

Hotspots of Subterranean Biodiversity Redux

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For most plants and animals the broad outlines of global species richness are well known, and often in some detail. The same cannot be said of subterranean communities in general and cave communities in particular. A set of challenges face any attempt to describe the biodiversity of cave communities. First, cave habitats are often difficult to access, and the fauna is numerically rare. Second, the ranges of cave species are typically small [1,2], requiring extensive sampling to capture most of the species richness in a region. Third, the cave fauna, which shows highly convergent morphology at the gross morphological level (i.e., the loss of eyes and pigment, and the elongation of appendages [3]), is often considered as a unit comprising many individual clades. Some individual clades are diverse enough for patterns to emerge [4], but this is rarely the case. Fourth, many species remain undescribed and undiscovered [5].

Despite these challenges, there has been speculation concerning the pattern of subterranean biodiversity since at least the 1960s. Early ideas about cave colonization relied heavily on a climate-forcing model, where species were driven into caves by the climate changes instigated by the Pleistocene glaciations [6,7]. Thus, the highest diversity would be expected in those areas where climate effects were strongest, and opportunities for colonization greatest, i.e., near glacial margins in northern temperate zones. With their discovery of obligate cave-dwelling invertebrates in the tropics, Mitchell [8] and Howarth [9] raised objections to both the Pleistocene model of cave colonization and the scarcity of cave-limited species in the tropics. It is curious that obligate cave-dwelling fish were known from tropical Africa and Mexico well before that [10,11], but had little impact on the early discussions of species diversity.

These early studies raised doubts about the temperate richness model, but actual data were slow in coming; contrastingly, the amount of data now accumulated is significant. In 2009, Gibert and Culver [12] reported more than 3500 known species of stygobionts (aquatic species limited to subterranean habitats, typically caves). Of these, 2000 were from Europe—surely an overrepresentation due to much more thorough collection and description. While more data are accumulating outside Europe and the United States [13], the preponderance of data remains European (and, to a lesser extent, from the U.S.A). For example, Zagamajster et al. [14] report on the diversity patterns of 1570 stygobiotic European species, and Christman et al. [15] report on the diversity patterns of 750 stygobiotic and troglobiotic U.S. species based on nearly 10,000 records. For Europe, the continental pattern for both stygobionts and troglobionts is one of a ridge of high diversity at 45° N [14,16], along the spine of the Pyrenees and through the Dinaric karst of Italy, Slovenia, Croatia, Serbia, Bosnia and Hercegovina, and Montenegro. The pattern in the U.S. is less resolved, but there is an overall hotspot of troglobiotic (terrestrial) species richness in northeast Alabama and adjoining parts of Tennessee [16,17]. Explanations for these regional patterns are complex and highly scale dependent [16,18].



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Information on the patterns of global subterranean biodiversity derive almost exclusively from data on individual “hotspot” caves [19]. Outside of Europe and the United States, no extensive regional collection of the scores of caves needed for species accumulation curves [20] has been conducted. Well-sampled tropical caves are listed by Deharveng and Bedos [13]. Given the high β diversity compared to α -diversity [19], inferences from the data about a few very diverse caves would seem unlikely to be informative. However, in their classic paper on subterranean biodiversity, Gibert and Deharveng [1] point out that regional diversity is a good predictor of local diversity and vice versa. This was buttressed by later findings that species accumulation curves infrequently crossed, and thus, the regional pattern could be captured by a relatively small number of samples [16,21]. Culver and Sket [22] 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, which were extensively sampled, were known from most large karst areas. The publication of their paper stimulated both the further sampling of high diversity caves throughout the world, and the compilation of species lists for high diversity caves. Due to this activity, the criterion for the inclusion of a cave in the hotspot list in 2021 was set at 25, with a total of 23 sites meeting this criterion [19,22]. Of these 23 caves, six had over 50 stygobionts and troglobionts [23–27].

An explanation of the observed hotspot patterns, especially for terrestrial hotspots, has proved elusive. For stygobionts, Culver and Sket [22] note that they tended to be from the Dinaric karst, were chemoautotrophic or anchialine, or were connected to ground (phreatic) water. Culver et al. [18] also noted that the stygobiotic hotspots tended to be in chemoautotrophic or in the Dinaric karst. Terrestrial hotspots are more dispersed and occur in both temperate and tropical zones. Part of the problem may be data limitations. There are regions of high species richness but without any one cave being rich, as is apparently the case for a cave region in Brazil [28]. Second, there may be unsampled cave hotspots, ones which will clarify the causes of the patterns.

In a Special Issue of *Diversity*, which was published in 2021 [29], 13 of 23 hotspot caves and their fauna were described in detail, and one other was described elsewhere [30]. Due to the positive response to calls for papers about hotspot caves and the fact that nine hotspot caves require updating, we have added a second Special Issue devoted to this topic. As in the first Special Issue, there will be a species list for each hotspot cave—information that is often unpublished for these caves. This is especially important given the controversy around the ecological status of cave species. Deharveng and Bedos [31] 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 [32,33], i.e., 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 that are found in caves [34]. 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.

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