Subterranean Biology 25: 1–7 (2018)
doi: 10.3897/subtbiol.25.23530
http://subtbiol.pensoft.net

SHORT COMMUNICATION

A peer-reviewed open-access journal
Subterranean Biology
Published by The International Society for Subterranean Biology

The deep subterranean environment as a potential model system in ecological, biogeographical and evolutionary research

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Academic editor: *O. Moldovan* | Received 10 January 2018 | Accepted 15 January 2018 | Published 18 January 2018

http://zoobank.org/ECB34A3E-6776-4E9E-9C51-C5DB25F86527

Citation: Sánchez-Fernández D, Rizzo V, Bourdeau C, Cieslak A, Comas J, Faille A, Fresneda J, Lleopart E, Millán A, Montes A, Pallarés S, Ribera I (2018) The deep subterranean environment as a potential model system in ecological, biogeographical and evolutionary research. Subterranean Biology 25: 1–7. https://doi.org/10.3897/subtbiol.25.23530

Abstract

One of the main challenges in ecology, biogeography and evolution is to understand and predict how species may respond to environmental changes. Here we focus on the deep subterranean environment, a system that minimizes most of the typical uncertainties of studies on epigean (surface) environments. Caves are relatively homogeneous habitats with nearly constant environmental conditions and simplified biological communities, allowing to control for biotic interactions. Thus, this particular system could be considered a natural habitat whose environmental conditions are similar to what can be reproduced in a laboratory, being an ideal model system for ecological, biogeographical and evolutionary studies. Subterranean species may potentially be used to assess the capability to persist in situ in a global change scenario, as they cannot accommodate to drastic changing conditions by behavioural plasticity, microhabitat use or by migrating to distant, more suitable areas, something frequent in epigean environments. In order to provide accurate predictions of the response of the subterranean biodiversity to climate change, we encourage evolutionary biologist, biogeographers and conservation biologist to work in this interesting ecosystem.

Keywords
caves, climate change, subterranean biodiversity, thermal tolerance, persistence capability

One of the main challenges in ecology, biogeography and evolution is to understand and predict how species may respond to environmental alterations, especially in the context of global change. If we aim to develop effective management strategies, accurate predictions of species response are mandatory. These predictions will be more accurate as we can obtain more reliable estimates of species dispersal ability, biotic interactions and species fundamental niche (and its geographical projection, understood as potential distribution; see Soberón et al. 2005).

Species fundamental niches can be defined as the multidimensional spaces of scenopoetic variables, typically measured at coarse spatial resolutions and over broad geographic extents (Peterson et al. 2011), and they are commonly inferred exclusively from the current climatic conditions of the localities in which the species are known to occur. In practical terms, this means that the simple presence of a species in a cell grid of a certain dimension is related to some average characteristics of this cell grid.

It is widely recognized that there are many sources of uncertainty (both conceptual and methodological) when relating species ecological niche to the environmental conditions of their distributions (Jiménez-Valverde et al. 2008). Thus, it is assumed that the variables affecting species performance and distribution are known, that species are found in their optimal climatic niches, and what is more important, that these environmental conditions are homogeneous through the spatial units used (usually grid cells), ignoring both temporal (daily and often even seasonal) and spatial (micro-habitat) heterogeneity (Hannah et al. 2014, Klečková et al. 2014, Rezende et al. 2014). Consequently, both behavioural and phenological accommodation to different environmental conditions (Parmesan 2006, Sunday et al. 2014) are frequently ignored, assuming that organisms have no control over the conditions to which they are exposed (see Charmantier et al. 2008, Wong and Candolin 2015). Lastly, it is assumed that species occur at all locations where environmental conditions are favourable, likely overestimating dispersal capabilities and underestimating the influence of biotic interactions (Guisan and Thuiller 2005, Araújo and Luoto 2007, Jiménez-Valverde et al. 2008, Wiens et al. 2009).

