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

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

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

In order to minimize confounding effects, scientists have often used isolated ecosystems—and specific organisms within them—as models to unravel ecological responses to recent climate alterations, upscaling results and conclusions to a wider range of systems and organisms. Under this perspective, mountain summits, oceanic islands, lakes and other confined habitats have offered insightful models for determining the effects of climate change on biodiversity in situ (Hortal et al., 2014; Warren et al., 2015; Whittaker et al., 2017; Itescu, 2018; Mammola, 2018). Even if the potential of subterranean habitats as ideal biological laboratories has been long ago foreseen (Barr, 1968; Poulson and White, 1969; Culver, 1982), little has been written about the specific contribution of cave-based studies to the understanding of patterns and processes in global change biology (Mammola, 2018; Sánchez-Fernández et al., 2018). As a direct consequence, most syntheses focusing on the effect of climate change on ecosystems did not feature terrestrial caves in the potential study systems (e.g. Walther et al., 2002; Parmesan and Yohe, 2003; Scholze et al., 2006). However, there exists an emerging trend in
environmental, physical, and ecological studies alike to use caves and other subterranean habitats as models for unraveling current climate change dynamics. Recent relevant studies focused on the role of climatic alterations on the geophysical components of the cave environment (Domínguez-Villar et al., 2015; Colucci et al., 2016; Pipan et al. 2018), the potential of caves as methane-sinks (Fernandez-Cortes et al., 2015) and the general effects of global temperature increase on different subterranean animals (Colson-Proch et al., 2010; Lencioni et al., 2010; Brandmayr et al., 2013; Mermillod-Blondin et al., 2013; Rizzo et al., 2015; Sánchez-Fernández et al., 2016; Mammola and Isaia, 2017; Di Lorenzo and Galassi, 2017; Mammola et al., 2018), and microorganisms (Brielmann et al., 2009, 2011; Gribler et al., 2016).

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

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

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

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

iv) subterranean organisms have evolved a suite of morphological and physiological adaptations to thrive under the peculiar environmental conditions found in caves, which are often convergent even across phylogenetically distant groups (Culver and Pipan, 2009; Juan et al., 2010; Protas and Jeffrey, 2012).
However, a lack of synthesis on this topic is possibly holding back the establishment of caves as standard models for the study of the effects of climate change in the field. By bringing together literature focusing on cave biology, ecology, and physics that were previously disconnected, we illustrate the rationale supporting the use of subterranean habitats as ideal model for studies of global change biology. We describe the potential effects of the anthropogenic climate alterations on the abiotic and the biotic components of the cave ecosystem, giving special reference to the cave climate, subterranean organisms and the interconnection between caves and other ecosystems (surface and soil). We focused here mostly on terrestrial subterranean habitats and only partly on groundwater systems (see Green et al., 2011; Taylor et al., 2013 for more arguments on groundwaters). We did not considered marine caves. A definition of the jargon used in the text is presented in Box 1. Throughout the text, the term “cave” is used to refer to the extended network of fissures and cracks that permeate most substrates, even if their size is not commensurable to the human-scale (Romero, 2012).

II. ABIOTIC FEATURES

(1) Subterranean climate

A wealth of literature documents the ecological peculiarity of the subterranean realm, and how distinct it is from surface habitats. Whilst the absence of solar radiation is possibly the most crucial factor conditioning the ecology of subsurface habitats (Culver and Pipan, 2015), the most important feature that corroborates the idea that caves are ideal laboratories for the study of climate change in natural environment is their unique climatic stability. Indeed, deep subterranean habitats have, in most cases, an almost constant temperature over the year and a relative humidity often close to saturation (Cigna, 2002; Badino, 2010).
The cave temperature is coupled with surface atmosphere temperature. The surface ground thermal signal is transferred by conduction through the bedrock, eventually reaching the depth of the cave (Domínguez-Villar et al., 2013). External air penetrating caves rapidly reaches a nearly constant temperature along the entrance sectors due to the buffering effect associated to the increase of relative humidity, and the progressive equilibration with the temperature of the rock (Wigley and Brown, 1971; Wigley and Brown, 1976). As a result of this process, mean air temperature in cave interiors correspond almost exactly to the average annual value of the outside temperature (Moore, 1964, Moore and Nicholas, 1964; Figure 1).

