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Functional ecology of soil organisms in tundra ecosystems: towards the future

I.D. Hodkinson[a,*], P.A. Wookey[b]

[a] School of Biological & Earth Sciences, Liverpool John Moores University, Byrom St., Liverpool L3 3AF, UK
[b] Department of Geography, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK and Uppsala University, Institute of Earth Sciences, Physical Geography, Villavägen 16, S-752 Uppsala, Sweden

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Abstract

The need to understand the functional linkages between Arctic/alpine soil communities and the major soil processes is stressed. Soil organisms are classified into broad functional groups and it is suggested that the functional success of any organism can be defined by its position along four axes, namely population responsiveness, dispersability, ecophysiological flexibility and resource use flexibility. Each of these axes is defined by reference to a spectrum of relevant ecological attributes. The resilience and response of tundra communities to change are discussed and the possible alteration in community structure and function that may result from shifting climate patterns are reviewed. The interrelationship between the spatial distribution patterns of organisms and their dispersability is highlighted and the significance of the thermal environment in moderating the competitive interaction between species is emphasised. The advantages and disadvantages of various approaches to studying the effect of climate change on Arctic/alpine community structure and function are contrasted. In particular, the manipulative experimental approach is distinguished from the comparative approach that makes use of measurements taken along geographical/ecological transects as analogues for climate change. © 1999 Elsevier Science B.V.

Keywords: Arctic soil; Tundra ecosystem; Community structure and function; Biodiversity; Climate change

1. Introduction

The International Biological Programme (IBP) provided a major stimulus for comparative studies on tundra ecosystems and their constituent processes. It drew together specialist scientists from a variety of disciplines from around the northern hemisphere to work within a unifying conceptual and co-operative framework. If publication is a measure of scientific activity, then the IBP and the synthesis volumes that flowed from it, represents the azimuth of scientific effort in tundra soil biology (Wiegolaski, 1975; Rosswall and Heal, 1975; Bliss, 1977; Heal and Perkins, 1978; Brown et al., 1980; Bliss et al., 1981; Petersen and Luxton, 1982). The nadir was soon to follow and over the next 20 years, except for smaller concerted programmes, such as the UK Arctic Terrestrial Ecology Special Topic Programme, the Norwegian TERRØK initiative and the US Long Term Environmental Research Programme at Toolik Lake, studies on arctic soil biology have languished (Chapin et al., 1991).

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*Corresponding author. Tel.: +44-151-231-2030; fax: +44-151-298-1014.

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Table 1
Comparison of the important ‘buzzwords’ and concepts from the IBP era with those of contemporary ecology to illustrate the changing emphases

IBP era	*Contemporary ecology*
Biomass	Biodiversity
Population	Metapopulation dynamics
Standing crop	Community dynamics
Energy flow	Process ecology
Productivity	Carbon budgets
Nutrient cycling	Functional relationships
Food chains	Molecular ecology, genetic adaptation
Site typology	Chemical ecology
Word and compartment models	Dynamic models in space and time
Description	Experimentation and prediction
Variability a nuisance	Variability and heterogeneity important
Ecophysiological understanding rudimentary	Ecophysiological understanding advanced
Anthropogenic effects ignored	Anthropogenic effects important
Computing rudimentary	Computing powerful
Automatic data logging in infancy	Data logging routine
Comparison	Scaling and integration

Table 1 lists the ‘buzzwords’ and concepts from the tundra IBP era of the 1970s to characterise the types of measurement that were being made, the concepts that were deemed important and the way in which technology was progressing at the time. Alongside this is a list of ideas that excite many ecologists today. The table highlights how the emphases have changed and stresses some of the concepts and ideas that we need to incorporate more fully into our thinking if our understanding of tundra soils as functional systems is to advance.

The major challenge facing us is to identify the significant major questions we should be asking concerning the functioning and control of tundra soil processes and exploring how we might develop and mould new and existing ideas into a coherent framework for future research. It appears to us that the major challenge is to explore and understand the functional linkages between the communities of living organisms and the soil processes with which they are involved (Bengtsson et al., 1995; Huntly, 1995; Parmelee, 1995; Rastetter and Shaver, 1995; Collins and Benning, 1996; Johnson et al., 1996). How does the composition of the biotic community determine the rates of major ecological processes? How variable are the process rates in time and space and to what extent is this variation linked to measurable features of the soil biotic community? To what extent is there functional redundancy among organisms within the soil system (i.e. redundant biodiversity)? Can we recognise and separate the essential from the non-essential biotic components? Can we translate a species list into a set of units that will perform a known ecological function. Can we predict how a changing biotic community, responding to shifting environmental conditions resulting from short-term fluctuations or longer term trends, will determine process rates? On what sort of scale, both spatial and temporal, should we be working? Can we link variation at the microtopographical scale to broader generalisations at the landscape scale?

