Chapter 4
Biodiversity: Extracting Lessons from Extreme Soils

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4.1 Introduction

The organisms that live in extreme environments have justifiably captured the imagination of people fascinated with the detection of life and exploration. Reasons for this captivation vary. Some see exploration of these organisms and their environment as a scientific area to provide insight about life on earth, whereas others see economic potential. Whether the extreme environment is human-caused, such as a polluted soil, or a more natural environment (aquatic hot springs, ice, ocean depths, atmosphere, or land), unravelling and understanding the resident organisms, their mechanisms of survival, and the intricate relationship between the habitat and other species, can help us understand life on this planet and elsewhere. Because of global changes, many aspects of extreme environments, such as the identity and types of organisms and communities, the biological traits that allow evolutionary success in a harsh environment, the patterns of distribution of these organisms, the factors controlling their distribution, and their influence on and feedback from ecosystem processes, have increasing relevance to all terrestrial ecosystems. This chapter examines how extreme soils as a habitat for biota can inform our general knowledge of terrestrial biodiversity in many other ecosystems. A brief background on soil biodiversity from other terrestrial systems is presented to set the stage for lessons derived from studies of extreme soils.

Biodiversity is defined by the United Nations Convention on Biodiversity (CBD) as the "variability among living organisms from all sources … and the biological complexes of which they are a part: this includes diversity within species, between species and of ecosystems" (Convention on Biodiversity 2004). This expansive definition is extremely useful for describing life on earth, determining the biotic composition of an ecosystem, and addressing the rapid changes occurring at temporal and spatial scales to the ecosystem, such as the increasing rate of

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P. Dion and C.S. Nautiyal (eds.), *Microbiology of Extreme Soils*. *Soil Biology 13*

extinctions of species. Scientists have emphasized that entire populations, as well as single individuals of a species, are being lost at an accelerating rate. The CBD definition is based on both classical morphological and/or genetic taxonomic knowledge of the biological distribution of species, whether endemic or widespread.

The numbers of species of plants and large animals across landscapes and their global distribution are better known than for smaller invertebrates or microbes, and likewise, more is known about biodiversity above- than belowground (Wardle 2002). Whether there are accelerating rates of extinction for less visible organisms such as bacteria or fungi, and particularly for belowground biota, has yet to be determined. Instead, in many cases, protection of a land area for aboveground species assumes belowground species are also conserved. Whether the spatial scale of the protected area is adequate for conservation of both above- and belowground species and food webs is less studied, but land conserved for a plant in a small habitat might be inadequate to conserve significant levels of diversity belowground.

The world's soils have a large abundance and wealth of biotic diversity with species numbers estimated to be greater than aboveground diversity (Wardle 2002). Taxa include microbes (bacteria among which are cyanobacteria and actinomycetes, fungi, Archaea), protozoa, microscopic invertebrates (microarthropods, nematodes, rotifers, tardigrades), large invertebrates (snails, millipedes, centipedes, termites and earthworms), vertebrates (moles, gophers, lizards), vascular plant roots and lichens, cryptogamic crusts, algae, and mosses. Many of these smaller groups can be found in a handful of soil (Wall and Virginia 2000). Because of the abundance and diversity of the multiple taxonomic groups, identifying all species and their interactions in a single soil sample has been problematic. Instead, our understanding of soil biodiversity is largely based on trophic or functional classifications (e.g., herbivore, predator, microbial feeder, detritus feeder) derived from scientific literature on the feeding habits and morphology of a few species. This approach can then be extrapolated to assemble other unnamed species into functional groups in complex food webs. The contribution of soil biota components in ecosystem processes has thus been postulated based on functional grouping of similar species into food webs. This has proven useful to quantify the role of soil biota in processes such as regulating the rate of soil organic matter decomposition, nitrification, primary production, and nutrient cycling (Hunt and Wall 2002). However, research is needed, as assumptions regarding functionality of large groups of soil organisms may not provide realistic measures of these processes.