Most of the research to date has been based on distributional data of vertebrate species (using grid cells at different spatial resolutions) from terrestrial ecosystems. However, all these assumptions should be questioned when we consider the great variety of environments that can co-occur in a spatial unit of typical dimensions (e.g. cells of 10×10 km), the importance of extreme or unusual rather than average conditions (Schoepf et al. 2015), the possibility to be exposed to different environmental conditions simply through behavioural adaptations and adjustments in microhabitat use (Visser and Both 2005), or the possibility of competitive exclusion of a species from an environmentally suitable area.

We would like here to bring attention to a system in which most of these uncertainties are minimised: the deep subterranean environment. Contrary to what happens in epigean (surface) environments, the range of variables affecting a species in this environment is very limited. The humidity in the deep parts of a cave is always near the saturation point and the temperature is relatively constant through the day and year, and what is more interesting, it can be easily (though approximately) estimated from the mean annual temperature of the surface (Jeannel 1926, Poulson and White 1969, Juberthie and Decu 1994, Culver and Pipan 2009). To obtain a numerical estimation of this relationship, even if very crude, we compiled records of temperature inside 59 caves (28 from the North-eastern Iberian Peninsula, Sánchez-Fernández et al. 2016, and 31 from the western Alps, Mammola et al. 2017) and compared these values with those obtained from raster with the Mean Annual Temperature of the surface at 0.08 degree spatial resolution cells from WORLDCLIM version 1.3 (http://www.worldclim.org; Hijmans et al. 2005). We found that the temperature of the cave can be estimated with an average error of 1.90 °C using as only predictor the Mean Annual Temperature of the surface ($r = 0.79$, $n = 59$; $p < 0.01$; see Figure 1).

Compared with epigean habitats, most of the environmental conditions are also virtually homogeneous through all possible microhabitats within the deepest parts of a cave system, so small-scale spatial heterogeneity and the possibility of behavioural adjustments, phenotypic plasticity or adaptive evolution are limited. Mammola and Isaia (2016) studied the environmental niche of a subterranean spider (*Troglohyphantes vignai* Brignoli, 1971) during a year, concluding that although some minimal spatial climatic variation was detected, neither temporal nor spatial variation of the niche of this species was found through the year. Finally, caves harbour comparatively simple biological communities (Racovitza 1907, Culver and Pipan 2009, Cardoso 2012), which minimizes the additional complexity of biological interactions. Most highly specialized cave species have also a well-defined distribution, as they show low mobility and extremely narrow geographical ranges, which minimizes sampling uncertainties. In summary, and unlike in surface environments, here the real and accurate environmental conditions that species experience are known.

However, there are not only advantages in this study system. Subterranean species violate a key assumption especially relevant for biogeogeographical research: compared with epigean species, they show low dispersal abilities (Rizzo et al. 2013, 2017). Thus, they cannot be expected to occupy most of their suitable habitat, which means that they are then not in equilibrium with climatic conditions (see Svenning and Skov 2005, Sánchez-Fernández et al. 2012). In other words, in addition to climate, other factors (such as biotic interactions or limited dispersal) are important shaping their distributions. This situation could compromise biogeographical studies, especially those that are exclusively supported by species distribution models used for epigean fauna (but see Mammola et al. 2017, Mammola and Leroy in press). However, in some situations this drawback could be seen as an opportunity, as i) their low mobility could also favour more accurate estimates of the climatic conditions that species experience, allowing to include past climates to estimate species climatic niches, as current records can in most cases be considered to reflect ancient distributions (Sánchez-Fernández et al. 2016), and ii) as for most of these species dispersal to more suitable locations is not an option, the only pos-

