Chapter 8
Microfauna Within Biological Soil Crusts

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8.1 Introduction

A variety of microfauna inhabit the biological soil crusts (biocrusts) of arid soils from all parts of the globe, including the southwestern USA (Bamforth 2004, 2008; Darby et al. 2006, 2007a, b; Neher et al. 2009), the Negev Desert of Israel (Jones and Shachak 1990; Pen-Mouratov et al. 2011), the Tengger Desert of northern China (Liu et al. 2011; Li et al. 2011), Australia (Robinson et al. 2002), and Antarctica (Bamforth et al. 2005; Sohlenius et al. 2004; Schwarz et al. 1993; Colesie et al. 2014). The objective of this chapter is to review the literature on microfauna associated with biocrusts and identify the major microfaunal groups that inhabit biocrusts, the functions they perform in the biocrust ecosystem, when they are most active, where they are located in the soil and biocrust profile, and how they are affected by surface disturbances and altered abiotic conditions. We conclude by proposing three research priorities that are most necessary to improving our understanding of the ecology of biocrust microfauna.

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8.2 Who Are the Microfaunal Inhabitants of Biocrusts?

8.2.1 Protozoa

Protozoa may be the least understood of the biological soil crust consumers because they are small and numerous, but difficult to quantify, observe, manipulate, and identify taxonomically. Most protozoans are generally considered bacterivorous, or predators of other protozoans and small invertebrates, but many species are known to feed on fungal spores and hyphae, and it is likely that many also feed on cyanobacteria in biocrust systems. Predation of cyanobacteria by protozoans is prevalent (Dryden and Wright 1987), but most reports are from aquatic species and it is not clear how many cyanobacteria-feeding species occur in biocrusts. Ghabbour et al. (1980) suggested that protozoans from desert soils (particularly a species of Acanthamoebae) consumed the cyanobacteria *Anabaena* spp. and *Nostoc* spp. in a liquid culture and contributed to the reduction of chlorophyll-α, but there was no definitive evidence that this was not due to grazing from the nematode microfauna also present. Protozoan predation of bacteria, spores, and other protozoans is generally by phagocytosis or engulfing of the whole cells, while predation of filamentous fungal hyphae and cyanobacteria can be either through phagocytosis of the cells/filaments or by a more specialized piercing mechanism. Filose pseudopods (in the case of certain amoebae), or specialized internal structures (in the case of some flagellates and ciliates), pierce fungal hyphae or cyanobacterial filaments to access the prey cells' cytoplasm. This method of feeding by piercing has been found in diverse protozoans, such as in the amoeboid genus *Vampyrella*, the flagellate family Viridiraptoridae, and the ciliate family Grossglockneridae, but it remains to be determined how many of these species are to be found in biocrust systems.

Much of the ecological research on biocrust protozoa distinguishes between mobility groups, which include "amoebae," "flagellates," and "ciliates." These mobility groupings are not monophyletic groups, nor do they necessarily perform distinct functions, but this does not necessarily mean that mobility groupings are invalid methods of understanding the ecology of biocrust protozoa. Protozoa live within a network of water films and water-filled pore spaces, which constrains the size and number of organisms that can inhabit soil and organic matter. Presumably, small, amoeboid protozoa are able to occupy smaller pore sizes that are slow to dry out compared to larger, rigid-bodied protozoans like ciliates. If true, this would have significant implications for which species can be physiologically active in different levels of soil moisture. The difficulty that comes with counting, observing, and identifying protozoa also impedes our ability to distinguish specific niches or feeding habits of different protozoan species. Desert amoebae have been distinguished at finer mobility forms to differentiate between amoebae with (1) extended pseudopodia, (2) limax amoebae (see Fig. 8.1a, roughly cylindrical in shape, resembling a slug) with a single leading pseudopod and no subpseudopodia, (3) limax amoebae with eruptive cells, and (4) flattened, fan-shaped cells