2. Functional groups in soil ecology

Many workers on soil organisms are specialists who have a deep knowledge of the biology of their particular group, an abiding passion that often precludes the consideration of broader issues. We lack the coherent framework that enables us to reach beyond our specialisms and see soil organisms as mere functional units that drive and control the major processes within the ecosystem (Anderson, 1994; Anderson, 1995; Lawton and Jones, 1995). Such a system of functional groupings, which transcends taxonomic similarities, is well-developed in plant ecology (Grime, 1977; Grime, 1979). The Grime triangle classifies plants according to their life strategies into ruderals, competitors and stress tolerators, each group being defined by particular ecological/biological parameters. This system has high predictive value with respect to both the individual species and at the ecosystem level of organisation. Some attempt has been made to develop similar functional classifications for restricted groups of soil organisms but these often lack wider applicability. For example, the existing concepts of the ecological niche, trophic guilds or leagues, with their emphases on resource utilisation and/or species interactions, have been widely used to categorise the soil fauna (Luxton, 1979; Faber, 1991). While these concepts are useful, they do not directly address the major problem, namely the classification of organisms according to their functional attributes and their potential effect on ecological processes. Southwood (1977) viewed the habitat as a varying space–time continuum or templet towards which organisms can adapt using two principal strategies (r and K selection) for success. This concept was applied to soil fungi by Swift (1984) and extended to the soil microflora in general by Heal and Ineson (1984). Heal and Ineson added a third group of organisms (A or adversity adapted) to the r and K categories and suggested that adaptation was to two principal environmental axes, durational stability and adversity. The latter axis was represented by two major variables: resources (continuous); and climate (discontinuous). Panikov (1995), in a simulation model of microbial dynamics in tundra ecosystems again recognised selection under adverse conditions, which he referred to as L selection. He also attempted to align earlier functional classifications of microorganisms, such as zymogenic versus autochthonous or copiotrophic versus oligotrophic, with the r–K continuum.

The problem with all these classifications, however, is that they are organism-centred, rather than process-centred. They define the strategies that organisms may use to be successful within a varying habitat, they pay little attention to how the organism influences the ecological processes. We, therefore, need to turn this question around to focus on the processes and ask what are the functional characteristics required of an organism for it to continue to perform a particular function as part of an integrated ecological process.

Table 2 tentatively classifies soil organisms into a number of identifiable functional groupings. When considering the functional role of these groups it is important to bear in mind that the substrate is of variable quality, often being derived from a mixture of plant species. Furthermore, decomposition is a successional process that means that the activities of some functional groups are temporally and spatially separated, operating at different stages of the succession or at different depths within the soil profile (Clapp et al., 1995). The difficulty of categorising soil organisms within functional groups is compounded by the fact that many perform more than one function and thus lie simultaneously within different groups. Thus, some omnivorous soil invertebrates perform both a physical and a chemical function on a mixed substrate and this may include, in a limited number of species, cellulolytic activity (Petersen and Luxton, 1982). Although overall diversity in tundra ecosystems is low, most functional groups appear to be represented most of the time. Exceptions appear to include the general absence of larger comminutors such as earthworms, apart from at restricted sites in the Russian Arctic where *Eisenia nordenskioldi* is found (Chernov et al., 1975), and the absence of the predatory beetle *Atheta graminicola* from sites on Svalbard where its main collembolan prey species, *Onychiurus arcticus*, is found (Hodkinson et al. unpublished). Flanagan and Scarborough (1974) reported a full range of functional/physiological groups of fungi in Devon Island soils, although there were relatively few cellulolytic and ligninolytic strains present. This might suggest that decomposition rates might be compromised by a lack of available isolates (Robinson and Wookey, 1997).

The functional 'success' of an organism can best be categorised by its relative position along four linked axes (Fig. 1). These axes determine the reliability or dependability of a species as a functional component of the ecosystem. Organisms with high scores along each axis will tend to be the most reliable and persistent functional components of the community. Thus, in Fig. 1 the shaded inner circle defines the domain within which species show characteristics that confer reliability and persistence, the outer circle represents increasing unreliability and transience. The characteristics of each organism or functional group, such as A or B, can be mapped as a trapezoid.

Table 2
Suggested classification of soil organisms into functional types, depending on their role in soil ecosystem function. Examples are given of organisms within each group. Some organisms may perform more than one function

Groups performing physical functions
- Comminuters (some earthworms)
- Mixers/aerators (some earthworms etc.)
- Small particle organic matter processors (physical abrasion) (many invertebrates)

Groups performing chemical functions
Modifying soil nutrient levels
- N fixers (bacteria)
- Denitrifiers (bacteria)
- Anaerobes (sulphur, iron modifiers) (bacteria)

Controling the chemical breakdown of organic matter
- Invasive/disruptive of cellular structure (fungi)
- Non-invasive (bacteria, including Actinomycetes)

Both groups can be broken down further in relation to their ability to decompose the following important substrates:
- Cellulose and cellobiose
- Hemicellulose including xylan
- Pectin
- Lignin
- Proteins
- Soluble sugars
- Soluble amino acids

Groups regulating or modifying the populations of other groups
- Predators (many invertebrates)
- Fungal browsers (many invertebrates)
- Bacterial feeders (many invertebrates)

Groups adding dead organic matter to the soil
- Root feeders (subsurface) (nematodes, collembola etc.)
- Algae, cyanobacteria, lichen feeders (some collembola)

For a reliable species (A) the trapezoid will lie within the inner circle whereas for an unreliable species (B) the trapezoid will lie predominantly outside the inner circle.

Clearly, the axes combine elements that determine the organism's response to both its abiotic environment and its interaction with other organisms. Those in the figure are for simplicity drawn symmetrical but this need not necessarily be so, particularly where it can be shown that functional characteristics are positively or negatively correlated.

