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

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Abstract

Scientists of different disciplines have recognized the valuable role of terrestrial caves as ideal natural laboratories in which to study multiple eco-evolutionary processes, from genes to ecosystems. Because caves are semi-closed systems characterized by a remarkable thermal stability and buffered from external variations, they 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 potential use of caves as standard models for the study of the recent climatic alteration. In this review, we illustrate the rationale supporting the use of subterranean habitats as ideal laboratories for studies of global change biology. In light of the results recently presented in scientific literature, we provide a critical evaluation of the studies describing the response of different subterranean organisms to temperature variations. Finally, we bring up a forward-looking view of prospects offered by cave studies for deepening our knowledge of the eco-evolutionary response of biological organisms to recent climate change. Together with other species living in confined habitats, such as oceanic islands and mountain summits, we argue that cave species are particularly sensitive to climate change, and we stress out the urgent need for future research and conservation measures.

INTRODUCTION

Climate change is considered to be one of the most challenging concerns for humanity (Walther et al., 2002; Parmesan & Yohe, 2003; Scholze et al. 2006). 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 & Yohe 2003; Root et al., 2003), complex interactions among previously isolated species (Williams & 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* (Whittaker et al., 2017). Even if the potential of subterranean habitats as ideal biological laboratories has been long ago foreseen (Poulson & White, 1969), little has been written about the specific contribution of cave-based studies to the understanding of patterns and processes in global change biology (Mammola et al., 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 & Yohe, 2003; Scholze et al., 2006). However, there exists an emerging trend in environmental, physical and ecological studies 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), the potential of caves as methane-sinks (Fernandez-Cortes et al. 2015) and the effects of global temperature increase on different species of subterranean arthropods (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 & Isaia 2017, Di Lorenzo & Galassi 2017, Mammola et al. 2018).

We argue here that caves are one of the most informative system for the study of climate change across its biotic and abiotic components, for multiple reasons: i) they are semi-closed ecosystems that are extensively replicated across the Earth (Culver & Pipan, 2009); ii) they are buffered from external variations and generally characterized by a remarkable thermal stability (Badino, 2004, 2010); iii) temperature inside caves correlates significantly with the mean annual temperature outside, at least in temperate areas (Moore & Nicholas, 1964, Sánchez-Fernández et al. 2018); 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 & Pipan 2009; Juan et al. 2010).

However, the 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. With this review we aim to overcome this impediment, providing a forward-looking view of prospects offered by these ecosystems for future advances in our understanding of eco-evolutionary responses to recent climate change. In this contribution, we describe the potential effects of the anthropogenic climate alterations on the abiotic and the biotic components of the cave ecosystem. Special focus is given to terrestrial and freshwater ectothermic subterranean organisms. A definition of the speleological jargon used in the text is presented in Box 1.

Box 1. Glossary

Epigean (species/habitat/ecosystem) Living or occurring in superficial habitats.

Hypogean (species/habitat/ecosystem). Living or occurring in subterranean habitats (as defined below).

Shallow Subterranean Habitats (acronym SSH). The aphotic 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 aphotic subterranean spaces harbouring species showing adaptation to subterranean life (troglomorphic traits). These include human-accessible natural subterranean spaces (i.e. caves), 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 populations both in subterranean and surface habitats, with individuals regularly commuting between these habitats thus maintaining gene flow (Trajano & Carvalho 2017).

Troglomorphism

PHYSICS OF CAVE WARMING

Subterranean climate

A wealth of literature documents the ecological peculiarity of the subterranean realm, and how distinct it is from surface habitats. Subterranean ecosystems may be considered extreme, lacking solar radiation and receiving poor energy inputs (Poulson & White 1969; Culver & Pipan 2009). The most notable feature that corroborates the idea that caves are ideal laboratories for the study of climate change in natural environment is their peculiar climatic stability.

Caves have almost constant temperature over the year and a relative humidity often close to saturation (Badino 2010). 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 & Brown, 1971; Wigley & Brown, 1976). Therefore, beyond the entrance, air temperature reaches stable values, in equilibrium with the temperature of the cave walls (Moore & Nicholas, 1964).

Moreover, air temperature in cave interiors is similar to the average annual value of the outside temperature (Moore, 1964) (Figure 1). The link between cave and mean annual atmosphere temperature is represented by the temperature of the ground over the cave, which 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, thus linking air temperature in the cave with the external one (Domínguez-Villar et al., 2013). The geothermal gradient is buffered in karst regions by the advection of groundwater (Bögli, 1980), limiting the sources of heat variability affecting caves.

