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Wind dispersal of soil invertebrates in the McMurdo Dry Valleys, Antarctica

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Abstract Dispersal of soil organisms is crucial for their spatial distribution and adaptation to the prevailing conditions of the Antarctic Dry Valleys. This study investigated the possibility of wind dispersal of soil invertebrates within the dry valleys. Soil invertebrates were evaluated in (1) pockets of transported sediments to lake ice and glacier surfaces, (2) wind-transported dust particles in collection pans (Bundt pans) 100 cm above the soil surface, and (3) sediments transported closer to the surface (< 50 cm) and collected in open top chambers (OTCs). Invertebrates were extracted and identified. Nematodes were identified to species and classified according to life stage and sex. Three species of nematodes were recovered and *Scottnema lindsayae* was the most dominant. There were more juveniles (~71%) in the transported sediments than adults (29%). Tardigrades and rotifers were more abundant in sediments on lake and glacier surfaces while nematodes were more abundant in the dry sediment collections of Bundt pans and OTCs. The abundance of immobile (dead) nematodes in the Bundt pans and OTCs was three times greater than active (live) nematodes. Anhydrobiosis constitutes a survival mechanism that allows wind dispersal of nematodes in the McMurdo Dry Valleys. Our results show that soil invertebrates are dispersed by wind in the Dry Valleys and are viable in ice communities on lake surfaces and glaciers.

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Introduction

The McMurdo Dry Valleys of Antarctica are an extreme environment. They comprise a large (~4,000 km^2) ice-free area considered to be the driest and coldest desert on Earth, (Fountain et al. 1999; Priscu et al. 1998) limiting to the survival of many forms of life (Convey 1996). Nevertheless, there are soil invertebrates in this environment among which are soil nematodes, protozoa, rotifers and tardigrades (Freckman and Virginia 1997, 1998, Virginia and Wall 1999; Bamforth et al. 2005).

Soil nematodes disperse by slow migration in soil, and transportation with water and air currents (Carroll and Viglierchio 1981; Janiec 1996; Prot and VanGundy 1981a, b; de Rooij-van der Goes and van der Putten 1998). Active nematode migration and dispersal occurs within the soils of the dry valleys of Antarctica to avoid the prevailing dry soil conditions (Treonis et al. 1999). Wind is an important abiotic factor responsible for dispersion of soil nematodes in terrestrial ecosystems, including the moist maritime Antarctic (Carroll and Viglierchio 1981; Orr and Newton 1971; Baujard and Martiny 1994; Benninghoff and Benninghoff 1985; Gressitt et al. 1960; Janiec 1996; Weicht and Moorhead 2004). Wind dispersal is supposedly facilitated when the nematodes, rotifers and tardigrades are in anhydrobiosis. Anhydrobiosis is a form of cryptobiosis, an ametabolic stage during which nematodes, rotifers and tardigrades undergo physiological adjustment resulting in body mass reduction induced during periods of environmental stress such as desiccation (Crowe and Clegg 1978; Freckman 1978; Treonis et al. 2000; Treonis and Wall 2005, in press).

Dry Valley soils receive little precipitation (< 10 cm water equivalent annually, Doran et al. 2002) or free soil moisture (Barrett et al. 2004; Virginia and Wall 1999) except during decadal events (Lyons et al. 2005, in press). Moving water exists primarily in ephemeral glacial meltstreams (McKnight et al. 1999). In the dry valleys and in hot deserts, low soil moisture triggers anhydrobiosis in nematodes (Freckman 1978; Freckman et al. 1975; Treonis et al. 2000). Anhydrobiotic nematodes are presumably more likely to survive the desiccation extremes of wind transport than many other organisms. Freckman and Virginia (1998) hypothesized that wind is a primary dispersal mechanism for soil nematodes in the dry valleys. In a conceptual model predicting soil habitat suitability they assumed that wind dispersal occurs and that soil heterogeneity (variation in moisture, salinity, organic matter) is the main factor determining invertebrate distribution, establishment and diversity across small (< meter) and large (meter–kilometer) scales in the dry valleys (Courtright et al. 2000; Freckman and Virginia 1998; Barrett et al. 2004).

