

Chapter 10

Managing Microbial Communities in Caves

Diana E. Northup

Abstract Microbial communities in caves vary from striking microbial mats observed in many lava tubes worldwide, to occasional colonies on the wall, to invisible biofilms on rock walls and ceilings of caves, to microbial end products, such as manganese oxides. The investigations of the last decade, using culture-independent techniques in which we extract DNA from environmental samples and sequence clones to identify organisms present based on their genetic sequence, have revealed a wealth of microbial species never before described. These microorganisms represent a minimally explored treasure trove of organisms that can be impacted by the actions of humans living above caves and exploring within caves. The degree to which we impact cave microbial communities depends on the nature of the cave. Mammoth Cave in Kentucky, USA, and other similar caves, have rivers or streams running through major portions of the cave. Water flowing into caves may either bring plumes of pollutants to many parts of the cave and/or may help to wash away some impact caused by human visitation. Arid-land caves, such as Lechuguilla Cave in New Mexico, USA, that lack much in the way of flowing water, may be subjected to other kinds of impacts. Several strategies have been suggested to lower the impact that we explorers, scientists, and people living above caves have on cave microbial communities in order to preserve them for future study. Cave microbial communities can represent an extremely valuable resource that is worth protecting by modifying our behavior in visiting and living above caves.

D.E. Northup (✉)
Biology Department, University of New Mexico, MSC03 2020,
87131 Albuquerque, NM, USA
e-mail: dnorthup@unm.edu

10.1 Introduction

Microorganisms in caves range from completely invisible to highly colorful microbial mats (Fig. 10.1) that line the walls of lava tubes to microbial waste products, such as iron oxides. It is hard to appreciate and value something that you cannot even see (Fig. 10.2), but there are many compelling reasons to protect and conserve cave microorganisms and their habitat, including the immense amount of novel diversity that we are finding, the roles that microorganisms play in the formation of speleothems in caves, and the potential compounds of biomedical and biotechnological use that cave microorganisms may produce.

In the last two decades, we have seen a major increase in research concerning the role that microorganisms play in the dissolution of bedrock and other surfaces and the precipitation of secondary mineral deposits (Barton and Northup 2007; Northup and Lavoie 2001). New discoveries of sulfur oxidizing bacteria in caves are revealing microbial roles in cycling sulfur in caves (Fig. 10.3) and enlargement of cave passages through sulfuric acid dissolution, as well as a possible role in sulfuric acid driven speleogenesis (Engel et al. 2004; Hose et al. 2000; Macalady et al. 2007).



Fig. 10.1 Colorful microbial mats adorn the walls of many Azorean lava tubes. The photo on the left gives an overview of a yellow microbial mat, while the photo on the right shows a closeup of yellow microbial colonies growing on organic ooze on a basalt formation. Photos courtesy of Kenneth Ingham



Fig. 10.2 Microscopic organisms that live on cave walls in limestone caves and lava tubes present an amazing array of shapes when viewed with a scanning electron microscope. **(a)** Putative bacterial filamentous morphology was found in a gold mineral-like deposit from Four Windows Cave, El Malpais National Monument, New Mexico, USA. **(b, c)** Rods, filaments, beads-on-a-string, and fuzzy coccoid morphologies were observed in white microbial mats from an Azorean lava tube on the island of Terceira, Portugal. **(d)** Fuzzy cocci and segmented filaments were revealed in a sample from a Cape Verde lava tube. Photomicrographs by Michael Spilde, Penelope Boston, and Diana Northup

