Global change tipping points: above- and below-ground biotic interactions in a low diversity ecosystem

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Low diversity ecosystems are expected to be more vulnerable to global changes although they have received less attention than high diversity ecosystems. Addressing the present state of the Antarctic Dry Valley region by focusing on the potential global changes that may alter the coupling of above- and below-ground species and ecosystem processes is a realistic and critical need that has value beyond the Antarctic community. Presented here are suggested implications of global change on the Dry Valley terrestrial systems and how these effects might be manifested in the future.

Keywords: soil; biodiversity; Antarctica; Dry Valleys; climate change

1. INTRODUCTION

Antarctic scientists are increasingly being asked to explain the relevance of their investigations in regions with low biodiversity, such as the McMurdo Dry Valleys (approx. 78° S), to those regions having higher biodiversity and experiencing unprecedented and rapid transformations. Antarctica's terrestrial biodiversity is not immune to global changes affecting biodiversity and ecosystem functioning elsewhere (Kennedy 1995; Freckman & Virginia 1997; Sinclair 2002; Cowan & Tow 2004; Frenot *et al.* 2005; Turner *et al.* 2005; Wall 2005). However, less attention is given to changes affecting these Antarctic ecosystems, possibly because the ice-free land mass is less than 0.5% (332 000 km^2) of the continent (Drewry *et al.* 1982) and the role of the few species in the functioning of these cold desert terrestrial ecosystems seems minor compared with physical controls (Campbell & Claridge 1987; Fountain *et al.* 1999) or compared with the role of less cryptic biota in the maritime Antarctic or Arctic regions (Convey 2003; Callaghan *et al.* 2004).

In the Arctic, there are profound and obvious global changes affecting biodiversity, ecosystems and humans at local and regional scales (Walker *et al.* 2001). The Antarctic, in contrast, has no indigenous human population and terrestrial natural resource use has been negligible, as have opportunities to investigate effects of changes on resource distribution and availability. Therefore, it is still unclear whether similar changes occurring to low diversity terrestrial ecosystems such as in the McMurdo Dry Valleys are of consequence, and if they extend to and influence biodiversity and ecosystem functioning and, thus, human well-being, elsewhere (Wall 2004, 2005).

Globally, humans are causing major perturbations and significant shifts in the functioning of ecosystems. For example, there is a rapid acceleration of species extinctions, increased exchange of species, losses of populations of species and multiple changes to global nitrogen, carbon and hydrological cycles (Vitousek *et al.* 1997; Millennium Ecosystem Assessment 2005). A large proportion of the Earth's terrestrial vascular plant and vertebrate species are concentrated in warmer, tropical and temperate ecosystems and have become a priority for conservation, due to the high species richness (number of species), concentration of endemic species and the role of these species in ecosystem functioning (Dobson *et al.* 1997; Reid 1998; Myers *et al.* 2000; Araujo 2002; Brooks *et al.* 2002; Hobohm 2003). Areas of poor plant and animal species diversity, or 'coldspots', have also gained attention as a high priority for conservation because loss of a few species in these ecosystems due to global changes may more quickly result in loss of ecosystem function (Kareiva & Marvier 2003*a*,*b*). Although Antarctica is managed for scientific research (Waterhouse 1997) and could be considered as protected as agreed by nations signing the Antarctic Treaty, it is not isolated from human-related, global changes (land use change, pollution, invasive species and atmospheric change). Local to regional responses that occur in this polar desert may be magnified and have nonlinear feedbacks to the Dry Valleys and other distant ecosystems.

Global changes have tremendous significance for human well-being (Millennium Ecosystem Assessment 2005). People are dependent on benefits, such as clean air, water, fertile soils and nutrient cycles, which are provided by nature's ecosystems. It is now apparent (Millennium Ecosystem Assessment 2005) that the future ability of the Earth's biodiversity and ecosystems to provide these services is endangered. As governments, businesses and the public are making international efforts to address the enormity of these

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problems over the next 20–50 years, it is appropriate for the Antarctic scientific community to assess the state of knowledge of low diversity ecosystems and with data from more diverse systems develop scenarios of how biodiversity and ecosystems may change in the next 50 years. Compilation of information such as species distributions, vulnerabilities and potential global changes, which may shift the functioning of species-poor ecosystems to a new state, is highly relevant and needed for understanding and sustaining more diverse ecosystems and our global environment.

This paper does not attempt to compile information on global changes (Kennedy 1995; Sinclair 2002; Frenot *et al.* 2005), species diversity or distributions and functioning for all terrestrial habitats in Antarctica (but see Chown & Convey 2007). Instead, using one region of low diversity, the McMurdo Dry Valleys, I suggest ways in which biodiversity and ecosystem functioning in above- and below-ground coupled systems may be affected by a few of these global changes and the potential implications for the region. The relatively minimal anthropogenic activity compared with the level seen in complex systems, combined with the low biodiversity and relatively simple terrestrial habitats, helps us understand that disturbances in the Dry Valleys influencing species and ecosystem function can be extrapolated to more complex ecosystems (Freckman & Virginia 1997).

2. THE MCMURDO DRY VALLEY REGION

Known as one of the most extreme environments in the world, the McMurdo Dry Valleys ($76°30'–78°00'$ S, $160°00'–1645°00'$ E) of southern Victoria Land, are the largest (4800 km^2) ice-free region on the Antarctic continent, and are composed of multiple valleys formed by the Transantarctic mountain range near the Ross Sea. They are thought to have the lowest species diversity on Earth (Procter 1984; Adams *et al.* 2006). These valleys vary in size, elevation, geological age and orientation to the polar plateau, all of which contribute to each valley having unique local environments (Moorhead & Priscu 1998; Bockheim 2002). Valleys are typically characterized by a mosaic of glaciers, perennially ice-covered lakes, ephemeral meltstreams and wide expanses of exposed soil underlain with ice and permafrost at 10–50 cm depth (Pastor & Bockheim 1980; Bockheim 1997). Each of these habitats contains viable life, including invertebrates that are capable of surviving severe climatic conditions and returning to activity when liquid water becomes available. For information on species diversity, abundance and role in ecosystem functioning of glaciers see Fountain *et al.* 1998, 1999, 2004*a*,*b*; Porazinska *et al.* 2004; Ebnet *et al.* 2005 and for streams see Utermohl 1958; Broady 1982; Vincent & Howard-Williams 1986; Alger *et al.* 1997; McKnight *et al.* 1998; Barrett *et al.* 2004. A synthesis of lake biodiversity is yet to be compiled (but see Fritsen & Priscu 1999; Priscu *et al.* 1999; Roberts & Laybourn-Parry 1999; Laybourn-Parry & Pearce 2007). For soils, reviews of Victoria Land terrestrial ecosystems include information on the McMurdo Dry Valley biodiversity and distributions (Adams *et al.* 2006), biotic interactions (Hogg *et al.*

2006) and ecosystem functioning (Barrett *et al.* 2006*a*,*b*). The emphasis of this paper will be the large land portion of the McMurdo Dry Valleys, which is heterogeneous: bare ground with sand to soil that can be free of, or patterned with, small pebbles to large-size boulders and intersected by moist to aquatic habitats, such as ponds, snow patches, lake margins and meltstreams.

