Controls on soil biodiversity: insights from extreme environments

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Abstract

Research in low biodiversity extreme environments allows separation of the climatic, soil and biological interactions that determine soil biodiversity and community structure. Studies focused on the response of low diversity communities in soils of the Antarctic Dry Valleys and the Chihuahuan Desert of the southwestern USA, to manipulations of soil resources and climate, offer the best opportunity to learn about the environmental controls on soil biodiversity and the role of biodiversity in soil functioning. We propose that insights based on research in these extreme environments should be applicable to understanding soil biodiversity in more complex, temperate and tropical ecosystems. The study of extreme soil ecosystems may also provide information on the response of soil biodiversity to increasing occurrences of environmental extremes that are predicted to occur from global change models. Studies from hot and cold deserts show that decomposition-based food webs can be very simple, that aridity produces similar mechanisms for survival and dispersal of organisms in temperate and polar systems, that suitable soil habitats are patchily distributed in arid environments, and the low biodiversity of extreme soil ecosystems creates little or no functional redundancy making these systems susceptible to disturbance. We suggest that species within the same functional group can have small differences in ecology that are sufficient to affect ecosystem processes. When this occurs, differential responses of species to disturbance within a functional group will not stabilise the soil ecosystem, but rather lead to dramatic changes in community composition and ecosystem process rates. © 1999 Elsevier Science B.V. All rights reserved.

1. Introduction

Knowledge of the distribution and diversity patterns of soil species and their influence on ecosystem processes is currently inadequate, partially due to the high species richness and complexity of below-ground ecosystems (Brussaard et al., 1997). Previous research has addressed this problem by pooling species into functional groups to reduce the complexity, and approach that helps us to describe the critical tasks that organisms perform in ecosystems, e.g. decomposition, nitrogen fixation, etc. However, this approach tells us nothing about interactions between, and redundancy of, functions among species. Another possible approach is to examine species in ecosystems with naturally reduced complexity, such as extreme environments. These studies on individual species within soil communities can be used to unravel mechanisms that are hidden in more complex ecosys-

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tems, and to predict how ecosystems will respond to increasing environmental change and disturbance (Freckman and Virginia, 1998).

Environmental changes, e.g. atmospheric composition and climate, have increased in importance today because of the rate and intensity, and the global scale at which they are occurring (Vitousek et al., 1997). These changes will determine the above- and below-ground diversity of plants, animals and microbes that will exist in the future (Swift et al., 1998; Wardle et al., 1998). In geological time, climate changes have resulted in the extinction of many animal and plant species. Today, we see, as a result of human activities, an accelerated frequency and magnitude of both catastrophic and milder environmental events (e.g. soil erosion and salinisation, pollution of air, soil and water) at local, regional and global scales, resulting in extinction of entire plant and animal communities (Hoffman and Parsons, 1997; Vitousek et al., 1997).

The consequences of these accelerated changes for soil biotic communities and ecosystem functioning must be identified and evaluated. Research is focusing on the effects on soil biota (Smith et al., 1998; Wardle et al., 1998) of increased atmospheric nitrogen deposition (Holland and Lamarque, 1997), deforestation (Bloemers et al., 1997), agricultural practices (Matson et al., 1997) ecosystem reclamation and restoration (Zink and Allen, 1998), pollution (Bongers, 1990) and desertification (Freckman and Virginia, 1989), as well as the consequences of soil biodiversity loss, for sustainable land use.

These natural and human-induced changes may represent new environmental extremes or challenges for many organisms, and concerns are raised about their response and survival. Yet, extreme conditions exist in natural ecosystems around the world where low-diversity soil communities have reproduced and survived. The study of these systems can provide insights into the response of soil species to perturbation and environmental change (Hoffman and Parsons, 1997). This paper uses soil nematodes as a model for the soil biota to provide some of the insights from these extreme ecosystems on the responses of soil biodiversity, soils and ecosystem functioning to changes in the environment. We propose these insights will be useful (a) to elucidate similar mechanisms and relationships that occur, but may be masked, in more complex ecosystems, and (b) to predict the effects of environmental change on soil organisms and communities.

2. Soil nematodes

The impacts of a changing environment, or other perturbation, on soil organisms, as measured by their diversity, abundance, survival or extinction, and how their response may affect ecosystem processes, is much more difficult to measure than for above-ground biota. Microscopic soil organisms, including invertebrates such as nematodes, represent a major component of the Earth's biodiversity, one whose importance is well acknowledged, but whose taxonomic dimensions remain obscure (May, 1988). Although soil organisms are vital to the functioning of terrestrial habitats (Brussaard et al., 1997), the abundance, diversity, habitats, distribution and interactions, remain undetermined for a large majority of soil organisms (Wall and Virginia, in press). The number of possible interactions among the diversity of soil organisms (encompassing vertebrates to microorganisms) as well as a limited knowledge of their physiology (metabolism, reproductive rates) and tolerance to environmental fluctuations, makes it difficult to assess trends or patterns of responses, or how 'resistant' or 'resilient' the organisms will be under environmental change.

