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Please refer to the corresponding final paper in BG if available.

**Where
microorganisms meet
rocks in the Earth's
Critical Zone**

D. M. Akob and K. Küsel

Where microorganisms meet rocks in the Earth's Critical Zone

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Received: 12 February 2011 – Accepted: 17 February 2011 – Published: 9 March 2011

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

The Earth's Critical Zone (CZ) is the critical, outer shell of the Earth that provides an arena for the interplay of diverse physical, chemical, and biological processes that are fundamental for sustaining life. As microbes are the principle drivers of biogeochemical cycles, it is necessary to understand the biodiversity of the CZ unseen majority and their impact on life-sustaining processes. This review aims to summarize the factors controlling where microbes (prokaryotes and micro-eukaryotes) live within the CZ and what is known to date about their diversity and function. Microbes live in all regions of the CZ down to 5 km depth, but due to changing habitat complexity, e.g., variability in pore spaces, water, oxygen, and nutrients, their functional role changes with depth. The abundance of prokaryotes and micro-eukaryotes decreases from a maximum of 10^{10} or 10^7 cells g soil⁻¹ up to eight orders of magnitude with depth. Symbiotic mycorrhizal fungi and free-living decomposers are best understood in soil habitats, where they are up to 10^3 cells g soil⁻¹. However, little is known about their identity and impact on weathering in the deep subsurface. The relatively low abundance of micro-eukaryotes in the deep subsurface suggests that these organisms are either limited in space or nutrients or unable to cope with oxygen limitations. Since deep regions of the CZ are limited in the recent input of photosynthesis-derived carbon, microbes are dependent on deposited organic material or on chemolithoautotrophic metabolism that allows for the establishment of a complete food chain independent from the surface. However, the energy flux available might only allow cell growth over tens to thousands of years. The recent development of “omics” technologies has provided microbial ecologists with methods to link the composition and function of in situ microbial communities. We should expect new metabolic discoveries as we have a closer look utilizing a polyphasic approach into the microbial communities of the CZ. Thus, future work is still needed to link microbial biodiversity to the exact role of microbes in weathering and geochemical cycling in the CZ, especially in subsurface habitats.

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1 The Critical Zone – where rocks meet life

The Earth's Critical Zone (CZ) defines the heterogeneous environment in which complex interactions involving rock, soil, water, air, and living organisms regulate the natural habitat and determine the availability of life-sustaining resources (NRC, 2001).

It is a huge region that ranges from the outer extent of vegetation through the soils or pedosphere down to the unsaturated and saturated bedrock (Fig. 1). The deeper boundary, marking the limits of the influence of life on the rock environment, is still not defined. This outer shell of the Earth provides a “critical” arena for the interplay of diverse physical, chemical, and biological processes that are fundamental for sustaining ecosystems and human societies (Amundson et al., 2007; Brantley et al., 2007; Chorover et al., 2007; Lin, 2010). For example, the global net primary production, the net transformation of solar radiation into biochemical energy, is one of the most important ecosystem services provided by plants. These processes are controlled in the CZ by a coupled system of biological and geological cycles that are unified via fluid transport, as water is means of transferring both energy and mass (Lin, 2010). Water flow, horizontal or vertical, is controlled in part by the composition of soils and sediments as well as the occurrence of fractures and impermeable bedrock. Interfaces between and within layers of the CZ can affect dynamic interactions between the biological and geological cycles. Thus, water flow is crucial by linking these complex networks as it is transported down through the layers of CZ (Fig. 1).

Life within the CZ is directly impacted by geology, as organisms cannot survive on intact, unweathered bedrock. The creation of porosity in rock is crucial to the transformation of bedrock into a medium that can support life and is driven by abiotic and biotic weathering processes (Jin et al., 2010). Abiotic weathering occurs when water enters the rock through vertical fractures, allowing for the contact of water with rock walls, dissolving trace minerals and oxidizing iron silicates. These reactions proceed as the rock equilibrates with acidic and oxidizing gases dissolved in surface waters leading to a fractured rock. Plants contribute to this weathering by extending roots into fractures

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to extract water, sometimes reaching down to over 20 meters in depth (Jackson et al., 1999). Root-associated fungi can speed up the process by extending hair-like structures, termed hyphae, into small cracks, channeling water to plants. However, little is known about the functional consequences of fungal biodiversity in the deeper regions and aquifers of the CZ (Wall et al., 2010).

Modern microbiology has increased the thickness of the CZ biosphere by showing that microorganisms live in areas that were long thought to be uninhabitable (Gold, 1992). The primary limit to the depth that life can penetrate into the Earth's surface is temperature rather than energy, which increases rapidly with depth and is influenced by the type of crust, rock, location, etc. Under the continents, temperature increases on average at a rate of $25^{\circ}\text{C km}^{-1}$ (Bott, 1971), which suggests that with an upper temperature limit of 130°C for bacteria (Kashefi, 2003), life could exist up to a depth of 5.2 km. Pushed by the coordinated activities of the Ocean Drilling Program (ODP) and the Integrated Ocean Drilling Program (IODP), marine scientists have started to explore the hidden biological diversity beneath the ocean floor, in conjunction with basic research addressing the history of the Earth recorded in marine sediments and rocks. Their spectacular findings, especially from sites where chemical energy is fuelling rich and diverse microbial communities at vents and seeps, (e.g., Hinrichs et al., 1999; Boetius et al., 2000; Michaelis et al., 2002) is now stimulating research in the terrestrial subsurface. Improved drilling techniques now allow for sterile sampling that provide scientists the ability to focus on the critical interaction between the biosphere and the Earth's crust. Therefore, continued work is needed to fully understand the role of microbial communities in the interplay of diverse physical, chemical, and biological processes in all regions of the CZ.

The purpose of this article is to review the current knowledge about microbiology within CZ ecosystems. The physical and hydrological aspects of CZ processes have been described previously in detail in the excellent review of Lin (2010). Many reviews are available which summarize the microbiology of specific, distinct CZ habitats, i.e., soils (Buckley and Schmidt, 2002), groundwater (Griebler and Lueders, 2009), and

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caves (Northup and Lavoie, 2001). This review focuses on synthesizing the current knowledge of microbial biodiversity within specific habitats and placing this information within the larger context of the CZ. We intend to show that the sum of all microbial biodiversity within the linked ecosystems and zones of the CZ is greater than the individual components. The aim is that microbiologists and ecologists will begin to evaluate their data within the global CZ network and provide a fuller understanding of complex Earth processes.

2 The biological cycle within the CZ

The CZ biological cycle is a combination of ecological and biogeochemical cycles, involved in the production and consumption of food and energy in an ecosystem (Lin, 2010). Microorganisms are central to both aspects of the biological cycle as they have the potential to control food web trophic interactions (the ecological cycle) and biogeochemical cycling of nutrients. The ecological cycle is the combination of processes that support a food chain via the generation of biomass and trophic interactions. The bottom rung of the food chain is primary production, which is carried out by producers, such as plants and autotrophic microbes (Fig. 2). Fixed carbon then moves up the food chain reaching consumers and ultimately being recycled by detritivores, e.g., prokaryotes, fungi, and higher animals. The biogeochemical cycle is intimately linked to the ecological cycle because it is a combination of biotic and abiotic processes that determines the bioavailability of elements. Bioavailability of elements necessary for life, such as carbon, oxygen, and nitrogen, is controlled by biogeochemical cycling in water, solid material (e.g., minerals), and gas (e.g., air). Two types of ecological cycles exist within the CZ, that which is driven by surface energy inputs, e.g., photosynthesis-driven food chain, and that which is dependent on subsurface energy inputs, e.g., a chemolithoautotrophic-driven food chain, are discussed in detail below (Fig. 2).