3. ABOVE- AND BELOW-GROUND INTERACTIONS

To understand how the McMurdo Dry Valley systems may change, consider the linked above- and below-ground subsystem approach (figure 1*a*) employed to examine the regulation and functional significance of biodiversity in all plant-dominated terrestrial ecosystems (Porazinska *et al.* 2003; Wardle *et al.* 2004; Bardgett *et al.* 2005*a*; De Deyn & Van der Putten 2005). A common feature of terrestrial ecosystems with vascular plants is coupled above- and below-ground systems that interact through positive and negative feedbacks to influence and regulate community and ecosystem functioning (Wardle *et al.* 2004; Bardgett *et al.* 2005*a*). Above-ground plant species communities differ in the quantity of biomass and quality—or chemical complexity and structural composition—of the organic matter they produce (Swift *et al.* 1979). As the above-ground plant parts and below-ground roots die, the quantity and quality of the organic matter becomes the basis for the energy and functioning of the below-ground community and contributes to soil habitat heterogeneity.

The below-ground system, in turn, responds by breaking down dead organic matter (Wall *et al.* 2004, 2005), altering plant metabolism, regulating the availability of soil nutrients for plant growth (Hunt *et al.* 1987; Moore *et al.* 2004), affecting plant community composition and, possibly, influencing plant distributions (Van der Putten *et al.* 2001; De Deyn *et al.* 2003; De Deyn & Van der Putten 2005). Soil, climate and the variation in quantity and quality (e.g. C : N and lignin) of organic matter inputs from the plant can drive the species composition of the below-ground community (Swift *et al.* 1979; Wardle 2002; Bardgett *et al.* 2005*b*). In the world's terrestrial soils, for example, the numbers or types of species (or OTUs—operational taxonomic units) may be in the millions of genomes of microbes per 10 g soil (Gans *et al.* 2005) and there may be hundreds of species of microscopic animals, rotifers, tardigrades, nematodes, mites, Collembola, and many species of larger animals such as isopods, millipedes, earthworms, termites and ants (Wardle *et al.* 2004). Each of these has roles in ecosystems (table 1) through their interactions within complex food webs.

There are two soil food webs, root-associated and decomposer, with different functions. Root-associated webs affect plant architecture, metabolism and growth, while decomposer-based webs influence organic matter breakdown, nutrient availability for roots, and soil morphology by modifying soil porosity, soil structure and hydrology (Anderson 1988; Crossley *et al.* 1989; Bardgett *et al.* 2001; Hunt & Wall 2002; Wall 2004). Macroinvertebrates (termites, earthworms, millipedes, etc.) rip and shred complex organic matter. Smaller
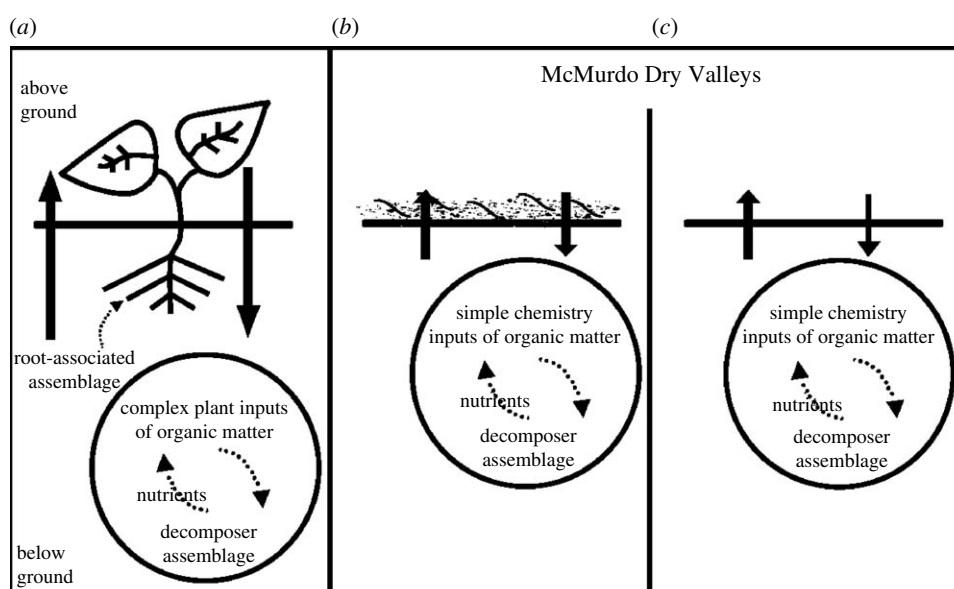
Figure 1. Above-ground and below-ground interactions in (*a*) vascular plant-dominated ecosystems, compared to the terrestrial landscape of the McMurdo Dry Valleys. In the Dry Valleys, the highest productivity and diversity are found in the smallest area of the landscape, (*b*) the algal, moss and cyanobacterial-dominated above- and below-ground systems, and the lowest diversity in the largest area of the landscape (see text), (*c*) the dry soil-dominated ecosystems. Note the vascular plant dominated system (*a*) has greater depth compared with the shallow Dry Valley systems (*b*,*c*). Vertical arrows indicate the feedbacks and contributions to ecosystem processes above and below ground.

Table 1. Examples of some of the taxa below ground, the functional groups within soil food webs and their role in ecosystem processes in plant-dominated ecosystems. (The biodiversity of each functional group regulates or influences various ecosystem processes and thus provides benefits or ecosystem service for human well-being. See Wall (2004) and the Millennium Ecosystem Assessment (2005).)

biodiversity	functional groups	ecosystem processes
vertebrates, invertebrates (oligochaetaes, polychaetaes, crustaceans, molluscs, ants, termites), plant roots	bioturbators, ecosystem engineers	soil alteration, soil structure, organic matter and microbes mixing laterally and vertical depths
plant roots, algae	primary producers	create biomass, stabilize soils and sediments, provide C and N at depth
millipedes, centipedes	shredders	fragment, rip and tear organic matter
bacteria and fungi, Collembola, mites, nematodes, rotifers, tardigrades, protozoa	primary decomposers and secondary decomposers	recycle nutrients, increase nutrient availability for primary production
symbiotic (e.g. *Rhizobium*) and asymbiotic bacteria (e.g. *Cyanobacter*, *Azobacter*)	nitrogen fixers	biologically fix atmospheric N_2
methanogenic bacteria, denitrifying bacteria	trace gas producers	C, N_2, N_2O, CH_4 transfer and denitrification
roots, soil organisms	CO_2 producers	respiration, emission of CO_2

aquatic animal species such as rotifers, tardigrades and nematodes living in water films around soil particles have less obvious but numerous roles in the soil food webs. Two of the five nematode functional groups, fungivores and bacterivores, consume and regulate populations of primary decomposers (bacteria, yeast and fungi) and the release of inorganic nutrients (Ingham *et al.* 1985; Overhoff *et al.* 1993; Hunt & Wall 2002). Species in many functional groups of microarthropods living in air-filled pores in soils also feed on bacteria and fungi, adding to the complexity of the below-ground food web (Stevens & Hogg 2003; St. John *et al.* 2006). At the top of the food webs are predators, represented by species of macro- and microfauna, which feed on smaller invertebrates and protists. The complex interactions within a soil food web are notably confounded by the sheer abundance and types of soil biota (Wall *et al.* 2005).

How might the above- and below-ground inter-dependence in a diverse vegetated system (figure 1*a*) contrast with that of a cold desert ecosystem, such as the McMurdo Dry Valleys where many of these components are absent (figure 1*b*,*c*)? Major differences between these linked subsystems include:

(i) the primary producer phototrophs are cyanobacteria, eukaryotic algae, mosses or lichens, not communities of vascular plants,

(ii) the Dry Valley system is horizontal and microbial, with nearly microscopic to invisible surface 'plant-autotroph' cover, no roots and only microscopic biota (figure 1*b*,*c*) compared with the vertical plant system (figure 1*a*) where plant cover extends upwards and roots penetrate

to depths transporting large amounts of carbon and nutrients below ground,

(iii) the quality of organic inputs to the soil from surface algae is higher (greater C : N ratio) and has less variation in chemical composition than in vascular plant systems, and

(iv) the below-ground assemblage is depauperate in functional groups and diversity compared to vascular, plant-dominated systems (figure 1c).