Despite the potential importance of wind dispersal as an important factor controlling the distribution and diversity of life in Antarctic soils, no study has directly addressed the ability of soil invertebrates to disperse by wind and survive in these extreme soil habitats of the dry valleys. Here we report results from field studies in Taylor Valley (77°40′S 162°E) site of the McMurdo Dry Valley Long-Term Ecological Research LTER), on wind dispersal of nematodes and other invertebrates.

Materials and methods

Three methods were used to collect wind-transported sediments and invertebrates. One was conducted by analyzing sediment accumulated on frozen lake ice or glaciers and the other two were conducted on land and collected windblown sediment after 1 year at two heights above ground level. Invertebrate diversity and nematode survival, active or live and immobile or dead nematodes were determined.

1. Sediment pockets on lake ice or glaciers: In the austral summer of 1997/1998, soil invertebrates were evaluated in pockets of soil sediments deposited on frozen surfaces of Lake Hoare (77°38′S, 162°52′E, elevation of ~77 m asl) and Canada Glacier (77°37′S, 162°59′E, elevation of ~264 m asl). Soil sediment pockets are formed as soil particles transported by wind and deposited on ice surfaces of lakes and melt glaciers. They may eventually melt into the ice forming biologically active cryoconite holes (Porazinska et al. 2004). These were sampled along three perpendicular transects of five sampling positions at varying distances along each transect wherever a soil deposit was found. The soil was collected with sterile plastic scoops and put into sterile Whirlpak® bags (NASCO Plastics Inc., ON, Canada) (Freckman and Virginia 1993). The soil samples were stored in a cooler and transported to the McMurdo Station Crary Laboratory where they were stored at 4°C until processed.
2. Bundt pan soil traps: Bundt pans (Lancaster 2002) with approximately 25 cm diameter and 10–20 cm depth were mounted approximately 100 cm aboveground on PVC posts (Fig. 1) at three locations across Taylor Valley. Twenty seven Bundt pan traps, nine at each site, were placed along a transect on the south side of Lakes Fryxell (77°35′S, 163°22′E), and Hoare in the 1998–1999 summer season, and Lake Bonney (77°55′S, 162°27′E) in 1999–2000 summer season. Each pan contained about 100 glass marbles (1 cm diameter), on top of a coarse wire screen. The marbles and screen created a rough surface for trapping airborne particles and protecting them from being blown away. For sampling, the pans were removed, each covered with aluminum foil, and placed upright into polythene bags during transportation to prevent sediment loss. A portion of the amount of sediment collected in each Bundt pan was weighed and soil moisture determined gravimetrically by oven-drying a sub-sample of known weight at 105°C for 24 h (Courtright et al. 2001; Porazinska and Wall 2002). Soil invertebrate numbers recovered (see below) were expressed as per dry weight of soil.
3. Open top chambers at ground surface: The open top cone-shaped chambers (Fig. 1) (Marion et al. 1997) complemented the Bundt pans, and targeted sediment transport just above ground level (< 1 m). The OTCs were placed on level ground surfaces (< 3–4% slope) at the south side of Lakes Fryxell, Hoare and Bonney in the summer of 2001–2002. Three plexiglass chambers (85 cm bottom diameter and 50 cm top diameter; Sun-Lite®, Solar Components Corporation) were anchored into the ground with four metal stakes and

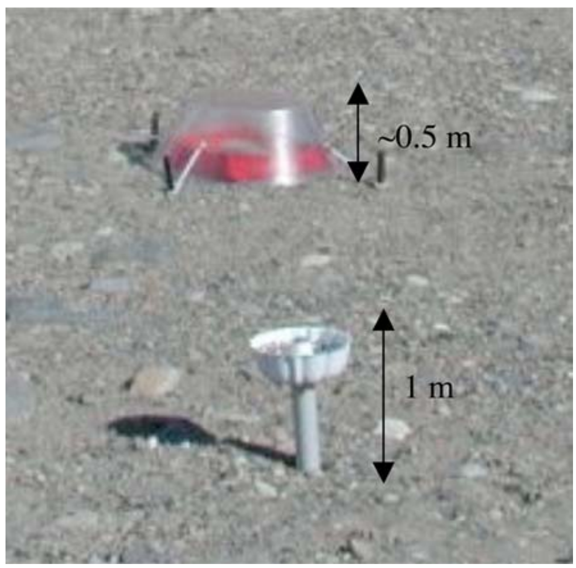

Fig. 1 A Bundt pan and an open top chamber (OTC) with the *red square carpet cloth* for wind-dislodged sediment collection (not to scale)

