

Hotspots of Subterranean Biodiversity

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Received: 18 May 2020; Accepted: 21 May 2020; Published: 25 May 2020



Abstract: Worldwide, caves and groundwater habitats harbor thousands of species modified and limited to subterranean habitats in karst. Data are concentrated in Europe and USA, where a number of detailed analyses have been performed. Much less is known with respect to global patterns due to a lack of data. This special issue will focus on and discuss the global patterns of individual hotspot caves and groundwater habitats.

Keywords: α -diversity; biogeography; biospeleology; cave biology; caves; hotspots; invertebrates; subterranean biodiversity

1. Introduction

The denizens of caves and other habitats without light hold a special interest for students of biodiversity [1]. The fauna have bizarre and very distinctive morphology, including the lack of or reduction in eyes and pigment, elongated appendages, and often a ghost-like appearance [1–4]. How these species from disparate groups, including both vertebrates and invertebrates, evolved this convergent morphology remains a subject of intense research, both in the laboratory [5–7] and in the field [8,9]. Whatever the details, cave fauna are a magnificent example of convergent evolution and adaptation [10,11].

What is less well known is that there are thousands of species specialized for life in darkness, especially in caves. While speciation can occur as a result of isolation in caves, followed by subterranean dispersal and more isolation, opportunities for subterranean dispersal are restricted [4,12,13], and the specialized subterranean fauna is the result of many hundreds if not thousands of separate colonizations from the surface to the subsurface. These numbers are sufficient to expect predictable geographic patterns to emerge from their analysis [14].

While there are now several datasets on the georeferenced occurrence of specialized subterranean species from both Europe and the United States with over 2000 records [15–18], these records were hard-won and without parallel in other continents and regions. Brazil is the best-known region outside of Europe and the United States and the number of records is much smaller, and mostly for as yet undescribed species [19,20]. Exploration and access to caves is often formidable, and the number of caves is very large. For example, 45,000 caves were known from the USA in 1999 [21], and that number has grown considerably since that time. Of course, not all caves need to be sampled to obtain a good estimate of species richness for a region, but a rather large number do. This is because β -diversity dominates α -diversity [22,23]. One study of the European terrestrial fauna found that approximately 100 caves were needed to have accumulation curves of species numbers approach an asymptote [24].

The availability of large numbers of records for non-cave subterranean habitats is almost non-existent, with two exceptions. One is the analysis of epikarst communities in Slovenia [25], a habitat that is indirectly sampled through the continuous sampling of water dripping from cave ceilings [26]. The other is the larger scale sampling of porous aquifers in Europe as part of the PASCALIS project (Protocol for the ASsessment and Conservation of Aquatic Life in the Subsurface) [27]. There are also several studies that combine cave and non-cave subterranean aquatic diversity [28,29]. This sampling deficiency in subterranean habitats not directly accessible to humans has been named the “Racovitza impediment” [30].

In spite of these impediments, we know a great deal about cave biodiversity patterns in Europe and, to a lesser extent, the United States. In Europe, there is a ridge of high species richness for both aquatic and terrestrial species at a latitude of approximately 45° N along the spine of the Pyrenees and through the Dinaric karst of Slovenia, Croatia, Serbia, and Montenegro [16,24]. Species range sizes follow Rapoport’s Rule and increase with increasing latitude [16], and species turnover is high over short distances [16,23]. Explanations of patterns are highly scale-dependent. For example, the ridge of high species richness is largely concordant with areas of high productivity [24], but productivity is unimportant in determining hotspots within hotspots [15]. The explanations for regional differences have proven to be complex, often involving a combination of energy availability, spatial heterogeneity, and history, and the explanations vary from region to region, being spatially non-stationary [31].