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

One may argue about the possible effect of the geothermal gradient, as temperature below the surface slowly increases with the vertical distance under the
surface (ca. 30 °C/km away from tectonic plates). However, the geothermal gradient is generally so small that tens to hundreds of meters are required to notice a shift in the thermal equilibrium between the external air temperature and the cave one (Luetscher and Jeannin, 2004). Moreover, in karst regions the geothermal gradient is further buffered by the advection of groundwater (Bögli, 1980), limiting the sources of heat variability affecting caves (Badino, 2010).

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

(2) Climate change and the thermal inertia of caves

Theoretical models have predicted that climate warming will impact temperature in caves (Badino, 2004; Covington and Perne, 2015), and model-data comparisons have confirmed such scenario (Domínguez-Villar et al., 2015; Šebela et al., 2015; Pipan et al., 2018), indicating that anthropogenic climate alterations are currently modifying the subterranean microclimate. Most caves show fairly stable air temperature in their interiors, as a result of the slow mechanism conveying underground the outer thermal signals by conduction. Consequently, there is lag-time between the air temperature increase recorded at the surface and its record in cave interiors. The delay depends on the cave depth (that is, the thickness of the rock above the cave) and on the duration of the anomaly (Domínguez-Villar, 2012). In the pioneer synthesis of Moore and Nicholas (1964), the authors speculated with delay times in the order of hundreds to thousands of years for climate anomalies at the surface to reach the deeper sectors of karst massifs. In a study set in a Slovenian cave located 37 m under the surface, the signal of the onset of global warming
was recorded 20 years later (Domínguez-Villar et al., 2015). However, it should be noticed that at the same site, cave conduits located closer to the surface were expected to record thermal anomalies earlier, whereas cave conduits located deeper into the karst massif are unlikely to have registered the thermal impact of climate warming yet.

(3) Potential implications of subterranean warming on abiotic features

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

Concentration of CO$_2$ in caves is a major control on the dissolution and precipitation of carbonates. However, at the inter-annual timescale, the CO$_2$ concentration does not depend on the cave temperature but on the soil CO$_2$ production and cave ventilation (Fairchild and Baker, 2012). Therefore, subtle changes in cave temperature are not expected to produce large geophysical changes.

However, the warming rate during the last decades is unusually large compared to changes recorded during previous millennia (Moberg et al., 2005), affecting the magnitude of thermal change per unit of time. Due to the required time to transfer the external thermal signal to caves, a thermal decoupling exists between the external temperature and the cave interior temperature during a climate change period. This decoupling affects the seasonal air flow in caves that, in most cases, is driven by gradients in air density, depending, in turn, from temperature differences between external
atmosphere and the cave interior. Thus, in most caves, enhanced ventilation occurs when the external temperature is below the cave temperature, whereas limited ventilation is recorded during the rest of the year (e.g., Kowalczk and Froelich, 2010). Under a scenario of thermal decoupling, the thermal difference between the external and the cave atmosphere increases during winters, and decreases during summers. This large thermal decoupling may be affecting the duration of air flow regime in caves, causing longer periods of enhanced ventilation and reducing the periods with limited ventilation. Despite their potential implication for cave environments and their importance in determining seasonal concentrations of CO$_2$ and other cave environmental parameters, changes in the duration of seasonal air flows have not been studied in detail yet.