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2.1 Surface energy inputs to the CZ

The biological cycle in the CZ is primarily dependent upon input of fixed carbon from primary production at the surface. Photosynthesis-derived carbon is known to enter upper soil layers of the CZ via litter and roots but it can be returned to the atmosphere via respiration, stored in plant tissues or as soil organic matter (SOM), or transported elsewhere within the CZ (Fig. 2). In addition, carbon can also enter soils via non-photosynthetic CO₂ fixation by microbes and, although it is only a minor input of C to the bulk soil (0.05% of soil organic carbon), this carbon can be important to soil microenvironments (Miltner et al., 2004, 2005) (Fig. 2).

Respiration can be divided into two pools resulting in CO₂ release: autotrophic respiration by living plant leaves, stems, and roots and heterotrophic respiration resulting from decomposition of dead organic matter (OM). Heterotrophic respiration primarily occurs in surface soil horizons and is catalyzed by fungi and prokaryotes (Fig. 2). Substrates for this heterotrophic respiration include fresh plant litter, dead plant roots and root exudates, and C from parent rocks. Transport of such substrates is a major factor determining the availability of carbon for respiration in deeper regions of the CZ. Input of photosynthesis-derived carbon to the depths of the CZ is obviously dependent on plant rooting depth, which can act as a means of transporting fixed organic carbon, but also on vertical water flow. The CZ must be considered an open system, which continuously receives organic C and loses gaseous carbon compounds and dissolved organic carbon (DOC) via leaching and mineralization.

The fate of carbon transported to soils and deeper regions of the CZ is highly dependent on the presence and metabolic potential of microbial communities. Carbon can be cycled rapidly by soil microorganisms or transported to fuel subsurface food webs or stored as buried organic C (Fig. 2). Variability in the decomposition rate of plant material by soil microorganisms can be affected by the input source as well as community structure, as different microbial communities prefer different carbon substrates. Two populations of microbes have been identified that differ in their substrate usage:

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r-strategists, which are specialized for feeding on fresh organic matter (FOM), and k-strategists that utilize remaining polymerized substrates (summarized in Fontaine et al., 2003). In addition to stimulating microbial populations, the input of FOM can cause a priming effect in soils. Priming effects are strong short-term changes in the turnover of soil organic matter (SOM) caused by a trigger, such as the input of an easily decomposable energy source (as reviewed in Kuzyakov et al., 2000). Thus, addition of carbohydrates, amino acids, or simple organic acids can increase SOM mineralization in many soils indicating that stability may also be caused by substrate limitations. For example, the addition of FOM from plant litter resulted in fast turnover of soil C and lower carbon storage (Steinbeiss et al., 2008).

Carbon storage times in soils range from seasonal to inter-annual timeframes to decadal or longer time scales (Trumbore, 2006). Residence of carbon on the millennia scale appears to be due to stabilization by association with mineral surfaces, limitations in the potential for decomposition, or by physical protection from aggregates (Trumbore, 2006). For a long time, the formation of recalcitrant humic substances has been considered to be the major pathway for SOM stabilization. However, lignin is altered relatively quickly and does not appear to be stabilized in the long-term in any soil fraction (Marschner et al., 2008). It has been argued that the degradability of the readily bioavailable dissolved or water-extractable OM fraction is due to its low aromatic compounds content, but DOC aromaticity and biodegradability are very low in deeper soil horizons indicating that other factors or compounds limit its degradation. However, key factors controlling the decomposition of C in plant residues vs. the storage of SOM are still poorly understood due to method limitations (Trumbore, 2006). As long-term stored carbon pools are a minor contribution to soil respiration fluxes, they likely are the majority of soil carbon stocks (Schoor and Trumbore, 2006; Trumbore et al., 2006) that can also be transported within the deeper CZ (Trumbore, 2006). Therefore, it is important to recognize that future work is needed to identify how plants allocate C and the factors that control respiration and burial.

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2.2 Subsurface energy inputs to the CZ

Deep regions of the CZ are limited in the recent input of photosynthesis-derived carbon and are dependent on old organic material deposited in sedimentary rocks. Otherwise microbial communities in the deep CZ have to make their living on sources of inorganic electron donors and inorganic carbon for chemolithoautotrophic metabolism. Lithoautotrophy is a secondary input of fixed carbon to the CZ thereby allowing for the establishment of a complete food chain that is distinctly independent from the surface (Fig. 2). In this case, *Bacteria* and *Archaea* make up the base of the food chain by catalyzing lithoautotrophic primary production in the deep biosphere. In deep biosphere basalt and granitic systems, there is evidence that the base of the food chain is composed of methanogens and acetogens that utilize geologically produced H₂ and CO₂ for the production of methane and acetate, respectively (Pedersen, 1997; Chapelle et al., 2002) (Fig. 2). The production of methane and acetate can then support the growth of acetoclastic methanogens, sulfate- (SRB) and iron-reducing bacteria (FeRB). Communities in basalt aquifers can harbor methanogenic *Archaea* at an abundance of 2.8×10^5 microbial cells ml⁻¹ (Chapelle et al., 2002). As secondary consumers synthesize biomass they in turn provide a source of carbon and energy for anaerobic heterotrophs (Fig. 2).

Lithoautotrophy in the deep biosphere can also be driven by energy sources other than H₂. Organisms that require neither H₂ nor photosynthesis-derived organic carbon are rare, but their potential to contribute to a deep biosphere food chain cannot be ignored. Disproportionation of sulfur (S⁰), sulfite (SO₃²⁻) or thiosulfate (S₂O₃²⁻) or the oxidation of Fe(II), S⁰ or S₂O₃²⁻ with reduction of nitrate or Fe(III) may be providing sufficient energy for microbial populations to act as primary producers (Stevens, 1997; Amend and Teske, 2005). Intricate weathering textures, like specific styles of pits, channels, tunnels, and voids, detected in oceanic pillow basalt support the hypothesis that these unusual features are of microbiological origin (Fisk et al., 1998) related to lithoautotrophy. Reduced iron, manganese, and sulfur present in the basalt could

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have served as electron donors, and Fe^{3+} as an electron acceptor. However, conclusive evidence that the diverse weathering patterns are the direct consequences of biological activity still awaits further analyses, e.g., the identification of microorganisms associated with these phenomena.