A further and critical recognition of the dependence of humans on the benefits provided by soil biodiversity is the concept of ecosystem services (Millennium Ecosystem Assessment 2005; Wall 2004). These include carbon sequestration, generation and renewal of soil structure and soil fertility, flood and erosion control, bioremediation of wastes and pollutants, modification of the hydrologic cycle, regulation of atmospheric trace gases, and biocontrol of human, animal, and plant pathogens and parasites. Alterations and loss of the world's terrestrial soils are occurring rapidly, raising concerns that some of these services may be largely interrupted, as they are currently rendered by unsustainable soils (Millennium Ecosystem Assessment 2005).

Given this background on soil biodiversity, can soil biodiversity of extreme environments inform us about biodiversity and ecosystems elsewhere? My intent here is to augment lessons from microbes living in extreme soils with examples of their consumers, primarily invertebrates, in order to better extract and extend lessons to biodiversity inhabiting global soils. It is hoped that these lessons will be further expanded and clarified by the many scientists who are developing exciting new approaches for detecting these amazing organisms and learning how they live in extreme soils and are integral to the working of ecosystems.

4.2 Lesson One: Biodiversity in Soils Is Hidden

Although this statement appears obvious to those working on extreme soils, scientists often bring their biases of larger, visible, and more easily detected organisms to the study of soils. However, most life in soils is microscopic. In extreme soils, an emphasis is to detect and study microbes and microscopic life, particularly at the species or molecular level, whereas in other ecosystems the attention to larger, mostly visible life sometimes dismisses the variety of life below the surface.

In extreme soils of lower plant and animal species diversity, multiple techniques are used to detect life. Without familiarity and testing of the correct extraction technique, microscopic animals and microbes may be considered absent and soils, ‘sterile’. Scientists working on extreme soils recognize that techniques used to isolate microscopic invertebrates are varied and require a basic understanding of the limitations of the method as well as the general biology of each particular group. Techniques for extraction, identification, and enumeration (based on classical morphology) are specialized and may differ for each group of taxa occurring in soils. For example, to extract microarthropods and nematode roundworms, two groups of mesofauna that occur in soils worldwide, a single technique should not be used.

Microarthropods (mites and Collembola) live in air-filled pores of soil whereas nematodes are aquatic animals living in water films around soil particles. Nematologists may extract nematodes from soil with methods depending on soil type and organic matter content and whether they want to recover the whole community or just a targeted species. Such methods are based on movement in water by gravity, sieving-centrifugation, or flotation techniques. Microarthropods have a different physiology and behavior and are removed from air pores in soil by methods based on active avoidance (e.g., avoidance of heat using Berlese–Tullgren funnels), aspiration, and flotation (Coleman et al. 1999; Ducarme et al. 1998). Within these two major groups of soil fauna, species differ in body size, movement, life histories, temperature requirements, feeding habits, and physiologies. In addition, many species are rare, and may not be detected without prior evaluation and use of several techniques. For example, the drier, saltier, low carbon soils of the Antarctic Dry Valleys (see Chapters 2 and 12) located away from meltstreams were considered almost sterile until the early 1990s, but different extraction techniques for nematodes and molecular analyses of microbes have shown greater diversity and distribution than previously thought (Aislabie et al. 2006; Barrett et al. 2006; Freckman and Virginia 1997; Wall and Virginia 1999). Rapid faunal analysis from soil using bulk animal DNA for identification is emerging as an addition to classical morphological techniques. However, as with microbial molecular tools, faunal DNA analysis will need to be related to activity of viable populations. As with extreme soils, using numerous techniques in a coordinated manner will increase detection of organisms in all terrestrial soil systems, no matter the location or depth of the soil. This information will increase our knowledge of Earth's biodiversity.

