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Experimental approaches to predicting the future of tundra plant communities

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Abstract

(a) **Background:** Predicting the future of tundra plant communities is a major intellectual and practical challenge and it can only be successful if underpinned by an understanding of the evolutionary history and genetics of tundra plant species, their ecophysiology, and their responsiveness (both individually and as component parts of communities) to multiple environmental change drivers.

(b) **Aims:** This paper considers the types of experimental approaches that have been used to understand and to predict the future of tundra plant communities and ecosystems. In particular, the use of ‘environmental manipulation’ experiments in the field is described, and the merits and limitations of this type of approach are considered with specific reference to the International Tundra Experiment (ITEX) as an example to indicate the key principles. The approach is compared with palaeoenvironmental investigations (using archives – or proxies – of past change) and the study of environmental gradients (so-called ‘space-for-time substitution’) to understand potential future change.

(c) **Conclusions:** Environmental manipulation experiments have limitations associated with, for example, short timescales, treatment artefacts, and trade-offs between technical sophistication and breadth of deployment in heterogeneous landscapes/regions. They do, however, provide valuable information on seasonal through decadal phenological, growth, reproductive, and ecosystem responses which have a direct bearing on ecosystem-atmosphere coupling, species interactions and, potentially, trophic cascades. Designed appropriately, they enable researchers to test specific hypotheses and to record the dynamics of ecosystem responses to change directly, thus providing a robust complement to palaeoenvironmental investigations, gradient studies and ecosystem modelling.

Introduction

Tundra ecosystems are reported to be undergoing pan-arctic changes in community composition (Myneni et al. 1997; Sturm et al. 2001; Tape et al. 2006), with evidence of related changes in the mid-latitude Alpine (Grabbherr et al. 1994; Walther et al. 2005; Cannone et al. 2007; Pauli et al. 2007). These changes are being linked to climate warming, and more specifically to earlier snow-melt and a lengthening growing season. There is a strong consensus among general circulation models of the earth's climate that climate change at northern high latitudes will accelerate into the 21st Century (ACIA 2005; IPCC 2007). The rate and magnitude of warming in these regions are predicted to exceed the global average substantially, although regional variations in precipitation (and hence surface water balance) are much less clear. The tundra biome will, nonetheless, represent a sensitive indicator of change. Furthermore, the land surface and atmosphere are strongly coupled in the Arctic, and changes in the structure and functioning of tundra ecosystems have the potential to impact on global biogeochemistry and the climate system through changes in surface energy balance, biogenic trace gas fluxes, and regional hydrology (Chapin et al. 2000, 2005). There is therefore considerable urgency to improve the understanding and prediction of ecosystem dynamics in response to global change drivers.

But climate change is not operating in isolation from other drivers of change in the Arctic: Environmental change has multiple facets (including direct land-use change). This makes prediction of ecosystem effects of change a serious intellectual and practical challenge. For example, increasing concentrations of carbon dioxide (CO₂) in the atmosphere have a global dimension (IPCC 2007), and are unequivocally-linked with anthropogenic activity. More variable regionally, but also with a strong global dimension, is the increased deposition of airborne N-containing contaminants into remote locations, including arctic and alpine ecosystems. Furthermore, stratospheric ozone depletion over high latitudes increases fluxes of UV-B radiation

to the surface, but is associated with strong temporal and spatial variability. Thus environmental change in the broadest sense involves several individual ‘drivers’ of change which are co-occurring, but which have regional contrasts.

This is one reason why palaeoenvironmental investigations, though critical for establishing the magnitude and rate of environmental change in the past, may have limited applicability for predicting future change. Thus the notion of “the past as a key to the future” (Adams and Woodward 1992; Jackson and Williams 2004) is valid to some extent, but should be applied with caution. Likewise, a reliance on transect approaches (or ‘space-for-time’ substitution) to predict the end-points of change based upon existing communities and ecosystems is potentially flawed for several reasons that will be discussed later.