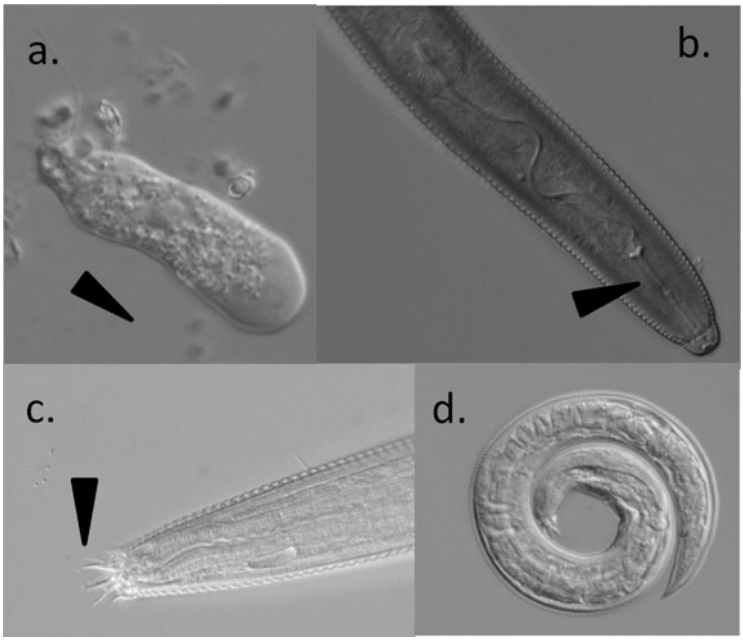

Fig. 8.1 Biological soil crust biota. (**a**) Limax (snail-like) amoebae (*arrow* points in the direction that the amoebae are moving). (**b**) Stylet-bearing fungivorous/omnivorous nematode of the genus *Tylenchus* (*arrow* points to needlelike stylet that is used to pierce fungal hyphae and filamentous cyanobacteria). (**c**) Bacterial-feeding nematode of the genus *Acrobeles* in an active, hydrated form (*arrow* points to probolae). (**d**) Bacterial-feeding nematode of the genus *Acrobeles* in a coiled, anhydrobiotic form. Images by B. Darby

(Rodriguez-Zaragoza et al. 2005; Zaragoza et al. 2007). Some studies have been able to further identify individual species belonging to some functional groups (Bamforth 1984, 2004, 2008; Bamforth and Bennett 1985; Bamforth et al. 2005; Robinson et al. 2002). The results of these meticulous studies at finer resolution have led to the observation that biocrusts contain numerous species of non-encysting protozoa (like Thecamoebae), which may suggest that biocrusts serve as microrefugia with pockets of adequately moist pores for some protozoa (Robinson et al. 2002).

8.2.2 Nematodes

Nematodes are not as abundant as protozoa in either numbers or biomass, nor are they as phylogenetically diverse as protozoa, but we have a greater understanding of nematode ecology in biocrust habitats, mostly because we can count, identify, and manipulate nematodes easier and with a finer level of taxonomic resolution. However, most of our understanding of feeding habits and life history traits of

specific nematode species is still based on generalizations made at the taxonomic level of family or genus. One of the outstanding questions of biocrust nematode ecology is whether the species that are found in biocrusts have similar or different feeding habits of comparable species of the same genus in non-biocrust habitats. Nearly every component of the biocrust food web has some potential nematode predator. For the purposes of estimating general trophic links in the nematode community, species of nematodes are typically grouped into one of several feeding types identified largely on the basis of the size and shape of feeding apparati (Yeates et al. 1993). One of the most distinguishing factors is the presence or absence of a stylet (see Fig. 8.1b), a fine, needlelike piercing apparatus of organisms that pierce (rather than fully engulf) their prey. There are five types of nematodes: herbivores, fungivores, bacterivores, predators, and omnivores. Herbivores have a fine-apertured stylet with a length depending on whether the species tends to be an endo- or ectoparasite. Fungivores have a fine-apertured stylet that is typically short. Bacterivores do not have a stylet and instead have an open buccal cavity with various types of lips surrounding the anterior opening, from smooth and low-rounded to very elaborate, branched processes extending from the lips (called probolae, see Fig. 8.1c). Predators (order Mononchida) have a large, open stoma (oral opening), often with a prominent tooth or row of denticals (Fig. 8.2). There are two main types of omnivores that deserve to be acknowledged in biocrust systems. Nematodes in the orders Tylenchida and Aphelenchida have fine-apertured stomato-stylets and can potentially pierce filaments to feed on the cytoplasm of fungi, fine root hairs, moss rhizoids, and cyanobacteria (Fig. 8.3a). Nematodes in the order Dorylaimida have a broad-apertured odontostylet and can feed on fungi, cyanobacteria, and other microinvertebrates including nematodes, tardigrades, and rotifers. Previous outlines of nematode feeding habits advised against assigning the name of omnivore whenever possible, due to the ambiguity of the designation. However, they also acknowledged the significant "gaps in knowledge of feeding in the smaller tylenchids and many dorylaims" (Yeates et al. 1993). The nematodes that are most likely to consume cyanobacteria are those with a piercing/sucking stylet (such as those traditionally identified as fungivores or predator/omnivores) rather than those with an open buccal cavity (otherwise called bacterivores). This is supported by some of the earliest studies that documented nematode feeding habits as they demonstrated that feeding on algae (both green algae and cyanobacteria) was just as prevalent as feeding on fungal hyphae among the small Tylenchidae (Wood 1973a, b). Because cyanobacteria are such a significant portion of the biocrust soil food web, we consider it prudent to assume for now that many nematodes in genera thought to be primarily fungivorous in temperate ecosystems may also feed on cyanobacteria in biocrust systems (Fig. 8.3b).

