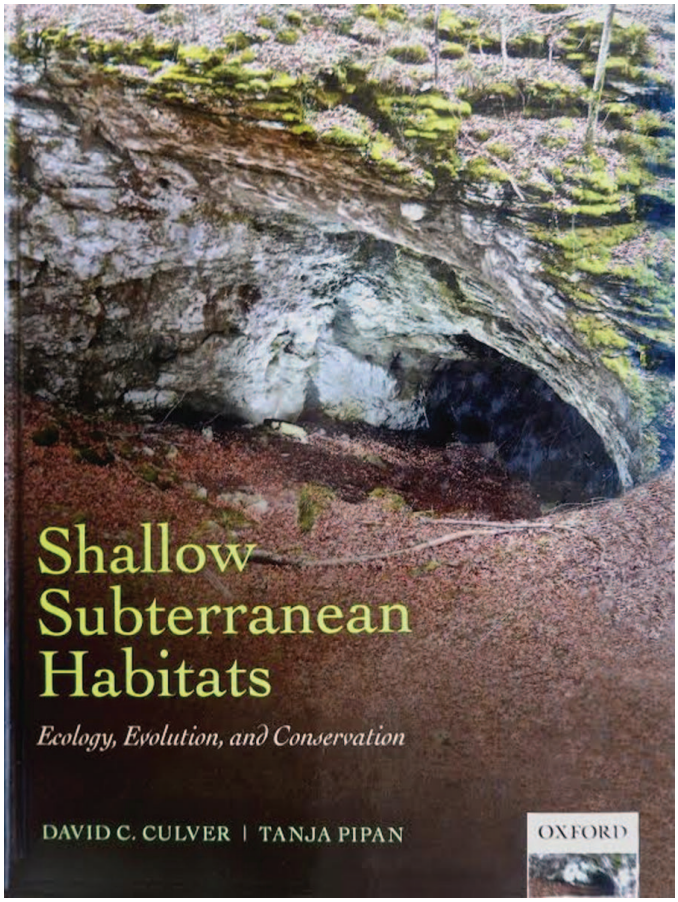
BOOK REVIEW



Shallow Subterranean Habitats: Ecology, Evolution, and Convervation

David C. Culver and Tanja Pipan, 2014. Oxford University Press, UK, 258 p., 10 × 7.5 inches, ISBN 978-0-19-964617-3, hardbound, $99.95.

Overview

As the authors point out in their preface, this book is unlike their 2009 introductory textbook *The Biology of Caves and Other Subterranean Habitats*. It extends their studies to many other shallow subterranean habitats. Their first book emphasized caves, but they later expanded their scope to include many other subterranean habitats with spaces of various sizes. In particular, they extend European workers' hypothesis that interstitial spaces among gravels in the beds of surface streams are the "staging areas" for colonization of deeper spaces, including caves. The shallow subterranean habitats discussed are seepage springs and other hypotelminorheic habitat of the soil-rock epikarst interface, intermediate-sized terrestrial shallow habitats in calcareous aquifers, interstitial habitats along rivers and streams, and soil and lava tubes. Like caves, these habitats have many eyeless and de-pigmented species.

Their approach is heavily quantitative, with 76 graphs and 65 tables, but not nearly as theoretical, in terms of testing of ecological and evolutionary models, as Culver's incredible 1982 book *Cave Life*. They do report cases of rigorous multivariate analyses that associate past and ongoing competition with morphological divergence in size and shape among closely related species, as a result of past and ongoing competition, and they approach the problem of the impossibility of direct sampling of shallow subterranean habitats by substituting statistical approaches to estimate species diversity at increasing spatial and temporal scales. A surprising example of copepods collected from ceiling drips in caves is that 12% of all species ever collected from drips over time, 20% between drips with very different chemistry only a meter apart, and 68% between different caves.

Chapter-by-Chapter Review

Culver and Pipan's book is divided into two parts. After the first chapter, which summarizes the whole book, the next seven chapters provide "a detailed description of shallow subterranean habitats," and the next six chapters are "an exploration of the biological consequences of the existence of these habitats." There follows a short chapter on conservation. Finally a four-page "Epilog and Prospects" discusses what unites and divides shallow subterranean habitats and whether they are "staging areas" for colonization of deeper habitats and, finally, attacks the efficacy of troglomorphy as a unifying theme.