Nevertheless, in the vadose (i.e. unsaturated) zone of karst regions, there is certain thermal gradient linked to infiltrating water (Badino 2010). Although the temperature slowly increases with the vertical distance under the surface, the 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 & Jeannin, 2004). Strong air circulation or significant water streams can impact the cave temperature by the advection or radiation of heat from the fluids (De Freitas & Littlejohn, 1987; Covington et al., 2011), although in those cases the internal temperature is also linked to the external one (Smithson, 1991; Kranjc & Opara, 2002). 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).

Depending on the characteristics of the material above the cave, thermal differences between the cave and the external mean annual temperature rarely exceed 3 ºC, with normal values ranging between 0 and 2 ºC. 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 - isolating the ground from atmosphere temperatures and the evaporative cooling in soils caused by evaporation are other factor which may contribute to explain small thermal disequilibria between cave and mean annual atmosphere temperatures (Beltrami and Kellman, 2003; Yzaki et al., 2013).

Figure 1. The (theoretical) amplitude of the thermal signal in a cave. Lines show the theoretical annual trend of mean daily temperatures deep inside the cave (dotted line), in the vicinity of the cave entrance (dashed line) and outside the cave (filled line). Note the strict correspondence between the inner temperature and the mean annual temperature outside, as highlighted in the left y-axis, and the reduction of the signal amplitude with increasing depths within the cave.

Climate change and the thermal inertia of caves

Theorethical models have predicted that climate warming will impact temperature in caves (Badino, 2004), and model-data comparisons have confirmed such scenario (Domínguez-Villar et al., 2015), 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 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.

Shallow Subterranean Habitats

Besides caves and the associated networks of fissures, Superficial Subterranean Habitats (SSHs; Box 1) stand out as a peculiar 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).

The increased flux of energy from the atmosphere to the subterranean environment induced by climate change is expected to be primarily deposited in the SSHs—see physical modelisations 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 hypogean sectors, effects on the SSH fauna are expected to be more immediate (Wynne et al., 2014).

Potential implications of subterranean warming

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), 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 is registered when the external temperature is below the cave temperature, whereas limited ventilation is recorded during the rest of the year (e.g., Kowalczk & 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 details yet.

ECO-EVOLUTIONARY RESPONSES TO GLOBAL CLIMATE CHANGE IN CAVES

Cave 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. 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 cave 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 & Renault 2002, Mezec et al. 2010, Voituron et al. 2011). A charismatic example is offered by the first cave species ever described, the olm *Proteus anguinus*. 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).

Potential species sensitivity to climate change

While much attention has been given to the effects of global climate change on epigean 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 hypogean species should exhibit a stenothermal profile (*sensu* Huey and Kingsolver, 1989), which maximizes 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 troglophile invertebrates living in the vicinity of the surface have the capacity to withstand temperature variations, most troglobionts lack such thermoregulatory mechanisms (Novak et al., 2014). 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. 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* have the ability to synthesize 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 cave-dwelling amphipods in the genus *Niphargus* (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 other have not (Issartel et al., 2005; Colson-Proch et al. 2010; Mermillod-Blondin et al., 2013). Moreover, an intra-specific variability in the thermal performance across different populations of …. was demonstrated (Colson-Proch et al., 2009). 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 considered to be one of the most important limiting factors for terrestrial cave obligate species (Howarth, 1980, 1983; Simões et al. 2015). Accordingly, the maintenance of high humidity levels appears to be essential for the survival of 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.

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.

Area	Model organism(s)	Subterranean adaptation	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	Beetles (gen. *Troglocharinus* + 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
Eastern 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. *Niphargus*)	Stygobiont	Expression gene profile	Subterranean species maintain the expression of heat shock protein	Colson-Proch et al. 2010
Western Alps (Italy)	Spiders (gen. *Troglohyphantes*)	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. *Proasellus*)	Stygobiont	Physiological tests	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).	Mermillod-Blondin et al., 2013.
Medio Valdarno porous aquifer (Italy)	Aquatic copepod (*Diacyclops belgicus)*	Stygophile/Stygobiont—widely distributed across Europe	Physiological test	No significant variations in the oxygen consumptions to a +3 °C change in temperature	Di Lorenzo & Galassi, 2017

Europe	Spiders (gen. *Meta*)	Troglophile	Species Distribution Modelling	Future poleward shift in the distribution ranges	Mammola 2017
Europe	Spiders (gen. *Meta*)	Troglophile	Species Distribution Modelling	i) Future poleward shift in the distribution ranges ii) Niche overlap between congeneric species	Mammola & Isaia, 2017

Potential future responses

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 epigean 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 xxx).

