability is encompassed by a population, allowing for a change of
376 dominant traits over time, adaptive evolution of physiology may be the best response to
377 climate warming (Bradshaw and Holzapfel, 2006; Visser, 2008; Williams et al., 2008). In
378 particular, physiological adaptation to increasing temperatures has been reported in
379 surface organisms, resulting in increased metabolic rate and faster growth (Hughes,
380 2000). Although physiological modifications are hard to be measured or predicted,
381 previous studies suggest that subterranean organisms exhibit decreased metabolic
382 plasticity, i.e., show far less elevation of metabolism than their close surface relatives in
383 response to higher temperatures (Dresco-Derouet, 1959; Vandel, 1965; Hervant and
384 Mathieu, 1997). Indeed, habitat specialists often present low functional variability due to
385 specialisation (but see Faille et al., 2010; Juan et al., 2010; Ribera et al., 2010). This in
386 turn limits the evolutionary potential even within large populations (Kellermann et al.,
387 2006). With a relatively stable habitat and restricted distribution, genetic variability of cave
388 populations is in fact often very low (Juan et al., 2010; but see Cieslak et al., 2014; Stern et
389 al., 2017). In addition, cave species typically have low reproductive rates, slow
390 growing/maturing and long life-span (Voituron et al., 2011). These characteristics generally
391 constrain rapid evolutionary change (McKinney, 1997).

392

393 **(4) Inter-connection with other systems**

394

395 The arguments presented in the previous section illustrate the potential eco-evolutionary
396 responses of cave species to climate change within the subterranean domain. However, it
397 is worth noting that most subterranean habitats are semi-closed systems, thus
398 interconnected and strongly dependent of other environments, especially surface habitats.

399

400 Being light deficient, the subterranean ecosystem is strongly dependent from the
outside ecosystems providing the fundamental energy inputs for its maintenance (Gibert

401 and Deharveng, 2002)—although chemolithotrophic organisms may account for primary
402 production within caves (Northup and Lavoie, 2001). Trophic inputs mainly consist of
403 organic materials passively transported underground, as well as by active migration of
404 animals within some caves. Consequently, energy flow in a typical subterranean habitat is
405 strongly influenced by seasonal fluctuations (Culver and Pipan, 2009) and the supply of
406 organic matter might also increase with current surface land-use changes (Wilhelm et al.,
407 2006). Phenological shifts—the advancement or postponing of annual phenomena—in
408 relation to global change have been extensively documented in surface species (Peñuelas
409 and Filella, 2001), especially in plants (Cleland et al., 2007; Wolkovich et al., 2012). It is
410 thus theoretically expected that the amount and timing of allochthonous energy inputs in
411 caves will change accordingly, with direct effects on the subterranean biota.

412 It is also well documented how climate changes will enhance invasion
413 processes, causing the introduction and spread of alien species (Bellard et al., 2013),
414 which are expected to affect cave biology (Wynne et al., 2014). Accordingly, several
415 studies have documented the potential recent spread of pathogen fungi in terrestrial
416 subterranean habitats (Escobar et al., 2014) or of alien species in marine caves
417 (Gerovasileiou et al., 2016). Furthermore, dramatic modification of surface habitats (e.g.,
418 aridification and deforestation), may also induce changes in the hydrological regimes of
419 caves, with consequent further degradation of the cave ecosystem (Trajano et al., 2009,
420 Bichuette and Trajano, 2010).

421 From a slightly different perspective, it is likely that some soil and surface
422 organisms may exploit subterranean environments, especially cave entrances and SSHs,
423 as refugial area in a climate change scenario. Indeed, it can be argued that the critical
424 difference between caves or other subterranean habitats and surface habitats is that
425 temperature extremes are buffered. If these extremes are what constitute a physiological

426 challenge, then these habitats may serve as a refuge. For instance, different soil
427 arthropods (e.g. springtails, woodlouse) may find more favourable conditions (e.g. lower
428 desiccation level, lower predation level) in the subterranean habitats than in surface
429 habitats (Fernandes et al., 2016; Mammola et al., 2016). Similarly, arthropods adapted to
430 cold environments may find safer places for survival in some subterranean habitats as in
431 karst areas (Raschmanova et al., 2015).

432 These examples do not intend to be exhaustive, but we rather aim to highlight
433 the importance of considering the deep relation between caves and other ecosystems, and
434 thus to consider the reciprocal interaction between the underground and the above-ground
435 world. However, in lack of specific studies involving the collaboration of cave-based
436 scientists and ecologists operating in other research fields, most of these interactions are
437 still difficult to disclose and predict.