4.3 Lesson Two: Soil Species Have More Than One Survival Strategy

Many survival strategies exist among the organisms in extreme soils that may contribute to evolutionary success. Distantly related organisms may share a strategy, and additionally may have developed multiple adaptations for maintaining populations. Evolution has selected for biota that express ecological traits such as long versus short life cycles, sexual versus other reproductive modes, numerous versus few eggs, multiple dispersal mechanisms, alterations in morphology, and active migration to avoid stress. Types of cryptobiosis, an ametabolic, reversible response to environmental stress known in many taxonomically distinct organisms such as most tardigrades, rotifers, and nematodes, are a response to desiccation (anhydrobiosis), freezing (cryobiosis), and salinity (osmobiosis; Block 1982; Pugh and Dartnall 1994; Sinclair and Sjursen 2001; Treonis and Wall 2005). In the Antarctic, soil nematodes have a variety of strategies including anhydrobiosis, cryobiosis, cold-hardiness (Pickup 1990), intracellular freezing (Wharton 2003), dispersal by wind (Nkem et al. 2006), and life histories. Microarthropods can supercool (Convey et al. 2003), be heat tolerant, or cold-hardy (Sinclair and Sjursen 2001), and can desiccate (Montiel et al. 1998; Worland and Lukesova 2000). Algae and mosses in extreme hot and cold deserts desiccate without water and in the polar deserts become freeze-dried through the long winters until temperature and moisture combine to trigger activity (McKnight et al. 1999). Examples of resistance mechanisms for microbes living in extreme soils are discussed throughout this volume, and add to the synthesis of the underlying evolutionary adaptations of all soil biota.

Survival mechanisms extend to more biodiverse soils in other ecosystems. Even within a diverse phylum such as nematodes, anhydrobiosis is widely distributed. Many nematodes in temperate and tropical soils undergo anhydrobiosis when soils dry, including phylogenetically different species such as the fungal-feeding nematode *Aphelenchus avenae* (Browne et al. 2004; Crowe and Madin 1975; Freckman et al. 1980), bacterial-feeding species, *Panagrolaimus* and *Acrobeloides*, the obligate plant parasites *Rotylenchulus reniformis* and *Scuttellonema brachyurum*, and many others (Demeure et al. 1979; Goyal et al. 2003). However, the degree to which anhydrobiosis, like other forms of cryptobiosis, protects different species can vary (Rothschild and Mancinelli 2001; Wharton 2003).

Thus, a combination of ecological and physiological traits has allowed species to successfully evolve and maintain active populations in extreme soil habitats. These few examples from extreme soils suggest multiple strategies that might also be expressed in nonextreme soils to enable responses to environmental change.

4.4 Lesson Three: Extreme Soils Are Ecosystems

Although there may be fewer species in extreme soils, these particular soils harbor all the characteristics of an ecosystem, for example, species variability, food webs, nutrient cycling, production, decomposition, and interaction with the environment. Food webs in extreme soils are simpler than in other ecosystems and usually have fewer trophic levels because of lower energy or primary production input. In extreme soils, controls on trophic levels in a food web are dependent more on abiotic controls than on top predators of lower trophic levels. Whether the food web is primary producer-based or detritus-based, most food webs will involve only two functional groups, microbes and their consumers (Moore and de Ruiter 2000). Detrital-based food webs could have an additional trophic level if they depend on two types of contemporary primary production: autochthonous (algae growing in soils) or allochthonous (detritus blown in from a nearby source); but if based on ancient legacy carbon alone, there will be only two trophic levels. Protozoa and larger-sized organisms (of size range from 500 µm to 2 mm), such as microfauna (rotifers, tardigrades) and mesofauna (microarthropods, nematodes) consume producers (cyanobacteria or algae), or consume decomposers (bacteria or fungi), and thus regulate the turnover of microbes and nutrients. As these organisms die, organic carbon and nutrients are recycled back to the soil. In some extreme soils such as in the Atacama Desert with their hypolithic communities of phototrophs, the organisms appear to interact solely as primary producers, but more data on heterotrophic microbes are needed (Warren-Rhodes et al. 2006; see also Chapter 6).