Set within the context of environmental change which is multifaceted, and with interpretational constraints on palaeoenvironmental and space-for-time approaches, this paper examines the strengths and weaknesses of environmental manipulation experiments in the field which seek to simulate environmental change and to measure directly the biological responses to change. It is out-with the scope of the paper to review comprehensively the full spectrum of experiments which have been undertaken in the tundra biome (the reader is referred to Callaghan et al. (2004a) for a synthesis), so the principal focus is the International Tundra Experiment (ITEX), which is one of the longest-running experiments seeking to understand the likely response of tundra (both arctic and temperate alpine) ecosystems to climate change.

An experimental approach to understanding global warming and the tundra biome

The International Tundra Experiment was launched in December 1990, and from the start it adopted a straightforward approach designed to encourage broad international participation. ITEX linked an international network of research scientists through the implementation of

experiments focusing on the impact of climate change on selected circumpolar, cold-adapted plant species, in tundra and alpine vegetation. At its core, ITEX had the ‘3 Ms’ - manipulation, monitoring, and meta-analysis (synthesis) – with a simple manipulation of growing season temperature (using small hexagonal greenhouses with open tops: OTCs; Open-Topped Chambers), un-manipulated ‘control’ plots (contributing also to monitoring), and exchange of ideas and data through regular synthesis meetings. A further three key elements included standardisation (of experimental treatment and measurement protocols), replication, and the provision of baseline community data prior to (or in parallel with) the initiation of the experimental warming treatment.

With the original focus on a selection of ‘ITEX species’ (including, for example, *Bistorta vivipara*, *Dryas octopetala* and *Silene acaulis*), the programme was constructed deliberately as a bottom-up approach (Fig. 1). This was also in recognition of the fundamental fact that ecosystems respond to environmental change in the first instance through individual organisms (Fig. 2) rather than through populations or communities. Reflecting this, both site- and species-specific results have been published in a large number of papers in peer-reviewed journals, including a supplement of *Global Change Biology* (see Henry and Molau 1997) devoted specifically to ITEX. The broad geographical coverage of ITEX (including arctic and alpine sites, as well as the Tibetan Plateau) also recognized that regional contrasts in ecosystem response to simulated environmental change might be anticipated as a function of, for example, where key ITEX species were located in their geographical range (Fig. 3) and the site characteristics in terms of opportunities for seedling recruitment, alterations in vertical development and lateral spread of existing plants.

In addition to the *Global Change Biology* supplement, the synthesis activities were achieved by implementing two statistical meta-analyses involving data from a suite of ITEX sites and

designed to provide added-value to the conclusions based on individual sites: This, in essence, is a key strength of ITEX as a network. The two meta-analytical works (Arft et al. 1999; Walker et al. 2006) deal, respectively, with plant phenological and growth responses (referred to subsequently as Synthesis I), and whole-community responses (Synthesis II) to experimental warming. This broad geographical coverage involving multiple arctic and alpine sites is unique to ITEX: other environmental manipulation studies have usually been limited to one or two sites, or specific gradients (e.g. the mountain birch forest-tundra heath ecotone in the Scandes mountains; see Sjögersten and Wookey 2002, 2004, 2005).

Henry and Molau (1997) reviewed and synthesized the results of the early (1-3 yr) site- and species-specific investigations of vegetative and reproductive growth and phenology without the benefit of statistical meta-analysis. They concluded that all species measured at that stage responded to ITEX temperature manipulations, but that they responded largely individually. Although it was difficult to distinguish clear patterns of response related to growth form, forbs (e.g. *Ranunculus glacialis*) appeared the most responsive group to warming (Molau 1997) but the range of responses within this group was large. Results also suggested that plants towards the colder limits of their ranges responded more strongly to warming than plants of the same species further south (e.g. *Saxifraga oppositifolia* and *Cassiope tetragona*), and there were indications of stronger responses to experimental warming during ‘colder’ growing seasons (both of which are consistent with Figure 3). Increases in reproductive growth (seed set, seed weight, and germinability) also appear to be general responses to warming in the short-term: Wookey et al. (1995), for example, reported a 141% increase in seed germinability of *Dryas octopetala* at a high arctic polar semi-desert, Svalbard, in association with warming over three growing seasons.