438

439 **IV. FUTURE DIRECTIONS**

440 We have discussed that caves represent remarkable examples of natural laboratories in
441 which the climatic conditions are as homogeneous as the one that could be obtained in a
442 laboratory. Thus, in contrast with fluctuating surface temperatures, temperature
443 measurements in caves allow researchers to readily detect temperature variations related
444 to climate warming (see, e.g., Fejér and Moldovan, 2013; Šebela et al., 2015; Domínguez-
445 Villar et al., 2015). Currently monitoring programs in caves mostly involves the analysis of
446 speleothems, which requires a single visit to obtain a sample (Pipan et al. 2018). Indeed,
447 the sheltered environment in which speleothems grow, and their capacity to preserve even
448 sub-annual climatic events, offers a certain potential for their use as climatic archives of
449 the Anthropocene (Fairchild and Frisia, 2014; Fairchild, 2017; Waters et al., 2017). On the
450 other hand, long-term monitoring programs within karst settings are currently very rare

451 (Brookfield et al., 2016; Pipan et al., 2018); we thus point out that monitoring programs
452 should be established for relevant abiotic and biotic variables—see, e.g., the notable case
453 of Postojna cave (Šebela and Turk, 2011; Šebela et al., 2015; Pipan et al., 2018).

454 With small distribution ranges (due to the isolation among subterranean
455 systems), small population size (due to low energy availability), and restricted habitat (by
456 definition), cave organisms often fulfil all forms of rarity (Rabinowitz, 1981; Gaston, 1994).
457 Species with small range and abundance are expected to have low adaptive potential in
458 the face of environmental change (Williams et al., 2008). Subterranean species are in fact
459 prevalent on conservation priority lists (Martín et al., 2010; Cardoso et al., 2011; IUCN,
460 2017). We have shown that a significant number of subterranean species cannot
461 accommodate to changing conditions by dispersal or microhabitat use, and the only
462 possibility to cope with climate change will be to persist *in situ*. However, if natural
463 populations cannot adapt to environmental change by means of adaptive shifts, they
464 should be more prone to local extinction due to the direct effects of climate change than
465 their surface counterparts. We therefore advocate the need for long-term monitoring
466 programs for cave species, namely those with high threat status.

467 Nevertheless, it is worth noting that not all subterranean species are likely to become
468 extinct in light of a warming climate. Depending on the organisms under consideration and
469 its degree of subterranean adaptation, a variety of possible responses to an altered
470 climate has to be expected. Whilst a great deal of attention is paid to troglobionts, there
471 are high-dispersal subterranean species which may, on the contrary, be able to respond
472 with dispersal to climatic alterations (e.g., Mammola and Isaia, 2017). We have also
473 discussed that movements of faunas from surface to subterranean habitats, and vice
474 *versa*, can be expected. The confrontation of these opposite displacements, even if they
475 are currently rare, might become a research priority in the next future, because of the rapid

476 changes observed in surface habitats and the loss of climatic stability of subterranean
477 ones. In that context, analytical approaches typically used in landscape and island
478 ecology—e.g. source-sink and metapopulations dynamics (Pipan et al., 2010; Moldovan et
479 al., 2012; Fattorini et al., 2016; Trajano and de Carvalho, 2017)—will become helpful to
480 document the amplitude of these reciprocal movements.

481 A general caveat to consider in discussing this topic is that studies conducted so far
482 have been mostly correlative, meaning that a causal attribution of recent biological trends
483 to climate change in subterranean species is currently lacking. Although it is difficult to
484 overcome this impediment, it is likely that advances can be done both by studying multiple
485 subterranean systems and by combining multiple lines of evidence (Mammola and Leroy,
486 2018; Pipan et al., 2018). For instance, the simultaneous use of physiological data, genetic
487 evidence and forecast derived from statistical projections has a great deal of potential.
488 There is little doubt that this integrated approach would greatly benefit the study of climate
489 change dynamics in deep subterranean habitats, prompting a fast and significant advance
490 in knowledge.

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494

V. CONCLUSIONS

495 (1) Due to their intrinsic environmental stability, subterranean ecosystems are unique
496 models for the study of global change biology. However, monitoring programs of caves
497 abiotic conditions are rare and we still have a limited understanding of the mechanisms
498 that underlie survival of the most adapted species to climatic and environmental
499 alterations, even more so in tropical regions.