The Antarctic Dry Valleys provide examples of soil communities with few species in trophic groups. These have both primary producer-based and detritus-based food webs. These include algal feeders – a single species of nematode, *Eudorylaimus antarcticus* (Wall 2007), bacterial feeders – two nematode species, and more rarely, fungal feeders – a mite and a collembolan species. Tardigrades and rotifers that feed on bacteria or algae occur in about 14% of the wet, organic matter-rich soils across the Dry Valley landscape (Freckman and Virginia 1997). In contrast to those that colonize plant-dominated soils, Dry Valley taxa rarely coexist as a community or more complex food web, and competitive interactions can be limited (Hogg et al. 2006). Extreme soils can also be characterized by an absence of consumer populations and their predators. About 60% of the soils in the Dry Valleys lack nematodes and about 50% of soils in Ellsworth Land, Antarctica, and areas in the Atacama Desert lack soil mesofauna (Convey and McInnes 2005; Freckman and Virginia 1997; Warren-Rhodes et al. 2006). Whether these unsuitable soil habitats are due to soil geochemical and/or food source limitations, or else to other factors, is being studied (Poage et al. in press; Warren-Rhodes et al. 2006).

It is somewhat easier to clarify the food sources within an extreme soil food web, and thus the role of a species in the ecosystem, than it is in highly diverse soils. All the consumers, micro- and/or mesofauna are usually known at the species level in an extreme soil ecosystem. For example, using stable isotopes, Bokhorst et al. (2007) showed that a polar collembolan species feeds preferentially on lichens and algae, rather than moss. Less is known about faunal species feeding on a selective bacterial species, particularly for extreme soils where microbial diversity is appearing to be higher than previously reported (Aislabie et al. 2006; Barrett et al. 2006; Cowan and Tow 2004). Nevertheless, compared to the study of more diverse food webs, analysis of the extreme soil food webs is particularly useful to reveal food web architecture, the role of the species in the ecosystem, and the degree of overlap in geographic species range for soil fauna.

Food webs in nonextreme soils have high energy input from plants and algae, more trophic levels, and potentially hundreds of species in a functional group. Larger macrofauna prey on smaller mesofauna, and so on through the food web. Food webs are thus extremely complex: for example, the diversity of fungal feeding mite species in soils might range in the hundreds of species whereas in an extreme soil, there may be only a single species, if any. Resolving food sources for each species in a functional group for most soils is thus extremely difficult due to the high number of species. Instead, transfer of nutrients, for example, carbon, nitrogen, and phosphorus, through the soil food web can only be estimated based on abundance and biomass of invertebrates within the various functional groups.

Because most functional groups have many species performing the same task or role in highly diverse soil ecosystems, it has been argued that there is considerable redundancy (Loreau and Thebault 2005). If a species were lost, another species would take its place and there would be little change in the ecosystem function. More recently, experiments (Heemsbergen et al. 2004; Roscher et al. 2004) suggest that functional diversity is more important to an ecosystem function than the number of species (see also Hunt and Wall 2002). This is not the case in low-diversity systems where both numbers of functional groups and species are low (e.g., a functional group is represented by one species) and, frequently, one species is key to a process (Wall 2007). Loss of one species could decrease an ecosystem process in an extreme soil. For example, a single nematode species in the Dry Valley soils, the bacterial feeder *Scottnema lindsayae*, is responsible for a disproportionate amount of soil carbon turnover, about 5–7% (Barrett et al. unpublished), such level of activity being unachievable in temperate ecosystems with their highly diverse and greater biomass (Schröter et al. 2003). As the Dry Valleys have cooled, populations of *S. lindsayae* have declined with as yet unknown implications for carbon cycling (Doran et al. 2002).

Knowledge at an ecosystem level gained from studying simple food webs and individual species in extreme soils can be transferred to other terrestrial soils. Simply stated, microscopic species placed in a functional group may not be equal in their roles in an ecosystem process. Their roles may differ on temporal, spatial, physiological, nutritional, and other measurable scales, but may be masked by sheer numbers of species. Combined field and laboratory experimentation to clarify food web interactions will enhance our ability to detect potential ecosystem effects involving loss of species or shift in composition of species (or functional groups). Synthesizing this information will enable us to better monitor how soil biodiversity is altered by global changes, to compare impacts across soil ecosystems, and to better formulate actions to assure long-term soil sustainability.