5 Geological processes can transport chemical energy, i.e., H_2 , CH_4 , H_2S , and Fe(II) , from the unweathered subsurface to the CZ. Rich and diverse microbial communities based on CH_4 or H_2S oxidation thrive at sites on the marine seafloor where chemical energy is delivered from below (Hinrichs et al., 1999; Boetius et al., 2000; Michaelis et al., 2002). However, most subsurface microorganisms live in conditions of extreme energy limitation, with mean generation times of up to thousands of years (Jørgensen and Boetius, 2007). Recent discoveries of prokaryotic communities that survive with little nutrients in ice, permafrost, or in the desert-like seafloor has profoundly altered our perspective on the limits of living organisms and their need for energy (Price and Sowers, 2004). Complex functions in microorganisms have to be maintained in these environments at an energy flux that barely allows cell growth over tens to thousands of years. The energy available might only be sufficient to maintain cell processes exclusive of biomass production (an energy which is called maintenance energy) or to allow the repair of macromolecular damage (an energy which is called survival energy). The lowest metabolic rate of immobile, likely dormant communities with an extremely weak metabolism can be clearly differentiated from that of communities with more access to nutrients and free to move but still at too low a level for growth (Price and Sowers, 2004). The metabolic rates per cell corresponding to growth, maintenance and survival can range over six orders of magnitude difference. Thus, our classical cultivation techniques designed to work with growing cultures in the laboratory will be inappropriate to understand microbial life under such extremely energy-depleted conditions.

25 It is now recognized that a photosynthesis-independent biosphere exists within the CZ using energy delivered from rocks or below. However, it is still unclear to what extent this deep biosphere affects weathering processes of sedimentary, metamorphic, and magmatic rocks. In addition, we should also consider a potential feedback from

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the deep subsurface to the shallow biosphere and to the atmosphere due to the fluid-driven transport of subsurface-fixed carbon and diffusion of gasses. These important links are key to understanding the complexity of the CZ and may be answered in future research.

3 Microbial ecology in the CZ

CZ habitats that can sustain microbial life are estimated to harbor the unseen majority of Earth's biomass with the total amount of carbon in subsurface organisms likely equal to that of all terrestrial and marine plants (Whitman et al., 1998). The microbial world in the CZ includes prokaryotes (*Bacteria* and *Archaea*), eukaryotes (fungi, algae, and protozoa), and viruses. Prokaryotes have been present on the Earth for at least 3.8 billion years and evolution has allowed them to evolve an extraordinary diversity of metabolic potential and adapt to a diversity of habitats (Torsvik et al., 2002). The discovery of submarine hydrothermal vents 30 yr ago influenced our hypotheses about the origin of life, because these chemically reactive environments, which are primordial and reminiscent of early Earth, constitute suitable conditions for sustained prebiotic synthesis (Martin et al., 2008). Indeed, there are striking parallels between the chemistry of the H_2 - CO_2 redox couple that is present in hydrothermal systems and the core energy metabolic reactions of some modern prokaryotic autotrophs, e.g., the acetogens (belonging to the *Bacteria*) and methanogens (belonging to the *Archaea*). These CO_2 -reducing, obligate anaerobic, modern microorganisms use the Wood–Ljungdahl (acetyl-CoA) pathway not only as a terminal electron accepting, energy-conserving process, but also as a mechanism for the synthesis of cell carbon from CO_2 (Drake et al., 2006). This combination presents a plausible starting point for biochemical evolution, because the synthesis of acetate and CH_4 from H_2 and CO_2 releases energy and might have supported the synthesis of more complicated biomolecules on early Earth (Martin et al., 2008).

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on the availability of appropriate nutrients and energy sources in each habitat. In the following, we will discuss how the physical complexity of subsurface CZ habitats influences microbial functional groups and what is known about the function and diversity of microbial communities.

3.1 Impact of physical complexity on CZ biology

CZ habitats vary in their physical, chemical, and biological heterogeneity with the most complex and productive regions occurring in the shallow, near surface and the less complex regions towards the interior of the Earth. The complexity of these habitats is related to the extent of weathering in which rocks are fractured, ground, dissolved, and bioturbated into transportable minerals (Brantley et al., 2007). Transport processes can then control the flux of water and nutrients through the CZ linking these regions and affecting microbial activity. Heterotrophic and chemolithoautotrophic microorganisms are detected in all regions of the CZ (Table 1), but their contribution to CZ processes varies depending on the complexity of the habitat. Habitat complexity in particular refers to the spatial and temporal variability that can influence the availability of pore spaces, water, oxygen, and nutrients for microbial life.

The three-dimensional matrix of the CZ, which is enhanced by weathering of rock material, forms a variety of heterogeneous microhabitats for biota that differ in the amount and source of water input. Microhabitats range in size from the nm to cm scale and refer to pore spaces, fractures, or particle aggregates. Pores with a small size range (nm to μm) are found within mineral particles, black carbon, or particle aggregates, and can be formed by abiotic processes, e.g., chemical weathering, fire, or aggregation, or via biological processes, e.g., bioturbation, root-soil interactions, or microbial activity (Jarvis, 2007; Chorover et al., 2007). Large pore sizes (mm to cm) in soils result also from biological activity, such as bioturbation by soil fauna or root penetration, or abiotic processes, such as shrinking and swelling of clay materials, rock fracturing and preferential weathering (Jarvis, 2007; Chorover et al., 2007).

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Water is a means of nutrient and gas transport through habitats via the fractures and pore spaces providing a constant source of elements to some regions of the CZ. Soils gain the majority of water from the atmosphere and interfaces with aquatic systems. In the unsaturated zone, pore spaces are only partially filled with water and water moves primarily by the force of gravity in a downward gradient. In the saturated zone, pore spaces are completely filled with water at a pressure equal to or higher than atmospheric pressure and water can also move horizontally in response to the hydraulic head. In deep regions of the CZ, water flow tends to decrease (Anderson et al., 2007) and can cause deep regions to be limiting in nutrients.

Prokaryotes live connected to water within CZ microhabitats, within water films or on the surface of particles, pores and fractures as microcolonies or biofilms, or in the interior of particle aggregates (Madigan et al., 2000; Young, 2008). Therefore, constraints of microbial life are the microhabitat size and the availability of water. In soils and the unsaturated zone, water saturation limits transport and as drying occurs the thickness of water films in pores decreases (Young, 2008). Water provides a connection between pores and availability controls the movement of organisms. Therefore, dry areas lead to niche separation and increasing habitat diversity. Soil aggregates provide a unique microhabitat for prokaryotes because micron-scale gradients in water, nutrients, and oxygen can be found within a small 3 mm sized aggregate (Madigan et al., 2000). Anoxic regions can form within the interior of soil aggregates due to variable diffusion of gases and consumption of oxygen near the aggregate surface. These microoxic or anoxic niches within a generally oxic soil habitat allows for the activity of organisms that vary in their need for oxygen (Madigan et al., 2000). Thus, the interior microhabitat of a single soil aggregate can support very different microbial communities as compared to the exterior (Drażkiewicz, 1994). The spatial and kinetic relationships between aerobic and anaerobic processes in soil are complex and subject to regulation via rainfall and drying patterns, leaching of DOC, and changes in oxygen consumption (Küsel and Drake, 1995). Acetate, a major fermentation product formed under anoxic conditions, e.g., in the centre of anoxic soil aggregates or within the litter layer, can

accumulate from SOM mineralization or diffuse to more oxic regions where it will be rapidly consumed by other microorganisms in the presence of electron acceptors, like Fe(III), nitrate, or O₂ (Küsel et al., 2002).