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

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

(1) Subterranean organisms

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

(2) Potential species sensitivity to climate change

While much attention has been given to the effects of global climate change on surface organisms, communities and ecosystems, studies about the influence of temperature increase on subterranean biota are still at their infancy (Table 1). The contrasting response obtained on different animal groups indicate that the sensitivity of subterranean species to altered climatic conditions is likely to depend on phylogeny, evolutionary history and by the degree of subterranean adaptations or other functional traits.
The most important, yet heterogeneous, evidence about the sensitivity of subterranean species to the ongoing climate change derives from physiological tests. As a direct result of a long evolutionary history in a thermally stable environment, it is theoretically expected that most subterranean species should exhibit a stenothermal profile (sensu Huey and Kingsolver, 1989), which maximises their physiological performance over a narrow temperature range. However, in a climate change perspective, adaptation to narrow ranges of temperature turns out to be a strong limitation. Indeed, while most invertebrates living in the vicinity of the surface have the capacity to withstand temperature variations, most deep subterranean species lack such thermoregulatory mechanisms (Novak et al., 2014; Raschmanová et al., 2018). In certain species, even a positive or negative variation of 2°C in respect to their habitat temperature proved to be fatal (Mermillod-Blondin et al., 2013). However, the figure remains rather crude, as most studies conducted so far focused on single model taxa and thus lacked a wider phylogenetic perspective (but see Pallarés et al., 2019). For instance, tests carried on subterranean beetles are divergent, pointing out a wide thermal niche for numerous species of Cholevidae (Rizzo et al., 2015; Sánchez-Fernández et al., 2016). In addition, it has been shown that two cold stenothermal cave-dwelling beetles in the genus Neobathyscia (Coleoptera: Catopidae) have the ability to synthesise heat shock proteins, which provide resistance to heat exposure (Bernabò et al., 2011). The same kind of pattern (inducible HSP70 heat shock response) has been observed in subterranean amphipods in the genus Niphargus (Crustacea: Amphipoda) (Colson-Proch et al., 2010).

Also, contrasting results were obtained by different authors focusing on survival and performance patterns in stygobiont crustaceans living in thermally buffered subterranean aquatic habitats. Physiological tests suggested that certain species have lost the mechanisms for withstanding thermal variation, while certain others have not (Mathieu,
Moreover, an intra-specific variability in the thermal performance across different populations of *Niphargus rhenorhodanensis* Schellenberg was demonstrated (Colson-Proch et al., 2009). Some of this variability may be the result of different cave habitats. For example, epikarst (an SSH) inhabitants face a wider range of temperatures than do deep cave inhabitants (see Pipan et al., 2011). One would expect species facing this increased range of temperatures to have an increased thermal tolerance, but there are no data to directly bear on this point. It seems clear that thermal tolerance is necessarily species-specific, and the resulting bioindicator potential should be evaluated on a case-by-case basis.

Apart from thermal tolerance, it is worth noting that air moisture content (i.e. humidity) is one of the most important limiting factors for terrestrial cave obligate species (Howarth, 1980, 1983; Simões et al., 2015). For example, Howarth (1980) tested in laboratory the longevity of spiderlings of *Lycosa howarthi* Gertsch (Araneae: Lycosidae) at three distinct values of relative humidity (100%, 95%, and 90%). At 90% the longevity dropped to one-fourth of the mean value at 100% (15.4±0.9 versus 61.8±1.3 days), pointing toward a pronounced sensitivity to saturation deficit. Accordingly, the maintenance of high humidity levels appears to be essential for the survival of different troglobionts. This is generally explained by the high cuticular permeability of many species, associated with a low resistance to desiccation (Howarth, 1980, 1983; Hadley et al., 1981). As previously explained, in caves from regions with limited water infiltration, relative humidity of cave environments may be reduced as a consequence of the cave temperature increase. However, the impacts associated to the alteration of relative humidity due to increased temperature is rather limited when compared to role of infiltrating water in karst (Eraso, 1962). Nevertheless, in many regions of the planet, such as the Mediterranean, it adds on
top of the decrease in precipitation (Xoplaki et al., 2004) that is reducing infiltration of water in karst, pushing caves towards lower relative humidity scenarios. Consequently, drops in the relative humidity in some regions of the planet are likely to play a critical role in the species response of subterranean species to climate change (Shu et al., 2013).