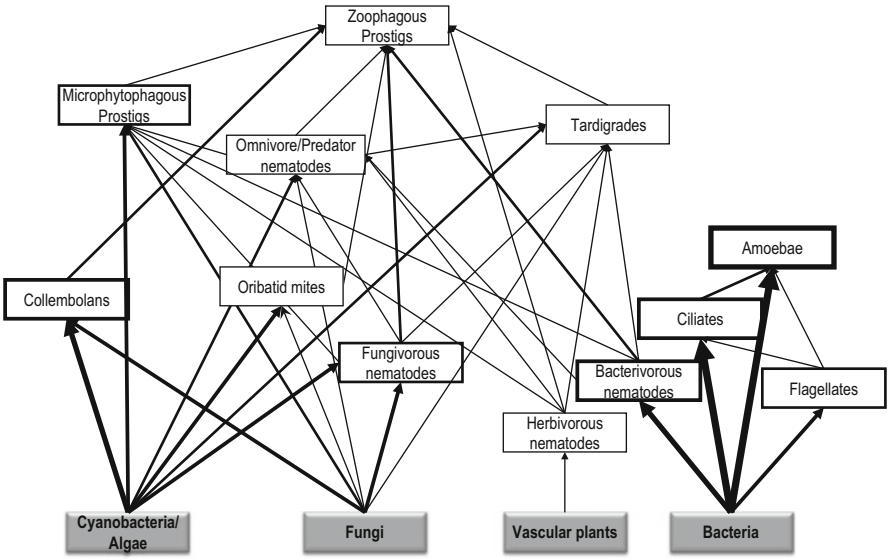

Fig. 8.2 Biocrust consumer food web. The consumer food web as based on the microfauna found in a Moab, Utah, biocrust system in southwestern USA (Darby et al. 2011; Neher et al. 2009). The width of the *arrows* linking prey to their consumer is proportional to the biomass nitrogen of that trophic link, and the width of the border around the consumer text box is proportional to the amount of inorganic nitrogen (N) being released from the consumer functional group [according to the results of the model as computed by Hunt et al. (1987) for the Moab, Utah, biocrust food web]. In contrast to a typical short-grass prairie soil food web, the biocrust food web: (1) has more N cycling through and from protozoans and (2) has more N cycling through and from the functional groups that are otherwise thought to be fungivorous (if, indeed, these functional groups are also capable of feeding on cyanobacteria, which is a reasonable but yet unconfirmed assumption)

8.2.3 Tardigrades and Rotifers

Tardigrades and rotifers are also among the microinvertebrates that one might find inhabiting the water films of a biocrust sample. Both tardigrades and rotifers are sometimes found exclusively on the surface of biocrusts as most species are extremely desiccation tolerant. Rotifers are filter feeders that primarily prey on small cells (e.g., bacteria, flagellates, and small unicellular algae), but probably not on filamentous cyanobacteria or large protist cells that are larger than their mouths. Tardigrades may be algivores, fungivores, cyanovores, or predators (on other microinvertebrates) depending on whether they have a piercing/sucking stylet or an open buccal tube. Compared to nematodes, there is less doubt that tardigrades feed on cyanobacteria (Fig. 8.3c), but it remains unclear which species of cyanobacteria are acceptable prey items and whether cyanobacteria are necessarily preferred over other potential foods (such as moss, fungi, or green algae).

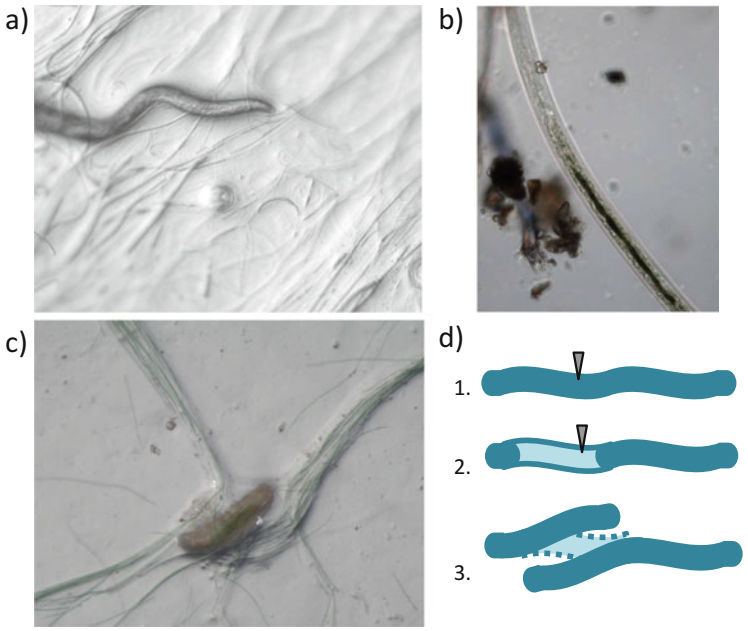

Fig. 8.3 Feeding on cyanobacteria. Digital images of microfauna feeding on cyanobacteria. (**a**) *Aphelenchoides* sp. feeding on *Microcoleus vaginatus* in monoxenic culture, (**b**) *dark green/cyan* pigmentation in the intestines of an Aporcelaimidae extracted from soil, (**c**) tardigrade *Haplomacrobiotus utahensis* feeding on *Microcoleus vaginatus*, (**d**) schematic of the regrowth of evacuated cyanobacterial filaments after being fed on by a piercing and sucking stylet-bearing nematode or tardigrade. First, the stylet-bearing nematode or tardigrade pierces the cyanobacterial filament with its piercing stylet (represented by the *triangle*). Second, the organism sucks out the cytoplasm of the segments adjacent to the initial stylet piercing. Finally, the ends of the filaments regrow into and out of evacuated segments, effectively creating two new ends from which the cyanobacteria grows