2.1. Population responsiveness (Table 3)

This axis combines two main interrelated parameters, speed and magnitude. A species population that responds quickly and produces many 'offspring' is more able to respond to changing conditions and to maintain its position within the community. Populations of both tundra soil invertebrates and micro-organisms are likely to respond rapidly to changes in both their physical environments and in the availability of resources, particularly food substrates. However, temperature and moisture constraints may limit the ability of an organism fully to exploit changes in resource availability: feeding by the collembolan *Onychiurus arcticus* is restricted to microsites with high humidity despite the abundance of potential food resources elsewhere (Hodkinson et al., 1994).

The life cycles in the dominant groups of tundra soil invertebrates such as mites, collembolans, dipterous larvae and enchytraeid worms are usually free

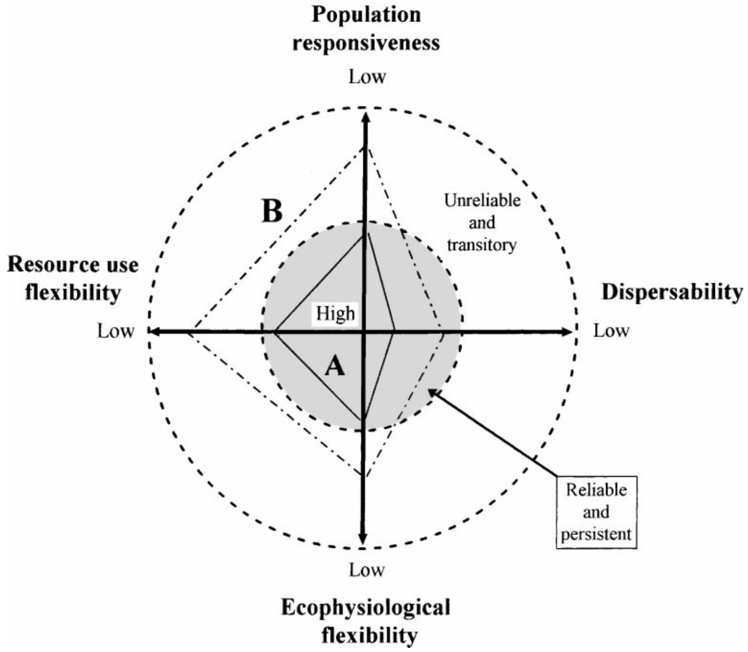

Fig. 1. Diagram plotting the distribution of a reliable and persistent species (A) and an unreliable and transient species (B) along the four recognised functional axes. The shaded central circle represents the domain of reliability, the outer unshaded part of the larger circle the domain of unreliability.

Table 3
Contrasting population characteristics of organisms showing high and low population responsiveness. See Table 1 and text for general context

High population responsiveness	*Low population responsiveness*
Generation time hours or days	Generation time months or years
Many offspring per generation	Few offspring per generation
Asexual reproduction	Sexual reproduction
Low mortality rates	High mortality rates
Lack of predation/parasitism	Predation/parasitism significant

running, often extending over two or more years (MacLean, 1975; Bale et al., 1997). There is little evidence for seasonal synchronisation, except in the case of adult emergence in Diptera, although population recruitment can show a seasonal trend in soil microarthropod populations (Douce and Crossley, 1977). Resulting populations normally have a mixed age structure. At the other extreme, the generation times of tundra bacteria, under optimal conditions, is measured in hours and population densities can fluctuate rapidly over periods of days (Parinkina, 1974). In both cases the speed of population change, providing no other constraints are operating, depends directly on the developmental response of the individual species to temperature. Mycelial growth in tundra fungi shows a similar functional response (Robinson and Wookey, 1997).

Population responses to resource availability are clearly demonstrated by the differential response speeds of various tundra soil bacteria to additional carbon sources (Panikov, 1995). MacLean (1974), however, demonstrated a clear paradox with respect to soil invertebrates at Barrow Alaska where faunal biomass in several animal groups, especially enchytraeids, was negatively correlated with the amount of accumulated organic matter.

Table 4
Contrasting dispersal characteristics of organisms exhibiting high and low rates of dispersal. Active and passive dispersal are considered separately. See Fig. 1 and text for general context

Active dispersal *High dispersal characteristics*	*Low dispersal characteristics*
Motile	Non-motile
High basal metabolic rate	Low basal metabolic rate
High Q_{10} response to temperature	Low Q_{10} response to temperature
Large size	Small size
Activity continuous	Diurnal/seasonal activity rhythms present
Passive dispersal *High dispersal characteristics*	*Low dispersal characteristics*
Small size	Large size
Abundant	Scarce
Resistant stages	No resistant stages
Asexual reproduction	Sexual reproduction
Wind or water dispersed	Not wind or water dispersed
Associated with motile organisms	Not associated with motile organisms

2.2. Dispersability (Table 4)

Dispersal is important on both microtopographical and broader geographical scales. The characteristics which favour dispersal are summarised in Table 4. On a microtopographical scale, organisms living in patchy environments subject to fluctuating climatic conditions will suffer differential mortality or extinction. Effective dispersal between, and recolonisation of, patches will ensure the functional reliability of the organism within the community. Poor dispersal will exclude the species, reducing its functional significance. Hertzberg et al. (1994) demonstrated the significance of such horizontal dispersal for *Folsomia* (Collembola) species populations along habitat moisture gradients between plant tussocks on Svalbard. The evidence, however, for pronounced seasonal changes in the vertical distributions of tundra soil microarthropods, perhaps in response to changing resource availability, is less convincing (Bale et al., 1997), although locomotary activity continues at subzero temperatures below snow packs (Coulson et al., 1995a). Similarly, the significantly higher proportion of sterile mycelium in the fungal communities of tundra compared with temperate soil environments (Dowding and Widden, 1974; Syzova and Panikov, 1995) suggests that dispersability may be restricted by a lack of airborne spores.