Spilde et al. (2005) have shown a microbial role in the production of ferromanganese deposits in arid-land caves, where little organic carbon exists to fuel microbial processes (Fig. 10.4). These and other studies are showing key geomicrobiological roles for microorganisms in caves. Although much remains to be learned about the microbial role in energy transfer and elemental cycling, some evidence suggests that microorganisms facilitate the transfer of energy between cave life and organic carbon and serve as food for the cave life (Simon et al. 2007). Perhaps, most exciting is the amount of novel biodiversity that culture-independent molecular studies are revealing in caves (e.g., Barton et al. 2004; Gonzalez et al. 2006; Northup et al. 2003). Some of these novel (and not so novel) species may produce chemical compounds that are very useful to humans, such as new antibiotics to replace those to which bacteria are now resistant (Dapkevicius, Terrazas and Northup, unpub. data). The geomicrobiological studies (Barton and Northup 2007) and those of novel

Fig. 10.3 Pendant acidic microbial structures, termed snottites, hang from the walls of sulfur caves such as Cueva de Villa Luz in Tabasco, Mexico. Photo courtesy of Kenneth Ingham

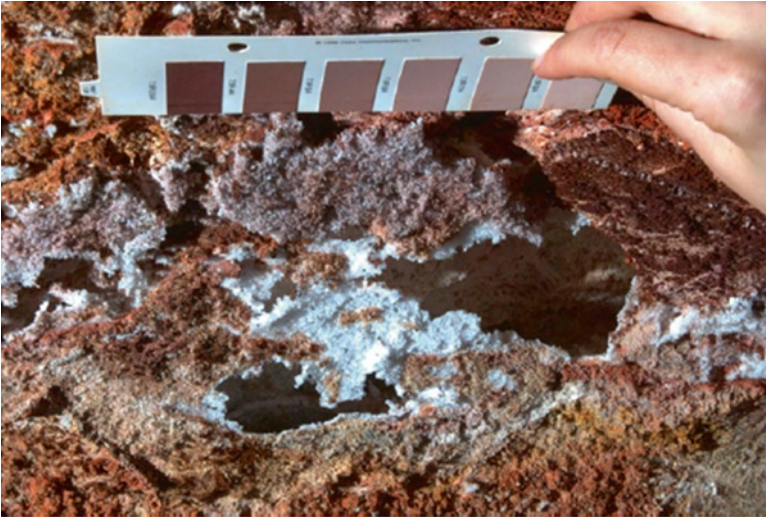


Fig. 10.4 Red, brown, and pink ferromanganese deposits, which contain varied microbial communities, adorn the walls of Spider Cave, Carlsbad Caverns National Park, New Mexico. Photo courtesy of Kenneth Ingham

microbial biodiversity also serve to aid our understanding of how to detect life on other planets, such as Mars, where life is likely to shelter from harsh surface conditions in the subsurface (Boston et al. 2001). Thus, our research emphasizes the critical nature of cave microbial communities and suggests that their conservation is vital. However, several threats to cave microbial populations exist.

10.2 Threats to Microbial Populations

Cave microorganisms are susceptible to a variety of threats, including human visitation, soil compaction, pollutant spills, cave restoration, habitation above caves, and organic carbon enrichment. Whether microorganisms reside in arid-land caves, or those in areas with more rainfall, affects the degree to which these threats are an issue for microbial populations. Rivers and streams running through caves can carry away pollutants and dampen the effects of various threats; however, rivers and streams can also be the vehicle for introducing pollutants. Such pollutants can have a major impact of aquatic microbial communities within caves with potential subsequent impacts on the invertebrate communities that feed on these microbial communities. Some threats are common across this spectrum, while others are more problematic in arid-land caves.