(3) Eco-evolutionary response to climate change

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

If the dispersal capacity is enough to accompany the spatial change in temperatures, one of the most common response of surface organisms to climate change is the altitudinal and/or latitudinal shift of distribution ranges (Parmesan and Yohe, 2003; Chen et al., 2011). However, most subterranean systems are geographically isolated, acting as islands for many species (e.g., Cardoso, 2012; Niemiller et al., 2013; Fattorini et al., 2016; Rizzo et al., 2017). This ecological feature, together with physiological constraints, caused an extreme reduction in the dispersal potential of most troglobionts (Bohonak, 1999). Indeed, as discussed in Juan et al. (2010), a breadth of studies
uncovered pronounced genetic structuring and low gene flow between populations inhabiting different caves. Thus, long range dispersal events in troglobionts are extremely unlikely and, in fact, available future projections point at reductions in troglobiont ranges rather than range expansions or shifts (Sánchez-Fernández et al., 2016; Mammola et al., 2018). In this respect, due to the same kind of barriers inhibiting local migrations, altitudinal shifts may be equally unlikely. However, it is worth noting that isolation between caves should be theoretically higher for troglobionts than for stygobionts, as subterranean waters present broader connections than subterranean terrestrial habitats (Christman and Culver, 2001), often resulting in aquatic subterranean species having wider ranges than terrestrial ones (Lamoreaux, 2004). Also, it has been recently shown that adaptation to subterranean habitats is not always a one-way evolutionary path, with subterranean species being occasionally able to recolonise and widely disperse in surface habitats (Prendini et al., 2009, Copilas-Ciocianu et al., 2018).

At a smaller scale, in response to climate change cave species could theoretically change their spatial distribution inside the cave system itself (Fejér and Moldovan, 2013; Mammola et al., 2015, 2017; Lunghi et al., 2017). Evidence suggests that a number of subterranean species are indeed able to seasonally migrate toward greater depths and vice versa (e.g., Juberthie, 1969; Crouau-Roy et al., 1992; Tobin et al., 2013). However, a permanent shift in the species spatial niche toward greater depths may be less likely, because this would affect the general energetic needs, as the energy input far from the surface is generally scarcer especially in temperate oligotrophic caves (Gers, 1998; Souza-Silva et al., 2011; Venarsky et al., 2014). Moreover, most of specialised subterranean arthropods are confined in caves lacking climatic heterogeneity to be exploited (Figure 2).
If enough genetic variability is encompassed by a population, allowing for a change of dominant traits over time, adaptive evolution of physiology may be the best response to climate warming (Bradshaw and Holzapfel, 2006; Visser, 2008; Williams et al., 2008). In particular, physiological adaptation to increasing temperatures has been reported in surface organisms, resulting in increased metabolic rate and faster growth (Hughes, 2000). Although physiological modifications are hard to be measured or predicted, previous studies suggest that subterranean organisms exhibit decreased metabolic plasticity, i.e., show far less elevation of metabolism than their close surface relatives in response to higher temperatures (Dresco-Derouet, 1959; Vandel, 1965; Hervant and Mathieu, 1997). Indeed, habitat specialists often present low functional variability due to specialisation (but see Faille et al., 2010; Juan et al., 2010; Ribera et al., 2010). This in turn limits the evolutionary potential even within large populations (Kellermann et al., 2006). With a relatively stable habitat and restricted distribution, genetic variability of cave populations is in fact often very low (Juan et al., 2010; but see Cieslak et al., 2014; Stern et al., 2017). In addition, cave species typically have low reproductive rates, slow growing/maturing and long life-span (Voituron et al., 2011). These characteristics generally constrain rapid evolutionary change (McKinney, 1997).

(4) Inter-connection with other systems

The arguments presented in the previous section illustrate the potential eco-evolutionary responses of cave species to climate change within the subterranean domain. However, it is worth noting that most subterranean habitats are semi-closed systems, thus interconnected and strongly dependent of other environments, especially surface habitats. Being light deficient, the subterranean ecosystem is strongly dependent from the outside ecosystems providing the fundamental energy inputs for its maintenance (Gibert
—although chemolithotrophic organisms may account for primary production within caves (Northup and Lavoie, 2001). Trophic inputs mainly consist of organic materials passively transported underground, as well as by active migration of animals within some caves. Consequently, energy flow in a typical subterranean habitat is strongly influenced by seasonal fluctuations (Culver and Pipan, 2009) and the supply of organic matter might also increase with current surface land-use changes (Wilhelm et al., 2006). Phenological shifts—the advancement or postponing of annual phenomena—in relation to global change have been extensively documented in surface species (Peñuelas and Filella, 2001), especially in plants (Cleland et al., 2007; Wolkovich et al., 2012). It is thus theoretically expected that the amount and timing of allochthonous energy inputs in caves will change accordingly, with direct effects on the subterranean biota.