a heavy gauge wire harness. The chambers were spaced 3 m apart along a (N–S) line perpendicular to the valley floor. An empty red polyester cloth formed into a wire-supported box (50×50 cm^2 and 10 cm height) was placed in the center of each chamber and anchored to the ground with nails at each corner and center of the box. At each sampling the chamber was removed, the cloth box with accumulated sediments dislodged by wind was cleaned into a plastic bag and transported to the laboratory, stored and analyzed as detailed for the Bundt pan traps.

The transport collection method of soil to lake ice and glacier was sampled once, and the other two methods annually (2 years for OTC traps, and 5 years for the Bundt pan sediment traps). For all studies, nematodes, tardigrades and rotifers were extracted within 48 h of sampling from 100-g soil subsamples, where possible by wet sieving followed by centrifugation (Freckman and Virginia 1993, 1997; Porazinska and Wall 2002; Powers et al. 1998). Nematodes, tardigrades and rotifers were counted, nematodes identified to species, and classified as active (living) or immobile (dead), male or female, adult or juvenile. Invertebrate abundance was expressed as kg^{-1} of dry soil before log (n + 1) transformation for statistical analysis (Courtright et al. 2001, Zar 1998) using analysis of variance in JMP 501 (2002). The annual amount of aeolian deposition was calculated based on the formula adapted from Lancaster (2002): aeolian deposition (g m^{-2} $year^{-1}$) = mass of sediment retained (g) × area of dust pan or OTC (m^2) × time exposed (year).

Results

Across the three methods of sediment collection, the OTCs collected more sediment than the Bundt pans (Fig. 2), and with a greater invertebrate diversity (Table 1) than the Bundt pans and the sediment to lake/glacier transport method. However, transport of live organisms was more evident in the sediments deposited on frozen lake surfaces and glaciers (Fig. 3). *Scottnema lindsayae* remained the most abundant nematode species (Fig. 4) recorded across the three methods of sediment collection.

The amount of sediment collected from pockets on ice in the soil to lake/glacier transport was not analyzed for comparison, because there was insufficient weight per sample.

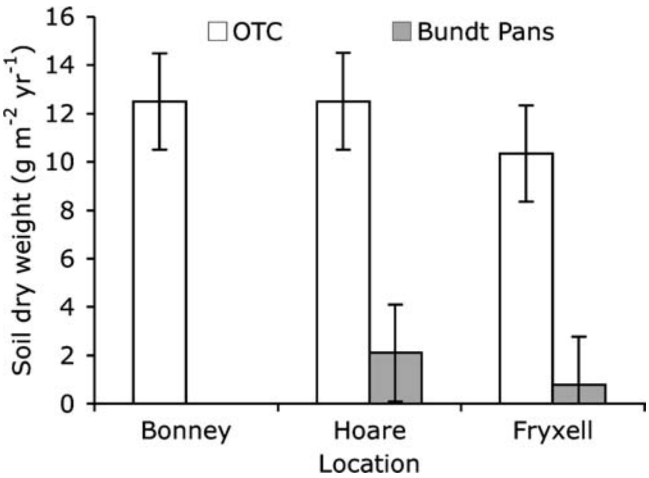

Fig. 2 Mean weight of aeolian sediments in three locations (Lakes Bonney, Hoare, Fryxell) in the OTCs ($n = 9$, over 2 years), and Bundt pans ($n = 27$, over 3 years), at the various locations. Material collected in the Bundt pans at Bonney was too small (< 10 mg) for dry weight estimation

In the sediment to lake/glacier transport method the abundance and diversity of soil invertebrates in sediments collected from the frozen lake surfaces did not differ from those deposited on glaciers. In both locations rotifers and tardigrades were the predominant invertebrates. The abundance of nematodes was significantly lower ($P < 0.001$) than the abundance of tardigardes and rotifers, and *Plectus antarcticus* was the only nematode species recorded in sediments deposited on frozen lake and glacier surfaces (Table 1). Although some active (living) soil invertebrates were recorded in the sediments from frozen lake surfaces and glaciers, overall, the number of immobile (dead) organisms was significantly higher ($P < 0.0056$) (Fig. 3).