10.2.1 *Organic Carbon and Other Nutrient Enrichment from Human Visitation*

Arid-land and caves are much more subject to the effects of organic carbon enrichment and other impacts that result from human visitation of caves due to their oligotrophic nature. When we visit caves, we shed tens of thousands of skin cells, many of which are life rafts for our own microbial inhabitants, as well as hair and fibers and mud from our clothing. If we are sick and vomit in the cave, we greatly enrich organic carbon in the habitat. Longer cave trips may bring the issues of urine and feces deposition (Fig. 10.5). While cricket and beetle feces are a natural part of the ecosystem, human feces are not. Humans obviously deposit much more feces than a cricket and human feces has almost 50% microorganisms. Urine can lead to the buildup of harmful compounds that change the microbial ecosystem (Lavoie 1995). Most cave visits are several hours in duration and often involve eating. Dropping crumbs of food in the cave may not seem much of an impact, but to the microbial communities it represents a large infusion of organic carbon, which may, over time, fuel the growth of “weedy” heterotrophic organisms such as the fungus pictured in Fig. 10.6. These microorganisms, which may be transplants from the surface, may then outcompete the resident microorganisms, if organic carbon levels throughout the cave have increased. Where native microbial populations reside in oligotrophic habitats within caves, we may see the most profound effects.



Fig. 10.5 A sign warns against depositing feces in the cave

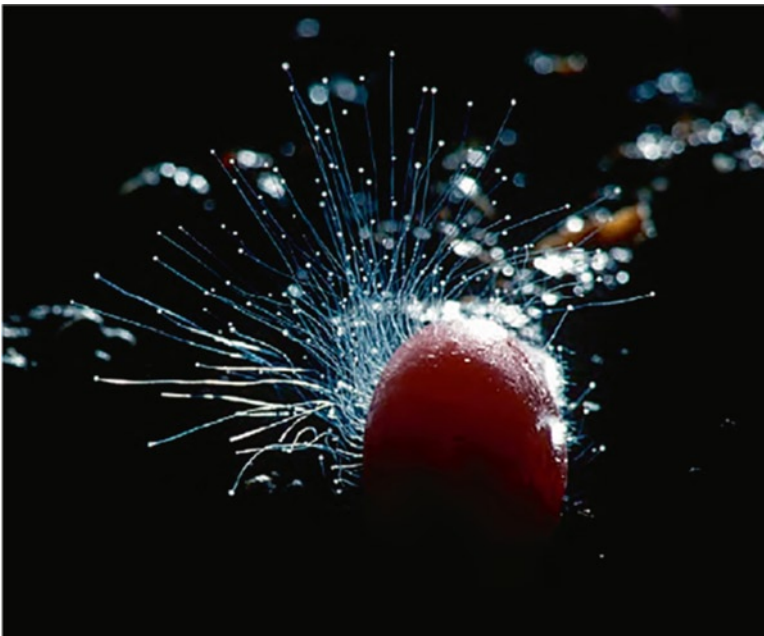


Fig. 10.6 Human visitors dropped a jelly bean, which fueled the growth of microorganisms in this lava tube. Photo courtesy of Kenneth Ingham

Oligotrophic microorganisms do not simply get “fatter” when you feed them more; they often die off, allowing more surface-adapted microorganisms to take their place. Koch (1997) suggests that organisms in low nutrient environments grow at very slow rates and that cultivation studies using standard amounts of nutrients simply provoke death, which suggests that carbon enrichment of the cave, may prove harmful to the native micro biota. Thus, human visitation can introduce new organic matter and exotic microorganisms into caves, which may harm native microbial populations.

Some organic carbon enrichment originates from the surface in a variety of ways (Fig. 10.7). Sinkholes have long been a favorite place for the dumping of trash.



Fig. 10.7 Sinkholes are convenient trash dumps; sewage pipes occasionally penetrate caves; and land use above caves, such as grazing, can provide higher levels of nutrients entering caves. Photos courtesy of Kenneth Ingham

Besides being a source of organic carbon enrichment into caves, some trash brings toxic chemicals which may harm microbial communities, or in some cases may stimulate the growth of microorganisms that can utilize chemical substances that are toxic to most life forms.

Sewage leakage into caves can be a major source of organic carbon and other nutrient enrichment. In some rural communities, sewage pipes have been known to penetrate caves (Fig. 10.7), dumping raw sewage into the cave. In other instances, cave visitor centers have had inadvertent sewage leaks into the caves when the aging sewer system cracked and failed without being detected for a prolonged period of time. This led to the growth of bracket fungi in one case. Leaks such as this, invariably test positive for fecal coliforms and pose a health hazard to cave visitors.

