

How Soils Structure Communities in the Antarctic Dry Valleys

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At no time in the history of the earth have the chemical and physical properties of soil and their biota been so radically transformed by human activities. In the past 100 years, cultivation, grazing, introduction of exotic species, and urbanization have erased legacies of previous ecosystems and accelerated change in the amount and spatial distribution of soil resources and soil biota, leading to changes in productivity, nutrient cycling, and linkages to global-scale processes (Schlesinger et al. 1990, Brussaard et al. 1997, Vitousek et al. 1997). By legacy, we mean a carry-over, or “memory,” of past events and processes that influences today’s soil habitats (Vogt et al. 1997). For example, agricultural cultivation has homogenized soil structure and erased the pre-agricultural spatial variation in soil (Robertson and Freckman 1995, Rasmussen et al. 1998), whereas replacement of native grasslands by invasive shrubs during desertification has increased spatial heterogeneity of soil nutrients (Freckman and Virginia 1989, Schlesinger et al. 1990). Will these recent changes in the spatial organization of soils affect biodiversity, nutrient cycling, and the ability of ecosystems to sustain human needs?

The overall importance of soil biodiversity to humans and ecosystem processes is just beginning to be acknowledged (Brussaard et al. 1997). Soil organisms (microbes, fungi, protozoa, invertebrates, and vertebrates) are responsible for soil fertility, maintenance of soil structure, decay and recycling of organic matter, biological control of agricultural and human pests, and cleansing of water; they also influence the composition of the atmosphere (Wall and Virginia in press). In addition to the need to know more about the roles of specific taxonomic groups, relationships between soil biodiversity, ecosystem processes (decomposition, nutrient cycling, productivity), and soil habitat (both physical and chemical properties) are difficult to discern.

The spatial distributions of nutrients and biota in today’s human-affected soils are “young,” especially in the context of the time required for soil development (Jenny 1980). The patterns characteristic of relatively young and disturbed soils may mask the underlying geological time-scale influences that have a major impact on soil communities. Given that many recent ecosystem changes in soil properties and their spatial variation are a result of vegetation disturbance, removal, and invasion (Schlesinger et

SOIL ORGANISMS IN EXTREME ENVIRONMENTS FUNCTION IN LOW-DIVERSITY COMMUNITIES. OUR FINDINGS INDICATE THAT TODAY’S DRY VALLEY SOIL COMMUNITIES ARE DEFINED IN PART BY THE LEGACIES OF PAST ECOSYSTEMS

al. 1990), factors that structure soil communities might be better identified in areas that are remote from human influence and that lack plants (Wall and Virginia 1999). The polar deserts of Antarctica are ideal for such studies. The McMurdo Dry Valleys lack higher plants, have simple soil communities with low species diversity, and are almost completely isolated from human influence on soils. In these valleys, the legacies of past ecosystems should be pronounced.

The legacy of a previous ecosystem and its influences on contemporary processes are not always apparent. For example, stable-isotope measurements of soil organic matter reveal that much of the carbon in the arid shrublands of New Mexico is a relatively short term legacy of the perennial grasslands that dominated the region until approximately 1900 (Connin et al. 1997). The dry valley environment has, in contrast, been remarkably stable over the past few million years, with extremely slow rates of landscape modification relative to those of temperate regions (Brown et al. 1991, Fountain et al. 1999). Current

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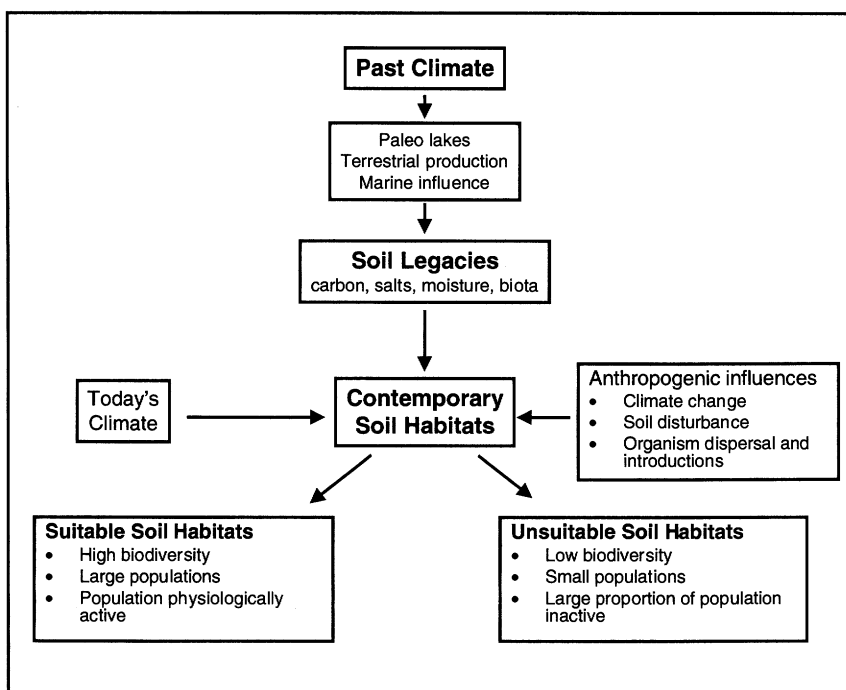


Figure 1. Conceptual model of factors and interactions involving climate, soil legacies, and anthropogenic influences that define suitable and unsuitable habitats for today's soil communities in Antarctic dry valleys.

patterns of biological activity and diversity in Antarctic soils may reflect past distributions of water, nutrients, organic carbon, and biota deposited by paleo-lakes and redistributed by glaciers (Moorhead et al. 1999, Priscu et al. 1999). In this article, we examine how legacies of past ecosystems influence the spatial distribution of habitats suitable for establishment of soil communities in the Antarctic Dry Valleys (Figure 1).