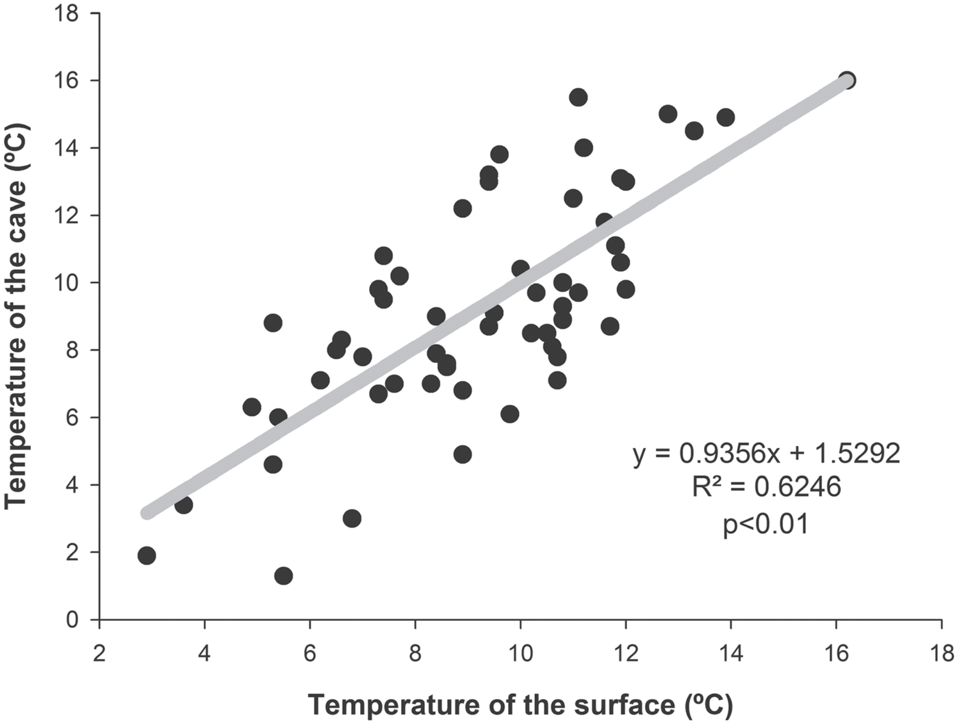

Figure 1. Relationship between the temperature inside the cave and the surface (Mean Annual Temperature (°C) of each pixel (0.08° cells).

sibility to cope with climate change is to persist in situ, so they can be used to estimate the capability of species to persist when facing climatic fluctuations. As an example, in a recent study Sánchez-Fernández et al. (2016) used the subterranean habitat to illustrate how traditional approaches to estimate species fundamental niche and potential distributions do not work for poor dispersing species. They make also a weak-up call on this issue, as these same methods have been applied (and are still being regularly applied) to many species for which dispersal ability or thermal tolerance are not known, but that they are assumed to disperse freely without any limit, and to be perfectly adapted to the temperatures they experience with their current distribution. We thus encourage biogeographers and conservation biologist to work in this interesting ecosystem in order to provide accurate predictions of the response of biodiversity to climate change.

Besides, other than to exemplify general principles, subterranean fauna is certainly of interest and value on its own, since it represents an often neglected but substantial part of our natural heritage. Although there is a general lack of knowledge of most subterranean groups worldwide, Culver and Holsinger (1992) estimated that there may be a total of 50,000 to 100,000 obligate subterranean species, with a high level of endemism (Gibert and Deharveng 2002). It is not surprising that biologists have long been fascinated by the peculiarities of typical subterranean organisms (e.g. Darwin 1859, Racovitza 1907, Jeannel 1943), as they show morphological, physiological, and life-history adaptations reflecting severe environmental constraints which result in an invaluable resource for evolutionary studies (Juan et al. 2010, Rohner et al. 2013). Thus, it is worth to note the interest of subterranean biodiversity also from a conservationist perspective. However, and in sharp contrast to its relevance, in conservation programs subterranean biodiversity is usually either neglected or protection measures are recommended based on misconceptions on the subterranean environment and a most incomplete knowledge of the biology of their species.

Acknowledgements

DS-F was supported by a post-doctoral contract funded by Universidad de Castilla-La Mancha and the European Social Fund (ESF). This work was partly funded by two projects funded by the Spanish Ministry of Economy and Competitiveness (CGL2016-76995-P to DSF and CGL2016-76705-P to IR).

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