139 The next logical step with the growing ITEX data-sets was to undertake an objective and
140 statistically-rigorous comparative analysis on the standardized data. This was undertaken, with
141 US NSF (National Science Foundation) support, in December 1996 at the National Center for
142 Ecological Analysis and Synthesis (NCEAS), Santa Barbara, California. The results of Synthesis
143 I (Arft et al. 1999) demonstrated that growth forms (which are related to plant functional types;
144 FTs) have some predictive value, thus enabling generalizations to be made on responses which
145 are not exclusively species-specific (Fig. 1): Herbaceous growth forms, for example, responded
146 more strongly than woody forms. Statistical meta-analysis was therefore able to confirm patterns
147 of response that a traditional literature review was unable to resolve unequivocally (see previous
148 paragraph). It should be acknowledged, however, that Synthesis I was based on a fuller data-set
149 (with up to 4 years of data from some sites, and 13 sites included) than the early synthesis of
150 Henry and Molau (1997). Phenological shifts were also consistent - with earlier bud-burst and
151 anthesis in response to warming - while plants growing in the low arctic were more responsive
152 than those at alpine and high arctic sites in terms of above-ground growth (the latter result
153 apparently contrasting somewhat with conclusions drawn by Henry and Molau (1997) on the
154 basis of single species' responses to warming in contrasting parts of their geographical range).
155 Synthesis I also indicated that a shift occurred over the first 3-4 years of warming from strong
156 vegetative responses early on toward greater reproductive effort and success in the fourth
157 treatment year (Arft et al. 1999). These results were interpreted as reflecting a possible depletion
158 of stored plant reserves or soil nutrients, so that sustained vegetative growth was constrained,
159 while investment in reproduction was a secondary response reflecting increased production of
160 flower buds in seasons prior to flowering (flower buds form one to several seasons prior to
161 flowering in many tundra plant species; Sørensen 1941, Diggle 1997).

During the drafting of the Arft et al. (1999) paper, and in the period up to publication, ITEX researchers continued with data collection. Synthesis I, together with the subsequent addition of new data, prompted emergence of the hypothesis that individual plant responses to warming will be modulated by the communities of which they are a part (Figs. 1 and 2), and by broader ecosystem properties (e.g. soil nutrient pools, permafrost conditions, herbivory). It was thus increasingly recognised that species-specific responses can only be interpreted in the context of communities and ecosystems. Data on community composition (based on point-quadrat methods) also indicated that significant changes in plant communities were occurring more rapidly than ITEX researchers first thought. These factors prompted Synthesis II, which demonstrated clearly that plant communities exhibited detectable responses to warming over time periods of only 3-4 yr (Walker et al. 2006), with the most significant changes being increases in deciduous shrub cover and height (consistent with the results of Synthesis I which indicated that deciduous shrubs as a growth form were particularly responsive to warming), decreases in cryptogam cover, and decreases in (apparent) species richness. Overall the results are consistent with the observations of increased 'shrubiness' in Alaska (Myneni et al. 1997; Sturm et al. 2001) which are now increasingly being considered pan-arctic in extent (Chapin et al. 2005; Tape et al. 2006) (although scope remains to question the robustness of the data being used to underpin such conclusions). The loss of cryptogam cover and diversity is also consistent with the observations of Cornelissen et al. (2001) and Jägerbrand et al. (2006).