As the variability in pore size decreases through regions of the CZ, biological complexity decreases in these habitats. Large pore sizes in soils allow the occurrence not only of prokaryotes (Table 1) and micro-eukaryotes (Table 2), but also of higher organisms (plant roots and macrofauna) with macrofauna and micro-eukaryotes inhabiting larger pore spaces than prokaryotes (Young and Ritz, 2000). This can be advantageous for prokaryotes, because they can be protected from grazing by higher trophic levels by inhabiting small pore spaces that are inaccessible to these organisms, e.g., (Wright et al., 1993). Pore space size has been also shown to constrain the viability and activity of microbes in core samples; with interconnected pore throats > 0.2 μm diameter being required for sustained activity (Fredrickson et al., 1997). In contrast to soils, the deep biosphere is characterized by unsaturated and saturated bedrock with a large, solid surface-area-to-water-volume ratio, leaving little pore space for water and microbes per volume of subsurface (Pedersen, 1993). Communities in the deep subsurface include prokaryotes (Table 1) and micro-eukaryotes (Table 2) with no reports of higher fauna to date. These organisms are restricted to living in pores or fractures within their habitat and are generally cut-off from subsurface inputs of energy.

In addition to water and space, microorganisms require resources, such as carbon, nitrogen, electron donors (carbon or inorganic compounds), electron acceptors (oxygen, nitrate, sulfate, Fe(III), etc.), and trace minerals, for life. The availability of these resources in the CZ is related to proximity to the nutrient source and competition for the source between organisms. Nutrients such as nitrogen, iron, and phosphorus can be scarce in many habitats causing competition between microbial populations and selecting for populations that are extremely nutrient efficient (Madigan et al., 2000). To overcome such nutrient limitations prokaryotes have evolved adaptive traits, such as the ability to fix nitrogen or scavenge iron or other metals with siderophores (Madigan et al., 2000). Fungal weathering can increase the availability of inorganic minerals to

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other soil organisms and increase habitat availability by fracturing rock and creating new pore spaces (van Schöll et al., 2008).

In the case of carbon and oxygen, the input source into the CZ differs with relationship to the surface (Fig. 2). Soils have the highest organic carbon inputs due to rhizodeposition from higher plants or macrofauna and high input of oxygen due to proximity to the atmosphere (as summarized in Hinsinger et al., 2009). The high quantity of OM input and availability of high-energy electron acceptors, e.g., oxygen and nitrate, can allow complex microbial communities and processes to thrive in soil ecosystems (Table 1). Carbon and oxygen availability in habitats can also be patchy due to variable input and consumption by organisms. Therefore, carbon-depleted and anoxic or microoxic niches can form within habitats that support the growth of autotrophic or oligotrophic organisms (Table 1). In deeper regions of the CZ, delivery of oxygen is impeded and conditions become more anoxic and oligotrophic and organisms must be well adapted to life under such conditions. Oligotrophic conditions can be variable, with some habitats experiencing long periods of time with little to no inputs of fixed carbon from the surface. These sporadic inputs will cause microbial communities to evolve different survival strategies compared to their counterparts living in environments that experience low but constant nutrient inputs in shallower CZ ecosystems. In contaminated subsurface sediments, microbial populations are often in an active state (Akob et al., 2007), but metabolic activity is difficult to measure without the addition of carbon substrates to fuel anaerobic growth (Akob et al., 2007, 2008).

The majority of characteristics discussed above refer to conditions that affect life in the major CZ habitats, e.g., soils, the shallow and deep subsurface. However, groundwater and cave ecosystems require a special note as to how physical complexity affects biology. Both of these ecosystems are distinguished from soil and surface habitats by having no photosynthesis and for the most part, lacking inputs of easily available carbon (Griebler and Lueders, 2009). Groundwater habitats include both shallow and deep aquifers and in many cases share space and nutrient characteristics with the shallow and deep subsurface. However, water flow through an aquifer can enhance

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microbial activity by replenishing nutrients to regions of an aquifer. Within aquifers, prokaryotes primarily live attached to surfaces, such as sediment particles, rock surfaces, and detritus (Griebler and Lueders, 2009).

Caves differ from groundwater ecosystems, as they are spaces in the subsurface that are characterized by different types of rock and mechanisms of formation (Northup and Lavoie, 2001). They can form by a variety of geological processes, including chemical dissolution, erosion by water, and activity of microorganisms. In a sense, caves are gigantic pores within the CZ and depending on their connectivity to the surface and to water sources, lack limitations in oxygen and water. The large size of a cave also provides many different microhabitats for microbes and provides space for higher animals. Microbes can be found within cave water bodies or sediments and on rock surfaces as biofilms. Although caves are oligotrophic, the conditions can be ideal for life because they are very stable in terms of physical parameters, e.g., temperature and humidity (Northup and Lavoie, 2001). Conditions in groundwater and cave ecosystems are known to support a diversity of microbial metabolisms, including aerobic and anaerobic heterotrophic and chemoautotrophic microbial populations (Table 1).

3.2 Prokaryote communities

Prokaryotes are the most abundant groups of organisms on the planet and are vital to the CZ as they are the engines of biogeochemical cycles, catalyzing life-sustaining processes. However, understanding the role of prokaryotes in the environment has posed a challenge to scientists, as they are invisible to the naked eye. Therefore, in order to put the knowledge to date about the functional role of prokaryotes into context it is necessary to have some background about how prokaryotes are studied. Historically the main approach to studying microbes was cultivation combined with identification based on morphology or physiology. However, it was well established that microscopic counts of bacteria were much higher than what was recovered by cultivation methods (< 1% of total bacteria) (Amann et al., 1995). With the advent of cultivation-independent techniques targeting small subunit ribosomal RNA molecules (SSU rRNA)

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a huge phylogenetic diversity was revealed (Hugenholtz et al., 1998). Detecting unknown microbial diversity was a huge step forward for microbiology but it did little to expand our knowledge of the functional role of uncultured organisms. The fact that < 1% of all prokaryotes can be cultured is likely due to the impact of time-consuming cultivation methods, which traditionally utilized nutrient-rich media. Nutrient-rich media varies greatly from conditions in the CZ and may not be ideal for obtaining organisms in isolation that have specific growth requirements, e.g., specific nutrients, pH conditions, incubation temperatures, or oxygen, or require interactions with other organisms (Vartoukian et al., 2010). With this perspective in mind, numerous methods have been developed that target “unculturable” prokaryotes (Vartoukian et al., 2010), so that the exact role of prokaryotes in biogeochemical cycles can be identified.