10.2.2 Physical Threats

As we walk through areas of the cave with soil or detrital material, we cause compaction of the soil, which decreases the available oxygen. Some organisms may be killed outright by this physical compaction. Because of the lack of substantial weathering in caves, such compaction takes a very long time to reverse. Some visitors draw their names and dates in microbial mats (Fig. 10.8), eliminating microorganisms in the path of their finger and leaving behind their own microorganisms and skin oils (Varela 2009). Some of the names and dates that we have observed in lava tubes have only minimal microbial re-growth after two decades.

10.2.3 Threats from Imported Exotic Microorganisms

Human visitors to caves shed many of their associated bacteria and fungi as they walk, climb, and crawl through caves. Our studies (Lavoie and Northup 2006; unpublished data) suggest that human associated bacteria (e.g., *Staphylococcus aureus*) are preferentially found in areas with more human impact (Fig. 10.9). Because fungi produce copious numbers of spores that travel easily through the air, they are often found in equal measure in low and high impact of more open caves. If the cave is given time to “rest” (i.e., no human visitation), and we limit the amount of organic carbon buildup, these exotic populations generally die off. However, some exotic populations of bacteria and fungi, brought in by humans and arthropods, can persist and damage cultural artworks, such as those found in the caves of France and Spain (Dupont et al. 2007; Jurado et al. 2008; Bastian et al. 2010 and references therein). Recently, a newly described fungus, *Geomyces destructans* (Gargas et al. 2009), has been hypothesized to contribute to the death of more than a million bats in the eastern United States. It is currently unknown whether the fungus is native to caves or whether humans have transported the fungus into the cave; research is ongoing to determine the cause of the massive die-off and



Fig. 10.8 Human visitors write their names (*top image*) in the microbial communities of these Azorean lava tubes, or leave finger smear marks behind when touching the walls (*bottom image*). Photos courtesy of Kenneth Ingham

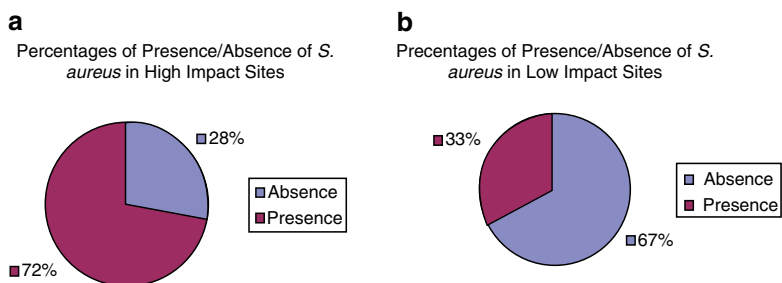


Fig. 10.9 (a, b) Relative proportion of *Staphylococcus aureus* in high (a) and low (b) human impact areas of Carlsbad Cavern, Carlsbad Caverns National Park, New Mexico, USA. Graphs courtesy of Jessica Snider

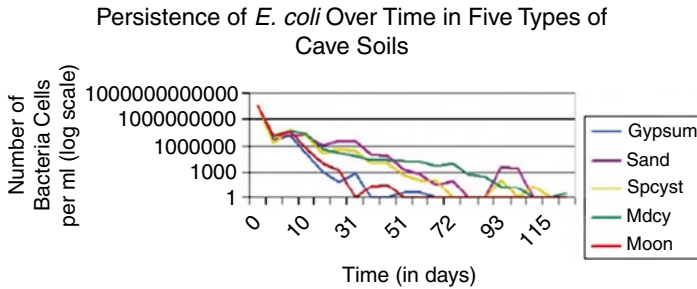


Fig. 10.10 *E. coli* inoculated into five different soil types from Carlsbad Cavern and Spider Cave in New Mexico, show different patterns of persistence over time. Graph courtesy of Amaka Nwagbologu

illustrates how little we actually know about the role that humans play in changing the makeup of microbial populations in caves.