The McMurdo Dry Valleys

The McMurdo Dry Valleys form the largest ice-free region in Antarctica (Priscu 1998). Soils in these valleys are the coldest, oldest, and driest on Earth. Dry valley desert soils are generally poorly developed, coarse textured, and low in biological activity (Campbell and Claridge 1987, Campbell et al. 1998). These soils are unique among desert soils in having large amounts of soluble salts, high pH, and permafrost at 10–30 cm depth (Pastor and Bockheim 1980, Bockheim 1997). Surface soil (0–20 cm depth) temperatures in December and January are consistently above freezing, permitting biological activity (Vincent 1988). However, the desiccation gradient in this cold desert can be so steep that permafrost cannot furnish adequate liquid water for the microbial growth that is necessary to stabilize the soil surface (Wynn-Williams 1990).

Taylor Valley, site of the McMurdo Long-Term Ecological Research (LTER) project, is being intensively studied to develop information on physical and biological processes operating at small to regional scales. The soil ecosystem in Taylor Valley occupies approximately 95% of the surface area (105 km²), compared to the aquatic habitats of lakes (4.7 km²) and streams (0.2 km²; Melody B. Burkins, Ross A. Virginia, Diana H. Wall, unpublished manuscript). Climatic legacies have strongly imprinted soil habitats in Tay-

lor Valley. One influential event was the inundation of the valley by Lake Washburn during the Late Pleistocene (24,000–6000 years ago; Denton et al. 1984). The rise and subsequent fall of Lake Washburn deposited lacustrine sediments and entrained organic carbon and salts in what are now the soils of the lower elevations in the valley. The contemporary soil variation among the three major lake basins (Fryxell, Hoare, and Bonney) that now occupy Taylor Valley is in part a legacy of Lake Washburn and the past climate (Figure 1).

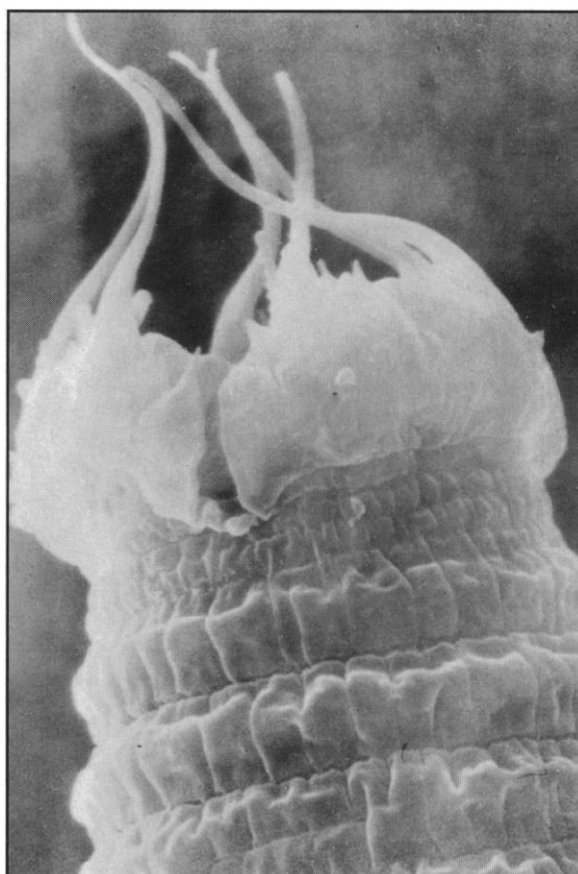
Studies of the natural abundance of carbon (¹³C/¹²C) and nitrogen (¹⁵N/¹⁴N) isotopes in organic matter from Taylor Valley confirm the existence of multiple sources of carbon in these soils and show the current importance of the legacy of productivity from paleo-lakes such as Lake Washburn (Burkins et al. in press). Transects from near the shores of Lakes Hoare (elevation 73 m), Fryxell (18 m), and Bonney (57 m) indicate that soil organic carbon sampled from low elevations in the valley is strongly influenced by legacy carbon derived from lacustrine and marine sources. In contrast, soil organic carbon at higher elevations (above 100 m) shows less potential contribution from past lakes and has an isotopic signature that is consistent with terrestrial production accumulated from the activities of cryptoendolithic microbial communities and soil algae over very long time scales. This pattern implies that today's soil food web in the valley may be supported by carbon fixed long ago.

Another legacy affecting present-day Taylor Valley soil communities is the spatial distribution of salts deposited during fluctuations in the level of paleo-lakes (Lyons et al. 1998) and the redistribution of these salts by aeolian transport. Soils that are now highly saline—either as a legacy or from prolonged weathering—may not be suitable for the development of today's soil communities (Freckman and Virginia 1997).

Biodiversity of Antarctic soil communities

Soil communities in the dry valleys are strikingly different from those of other terrestrial ecosystems. Dry valley soil communities are limited to a few phyla (rotifers, tardigrades, nematodes, protozoans, fungi, and bacteria; Freckman and Virginia 1998); these soil communities are much less diverse and abundant than the soil communities of

Figure 2. Head region of *Scottnema lindsayae*, a microbial-feeding nematode that dominates the soils of the McMurdo Dry Valleys. Scanning electron micrograph: Manuel Mundo, University of California–Riverside.



most terrestrial ecosystems (Friedmann 1982, Bamforth et al. 1996, Smith 1996, Vishniac 1996); a high percentage of dry valley soils lacks invertebrates or has only a single species of invertebrate (Freckman and Virginia 1998); and the highest invertebrate in the dry valley soil food web is the nematode (Freckman and Virginia 1997). The nematode community in the dry valleys has just four endemic species: *Scottnema lindsayae*, a microbial (bacteria and yeast) feeder (Figure 2); *Plectus antarcticus*, a bacterial feeder; and *Eudorylaimus antarcticus*, an omnivore–predator (Freckman and Virginia 1991). *Plectus frigophilus*, a bacterial feeder, has also been noted in a few soils (Amy Treonis, The Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen, UK, personal communication). Thus, unlike in most ecosystems, decomposition of soil organic matter in the dry valleys appears to be controlled by only two nematode functional groups, microbivores and omnivore–predators, and nutrient cycles and trophic interactions in the soil are limited to microbial populations and microinvertebrates (protozoa, rotifers, tardigrades, and nematodes; Vishniac 1996, Wynn-Williams 1996).