On a broader geographical scale the establishment of new species (functional units) in an area depends upon their long range dispersal ability. For most tundra soil organisms active dispersal is most effective over short distances whereas some form of passive dispersal allows the organism to spread its broader geographical range. For soil microarthropods their small size, lack of flying ability and absence of obvious resistant wind dispersed stages might suggest limited powers of dispersal. The evidence, however, suggests otherwise. Many of the important Svalbard Collembola are circumpolar (Fjellberg, 1986) and Norton and Palmer (1991) have suggested that the arctic mite *Opiella nova* is the world's most widespread and abundant arthropod. There is some evidence that surface water movement may be an important dispersal agency for many soil animals, particularly Collembola (Hertzberg et al., 1994).

2.3. Ecophysiological flexibility (Table 5)

Topographically complex tundra ecosystems provide a wide range of winter and summer physical environments, some climatically favoured, others climatically extreme. Superimposed on this is short and long-term climatic variation, including infrequent climatic events that have a dramatic impact on survival. The precise temperature tolerances of tundra organisms and the impact of temperature on their functional activity are reasonably well known, at least for the soil invertebrates (Bale et al., 1997), but the corresponding

Table 5
Contrasting ecophysiological characteristics of organisms exhibiting good or poor survival. Winter and summer survival are considered separately. See Fig. 1 and text for general context

Winter survival *High survival characteristics*	*Low survival characteristics*
Capacity to dehydrate	Remain hydrated
Produce antifreezes	Lack antifreezes
High supercooling ability	Low supercooling ability
High chill tolerance	Low chill tolerance
Freeze tolerance	Freeze intolerance
Behavioural selection of microhabitat	No microhabitat selection
Live in habitats with snow cover	Live in habitats without snow cover
Survive anoxia	Anoxia susceptibility
Summer survival *High survival characteristics*	*Low survival characteristics*
Desiccation resistance	Desiccation susceptibility
High Q_{10} value	Low Q_{10} value
Inhabit well-drained 'early' sites	Inhabit wet 'late' microsites

functional responses to water availability are poorly understood (Boddy, 1986; Kennedy, 1993). Often, during the period of summer activity the effects of temperature are inextricably linked to water availability and some combined function (saturated vapour pressure deficit) best defines the environment within which the soil organisms operate. Lack of water, and associated osmotic stress, inhibits the functional response of the organisms to temperature, especially in many tundra areas where soil moisture is low.

When considering the functional link between an ecological process and the biotic community it is most meaningful to subdivide the year into ecophysiologically important phases, each of which place different demands on the organisms. During the winter period organisms and processes are largely inactive but the organisms face the problems of surviving low temperature and possibly anoxia when encased in ice. Within the soil fauna different species of mite and Collembola display different population mortality characteristics in response to low temperature. On Svalbard the overwintering collembolans *Onychiurus arcticus, O. groenlandicus* and *Hypogastrura tullbergi* differ in their mean supercooling points and their mortality versus temperature curves. Even within a species, such as in the mite *Diapterobates notatus*, there may be considerable variation in cold tolerance between individuals within the same population but whether this is related to the particular microsite they occupy within the soil is not known (Coulson et al., 1995a).

During summer activity, high and low temperature extremes appear to pose few problems for survival and, provided water does not become limiting, the contribution of the organisms to ecosystem processes is largely temperature dependent, with some species, such as the collembolan *Onychiurus arcticus* displaying exceptionally high Q_{10} values, particularly at lower temperatures (Block et al., 1994). All the dominant mite and Collembola species on tundra heath and polar semi-desert at Svalbard sites are well able to survive limited exposure (1–3 h) to temperatures above 35°C, provided humidity remains at 100% (Hodkinson et al., 1996a). At zero humidity all species of Collembola succumb rapidly to high temperatures but the desiccation resistant mite species are relatively unaffected.

The transition between activity and inactivity in spring and autumn represents a period of stress during which normal physiological function is resumed or curtailed and may involve rapid change such as dehydration or rehydration with important consequences for cold hardiness. The freezing point of the collembolan *Hypogastrura tullbergi* changes rapidly from -20 to -8°C over a period of a few hours as hibernating individuals become active (Bale et al., 1997). This stress can be greatly accentuated if it involves a number of freeze thaw cycles. The reliability of each species within the community is thus dependent on its success in coping successively with these three phases of the year.

In fungi there may be substantial ecophysiological flexibility associated with the morphology of the mycelium, such that the hyphae of the same fungus, because of their dispersed nature within the soil, might experience simultaneously a broad range of environmental conditions. However, the significance of this flexibility for tundra fungi, which is analogous to the ‘guerrilla’ growth strategy of clonal tundra plants (Callaghan et al., 1992a), is unknown.

