

Are rates of thermal niche evolution in cave beetles enough to cope with climate change?



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Introduction and objectives

Climate change has become one of the main threats to global biodiversity. However, the extent to which species are threatened by climate change depends on how they respond to these new climatic conditions. They can disperse to more suitable locations, or they can cope through phenotypic or behavioural plasticity and, ultimately, via evolutionary adaptation. Most of the studies of the evolutionary and biogeographical consequences of climatic change have been done with terrestrial, mainly vertebrate species. These models present some important uncertainties, as depending on the use of different microhabitats at different times within the same area the species can be exposed to a range of temperature or humidity sometimes much wider than the change predicted by the most pessimistic scenarios of climate change. The possibility of range movement tracking suitable habitats is also a confounding factor when trying to infer the conditions at which these species were subjected in the past.

Here we present a system in which most of these uncertainties do not apply: the deep subterranean environment. The temperature of a cave is highly constant through the year and can be estimated from the mean annual temperature of the surface (Fig. 1), and the humidity is always near to the saturation point. These conditions are homogeneous through all possible microhabitats within a cave system, and constant through the year. Most highly specialized cave species have also extremely narrow geographical ranges, which allows to trace their geographical movements through several cladogenetic processes.

We focused on a well defined clade of troglobitic beetles of the tribe Leptodirini (Coleoptera, Leiodidae) living in the North-eastern Iberian Peninsula (from the Pyrenees to the coast of Catalonia; see Figure 3), including 88 taxa. Most of them are narrow endemic species with a well known distribution.

We aim to estimate the thermal niche and its geographical projection (here considered as potential distribution) of these species using i) the temperature data from its current distribution, and ii) including different estimates of the rate of thermal niche evolution. Finally we compare these results with the predicted climatic conditions from 2000 to 2080 for the same areas.

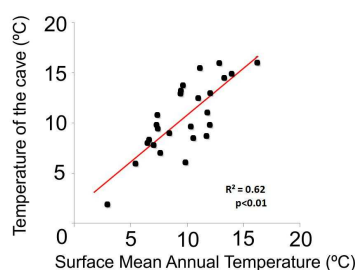


Fig. 1. The temperature of the cave can be estimated with an average error of 1.58 °C using as predictor only a raster with the Mean Annual Temperature of the surface ($R^2 = 0.62$, $n=28$; $p < 0.01$)

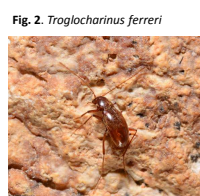


Fig. 2. *Tragocharinus ferreri*

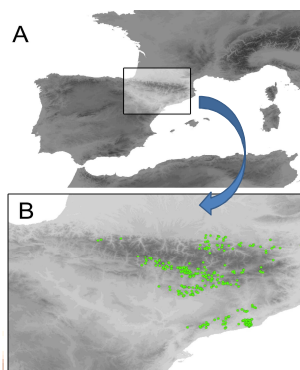


Fig. 3. Study area. Green dots show the sampling localities

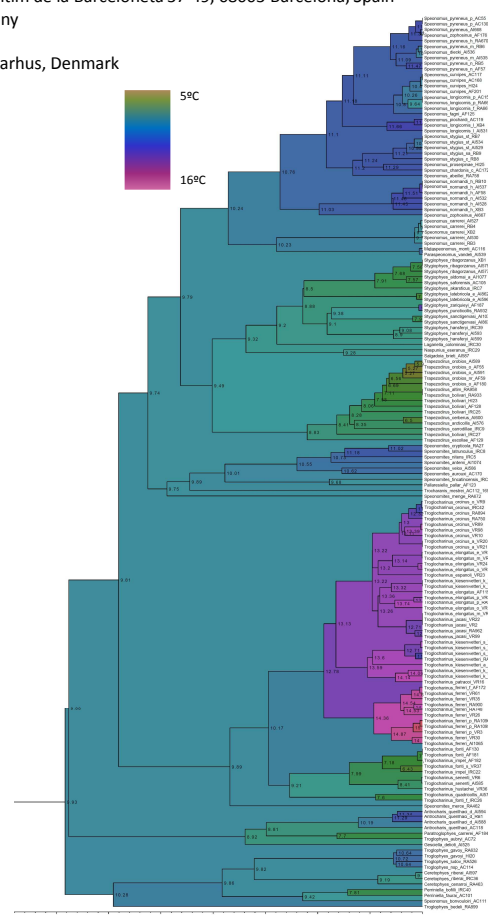


Fig. 4. Phylogenetic ultrametric tree. Colors indicate the thermal reconstruction of the ancestor using only the current temperature of the species

Approach and results

Estimating thermal niche and potential distribution

The maximum and minimum scores (extreme values) of the Mean Annual Temperature from the entire set of observed presences are calculated for each species. Then, all grid cells with climatic values falling within the mentioned range were designated as suitable, and all cells outside it as unsuitable. In this way, the extreme values were used to derive a binary distributional hypothesis about the areas having climatically suitable conditions (potential distribution), under the standard assumption that recorded occurrences reflect the spectrum of climatic conditions in which the species can survive and reproduce. We followed the same procedure projecting the thermal niche of each species to the predicted temperature for the 2080 (the A2 scenario for the CCCMA-CGCM2 climate model through the CIAT database (www.ccafs-climate.org)) in order to know how many of the current populations for each species would have suitable thermal conditions in 2080. Finally, we also calculated the thermal niche incorporating different rates of thermal niche evolution.