Therefore, the analogue for a coupled above- and below-ground system in the Dry Valleys has to be adjusted because the components interact at a different resolution than in vascular, plant-dominated ecosystems.

In the McMurdo Dry Valley landscapes, there are two basic types of habitats for above- and below-ground biotic interactions: algal and moss diverse habitats (figure 1b) located in moist to wet soils that are analogues to plant-dominated ecosystems; or less diverse, very dry soil habitats (figure 1c). Across the Dry Valleys, gradients of above- and below-ground coupling occur where the above-ground component disappears as distance increases from the algal and moss–below-ground coupled habitats (figure 1b) to drier soils of only a below-ground dominated subsystem (figure 1c). The surface soil area in both types of habitats is thus a critical zone in the Dry Valleys and sensitive to disturbance. Biotic populations that establish in suitable above- and below-ground linked habitats (higher soil moisture and carbon and lower salinity) would have more diversity and stable populations compared with inhospitable habitats (desiccated, lower carbon and higher salinity soils) with no mesofauna or only a single invertebrate taxa (Schwarz *et al.* 1992, 1993; Powers *et al.* 1995, 1998; Virginia & Wall 1999; Courtright *et al.* 2001).

Across the Dry Valleys, the landscape shows little visible evidence of any above-ground primary producers. Knowledge of the distribution of phototrophs (cyanobacteria) and estimates of primary production in soils remains undetermined. However, within valleys in depressions where snow collects, edges of melt pools associated with glaciers, or stream channels formed over years from periodic melting of glaciers during the summer, there are visible mosses, algae and mats of cyanobacteria (figures 1b and 2; Gooseff *et al.* 2003). These are typically the areas of greatest diversity and functioning above the surface in the Dry Valleys and represent the highest complexity among terrestrial ecosystems in the region. Although this vegetation is technically considered aquatic and above sediment, not soil, it is most closely related to the above-ground component of vascular plant ecosystems.

Species richness (number of species) of the algal above-ground component in streambeds is higher than might be expected: the Dry Valleys have about 80 algal species, with 50 confirmed species of freshwater diatoms, many of which are endemic (Alger *et al.* 1997; Esposito *et al.* 2006). Distribution of species varies depending on the composition of the streambed and velocity of stream flow with some species submerged only a few hours a day and others for longer periods in faster-flowing channels. These surface microbial mats form a diverse assemblage of
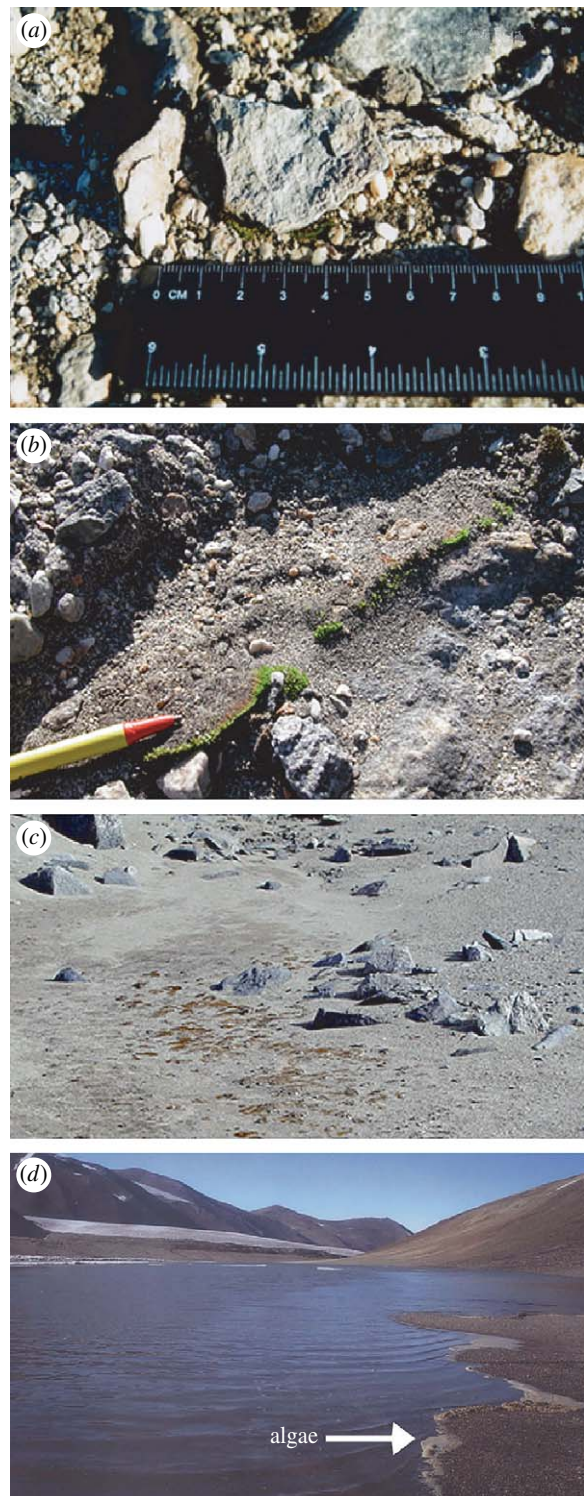
Figure 2. The Dry Valley above-ground surface (*a*–*d*) at small-to-landscape scales: (*a*) surface pavement of rocks and pebbles, (*b*) visible green algae amidst a larger, drier surface, (*c*) patchy clumps of algae occurring in moist areas near rocks and (*d*) landscape of soils, glacier and lake with lake algae that can be blown to soil surfaces. (Photos courtesy of D. W. Hopkins.)

species that contribute a narrow range of chemical quality as below-ground inputs to the sediments (figure 2c,d; Esposito *et al.* 2006). Organic compounds comprising mostly of simple mucopolysaccharides or slime and silica are degraded in soils to carbon and inorganic nutrients primarily by bacterial-dominated pathways. The cyanobacterial and algal mat biomass
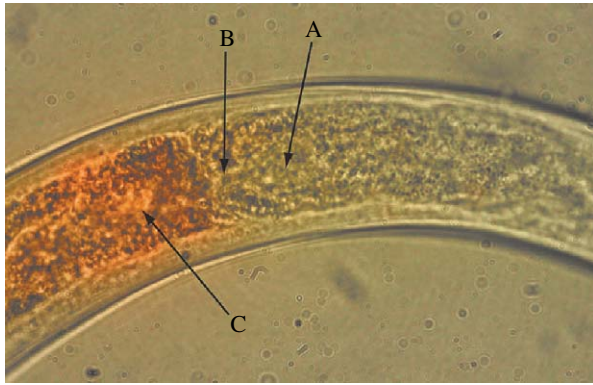
Figure 3. Picture of the nematode *Eudorylaimus* spp. depicting algal ingestion. Image is a composite of two separate images generated by transmitted white light microscopy, and fluorescence microscopy. An acridine orange filter was used to observe refraction by chloroplasts, which appear at the base of the oesophagus as a red mass ($100\times$, oil immersion). (Photo courtesy of Byron Adams.)