500
501 (2) Most subterranean species are expected to have fine-tuned their thermal physiology to
502 the narrow and stable condition of their habitats, and should have low adaptive potential in

503 the face of environmental change. The contrasting response obtained on different animal
504 groups suggest that the sensitivity of subterranean species to temperature variations is
505 likely to significantly differ depending on phylogeny, evolutionary history and degree of
506 subterranean adaptation.

507

508 (3) Subterranean communities are relatively depauperate, with less redundancy in
509 ecological roles among species. Disruption of trophic webs and species interactions is
510 therefore much likely in such communities.

511

512 (4) Some external organisms may be able to exploit subterranean environments as refugia
513 in a climate change scenario. However, if caves can be seen as shelters for preadapted
514 surface and soil species in the face of rapid climate change, they may become dead-end
515 traps for their current inhabitants, being characterised by a poor dispersal ability a low
516 adaptation potential.

517

518 (5) When thinking about the ecology of subterranean ecosystems, it is crucial to consider
519 their interconnections with other environments, especially surface habitats. Studies
520 involving the collaboration of cave-based scientists with ecologists operating in other
521 research fields are likely to produce a more realistic picture of the effects of climate change
522 in the underground world.

523

524 (6) We encourage renewed effort to better characterise the dynamic processes and
525 challenges associated with global climate change in deep subterranean habitats. Evidence
526 arising from such studies would not exclusively be important for the conservation of the
527 subterranean fauna, but more generally they would contribute to increase our

528 understanding about the effects of rapid global changes on the wider variety of
529 ecosystems exhibiting with low thermal seasonality, such as soils and deep sea waters.

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1093 **TABLES & BOXES**

1094 **Box 1. Glossary**

1095 **Shallow Subterranean Habitats (acronym SSH).** The aphotic subterranean habitats
1096 close to the surface, harbouring species showing subterranean adaptations. These include
1097 small emerging drainages (hypotelminorheic habitats), small cavities in the uppermost
1098 karst layers (epikarst), lava tubes, deep soil and litter strata, talus slopes, surface cracks
1099 and fissures (*Milieu Souterrain Superficiel*; MSS) (Culver & Pipan, 2014).

1100 **Subterranean habitats.** All the aphotic subterranean spaces harbouring species showing
1101 adaptation to subterranean life (troglomorphic traits). These include human-accessible
1102 natural subterranean spaces (i.e. “proper caves” *sensu* Curl, 1964), network of fissures
1103 with sizes smaller than the human-scale and artificial subterranean habitats (mines,
1104 blockhouses, cellars, etc.) (Culver & Pipan, 2009).

1105 **Troglobiont/Stygobiont.** A terrestrial (troglo-) or aquatic (stygo-) species having its source
1106 population in the subterranean habitat (Trajano & Carvalho, 2017). Usually shows
1107 pronounced adaptation to the subterranean conditions.

1108 **Troglophile/Stygophile.** A terrestrial (troglo-) or aquatic (stygo-) species forming source
1109 populations both in subterranean and surface habitats (Trajano & Carvalho, 2017).

1110 **Troglomorphism.** The suite of morphological, physiological and behavioral adaptations to
1111 the subterranean habitat (Christiansen, 2012). Examples of troglomorphic traits include
1112 pigment loss, eye regression and parallel increase in the development of other receptors
1113 and sensory organs, reduction in metabolic rate, increase in life span.