8.2.4 Microarthropods

A variety of animals that do not require thin films of water, including arthropods and mollusks, also inhabit biocrusts around the world (Shepherd et al. 2002; Colesie et al. 2014; Shachak and Steinberger 1980). Microarthropods such as mites and collembolans inhabit primarily air-filled pore spaces (unlike the water-film fauna that include protozoans, nematodes, tardigrades, and rotifers) and are typically more mobile than water-film fauna (both vertically and horizontally) across larger spatial scales (Shepherd et al. 2002). Like nematodes, the feeding habits of most microarthropods are predicted based on observations of closely related taxa and on the morphology of feeding structures. Most biocrust collembolans are microphytophages, feeding on cyanobacteria, fungi, and detritus, but some are also facultatively predaceous on smaller microinvertebrates such as nematodes. However, biocrust mites can feed on diverse food items such as cyanobacteria, fungi,

nematodes, detritus, mammals, carrion, arthropods, lichens, pollen, and plants (Neher et al. 2009). Larger invertebrates, including mollusks such as snails and macro-arthropods such as ants and pseudoscorpions, can also be significant components of some biocrusts (Li et al. 2011). Unlike microfauna, which are thought to have minimal impact on the physical structure of soil and biocrusts, arthropods like ants have been shown to alter the physical architecture of soil and biocrust hydrology (Chen and Li 2012; Li et al. 2014). Predators of microarthropods form the link between the soil microinvertebrate fauna and the aboveground insectivores. Snails graze lichens, cyanobacteria, and mosses of rocky surfaces (Jones and Shachak 1990; Shachak and Steinberger 1980).

8.3 What Microfauna Do in Soil Crust Ecosystems

Microfauna in biocrusts perform many of the same functions that microfauna perform in grassland or forest systems. This includes regulating their microbial prey populations, cycling nutrients by stimulating microbial growth and excreting waste nutrients as soluble inorganic or low molecular weight organic form, dispersing spores or vegetative microbial cells that are viable and not fully crushed during digestion, and serving as prey for macrofauna at higher trophic levels in the soil food web (Neher 2001; Freckman 1988). However, the relationship between microfauna and autotrophic (and in some cases diazotrophic) cyanobacteria in the soil food web is one of the primary questions that remains regarding the role of microfauna in biocrust systems: that is, how many microfauna consume cyanobacteria, and what is the significance of this trophic link for the biocrust food web? The nutrients that microinvertebrates mobilize are thought to depend on the elemental ratio of their prey (Hunt et al. 1987). For example, a nematode that feeds on fungi with a relatively high carbon(C)/nitrogen(N) ratio is thought to be N limited and therefore will mineralize more C by respiration than N by waste release. Additionally, the ecosystem function that would be affected by grazing would be the decomposition performed by fungal extracellular enzyme activity. However, if this same nematode species can also prey on N-fixing cyanobacteria with a low C:N in a biocrust system, then we would expect the nematode to be relatively C limited and would instead mineralize more N as a waste product instead of C by respiration. Additionally, the ecosystem function that would be affected by grazing would be photosynthesis and N-fixation from the cyanobacteria. These possibilities have not been demonstrated experimentally with nematodes, but they have been shown for protozoa feeding on *Azotobacter chroococcum* (Nasir 1923; Cutler and Bal 1926) and Collembola feeding on arctic cyanobacterial mats (Birkemoe and Liengen 2000). In both cases, the experimenters found that N-fixation increased with intermediate levels of grazing from their microfaunal predator.

To demonstrate the potential effect of biocrust fauna on nutrient cycling, N cycling through the biocrust food web was estimated for a field site in a cool desert location in the southwestern USA (Darby et al. 2011; Yeager et al. 2012; Zelikova