One conservation technique, designed to protect the pristine pools of Lechuguilla Cave in Carlsbad Caverns National Park, did not have the desired outcome. Explorers and land managers introduced plastic tubing into pools designated as drinking water sources in order to circumvent the need to dip water bottles in the pools, thereby hopefully preventing the contamination of the pools. However, the tubing used contained plasticizers that leaked into the pool, promoting the growth of native bacteria that grew to visible streamers within the tubing, putatively due to the enrichment of organic carbon from the plasticizers. This population explosion of a native bacterial population may have supported or introduced *E. coli* population growth in the pool (Hunter et al. 2004). In response to our study, Barton and Pace (2005) raised the issue of whether *E. coli* would persist in the cave environment. We believed that it would (Hunter et al. 2005), and subsequently conducted experiments with cave soils inoculated with *E. coli*. These studies demonstrate that *E. coli* can persist in a variety of cave soils at cave temperatures for extended periods of time (Fig. 10.10). *E. coli* appears to persist in clay soils, in particular. More research is needed into how human associated microorganisms affect microbial populations in caves and the extent to which they persist in the cave environment.

10.2.4 Threats from Cave Restoration Efforts

Our well intended efforts to restore and clean caves can lead to many problems for microbial communities as detailed in Boston et al. (2005). Some restoration efforts use chemicals that can harm cave macro- and microbiota. Chlorine bleach is one of the major hazardous chemicals that is often used in restoration work. The problem with chlorine bleach comes from its nature as a strong oxidant, which can lead to a major decimation of organic matter and the death of invertebrates and microorganisms. Techniques such as pressure water sprays also can be harmful from two perspectives.

The high pressure water can remove and kill biofilms. Secondly, depending on the source and nature of the water, it can introduce non-native microorganisms into the cave and may be acidic in nature. Another consideration in cave restoration is how to clean cave pearl nests. There is some evidence that microorganisms may play a role in cave pearl formation, or at least be associated with cave pearls. Removing the water from around them, or handling the pearls themselves, may either remove needed nutrients or may damage biofilms on the pearls. Extreme care should be taken in cleaning cave pearl areas until we know more about their formation. Thus, careful consideration of what techniques can be used in restoration, without major harm to microbial communities, is essential.

A major target of restoration work is algae and other organisms whose growth is associated with lights in show caves. This growth, which can be from algae, cyanobacteria, or other microbial partners, is often quite luxuriant (Fig. 10.11). Olson (2005) has recommended the use of lighting that employs wavelengths that are utilized extensively by the photosynthetic organisms growing in lampenflora.



Fig. 10.11 Show caves, such as this lava tube in Hawai'i, utilize lights to guide visitors to the caves. These lights result in the growth of lampenflora. Photo courtesy of Kenneth Ingham

Both Olsen (2005) and Mulec and Kosi (2009) offer additional strategies for controlling the growth of lampenflora, while lessening harm to native microbiota.

10.3 Is Protection Possible During Active Exploration and Scientific Investigation?

Should microbial communities in caves be protected at the expense of human access to some caves? Should we entertain the idea of creating “microbial preserves” that protect critical microbial populations within certain areas of caves? At one end of the spectrum is the case of Lascaux Cave in France, which houses some of the world’s most fabulous cave paintings. Microbial damage to the paintings, caused in part because of human visitation, led to the closure of the cave in order to protect the paintings and many investigations and mitigation strategies have ensued (reviewed in Bastian et al. 2010). The seriousness of the deterioration led to the formation of the International Committee for the Preservation of Lascaux and the passage of resolutions by UNESCO’s World Heritage Committee to work toward more effective means to save these paintings whose value is beyond measure. In the case of Lascaux, there is little doubt that extreme preservation is warranted. But what about less well-known caves, where what is threatened are microbial communities that are invisible to the unaided eye. Additionally, because the research is just beginning into how much of an effect that humans have on microbial populations, it is often hard to make a strong case for making some areas off limits to human visitation in order to protect microorganisms. What is clear is that we need to advance the study of microorganisms in caves and the effect that humans have on cave microbial populations.