Determining the global patterns of subterranean species richness has remained elusive. At one level, the possibilities of determining the patterns seem difficult at best and a long way in the future. If thousands of records are needed to describe and understand the European pattern, global studies with tens of thousands of records would be needed. However, there may be a shortcut at hand that at least holds promise of a global picture, albeit incomplete. It starts with the observation by Gibert and Deharveng [22] in their classic paper on subterranean biodiversity that regional diversity is a good predictor of local diversity and vice versa. This was buttressed by later findings that species accumulation curves rarely crossed, and thus the regional qualitative pattern could be captured by a relatively small number of samples [24,32]. Culver and Sket [33] took this idea to its logical extreme, and considered only caves and karst wells with the highest species richness, originally finding 20 sites with 20 or more species specialized for subterranean life. While the coverage of large numbers of caves in a relatively small area was (and is) limited to Europe and the United States, they reasoned that at least a few outstanding caves, extensively sampled, were known from most large karst areas. Since the publication of the first hotspot list in 2000, knowledge of the global cave fauna has grown exponentially. Species lists are available for several tropical countries [20,34,35], and a number of caves throughout the tropics and sub-tropics are now well sampled [36]. In a later update [37], the bar was raised to either 25 terrestrial or 25 aquatic species. In 2019, there were 24 examples of hotspot caves known [38]—16 from the temperate zone, 5 from the subtemperate zone, and 3 from the subtropics. The tropics have at least five caves with 20 or more species specialized for subterranean life, the original hotspot criterion [37]. The demonstration of hotspot caves in the tropics also raises some other issues. One is how to treat undescribed species, which is the case for the majority of tropical species [39]. If they are ignored, then tropical and subtropical caves will appear to be artificially depauperate. If they are fully counted, the likelihood that some of these species are not valid [40] is ignored. Of course, described species may also be wrongly thought to be limited to subterranean habitats. In addition, the tropical cave fauna often has a component specialized on guano but never found outside of caves. These guanobionts typically show less eye and pigment loss and less appendage elongation [38,39]. Should they be discounted as cave specialists? If so, then once again tropical and subtropical caves may appear to be artificially depauperate.

This special issue of *Diversity* aims to bring together information on hotspot caves and karst ground-watered habitats for in-depth analyses and comparisons. First and foremost, there will be a species list for each of the hotspot caves, information that is strangely unpublished for many of the hotspot caves. This is especially important given the controversy around the ecological status of cave