Soil nematodes, unlike other groups of soil invertebrates, such as enchytraeids, earthworms, and termites, are ubiquitous and abundant in all ecosystems (Petersen and Luxton, 1982). Nematodes can be used to assess changes in soils that occur as a result of disturbance or pollution (Bongers, 1990). On a global scale, nematodes are a species-rich fauna of 20 000 described species found in freshwater and marine sediments and soils. This is <5% of their estimated diversity (Bernard, 1992; Baldwin et al., in press). In soils, ≈5000 species have been described (Brussaard et al., 1997). Nematodes participate in nearly all the ecological processes in soil that contribute to soil fertility and biogeochemical cycling (Freckman, 1982). In soils of temperate, tropical and even Arctic regions, nematodes can be divided into five-to-eight functional groups including: predaceous nematodes; omnivorous nematodes; algal-feeding nematodes; plant-feeding nematodes that constrain primary productivity; and, the bacterial-

feeding and fungal-feeding nematodes that influence the rates of decomposition and the availability of nutrients (mineralisation) to plants (Yeates et al., 1993). A range of life-history strategies places nematodes at the centre of key processes such as decomposition, and plant productivity, and as a result, the structure of nematode communities can be used to indicate the status or 'health' of soil habitats (Bongers, 1990).

Nematode community structure, species distribution and activity in temperate systems are affected primarily by plants (plant species composition and chemistry) and secondarily by soil habitat (moisture and chemical and physical properties) and climate (Freckman, 1982). Less well known is the fact that competition and predation often limit nematode species populations (Ettema, 1998). Any environmental change or other perturbation that affects plant species composition or physiology, soil texture, soil chemistry, and soil climatic factors, like soil moisture and soil temperature, may alter nematode species and functional group diversity. Research on soil disturbances from many ecosystems indicates that, because of the complexity and numerous interactions of soil biota, the patterns of responses at the species level are difficult to predict (Niles and Freckman, 1998).

In temperate and tropical ecosystems, the high abundance of nematodes, the richness of nematode species in soils, the large number of species within nematode functional groups, their numerous interactions (mutualism, competition, predation) with other organisms (Wall and Moore, 1999), as well as spatial and temporal dynamics, have made it difficult to isolate the factors that (a) are responsible for small- and large-scale patterns of species diversity, (b) relate species diversity to ecosystem processes, or (c) determine the response of soil species to environmental change.

We propose that simple ecosystems in extreme environments can help elucidate the patterns of soil biodiversity and ecosystem functioning and also provide insight into the responses of soil biota to increasing occurrences of environmental extremes.

3. Extreme environments

Examples of naturally occurring soil environments that can be considered extreme include, but are not
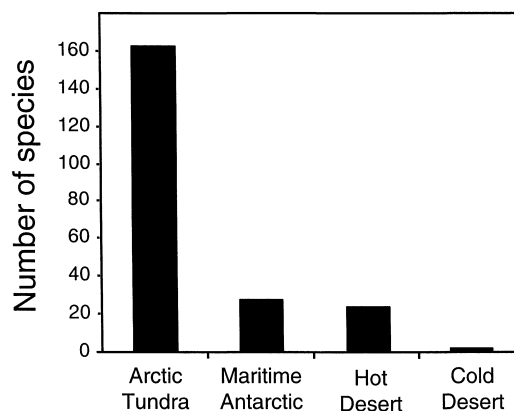

Fig. 1. The numbers of described nematode species in four extreme environments. Data are from Arctic tundra, (Sohlenius, 1980) maritime Antarctic, (Maslen, 1981) hot desert, (Freckman and Mankau, 1986) Antarctic cold desert (Freckman and Virginia, 1997). (Modified from Freckman and Virginia, 1998).

limited to, caves, deserts, high-altitude and high-latitude ecosystems, and saline soils and sediments. In addition, there are precipitous events, such as fire, hurricanes and floods, that allow us to examine how the soil biota and the ecosystem responds to sudden changes in the environment. Our discussion is limited to two desert systems. The biota in these two water-limited soil ecosystems offer an opportunity to study linkages between species diversity and ecosystem functioning that are masked by the overwhelming complexity of soil biodiversity in other, less extreme, terrestrial ecosystems (Fig. 1) (Freckman and Virginia, 1998).

Deserts are characterised by low and unpredictable rainfall, high evapotranspiration, low soil organic-matter content, high soil pH and salinity, and temperature extremes (Freckman and Virginia, 1989). The two contrasting thermal environments of hot and cold deserts are useful systems for understanding the impact of disturbance and environmental change on soil biodiversity in more complex ecosystems, in part because both have low soil biodiversity (Figs. 1 and 2).