et al. 2012), based on the approach of Hunt et al. (1987) and de Ruiter et al. (1993). The desert food web was constructed based on best estimates of feeding habits known for the organisms found at this site and accounted for the findings of grazing on cyanobacteria by stylet-bearing nematodes and tardigrades, as well as microphytophagous mites and collembolans. Biomass of micro- and mesofauna at this site was obtained from 2-year mean abundances of all functional groups previously measured at Colorado Plateau (Darby et al 2011). To facilitate comparison, and conform to published conventions, biomass per gram of dry soil was converted to biomass per area (to 10 cm depth) assuming a bulk density of 1.0 g cm^{-3} (Belnap 1995), and biomass N was estimated as 5 % of total dry biomass. Feeding preferences and physiological parameters were assigned according to Hunt et al. (1987) with the following exceptions. First, the generation time of omnivore nematodes in the order Dorylaimida was set to 50 days per year, representative of the slower-growing omnivore-predators in the desert such as *Aporcelaimellus* and Qudsianematidae (Wood 1973a, b). Second, the generation time of all protozoa was decreased from 6.67 days to 2 days, which is a conservative estimate of the maximum growth rate (0.5 per day) of these desert protozoa (Darby et al. 2006). Finally, microphytophagous prostigmatid and oribatid mites, collembolans, tardigrades, and tylench- and dorylaim-type omnivores were assumed to prey on cyanobacteria with the same preferences as on saprophytic fungi (Neher et al 2009; Wood 1973a; Yeates et al 1993). Microarthropods were assumed to be active and growing for 365 days per year because they are thought to be active even in dry, air-filled pores. Nematodes and protozoa were assumed to be active and growing for 40 days per year (Hunt et al. 1987). This model predicted that belowground soil fauna produce 311 mg N m^{-2} $year^{-1}$ inorganic N and 97 mg N m^{-2} $year^{-1}$ organic N from feces (Table 8.1) or 3.0 kg N ha^{-1} $year^{-1}$ inorganic N and 1.0 kg N ha^{-1} $year^{-1}$ organic N from feces. Like in temperate grassland systems, most of the inorganic N comes from protozoa and bacterivorous nematodes grazing on bacteria (Fig. 8.3). However, what is unique in this system is that a large portion of biologically fixed N from cyanobacteria would be mobilized by microfauna under the assumption that fungivorous functional groups also prey on cyanobacteria. This is a reasonable but unconfirmed assumption, which is why detailing the actual feeding habits of desert microfauna is so important to understanding overall ecosystem function.

Another significant function of microbe-feeding microinvertebrates is the dispersal of viable microbial spores and cells to new locations. In the case of biocrusts, this would include fungal spores and bacterial cells that are not crushed or enzymatically degraded by a predator that feeds by engulfing its prey. However, this would not include filamentous prey items (such as fungal hyphae and filamentous cyanobacteria) that are consumed by predators that feed by piercing their prey (Fig. 8.3). Even though piercing-type predators of filamentous cyanobacteria, such as nematodes or tardigrades, would not disperse vegetative cells, it may still be possible that these predators may nonetheless alter the distribution of filamentous cyanobacteria in biocrusts. As predators such as tardigrades pierce a cyanobacteria filament and suck out the cytoplasm, they leave a gap of evacuated cytoplasm. As

Table 8.1 Faunal contributions to nitrogen cycling

Functional Group	Biomass (mg N m^{-2})	Inorganic (mg N m^{-2} $year^{-1}$)	Feces (mg N m^{-2} $year^{-1}$)	Death (mg N m^{-2} $year^{-1}$)
Zoophagous	35.6	0.76	0.90	0.60
Microphytophagous	88.4	1.99	3.56	1.57
Oribatid	33.1	0.50	0.89	0.39
Collembolans	1070.7	24.14	43.10	18.97
Tardigrades	9.6	0.03	0.06	0.03
Dorylaim omnivore nemas	88.6	0.19	0.30	0.11
Tylenchid omnivore nemas	541.6	2.21	5.71	1.30
Herbivore nemas	2.7	0.007	0.03	0.004
Bacterivore nemas	1861.8	33.25	26.08	5.87
Amoebae	2406.7	161.14	11.01	(48.13)
Ciliates	1185.1	79.95	5.47	(23.88)
Flagellates	98.6	6.90	0.47	(2.06)
Total (mg N m^{-2})	7422.5	311.08	97.61	102.91

Nitrogen (N) cycling results from soil food web model [adapted from Hunt et al. (1987)], including standing biomass and nitrogen contributions to inorganic substrates and organic substrates through feces and death. Death of amoebae, ciliates, and flagellates was computed as for other organisms (inverse of generation time) but is presented in parentheses because they are thought to not die naturally but rather continue to divide. Thus, contributions to substrate from death may be much less than modeled and limited to environmentally induced mortality rather than natural turnover

the adjacent cells grow and extend into the gap, they sometimes extend past the opposing end, which results in lateral branching, creating twice as many ends from which the cyanobacteria can grow (Fig. 8.3d). This phenomenon was observed in laboratory cultures on flat agar surfaces, but it is unclear if it occurs similarly in a more complex natural environment.

8.4 When Are Microfauna Active?

The water-film fauna that are restricted to water-filled pores are often constrained to brief windows of activity in biocrusts. Most biocrust microfauna have diverse cryptobiotic ("hidden life," Crowe and Cooper 1971) capabilities that allow them to enter temporary dormant stages such as anhydrobiosis (to survive life without water, Crowe and Crowe 2000), cryobiosis (to survive freezing), and anoxybiosis (to survive life without oxygen, although this is less common in surface biocrusts). As soils dry, microinvertebrates enter anhydrobiosis by converting storage carbohydrates into low molecular weight cellular protecting sugars, such as trehalose (Crowe 2002; Madin and Crowe 1975). Specimens that have entered anhydrobiosis are often seen in a coiled, anhydrobiotic state (Fig. 8.1d). Entering and exiting