Examples of the vast phylogenetic diversity and functional role of prokaryote communities in the CZ known from both cultivation-dependent and -independent studies are summarized in Table 1. A common theme observed in Table 1 is the detection of aerobic heterotrophs. This is likely due to both the importance of this functional group to CZ processes and to the ease of cultivating these organisms. But, as cultivation-independent methods have confirmed that these organisms are a small fraction of the total community in oligotrophic habitats, new cultivation-dependent methods have expanded our knowledge about other important functional groups. This list is far from comprehensive, as much is still unknown about the microbial world, and with the development of new methods our understanding is broadening daily. For example, the anaerobic oxidation of ammonium with nitrite, previously believed to be impossible, is now recognized as an important process in the marine nitrogen cycle and may be responsible for up to 50% of the global removal of fixed nitrogen from the oceans (Dalsgaard et al., 2005). The identification of the microorganisms involved could be achieved by a modernization of conventional “cultivation based techniques” combined with the introduction of the molecular toolbox and modern bioreactor engineering to microbial ecology (Strous et al., 2002). An important step seems to be the postulation of an ecological niche based on simple thermodynamic considerations, in which various electron

donors and acceptors are combined to calculate which combinations are possible and which are not. Other sources of inspiration for interesting new microbial processes can be ecological field data such as spatial or temporal profiles. Thus, we should expect more discoveries as we have a closer look into the CZ using a polyphasic approach.

5 The abundance of prokaryotes tends to decrease with depth in the CZ, with the highest abundance observed in soils ($> 10^{10}$ cells g soil⁻¹, Table 1). Soil prokaryotes have a high metabolic diversity with most functional groups known to date being detected in numerous phylogenetic groups (Table 1). A vast diversity has been observed for soil prokaryotes and it is estimated that a single gram of soil contains at least 4000 different species (Buckley and Schmidt, 2002). Many of these organisms play an important role in nitrogen and carbon cycling with aerobic or anaerobic metabolism. Nitrogen-cycling bacteria in soils, e.g., nitrogen-fixers, denitrifiers, and nitrifiers, play a vital role for nitrogen availability soil ecosystems, thereby exerting some control on plant primary production (Buckley and Schmidt, 2002; Wall et al., 2010). Methanogens, methylotrophs, heterotrophs, acetogens, and CO₂-fixing bacteria are important components of the carbon cycle and can contribute to the fluxes of C in and out of soil (Buckley and Schmidt, 2002; Küsel and Drake, 1994, 1995).

Prokaryote communities in the shallow and deep subsurface, and groundwater ecosystems range in abundance from 10² to 10⁸ cells g⁻¹ (Table 1). These communities include organisms within diverse phylogenetic lineages that have a high metabolic capacity, although compared to soils fewer functional groups have been detected to date (Table 1). Surprisingly, the abundance of prokaryotes in the deep subsurface is on the same order of magnitude as shallower groundwater ecosystems. Over a depth range of 50–4200 m, prokaryotes in deep groundwater, sediments, and rock (granite, limestone, and basalts) ranged from 10² to 10⁸ cells ml groundwater⁻³ to 10² to 10⁸ cells g dw sediment⁻¹ (Table 1). Organisms in these habitats are phylogenetically diverse and both aerobic and anaerobic organisms involved in nitrogen, carbon, metal, and sulfur cycling have been detected (Table 1). Using a variety of cultivation-dependent and -independent techniques, it has been shown that members

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of many *Bacteria* phyla and a few novel lineages live in groundwater ecosystems (Table 1). Communities in pristine groundwater systems are distinct from surface communities, but still functionally diverse, including for example, heterotrophs and nitrifying, manganese- and sulfur-oxidizing bacteria, FeRB, and SRB (Griebler and Lueders, 2009).

Organisms cultivated from the deep display a wide array of metabolic potential, with oligotrophic heterotrophs, chemolithoautotrophs, SRB, FeRB, methanogens, thermophiles, fermenters, nitrogen-fixing bacteria, nitrifiers, and sulfur-oxidizers obtained by cultivation methods (Table 1). As discussed above, food webs in deep continental basaltic and granitic aquifers are primarily driven by chemolithoautotrophy (Pedersen, 1997; Chapelle et al., 2002; Amend and Teske, 2005). However, in other deep subsurface environments, heterotrophic SRB, living at geological interfaces between sandstone and clays, were found to gain energy and carbon from surrounding shale (Krumholz et al., 1997). SRB located in sandstones due to the high porosity of this rock appear to be dependent on old carbon in shales diffusing to their microhabitat. Within the *Archaea* phyla detected there is evidence that novel clades exist in the deep biosphere that are distinct from other environments although the functional role of these organisms is still unknown (Takai et al., 2001). Investigations of a biofilm from 1.7 km below surface in a platinum mine also uncovered a new prokaryotic morphotype (Wanger et al., 2008). This new star-shaped morphotype indicates that the deep subsurface holds an unexplored diversity of microbes and that further work is needed to fully understand the potential of these communities.

Caves harbor diverse microbial and macrofaunal communities and here we will describe the known microbial communities in a few well-studied cave systems that differ in their mechanism of formation. The Lechuguilla Cave in New Mexico is a gypsum and sulfur-bearing cave that is formed by sulfuric acid dissolution and contains ferromanganese deposits (Cunningham et al., 1995; Northup and Lavoie, 2001). This cave receives little OM, but is extensively colonized by heterotrophic, e.g., oligotrophs or Mn-oxidizers, and chemolithoautotrophic microbes, e.g., iron-oxidizers (Table 1). These

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studies suggest that the microbial communities in this cave are altering their environment by oxidizing metals and possibly contributing to the formation of ferromanganese deposits during corrosion of limestone (Northup and Lavoie, 2001). The Movile Cave in Romania and the Lower Kane Cave in Wyoming also formed via sulfuric acid dissolution (Sarbu et al., 1996; Engel et al., 2003). In these caves, it was shown that microbial food webs are based entirely on chemolithoautotrophic primary production, via methane and sulfide oxidation. Microbes identified in microbial mats of these caves included sulfur-oxidizing members of the *Beta-* (*Thiobacillus*) and *Epsilonproteobacteria* (Sarbu et al., 1996; Engel et al., 2003). The activity of sulfur-oxidizing microorganisms results in the production of sulfuric acid, which can then weather the carbonate bedrock of the caves (Sarbu et al., 1996). In karstic caves, calcium carbonate structures are a ubiquitous feature and microbial studies have shown that microorganisms (*Bacteria* and fungi) participate in carbonate mineral formation (Northup and Lavoie, 2001). These organisms precipitate carbonate under alkaline, Ca^{2+} -rich conditions, involving metabolic pathways associated with photosynthesis and nitrogen and sulfur cycling (Castanier et al., 1999).

Prokaryotes in CZ habitats vary in their abundance but a common theme is that these organisms are phylogenetically diverse. The list of organisms presented here show that the abundance of organisms generally decreases with depth and that many phyla within the domain *Bacteria* are ubiquitous in the CZ. As this list is far from complete and research is constantly expanding our knowledge of microbial ecology in the CZ, additional taxa may be revealed in the future to be in high abundance and common in all of the CZ. The function of some CZ prokaryotes revealed using cultivation-dependent techniques showed that most are heterotrophs, nitrogen and carbon cycling bacteria, chemolithoautotrophs, FeRB, and SRB. However, the function of the majority of microbes still remains unknown. With the application of new techniques and efforts to cultivate previously unculturable prokaryotes we can expect new functional roles of prokaryotes in the CZ to be revealed.