C : N ratios are consistently near the Redfield ratio of 6 : 1 (Barrett *et al.* 2007) compared to a wide C : N range of 12 : 100 for vascular plants (Hunt *et al.* 1999).

Intermingled and beneath the phototrophs, the sediments can have a complex assemblage of Collembola, mites, nematodes, tardigrades, rotifers, protozoa and microbes. The majority of these taxonomic groups can live in moist soils and sediments without visible algae, lending support to the linkage between sediments and soils across this landscape (Wall 2004). For example, Collembola are patchily distributed in moist soil areas under rocks to several centimetres depth, and can be dispersed in moving water sweeping across dry stream-beds although they are not aquatic inhabitants (Stevens & Hogg 2003). The species of nematodes found in these productive moist areas are consumers (*Plectus* spp.) of bacteria, or as recently seen for *Eudorylaimus* (figure 3), consumers of algae (B. J. Adams & D. H. Wall 2004, unpublished data; Treonis *et al.* 1999; Gooseff *et al.* 2003). Many *Eudorylaimus* spp. in other ecosystems are predators of small invertebrates, but this has not been documented in the Dry Valley soils. The level of feeding specificity by invertebrates has not been determined for the Dry Valley invertebrates, but data on mouthparts, gut contents and diets indicate tardigrades and rotifers graze on algae and bacteria, Collembola are fungal and algal feeders (Davidson & Broady 1996) and mites are fungal feeders (Stevens & Hogg 2003; Joaquim-Justo *et al.* 2004; Hogg *et al.* 2006). Compared with the wide variety of functional groups in plant-dominated ecosystems (figure 1*a*), the functional groups in the two types of Dry Valley habitats (figure 1*b,c*) are remarkably few compared with temperate ecosystems, consisting of microbial consumers (fungivores, bacterial feeders, omnivores or microbial feeders) and 'herbivores' or algal feeders. Predation is apparently absent or unobserved for species of mites, nematodes or tardigrades (Freckman & Virginia 1998; Adams *et al.* 2006; Hogg *et al.* 2006). The predatory tardigrade, *Macrobiotus*, observed elsewhere in Antarctica (Convey & McInnes 2005) has not been found in the Dry Valley soil samples.

The biotic contribution to the functioning of this above- and below-ground subsystem is activated in the austral summer when increased temperatures melt ice and affect soil relative humidity. The limiting factor for activity and production of cyanobacteria and algae in streams and lake margins is this brief pulse of liquid water (McKnight *et al.* 1998). When there is no available moisture, algae and mosses desiccate. The invertebrates have survival strategies that enable them to respond quickly to changes in the environment (temperature, moisture and corresponding changes in soil chemistry) even during Antarctic summers, by ceasing feeding, movement and metabolism until, as with algae and mosses, they are reactivated by liquid water (McKnight *et al.* 1998; Treonis & Wall 2005). When desiccated or frozen, cyanobacteria, algal mats, invertebrates and microbes are windblown, and thus are important sources of organic matter and biotic inocula for dry soils across the region (Gressitt *et al.* 1960; Nkem *et al.* 2006).

Extending from obvious aquatic areas of ponds, streams and lakes, the landscape has large areas of barren, dry soils mostly formed into polygons (Pastor & Bockheim 1980; Virginia & Wall 1999; Bockheim 2002; Barrett *et al.* 2004). In Taylor Valley, the site of the US National Science Foundation McMurdo Long Term Ecological Research, arid soil occupies > 95% of ice-free areas (105 km^2) below 1000 m, compared with streams (0.2 km^2) where productive cyanobacteria and algae (figure 1*b*) communities occur, and ice-covered lakes (4.7 km^2; Virginia & Wall 1999; Burkins *et al.* 2001). Factors such as elevation, high salinity, low carbon (0.01–0.5 mg C g soil^{-1}; Burkins *et al.* 2001) and moisture, limit life above and below the soil surface (figure 1*c*), resulting in biotic communities that are heterogeneously distributed across the valley. This vast area represents a unique extreme for the world: no apparent above-ground component coupled with the active below-ground.

Biotic carbon, primary productivity for the Dry Valleys, is supplied to soils primarily by above-surface algae and cyanobacteria. Carbon inputs include 'invisible soil algae' or cyanobacteria and algae, which are sparse on soil surfaces, windblown cyanobacterial and algal mats from streams, ponds and lakes (Eberling *et al.* 2006; Hopkins *et al.* 2006), cyptoendolithic rocks, marine inputs, and algae or mosses beneath quartzite rocks (Friedmann 1982; Wynn-Williams 1990; Burkins *et al.* 2001; Moorhead *et al.* 2003; Barrett *et al.* 2006*a,b*; Eberling *et al.* 2006; Hopkins *et al.* 2006). The below-ground system also contributes legacy carbon that has been stored during previous geological periods (Burkins *et al.* 2000; Barrett *et al.* 2006*a,b*). Legacy carbon is an important source of organic matter for drier soils over the long term, because there are no vascular plants above-ground contributing to the accumulation of below-ground storage of organic C (figure 1*a*), and above-ground algal subsidies are reduced and supplied on a short-term annual basis (Powers *et al.* 1995, 1998; Virginia & Wall 1999; Courtright *et al.* 2001). The persistence of this C pool in soils is a function of the original amount and turnover rates.

In contrast to the few algal and moss-dominated moist soils and streams where invertebrates live intertwined above and below ground (figure 1*b*), the
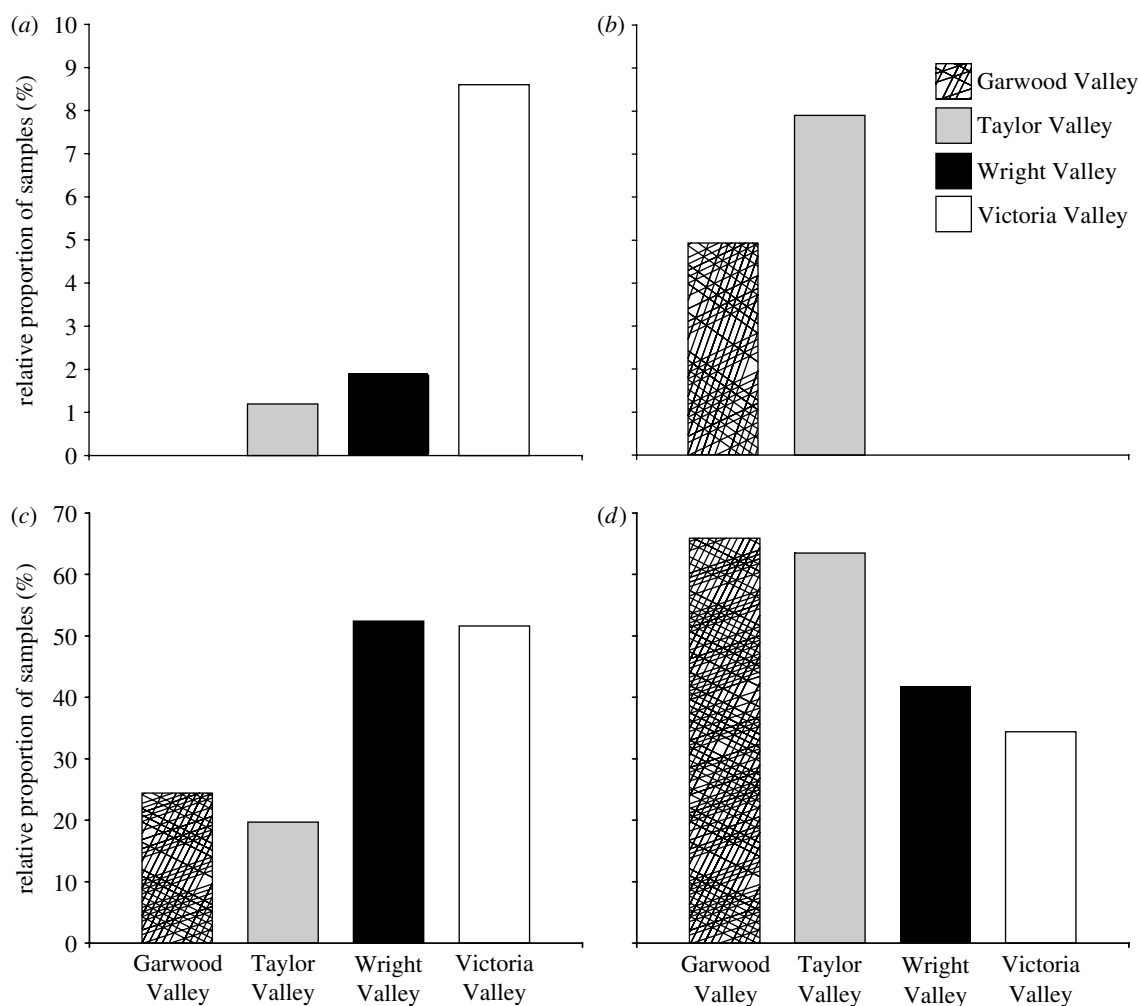
Figure 4. Relative proportion (%) of soil samples collected from four McMurdo Dry Valleys, Garwood Valley ($n=41$), Taylor Valley ($n=178$), Wright Valley ($n=103$) and Victoria Valley ($n=93$), which contained 0–3 invertebrate phyla: (a) rotifers and tardigrades, (b) three-taxa communities, (c) soils without invertebrates and (d) nematodes only. Other two-taxa communities represented less than 8% of all samples in all valleys and are not shown. Note the difference in scale on the y-axes.