2.4. Resource use flexibility (Table 6)

Soil organisms perform two basic functions in soil processes, the physical alteration of their environment (e.g. commination, soil aeration) and chemical functions involved in energy flow and nutrient cycling, which are dependent on the enzyme complements that the organisms possess. Both these functions have a measurable energy cost. An organism’s ability to conduct these functions depends on the extent to which it is able to exploit the food and other resources available and to cope with spatial and temporal variation in resource availability (Futuyama and Moreno, 1988). We can recognise various characteristics of resource flexibility (Table 6).

The low diversity of both invertebrates and microorganisms in tundra soils suggests that individual species have the opportunity to evolve broader niches, particularly with respect to food availability. Many mites and Collembola show varying degrees of catholicism in their food choice: the collembolan *Onychiurus arcticus*, for example, feeds on living bryophytes as well as unicellular algae, fungal mycelium and detritus (Hodkinson et al., 1994). Food availability can be an important determinant of the functional composition of the microarthropod fauna. The mite faunas of tundra heath and polar semi-desert on Svalbard are dominated by the same six species but the community composition differs markedly and is probably determined by food availability matched against trophic flexibility. The predominant species on the tundra heath are microphytophages that feed strictly on the microflora, whereas the fauna of the skeletal soils of the polar semi-desert is dominated by panphytophages that feed on a range of plant materials, including bryophytes as well as fungi and lichens (Webb et al., 1998). Similar measurement of trophic flexibility in fungi from tundra soils have mainly been made in vitro and results should be treated with some caution. Nevertheless, very few strains of fungi from Devon Island, Canada, decomposed cellulose, gallic acids and humic acids, but pectinolytic and amylolytic strains were common (Flanagan and Scarborough, 1974).

3. Community resilience and responses to change: the broad questions

Tundra ecosystems are relatively young systems that are subjected to repeated natural disturbances, such as cryoturbaton, and provide an unstable physical environment within which the biological processes operate. Long term directional changes in environmental factors such as temperature, precipitation, CO_2, UVB etc. are providing an underlying external ENVIRONMENTAL INERTIA that is driving change in the biotic composition and functioning of Arctic soil systems (Fig. 2) (Danks, 1992; Kareiva et al., 1993; Gates, 1993; Callaghan et al., 1992b). Natural autogenic succession, including cyclical events linked to cryoturbation, also creates a BIOTIC INERTIA that drives change. Superimposed on this directional change is the shorter term variation and change, induced by within and between year fluctuations in climate, which produces the seemingly random

Table 6
Contrasting characteristics of organisms that display flexibility or inflexibility in resource usage. See Fig. 1 and text for general context

High resource use flexibility	*Low resource us inflexibility*
Generalism, use of a wide range of resources (e.g. polyphagy)	Specialism, use of a single resource (e.g. monophagy)
Compensatory ability to switch resource use in time and space	Inability to switch resources
Ability to supplement or ameliorate resources (e.g. N fixation)	Inability to supplement resources
Synergistic association with other organisms	No synergistic association

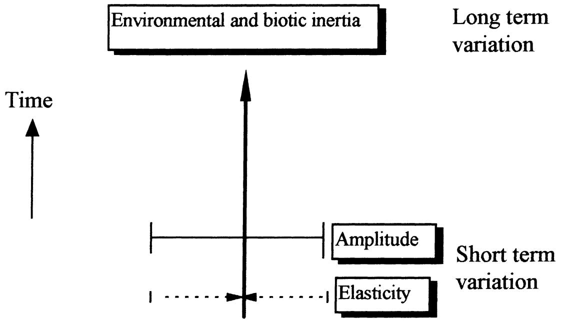

Fig. 2. Schematic representation summarising the responses of tundra soil ecosystems over time to changing climate.

fluctuations around the long term trend. Two important components of this fluctuation determine the resilience of both the biotic community and the underlying soil processes. The AMPLITUDE determines how far the system can be perturbed yet still be capable of returning to its original state, the ELASTICITY determines how quickly the system returns to its equilibrium state (Orians, 1975; Harrison, 1979). Results of temperature enhancement experiments illustrate simultaneously both the inherent resilience and potential fragility of some components of tundra soil communities. For example, soil microarthropods on tundra heath and polar semi-desert sites on Svalbard showed no significant initial population response to an 8–10% increase in their thermal budget (Coulson et al., 1996). This suggested a strongly buffered response to an increase in heat availability similar to the normal year-to-year or between site variations normally experienced, i.e. a wide normal amplitude. However, an extreme event in the form of an exceptionally warm and dry year, produced significant mortality in the Collembola but not the mite populations at the polar semi-desert site, where the soil was most susceptible to drying. Collembolan populations, with their long generation times, when pushed beyond a set amplitude, thus probably display weak elasticity. These experiments suggest that the effects of infrequent extreme events on soil organisms should be given greater consideration (Wigley, 1985). The challenge for soil ecologists is to untangle the short term variation from the general inertia and to separate the effects of the environmental from the biotic inertia (Coulson et al., 1996). Only then will the consequences of variation and change for the functioning of soil communities be fully understood.