species [41]. Deharveng and Bedos [41] pointed out that considerable confusion exists in the literature about the terms troglobiont—which should be used only for species not found outside of caves, irrespective of their morphology—and troglomorph [42,43], species with reduced eyes and pigment and elongated appendages. The two are not identical, a problem that arises not only with guanobionts but also with all species without troglomorphic features occurring in caves [44]. The special issue will also provide a physical setting for the caves and groundwater habitats, including their hydrogeological and environmental context, their use by humans, the nature of the karst in which they are situated, and the knowledge on nearby cave biodiversity. An interesting side note is that a number of hotspot caves are or have been commercial caves, including Mammoth Cave in Kentucky, USA; the Postojna-Planina Cave System in Slovenia; and Vjetrenica in Bosnia and Hercegovina. Meanwhile, some groundwater hotspots are industrially exploited for water consumption. Finally, there will also be a summary of what we know, the patterns of distribution, and future research directions. For more information, contact any of the editors.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Fenolio, D. *Life in the Dark: Illustrating Biodiversity in the Shadowy Haunts of Planet Earth*; Johns Hopkins University Press: Baltimore, MD, USA, 2016.
2. Juberthie, C. *Encyclopaedia Biospeologica*; Decu, V., Ed.; Société Internationale de Biospéologie: Moulis, France, 1994; Volume 3.
3. Botosaneanu, L. *Stygofauna Mundi*; E.J. Brill: Leiden, The Netherlands, 1986.
4. Culver, D.C.; Pipan, T. *The Biology of Caves and Other Subterranean Habitats*, 2nd ed.; Oxford University Press: Oxford, UK, 2019.
5. Keene, A.C.; Yoshizawa, M.; McGaugh, S.E. *Biology and Evolution of the Mexican Cavefish*; Academic Press: Waltham, MA, USA, 2016.
6. Wilkens, H.; Strecker, U. *Evolution in the Dark. Darwin's Loss without Selection*; Springer Nature: Berlin, Germany, 2017.
7. Rohner, N.; Jarosz, D.F.; Kowalko, J.E.; Yoshizawa, M.; Jeffery, W.R.; Borowsky, R.L.; Lindquist, S.; Tabin, C.J. Cryptic variation in morphological evolution: HSP90 as a capacitor for loss of eyes in cavefish. *Science* **2013**, *342*, 1372–1375. [[CrossRef](#)] [[PubMed](#)]
8. Poulson, T.L. Cave adaptation in amblyopsid fishes. *Am. Midl. Nat.* **1963**, *70*, 257–290. [[CrossRef](#)]
9. Culver, D.C.; Kane, T.C.; Fong, D.W. *Adaptation and Natural Selection in Caves. Gammarus minus as a Case Study*; Harvard University Press: Cambridge, MA, USA, 1995.
10. Pipan, T.; Culver, D.C. Convergence and divergence in the subterranean realm: A reassessment. *Biol. J. Linn. Soc.* **2012**, *107*, 1–14. [[CrossRef](#)]
11. Culver, D.C.; Pipan, T. Shifting paradigms of the evolution of cave life. *Acta Carsologica* **2015**, *44*, 415–425. [[CrossRef](#)]
12. Trontelj, P. Vicariance and dispersal in caves. In *Encyclopedia of Caves*, 3rd ed.; White, W.B., Culver, D.C., Pipan, T., Eds.; Academic Press: Waltham, MA, USA, 2019; pp. 1103–1109.
13. Eme, D.; Malard, F.; Konecny-Dupré, L.; Lefébure, T.; Douady, C.J. Bayesian phylogenetic inferences reveal contrasted colonization dynamics among European groundwater isopods. *Mol. Ecol.* **2013**, *22*, 5865–5899. [[CrossRef](#)]
14. Zagamajster, M.; Christman, M.C. Mapping subterranean biodiversity. In *Encyclopedia of Caves*, 3rd ed.; White, W.B., Culver, D.C., Pipan, T., Eds.; Academic Press: Waltham, MA, USA, 2019; pp. 678–685.
15. Bregović, P.; Zagamajster, M. Understanding hotspots within a global hotspot—Identifying the drivers of regional species richness patterns in terrestrial subterranean habitats. *Insect Conserv. Biodivers.* **2016**, *9*, 268–281. [[CrossRef](#)]
16. Zagamajster, M.; Eme, D.; Fišer, C.; Galassi, D.; Marmonier, P.; Stoch, F.; Cornu, J.; Malard, F. Geographic variation in range size and beta diversity of groundwater crustaceans: Insights from habitats with low thermal seasonality. *Glob. Ecol. Biogeogr.* **2014**, *23*, 1135–1145. [[CrossRef](#)]