The hot desert site we examined was located in the northern Chihuahuan Desert on the Jornada Basin Long-Term Ecological Research site, located 40 km NNE (32°30′ N, 106°45′ W) of Las Cruces, New Mexico, USA. The hundred-year annual precipitation is 211 ± 77 mm, with 60% of the annual precipitation
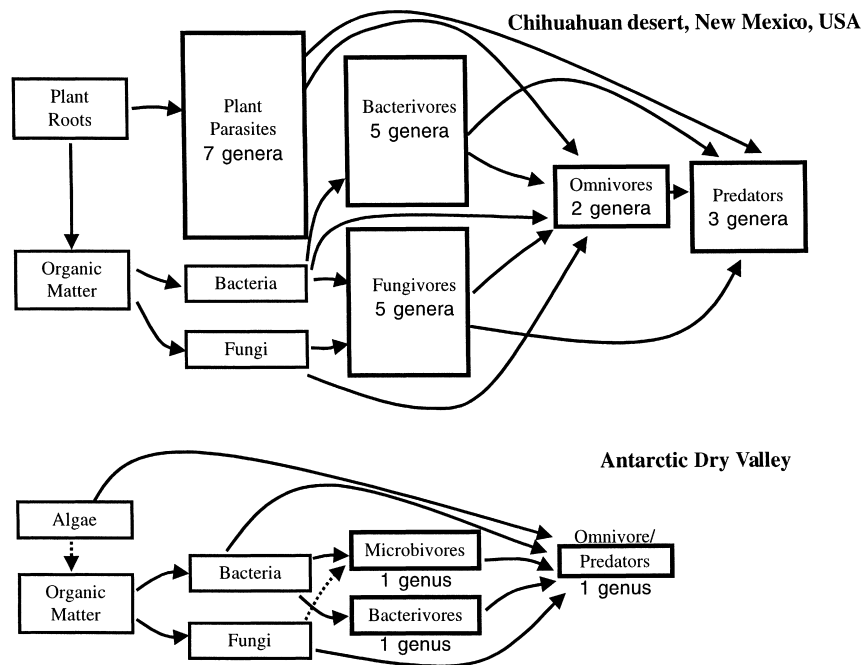
Fig. 2. Complexity of soil nematode food webs in a hot desert (Chihuahuan, Jornada LTER, New Mexico, USA) with 22 nematode genera, and a cold desert (Taylor Valley, McMurdo LTER, Antarctica) with three genera. For the nematodes, the height of the boxes illustrates the number of genera. The Antarctic Dry Valley has one species of a microbivore, *Scottnema lindsaye*, that feeds on bacteria and yeast, one bacterivore, *Plectus antarcticus*, that feeds on bacteria, and an omnivore-predator, *Eudorylaimus antarcticus*, that probably feeds on algal cells, bacteria, yeast, fungi, nematodes and other small fauna.

occurring between July and October (Houghton, 1972). Maximum temperatures in summer range from 36° to 40°C and winter minimum temperatures regularly drop below 0°C. Soil temperatures are 0–40°C at 5 cm depth (Parker et al., 1984). In the past century, the woody legume mesquite (*Prosopis glandulosa*), formerly restricted to playa and arroyo habitats, has expanded across the landscape and invaded grasslands and formed extensive areas of coppice dunes (Buffington and Herbel, 1965). The soil at the playa and grassland sites is a Haplargid; the arroyo a Torrifluvent; and the dunes a Torrispsamment (Gile et al., 1981; Wierenga et al., 1987).

The cold desert of Antarctica is a much simpler soil ecosystem than even the Jornada Basin (Freckman and Virginia, 1998). Although the Antarctic Peninsula has visible vegetation with vascular plants (two species of angiosperms, mosses and lichens), higher plants are absent on the continent and mosses and lichens are rare in the Antarctic Dry Valleys (77°00′ S, 162°52′ E) (Kappen, 1993). Here, the soils which pervade the

valleys are the coldest, and are among the oldest and driest on Earth (Campbell et al., 1997). Soil temperatures (5 cm depth) in the McMurdo Dry Valleys during December and January range from −2.7° to 15.9°C and annual mean air temperatures is −20°C (Clow et al., 1987). Because of the high surface roughness, there is a layer of relatively calm air immediately above the ground so that surface temperatures are often considerably higher than ambient. However, although soil temperatures may be favourable, no liquid water is available. The desiccation gradient can be so steep that even when the reservoir of ice in the permafrost starts to melt, it cannot furnish adequate liquid water for the microbial growth necessary to stabilise the soil surface (Wynn-Williams, 1990).

Due to the low precipitation (∼10 cm rainfall equivalent per year), the soils of the Dry Valleys are not leached and weathering products accumulate in the soil profile (Pastor and Bockheim, 1980). Dry Valley soils are generally poorly developed, coarse

textured, and have low biological activity (Campbell and Claridge, 1987). Dry Valley soils have greater variation in chemical and physical properties at smaller scales ($<1\ m^2$) than do temperate soils (Bockheim, 1997) or hot desert soils at the Jornada LTER (Virgina and Wall, in press). Organic C and N levels are extremely low due to the lack of plant cover and low rates of primary production, and are much lower (0.08% organic C; 0.038–0.047 g kg^{-1} total N) than hot desert soils (0.28–2.06% organic C; 0.44–2.49 g kg^{-1} total N) (Freckman and Virginia, 1997).

4. Insights on soil biodiversity from extreme environments

4.1. Decomposition-based food webs can be very simple

The main difference between the polar deserts of Antarctica and the Jornada is the presence in the Jornada of woody vegetation that acts to concentrate biological activity in discrete patches. The factors responsible for creating suitable soil habitats are not visible in the Dry Valleys, but rather result from long-term dynamics of glaciers, lakes and their influences on primary productivity (Virgina and Wall, in press). Antarctic Dry Valleys represent the most extreme soil habitat on earth (Wynn-Williams, 1990). There are no other soil systems known where nematodes represent the top of the food chain and where food webs appear so simple in structure (Fig. 2) (Virgina and Wall, in press). Nematode species richness in the Dry Valleys appears to be the lowest of any ecosystem on Earth (Freckman and Virginia, 1998) (Fig. 1). In the Dry Valley soils we examined, there are only three nematode species (Fig. 2), a microbivore, a bacterivore and an omnivore-predator, and no higher invertebrates in the driest soils of the valleys. Tardigrades and rotifers are absent in >80% of the soils sampled ($n = 415$) (Freckman and Virginia, 1998).