arid soils (figure 1c) have no above-surface animals. However, data collected in the past 15 years show that vast areas of these dry soils once considered nearly sterile have a surprising biotic diversity. The richness (number of species) of the dry below-ground system (figure 1c) is still unknown, but can range from 1 to 10 metazoan taxa for the Dry Valleys (Adams *et al.* 2006). This is an order of magnitude less than the hundreds of invertebrates in temperate soil (Wardle 2002), although a coordinated taxonomic analysis (combining molecular and classical morphological techniques) of the Dry Valley soils would most probably discover additional species. While molecular techniques are crucial to delineating species of mites, Collembola and other invertebrates (Adams *et al.* 2006), ecological investigations are also important to assure that the species exist as active inhabitants of communities.

The distribution of mesofauna is more heterogeneous across the Dry Valley landscape than that in other ecosystems (Freckman & Virginia 1998; Virginia & Wall 1999; Barrett *et al.* 2004). For example, Beacon Valley has a high elevation, high soil salinity and no invertebrate soil species. Across the four other valleys sampled (figure 4; 415 soil samples), less than 5% of the samples had all three (rotifers, tardigrades and

nematodes) groups of invertebrates represented (Freckman & Virginia 1998). A high percentage (approx. 35%) of these soils had no invertebrates (figure 4a–d) attesting to how geology, habitat, climate and dispersal dynamics all contribute to assembly of species communities. Of the 60% of Dry Valley soils with invertebrates, the most inhabitable valleys appeared to be Wright and Victoria (figure 4b–d). Taylor Valley had a higher proportion of three-invertebrate communities (figure 4b), and nematodes occurred in a higher proportion of soils in the Taylor and Garwood Valleys (figure 4d). Peak densities of nematodes (4000 kg dry soil^{-1}) were comparable to plant-dominated hot desert soils (Freckman & Mankau 1986). Nematode species distributions in drier soils are limited by salinity, carbon and moisture, with the abundance and biomass of one species, *Scottnema lindsayae*, dominating the drier, salty soils (Freckman & Virginia 1997; Courtright *et al.* 2001). Soil protozoa, as measured by culture techniques, can occur in soils with or without nematodes (Bamforth *et al.* 2005).

Much less is known about microbial diversity and distribution, but as with recent studies of all ecosystems, molecular evidence is revealing greater diversity. In the Dry Valleys, yeasts are more widely distributed

(Connell *et al.* 2006) and diverse than that previously thought (Atlas *et al.* 1978). Cowan *et al.* (2002), using luminometry to estimate ATP levels, also concluded that the richness of bacterial taxa in Taylor Valley soils is higher than that previously believed. An unexpectedly high diversity in soils of Arctic tundra compared with boreal forests was recently noted, but whether species are transient and/or inactive remains to be resolved (Cowan *et al.* 2002; Neufeld & Mohn 2005).

4. THE FUNCTIONING OF LOW DIVERSITY SYSTEMS

The relationship of below-ground biodiversity (species richness) to an ecosystem function such as primary production or decomposition is still ambiguous for high diversity terrestrial ecosystems (Loreau & Thébault 2005; Setälä 2005). This is partially because designing realistic experiments to include the numbers of invertebrates and microbes in soil assemblages becomes complex and the role of each species in an ecosystem process is seldom known (see Mikola *et al.* 2002 for review). A consensus arising from the results of laboratory microcosm experiments (Liiri *et al.* 2002; Setälä 2002), in which invertebrate species richness was related to an ecosystem process, decomposition, is that in high diversity, complex systems, functional diversity is more important than increased numbers of species (Heemsbergen *et al.* 2004; Roscher *et al.* 2004). The number of species appears more critical to ecosystem functioning in low diversity (1–10 species) systems, because if disturbed, there is less redundancy, i.e. fewer 'back-up' species to take on lost functional roles. In other words, if the amount of primary productivity and physico-chemical environment were held constant in all ecosystems, fewer species would be responsible for a greater amount of a particular ecosystem function in low diversity systems. This suggests that the few species involved in ecosystem functioning in the McMurdo Dry Valley ecosystems are crucial and may play a larger proportional role than that previously thought (Barrett *et al.* 2006b). In turn, they and related ecosystem processes may be more vulnerable to global changes than those in high diversity, more complex ecosystems.

5. IMPLICATIONS OF GLOBAL CHANGES ON COUPLED ABOVE- AND BELOW-GROUND SUBSYSTEMS

What are tipping points (Kemp 2005; Schellnhuber *et al.* 2006; http://kron1.eng.ox.ac.uk/climate/) or disturbances that might take this low diversity region to a different equilibrium state? Schellnhuber *et al.* in a workshop, which identified regions where the balance of a system has reached the critical point due to climate change, defined a tipping point as a point at which potentially irreversible change is about to occur, or is already occurring. The tipping point for the Dry Valley region may be climatic but could also include other significant human-induced changes that feedback to climate. Global changes that directly impact ecosystem processes and services in plant-dominated systems, such as land use change, increased urbanization, slash

and burn of tropical forests or inputs of agricultural chemicals, become indirect drivers affecting climatic, atmospheric and hydrological cycles elsewhere, including the Dry Valleys, and might be potential tipping points. Direct human impacts on the Dry Valleys, which could be candidates for tipping points, might be invasive species, pollution and/or human trampling.