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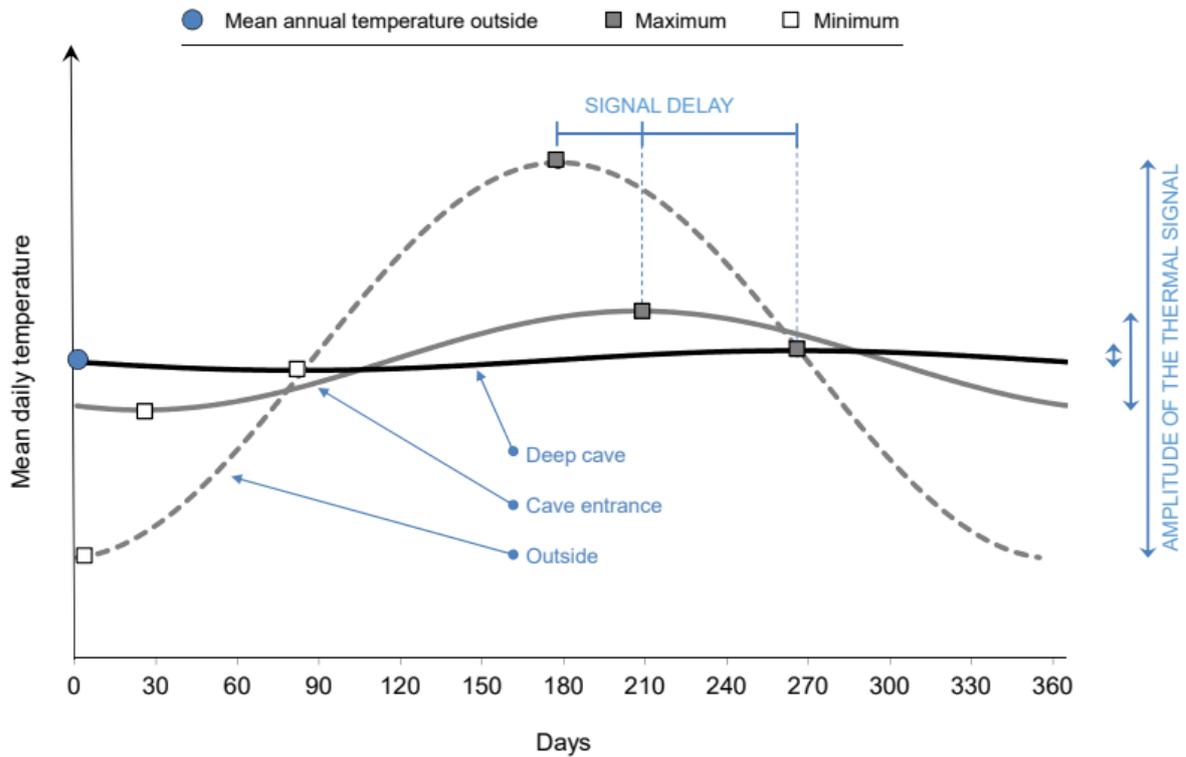
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1118 **Table 1.** A selection of recent experimental studies investigating the response of
 1119 subterranean organisms to global climate change. Only articles written in English are
 1120 reported.

Area	Model organism(s)	Ecological classification	Method(s)	Observed/predicted effect(s)	Reference
Europe	Beetles (various genera)	Troglobiont	Indirect evidence extrapolated from species accumulation curves	Expansion of the spatial niche of cave species toward the surface—i.e., into superficial cavities and Shallow Subterranean Habitats.	Brandmayr et al., 2013
Pyrenees (France, Spain)	Beetles (gen. <i>Troglocharinus</i> + outgroups)	Troglobiont	Physiological tests	i) Most lineage have lost some of the thermoregulatory mechanisms common in temperate insects ii) Broader thermal tolerance than expected by habitat climatic seasonality	Rizzo et al. 2015
Pyrenees (France, Spain)	Beetles (Tribe Leptodirini)	Troglobiont	i) Species Distribution Modelling ii) Molecular data iii) Physiological test	A slight future decline in habitat suitability, but a broad thermal tolerance in most subterranean species	Sanchez-Fernandez et al., 2016
Jura Mountains (France)	Crustacean (gen. <i>Niphargus</i>)	Stygobiont	Expression gene profile	Subterranean species maintain the expression of heat shock protein	Colson-Proch et al. 2010
Western Alps (Italy)	Spiders (gen. <i>Troglohyphantes</i>)	Troglobiont	Species Distribution Modelling	i) Future decline in habitat suitability ii) Potential local extinction in a number of populations	Mammola et al., 2018
Jura Mountains (France)	Aquatic isopods (gen. <i>Proasellus</i>)	Stygobiont	Physiological test	i) Some species are sensitive to changes in temperature ($\pm 2^{\circ}\text{C}$), although one exhibited a higher thermal tolerance breadth (11°C) ii) Extinction risk of groundwater endemics is higher than that of widely distributed species (inferred).	Mermillod-Blondin et al., 2013.
Medio Valdarno porous aquifer (Italy)	Aquatic copepod (<i>Diacyclops belgicus</i> Kiefer)	Stygophile/Stygobiont	Physiological test	No significant variations in the oxygen consumptions to a $+3^{\circ}\text{C}$ change in temperature	Di Lorenzo & Galassi, 2017
Great Britain	Spiders (gen. <i>Meta</i>)	Troglophile	Species Distribution Modelling	Future poleward shift in the distribution ranges	Mammola 2017
Europe	Spiders (gen. <i>Meta</i>)	Troglophile	Species Distribution Modelling	i) Future poleward shift in the distribution ranges ii) Niche overlap between congeneric species	Mammola & Isaia, 2017