To me, the most interesting shallow subterranean habitat is the epikarst, since Pipan has made this her research focus. The authors show that certain copepod species are epikarst specialists, since they are only found in ceiling drips and drip pools in caves. Their tantalizing results beg, to me, for simple behavioral experiments, as done by Culver in the 1970s to use the diversity of biotic interactions, such as competition, predation, cannibalism, and indirect mutualism, to explain patterns of co-occurrence among species of Appalachian cave-stream isopods and amphipods. For example, it would be easy to put different species of copepods in a bowl alone with a food particle and to watch them, or to make a shallow subterranean analogue of artificial streams to see what aspects of size and leg morphology explain differences in washout rate. These behavioral studies could be complemented with measures of activity and metabolic rate. And raising species in the lab could give data on growth rate, fecundity, and egg size. Sadly, such data are virtually lacking for any species in any such habitat.

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Some of the later chapters in the book are the most interesting and controversial. Chapter 9, ''The role of light in shallow subterranean habitats,'' is merely descriptive. Chapter 10, ''Environmental fluctuations and stresses in shallow subterranean habitats,'' is more analytical. Culver and Pipan point out a seeming contradiction: such habitats provide a refuge from unfavorable surface conditions (climate adversity colonization) or an opportunity to exploit new or better resources (habitat shift colonization), or else they are an extreme environment with many environmental barriers, especially absence of cyclic changes that entrain circadian rhythms and rest homeostasis on the surface.

Chapter 13, ''Colonization and dispersal in shallow subterranean habitats'' is an area of special expertise of the authors, and I have written nothing but ''great'' and ''wonderful'' in the margins. My only slight quibble is in their use of the term *exaptation*. They define it correctly in their glossary, but with no examples that fit the definition. To be fair, they do say that both exaptation and preadaptation ''remain rather elusive concepts.'' I believe that the fact that some soil and litter taxa do not occupy caves does not imply that the adaptations of many surface taxa to dark and cryptic habitats were not necessary for successful colonization of caves and some shallow subterranean habitats.

I also have nothing but praise for the authors' perspectives and choices of a few excellent papers to review in Chapter 14, ''Phylogeny in shallow subterranean habitats.''

Chapter 15, ''Conservation and protection of shallow subterranean habitats'' is mostly standard fare, but well done. They go beyond the usual by discussing types of rarity and a landscape approach to protection on different spatial scales. They show the importance of both these issues in connection with the various types of habitat of the first half of the book.

In their final chapter, ''Epilog and Prospects,'' the authors start with a discussion of what separates and what unites different types of shallow subterranean habitat and then consider which, if any, are ''staging areas'' for colonization of deeper subterranean habitats and caves. There is a brief bit on the confusing proliferation of terms, with a plea to focus on the selective factors in each type of habitat. They end with a very brief ''What about troglomorphy?''

Kudos and Criticisms

The authors do their usual excellent job of discussing the areas of their particular expertise in biogeography and species diversity at different spatial scales and in patterns of morphological variation among species. They discuss pitfalls and limitations of some approaches, especially multivariate statistics, and they are clear where more and better data are needed. Their care in discussing alternatives and the data of others is shown in just one chapter by the phrases *incomplete sampling* (four times), *correlation* (three times), *possibly* (twice), *conflated distance and chemistry* (twice), *may or may not*, *perhaps*, and *many possibilities*. On the other hand they do not hedge when discussing in detail the few very best research studies in several areas.