17. Christman, M.C.; Doctor, D.H.; Niemiller, M.L.; Weary, D.J.; Young, J.A.; Zigler, K.S.; Culver, D.C. Predicting the occurrence of cave-inhabiting fauna based on features of the Earth surface environment. *PLoS ONE* **2016**, *11*, e0160408. [[CrossRef](#)]
18. Deharveng, L.; Stoch, F.; Gibert, J.; Bedos, A.; Galassi, D.; Zagamajster, M.; Brancelj, A.; Camacho, A.; Fiers, F.; Martin, P.; et al. Groundwater biodiversity in Europe. *Freshw. Biol.* **2009**, *54*, 709–726. [[CrossRef](#)]
19. Trajano, E.; Bichuette, M.E. Diversity of Brazilian subterranean invertebrates, with a list of troglomorphic data. *Subterr. Biol.* **2010**, *7*, 1–16.
20. Souza-Silva, M.; Ferreira, R.L. The first two hotspots of subterranean biodiversity in South America. *Subterr. Biol.* **2016**, *19*, 1–21. [[CrossRef](#)]
21. Culver, D.C.; Hobbs III, H.H.; Christman, M.C.; Master, L.L. Distribution map of caves and cave animals in the United States. *J. Cave Karst Stud.* **1999**, *61*, 139–140.
22. Gibert, J.; Deharveng, L. Subterranean ecosystems: A truncated functional diversity. *Bioscience* **2002**, *52*, 473–481. [[CrossRef](#)]
23. Malard, F.; Boutin, C.; Camacho, A.I.; Ferreira, D.; Michel, G.; Sket, B.; Stoch, F. Diversity patterns of stygobiotic crustaceans across multiple spatial scales in western Europe. *Freshw. Biol.* **2009**, *54*, 756–776. [[CrossRef](#)]
24. Culver, D.C.; Deharveng, L.; Bedos, A.; Lewis, J.J.; Madden, M.; Reddell, J.R.; Sket, B.; Trontelj, P.; White, D. The mid-latitude biodiversity ridge in terrestrial cave fauna. *Ecography* **2006**, *29*, 120–128. [[CrossRef](#)]
25. Pipan, T.; Culver, D.C.; Papi, F.; Kozel, P. Partitioning diversity in subterranean invertebrates: The epikarst fauna of Slovenia. *PLoS ONE* **2018**, *13*, e0185991. [[CrossRef](#)]
26. Pipan, T. *Epikarst—A Promising Habitat*; Založba ZRC: Ljubljana, Slovenia, 2005.
27. Gibert, J.; Culver, D.C. Assessing and conserving groundwater biodiversity: An introduction. *Freshw. Biol.* **2009**, *54*, 639–648. [[CrossRef](#)]
28. Hof, C.; Brändle, M.; Brandl, R. Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types. *Glob. Ecol. Biogeogr.* **2008**, *17*, 539–546. [[CrossRef](#)]
29. Stoch, F.; Galassi, D.M.P. Stygobiotic crustacean species richness: A question of numbers, a matter of scale. *Hydrobiologia* **2010**, *653*, 217–234. [[CrossRef](#)]
30. Ficetola, C.F.; Canadoli, C.; Stoch, F. The Racovitza impediment and the hidden biodiversity of unexplored environments. *Conserv. Biol.* **2019**, *33*, 214–216. [[CrossRef](#)]
31. Zagamajster, M.; Malard, F.; Eme, D.; Culver, D.C. Subterranean biodiversity patterns from global to regional scales. In *Cave Ecology*; Moldovan, O.T., Kováč, L., Halse, S., Eds.; Springer: Cham, Switzerland, 2018; pp. 195–228.
32. Dole-Olivier, M.J.; Castellarini, F.; Coineau, N.; Galassi, D.M.P.; Martin, P.; Mori, N.; Valdecasas, A.; Gibert, J. Towards an optimal sampling strategy to assess groundwater biodiversity: Comparison across six regions of Europe. *Freshw. Biol.* **2009**, *54*, 777–796. [[CrossRef](#)]
33. Culver, D.C.; Sket, B. Hotspots of subterranean biodiversity in caves and wells. *J. Cave Karst Stud.* **2000**, *62*, 11–17.
34. Palacios-Vargas, J.G.; Reddell, J.R. Actualización del inventario cavernícola (estigobiontes, estigófilos y troglóbios) de México. *Mundos Subterráneos* **2013**, *24*, 33–95.
35. Trajano, E.; Gallão, J.E.; Bichuette, M.E. Spots of high diversity of troglóbites in Brazil: The challenge of measuring subterranean diversity. *Biodivers. Conserv.* **2016**, *25*, 1805–1828. [[CrossRef](#)]
36. Deharveng, L.; Bedos, A. Biodiversity in the tropics. In *Encyclopedia of Caves*, 3rd ed.; White, W.B., Culver, D.C., Pipan, T., Eds.; Academic Press: Waltham, MA, USA, 2019; pp. 146–162.
37. Culver, D.C.; Pipan, T. Subterranean ecosystems. In *Encyclopedia of Biodiversity*, 2nd ed.; Levin, S.A., Ed.; Elsevier: Amsterdam, The Netherlands, 2013; Volume 7, pp. 49–62.
38. Deharveng, L.; Bedos, A. The cave fauna of southeast Asia. Origin, evolution, and ecology. In *Subterranean Ecosystems*; Wilken, H., Culver, D.C., Humphreys, W.F., Eds.; Elsevier: Amsterdam, The Netherlands, 2000; pp. 603–632.
39. Deharveng, L.; Lips, J.; Rahmali, C. Focus on guano. In *The Natural History of Santo*; Bouchet, T., Le Guyader, H., Pascal, O., Eds.; Museum National d'Histoire Naturelle: Paris, France, 2011; pp. 300–306.
40. Culver, D.C.; Trontelj, P.; Zagamajster, M.; Pipan, T. Paving the way for standardized and comparable subterranean biodiversity studies. *Subterr. Biol.* **2012**, *10*, 43–50. [[CrossRef](#)]

41. Deharveng, L.; Bedos, A. Diversity of terrestrial invertebrates in subterranean habitats. In *Cave Ecology*; Moldovan, O.T., Kováč, L., Halse, S., Eds.; Springer: Cham, Switzerland, 2018; pp. 107–172.
42. Christiansen, K.A. Proposition pour la classification des animaux cavernicoles. *Spelunca Mem.* **1962**, *2*, 76–78.
43. Christiansen, K.A. Morphological adaptation. In *Encyclopedia of Caves*, 2nd ed.; White, W.B., Culver, D.C., Eds.; Academic Press: Waltham, MA, USA, 2012; pp. 517–528.
44. Culver, D.C.; Pipan, T. *Shallow Subterranean Habitats. Ecology, Evolution, and Conservation*; Oxford University Press: Oxford, UK, 2014.



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