Jiang & Morin (2004) noted from laboratory experiments that climate change effects on species interactions within complex communities would be extremely difficult to predict. This suggests that it may be easier to forecast change in simple, low diversity communities. The questions are as follows: do we presently understand the role of species in these low diversity systems and the pattern of their responses to disturbance? Can observations of simple community-level responses to perturbations be used as a basis for extrapolating how species, processes and ecosystems may respond to more realistic multiple, rather than single, global changes in the future? Here, I use the 'press' and 'pulse' concepts of Bender *et al.* (1984) to frame disturbances that may alter responses of the species in above- and below-ground subsystems in the Dry Valleys. When an ecosystem is disturbed, it may respond by altering species composition and then return to its previous equilibrium. In this case, the system has been simply 'pulsed'. Or, it may respond by being 'pressed' to a new equilibrium state due to sustained alteration to species composition or extinction of species. A pulse disturbance will alter the system perhaps notably within the boundaries of a stable ecosystem, but a press will be a type of change that brings the Dry Valleys to a tipping point (Kemp 2005) resulting in a new organization of species and a potentially irreversible change and new state for the ecosystem (figure 4). The disturbances discussed below are examples of global changes (climatic or land use) that may have direct and measurable impacts on the above- and below-ground coupling at local and regional scales, and perhaps become tipping points for the Dry Valleys over the next 50 years. While increased atmospheric CO_2 concentration will certainly have an effect on biological communities, this has not been explicitly examined for the Antarctic Dry Valley terrestrial biota and is not discussed here (see Chown & Convey 2007 for a discussion of changes in maritime Antarctica).

(a) *Temperature change: warming*

The effect of a temperature increase in Antarctica during the austral summer would be more liquid water (Kennedy 1993), but these differences would vary across local, landscape and regional scales. In the Dry Valleys, for example, liquid water is mostly unavailable to biota. Fifty per cent of the arid soils are underlain with subsurface ice, either ice-cemented soil, or large, massive ice (Bockheim 2002). Because of low precipitation and air temperatures, snow sublimates and only a small amount melts (Gooseff *et al.* 2003). This moisture moves as a vapour, with limited migration of melt water from snow (Campbell & Claridge 1982). Most biological activity appears to occur in thin water films (Kennedy 1993; Treonis *et al.* 2000). The liquid water might be localized such as run-off from a
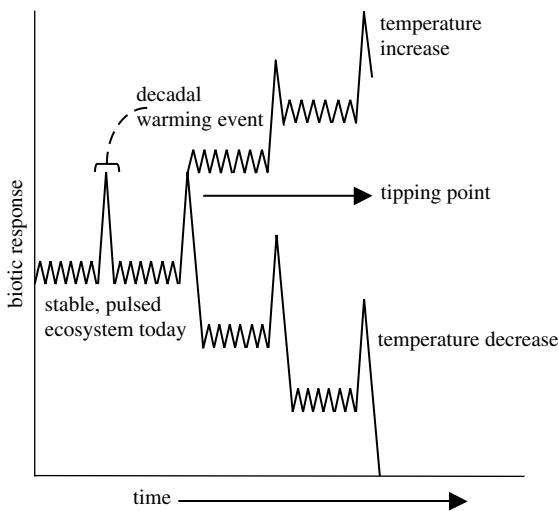
Figure 5. Conceptual figure of the response of terrestrial biota to alterations to climate over time. Biotic individual species and populations respond differently from year to year and with some large events such as a decadal warming event, but rebound to their previous stable, ecosystem state. When a tipping point occurs (see text), communities may reorganize, causing changes in ecosystem properties and rates, and move to a new ecosystem state with unknown effects within a region or globally.

north-facing glacier, melt of a shallow frozen melt pond, or non-uniform, patchy melt seen in normally dry soils due to variations in depth of permafrost.

At regional scales, evidence accumulating from lake levels in Wright and Taylor Valleys (Taylor Valley's record began with R. F. Scott in 1903), with models (Bomblies *et al.* 2001; Ebnet *et al.* 2005) and more recent temperature and Onyx River flow data from New Zealand and US scientists, suggests that decadal events of warming have occurred in the past 100 years, even though overall, the Dry Valley region is cooling (Doran *et al.* 2002; Lyons *et al.* 2005). Decadal warming would be considered a pulse disturbance (figure 5) and an example of a stable, resilient system that oscillates back and forth in response to a periodic temperature event. Species diversity is not altered significantly and species are not lost, because the system rebounds to the dynamics of the previous condition. Experience gained from observations in Taylor Valley in the 2001–2002 austral summer on the pulse effects of the warmest temperature since continuous records were maintained, provides a case study for projecting how the two types of above- and below-ground ecosystems (figure 1b,c) may respond in the future if pressed to a new equilibrium state (figure 5).

In Taylor Valley, the Lake Bonney weather station recorded an average air temperature increase from −3.9°C in the previous year to a very warm −1.7°C. The temperature increase and corresponding hydrological melt response (glaciers, frozen lake ice, permafrost, snowmelt, etc.) altered the dry appearance of the soils to a wet surface flow and puddles of water in areas across the landscape. As would be expected in the annual ephemeral melt ponds and streams (algal and cyanobacterial-dominated systems, figure 1b), the response was more liquid water: increased glacial run-off; wider streambeds; more rapid stream flow; and greater water volume. For the stream phototrophs, this

translated to altered species composition, and decreases in abundance and biomass due to water volume and scouring (Alger *et al.* 1997). The above-ground response to increased temperature and moisture would potentially produce a different quantity of organic matter below-ground to the soil–sediment biota and, in turn, perhaps alter composition of the microbes and invertebrate consumers and the bacterial or fungal (or physical) pathway of decomposition. For example, an increase in the proportion of biomass of diatoms in streams might change the percentage of silica. Modification in the uptake of dissolved silica and transformation into biogenic silica during diatom blooms in rivers could occur, as noted by Conley (1997). In other more vegetated ecosystems, the composition of the below-ground food web shifts to a bacterial pathway when the source of organic matter is more labile, and to a fungal-dominated food web when the organic matter is more complex and recalcitrant. Invertebrates and microbes respond by increasing their populations and altering the rate of nutrient turnover.

Surprisingly, in previously unwetted areas of the below-ground dominated (figure 1c) Taylor Valley landscape, two unusual but distinct features appeared in response to increased temperature: subsurface seeps of flowing water of unknown origin, which surfaced and spread much like a stream over areas of dried soil, and small circular patches that were wetted possibly due to snow or permafrost melt. Flows from a seep near Lake Bonney, which surfaced in Taylor Valley, differed considerably in geochemistry from nearby ephemeral annual streams during that year (Harris *et al.* 2007). Lyons *et al.* (2005) discovered a seep flow surfacing in soils near Lake Bonny that originated from a nearby snow plateau. They suggested that the seep flows dissolved and transported soluble salts in the soils, thereby making the soils a more suitable habitat for biota (Lyons *et al.* 2005). Across the Taylor Valley landscape, the many wet patches from seeps and melting permafrost showed an instantaneous above-ground response to moisture, but a delayed, 'uncoupled' below-ground response. The presence of algae, mosses and lichens in the wetted areas became a thin visible light green layer of contrast against the drier surrounding soil, but the below-ground response of invertebrates was inconspicuous and lagged by a year. In the following 2002–2003 season, when air temperatures and soil temperatures returned to colder, drier, unwetted norm for Taylor Valley, nematode assemblages located the prior year in wet areas had altered composition: *Eudorylaimus*, the rarer species in dry soils in previous cold years, and limited by water and carbon, increased; while *Scottnema*, the species widespread in drier, saltier soils, declined. Long life cycles (approx. 218 days at 10°C) have been shown for *Scottnema* in laboratory conditions (Overhoff *et al.* 1993), suggesting delayed and prolonged responses to environmental changes that affect life-history traits or distribution ecology.

