Quantifying troglomorphism in hyperspace

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Abstract

Many ecological and evolutionary studies require to quantify the degree of adaptation of subterranean species to caves or other subterranean systems. In 1962, Kenneth A. Christiansen (1924–2017) coined the term "troglomorphism" to illustrate the process of subterranean adaptation and the suite of adaptive traits of organisms ("troglomorphic traits" or "troglomorphies") (Christiansen 1962). Although this term was proposed in a paper published in French, "troglomorphism" and its derivatives (e.g. "troglobiomorphism") became widely adopted jargon in subterranean biology. Yet, after decades of work and countless discussions around the subtle meanings of the term, there is still no consensus on how to best quantify troglomorphism in a simple operational way to support eco-evolutionary research. In a recent interview, Boris Sket made the excellent point that "*nothing [makes] sense in speleobiology without a comparison of cave animals with the 'normal' epigean ones*" (Lučić 2021). Building on this idea, we contend that one could quantify troglomorphism on a continuous scale within a given group of organisms (e.g., family or genus) as the functional distance of each species to the phylogenetically closest surface species or the "average" surface species (depending on whether phylogenetic information is available or not). We illustrate this approach using subterranean spiders in the genus *Troglohyphantes*, a well-studied group for which both a phylogeny and functional traits are available (Isaia et al. 2017, Mammola et al. 2020). We tested two approaches: i) quantifying adaptation as the morphological distance of each species to the phylogenetically closest surface-dwelling relative; ii) using a kernel density n-dimensional hypervolume (*sensu* Blonder et al. 2014) to construct the morphospace occupied by all surface-dwelling species of *Troglohyphantes*, and quantifying the degree of adaptation of subterranean species as their distance from the centroid of this "average" surface species. To test the effectiveness of these alternative methods, we compare how functional distance varies in relation the habitat occupied by each species (deep caves vs cave entrances vs interstitial habitats) and its range size. We suggest our approach could be applied to any

group of subterranean organisms for which a surface relative is known, allowing to explore a range of questions on the degree to which the specialization of a given community relates to local environmental conditions, interspecific interactions, and more.

Keywords

Presenting author

Stefano Mammola

Funding program

Grant title

Hosting institution

Finnish Museum of Natural History – University of Helsinki

Author contributions

S.M. and P.C. conceived the study and designed the methodology. S.M. conducted analyses. F.M. and R.M. collected distribution data. M.I. and M.T. collected functional traits. M.A.A. and M.P. analysed phylogenetic data.

Conflicts of interest

None declared.

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