anhydrobiosis is metabolically costly (Crowe et al. 1977; Madin et al. 1985), and the frequency and duration with which microinvertebrates must endure hydration cycles is thought to affect their fitness in a biocrust habitat. The microinvertebrate species that exist in surface biocrusts must be able to tolerate frequent wetting/drying cycles, brief periods of activity following hydration events, prolonged periods of drought, and extreme temperatures while anhydrobiotic. The surrounding soil conditions, such as texture, depth, and cover, can influence the severity of the abiotic stresses. Soil pores dry out more quickly at the surface than at depth, in coarse relative to fine soils, and in soils with very low organic or vegetative cover than soils with higher cover. As a result, the biocrust microinvertebrate community composition differs somewhat between soils of different depth, texture, and cover (Darby et al. 2010), as does the mobility of microfauna after rain events (Whitford et al. 1981; Parker et al. 1984).

8.5 Where Are Microfauna Found in Biological Soil Crusts?

Perhaps the best characterized aspect of biocrust microfaunal ecology, more so than their feeding habits or life history traits, is the overall abundance and distribution of organisms relative to soil depth, cover type, successional stage, and proximity to vascular plants. Microfauna can generally exist wherever sufficient microbial prey exists, and this usually matches the distribution of plant biomass or organic matter. This means that microfauna are associated with diverse types of biocrusts even in relatively extreme environments or with little moisture, such as sand savannas (Neher et al. 2003), desert biocrusts (Belnap and Phillips 2001; Shepherd et al. 2002), tropical inselbergs (Vaculik et al. 2004), and Antarctic soils, glaciers, and hypoliths (Sohlenius et al. 2004; Schwarz et al. 1993; see Chap. 11 by Pointing). In arid systems, nematodes can be found as deep as 11–12 m (Freckman and Virginia 1989), but the peak abundance of microfauna in soils covered by biocrusts is usually within the top 10–20 cm. In most soils, protozoa, nematodes, and microarthropods are more abundant in the surface 0–10 cm than in the next 10–20 cm or 20–30 cm (Darby et al. 2006, 2007a, b, 2010; Housman et al. 2007; Neher et al. 2009). However, the proportion of microfauna that are anhydrobiotically inactive is inversely proportional to soil moisture or relative humidity, and relative humidity in soils below 10 cm is generally greater than in surface 0–10 cm soils. Thus, the abundance of active, hydrated water-film fauna may actually be greater below 10 cm than above 10 cm depth because even though microfauna are generally more abundant above 10 cm than they are below 10 cm, most of them are inactive at the surface (Darby et al. unpublished results). This is potentially significant because if the autotrophic biocrust components are most active at the surface during brief periods after rain events, but the heterotrophic consumers are most active at depth in between rain events, then this means that

productivity and consumption is potentially decoupled in both space and time. The full implications of this spatial and temporal decoupling have not been explored experimentally.

The second most determining factor of the abundance and distribution of microfauna is the distribution of vascular plants. Microfauna are generally more abundant and taxonomically diverse close to plant rhizospheres than in the interspace between plants (Darby et al. 2010; Housman et al. 2007). This is generally true for all ecosystems, but it is easier to quantify in arid systems with more sparsely distributed vascular plants. Furthermore, microfauna are more abundant and taxonomically diverse beneath and associated with late-successional stage "dark" lichen and moss biocrusts than when associated with early-successional stage "light" cyanobacteria biocrusts (Darby et al. 2006, 2007a, b, 2010). This can reasonably be explained, as greater productivity and microbial prey biomass is found in lichen and moss biocrusts than in cyanobacteria crusts. It has also been observed that nematode communities are more "ecologically mature" in late-successional stage biocrusts than early-successional stage crusts (Darby et al. 2007a, b). A greater proportion of the individuals associated with late-successional stage crusts are "K-strategists" (sensu Pianka) that are late to develop and have low reproductive output, slow generation times, and longer life spans (Bongers 1990). However, the persistor-type "K-strategist" nematodes that are associated with late-successional stage crusts also tend to be higher trophic levels (such as predators and omnivores). We cannot necessarily distinguish whether predatory K-strategist nematodes are associated with late-successional stage biocrusts due to increased biomass and autotrophic productivity going into the soil food web, or because late-successional stage biocrusts tend to ameliorate temperature and moisture fluctuations that promote persistor-type nematode species. Similarly, physical trampling of surface crusts reduces the biomass and architectural complexity of the lichen, cyanobacteria, and moss cover. This is associated with reduced abundance and species richness of nematodes relative to that of non-trampled biocrusts (Darby et al. 2010). However, we are not yet able to determine whether the effect of physical trampling on reducing nematode abundance and richness is due to the reduced biomass of microfloral prey items or because of the altered hydrology and reduced architectural complexity and pore size distribution of the trampled biocrust surface.

8.6 How Are Microfauna Affected by Surface Disturbance and Altered Climate?

The effect of altered climate on crust microfauna is a complex interaction of temperature, moisture, and the seasonality of these changes. Most microfauna can tolerate relatively high temperatures (>40–50 °C) if they gradually enter their anhydrobiotic state, but cannot tolerate being hydrated at high temperatures.