1121

1122 **FIGURE LEGENDS**



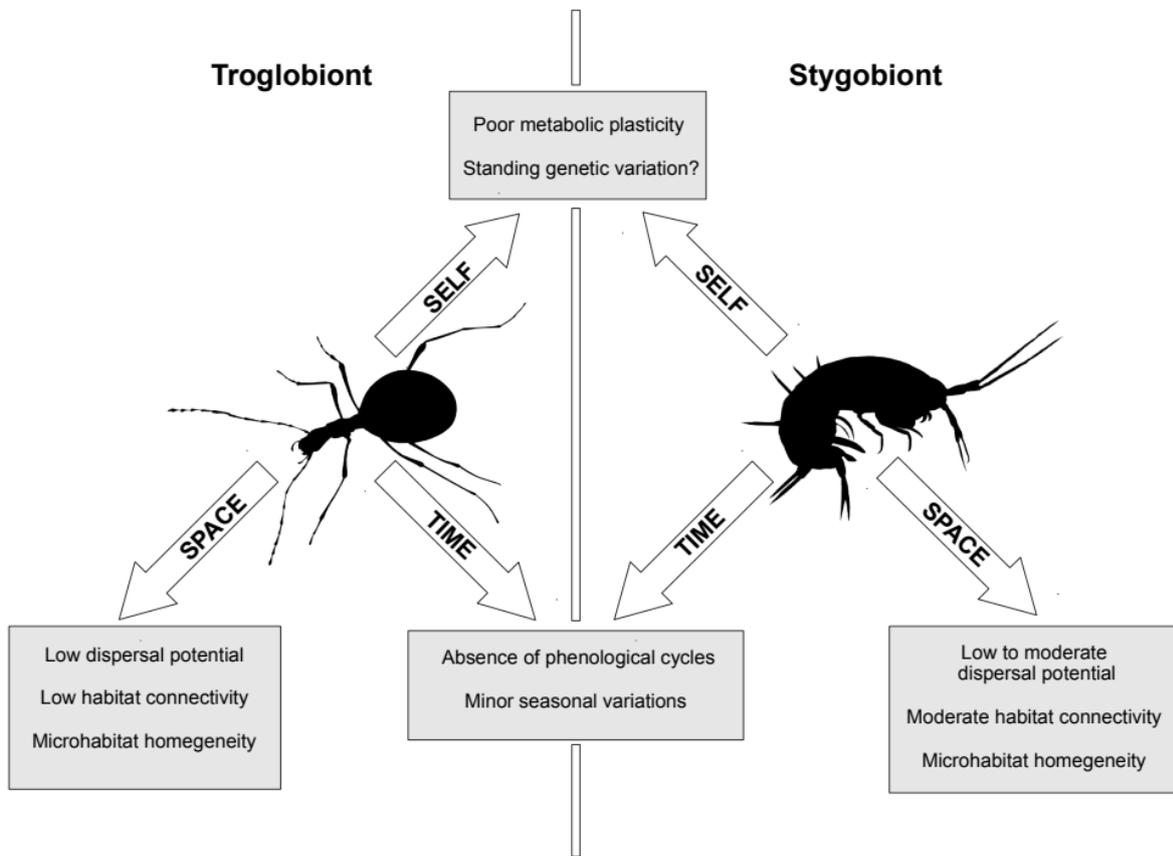
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1125 **Figure 1. The (theoretical) sinusoidal conduction dominating the thermal signal of a**
 1126 **cave.** Lines show the theoretical annual trend of mean daily temperatures deep inside the
 1127 cave (filled black line), in the vicinity of the cave entrance (filled grey line) and outside the
 1128 cave (dotted line). Note the reduction of the signal amplitude with increasing depths (i.e.
 1129 buffering effect), the delay of the signal (i.e. thermal inertia), and the strict correspondence
 1130 between the inner temperature and the mean annual temperature outside (highlighted in
 1131 the y-axis).

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1133



1136 **Figure 2. Eco-evolutionary response to climate change.** Potential shifts in the thermal
 1137 niche of a hypothetical troglobiont and stygobiont along three non-exclusive axes

1138 r
 1139 e
 1140 p
 1141 r
 1142 e
 1143 s
 1144 e
 1145 n
 1146 t
 1147 i
 1148 n