4.5 Lesson Four: Soils Are Major Drivers of Biodiversity

The geochemical component of extreme soils structures the diversity of life to a greater extent than the corresponding component in nonextreme soils, where biotic influences on soil organic matter and soil structure have masked effects of parent material. Many undisturbed extreme soils today reflect the past geologic history and parent material, and contribute to soil habitats that are highly heterogeneous at small and large spatial scales across the landscape. In ecosystems where plants are absent, for example, the hot hyperarid Atacama desert and the cold polar desert soils of the Dry Valleys, Antarctica, soils are relatively unchanged by centuries of biological (including human) activity and thus, the legacy of previous soil geochemistry patterns still remains. These deserts have extremely low water (<25 mm mean annual rainfall for the Atacama, and <10 cm rainfall equivalent for the Dry Valleys), low soil carbon, low organic matter, high pH, and high salinity (Barrett et al. 2004; Warren-Rhodes et al. 2006) compared to other ecosystems. As with other arid ecosystems, however, there is high spatial variability because soil chemical (e.g., C, N, P, organic matter, pH, salinity) and physical factors (structure, texture, soil type, pore space, bulk density) combine in varying proportions to form numerous habitats for organisms, which can range from suitable to poor (Barrett et al. 2004; Courtright et al. 2001; Wall and Virginia 1999). The soil geochemical heterogeneity affects the abundance of suitable habitats for life and contributes to patchily distributed fauna. Organisms, whether microbes, plants, or invertebrates, are limited by availability of soil resources at centimeter to kilometer scales (Ettema and Wardle 2002; Freckman and Virginia 1989; Poage et al. in press; Schlesinger et al. 1996; Wall and Virginia 1999; Warren-Rhodes et al. 2006).

In this way, spatial segregation of species occurs in extreme soils without the influence of plant roots. For example, in the hyperarid hot Atacama Desert, absence of water determined the spatial scale distribution and presence of photosynthetic and heterotrophic bacteria (Warren-Rhodes et al. 2006). In cold desert Dry Valley soils, where vascular plants are lacking and average mean annual surface soil temperatures are −26°C, four nematode species are distributed across the landscape according to food sources and soil habitat geochemical characteristics (Barrett et al. 2007; Porazinska et al. 2002; Treonis et al. 1999; Wall and Virginia 1999). *S. lindsayae*, the bacterial feeder that is widely distributed and has a greater abundance than the other nematode species, occurs in soils that are drier, saltier, and less organically rich. Another bacteria feeder, *Plectus* spp., is associated with soils that are moist, less saline, and with higher organic carbon; thus, this species rarely overlaps geographically for food with *S. lindsayae. Eudorylaimus antarcticus*, the algal feeder (Wall 2007), is found in soil habitats that are moist and highly organic, but its highest abundance occurs in lake sediments and streams (Ayres et al. 2007; Treonis et al. 1999). *Eudorylaimus* and *Plectus* frequently co-occur, but infrequently are found with *S. lindsayae*, or with a rarely found fourth species, *Geomonhyster*a sp. This soil food web in the Dry Valley soil ecosystem has no predators and is likely limited by physical constraints rather than species' competition (Wall 2007). Other examples of simple food webs, broad niches, and spatial segregation have been seen in other extreme soils (Convey and McInnes 2005; Richard et al. 1994). These examples illustrate how the heterogeneity in soil habitats alone can be a major driver of local biogeographical patterns.