What are the consequences of change for soil community composition and the rates of soil process? We can view each process (Fig. 3) as being controlled by a set of interacting functional groups, each of which is made up of interacting different functional units (species). Environmental changes will act on all such functional groups. The latent functional groups are those that may initially be absent and thus functionally inactive but which can enter the community and become ‘switched on’ as the environment changes. These may include parasitoid or

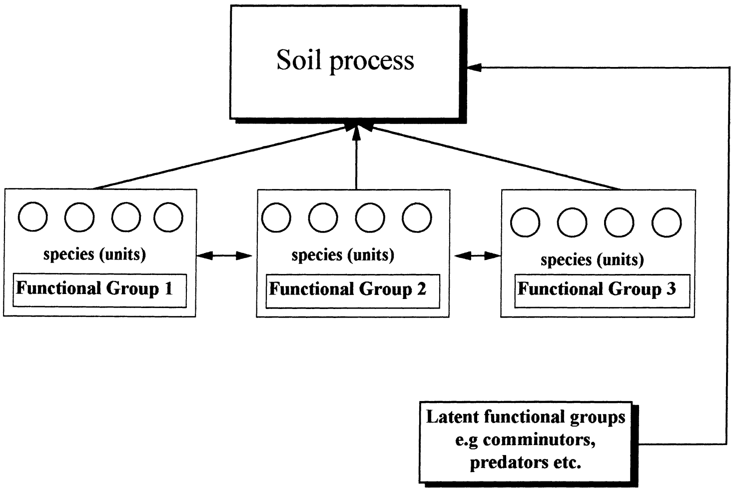

Fig. 3. Simplified schematic representation showing the interrelationships between functional units, functional groups and soil processes.

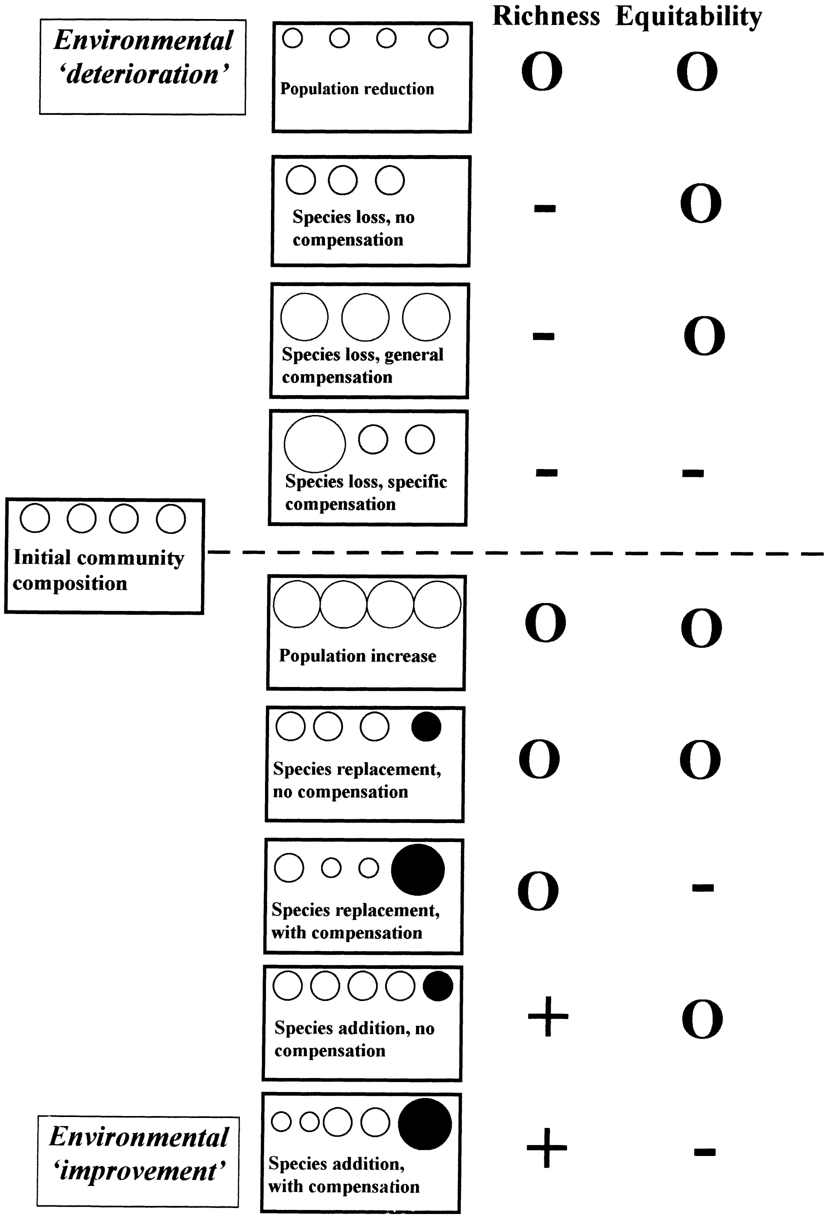

Fig. 4. Schematic representation of some of the changes in soil community composition that may result from climate change. Implications for community diversity measured as species richness and equitability are summarised on the right-hand side of the diagram. The size of each shaded circle is proportional to population density. Open circles represent existing species, dark shaded circles are invasive species. (+) represents an increase and (−) a decrease in the diversity parameter.

predator groups that occupy a narrower thermal range than their prey or functional groups, like earthworms, that can perform a unique function in the soil but where climate restricts their present distribution. The possible outcomes of change on the composition of one such group is summarised in Fig. 4, in which each circle represents an hypothetical population of a functional unit. These effects represent outcome scenarios of climate change on community composition and show how these will be reflected in changes in the two important parameters of biological diversity, species richness and equitability. Ultimately we need to know how these variations will affect the ecosystem process with which the community is involved.