In the meantime, there are some relatively simple things that can be done to protect microbial communities in caves. The success of recommendations for protecting cave microbial populations rests in the acceptance of the value of these microbial populations by cavers, scientists, and other visitors to caves. It is hard to think about and protect things that you cannot even see. If cave microorganisms are perceived to be a key component of the cave ecosystem, or an effective treatment for cancer or a new antibiotic that could save a life someday could come from a cave microorganism, then people may be more willing to go the extra mile for the microbes. To provide the information to increase motivation for microbial conservation in caves, we will need to conduct more research into what harms and what protects microbial communities in caves, in conjunction with using that information to educate cave visitors about the problems and solutions. One of the payoffs is that educational programs about cave microorganisms often excite and engage cave visitors – the microbes have wonderful stories to tell. We have begun efforts to share our scanning electron micrographs of cave microbes through the IDEC (Imagery Data Extraction Collaborative) website (<http://idec.aisti.org>). This site allows viewers of all backgrounds to comment on images and the features contained in them and allows teachers to download images that they can use in their curriculum.

10.4 Recommendations

To protect a subject of interest, you need to understand it. Our knowledge of cave microbial communities is rudimentary, limiting our ability to know precisely what efforts will protect microbial communities in caves. Several laboratories around the world are conducting outstanding culture-independent molecular studies of cave microbial communities to identify novel biodiversity, while others are culturing cave microorganisms to shed light on their physiology and biochemistry, but we need more scientists involved. The first molecular study of microbial diversity was published in 1997, and while many others have followed it, much remains to be learned. Microbial inventories across gradients of depth, nutrient richness, distance from entrances, human impact, etc. are needed to compile a more complete picture of cave microbial communities. Many interesting ecological and evolutionary questions about cave microorganisms await researchers (e.g., Snider et al. 2009). Thus, research and inventory are key steps in our efforts to protect cave microorganisms.

Several research questions concerning the impact of humans on microbial communities in caves require additional research. These include, but are not limited to:

- How do we differentiate native microorganisms from non-natives?
- What human associated microorganisms can be used as tracers of human impact?
- Do human associated microorganisms persist in cave soils and surfaces? Are they metabolically active?
- To what extent does human visitation in caves contribute to organic matter buildup?
- Does organic matter and other nutrient enrichment harm native microbial communities?
- What effects do surface land use practices in karst areas, such as grazing and other human activities, have on cave microbial communities? Do these activities result in increased nutrients entering the cave?
- What techniques can we employ to decrease organic matter enrichment from cave visitation and surface activities?
- We also need to identify critical microbial habitats within cave and karst areas that need additional protection. Different kinds of caves are going to vary in their microbial community makeup and vulnerability. We know little about these differences as yet.
- The following recommendations to conserve microbial habitat and microorganisms are based on our preliminary investigations and insights into microbial communities in arid-land caves, but their effectiveness remains to be tested:
- *Establish trails for movement through the cave.* When you establish trails, use inert markers that do not enrich organic carbon in the cave and do not degrade. Some forms of flagging have proven to be “tasty” to microorganisms and invertebrates, such as camel crickets. If there are no marked trails, always walk where the “elephant tracks” are.
- For caves in which camping is necessary for exploration, *establish camps to concentrate human impact.* If at all possible, carry out all human waste.

- *Eat over bags to catch all crumbs.* What is a crumb to you is a supermarket to a microorganism.
- *Clean your clothes and boots between cave trips to prevent cross contamination of microorganisms between caves.*
- *Brush your hair and beard to remove loose hairs before going caving.*
- *Find ways around pristine pools and avoid dipping anything, including yourself, in the pool.* Establish a clean pitcher for obtaining water. If you use plastic tubing to siphon water, make sure that the tubing does not leak plasticizers that can support microbial growth (Hunter et al. 2004).
- Educate new cavers about cave microbial communities and the ways to preserve and protect microbial communities.