What factors explain the distribution of soil biodiversity across the dry valley landscape, and are legacies part of this story? Since 1989, our research has focused on elucidating the primary soil factors responsible for the distribution of soil communities in the dry valleys, with the long-term goal of developing a synthesis of the controls on patterns of soils and biota at the valley to regional scale. We have found that moisture, carbon, and salinity are important in determining whether habitats are suitable or unsuitable for soil communities (Freckman and Virginia 1998). A suitable soil habitat for nematodes is one that supports a large and relatively diverse population with an age structure that indicates reproduction and persistence. Most individuals in such a habitat are physiologically active, and other soil invertebrates—protozoa, tardigrades, and rotifers—are present. Unsuitable soil habitats are characterized by low invertebrate diversity, or they may lack nematodes and other invertebrates entirely. Invertebrate populations, when present, are small and largely inactive. In this article, we discuss findings at a variety of spatial scales to show the nature and complexity of relationships between soils and biota in an extreme environment.

What are suitable and unsuitable habitats at varying scales?

The scale of the study of soil biota is often linked to the distribution and structure of the dominant vegetation. In patchy, arid ecosystems, such as shrublands (Virginia et al. 1992, Schlesinger and Pilmanis 1998) and grasslands (Kel-

ly and Burke 1997, Wall-Freckman and Huang 1998), scientists typically compare the soil biota found beneath plants with that in adjacent spaces that are barren of plants. However, in low-productivity ecosystems lacking vegetation, older legacies persist, making geological features the most apparent and relevant units for study. We have used the landscape features described in Figure 3 in a hierarchical approach to investigate soil habitats at local to regional scales and across gradients of legacy carbon, moisture, and salinity in the dry valleys.

Because soil invertebrates (protozoa, rotifers, tardigrades, and nematodes) require water for activity, their distribution in the dry valleys should be limited to suitable (i.e., high-moisture) habitats (Kennedy 1993). Such habitats are restricted to small areas near glaciers, streams, edges of frozen lakes, and snowmelt depressions. The vast majority of the Taylor Valley landscape is a dry soil habitat that was long thought to be an unsuitable habitat for life and was largely ignored in early biological surveys (Timm 1971, Vishniac 1993). The abundance of life in dry habitats became apparent, however, with the systematic sampling of dry valley soils. In a survey of three dry valleys, we found that moisture was not the primary limiting factor for nematode abundance and that other soil factors (e.g., salinity) and climate better defined suitable habitats and community composition (Freckman and Virginia 1997). To relate this knowledge of suitable and unsuitable habitats to soil biodiversity at larger scales, we organized our studies to

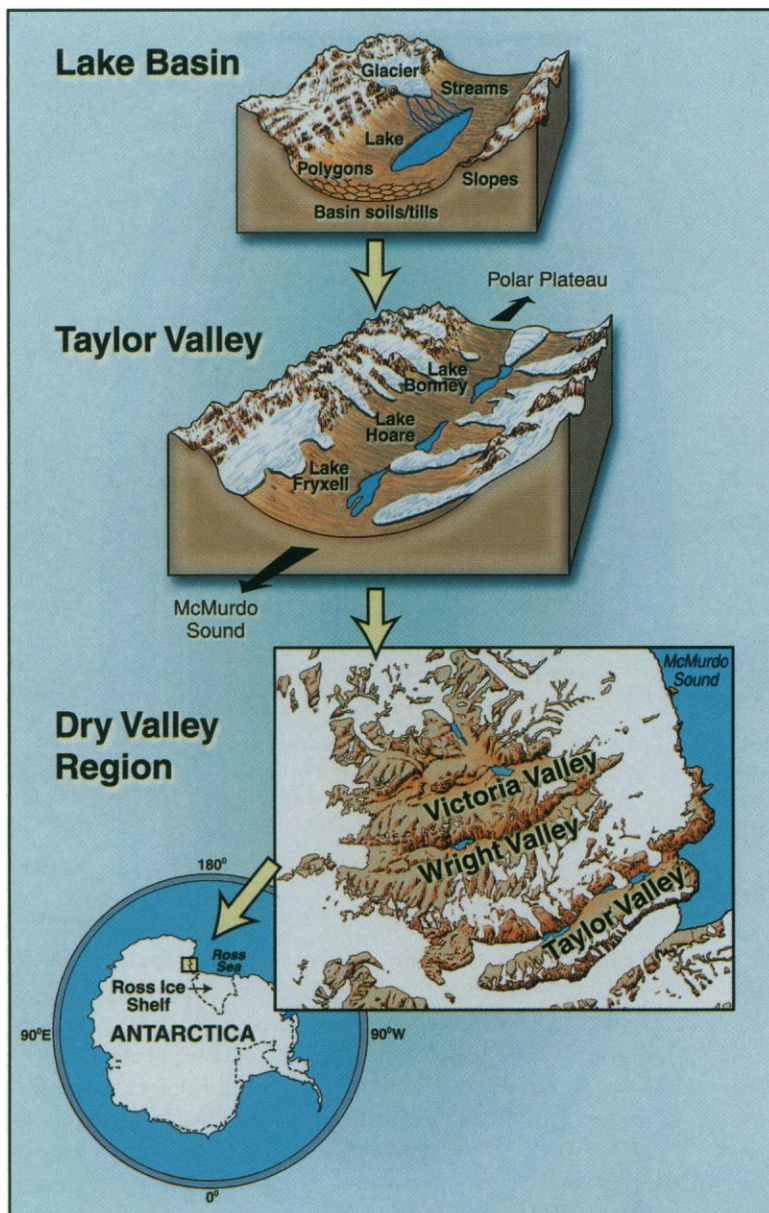


Figure 3. Hierarchical arrangement of the scales studied to assess relationships between soils and their biota in the McMurdo Dry Valley Region, Antarctica. In Taylor Valley, site of the McMurdo LTER program, there are three lake basins: Lake Bonney, nearest the polar plateau; Lake Hoare; and Lake Fryxell, nearest McMurdo Sound. The landscape units represented in each lake basin that we examined include soil-to-meltstream transects, soil polygons, elevational transects, and valleys themselves.