Globally, geographical patterns of soil biodiversity are driven primarily by climate and vegetation with soil heterogeneity having a variable role in determining biodiversity across spatial scales (Ettema and Wardle 2002). In younger soil systems, the soil biota, including plant roots, have contributed to the organic matter, total carbon, and soil structure by the formation of soil pores and channels. Thus, younger soils are subject to variation in biological, physical, and chemical alterations across shorter temporal and spatial scales than polar deserts, which tend to be older (Young and Crawford 2004). There are, however, examples of plant-dominated ecosystems where the soil substratum may be a stronger driver of belowground biogeographical patterns (Ettema and Wardle 2002). Fierer and Jackson (2006) show the influence of one soil factor, soil pH, as a predictor of soil microbial diversity across ecosystem types in North and South America. However, pH did not explain distribution of hypolithic soil bacteria in the Atacama Desert (Warren-Rhodes et al. 2006). In Arctic soils, where plants occur, variation in soil moisture was a major determinant of CO_2 respiration, which represents an overall measure of soil biotic metabolism (Sjögersten et al. 2006).

Globally, the aboveground distribution patterns of animal and plant diversity generally follow the latitudinal gradient hypotheses (Gaston 1996) of increasing species diversity from the poles to the tropics (Willig et al. 2003). The question of whether microbes are everywhere globally (Fenchel and Finlay 2004; Finlay 2002), or instead have spatial biogeography such as a latitudinal gradient, has resurged as a scientific debate and spawned research to examine constraints to dispersal and colonization for microbes less than 500 µm in addition to organisms of larger size (Fierer and Jackson 2006; Hughes Martiny et al. 2006; Lawley et al. 2004). The discussion on microbes and biogeography has extended to include bacteria, Archea, and some Eukarya (e.g., unicellular algae, Protozoa). In extreme soils, recent studies support unique organisms (Smith et al. 2006; Warren-Rhodes et al. 2006), but it is difficult to prove that these microbes are indeed unique (missing from other ecosystems) because of limited studies using similar molecular detection techniques or descriptions of soil habitat data.

Termites are one of the few groups of soil invertebrates that appear to follow the latitudinal gradient pattern (Eggleton et al. 1996, 1995). Global biogeography for the majority of soil fauna, particularly the micro- and mesofauna is less well known (Bardgett et al. 2005; Hughes Martiny et al. 2006; Maraun et al. 2007) partially because a greater proportion of soils have been sampled in temperate ecosystems (Bardgett 2005). One diverse group of soil microarthropods, oribatid mites, increases in diversity from boreal to temperate ecosystems but this trend does not extend to the tropics (Maraun et al. 2007), which may indicate a sampling problem. This problem has also been noted for global distribution patterns of soil nematodes (Bardgett 2005; Boag and Yeates 1998).

Given the variation in global ecosystems, it is challenging to establish ecological hypotheses explaining patterns of biogeography for soil biodiversity (Willig et al. 2003) or to determine if, at local regional or global scales, species-rich soils correspond to more productive ecosystems (Ettema and Wardle 2002; Young and Crawford 2004). Research in extreme ecosystems has already shown clearly that variation in soil geochemistry alone creates numerous soil habitats that are distinctly different and suitable for some species, but not others. This information, combined with information on species dispersal and colonization and with further knowledge on other drivers (vegetation, climate) of soil biodiversity, should contribute to better predictions of global soil biogeography.