This unique nematode community of the Dry Valleys consists solely of three species: the endemic species *Scottnema lindsayae*, (Timm, 1971), a microbivore (bacteria and yeast); an additional species, *Plectus antarcticus*, a bacterivore; and *Eudorylaimus antarcticus*, an omnivore-predator (Freckman and Virginia, 1991). In culture, *S. lindsayae* can signifi-
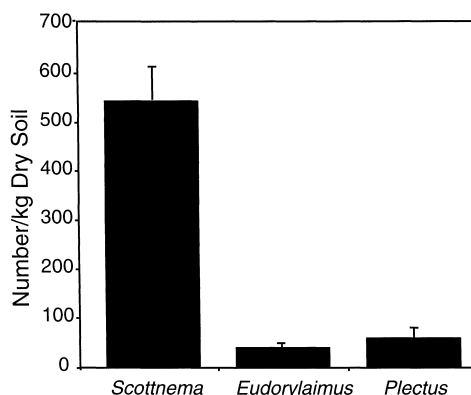

Fig. 3. The mean abundance (numbers kg^{-1} dry soil) of three nematode species (*Scottnema lindsayae*, *Eudorylaimus antarcticus*, and *Plectus antarcticus*) in soils from four Antarctic Dry Valleys ($n = 415$). (Modified from Freckman and Virginia, 1998).

cantly reduce bacterial and yeast populations (Overhoff et al., 1993). Based on other studies of related nematode species (Ingham et al., 1985) the presence of *S. lindsayae* and *P. antarcticus* is expected to increase carbon and nitrogen mineralisation. Although the food source of the omnivore-predator has not been confirmed, other species of *Eudorylaimus* are fungal or algal grazers or predators on other nematodes (Yeates et al., 1993). In some localised parts of our study area, tardigrades may be predators on nematodes. *S. lindsayae* dominates at a regional scale across the four Dry Valley soils we sampled, whereas abundances of the other two nematode species are considerably lower and they are rare in the Victoria Valley (Freckman and Virginia, 1998) (Fig. 3). The sources of organic matter supporting the simple soil communities are either carbon, recently fixed by soil algae, contemporary allochthonous inputs from lakes, streams or the oceans, or old organic matter (legacy organic matter) accumulated from past lake communities in the Dry Valleys (Burkins et al., 1998; Virgina and Wall, in press).

The lack of plant roots in the Dry Valley soils means that carbon is not easily moved to depth in the soil profile. Thus, the dominant food web in this soil ecosystem without higher plants is a decomposition-based food web and is limited to the near-surface environment (Virgina and Wall, in press). The decomposition of soil organic matter in the Dry Valleys appears to be controlled through regulation of micro-

bial abundance by three groups in the food web, namely microbivores, bacterivores and omnivore/predators (Freckman and Virginia, 1997). Nutrient cycles and trophic interactions in these low-diversity soils are limited to microbial (yeast and bacteria) populations and micro-invertebrates (Vishniac, 1996). Nematodes and protozoa help to maintain microbial diversity and nutrient turnover rates by grazing on and dispersing soil microbes. In cold ecosystems, microbial biomass is potentially a greater reservoir of nutrients with a more rapid turnover than in many other ecosystems (Wardle, 1992). Soil food webs in ecosystems with vascular plants have numerous functional groups and much longer food chains involved in the decomposition and herbivory pathways.

4.2. There are common mechanisms for survival and dispersal of soil organisms in arid environments, whether hot or cold

Survival in deserts requires that the soil biota have mechanisms to avoid or tolerate extremes that occur in the soil abiotic environment. Survival mechanisms can include avoidance by migration from the stress, physiological adaptations, and changes in sex ratio and fitness (ability to leave offspring) (Norton and Burns, 1971). In the Antarctic Dry Valleys, organisms must be capable of prolonged survival in soils with low moisture and prolonged periods with temperatures below freezing. In hot deserts, soil biota use a number of mechanisms to withstand high temperatures and low soil moistures (Freckman et al., 1987).

Nematodes live in water films around soil particles and generally do not migrate to greater depths to avoid the soil surface temperature and moisture extremes (Freckman et al., 1987). However, their survival mechanisms are well suited for harsh conditions, such as those found in hot and cold deserts. They enter into a cryptobiotic state at any stage in their life cycle when environmental conditions are severe (Crowe and Cooper, 1971). An undetectable metabolism—essentially no life—and the induction of physiological and morphological changes in the organism characterise cryptobiosis. Cryptobiotic nematodes are resistant to extremes, such as desiccation, extremely low temperatures, 0% relative humidity, vacuum, and nematicides, and quickly revive when favourable environmental conditions return (Freckman and Womersley, 1983).

Three of the four types of cryptobiosis (anhydrobiosis, cryobiosis and osmobiosis) are induced by the unavailability of water needed for normal metabolic reactions. Anhydrobiosis (life without water) differs from cryobiosis (freezing-induced cryptobiosis). In soil and laboratory studies, the morphological change of the nematode into a tight coil has been used as an indicator of anhydrobiosis, since active and dead nematodes are straight, and usually vermiform (Crowe, 1971).