Scientists, cavers, and cave managers who find unusual deposits that may be microbial should consider establishing a microbial preserve to allow investigation before visitation occurs to any extent. If you see something really intriguing, send a photo to one of the microbiologists around the world who studies these communities in caves. Scientists often study a few areas very intensively and may miss key discoveries. Cavers and scientists should collaborate on microbial discoveries for mutual benefit. Scientists can excite cavers and visitors by providing engaging information about their findings through public talks, articles, and other media that bring the science to the public.

10.5 Conclusions

Our knowledge of microbial diversity in caves is growing rapidly and revealing a wonderland of microorganisms that participate in precipitation and dissolution of cave mineral deposits that have roles in nutrient cycling within the cave ecosystem, that may produce chemical substances of great use to humans, and that serve as an analog for possible life on other planets. These important communities are, however, threatened by some of our actions when we visit or live and work above caves. By being conscious of the ways in which we may enrich organic carbon in caves, explorers, scientists, and landowners can do much to protect microbial habitats and microorganisms in caves. Are cave microorganisms threatened? In 1997, Jim Staley wrote the following concerning microorganisms in general:

Our knowledge of microbial diversity, particularly bacterial diversity, is so meager that we do not yet know if and when most species are threatened.

This is particularly true of cave microorganisms and enhanced efforts to study and understand cave microbial communities are essential to our being able to truly answer the question of whether these populations are threatened. Through a variety of ways, we provide challenges to subterranean microbial populations, but you are not yet fully informed about what these challenges are and the best ways in which to mitigate them.

Acknowledgements Many cavers and fellow scientists over the years have provided immeasurable help in carrying out the various research projects that led to observations that formed the basis for the ideas contained in this manuscript, and in providing leads to new microbial habitats. They include, but are not limited to: Kathy Lavoie, for being my partner in many of the research projects that have begun to explore the impact of human associated bacteria in caves; Amaka Nwagbolu, Jessica Snider, and Elizabeth Lavoie carried out several of the experiments and analyzed data; Kenneth Ingham, for all his great microbe photography; Val Hildreth-Werker and Jim Werker, for photography, engineering, and lots of great research; Andi Hunter, for her invaluable research into the contamination of pools in Lechuguilla Cave; the staff of the Cave Resources Office at Carlsbad Caverns National Park, including Dale Pate, Harry Burgess, and Stan Allison for supporting the project; and Penny Boston and Mike Spilde, with whom I have had many stimulating conversations about microbes. The Charles A. and Anne Morrow Lindbergh Foundation, Mammoth Cave National Park, and T & E, Inc. provided financial support for the human impact studies that were carried out in collaboration with Kathy Lavoie who contributed substantially to the ideas on human impact. Thanks go to Leslie Melim and Kenneth Ingham for insightful comments on the manuscript.