Similarly, many microfauna can tolerate frequent wetting and drying cycles in moderate temperatures, but they incur significant mortality if these wetting and drying cycles are at high temperatures (>35–40 °C). Thus, we predict that neither increased temperature during drought nor decreased moisture during warm seasons is necessarily going to alter microfaunal communities if they are already dormant. Instead, the combination of altered temperature and moisture is likely to be more influential than either alone. However, empirical evidence of the effect of altered temperature and precipitation on microfaunal communities is likely to come only after long-term experimentation (Darby et al. 2011). The primary literature does not have sufficient empirical evidence of the influence of altered climate on desert soil fauna community composition and their role in soil ecosystem functioning, so instead we rely on model predictions. Hunt and Wall (2002) addressed this challenge in temperate food webs by asking the question "how many species does it take to maintain ecosystem function?" They compared food web dynamics run to steady state after deleting each of the 15 functional groups, one at a time. They found that only two functional group deletions (i.e., bacteria and saprophytic fungi) resulted in the extinction of other groups, and only three functional group deletions (i.e., bacteria, saprophytic fungi, and herbivorous nematodes) resulted in a 10 % alteration in some index of ecosystem function (i.e., nitrogen mineralization or primary production). They concluded that "the results suggest that ecosystems could sustain the loss of some functional groups with little decline in ecosystem services, because of compensatory changes in the abundance of surviving groups." However, we suggest that the wholesale loss of entire functional groups is an unlikely scenario from climate change predictions. Instead, the more likely changes appear to be subtle and sometimes idiosyncratic shifts in the relative proportions (or species composition) of existing functional groups (Sohlenius and Bostrom 1999; Todd et al. 1999; Convey and Wynn-Williams 2002). Intolerant species that are lost from a functional group are often replaced by what appears to be redundant species of a similar functional group (Todd et al. 1999; Bakonyi and Nagy 2000). Thus, rather than addressing the question "how many species does it take to maintain ecosystem function," it would be more prudent to ask, "what happens to ecosystem function after a directional shift in species and functional group composition?"

To address the question "what happens to ecosystem function after a directional shift in species and functional group composition?" we first have to identify a likely directional shift in community composition and the functional significance of that change. In the case of biocrusts, we have observed that nematodes are affected more negatively by these abiotic stresses than amoebae (Darby et al. 2011). Because nematode body size is an order of magnitude greater than amoebae, they are expected to respire less per unit of biomass than amoebae (West et al. 1997, 1999; Ryszkowski 1975). Thus, nematodes contribute proportionately more to nitrogen cycling through dissolved organics (Wright 1975a, b), while amoebae contribute more to nitrogen cycling through excretion of inorganic nitrogen (Hunt et al. 1987). In sum, climate changes of increased temperature and summer precipitation could decrease the abundance of nematodes more than that of amoebae and shift the balance of nitrogen cycling by reducing the relative contributions of

dissolved organics and increasing the relative contributions of labile inorganics. This is significant because ammonium, the form of inorganic nitrogenous wastes by nematodes and protozoa, can be oxidized rapidly in this system (Johnson et al. 2005) and exported through leaching of nitrate (Johnson et al. 2007). Future research should be careful to compare the balance of organic and inorganic nitrogen in desert soils and determine whether changes in soil microfauna affect these substrate pools (Belnap et al. 2005).

8.7 Future Directions and Research Priorities

In the last decade we have learned much about the microfauna in biocrusts, including who are the main taxa and functional groups, what important functions they perform, when they are most active, where they exist in relation to depth and vegetative cover, and how they are affected by physical disturbance and abiotic stresses. We have identified three areas of research that we believe will be most beneficial in leading us toward a more complete understanding of the importance of microfauna in biocrust systems: (1) identify specific feeding behaviors of individual species, (2) increase the taxonomic resolution of ecological studies to the level of species, and (3) identify the ecologically relevant genetic and genomic aspects of microfaunal adaptations to the biocrust habitat.

8.7.1 Feeding Behavior

For most families and genera in biocrusts, we have a reasonable idea of what potential prey items they *could* consume (largely based on the size and shape of feeding structures), and what some of their sister species *likely* consume (largely based on published reports of feeding trials or tissue analysis), but we most likely do not know what the biocrust species *actually* consume. The two main pieces of information that need to be distinguished for each species are (1) the full breadth of *acceptable* prey items and (2) the subset of *preferred* prey items. Accomplishing this goal will require multiple different empirical approaches, such as culturing assays with feeding trials (Wood 1973a, b), molecular gut content probing (Treonis et al. 2010), stable isotopes (Darby and Neher 2012), and phospholipid fatty acid signatures (Buse et al. 2013; Ruess et al. 2005). This is important information because even though each functional group of biocrust fauna is represented by multiple species, we have no way to confirm whether or not these species are truly functionally redundant as we do not know if there are actually more subtle feeding preferences. This is especially true for taxa that are broadly considered omnivorous (e.g., stylet-bearing nematodes of Dorylaimida and some Tylenchidae). In many of these cases, we do not know whether omnivorous genera represent many species who themselves are all omnivorous, or if they represent many species who

themselves are all specialists but on different trophic levels, so that the genus as a whole appears omnivorous.