Nematode activity is closely related to levels of soil moisture, since nematodes enter anhydrobiosis and become inactive when the soil is dry (Freckman, 1978; Freckman and Womersley, 1983; Whitford et al., 1986; Freckman et al., 1987). It is this enhanced resistance to environmental stress (i.e. low soil moisture, cold) that allows nematodes to survive in extreme environments. In the Dry Valleys, the proportion of anhydrobiotic nematodes increased with distance from the stream sediments to drier soils (Treonis et al., in press). Different species occurred in the wet and dry habitats, suggesting species vary in their tolerance to desiccation and, perhaps, in their ability to enter anhydrobiosis. In the Jornada, 60% of the nematodes were anhydrobiotic at -0.4 MPa soil-water matric potential ($\sim$4.7% soil moisture) (Freckman et al., 1987). We know less about Antarctic nematodes and the relationships between soil moisture and activity. However, Treonis et al. (in press) have shown that *S. lindsayae* is capable of anhydrobiosis. Studies by (Freckman and Virginia, 1997, 1998) report living nematodes extracted from very dry soils (moisture content often below 1%)—water contents that would limit soil biota in nearly all other ecosystems.

Dispersal to other habitats can also increase chances of species survival (Hoffman and Parsons, 1997). Nematodes in temperate arid environments are dispersed as anyhydrobiotes in wind, possibly 100 km, to suitable habitats for establishment of new communities (Orr and Newton, 1971; Carroll and Viglierchio, 1981; Whitford and Freckman, 1988). The wide distribution and the ecology of nematodes in the cold desert indicate these organisms can survive, disperse and establish communities under the most extreme climatic conditions (Freckman and Virginia, 1997, 1998; Courtright et al., 1998).

The fact that the nematode species share a common mechanism for survival and dispersal across very

different arid habitats could have implications for their establishment into increasingly desertified areas in temperate climates. For example, species that are able to survive extreme temperatures and moistures would be expected to adapt more easily to the transition of arid habitats into newly desertified ecosystems. Nematodes from moister ecosystems, such as wet tropical forests, may be locally eliminated, as they are dispersed in water (irrigation, rain, flooding), have different survival mechanisms, and may not be able to survive a sudden exposure to higher temperatures and lower moistures (e.g. due to slash and burning or clear-cutting). As ecosystems lose biodiversity in response to stress and perturbations, soil organisms with adaptations to environmental extremes may be favoured. Identifying shared mechanisms of survival for different phyla may provide clues as to the species that can survive under human-induced environmental changes.

4.3. Suitable habitats to support soil biodiversity are patchily distributed in extreme environments

In hot deserts, there are below-ground representatives of many phyla: pack rats, beetles, termites, ants, millipedes, mites, springtails, nematodes, protozoans, microbes, roots, and microbial symbionts (Wallwork et al., 1986). The complexity of these possible interactions is magnified further when species richness is considered. Soils of deserts usually have >18 nematode genera (Freckman and Mankau, 1986), arid grasslands can have 117 nematode taxa (Freckman and Huang, 1998) and in a tropical Cameroon forest there were >423 nematode species of which 90% were unidentified (Lawton et al., 1996).

In most terrestrial ecosystems, higher plants are the dominating influence controlling the distribution and diversity of soil biota. In most ecosystems, plants and plant-related factors, (soil organic C and N, root and litter quality, species composition and abundance), as well as climate, are the major factors structuring the patchiness of below-ground diversity (Swift et al., 1979). The influence of micro-climatic and edaphic patterns are less studied. In hot deserts, soil biota are patchily distributed because they are concentrated beneath or near plants which provide islands of resources in an otherwise less fertile environment (Reynolds et al., 1999).

In contrast, in an ecosystem where organic matter content is extremely low, the influence of plant distribution is reduced and the abiotic and soil factors structuring the community become apparent. The extremes of the Antarctic Dry Valleys often fall outside the tolerance limits for soil invertebrates. A notable feature is the high percentage of soils that contain no invertebrates (Freckman and Virginia, 1998), a contrast to other systems where most soils contain more than eight invertebrate phyla (Heywood, 1995). Freckman and Virginia (1998) found that, of the 415 soils sampled across four Dry Valleys, about 35% had no animals. Of the remaining soils with fauna, communities containing only nematodes were by far the most abundant, and in these soils, their higher densities (4000 kg^{-1} dry soil) (Freckman and Virginia, 1998) are comparable to hot deserts. Communities of either rotifers or tardigrades, or of two and three invertebrate phyla, are scarce, occurring in <5% of the soil samples. Higher invertebrates, in this system, mites and Collembola, occur in only a minimal fraction of the landscape (<1%) on mosses growing where melt water accumulates from glaciers.

It is striking that soils with a complexity of more than two phyla rarely occur in the Dry Valleys, which indicates either that the majority of soils are unsuitable habitats for the development of complex communities or that organisms have not dispersed and developed in these locations (Freckman and Virginia, 1998). (Powers et al., 1995, 1998) described the distribution of soil biodiversity in Taylor Valley as patchy and dependent on the distribution of soil chemical and physical properties. The spatial heterogeneity of soil properties that appears to influence the establishment of the nematode community is a result of minimal leaching in soils, freezing and desiccation of soils, the influence of parent material, and wind dispersal of cations and other soil constituents (Virgina and Wall, in press). The resulting spatial variability of the substrate quality and quantity is much greater in the Dry Valleys than in the Jornada (Virgina and Wall, in press). In the Dry Valleys, salinity, moisture and acidity were the primary factors determining presence or absence of nematode communities (Table 1) (Freckman and Virginia, 1997). The fact that soils at this wide spatial scale exist without nematodes is surprising, since nematodes were considered to be ubiquitous (Bernard, 1992). Virgina and Wall (in

Table 1
Measures of chemical and physical properties for Antarctic Dry Valley soil samples ($n = 130$). Sites in which nematodes were present (86 soil sites) are compared (using ANOVA) with those without nematodes (44 soil sites).