References

- Barton HA, Northup DE (2007) Geomicrobiology in cave environments: past, current and future perspectives. *J Cave Karst Stud* 69:163–178
- Barton HA, Pace NR (2005) Discussion: persistent coliform contamination in Lechuguilla Cave pools. *J Cave Karst Stud* 67:55–57
- Barton HA, Taylor MR, Pace NR (2004) Molecular phylogenetic analysis of a bacterial community in an oligotrophic cave environment. *Geomicrobiol J* 21:11–20
- Bastian F, Jurado V, Nováková A et al (2010) The microbiology of Lascaux Cave. *Microbiology* 156:644–652
- Boston PJ, Spilde MN, Northup DE et al (2001) Cave biosignature suites: microbes, minerals and Mars. *Astrobio J* 1:25–55
- Boston PJ, Northup DE, Lavoie KH (2005) Protecting microbial habitats: preserving the unseen. In: Hildreth-Werker V, Werker JC (eds) *Cave conservation and restoration*. National Speleological Society, Huntsville, pp 61–82
- Dupont J, Jacquet C, Dennetière B et al (2007) Invasion of the French Paleolithic painted cave of Lascaux by members of the *Fusarium solani* species complex. *Mycologia* 99:526–533
- Engel AS, Stern LA, Bennett PC (2004) Microbial contributions to cave formation: new insights into sulfuric acid speleogenesis. *Geology* 32:369–372
- Gargas A, Trest MT, Christensen M et al (2009) *Geomyces destructans* sp. nov. associated with bat white-nose syndrome. *Mycotaxon* 108:147–154
- Gonzalez JM, Portilo MC, Saiz-Jimenez C (2006) Metabolically active Crenarchaeota in Altamira Cave. *Naturwissenschaften* 93:42–45
- Hose LD, Palmer AN, Palmer MV et al (2000) Microbiology and geochemistry in a hydrogen sulphide-rich karst environment. *Chem Geol* 169:399–423
- Hunter AJ, Northup DE, Dahm CN et al (2004) Persistent coliform contamination in Lechuguilla Cave pools. *J Cave Karst Stud* 66:102–110
- Hunter AJ, Northup DE, Dahm CN et al (2005) Persistent coliform contamination in Lechuguilla Cave pools – response: Barton and pace discussion. *J Cave Karst Stud* 67:133–135
- Jurado V, Sanchez-Moral S, Saiz-Jimenez C (2008) Entomogenous fungi and the conservation of the cultural heritage: a review. *Int Biodet Biodeg* 62:325–330
- Koch AL (1997) Microbial physiology and ecology of slow growth. *Microbiol Mol Biol Rev* 61:305–318

- Lavoie KH (1995) The effects of urine deposition on microbes in cave soils. In: Pate DL (ed) Proceedings of the 1993 National Cave Management Symposium, Carlsbad, New Mexico, 27–30 Oct 1993. National Cave Management Symposium Steering Committee, Huntsville, pp 302–11
- Northup KH, Northup DE (2006) Bacteria as indicators of human impact in caves. In: Proceedings of the 17th National Cave and Karst Management Symposium, Albany, New York, 31 Oct to 4 Nov 2005. The NCKMS Steering Committee, pp 40–47
- Macalady JL, Jones DS, Lyon EH (2007) Extremely acidic, pendulous cave wall biofilms from the Frasassi cave system, Italy. *Environ Microbiol* 9:1402–1404
- Mulec J, Kosi G (2009) Lampenflora algae and methods of growth control. *J Cave Karst Stud* 71:109–115
- Northup DE, Lavoie KH (2001) Geomicrobiology of caves: a review. *Geomicrobiol J* 18:199–222
- Northup DE, Barns SM, Yu LE et al (2003) Diverse microbial communities inhabiting ferromanganese deposits in Lechuguilla and Spider Caves. *Environ Microbiol* 5:1071–1086
- Olson R (2005) Control of lamp flora in developed caves. In: Hildreth-Werker V, JC Werker (eds) National Speleological Society, Huntsville, pp 343–348
- Simon KS, Pipan T, Culver DC (2007) Conceptual model of the flow and distribution of organic carbon in caves. *J Cave Karst Stud* 69:279–284
- Snider JR, Goin C, Miller RV et al (2009) Ultraviolet radiation sensitivity in cave bacteria: evidence of adaptation to the subsurface? *Int J Speleol* 38:1–12
- Spilde MN, Northup DE, Boston PJ et al (2005) Geomicrobiology of cave ferromanganese deposits: a field and laboratory investigation. *Geomicrobiol J* 22:99–116
- Staley JT (1997) Biodiversity: are microbial species threatened? *Cur Opin Biotech* 8:340–345
- Varela AR, Dapkevicius MLNE, Northup DE (2009) Microorganisms isolated from Azorean lava tubes have antimicrobial activity towards food-borne pathogens. *Actas do 9 Encontro de Quimica dos Alimentos*, pp 146