the stream, where chlorophyll *a* concentrations (an indicator of contemporary primary productivity) were highest and salinity was lowest. However, striking differences were seen in factors defining suitable soil habitats for the animals. Tardigrades and rotifers occurred only in the stream center. The three nematode species appeared to have distributions based on habitat factors. *S. lindsayae*, the most abundant nematode in the dry valleys, was absent from the stream center and dominated the dry soils; *E. antarcticus* was restricted primarily to the stream center and was rarely found in soils; and *P. antarcticus* was absent in soils but present in streams (Figure 4). Tardigrades and rotifers had the same distribution as *E. antarcticus*. These results show that soil biodiversity is structured by small-scale spatial variations (across a few meters) in moisture, salinity, and perhaps carbon.

Legacy effects of past lake levels and glaciers are distributed along the Taylor Valley floor and also along gradients of increasing elevation on the slopes of the Fryxell, Hoare, and Bonney lake basins (Figure 3). Powers et al. (1998) examined spatial heterogeneity of soil habitats at three scales, taking samples at 1 m and 10 m intervals in nested grids at sites along an elevational transect extending from 83 m to 188 m near Lake Hoare. If soil properties and biota were homogeneous, mean estimates of soil properties from the 1 × 1 m grids should be the same as those from the 10 × 10 m grids. However, estimates of soil moisture, organic carbon, and salinity at each elevation site differed significantly with grid size, indicating high spatial variation (Figure 5). Powers et al. (1998) suggested that this habitat heterogeneity was associated with changes in the distribution, abundance, and biodiversity of the nematode communities found along the elevational transect. This interpretation is consistent with the results of the stream-to-soil transition study of Treonis et al. (in press; Figure 4), in which nematode species were found to have differing requirements for establishment in soil habitats. One species, *S. lindsayae*, was found more frequently in drier and more saline soil habitats than *E. antarcticus*.

examine repeating landscape units of the dry valleys: transition zones between aquatic and terrestrial habitats, gradients of increasing elevation, and soil polygons.

The stream-to-soil transition zones provide a steep gradient of sediment and soil properties (Figure 4; McKnight et al. 1999). Dry valley streams flow intermittently during the austral summer and, along with the hyporheic zone, have high productivity that decreases over short distances into the surrounding dry soil habitats (Conovitz et al. 1998, McKnight et al. 1998). Information about soil invertebrate biodiversity across this environmental gradient can then be extrapolated to larger spatial scales in the dry valleys.

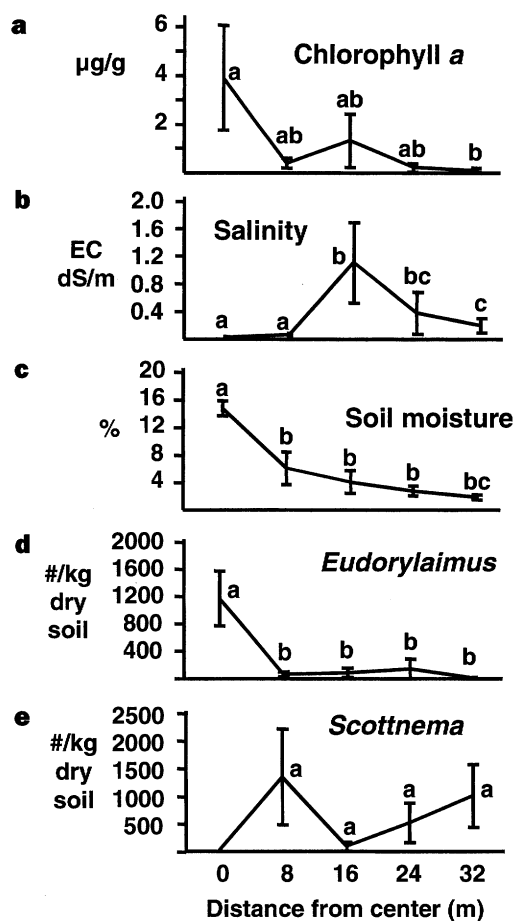
Biodiversity across the stream-to-soil transition was measured along 32 m transects from the center of a stream in the Lake Fryxell basin into the adjacent dry soils (Figure 4; Treonis et al. in press). Invertebrate (nematode, rotifer, and tardigrade) biodiversity was highest in the center of

Figure 4. Variation in three soil properties and in the abundance of two nematode species along transects extending from the center of a meltstream into adjacent soils of the Lake Fryxell basin of Taylor Valley. Values are means of three transects; error bars represent ± 1 SE. (a) Chlorophyll *a* (a measure of primary productivity). (b) Salinity, measured as electrical conductivity. (c) Soil moisture, as a percentage of soil mass. (d) Number of *Eudorylaimus antarcticus* individuals per kilogram of dry soil. (e) Number of *Scottnema lindsayae* individuals per kilogram of dry soil. Means identified by the same letter are not significantly different ($P \geq 0.05$) by the Student-Newman-Keuls Multiple Range Test. Modified from Treonis et al. (in press).

Soil polygons are the most obvious landscape feature of dry soil habitats that could be used for “scaling up” of biological information (Figure 6). They form from freeze–thaw cycles that create a physical sorting of rocks and soils (Campbell and Claridge 1987). Soil morphology, physical and chemical factors, and moisture vary across the polygons, changing from the polygon edges or troughs to their centers. Polygon size also changes with soil age, being smaller in younger soils and larger (more than 10 m wide) in older moraines (Campbell and Claridge 1987). We sampled well-formed polygons in the Fryxell, Hoare, and Bonney lake basins to determine relationships between soils and biotic communities at the basin and valley scales (Figure 7). We looked at two sources of carbon across the polygons, older legacy organic carbon and more contemporary carbon, using soil chlorophyll *a* concentrations as an indicator of recent primary production. We expected that at the landscape scale, soil biodiversity and abundance in drier polygons would be structured by the presence of high legacy organic carbon, not contemporary carbon and soil moisture.