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

From a slightly different perspective, it is likely that some soil and surface organisms may exploit subterranean environments, especially cave entrances and SSHs, as refugial area in a climate change scenario. Indeed, it can be argued that the critical difference between caves or other subterranean habitats and surface habitats is that temperature extremes are buffered. If these extremes are what constitute a physiological
challenge, then these habitats may serve as a refuge. For instance, different soil arthropods (e.g. springtails, woodlouse) may find more favourable conditions (e.g. lower desiccation level, lower predation level) in the subterranean habitats that in surface habitats (Fernandes et al., 2016; Mammola et al., 2016). Similarly, arthropods adapted to cold environments may find safer places for survival in some subterranean habitats as in karst areas (Raschmanova et al., 2015).

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

IV. FUTURE DIRECTIONS

We have discussed that caves represent remarkable examples of natural laboratories in which the climatic conditions are as homogeneous as the one that could be obtained in a laboratory. Thus, in contrast with fluctuating surface temperatures, temperature measurements in caves allow researchers to readily detect temperature variations related to climate warming (see, e.g., Fejér and Moldovan, 2013; Šebela et al., 2015; Domínguez-Villar et al., 2015). Currently monitoring programs in caves mostly involves the analysis of speleothems, which requires a single visit to obtain a sample (Pipan et al. 2018). Indeed, the sheltered environment in which speleothems grow, and their capacity to preserve even sub-annual climatic events, offers a certain potential for their use as climatic archives of the Anthropocene (Fairchild and Frisia, 2014; Fairchild, 2017; Waters et al., 2017). On the other hand, long-term monitoring programs within karst settings are currently very rare
(Brookfield et al., 2016; Pipan et al., 2018); we thus point out that monitoring programs should be established for relevant abiotic and biotic variables—see, e.g., the notable case of Postojna cave (Šebela and Turk, 2011; Šebela et al., 2015; Pipan et al., 2018).

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

Nevertheless, it is worth noting that not all subterranean species are likely to become extinct in light of a warming climate. Depending on the organisms under consideration and its degree of subterranean adaptation, a variety of possible responses to an altered climate has to be expected. Whilst a great deal of attention is paid to troglobionts, there are high-dispersal subterranean species which may, on the contrary, be able to respond with dispersal to climatic alterations (e.g., Mammola and Isaia, 2017). We have also discussed that movements of faunas from surface to subterranean habitats, and vice versa, can be expected. The confrontation of these opposite displacements, even if they are currently rare, might become a research priority in the next future, because of the rapid
changes observed in surface habitats and the loss of climatic stability of subterranean ones. In that context, analytical approaches typically used in landscape and island ecology—e.g. source-sink and metapopulations dynamics (Pipan et al., 2010; Moldovan et al., 2012; Fattorini et al., 2016; Trajano and de Carvalho, 2017)—will become helpful to document the amplitude of these reciprocal movements.

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

V. CONCLUSIONS

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

(2) Most subterranean species are expected to have fine-tuned their thermal physiology to the narrow and stable condition of their habitats, and should have low adaptive potential in
the face of environmental change. The contrasting response obtained on different animal
groups suggest that the sensitivity of subterranean species to temperature variations is
likely to significantly differ depending on phylogeny, evolutionary history and degree of
subterranean adaptation.

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

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

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

(6) We encourage renewed effort to better characterise the dynamic processes and
challenges associated with global climate change in deep subterranean habitats. Evidence
arising from such studies would not exclusively be important for the conservation of the
subterranean fauna, but more generally they would contribute to increase our
understanding about the effects of rapid global changes on the wider variety of ecosystems exhibiting with low thermal seasonality, such as soils and deep sea waters.