3.3 Fungal communities

Fungi are heterotrophic organisms that are found in all regions of the CZ and are identified via their morphological characteristics, physiology, or molecular genetic characterization. They have surprisingly diverse physiologies, which are summarized briefly below, but for a detailed account of the potential role of fungi in geomicrobiology we refer the reader to the excellent review of Gadd and Raven (2010). The fungal role in the CZ is best understood in soil habitats, where they range in abundance up to 10^3 cells $g\text{ soil}^{-1}$ (Table 2) and include symbiotic mycorrhizal fungi and free-living decomposers. Mycorrhizal fungi live in association with plants either as intracellular (arbuscular mycorrhizal fungi) or extracellular symbionts (ectomycorrhizal fungi) (Malloch et al., 1980). These organisms directly affect nutrient cycling and primary productivity in soils by decomposing SOM, taking up inorganic minerals, producing plant growth substances, and improving nutrient absorption for plants. In addition, ectomycorrhizal fungi contribute to mineral weathering in soils, accounting for up to 50% of total weathering via hyphae tunneling or the excretion of organic acids (van Schöll et al., 2008). Fungal weathering can increase the availability of inorganic minerals to other soil organisms and increase habitat availability by fracturing rock and creating new pore spaces. The role of fungi in weathering shallow rocks has been extensively investigated (Gadd, 2007) and production of low molecular weight organic acids by ectomycorrhizal fungi enhances weathering rates (van Schöll et al., 2008).

In the shallow subsurface and groundwater, fungi have been detected but their abundance is low (Table 2). In groundwater, the majority of reports were based on microscopic observations of spores or fungal hyphae, so little is known about their identity and functional role in the ecosystem (Krauss et al., 2003). However, the abundance of fungi was typically higher on the rock material compared to the interstitial water of an aquifer (Ellis et al., 1998) (Table 2). Many of the fungal groups detected in groundwater were related to fungi that are known to be well adapted to oligotrophic conditions (Göttlich et al., 2002). Although little is known about the functional role of fungi in

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groundwater, it is likely that these organisms are heterotrophs, feeding on prokaryote biomass and decaying organic matter. In cave ecosystems, fungi appear to play a unique role in the geology of their habitat. Fungal hyphae have been shown to act as nucleation sites for the crystallization of calcium carbonate (Northup and Lavoie, 2001), therefore, these organisms may be directly involved in forming speleothems that are characteristic to cave habitats.

Fungi have been isolated from the deep subsurface biosphere, 200 to 450 m below sea level, and were found to be at the lowest abundance (Ekendahl et al., 2003) compared to the other CZ habitats. In this study, 5 yeast, 3 yeast-like, and 17 mold strains were isolated and the yeast strains appeared to be well adapted to subsurface conditions as apparent by their small size and growth in a wide pH and temperature range (Ekendahl et al., 2003). It is thought that the small size of these yeasts is an adaption to living in small pore spaces or rock fractures. The lower abundance of these micro-eukaryotes in the deep subsurface as compared to prokaryotes, suggests that these organisms are either limited in space or nutrients or unable to cope with the anoxic conditions of the environment. However, a recent study showed that up to 2% of fungi in soils are facultative anaerobes (Kurakov et al., 2008), suggesting that anoxic conditions in the CZ may not limit the activity of fungi. Although, this number is a small percentage of the total population, it can have important implications for CZ processes. As fungi are important drivers of weathering it cannot be ruled out that fungi may be playing an important role within anoxic microzones or habitats.

3.4 Protozoa in the CZ

Protozoa have been found in the upper habitats of the CZ, with their abundance decreasing with depth (Table 2). Traditionally, protozoa were studied using direct or cultivation-dependent morphological observations, however, with the recent application of molecular techniques the diversity of this group has expanded (Finlay and Fenchel, 2001). In soils, many types of protozoa are found and their abundance ranges from 10^1 to 10^7 cells g dw soil⁻¹ (Table 2). These organisms can affect nutrient cycling in soils

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via consumption of bacteria, excretion of ingested nutrients directly into the soil system (Griffiths, 1994), and their ability to influence plant root growth (Bonkowski, 2004). In the shallow subsurface, flagellates and amoeba have been observed at an abundance of $> 10^3$ cells g dw soil or sediment⁻¹ (Table 2). In groundwater habitats, protozoa are a key part of the microbial loop in as they are effective predators, feeding on bacteria and other protozoa, and detritivores (Novarino et al., 1997). Their abundance is estimated to be low in pristine aquifers but can be as high as 10^8 cells g dw aquifer material⁻¹ in contaminated environments (Table 2). Cultivation-independent methods also suggest that protozoa are present in the deep subsurface (Pfiffner et al., 2006), although additional work is needed to confirm this observation. Research documenting the community structure and functional role of protozoa in CZ habitats is still limited, although a breadth of knowledge is available for understanding their role in soils. It appears that protozoan community structure in soils is dependent on habitat space and energy requirements (Finlay and Fenchel, 2001) and we can hypothesize that similar constraints influence communities in other CZ habitats.

4 Implications for future studies

As the CZ is the location of all life-sustaining processes on the Earth, there is a need for research to understand the complex dynamics of aboveground and belowground biodiversity and the response of biodiversity to global climate change. Research into the function of microbial populations in the CZ has focused up to now primarily on the role of soil microbiota and fungal-associated weathering process mediated especially by ectomycorrhizal fungi (e.g., Balogh-Brunstad and Keller, 2010; Holmström et al., 2010; Schmalenberger et al., 2010; Bridge et al., 2010). These studies and others (e.g., Balogh-Brunstad et al., 2008) have provided valuable insight into the role of fungal weathering processes in the rhizosphere or the upper 1–2 m of the CZ. But diverse communities of organisms live in all regions of the CZ and have the potential to impact many geochemical processes. In particular, it is necessary to assess the role of fungi in deep subsurface (> 200 m) weathering and biogeochemical cycles.

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For lithoautotrophic microorganisms, weathering of bedrock is necessary for sustain-
ing life by providing solutes for primary production. But in addition to utilizing solutes, it
is necessary to evaluate whether subsurface prokaryotes and fungi contribute directly
to weathering. Microorganisms are also known to modify their microenvironments via
pH modifications and biofilm formation. The latter has the potential to reduce or im-
pede water flow by clogging pores. Therefore, future work should determine if the
activity of microorganisms could also have a negative feedback on weathering and
transport. Specifically, the potential for microbes to form secondary minerals needs
to be assessed. In order to do this, it is necessary to determine the total biodiver-
sity of surface-associated microbial communities and not only the free-living, water-
associated organisms which can be obtained more easily from aquifers.

Therefore, future work is needed to understand the exact role of microbes in weath-
ering and geochemical cycling in the CZ, especially in subsurface habitats. Providing
a link between observed microbial populations and geochemical processes is a key
goal of microbial ecology and is especially important for understanding complex pro-
cesses in the CZ. As mentioned above, molecular-based approaches and new cultiva-
tion techniques expanded our ability to characterize the diversity of microbial commu-
nities and to study prokaryotes in isolation. The recent development of new “omics”
technologies has provided microbial ecologists with methods to link the composition
and function of in situ microbial communities. Genomics and metagenomics tech-
niques can provide information regarding the genetic potential of microbes (Cardenas
and Tiedje, 2008), whereas, proteomics targeting end-stage products, proteins, convey
functional information about microbial activity (Dill et al., 2010). Differentiating between
populations present in an environmental sample from those that are actively catalyzing
observed geochemical processes has been a difficult task for microbial ecologists in
the past. However, methods such as DNA- and RNA-stable isotope probing are now
widely used and provide an advantage over traditional molecular methods by directly
linking activity to phylogeny (Radajewski et al., 2002; Dumont and Murrell, 2005; Mane-
field et al., 2002). These methods rely on the additional of a labeled substrate, which is

metabolized by living cells and incorporated into their biomass carbon atom. All these technologies are best applied as a polyphasic approach, as the analysis of an environmental proteome is dependent on the current knowledge of genomic information.