Elsewhere in this issue, Fountain et al. (1999) have proposed that physical controls on Taylor Valley productivity and aeolian transport produce a general gradient of increasing soil organic carbon that extends from the Lake Bonney to the Lake Fryxell basins. Our polygon soil chemistry data are consistent with this hypothesis because we found that soil organic carbon was lowest at Lake Bonney and increased significantly moving down the valley to Lake Fryxell. In contrast, soil chlorophyll *a* concentrations were significantly higher at Lake Bonney (0.046 $\mu\text{g}/\text{mg}$) than at Lake Hoare (0.007 $\mu\text{g}/\text{mg}$) or Lake Fryxell (0.011 $\mu\text{g}/\text{mg}$). These differences indicate that a site with high legacy organic matter may not necessarily have the highest contemporary primary productivity (e.g., chlorophyll *a*). The activity of soil autotrophs should be less coupled to levels of soil organic matter than that of soil heterotrophs as long as adequate supplies of inorganic nutrients are present. In fact, dry valley soils typically have adequate amounts of inorganic nitrogen and phosphorus for most biota because these minerals are not leached and biotic uptake rates are very low.

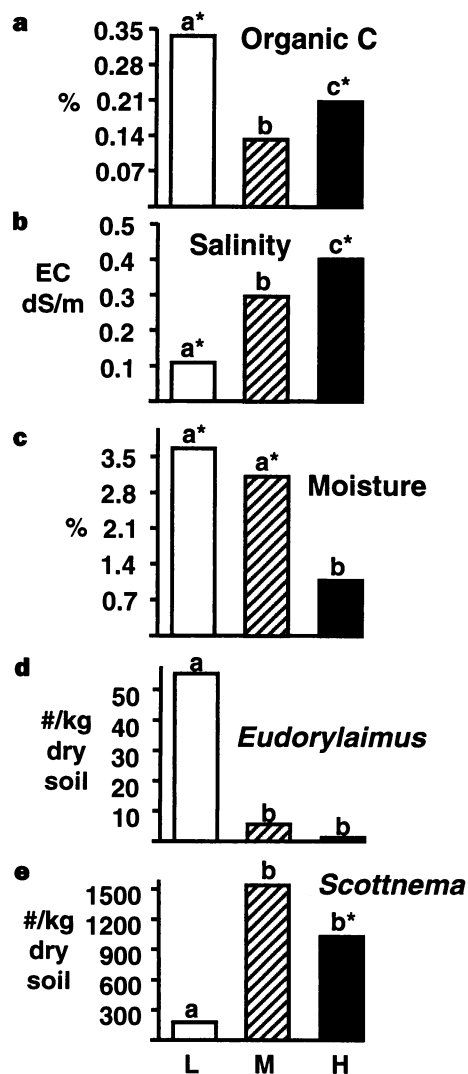
At the landscape scale, moisture appears to be of sec-



ondary importance to legacy carbon in patterning the distribution of soil communities across the valley. All basin soils had very low gravimetric moisture, ranging from 0.40% at Lake Hoare to 1.07% at Lake Fryxell (Figure 7). These levels of soil moisture would severely limit life in nearly all soil ecosystems, yet we recovered abundant and active nematode populations of *S. lindsayae* from the entire valley (Treonis et al. in press, Amy M. Treonis, Diana H. Wall, Ross A. Virginia, unpublished manuscript). At the time of polygon sampling, all basin soils in Taylor Valley were extremely dry, and the large-scale and long-term soil moisture patterns discussed by Fountain et al. (1999) were not observed. However, Lake Bonney basin is, as Fountain et al. (1999) note, the driest and windiest of the three Taylor Valley lake basins and, thus, the location with the most extreme (arid) climate. The nematode abundance results are consistent with this interpretation. Total nematode abundance at Lake Bonney was less than 25% of that at Lakes Hoare and Fryxell, and the number of unsuitable habitats for *S. lindsayae* was much greater at Lake Bonney (37%, $n = 93$) than at Lake Hoare (5%, $n = 93$) or Lake Fryxell (16%, $n = 96$). The distribution pattern of nematode species at larger polygon scales across the valley was, therefore, consistent with the stream-to-soil transition and elevational pattern.

E. antarcticus, a rarer nematode species in the dry val-

Figure 5. Variation in three soil properties and in the abundance of two nematode species at three sites forming an elevational transect located near the southern side of Lake Hoare, Taylor Valley. The three sites were located at elevations of 83 m (L), 121 m (M), and 188 m (H). At each elevation, nine samples each were collected from a 1 × 1 m grid and from a 10 × 10 m grid. (a) Organic carbon. (b) Salinity, measured as electrical conductivity. (c) Soil moisture, as a percentage of soil mass. (d) Number of *Eudorylaimus antarcticus* individuals per kilogram of dry soil. (e) Number of *Scottinema lindsayae* individuals per kilogram of dry soil. Means identified by the same letter are not significantly different ($P \geq 0.05$) by ANOVA. An asterisk indicates that means at a given elevation for the 1 m and 10 m sampling scales were significantly different ($P < 0.05$). This difference is a measure of soil variation. Modified from Powers et al. (1998).



leys, was most abundant in the moister habitats, in which greater amounts of contemporary carbon are assumed to be present (Powers et al. 1998, Treonis et al. in press). *S. lindsayae*, by contrast, is more clearly associated with the drier, saltier soils in which the relative importance of legacy soil organic carbon is hypothesized to be greater (Powers et al. 1998). The frequency of suitable habitats for *E. antarcticus* was greater at Lake Bonney (51%, $n = 93$), where soil chlorophyll *a* levels were higher, and organic carbon lower, than at Lake Fryxell (42%, $n = 96$) or at Lake Hoare (16%, $n = 98$).