Soil property	Nematodes	
	present	absent
Significant variables ($p < 0.05$)		
pH (1 : 2, soil : water)	8.51 ± 0.07	8.12 ± 0.07
NO_3-N (mg kg^{-1})	3.64 ± 1.07	19.2 ± 5.81
PO_4^{3}-P (mg kg^{-1})	1.23 ± 0.14	0.75 ± 0.15
Electrical conductivity (saturation extract, dS m^{-1})	0.19 ± 0.04	1.0 ± 0.21
Nonsignificant variables		
Soil texture		
sand	96.0 ± 0.31	97.3 ± 0.40
silt	1.0 ± 0.27	0.4 ± 0.16
clay	2.8 ± 0.27	4.3 ± 0.29
Soil moisture (%)	5.83 ± 0.78	4.3 ± 0.98
Organic carbon (%)	0.08 ± 0.008	0.08 ± 0.008
Total nitrogen (g kg^{-1})	0.047 ± 0.005	0.038 ± 0.008
NH_4-N (mg kg^{-1})	1.13 ± 0.13	1.06 ± 0.26

Note: Soils lacking nematodes had significantly higher total salinity (electrical conductivity). Data are mean $\pm$ 1 SE. (Modified from Freckman and Virginia, 1997). Soil texture is particle size distribution (% by mass).
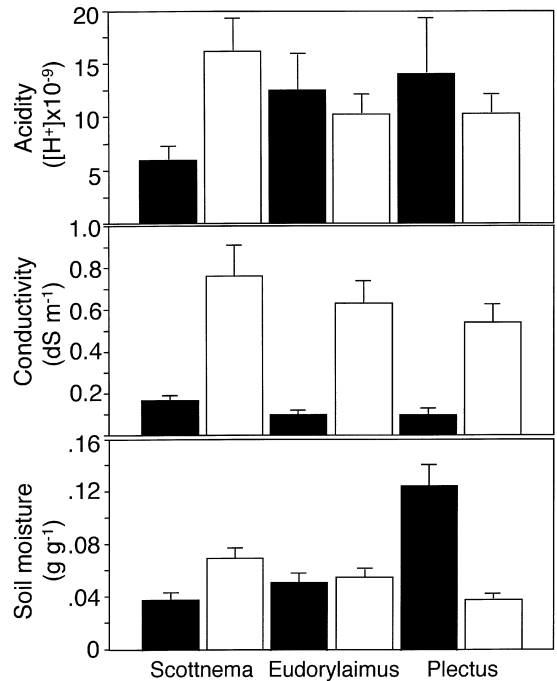

Fig. 4. Soil pH, electrical conductivity (dS cm^{-1}) and soil moisture content (g g^{-1} dry weight) in four Antarctic Dry Valley soils in which three nematode species (*Scottnema lindsayae*, *Eudorylaimus antarcticus*, and *Plectus antarcticus*) (mean $\pm$ 1SE) were present (solid bars) or absent (white bars). (Total $n = 130$).

press) found that soil moisture, carbon and salinity were the primary variables explaining nematode communities at both small (patch) and large-spatial scales in the Dry Valley region.

Nematode species biodiversity is also structured by soil factors across the landscape, enabling predictions of 'hot spots' with a higher number of species within the valleys. *S. lindsayae* occurred as the only nematode species in 38% of the soils, and with one other species in an additional 34% of the soils, whereas three-species communities were rare (Freckman and Virginia, 1997). *S. lindsayae* occurred in soils with a wide range of salinity, higher pH and lower soil moistures than the two rarer species (Fig. 4). The distribution of the omnivore *E. antarcticus* was closely related to lower pH, organic carbon and soil moisture, while the microbivore *P. antarcticus* was dependent on organic carbon, soil moisture, total nitrogen and phosphorus (Powers et al., 1998). *Scottnema* was found in soils with a mean conductivity of 0.16 dS m^{-1}, whereas *Plectus* and *Eudorylaimus* were not found in soil with a conductivity greater then 0.1 dS m^{-1}

(Fig. 4). This trend of greatest salinity tolerance by *S. lindsayae* supports that observed by Powers et al. (1998). In a transect from stream sediment to soil, Treonis et al. (in press) found a two-species community in the stream sediment (*P. antarcticus* and *E. antarcticus*), and the drier and more saline soil community to be dominated by or solely occupied by *S. lindsayae*. This pattern was consistent with the findings from an elevational transect in the Dry Valleys (Powers et al., 1998). The heterogeneity of soil habitats along an elevational transect was associated with changes in distribution, abundance and biodiversity of the nematode community. *S. lindsayae* occurred at much higher and lower soil moistures than *E. antarcticus*. When gross effects of plants on soil properties are absent in extreme environments, patchiness of other soil properties defines a favourable soil habitat and determines the invertebrate biodiversity in this extreme environment.