If the dispersal capacity is enough to accompany the spatial change in temperatures, one of the most common response of epigean organisms to climate change is the altitudinal and/or latitudinal shift of distribution ranges (Parmesan & Yohe 2003; Chen et al. 2011). However, most subterranean systems are geographically isolated, acting as islands for many species. This ecological feature, together with physiological constraints, caused an extreme reduction in the dispersal potential of most troglobionts. Indeed, as resumed 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 species ranges rather than range expansions or shifts (Sánchez-Fernández et al., 2016; Mammola et al., 2018; but see Mammola & Isaia, 2017). In this respect, due to the same kind of barriers inhibiting local migrations, altitudinal shifts may be equally unlikely.

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). Also, it has been recently shown that adaptation to groundwater is not always a one-way evolutionary path, with subterranean species being occasionally able to recolonize and widely disperse in surface waters (data on *Niphargus*; Copilas-Ciocianu et al. 2018). However, the connections among subterranean aquifers may change due to geological and hydrological processes potentially causing their isolation (Fattorini et al. 2016), thus this enhanced dispersal potential of stygobionts may not represent a real advantage in facing climate change.

At a smaller scale, in response to climate change cave species could theoretically change their spatial distribution inside the cave system itself. Evidence suggests that a number of subterranean species are indeed able to seasonally migrate toward greater depths and vice versa (e.g., 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 entrance is generally scarcer. Moreover, most of specialized subterranean arthropods are confined in caves lacking climatic heterogeneity to be exploited.

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 & Holzapfel 2006; Visser, 2008; Williams et al. 2008). In particular, physiological adaptation to increasing temperatures has been reported in

epigean 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 cave organisms exhibit decreased metabolic plasticity, i.e., show far less elevation of metabolism than their close epigean relatives in response to higher temperatures (Dresco-Derouet 1959; Vandel 1965; Hervant & Mathieu 1997). Indeed, habitat specialists often present low functional variability due to specialization (but see Juan 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). 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).

Inter-connection with other systems

The argumentation presented in the previous section illustrates the potential eco-evolutionary responses of cave dwelling species to climate change within the subterranean domain. However, it is worth noticing that most subterranean habitats are semi-closed systems, thus deeply interconnected and strongly dependent of other environments, as the soil and epigean habitats.

Being light deficient, the cave ecosystem is strongly dependent from the outside ecosystems providing the fundamental energy inputs for its maintenance (Gibert & Deharveng 2002)—although chemolithotrophic organisms may account for a little primary production within caves (Northup & Lavoie 2001). Trophic inputs mainly consist of organic materials passively transported underground, as well as by active migration of animals. Consequently, energy flow in a typical subterranean habitat is strongly influenced by seasonal fluctuations (Culver & 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 epigean species (Parmesan & Yohe, 2003), especially in plants (Cleland et al., 2007). It is thus theoretically expected that the amount and timing of allochtonous energy inputs in caves will change accordingly, with direct effects on the subterranean coenosis.

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 seriously 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 & Trajano, 2010).

From a slightly different perspective, it is likely that some soil and epigean organisms may exploit subterranean environments, especially cave entrances and SSHs, as refugial area in a climate change scenario. 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.

FUTURE DIRECTIONS

We have shown 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. Unfortunately, there is currently a lack of long-term temperature data series within karst settings (Brookfield et al. 2016); we thus point out that monitoring programs should be established for relevant abiotic variables, namely temperature and humidity.

With small distribution ranges (due to the isolation among cave systems), small population size (due to low energy availability), and restricted habitat (by definition), cave organisms often fulfil all forms of rarity (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). Troglobionts and stygobionts are in fact prevalent on conservation priority lists (Cardoso et al. 2011). 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 (Mammola & Isaia, 2017). We have also discussed that movements of faunas from surface to subterranean habitats, and vi*ce 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—will become helpful to document the amplitude of these reciprocal movements (Fattorini et al. 2016, Trajano & de Carvalho 2017).

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 cave 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. In fact, the simultaneous use of physiological data, genetic evidence and forecast derived from statistical projections has a great deal of potential (Mammola & Leroy 2017). There is little doubt that this integrated approach would greatly benefit the science of subterranean biology, prompting a fast and significant advance in knowledge.

Author contribution statement

SM conceived the idea and led the writing. SM, EP, PC, PV, and MI provided general arguments for all biological sections. DDV provided physical and climatological arguments.

All authors contributed significantly to the submitted manuscript through discussions and bibliographic additions.

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