Sediments collected in the Bundt pans had a different taxonomic composition to those collected from the sediment to lake/glacier transport study, with nematodes more dominant than rotifers and tardigrades (Table 1). Similar to the OTCs, in the Bundt pans there were more dead than live invertebrates ($P < 0.0105$). Sites near Lake Fryxell had higher numbers of invertebrates recorded than near Lakes Hoare and Bonney but this was not statistically significant ($P < 0.051$).

Three groups of invertebrate taxa were also recorded in the OTCs with nematodes significantly higher in abundance ($P < 0.0001$) than the other two taxa. Both the Bundt pan and OTC had more dead nematodes

Table 1 Mean number of soil invertebrates per kg of dry soil (SD of mean) recorded by three soil sediment collection methods

Organisms	Soil to lake/glacier transport	Bundt pans	OTC
Nematode (Total)	83.39 (2.3)	43.90 (23.4)	166.11 (42.4)
Scottnema lindsayae	0.0 (0)	1.62 (0.9)	159.42 (67.3)
Eudorylaimus antarcticus	0.0 (0)	0.62 (0.4)	5.57 (2.9)
Plectus antarcticus	83.39 (2.3)	41.66 (13.6)	1.12 (0.5)
Tardigrades	2,463.54 (342.1)	0.0 (0)	1.12 (5.2)
Rotifers	3,150.66 (146.1)	0.0 (0)	1.10(3.2)

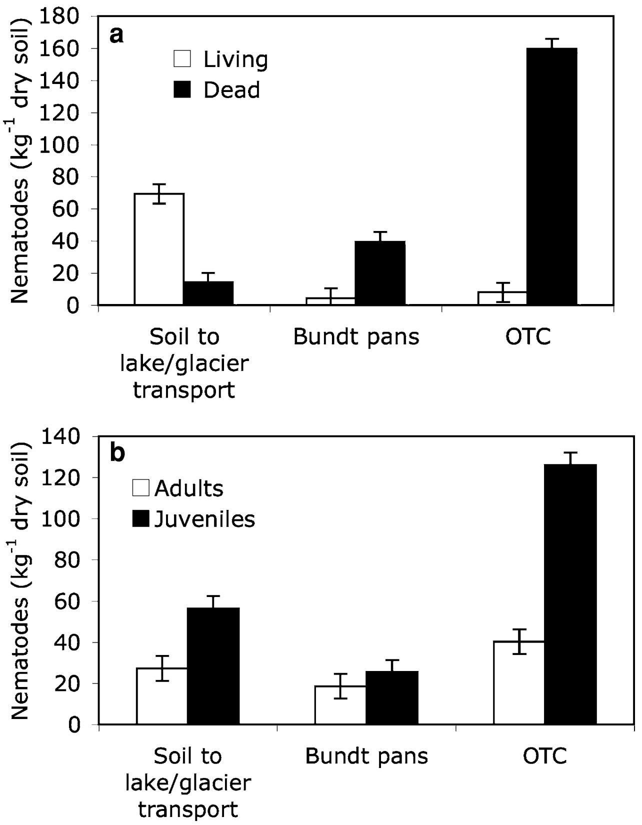

Fig. 3 The mean abundance of **a** living and dead, **b** adult and juvenile nematodes, recorded in soil to lake/glacier transport, Bundt pans and OTCs in the Dry Valleys

($P<0001$) than live nematodes (Fig. 3a). Unlike the Bundt pans, there were more nematode juveniles in the OTC sediments ($P<0.001$) (Fig. 3b). Similar to the Bundt pans, in the OTC sediments, nematodes were the most abundant invertebrates recorded, with *S. lindsayae* the most abundant species (Table 1). The lake and glacier sediments had more living than dead nematodes ($P<0001$). Among the lake basins, more invertebrates were recorded at Lake Fryxell ($P<0.0088$) than the other two locations.