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Box 1. Glossary

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

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

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

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

Troglomorphism. The suite of morphological, physiological and behavioral adaptations to the subterranean habitat (Christiansen, 2012). Examples of troglomorphic traits include pigment loss, eye regression and parallel increase in the development of other receptors and sensory organs, reduction in metabolic rate, increase in life span.
**Table 1.** A selection of recent experimental studies investigating the response of subterranean organisms to global climate change. Only articles written in English are reported.

<table>
<thead>
<tr>
<th>Area</th>
<th>Model organism(s)</th>
<th>Ecological classification</th>
<th>Method(s)</th>
<th>Observed/predicted effect(s)</th>
<th>Reference</th>
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<tbody>
<tr>
<td>Europe</td>
<td>Beetles (various genera)</td>
<td>Troglobiont</td>
<td>Indirect evidence extrapolated from species accumulation curves</td>
<td>Expansion of the spatial niche of cave species toward the surface—i.e., into superficial cavities and Shallow Subterranean Habitats.</td>
<td>Brandmayr et al., 2013</td>
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<tr>
<td>Pyrenees (France, Spain)</td>
<td>Beetles (gen. <em>Troglacharinus</em> + outgroups)</td>
<td>Troglobiont</td>
<td>Physiological tests</td>
<td>i) Most lineage have lost some of the thermoregulatory mechanisms common in temperate insects; ii) Broader thermal tolerance than expected by habitat climatic seasonality</td>
<td>Rizzo et al. 2015</td>
</tr>
<tr>
<td>Pyrenees (France, Spain)</td>
<td>Beetles (Tribe Leptodirini)</td>
<td>Troglobiont</td>
<td>i) Species Distribution Modelling; ii) Molecular data; iii) Physiological test</td>
<td>A slight future decline in habitat suitability, but a broad thermal tolerance in most subterranean species</td>
<td>Sanchez-Fernandez et al., 2016</td>
</tr>
<tr>
<td>Jura Mountains (France)</td>
<td>Crustacean (gen. <em>Niphargus</em>)</td>
<td>Stygobiont</td>
<td>Expression gene profile</td>
<td>Subterranean species maintain the expression of heat shock protein</td>
<td>Colson-Proch et al. 2010</td>
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<tr>
<td>Western Alps (Italy)</td>
<td>Spiders (gen. <em>Troglophyphantes</em>)</td>
<td>Troglobiont</td>
<td>Species Distribution Modelling</td>
<td>i) Future decline in habitat suitability; ii) Potential local extinction in a number of populations</td>
<td>Mammola et al., 2018</td>
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<tr>
<td>Jura Mountains (France)</td>
<td>Aquatic isopods (gen. <em>Proasellus</em>)</td>
<td>Stygobiont</td>
<td>Physiological test</td>
<td>i) Some species are sensitive to changes in temperature (±2°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).</td>
<td>Mermillod-Blondin et al., 2013.</td>
</tr>
<tr>
<td>Medio Valdarno porous aquifer (Italy)</td>
<td>Aquatic copepod (Diacyclops belgicus Kiefer)</td>
<td>Stygophile/Stygobiont</td>
<td>Physiological test</td>
<td>No significant variations in the oxygen consumptions to a +3°C change in temperature</td>
<td>Di Lorenzo &amp; Galassi, 2017</td>
</tr>
<tr>
<td>Great Britain</td>
<td>Spiders (gen. <em>Meta</em>)</td>
<td>Troglophile</td>
<td>Species Distribution Modelling</td>
<td>Future poleward shift in the distribution ranges</td>
<td>Mammola 2017</td>
</tr>
</tbody>
</table>
Figure 1. The (theoretical) sinusoidal conduction dominating the thermal signal of a cave. Lines show the theoretical annual trend of mean daily temperatures deep inside the cave (filled black line), in the vicinity of the cave entrance (filled grey line) and outside the cave (dotted line). Note the reduction of the signal amplitude with increasing depths (i.e. buffering effect), the delay of the signal (i.e. thermal inertia), and the strict correspondence between the inner temperature and the mean annual temperature outside (highlighted in the y-axis).
Figure 2. Eco-evolutionary response to climate change. Potential shifts in the thermal niche of a hypothetical troglobiont and stygobiont along three non-exclusive axes.