Is Taylor Valley representative of the other McMurdo Dry Valleys in terms of the distribution of soil communities? Taylor is just one of several major valleys forming the McMurdo Dry Valley region. The geological and glacial history of the region is complex and is therefore of considerable interest to scientists reconstructing the long-term dynamics of the Antarctic ice sheet (Ingolfsson et al. 1998, Prentice et al. 1998). The amount and types of salts found in the dry valleys are a function of timing and extent of paleolake influence and soil age (i.e., degree of weathering; Campbell et al. 1998). The amount and quality of soil organic matter are derived largely from aquatic ecosystems of the geologic past and from much smaller amounts of today's primary productivity in lakes, streams, and soils. At a regional scale, the dry valley soil legacies interact with valley climate, which is determined by elevation, orientation of the valley in relation to katabatic winds, distance from marine ecosystems, and local topography, resulting in a spatial distribution of soil habitats that are suitable or not suitable for soil life.

An examination of valley-scale relationships between biota and soil habitats indicated that Taylor (80%, $n = 178$) and

Figure 6. Soil polygons outlined by snow accumulation in Taylor Valley, Antarctica. These landscape features are common at lower elevations and are useful units of study for scaling up information about soils and their biota. Photo: Kathy Welch, University of Alabama, Birmingham.

Garwood (77%, $n = 41$) Valleys have more suitable habitats for soil invertebrates than the more remote and climatically "extreme" Victoria (50%, $n = 93$) and Wright (49%, $n = 103$) Valleys. Nevertheless, some soil habitats in Victoria Valley support nematodes at population densities that are comparable to those in soils in Taylor and Garwood Valleys (Freckman and Virginia 1998). The question then becomes, is a more remote and extreme environment such as Victoria Valley generally less suitable for soil life than Taylor Valley? Or have the soil invertebrates simply been unable to reach and colonize all possible suitable habitats in the more remote valleys?

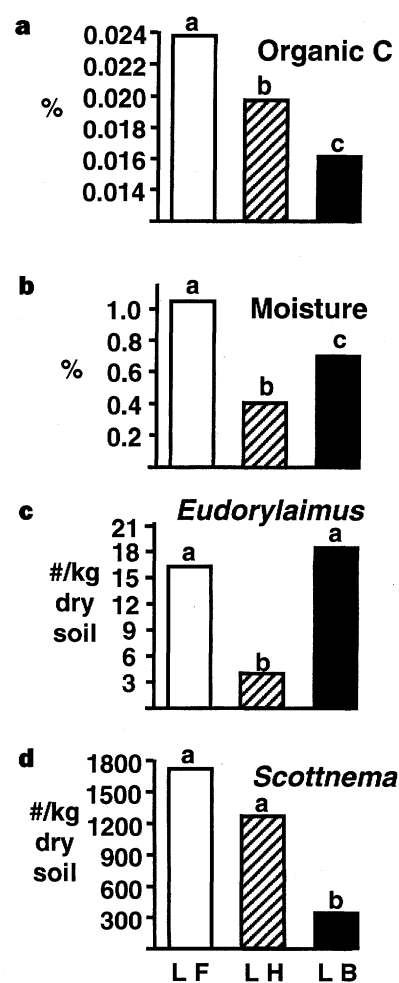
Dispersal and genetic variation

Nematodes can be wind dispersed in an anhydrobiotic state (Orr and Newton 1971, Carroll and Viglierchio 1981), or they may be transported in an active state by streams. Janiec (1996) observed that, in the maritime Antarctic, nematodes are dispersed by wind and the presence of plant fragments facilitates invertebrate movement. If dispersal to suitable habitats controls the makeup of dry valley soil communities, one would expect to see high rates of genetic exchange within and between the organisms in the valleys forming the McMurdo region, with a tendency toward a few dominant genotypes. Alternatively, soil biota might have limited opportunities for dispersal in this extreme environment, creating geographically isolated populations that are subject to genetic drift and adaptation to small-scale (local) soil conditions.

One way to determine the significance of dispersal is to examine the genetic diversity of a widely distributed soil invertebrate from the Antarctic continent; the first such analysis has recently been carried out (Courtright et al. in press). The pattern of variation in *S. lindsayae* nuclear rDNA and mitochondrial DNA, extracted from 188 individuals from small (less than 1 m²) plots in Garwood, Taylor, Wright, Victoria, and Alatina Valleys, was consistent with the interpretation of a single species defined morphologically as *S. lindsayae*. Mitochondrial analysis showed significant differences in the frequency of haplotypes in each geographic sample, with 12 distinct maternal lines (Figure 8). The mitochondrial results suggest that gene flow within and between valleys is restricted, indicating that wind-dispersal rates may be low.

Further work will be required to understand the soil

Figure 7. Soil properties and nematode abundance in polygon units in the Lake Fryxell, Lake Hoare, and Lake Bonney basins in Taylor Valley, Antarctica. We defined a polygon unit as three congruent polygons in a triangular formation. Soils were collected from transects joining midpoints of the polygon unit. Multiple samples from two polygon units, consisting of a total of six polygons, were examined at each lake basin. Numbers of samples: Lake Fryxell (LF), 96; Lake Hoare (LH), 98; Lake Bonney (LB), 93. The mean distance between centers of polygons was 14.9 m at Lake Fryxell, 19.5 m at Lake Hoare, and 17.5 m at Lake Bonney. Soil samples (0–10 cm depth) were collected from replicated sets of three congruent soil polygons at each site, and nematodes were extracted by sugar flotation (Freckman and Virginia 1993). Open bars, LF; hatched bars, LH; solid bars, LB. (a) Organic carbon. (b) Soil moisture, as a percentage of soil mass. (c) Number of *Eudorylaimus antarcticus* individuals per kilogram of dry soil. (d) Number of *Scottinema lindsayae* individuals per kilogram of dry soil. Means identified by the same letter are not significantly different ($P \geq 0.05$) by ANOVA. (Unpublished data from Ross A. Virginia and Diana H. Wall.)



and environmental factors underlying the genetic diversity of Antarctic soil communities. Human activities and disturbance to soils in the Antarctic will undoubtedly increase (Harris 1998). As more people enter the dry valleys, movement of soil and associated nematodes will increase the rates of nematode dispersal and introductions into the remote regions, as has occurred with temperate nematodes in agroecosystems and other terrestrial ecosystems.