8.7.2 Increased Taxonomic Resolution

Most studies of biocrust microfauna are performed at the taxonomic resolution of family or genus. This provides enough information on the broad feeding or functional groups that are present but does not provide enough information to distinguish between biocrust and underlying soil species, nor does it allow comparison of species composition across studies in geographically distinct locations. We still do not know whether the species of a particular genus inhabiting biocrusts of one site are the same species of that genus inhabiting the soil beneath the biocrust or even if they are the same species of that genus inhabiting biocrusts at a different site. There is a clear possibility that many of the species found in biocrusts have yet to be described (as in Pilato and Beasley 2005). To further our understanding of the ecology of biocrust food webs, there is a need for future ecological studies to aim for species-level taxonomic resolution in their enumeration of biocrust microfauna. This is challenging, but molecular techniques such as high-throughput amplicon sequencing (Bik et al. 2012; Darby et al. 2013; Steven et al. 2014) are making high-resolution enumerations rapid, accessible, and informative. Various methods of specimen preservation are available to allow for the recovery of both molecular and morphological information (Yoder et al. 2006). Thus, species-level taxonomic resolution can be obtained by combining, from the same specimen, both molecular sequence data and virtual morphological vouchers by digital multifocal imaging (De Ley and Bert 2002). The cumulative benefit of increasing taxonomic resolution to the species level will be to allow more reliable comparison of species composition between communities of different study sites or of different habitats (e.g., biocrust versus underlying soil) within a site.

8.7.3 Ecological Genomics

The effects of abiotic stresses on biocrust microfaunal communities have been studied mostly by the application of acute short-term experimental treatment (such as heat, desiccation, and UV radiation). However, the chronic, long-term implications of abiotic stresses on biocrust microfauna community composition have not been well studied, nor have we been able to quantify the consequences of changes in community composition on ecosystem processes. We believe this is largely because our understanding of the genetic and genomic adaptations of biotic and abiotic stress on biocrust microfauna lags behind that of the research on biocrust microflora (Zelikova et al. 2012; Steven et al. 2014). This is a significant research need, because the role of microfauna in ecosystem-wide functioning is

linked to the physiological traits that allow biocrust microfauna to survive in this unique habitat. If we can understand how biocrust microfauna are adapted to the biocrust habitat at a genetic and genomic level, then we may be better able to predict the ecosystem implications of changes in species composition. For example, the relative composition of waste nutrients that are mobilized by microfauna is thought to be related to the stoichiometry of the biomolecules that are used and extracted by the organism (Sterner and Elser 2002). Sugars and simple carbohydrates are high C-containing biomolecules, proteins are rich in N, and nucleic acids are one of the molecules that contain a large proportion of phosphorous. Thus, the biomolecules that microfauna use and synthesize in response to biotic and abiotic stress are biased in their chemical stoichiometry (Elser et al. 2000), and we can use ecological genomics approaches to understand how microfauna are adaptations to environmental stress and how these adaptations will influence the environmental cycling of key nutrients. Fortunately, advances in high-throughput sequencing technologies allow for more advanced genomic analysis of non-model organisms from ecological systems (Ungerer et al. 2008). Ecological genomics approaches can be used to identify the adaptively significant genomic variation that may lead to our understanding of how changes in community composition affect the functioning of biocrust microfauna.

8.8 Conclusion

In conclusion, biocrusts serve as unique habitat for a broad range of microfauna, including protozoa, nematodes, tardigrades, rotifers, mites, collembolans, and even larger arthropods and mollusks. These microfauna feed on the bacteria, cyanobacteria, algae, fungi, bryophytes, and plant roots that are found in the biocrusts. Consumer food web as a whole performs several important functions, such as cycling nutrients, dispersing propagules, and moderating their microbial prey populations. Many species of biocrust microfauna tolerate periods of drought in an anhydrobiotic dormant state, so they are typically active only during brief windows of time. Most microfaunal groups tend to be more abundant, species rich, and diverse in mature, late-successional stage biocrusts that are dominated by diverse microflora (such as lichens, bryophytes, fungi, and cyanobacteria) than in early-successional stage biocrusts that are dominated by less diverse microflora (such as cyanobacteria alone). Biocrust microfauna are susceptible to the same surface disturbances that affect biocrust microflora, such as physical trampling or altered temperature and summer precipitation, but the specific ecosystem consequences of altered community composition due to surface disturbances are still largely unknown. To fully understand the ecosystem consequences of biocrust microfauna, we propose that the three main research needs in the future are to: (1) identify specific feeding behaviors of individual species, (2) increase the taxonomic resolution of ecological studies to the level of species, and (3) identify

the ecologically relevant genetic and genomic aspects of microfaunal adaptations to the biocrust habitat.

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