4.4. Low biodiversity of extreme soil ecosystems creates little or no functional redundancy making these systems susceptible to disturbance

In all soil communities, environmental change or disturbances that affect soil properties can have an adverse impact on the species that are adapted to a particular set of properties. As there is no functional redundancy for nematode species within the trophic groups in the soil food web of the Antarctic Dry Valleys, the impact of change and disturbance can be measured at the species and functional level. Our field research shows that the soil food wed of the Antarctic Dry Valleys is sensitive to disturbance at the species level.

Powers et al. (1996) noted a greater number of dead *S. lindsayae* in soils that had been subjected to heavy trampling compared with non-trampled or lightly trampled soils. At a site on the north shore of Lake Hoare in Taylor Valley, a soil experiment with randomised treatments of increased temperature, moisture, and carbon (sucrose), and combinations of these additions, was established and examined one year later (Freckman and Virginia, 1997). All treatments resulted in a decline in the omnivore density (*E. antarcticus*), and an increase in the microbivore and possible prey (*S. lindsayae*) of *Eudorylaimus* (Fig. 5).
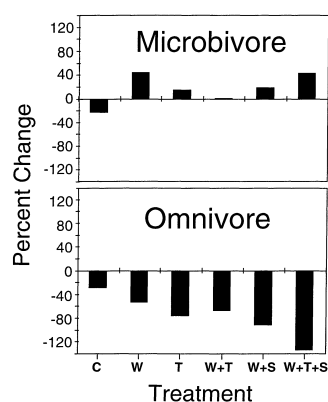

Fig. 5. Changes in nematode population density of a microbivore, *Scottnema lindsayae*, (mean ± 1SE, *n* = 5) and an omnivore, *Eudorylaimus antarcticus* (mean ± 1SE, *n* = 5), in response to manipulation of soil moisture, carbon, and temperature in Taylor Valley, Antarctica. (C = control, W = water amendment, T = increased temperature, W + T = water + temperature, W + S = water + sucrose, W + T + S = water + temperature + sucrose solution amendment). Modified from Freckman and Virginia (1997).

Whether these changes are top-down or bottom-up effects (Mikola and Setälä, 1998), is not known, but this shift in prey abundance is most likely due to the release of the prey species from predation. Alternatively, the treatments may have increased the food source (sucrose) of the microbes that are preyed upon by *S. lindsayae*. In this extreme environment, the individual invertebrate species within a soil community were impacted by perturbations that affected soil resources and climate. This suggests that decomposition and nutrient cycling could be affected (Freckman and Virginia, 1997).

In the Chihuahuan Desert, overgrazing by cattle in the late 1800s contributed to a transition from a C_3 grassland to a C_4 mesquite shrubland (Buffington and Herbel, 1965). Mesquite existed in the historically older habitats (playa and arroyo), but has expanded into grasslands and formed dunes. The comparison of soil biodiversity in soils of mesquite in older and newer desertified habitats presented an opportunity to see if change or loss of species within a nematode functional group occurred in response to rapid changes in vegetation and the associated soil organic matter (Connin et al., 1997).

We examined the species within the plant parasitic nematode functional group for two reasons:

(a) the taxonomy is relatively well known; and
(b) the feeding habits and ecology of the parasites and the physiological reaction of the plant to the nematode species is understood from agricultural research (Freckman and Virginia, 1989).

Plant parasitic species have differential effects on plants, and it is the species and its mode of feeding, not necessarily the abundance, which determines the level of plant damage or impact of herbivory (Freckman and Caswell, 1985). Plants in less disturbed systems may support greater species richness of plant parasites without a loss of plant productivity, because nematode species do not seem to compete for the same feeding locations on roots (van Gundy and Freckman, 1977) or, because natural vegetation may tolerate more species (Wallace, 1987).

We sampled to the rooting depth (15 m for mesquite at the playa; 5 m for mesquite at the dunes). The nematode community occurred to the rooting depth at the playa, but only to 3-m depth at the desertified dune site, perhaps because the soil resources required
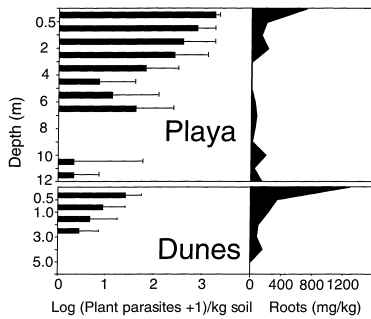
Fig. 6. Depth distribution of plant parasitic nematodes (numbers kg^{-1} dry soil) and *Prosopis glandulosa* roots (right) at a historical (playa) and a desertified (dunes) site in the Chihuahuan Desert, Jornada LTER, New Mexico, USA. ($n = 3$, mean $\pm$ SE). (Modified from Freckman and Virginia, 1989).

for the nematode community were not present, or, the soil properties were lost (Fig. 6). A similar distribution was observed for soil mites (Silva et al., 1989). Species richness differed also, with seven species associated with the mesquite at the older site and three at the desertified site (Fig. 7).