4. Spatial effects in the functional composition of soil communities – the significance of dispersability

The long term effectiveness of dispersability is reflected in the geographic distribution patterns of Arctic soil organisms (see section on dispersability). These patterns are susceptible to objective community analysis and comparison at the functional level. For many soil organisms, with limited dispersability, absence from a community does not indicate that a particular organism cannot play a functional role in that community, merely that it may never have arrived or may not have been able to establish. Measured biodiversity is a function of dispersability and may not indicate true potential biodiversity. Much of the high Arctic comprises scattered island archipelagos and transoceanic dispersal is important. The Arctic regions receive a steady 'rain' of autochthohous, wind-dispersed colonisers, especially insects (Elton, 1925). Continuous latitudinal land 'bridges' exist in the low Arctic, extending to the northern limits of the continental land masses. By contrast, the only 'continuous' land transect from low to high Arctic is in Greenland. Dispersal of organisms can be by two processes: GRADUAL DIFFUSION and JUMP DISPERSAL (Table 7).

On the broader geographical scale, climate represents the major barrier to diffusion. Such diffusion has significance on both short and long time scales. Diffusion within a heterogeneous environment permits continuous recolonisation of habitats from favourable refuges – the sink/source relationships of meta-population dynamics (Hanski and Gilpin, 1991; Lawton, 1995). Over the longer term it permits the gradual spread of organisms in response to directional change in the environment, i.e. the incorporation of new functional units into established communities. Jump dispersal is governed by the rules of biogeography and depends both on dispersability and on a stochastic element, the random chance of a species locating a favourable habitat within a matrix of hostile habitats. Thus, additions to communities may be chance elements that differ from place to place.

Little is known about how the functional composition of communities and the rates of processes vary with respect to microtopographical relief and how this relates to patterns on a broader geographic scale (Broll, 1994; O'Lear and Seastedt, 1994; Klimowicz and Uziak, 1996). To what extent is the continuity of a functioning community at a given point dependent on the dispersability of the constituent organisms, particularly when the microenvironment is subject to continual change, such as seasonal variation in water availability? Often microclimatic differences over a few centimetres, resulting from differences in aspect, can mirror changes that are obvious on a much larger geographical scale (Coulson et al., 1995b).

5. The thermal dimension in community composition

Different functional groups of ectothermic organisms respond to temperature change at different rates. However, the role of temperature in constantly fine tuning the competitive and functional interactions between organisms in the community is neglected (Gilchrist, 1995). Such interactions are well understood in model laboratory systems involving bacteria

Table 7
Contrasting dispersal characteristics of organisms spreading by diffusion and jump dispersal. Further explanation of the functional axes is given in Tables 3–6 and in the text

Diffusion	*Jump dispersal*
Continuous	Disjunct
Slow	Potentially rapid
Predictable in time and space	Stochastic in time and space
Potential for gradual genetic adaptation	No gradual genetic adaptation
Gradual assimilation into community	Potentially disruptive to community

or flour beetles but are less well understood for natural communities of tundra organisms in the field. Examples from Arctic/alpine situations include changes in the relative abundance of mesophilic and psychrophilic soil bacteria in response to varying temperature, shifts in insect community composition along thermal gradients and changes over longer time periods in plant community composition (Panikov, 1994, 1995; Hill and Hodkinson, 1995; Harte and Shaw, 1995). It is feasible that if the 'resources' available to two competing species remain constant and the initial populations of the competitors remain unaltered, the outcome of competition between the species can be shifted by altering the temperature (Hodkinson et al., 1996a). Climate warming models predict that temperature rises will be greatest in the winter when organisms are largely inactive. Changes in patterns of winter survival may again modify the competitive balance between competing organisms. In particular we need to know how:

(a) changing temperatures affect the composition and balance of the functional units within the community and how this is expressed in process rates.
(b) raising or lowering temperature will permit the assimilation of additional competitor species into, or the elimination of existing species from, the community. This needs to be viewed within the context of a naturally fluctuating temperature environment.

There is some evidence that predation, at least in the high arctic, may be temperature limited, allowing prey species to exist in predator free or predator restricted space (Bale et al., 1997). The extent to which this occurs in the soil ecosystem is uncertain but the *Onychiurus/Atheta* example cited earlier suggests that it may not be uncommon: the beetle is only found in the warmer microhabitats.

It is likely that the metabolic response of communities to temperature will change under directional climate forcing, depending on mean generation times, polymorphisms, modes of reproduction, etc. The magnitude and speed of such changes are unlikely to be uniform, either within or between functional groups, making forward prediction difficult. In this context the comparative approach becomes significant. In many cases changes will be linked to a general shortening of organisms life cycle, as has been demonstrated for terrestrial chironomid larvae on Svalbard (Hodkinson et al., 1996b)

6. Experimental approaches

Two contrasting but complementary approaches lend themselves to the functional analysis of Arctic soil communities, the EXPERIMENTAL/MANIPULATIVE approach (in field and laboratory) and the COMPARATIVE approach (field based). The aim of both approaches is to develop a predictive link between community composition and ecosystem process. Both approaches are interdisciplinary, requiring co-operation between specialisms. The difference between the approaches is illustrated by example below.

6.1. The experimental/manipulative approach

This approach tests how soil processes react to experimental manipulation of (a) the abiotic environment and (b) the composition of the soil community.