Based on this case study of a short-term (2 years) response to a decadal warming event, how might a climate change of increased temperatures in the next 50 years impact above- and below-ground biodiversity and functioning and tip the ecosystem to a new equilibrium state? Convey *et al.* (2003) suggested that warming

might lead to increased desiccation stress, while Harris *et al.* (2007) suggested that warming soils approximately 1°C would be sufficient to increase the thaw depth and result in permafrost melt as well as alter changes in geochemistry of the Dry Valley lakes and soils. If the frequency of decadal warming events increased over the next 50 years, reversing the current cooling trend, or if there was a smaller average temperature increase, this would possibly enlarge and meld the wetted areas (seeps and patches) and in effect be a tipping point (figure 5) moving this desert to a more homogeneous landscape with less patchiness, similar to warmer, moister ecosystems. More numerous suitable habitats for algal and moss-dominated systems would increase the sources of biota, which are dispersed by water and wind across the region and improve the chances that communities would establish. Increased variety and biomass of carbon inputs above (algal and moss production) and below ground (dead organic matter and invertebrates) would affect species diversity and feedbacks above and below ground. Soil assemblages would homogenize, reducing the number of areas that were once single-taxa communities, and change species composition through competition, parasitism, etc. Species distributions would contract or expand depending on habitat suitability and population and community dynamics. Collembolan, mites, tardigrades, rotifers, and the nematodes *Eudorylaimus* and *Plectus*, which favour moist soils, would expand their distribution. *Scottnema*, presently the nematode species with the greatest biomass and density and distribution across the McMurdo Dry Valleys, would become more restricted and a rare, less abundant species in wetter soils. With fewer, less abundant populations as a source to be distributed by wind, and possibly because *Scottnema* evolved slowly over time, a sudden or greater intensity of disturbance might switch this more stable, dominant animal population to a new equilibrium. Invasive species could possibly have a greater competitive advantage over the many endemic species from the valleys following perturbations (Adams *et al.* 2006; Hogg *et al.* 2006). The temporal lag below ground in response to above-ground algal and moss production noted in Taylor Valley might be shortened with long-term or more frequent decadal warming, altering the rates of decomposition and primary production.

Thus, the potential impact of temperature warming could dramatically change the Dry Valley landscape and press the system beyond the present decadal-pulsed (figure 5) and heterogeneous landscape (figure 1*b,c*) towards a wet algal and moss-dominated system and a homogeneous landscape (figure 1*b*). The fundamental properties, interactions of species, e.g. mutualism, parasitism and symbioses, and population processes, which are typical of all ecosystems, will become a characteristic of the biotic dynamics in the Dry Valleys.

(b) *Temperature change: cooling*

Continental climate trends remain the subject of much study, but data showing the Dry Valley region of Antarctica have demonstrated a cooling trend over the past 15–20 years is incontrovertible (Comiso 2000; Doran *et al.* 2002; Kwok & Comiso 2002; Thompson &

Solomon 2002; Walsh *et al.* 2002; Vaughan *et al.* 2003; Bertler *et al.* 2004; Shindell & Schmidt 2004). The effects of cooling on biodiversity and ecosystem functioning on below-ground dominated systems (figure 1*c*) appear to have driven the system to a different state of declining soil moistures, decreasing population sizes of nematodes, decline in relative abundance of *Plectus* and *Eudorylaimus* and changes in species assemblages. What might be the effect of continued cooling in this region in the next 50 years?

A major result of continued decreasing temperatures in the Dry Valleys would be a press disturbance resulting in a shift to fewer moist, highly productive, coupled systems and increased drier below-ground systems (figure 1*c*). The present arid-dominated landscape would expand in area because the frequency of wetted patches and number of annual ephemeral streams would be reduced. The quantity of biotic inocula dispersed from the reduced algal and moss-dominated systems across the dry landscape would be constrained, even during decadal warming events. The scarcity or loss of wet soil patches and species (tardigrades, rotifers, mites, Collembola and some nematode species) would drive the above- and below-ground system into lower diversity below ground and potentially affect rates or losses of ecosystem functions. The cooling would keep soil water frozen and biota potentially in a survival state uncoupled from ecosystem processes for a longer period of time, thus altering rates of functioning.

Climate changes will drive the low diversity systems to a new ecosystem state. How the mechanisms of species interactions will operate, and over what time period, are subjects for modelling and a terrestrial above- and below-ground assessment of this region.

(c) *UV radiation*

Antarctic communities may experience alterations in the surface conditions of temperature, moisture and ultraviolet (UV) radiation caused by humans and changes in atmospheric chemistry (Antarctic ozone hole; Farman *et al.* 1985; Solomon *et al.* 2005). Concerns have mounted about the deleterious effects of increased UV-B (280–320 nm) and UV-A (320–400 nm) radiation reaching the surface of Antarctic ecosystems (Solomon 1990; Weiler & Penhale 1994; Callaghan *et al.* 2004). Thirty years of ozone depletion has occurred (Farman *et al.* 1985; Solomon 1990; Solomon *et al.* 2005) and communities may already be undergoing adaptation, species selection and changes in species assemblages, communities and distribution with effects on ecosystem function. For the Antarctic terrestrial communities, a significant change associated with the ozone hole is not in the magnitude of UV-B exposure, but in the timing of the exposure in early spring when organisms may be in a physiologically inactive state and unaccustomed to these levels. UV-B levels at the Antarctic soil surface in spring if there is snow cover may be similar to those normally received in mid-summer at the same locations (Cockell & Córdoba-Jabonero 2004). The UV-B effects considered most harmful to life include mutagenic interactions with DNA and RNA and absorption by proteins, and damage to membranes and pigments with negative

effects on photosynthesis and primary productivity (Karentz 1994).

Wynn-Williams (1994) suggested that UV-B levels in Antarctica are deleterious to terrestrial surface cyanobacteria and the below-ground short food chains (Freckman & Virginia 1997) they support. Organisms most susceptible to UV-B damage will either be at or near the surface of soils and waters, or as they are dispersed by wind. Thus, UV-B exposure may alter the ability of both above-ground and below-ground organisms to successfully disperse and colonize new soil habitats (Wynn-Williams 1994). UV effects on Antarctic communities have been studied primarily in aquatic systems (Neale *et al.* 1994; Vincent & Quesada 1994) and in maritime terrestrial systems (Convey 2003; Newsham 2003; Frenot *et al.* 2005; Newsham *et al.* 2005). In Victoria Land, UV resistance has been shown in mosses (Green *et al.* 2005) and Tosi *et al.* (2005) found UV radiation-limited soil fungal assemblages and diversity.

The response of soil communities to UV-B is poorly studied in the Dry Valleys. In cryptoendolithic sandstone, UV radiation apparently attenuates and biota living in the rocks are relatively protected (Nienow *et al.* 1988; Onofri *et al.* 2004). In Antarctic regions that are warming, Cockell & Córdoba-Jabonero (2004) found that a thin layer of snow can protect underlying terrestrial communities from UV radiation and suggested that in regions that are cooling, such as the Dry Valleys, snow covers would be prolonged and provide protection. While this scenario is possible, it is also likely that in the future, the high rates of sublimation and strong katabatic winds that have been occurring with cooling in recent years, would continue to reduce available snow cover in early spring and leave terrestrial communities exposed to UV. At present, there is insufficient research on the response of terrestrial soil and sediment species in the Dry Valleys to UV radiation.