They do an especially nice job of picking critical research studies and discussing both the data and the implications. In addition to their own studies on copepods in the epikarst, I especially liked the following:

1. Gers's (1992) special traps that sample living fauna from the surface to 2-m deep in the epikarst.
2. A number of studies of calcrete aquifers in Australia and the amazing radiation of Dytiscid beetles.
3. Canonical variate analyses of size, shape, and other morphology in relation to habitat metrics. These include their own on copepods, another on *Niphargus* amphipods, and another on cholevine beetles. Each unmasks unexpected relationships that suggest experimental studies.
4. Rouch's (1988) many-year and all-season studies of the entire fauna in a 75 m^2 stream sample with its surface and shallow subterranean microhabitats.
5. As reviewed by Peck and Finston (1993) for Hawaii, Galapagos, and Canarys there are many sister species and on this basis researchers have championed habitat shift colonization with parapatric speciation.
6. Pioneering work by Howarth et al. (1980) in pointing out high tropical Hawaiian troglobite diversity, as opposed to some views that tropical caves have few troglobites.
7. In discussing organic carbon and nutrients in shallow subterranean habitats, the emphasis on Huppop's comprehensive review (2012) that cave fish of several species show a number of metabolic economies that are best explained by restricted food input into caves. In aquatic shallow subterranean habitats Simon and colleagues show a change in the quality of organic carbon with depth in the epikarst and into caves with increasing carbon limitation.

The authors provide a less unbiased review, and less complete citation, of examples that do and do not support their favorite hypotheses. ''Our first book was in a way a consensus view... and we did not emphasize the controversies of the field.'' ''This book is different, and we have put forward our views, even when it is perhaps a minority view.'' Since their book is intended for students and advanced researchers, this is excusable. But I would have liked them to address other views and give evidence to support their favorite hypotheses. I agree that absence of light is the only universal agent of selection with universal

reduction in eyes and pigment. But they miss a pattern that there are increasing degrees of troglomorphy, as taxa have increasing costs of doing business (Poulson, 2012) such as finding food in the face of increasing scarcity and dealing with circulation and respiration costs of increasing size. In some cases, they have missed important papers and not given due credit to earlier researchers. The most important example is the quasi-annual timing of flooding and its relation to circannual cycles of reproductive readiness. In other cases, they do not make sufficiently critical analyses where data are incomplete or even lacking. The most important example is the poorly conceived and supported hypotheses about the supposed stress of high humidity and the importance of ''bad air'' with high CO_2 and low O_2 in the habitat of troglobites. I would have liked to see an update of their table (12.1), which reproduces verbatim Christiansen's (1962) list of troglomorphic features that does not distinguish reducing and increasing traits, has many traits found only in a few taxa, and is incomplete on behavioral, physiological, and life history. They selectively, and sometimes incorrectly, cite studies that support their thesis that natural selection for reducing traits is ubiquitous and that neutral mutations are rare. Examples are some new papers on *Astyanax* cavefish and both old and new papers on amblyopsid cavefish. They give too much emphasis and uncritical support to a study of an evolutionarily new troglobitic beetle that supposedly uses remnant eyes and has vision genes that are supposedly functional. A main critique centers on a few pages at the end of Chapter 12 subtitled ''A new look at troglomorphy.'' They laud early studies and a landmark review on convergent evolution, but then say that ''cracks have appeared in the façade of convergent evolution of troglomorphy.'' In my view, they have been selective in citing support for this statement and in two cases are incorrect about facts.

There are several additions that I suggest would have improved their book. At the top of my list are:

1. A detailed look at whether different shallow subterranean habitats are source populations, with sustaining reproduction, or sinks.
2. Comparative drawings of surface formas, troglophile generalists, and troglobites, including epikarst specialists.
3. Inclusion of discussion of elaborated troglomorphies of physiology, behavior, and life history.
4. Simple lab experiments, since most of the species in their habitats cannot be watched in the field. Good models are Culver's own studies of amphipods in artificial streams and Christiansen's clever experiments on Collembola that showed how behavioral deployment of their tiny foot complex allows them to essentially walk on water.
5. Discussion of leaf litter as a staging area for colonization of some small-volume subterranena habitats. What traits are really pre-adaptations?

Summary

This book is the second coauthored by Culver and Pipan, and the fourth that Culver has authored or coauthored. Like those, this book is well-written and very professional. Some indicators of its rigor are the 76 graphs, 65 tables, 40 drawings and diagrams, 24 photos, 16 maps, 550 literature citations, and an 8-page glossary. This book will best serve professionals and advanced students with some background in biospeleology.

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