This study showed that changes in the nematode community do occur in response to rapid changes in vegetation. The soil properties associated with desertification (lower soil C, N, P) were also associated with fewer plant parasitic species (Fig. 7) and a shift in their densities and the composition of their feeding strategies from endoparasites to ectoparasites (Freckman and Virginia, 1989; Virginia et al., 1992). The endo- and ectoparasitic species have specialised feed-

ing strategies resulting in differing effects on plants, including changes in root architecture, disruption of nutrient uptake and water, and subsequent reduction in root biomass and above-ground function (Freckman and Caswell, 1985). For example, *Meloidogyne*, one of three endoparasites of mesquite at the playa, secretes cellulases (Rosso et al., in press), and affects plant nutrient and water uptake. Combining knowledge on each genus of plant parasitic nematode at the playa and the dunes allows us to assess whether the shift in the composition of the nematode species with desertification might have consequences for plant performance. We calculated a potential damage index for mesquite at the playa and the dunes, based on nematode density and a pathogenic impact factor for each genus within the plant parasitic functional group. This indicated that the more disturbed and desertified dunes site will be less affected by nematode herbivory (Fig. 8) (Freckman and Virginia, 1989). This lessened herbivory, compared to the playa, could allow a faster establishment of mesquite in disturbed systems or, due to the great abundance at the dunes of an endoparasitic species with a high pathogenic impact factor, *Meloidodera*, and a lessened competition from other endoparasites, could result in a greater loss in plant productivity over time.
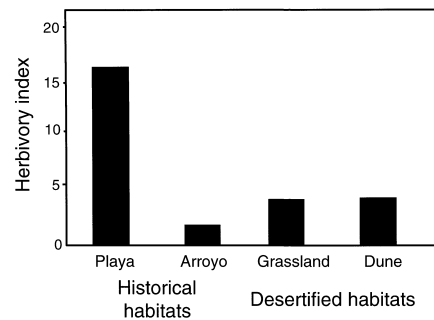
Fig. 8. Expressions of nematode herbivory across four *Prosopis glandulosa* habitats: two historical (playa, arroyo) and two recently desertified (grassland, dunes) in the Chihuahuan Desert, Jornada LTER, New Mexico, USA. The herbivory impact factor was calculated as [($\sum$), (number of nematodes/genus) $\times$ impact factor] where the impact for endoparasitic species was *Meloidogyne* (1), *Meloidodera* (1), *Pratylenchus* (0.5), and for ectoparasites *Helicotylenchus* (0.4), *Paratylenchus* (0.05), *Tylenchorhynchus* (0.05) and *Xiphinema* (0.07). (Modified from Freckman and Virginia, 1989).
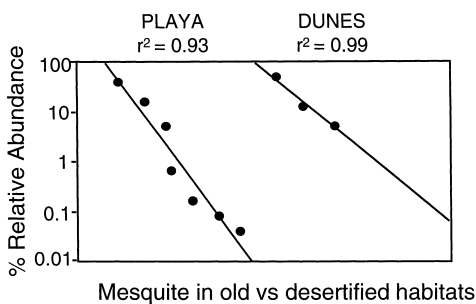

Fig. 7. Relative abundance of plant parasitic nematode species at a historical playa and a desertified dunes site in the Chihuahuan Desert, Jornada LTER, New Mexico, USA. (Modified from Freckman and Virginia, 1989).

5. Conclusion

These two studies of nematode communities in the extreme environments of the Antarctic and Chihuahuan deserts show that, in simple systems, effects of disturbance on individual species in soil communities could have a high impact on ecosystem processes (e.g. decomposition, herbivory, energy flow). Korthals et al. (1996), (see also Niles and Freckman, 1998) noted that closely related nematode genera have different responses to pollutants. Research on feeding behaviours and life histories (Ferris et al., 1995, 1996) at a finer taxonomic resolution are needed to fully assess impacts of disturbance on nematode communities and processes. Field studies in extreme environments allow identification of responses at a finer level of taxonomic resolution than the other systems studied to date. In the hot desert, the species within the plant parasitic functional group were not redundant as each had a different ecology. In the cold desert, where the soils frequently had functional groups consisting of a single species (microbivore, bacterivore or omnivore/predator), differential responses of species represented a major shift in energy flow to other consumers (bacteria and fungi).

These examples show that extreme environments have a simpler soil diversity and food web than other ecosystems (Fig. 2). Using low-diversity nematode communities, we gained insights that are applicable to more complex and diverse ecosystems where the interacting factors of climate, vegetation and soils influence the soil diversity and biotic-mediated ecosystem processes. Our work has shown that:

1. decomposition-based food webs can be very simple;
2. there are common mechanisms for survival and dispersal of soil organisms in arid environments, whether hot or cold;
3. habitat and resource requirements for soil biodiversity are patchily distributed in arid systems; and
4. low biodiversity of extreme soil ecosystems creates little or no functional redundancy, making these systems susceptible to disturbance.

From these results, we conclude that even rare species may be crucial to ecosystem functioning (Freckman and Virginia, 1997) and further, that contrary to Chapin et al. (1997), the stability of the ecosystem is not dependent solely on functionally similar species having different environmental sensitivities. We suggest that species within the same functional group can have small differences in ecology that are sufficient to affect ecosystem processes, such as decomposition or herbivory. When this occurs, differential responses of species to disturbance within a functional group will not confer stability on the soil ecosystem, but rather lead to dramatic changes in community composition and ecosystem processes. As Andrén et al. (1995) indicate, the presence or absence of key species within a functional group will have strong influences on ecosystem processes.

Our main results indicate that nematode species have specialised ecologies and that disturbance impacts biodiversity and potentially ecosystem function. These conclusions can also challenge us to examine fundamental concepts of how ecosystems function. Environmental problems create an urgent need for soil ecologists to synthesise and develop new information to better understand below- and above-surface linkages. Linking the taxonomy and individuality of soil organisms within functional groups to studies of interactions and biogeochemistry and ecosystem processes will increase our ability to predict responses to environmental change.

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