4.6 Lesson Five: Global Changes Are Rapidly Changing Soils

Global changes (climate change, atmospheric change, land use change, species extinctions, invasive species) are having an impact on soils at an increasingly rapid rate (Millennium Ecosystem Assessment 2005). Effects of soil degradation include loss of soil organic matter, erosion, salinisation, compaction, contamination, and sealing (Wall 2004). Several international agreements address the irreversible loss of productive soils and the impact on biodiversity. As an example, the UN Convention to Combat Desertification was signed in 1997 by 178 nations to mitigate the effects of drought by implementation of action plans (UN Convention to Combat Desertification 1997). As recent as September 2006, the European Commission adopted a strategy specifically for soil protection by the EU (European Commission on Soil Protection 2006). These and other agreements have as a basis the knowledge of the benefits to humans (called ecosystem services, see Section 4.1) provided by soils. The understanding that soil life is critically important for provision of ecosystem services is less well accepted as a basis for policy decisions than is the notion of the role of physical degradation (Wall 2004). Additionally, less attention has been drawn to extreme soils, with the exception perhaps of those organisms living in chemically impacted soils (see Chapters 15 and 16), partially because of the magnitude of the ecosystem change occurring to many species and habitats worldwide and because extreme soils do not produce crops (Alley et al. 2007). Can knowledge of biodiversity in extreme soil ecosystems apply elsewhere, when globally there is accumulating evidence that soil functional composition and some soil species are being altered by global changes (Swift et al. 1998; Wardle et al. 2004; Wolters et al. 2000)?

In extreme soils, global changes may homogenize habitat ranges of species, with differing effects on these systems. Rapid environmental climate change could alter species distribution as influenced by habitat requirements, physiological tolerances, and life histories. For example, warming in extremely cold ecosystems might increase soil moisture levels across large spatial scales and blend soil habitat chemistry by affecting decomposition rates and the amount of carbon in the soil, primary production, and salinity levels (Wall 2007). In ecosystems with extreme drought events, soils might have reduced heterogeneity in chemical and physical properties due to high wind erosion. Other global changes in extreme soil systems, such as land use change (resulting from increased human activity) and increased incidence of invasive species, could also alter the food web interactions and relative stability of extreme soils. Thus, the present habitats that specify species range could be altered significantly with consequent changes in species composition and geographic distributions and cascading effects on ecosystem processes across the landscape (Wall 2007).

Little is known about the effect of global changes at the individual species level for most soil systems (Convey and McInnes 2005; Doran et al. 2002). Evidence from the study of extreme soil biodiversity suggests that global change effects will differ with species and ecosystem, and that even species with broad niches can be vulnerable (Barrett et al. unpublished). Thus, in extreme but also in more diverse soils, it will be important to quantify which, if any, species are key to an ecosystem process or ecosystem service and whether they are vulnerable to the many global changes.

4.7 Conclusions

Extreme soils may initially appear to be vastly different from each other and from the rest of the world's soils. There are several unique features of extreme soils: their lack of easily detectable life, reduced number of mesofaunal species within a functional group, fewer trophic levels, less complex food webs, lack of small-scale geographic overlap of species within functional groups, marked periodicity of activity, and food selectivity by invertebrate species (Convey and McInnes 2005; Porazinska et al. 2002; Treonis et al. 1999; Wall 2007). Collectively, the study of extreme soil habitats has revealed information on their biodiversity and on species interactions that are difficult to examine in nonextreme soils. Although much is yet to be learned, there is now sufficient evidence that species diversity in extreme soils has similarities to soil biodiversity elsewhere. Researchers interested in both extreme and nonextreme soils have used some species' traits, revealed at the genetic, population, community, or ecosystem levels, to obtain quantitative measurements of biodiversity. All of these criteria for biodiversity estimation are compatible with the Convention on Biological Diversity definition of biodiversity mentioned earlier, which encompasses variability from species to landscapes levels (Convention on Biological Diversity 2004).

Extreme soil ecosystems are more than model systems or microcosms. The biodiversity found in extreme soil environments is an integral part of the diversity of terrestrial surfaces. The extreme soil ecosystems are not anomalies; they are local to relatively large terrestrial ecosystems with a range of life forms, albeit belonging to relatively few species, having several types of life histories and extraordinary physiological adaptations. For this reason alone, extreme soil habitats are worthy of conservation and protection. Kareiva and Marvier (2003) argued that ecosystems with fewer species, rather than those with high diversity, could be considered higher priorities for conservation. Extreme soils are also critically valuable as indicators of global changes likely to affect other soil systems. Our challenge is to define these habitats in more detail, to quantify their contribution to ecosystem processes and services, and to establish the relevance of biodiversity in extreme soils for sustaining life in all terrestrial soils.

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