(d) *Direct human influence: trampling*

Effects of human trampling on biodiversity as a type of land use change have been examined primarily in forests and recreational areas (figure 1*a*) in order to provide information on recovery and restoration. Much of this research shows that plant sensitivity to trampling is dependent on the species (Cole & Schreiner 1981; Kuss & Hall 1991), with some plant communities experiencing reductions in vegetation height, cover and species richness, and others increasing species diversity (Grime 1979). Effects of trampling on plants were similarly noted above ground in the Antarctic on Marion Island (Gremmen *et al.* 2003) and Macquaire Island (Scott & Kirkpatrick 1994). Studies below ground in both temperate and Antarctic environments have addressed soil physical properties and showed trampling increased soil temperatures, compaction and decreased soil porosity and moisture (Kobayashi *et al.* 1997; Campbell *et al.* 1998). In alpine habitats, soil moisture levels were instrumental in plant resilience (Bell & Bliss 1973; Holmes & Dobson 1976). In other habitats, compaction increased over five years of trampling, changes in bulk density and compaction influenced seedling establishment and recovery (Sun &

Liddle 1993), and changes noted in soil organic matter from trampling varied with habitat and vegetation (see Young & Gilmore 1976 and reviewed in Sun & Liddle 1993). This and other research on humans walking on soils illustrate that ecosystems sustaining damage above ground, also exhibit impacts below ground which, in turn, feedback to ecosystem recovery and restoration.

In contrast to these more complex ecosystems of high diversity, the terrestrial Dry Valley ecosystem has large areas that are characterized as essentially barren, absence of any protective vegetation except in algal and moss above- and below-ground systems. Campbell *et al.* (1998) presented data on three categories of human activities that impacted Antarctic Victoria Land soils: major disturbance (land surface change— Earth moving equipment, buildings, helicopter pads and re-contouring of land); moderate disturbance (camping, soil sampling and vehicles); and low disturbance (walking). Major disturbances were shown to have significant impacts on permafrost, soil physical properties and algal and moss-dominated communities, with some recovery of soil algae depending on the soil type (Balks *et al.* 1995; Campbell *et al.* 1998). Moderate impacts such as removal of small cobble size stones, and tents left impressions that remained for years. Even minor impacts of a few footsteps can be seen years later, although on covered stony surfaces, footprints are less visible. The scientific community has been proactive in addressing mechanisms to reduce impacts of trampling and other human activities on the Dry Valleys such as the use of paths, but consequences on the interdependence of biodiversity and functioning of the terrestrial ecosystem as a result of trampling and other activities are as yet unknown.

With the growth of human presence, including tourists, in the Dry Valleys since the R. F. Scott expedition into Taylor Valley in 1903, and relative growth in appreciation for the environment and biodiversity (Adams *et al.* 2006; Barrett *et al.* 2006*a*,*b*; Hopkins *et al.* 2006), the cumulative effects of human trampling on the interactions of the coupled above-ground and subsurface system must be considered as a significant press disturbance (not a pulse disturbance) that potentially will have a long-term effect. What changes to biodiversity and ecosystem functioning might result from this press disturbance of direct human impact on soils?

Above-ground algal-dominated systems associated with streams, ponds and moist soil areas might be altered in species composition and biomass due to changed soil and sediment physical and structural morphology. At the local level, walking could dislodge soil particles and pebbles and rocks that protect the soil interface. This could increase the potential for erosion, exposing deeper soil, changing soil temperatures, moistures and freeze–thaw patterns, and effectively modify the habitat for biota. This may fracture any microscopic biotic connections above and below ground affecting primary production, and potentially affect the return of biotic carbon inputs to soil organisms, as well as soil respiration, decomposition rates and availability of nutrients for above-ground algal and

moss communities. Deeper below-surface, compression and compaction in streams and soils could further convert soil habitat and hydrology. As soil and sediment habitats are modified, species abundance, survival and competition for resources could occur, transforming species assemblages. J. N. Nkem *et al.* (2005, unpublished data) conducted a long-term biodiversity study (1994–2004) on the cumulative effects of trampling in an arid below-ground dominated system (figure 1*c*) in Taylor Valley and documented a severe decline in the abundance of two nematode species, particularly in highly disturbed surface (0–2.5 cm depth) soils compared with controls. This and other work (Campbell *et al.* 1998) suggest that paths reduce disturbance to the rest of the landscape.

These local changes may be magnified at regional scales. Over time, local scale reduction in both abundance and types of biota and suitable habitats could affect the quality of sources for species dispersal and the ability of species to establish across the landscape. Based on data from plant-dominated ecosystems, the cumulative result might be reduced biodiversity, changes in community composition and alterations in rates of ecosystem processes. Whether this effect would be minor or major compared to regional climatic and physical controls on biodiversity and ecosystem functioning is unknown. However, for this low diversity system, increased human presence and the expansion of trampling, like temperature change, over several years, may be a tipping point that would significantly drive the Dry Valleys into a different state of functioning.

6. CONCLUDING REMARKS

There is sufficient evidence that the unusually low biotic diversity and low functional redundancy of the tightly coupled above-ground–below-ground Dry Valley system is both essential to ecosystem functioning and vulnerable to perturbations. Because the few faunal species are below ground and their response to global changes may operate at a different temporal scale than above-ground species, there is some uncertainty as to the detailed implications for the overall functioning of the Dry Valleys. In addition, climate change and land use changes (invasive species, pollution and human trampling) are occurring as multiple, cumulative interactions, not isolated events.

On other continents with plant-dominated systems, developing global change scenarios of how ecosystems may be tipped to a new state in the future is often complicated by responses and feedbacks from the higher biodiversity and number of colossal interactions. The above- and below-ground dependency is often overlooked, but in the Dry Valley region, developing predictions for responses of the whole system (biodiversity and ecosystem functioning) to single and multiple global changes for the next 50 years could be more easily accomplished. A short-term, field experiment as part of a polar network could be used to compare the reaction of soil biodiversity and ecosystem processes to increased temperature and UV across Antarctica regions. A scientific assessment of the geographic distribution of the few animal and 'plant'

(phototrophs—cyanobacteria, algae, mosses and lichens) species present in the Dry Valleys, would be high priority as a baseline for noting future change.

Learning how the tightly linked, above- and below-ground species will cope under increasing global changes has value beyond the Antarctic. Because the Dry Valley biota are interlinked northwards to coastal Victoria Land, further inland to the ice-free areas of the terrestrial Antarctic interior and to surrounding marine systems, global changes affecting species in the Dry Valley food webs could have profound feedbacks beyond this most extreme ecosystem on Earth. Similarly, changes occurring elsewhere in the continent will influence the Dry Valley biota. Climate warming, for example in the interior, may increase ice-free surface area, thus revealing new soil habitat for species invasions and expansion of species range. Focusing on the tipping points of global change that press the low biodiversity Dry Valley system to a different ecosystem state is important for understanding overall change on the Antarctic continent, and globally. Perhaps as important for ecologists, knowing the vulnerabilities of species and whether the loss or change to faunal species composition in a low diversity system will have a significant and rippling impact on ecosystem functioning is a fundamental scientific question. This, I believe, can be answered most appropriately, only in the Dry Valleys of Antarctica where all the faunal and phototrophic species of the whole ecosystem are close to being known. Providing the urgent attention needed now, to the global changes affecting disruptions to the coupling of above- and below-ground biodiversity and related ecosystem processes in the Dry Valleys, can provide a rigorous basis for determining how the changes in Antarctica in the next 50 years will also affect global human well-being.

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