To estimate the rate of thermal niche evolution we used three approaches:

i) we first reconstructed a minimum rate of evolutionary change from a time calibrated phylogeny using only the current thermal niche of the species. The rate of climatic niche evolution for each species was calculated as the average rate for all branches connecting the species with the tree root. For each branch, rate evolution was calculated as the absolute difference between the initial and final node and divided by the age of the branch. We found that *Tragocharinus ferreri* (Fig.2) is the species with the fastest rate of evolutionary change obtained from the time calibrated phylogeny (0.54 °C/MY; see Fig.4).

ii) as this pattern assume a constant amount of change over time and could lead to underestimated rates, we also considered the branch of the tree with higher rate of thermal niche evolution. Here, we estimated a rate of 1.4 °C/MY (found also in *T. ferreri* 0.5Ma; see Fig.4).

iii) we also introduced the constraint of the paleotemperatures of the areas occupied by these species during the Pleistocene glacial periods as the estimated range of temperature variation of these localities from the last 21000 years (and assuming that these species experience these temperatures *in situ*; i.e., they were not able to disperse to warm areas, see Fig. 5), using cartographical digital information with the current and Last Glacial Maximum (LGM) temperatures for the study area. In this case, we can estimate a maximum rate of thermal niche evolution of 0.0235 °C/100 years.

The IPCC estimated rates are 3-4 °C for mean annual temperature in the next ~100 years, depending on location. The rate of change observed among species obtained from the phylogenetic tree and considering the constrain of quaternary glaciations is then between ~10 000 and ~100 times slower than the expected rate of change from 2000 to 2100.

Only 11 of the 86 species would have a thermal niche broad enough to face climate change in some of the current localities (always below the 50% of their populations; see Fig.5). These results did not vary when considering the possibility of thermal niche evolution at the rates estimated above.

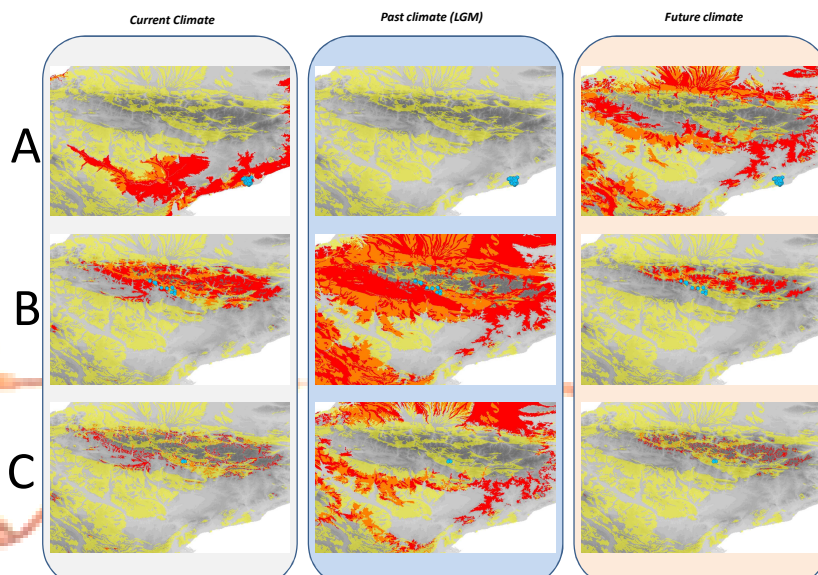


Fig. 5. Area with suitable temperature (red surface) for current, past and future for A: *Tragocharinus ferreri*; B: *Trapezodius orobius*; and C: *Stygiophyes ribagoranus*. Yellow surface represents karstic systems (i.e. the areas with probability to have caves). The overlapping between the two areas are represented in orange. Blue dots indicate current presences. For most of the species (e.g. *T. ferreri* and *S. ribagoranus*), the predicted distribution for the LGM climatic conditions falls outside the Pyrenees. Considering the current narrow and patchy distribution of these species it is highly unlikely that they moved to low warm areas in the LGM and then recolonizing the Pyrenees, so we assume that these species experience LGM temperatures *in situ*.

Only *Trapezodius orobius* is estimated to have suitable conditions in its current localities at the expected rates of climate change

Main conclusions

Taken at face value, our results suggest that to survive *in situ* the projected changes in climatic conditions subterranean species would require rates of climatic niche evolution that are largely unprecedented in their evolutionary history. This is reinforced by the fact that, unlike most study systems, ours fulfills all the assumptions of the models habitually used to estimate species distributions and niche evolution - all but one: we do not know to what extent the distributions of the species are limited by the temperature of the caves. Clearly, the standard approach that we apply here should not be the only one used to address how populations can respond to climate change. Experimental and modeling approaches are both essential, especially physiological experiments on long-term thermal tolerance, as well as comparative analyses among populations of the same species.

What we can say is that most species will be exposed to both rates of temperature change and absolute temperatures that have not been experienced in their evolutionary history since at least the early Miocene. But only an experimental approach can provide some evidence of the capability of these subterranean species to cope with temperatures outside those of their current environment.