The importance of genomics for understanding biogeochemical cycles was recently revealed in the marine literature. The genomic sequence of hyperthermophilic, marine *Archaea* indicated the presence of gene clusters that could be implicated in the metabolism of formate oxidation coupled to H₂ production (Kim et al., 2010). This finding was particularly interesting because this metabolism was not predicted to be thermodynamically favorable. By using genomic data as a guide, cultivation experiments showed growth and gene expression was correlated with formate oxidization. This polyphasic approach was able to reveal that a simple, previously unknown anaerobic respiration processes could support growth of microorganisms (Kim et al., 2010). The main message from this work for CZ science is that the application of “omics” technologies can be used to further target functional groups of prokaryotes and reveal new metabolic pathways that are relevant to biogeochemical cycling of nutrients. The most important challenge faced at this time is to determine the true potential and functionality of subsurface populations. But such work requires not only polyphasic approaches but also interdisciplinary approaches to truly understand the complexities of CZ microbiology. Microbiology alone cannot quantify the affect of microorganisms on CZ processes, although in collaboration with geologists and geochemists we can shed light on the mysteries of the CZ.

Acknowledgement. This study is a part of the research project AquaDiv@Jena funded by the ProExcellence Initiative of the federal state of Thuringia, Germany. The authors thank Anna Rusznyak, Ute Risse-Buhl, Peter Bouwma, Jonas Kley, Nina Kukowski, Beate Michalzik, Kai Uwe Totsche, and Susan Trumbore for helpful discussions.

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Table 1. Examples of prokaryote abundance, phylogenetic diversity, and functional role in CZ habitats.

Region	Habitat	Prokaryote abundance	Functional groups	Phylogenetic groups detected so far	References
Pedosphere	Soils	10^7 to 10^{10} cells g soil ⁻¹	<p>PHOTOAUTOTROPHS (e.g., CO₂-fixing bacteria)</p> <p>HETEROTROPHS (e.g., aerobes and anaerobes, nitrifiers, iron- and sulfate-reducers, nitrogen-fixing bacteria, denitrifiers, methyloprophs, acetogens)</p> <p>CHEMOLITHOAUTOTROPHS (e.g., ammonium oxidizers, methanogens, methanotrophs)</p>	<p><i>Bacteria</i> (<i>Proteobacteria</i>, <i>Acidobacteria</i>, <i>Actinobacteria</i>, <i>Bacteroidetes</i>, <i>Chloroflexi</i>, <i>Chlorobi</i>, <i>Cyanobacteria</i>, <i>Cytophagales</i>, <i>Deinococcus</i>, <i>Ferribacter</i>, <i>Firmicutes</i>, <i>Gemmatimonadetes</i>, <i>Planctomycetes</i>, <i>Verrucomicrobia</i>, candidate divisions)</p> <p><i>Archaea</i> (<i>Crenarchaeota</i>, <i>Euryarchaeota</i>)</p>	<p>Torsvik et al. (2002); Whitman et al. (1998); Beloin et al. (1988); Buckley and Schmidt (2002); Miltner et al. (2004); Brons and van Elsas (2008); Kowalchuk and Stephen (2001); Küsel and Drake (1995); Küsel et al. (2002)</p>
Unsaturated bedrock	Shallow subsurface	10^4 to 10^8 cells g ⁻¹	<p>HETEROTROPHS (e.g., aerobes and anaerobes, nitrifying bacteria, iron- and sulfate-reducers, nitrogen-fixing bacteria, methane-oxidizers)</p> <p>CHEMOLITHOAUTOTROPHS (e.g., Mn- and sulfur-oxidizers)</p>	<p><i>Bacteria</i> (<i>Proteobacteria</i>, <i>Acidobacteria</i>, <i>Actinobacteria</i>, <i>Bacteroidetes</i>, <i>Chloroflexi</i>, <i>Firmicutes</i>, <i>Planctomycetes</i>, <i>Verrucomicrobia</i>, candidate divisions)</p>	<p>Brockman and Murray (1997); Kieft et al. (1993); Balkwill and Ghiorse (1985); Wilson et al. (1983); Fliermans (1989); Hazen et al. (1991); Wang et al. (2008)</p>

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Table 1. Continued.

Region	Habitat	Prokaryote abundance	Functional groups	Phylogenetic groups detected so far	References
Saturated bedrock	Groundwater ecosystems	10 ³ to 10 ⁸ cells cm ⁻³ water	HETEROTROPHS (e.g., oligotrophs, nitrifiers, Mn-oxidizers, iron- and sulfate-reducers)	<i>Bacteria</i> (<i>Proteobacteria</i> , <i>Acidobacteria</i> , <i>Actinobacteria</i> , <i>Bacteroidetes</i> , <i>Chloroflexi</i> , <i>Firmicutes</i> , <i>Nitrospira</i> , <i>Planctomycetes</i> , <i>Spirochaetes</i> , <i>Verrucomicrobia</i> , candidate divisions)	Ghiorse and Wilson (1988); Madsen (2008); Pedersen (2000); Griebler and Lueders (2009); Ellis et al. (1998); Hirsch and Rades-Rohkohl (1990); Hazen et al. (1991); Emerson and Moyer (1997); Alfreider et al. (2009); Akob et al. (2007, 2008)
		> 10 ¹⁰ cells cm porous sediment ⁻³	CHEMOLITHOAUTOTROPHS (e.g., carbon-fixers, iron- and sulfur-oxidizers)		
	Caves	10 ² to 10 ⁸ cells cm ⁻³ water or sediment	HETEROTROPHS (e.g., oligotrophs, Mn-oxidizers, nitrifiers, carbonate precipitating bacteria, sulfate-reducers)	<i>Bacteria</i> (<i>Proteobacteria</i> , <i>Acidobacteria</i> , <i>Actinobacteria</i> , <i>Bacteroidetes</i> , <i>Chloroflexi</i> , <i>Cytophagales</i> , <i>Firmicutes</i> , <i>Gemmatimonadetes</i> , <i>Nitrospira</i> , <i>Planctomycetes</i> , <i>Verrucomicrobia</i>)	Gounot (1994); Farnleitner et al. (2005); Rusterholtz and Mallory (1994); Cunningham et al. (1995); Northup and Lavoie (2001); Northup et al. (2003); Pašić et al. (2010); Barton and Northup (2007); Engel et al. (2003, 2004)
			CHEMOLITHOAUTOTROPHS (e.g., iron-, methane- and sulfur-oxidizers)	<i>Archaea</i> (<i>Crenarchaeota</i> , <i>Euryarchaeota</i>)	
	The deep subsurface	10 ² to 10 ⁸ cells ml groundwater ⁻¹	HETEROTROPHS (e.g., oligotrophs, thermophiles, fermenters, nitrogen-fixers, nitrifiers, sulfate- and iron-reducers)	<i>Bacteria</i> (<i>Proteobacteria</i> , <i>Acidobacteria</i> , <i>Actinobacteria</i> , <i>Bacteroidetes</i> , <i>Chlorobi</i> , <i>Chloroflexi</i> , <i>Firmicutes</i> , <i>Gemmatimonadetes</i> , <i>Nitrospira</i> , <i>Planctomycetes</i> , <i>Verrucomicrobia</i> , candidate divisions)	Chapelle et al. (2002); Pedersen (1993, 1997); Madsen (2008); O'Connell et al. (2003); Rastogi et al. (2009); Pfiffner et al. (2006); Haldeman et al. (1993)
			CHEMOLITHOAUTOTROPHS (e.g., thermophiles, methanogens, acetogens, iron-, manganese-, methane- and sulfur-oxidizers)	<i>Archaea</i> (<i>Crenarchaeota</i> , <i>Euryarchaeota</i>)	