The dry valleys and other ecosystems

The extreme environment of the dry valleys and the biogeographic isolation of the continent create a set of selective pressures resulting in unusual, low-diversity soil communities (Vincent 1988, Vishniac 1993). The relationships between species diversity, ecosystem function, and soil environment should be more apparent in the dry valleys of Antarctica than in other terrestrial ecosystems because of the significant structural and functional differences between dry valleys and ecosystems with "young" patterns of soil spatial variation. In addition, dry valleys lack higher plants, which in other ecosystems have profound effects on soil biodiversity and the soil depths at which biological

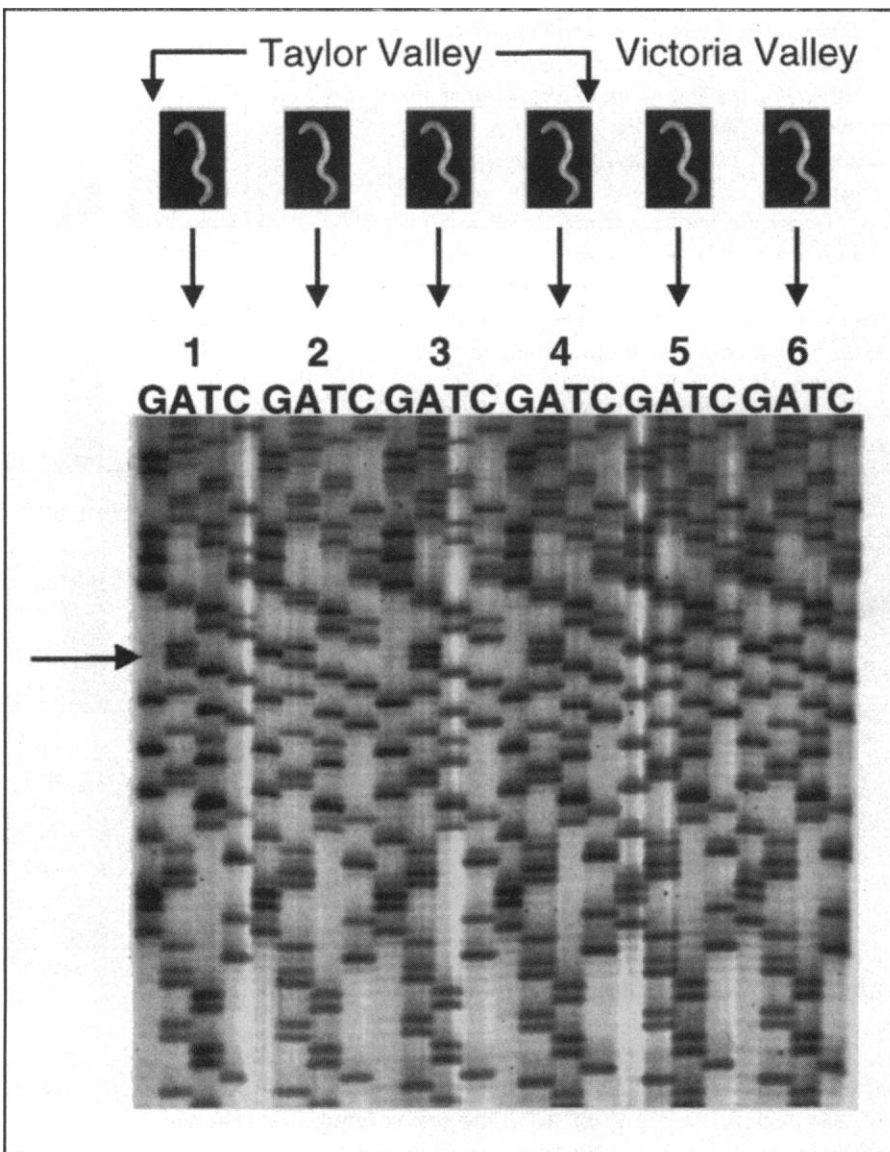


Figure 8. Genetic variation in *Scottinema lindsayae* within and between Taylor Valley and Victoria Valley. The DNA sequencing gel shows partial mitochondrial DNA sequences from six different individuals—four from Taylor Valley and two from Victoria Valley. Each sample was amplified and sequenced from the DNA extracted from an individual worm. The arrow indicates one of the variable positions found in the sequence. These and other results (Courtright et al. in press) indicate that gene flow between *S. lindsayae* populations in the frequently visited Taylor Valley and the more remote and isolated Victoria Valley is restricted. Modified from Courtright et al. (in press).

tem. In such an ecosystem, life processes are restricted to a narrow zone at or near the soil surface. Extreme aridity and a consequent lack of leaching, plus a lack of plant roots, mean that carbon and other materials are not easily moved from the surface to depth in the soil. Instead, legacies of productivity from past ecosystems have a marked influence on soil chemistry and organic matter. Movement of carbon into the soil profile is the result of material transport by wind and glaciers. Terrestrial primary productivity occurs at the soil surface, to

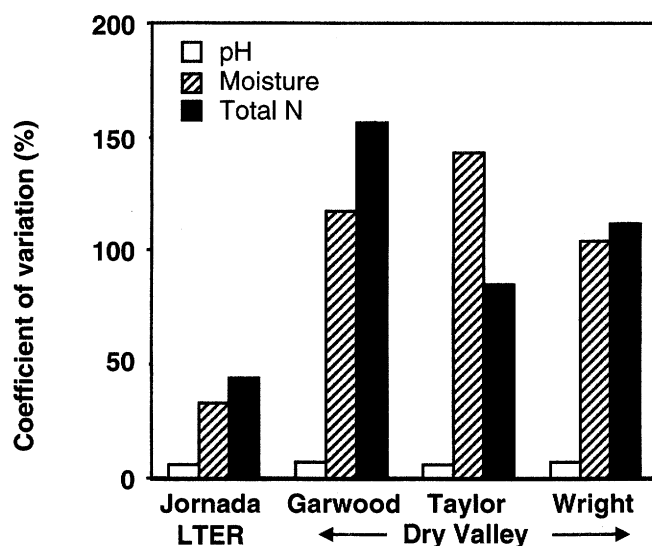
which cyanobacteria, algae, and the rest of the soil biota are largely confined. An important consequence of this horizontal structure is that the dry valley soil ecosystem should be highly susceptible to changes in surface energy balance (e.g., ultraviolet radiation, temperature, and moisture; Weiler and Penhale 1994) and soil physical disturbance (e.g., trampling; Freckman and Virginia 1997). These impacts on the fragile soil communities in dry valley have yet to be investigated.