6.1.1. Environmental manipulation

This approach involves measurement of the response of the selected system, both in terms of process rates and community composition, to manipulation of abiotic variables such as temperature, moisture, etc. It tests the resilience, amplitude and elasticity of an existing system in response to change. Several recent experimental/manipulative studies in the Arctic have measured the responses of communities or processes to manipulation. Manipulations have included the use of cloches or soil heating cables to modify soil temperature and the addition of inorganic plant nutrients (NPK) and/or water (Kennedy, 1995; Robinson et al., 1995; Wookey et al., 1995; Chapin et al., 1995; Coulson et al., 1993, 1996).

6.1.2. Community manipulation

This approach measures the response of both ecosystem processes and community composition to manipulation of the biotic communities under set environmental conditions. These experiments aim to discover the minimal shape of the functioning community and the significance of adding further functional units to the operation of the major ecosystem processes. Experiments may include:

Removal of functional groups and/or units within functional groups.
Addition of functional groups or functional units within groups.
Substitution of functional units with replacement units performing similar function.
Supplementation (or reduction) of the population size of selected functional units within the functional groups.
Simplification of the community by the development of simple laboratory microcosms.

A good example is the work of Sendstad (1981) who artificially removed lichen cover (simulation of reindeer grazing) to examine the effects on soil collembolan populations.

6.2. The comparative method

This approach compares and contrasts variation in rates of soil processes between sites and seeks to explain how differences are related to the functional composition of the soil communities. This is the approach that was widely used in the IBP and which underpins the current International Tundra Experiment (ITEX) and the High Latitude Transect in the Scandinavia/North European Region (SCANTRAN) initiatives (Molau and Mølgaard, 1996; Heal et al., 1996). Sites can be selected, particularly along ecological successions or environmental gradients (see below) to act as analogues for temporal change, i.e. space-for-time substitution (Pickett, 1989). Ideally, in broader comparisons, all types of site should be represented, from polar deserts to wet tundra. Studies should be carried out on different topographical scales, looking at variation linked say to surface relief and drainage, and on the broad geographic scale making intercontinental or latitudinal comparisons. Spatial scales should be linked whenever possible. For example, comparisons involving the impact of soil microarthropods on soil processes illustrate the significance of scale and show how ecosystem function can be linked to community composition. On a microtopographic scale such as on Devon Island, variation in populations of Collembola, linked to micro-organism populations, influenced rates of soil metabolism at different sites (Addison and Parkinson, 1978). These soil microarthropods form part of communities that differ in composition over wider spatial scales, such as along latitudinal gradients in northern Alaska (Thomas and MacLean, 1988).

Comparisons of community structure and ecosystem processes can therefore be made among geographically separate sites with different biotic and physico-chemical characteristics (Whittaker, 1974; MacLean, 1974).

Ultimately information from the experimental/manipulative and comparative approaches should be linked in multivariate and other models describing ecosystem composition, variation and function.

6.3. Ecological successions and gradients as possible study tools

Glacial successions could provide an opportunity to link the manipulative and comparative methods in the field. Succession is a spatial expression of the time series of events involved in the development of communities in response to changing climate (Crocker and Major, 1955; Downes, 1988; Pickett, 1989; Bennike and Böcher, 1994; Coope, 1995). Vegetation changes are often well documented but detailed studies of soil communities and ecosystem processes along succession gradients are few. Successions:

(a) permit the description of functional changes in the soil biotic community over time.
(b) allow the measurement of rates of community change.
(c) facilitate the measurement of dispersal rates of functional units within the community.
(d) provide an experimental arena for the experimental transplant of communities along a gradient in which community composition varies widely but macroclimate is relatively constant.

Latitudinal/altitudinal gradients provide similar arenas for transplant experiments on a wider geographic scale over which there are known directional changes in selected climatic parameters (Ottensen, 1996; Heal et al., 1996). It may also be possible to exploit experimentally the apparent different directions of climate change in different parts of the Arctic. Thus, comparisons between Svalbard, eastern Siberia and W. Canada/Alaska, which appear to be getting warmer and W. Greenland and E. Canada, which appear to be getting cooler, may be instructive.

7. Conclusion

The International Biological Programme established a baseline for studies on Arctic tundra soil systems, describing the limited taxonomic diversity of tundra communities and characterising the general physiological and growth responses of the dominant species. It demonstrated rates of productivity higher than anticipated but also showed slow rates of decomposition accompanied by high rates of litter accumulation resulting from low temperatures and poor litter quality. By comparison, recent studies have focused more on the impact of anthropogenic changes, particularly in environmental temperatures. The approach has shifted towards the experimental/manipulative and away from the comparative, although the comparative approach remains a vital component. Despite low species diversity, Arctic ecosystems appear capable of responding to change through the inherent functional flexibility of their component species. These species are well adapted to respond because natural fluctuations in time and space variation form part of their regular experience. Climate shifts, however, will inevitably produce a speeding-up of ecosystem function and it remains to be seen whether the organisms have the resilience over longer time scales to respond to such major changes and to increasingly frequent extreme events. The evidence suggests that there may be strong differential effects between taxa within functional groups and, given the current state of knowledge, the overall functional effects on ecosystem processes are difficult to predict with any certainty. However, the functional approaches to the study of Arctic soil systems, described in this paper, remain our best hope of achieving a deeper understanding of how such ecosystems operate.

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