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Table 2. Micro-eukaryote abundance and functional or phylogenetic diversity in CZ habitats.

Region	Habitat	Abundance	Functional or phylogenetic groups	References
Pedosphere	Soils	10^1 to 10^7 cells g dw soil ⁻¹	Protozoa (flagellates, ciliates, naked and testate amoeba)	Beloin et al. (1988); van Schöll et al. (2008); Brad et al. (2008); Strauss and Dodds (1997); Lara et al. (2007); Ekelund et al. (2001); Adl and Gupta (2006); Robinson et al. (2002)
		$> 10^3$ cells g sediment ⁻¹	Fungi (<i>Basidiomycota</i> , <i>Ascomycota</i> , <i>Chytridomycota</i> , <i>Zygomycota</i> , <i>Glomeromycota</i>)	Brad et al. (2008); Malloch et al. (1980); Kurakov et al. (2008)
Unsaturated bedrock	Shallow subsurface	$> 10^3$ cells g dw soil or sediment ⁻¹ > 18 cells g dw sediment ⁻¹	Protozoa (flagellates, amoeba) Fungi (yeasts)	Fliermans (1989); Ekelund et al. (2001)
Saturated bedrock	Groundwater ecosystems	$< 10^0$ to 10^8 cells g dw aquifer material ⁻¹	Protozoa (flagellates naked amoeba, ciliates, heliozoans)	Novarino et al. (1997); Ellis et al. (1998); Novarino et al. (1994); Ekelund et al. (2001); Loquay et al. (2009)
		< 3 flagellates ml ⁻¹ > 652 cells cm rock ⁻² > 91 cells ml water ⁻¹	Fungi (unclassified hyphomycetes, <i>Ascomycota</i> , <i>Zygomycota</i> , <i>Oomycetes</i>)	Krauss et al. (2003, 2005); Ellis et al. (1998); Göttlich et al. (2002); Solé et al. (2008); Kuehn and Koehn (1988)
	Caves	$< 10^0$ flagellates ml ⁻¹ in free water 2×10^1 flagellates ml ⁻¹ pore water $> 10^5$ cells g ⁻¹	Protozoa (flagellates, naked amoeba, ciliates, heliozoans) Fungi (<i>Ascomycota</i> , <i>Zygomycota</i> , <i>Rhizopus</i>)	Loquay et al. (2009) Cunningham et al. (1995); Northup and Lavoie (2001); Elhottová et al. (2006)
	The deep subsurface	0.01 to 1 cells ml groundwater ⁻¹	Fungi (yeasts (<i>Basidiomycota</i>) and molds)	Ekendahl et al. (2003)

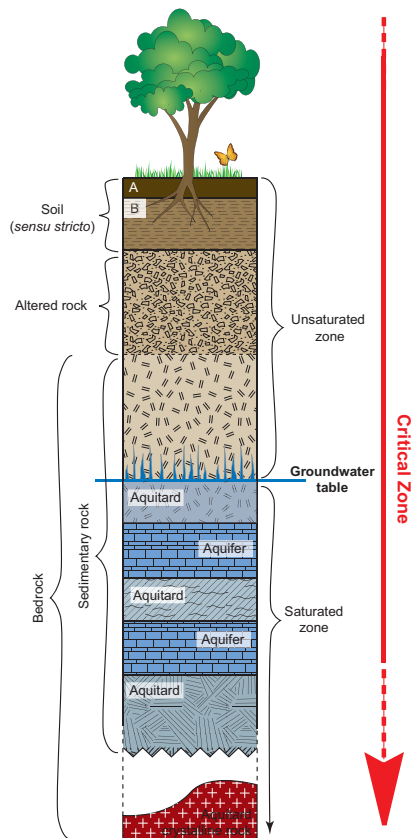


Fig. 1. The Earth's Critical Zone as exemplified for a sedimentary rock. The portion of the biosphere ranging from the outer extent of vegetation down through the lower limits of groundwater, including the soil, altered rock, the unsaturated zone, and the saturated zone (modified from Lin, 2010). **(A)** refers to the topsoil and **(B)** refers to the subsoil.

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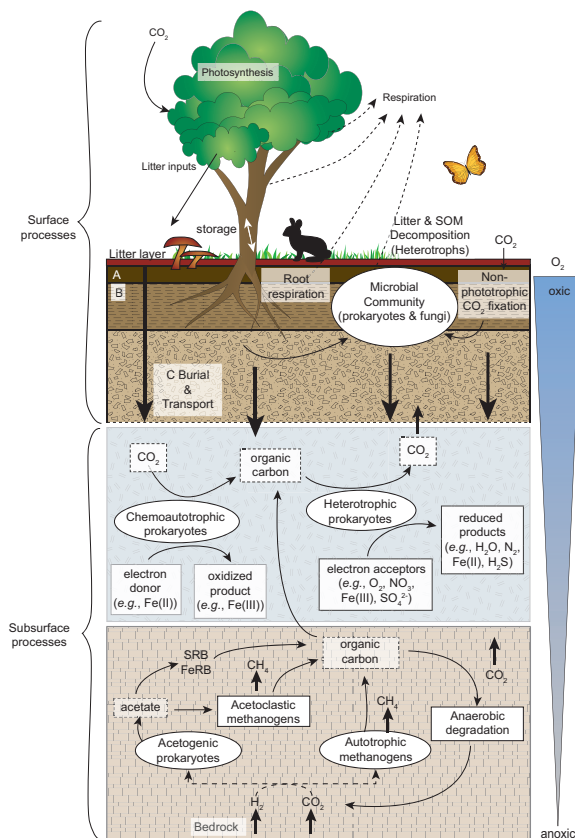


Fig. 2. The CZ biological cycle. Illustrated are the dominant biological processes driving the ecological cycle within the CZ. Cycles driven by surface- and subsurface-inputs of energy are shown and these cycles may overlap, as the extent of vertical transport of energy between layers of the CZ is unknown (modified from Pedersen, 1997; Trumbore, 2006).

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