The ecosystems whose distribution of soil biota is most similar to that of the dry valleys are other arid ecosystems (Wall and Virginia 1999). The Jornada Basin, site of an LTER project studying desertification, is also characterized by high spatial variation in soil properties (Schlesinger et al. 1990, Reynolds et al. 1999) and distribution of soil biota (Jenkins et al. 1988, Freckman and Virginia 1989). Unlike that in the dry valleys, the relatively high spatial variation in soil resources seen at the Jornada Basin is of recent origin, a newly created legacy of human activity

processes can occur (Brussaard et al. 1997). In a “vertical” three-dimensional soil ecosystem, plant roots move carbon deep into the soil profile (Canadell et al. 1996), providing high-quality organic substrates for soil microbes, increasing biodiversity, and providing the base for a complex food web of invertebrates (Freckman and Virginia 1989, Silva et al. 1989). Plant canopies and the plant litter layer alter the soil physical environment (e.g., the amount of light and ultraviolet radiation reaching the surface) and chemistry. Moreover, total productivity in ecosystems with vascular plants is high, and the amount of primary productivity contributed by soil organisms is a very small fraction of this total. Finally, human disturbance and changes in vegetation alter spatial patterns of soils and biota on much more rapid time scales (tens to hundreds of years) than in the dry valleys, where ecological and geological time scales converge.

By contrast to most other terrestrial ecosystems, dry valley soils can be conceptualized as a “horizontal” ecosys-

Figure 9. Coefficients of variation for soil properties at the Jornada Basin LTER site, New Mexico, and three McMurdo Dry Valleys. Open bars, pH; hatched bars, soil moisture; solid bars, total nitrogen content. Jornada Basin soils data from Schlesinger et al. (1990). Dry valley soils information was calculated from data in Freckman and Virginia (1997).



(e.g., introduction of domestic cattle). The McMurdo Dry Valleys have not been exposed to the human influences that generated spatial heterogeneity in the Jornada Basin. Instead, the research of the McMurdo LTER summarized in this issue of *BioScience* shows that legacies of soil development from past ecosystems persist in the dry valley landscape and contribute to a highly heterogeneous environment for soil organisms.

Chesson and Huntley (1997) argued that species coexistence leading to biodiversity is possible in harsh and fluctuating environments if niche differences between species exist and if a diversity of suitable habitats is created by spatial and temporal variations in environmental conditions (niche opportunities). The highly heterogeneous dry valley soil may have allowed the sorting of dry valley invertebrate biodiversity into discrete communities, such as those along the stream-to-soil landscape unit that we have described in this article. An important question for the future is whether the heterogeneity of soil properties we see today in the dry valleys will, much as we see in the Jornada Basin, be altered by human impact, with consequences for biota and ecosystem processes (Figure 9).

The legacies seen in Taylor Valley suggest that human disturbance of soils will have long-lasting effects (Campbell et al. 1998) and may later affect habitat suitability for soil biota. Coupled with increasing disturbance is the likelihood that humans will increase rates of organism dispersal within and between valleys, perhaps altering organism distributions and soil community structure. For these reasons, the soils of the McMurdo Dry Valleys should be considered sensitive to human disturbance (Freckman and Virginia 1997). The dominance of *S. lindsayae* in this system suggests that this organism might be a useful indicator of environmental change and disturbance in the dry valleys.

What does the nematode *S. lindsayae* tell us about the dry valleys?

The inhospitability of the dry valley soils to most soil phyla attests to the physiological challenges faced by soil organisms in Antarctica (Somme 1995). Yet, remarkably, *S. lindsayae* is found throughout the McMurdo Dry Valleys in high numbers. This single species dominates the most abundant habitat in the valleys, the dry and often saline soils with varying organic carbon (Figures 4, 5, and 7). Our goal is to define the niche of this unusual organism.

S. lindsayae is a generalist (Figure 2). It can feed on bac-

teria and yeasts (Overhoff et al. 1993), whereas *E. antarcticus* probably has a more specialized diet of algae or other soil invertebrates (Freckman and Virginia 1997). Distinct maternal lines of genetic variation for *S. lindsayae* suggest that this species is able to adapt to local-scale variations in soils and environmental conditions or to persist in patchily distributed soil habitats for long periods of time without exchange with other populations. The ability of *S. lindsayae* to enter anhydrobiosis and survive prolonged periods in the absence of water is perhaps the ultimate adaptation for success in this extreme arid environment (Powers et al. 1998, Treonis et al. in press). Knowledge of the distribution of this nematode can therefore be used in the future to track how dry valley soil ecosystems are responding both to global-scale perturbations (e.g., climate change) and to local disturbances caused by people visiting and studying this unique ecosystem.

Our research shows that small differences in climate and soil physical and chemical properties may have large effects on soil nematode abundance and biodiversity. The limited biodiversity of the dry valleys segregates into communities in response to a set of interacting soil factors (e.g., salinity, moisture, and organic carbon) operating at small to large spatial scales. These factors are in turn delineated by the legacies of past ecosystems. Perhaps more than in any other ecosystem, knowledge of the past is essential to understand communities that today function in the most extreme soil environment on Earth.

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