Discussion

Sediments seem to be transported predominantly near the soil surface based on the amounts recovered in the OTCs closer to the ground surface (< 50 cm), and the Bundt pans (100 cm above soil surface). Lancaster (2002) recorded over 110 g m^{-2} $year^{-1}$ of sediments in Bundt pans on the south side of Lake Bonney, but the amount of sediments he recorded on the south sides of Lakes Fryxell and Hoare were similar to the low values recorded in this study. These Bundt pan sediment amounts were more than five times lower than those collected in the OTCs. Lancaster (2002) noted that Bundt pans were inefficient for collecting sand, especially at a height of 100 cm above the soil surface. Our data show that OTC, located nearest to the soil surface, collected the largest amounts of sediments.

The amount of sediments transported by wind and the number of organisms recovered were related. Thus, soil invertebrates appear to be distributed with large amount of sediment movement, especially closer to the soil surface. Intense katabatic wind events (Nylen and Fountain 2004) may be particularly important for moving large amounts of sediments to entrain and then support invertebrates transported to new habitats, such as ice-covered lakes and glaciers. For nematodes, both juveniles and adults are dispersed by wind in all the methods we evaluated. However, except for the sediments examined on frozen lake and glacier surfaces, living (active) invertebrates were less abundant in the wind-transported sediments. Since we do not exactly know over what timeframe it took to build the invertebrates population found in the sediments on the lake and glacier surfaces, it is possible that sufficient moisture from surface melt, helped communities to develop over several years on the frozen lake and glacier surfaces, in contrast to the land-based traps that were exposed for only one season, with potentially less access to a moisture source. Also, moisture availability from surface melt could have facilitated reactivation of anhydrobiotic invertebrates on frozen lake and glacier surfaces resulting in the higher number of living organisms recorded on these surfaces.

The results of the three sediment collection methods in this study demonstrate the variety of invertebrates and the diversity of nematode genera (*Plectus, Scottnema, Eudorylaimus*) that are dispersed by wind in the Dry Valleys. We found the OTC traps to be the most efficient in collecting sediments, compared to the Bundt traps. Collecting sediments from frozen lake and glacier surfaces was also a good assessment of wind dispersion of soil invertebrates in the Antarctic Dry Valleys. Successful wind dispersion varied for different organisms. Tardigrades, rotifers and *P. antarcticus* coped better with deposition on fairly moist surfaces such as frozen

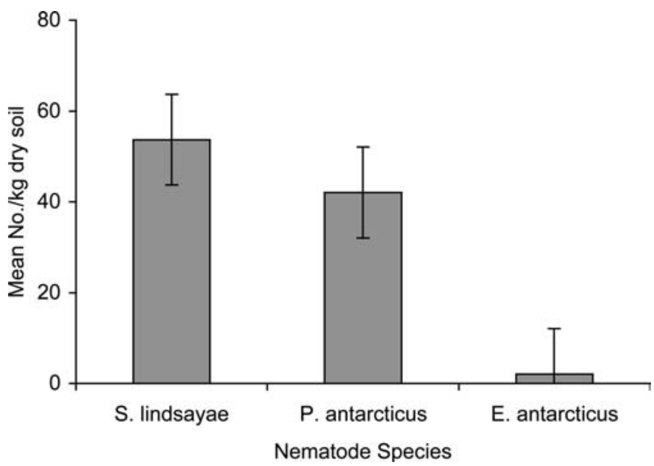

Fig. 4 The mean number of each nematode species recorded across all the three different soil sediment collection methods

lakes and glaciers. *S. lindsayae* are better adapted than *Plectus* to dry soil conditions (Treonis et al. 2000; Barrett 1976) and had a higher incidence of survival in the Bundt pans and OTC.

Similar observations of migration via the wind have been demonstrated as a mechanism for invasion of new species in the high Arctic (Coulson et al. 2003), and also nematode dispersal in other terrestrial ecosystems (Carroll and Viglierchio 1981; Shapiro et al. 1993; Steiner 1996). The individual weight of the organism and the wind speed are important factors in how far an organism can disperse (Ran et al. 2002). For example, body size and mass of protozoa were important factors determining their spatial dispersion by wind (Bamforth et al. 2005). While we did not determine whether nematodes were in anhydrobiosis, active nematodes have a heavier body mass and do not survive rapid desiccation (Crowe and Clegg 1978). Anhydrobiotic rotifers, tardigrades and nematodes have a reduced body mass due to loss of water (Demeure and Freckman 1981; Schill et al. 2004) and can survive desiccation (Crowe and Madin 1975).

Although the nematode survival rate is low, wind dispersal appears to be an effective method to increase gene flow and extend the geographic range. The higher percentage of dead nematodes recovered in wind-transported materials in dry sediments than is found in moist sediments could be due to: damage incurred to them during transport and deposition to harsh environmental conditions during transport (e.g., UV exposure, shearing force of sand particles, desiccation); deposition onto a less suitable habitat for growth and activity (highly saline soils); or, absence of either sex required for reproduction. Although signs of anhydrobiosis were not distinguished, nematodes reactivating in water after being in anhydrobiosis either become active, immobile or die. We counted many nematodes as dead that could have been inactive and anhydrobiotic at the time of sorting and identification. This is consistent with Marshall and Pugh's (1996) suggestion that wind transportation of larger invertebrates is only possible for those capable of anhydrobiosis. Then, it is not surprising that anhydrobiotic nematodes might be more successfully transported by wind than active nematodes in the McMurdo Dry Valleys (Virginia and Wall 1999; Wall and Virginia 1999; Orr and Newton 1971).

The potential for wind dispersal depends on the spatial distribution of soil communities, the density of organisms, and their proximity to the soil surface to allow entrainment by wind (Carroll and Viglierchio 1981; Courtright et al. 2001; Powers et al. 1995, 1998; Virginia and Wall 1999). Soil nematodes live below the soil primarily, and thus are less available for wind transport (Powers et al. 1998).

Soil invertebrate communities in the Antarctic Dry Valleys are thought to be restricted in part by extreme geographic isolation (Ellis-Evans and Walton 1990; Walton 1990), which makes dispersal critical for the maximum utilization of the limited resources. The desiccation of these cold desert soils may restrict biological dispersal of soil organisms, thereby limiting them to isolated patches of suitable habitats. This would be reflected in the greater evidence of restricted gene flow and higher endemism, which could retard the capacity of these populations to respond to environmental changes in the dry valleys. Hogg and Stevens (2002) noted limited gene flow in microarthropods between their study sites at Ross Island and southern Victoria Land on the Antarctic continent suggesting that gene flow and hence dispersal of Antarctic taxa may be limited to local events. For species already having small population sizes and an inability to exploit new habitats or disperse to optimal habitats, such conditions could lead to extinction risk. As part of an evolutionarily stable strategy in such situations, abiotic dispersion provides an optimal solution for organisms with small size, limited mobility and life in an extreme environment.

Our results support the conceptual model of Freckman and Virginia (1998), emphasizing wind as a dispersal mechanism for nematodes and other invertebrates across the dry valley landscape. Nematode abundance in the transported sediments of the three evaluation methods was similar to nematode abundance recorded in the top 0–2.5 cm of top soil that is removed by wind, at the south side of Lake Hoare (Powers et al. 1995). This study provides no indication on the spatial distances of invertebrate dispersal but does suggests that nematode species, rotifers and tardigrades are dispersed by wind within and, perhaps, across basin soils, lakes and glacier surfaces of the Dry Valleys. Depending on the suitability of the habitat, the nematodes may establish or not (Freckman and Virginia 1998). Establishment of populations would depend on the heterogeneity of soil chemical and physical factors and the organism's life history strategies. Finding live *Plectus* in sediments on frozen lakes and glacier surfaces is fascinating since there are no previous records of *Plectus*, living or dead, found in glacier cryoconite holes that were formed from soil deposition (Porazinska et al. 2004). There are indications from these collection experiments that although anhydrobiosis may have evolved to overcome periods of desiccation stress, it also constitutes a major adaptation facilitating wind dispersal.

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