In addition to the core ITEX focus on plant and plant community responses to warming, ITEX has contributed to a third recent meta-analysis (Cornelissen et al. 2007) comparing leaf litter decomposability of a range of species and FTs from several environmental manipulation experiments (including their unmanipulated control plots). These litters were decomposed in 'common-garden' conditions at two climatically contrasting sites, and the experiment aimed to

resolve direct climate-related effects on litter decomposition, and indirect effects mediated via changes in litter physico-chemical properties associated with the experimental manipulations. This analysis illustrates how ITEX, together with linked programmes, is addressing broader ecosystem-level processes (Figs. 1 and 2).

Limitations with environmental manipulation experiments

In situ environmental manipulation experiments designed to simulate the effects of environmental change on ecosystems and their component parts have several generic constraints. These should always be borne in mind when interpreting such experiments, but they do not invalidate the approach. Key issues concern (a) the environmental change scenarios being simulated, (b) time-scales, and (c) spatial scales and ‘scaling-up’. In addition, each environmental manipulation experiment is likely to be associated with specific experimental artefacts.

Experiments which are sophisticated in nature (involving, for example, CO₂, UV-B or ‘active’ temperature manipulations - e.g. heating cables or lamps - either singly or in factorial combination) are usually restricted geographically to a few sites with suitable infrastructure (Harte and Shaw 1995; Johnson et al. 2002). This carries with it the problem, however, that results might be difficult to extrapolate to regional, or even local scales (Epstein et al. 2004), depending on whether or not ‘zonal’, or other more specialized plant communities, were selected for investigation. A counter-argument in an arctic-alpine context, however, is that micro- or meso-topographic variations have a disproportionate effect on thermal environment and water-balance, and for this reason substantial community variability at the local scale (Walker 2000) can be exploited to make inferences about how ecosystems much further apart would respond to the same drivers of change. This hypothesis might have some validity, but ‘scaling-up’ to reach regional conclusions on the basis of results from one or a few sites in the same macro-climatic or

biogeographic region carries serious risks; responses to change likely differ depending upon initial community/ecosystem characteristics. Jónsdóttir et al. (2005), for example, reported contrasting responses to 3-5 years of ITEX warming at two sites in Iceland: A dwarf-shrub heath community showed an increased abundance of deciduous and evergreen dwarf shrubs, an increase in canopy height, and a decrease in bryophyte cover in response to warming, while no significant changes could be detected at a moss heath community. Likewise, Hobbie et al. (2005), demonstrated fundamental contrasts in community responses to fertilizer additions in moist acidic tundra compared with moist non-acidic tundra (associated with surfaces of contrasting age since deglaciation) in the northern foothills of the Brooks Range, Alaska; this was in spite of the fact that these communities share the same regional species pool. There is thus likely a necessary trade-off between the relative simplicity/physical robustness of environmental manipulation experiments that can be undertaken in a comparative way at multiple sites, and the technical sophistication of experiments at only a few sites. The latter might, through the application of advanced technology, reduce unwanted treatment artefacts, and might also enable the effects of combined drivers of change to be evaluated in fully orthogonal experiments, but they may be difficult to scale to the region.

Environmental manipulation experiments are generally designed to assess the potential responsiveness or resilience of ecosystem components and processes to global change. They must often, however, be temporally compressed in order to conform to standard research funding cycles (usually of 3-5 years), as well as for predictive purposes, so that mitigation and/or adaptation strategies can be designed for ecosystem management. For many ecosystem processes and components, however, the short- to medium-term responses to a step-change in environmental conditions imposed experimentally may not be a good predictor of longer-term responses to global change (see Fig. 4) (Hollister et al. 2005). There are very few experimental

studies that have been maintained for longer than a decade, but notable exceptions include manipulations of temperature, light and nutrient availability at wet sedge, moist tussock, and tundra heath communities near Toolik Lake, Alaska, initiated in 1981 (Chapin and Shaver 1985, Chapin et al. 1995; van Wijk et al. 2004), and at sub-arctic heath near Abisko, Swedish Lapland, initiated in 1989 (Havström et al. 1993; Graglia et al. 2001; Clemmensen et al. 2006; Rinnan et al. 2007). While ecophysiological processes such as photosynthesis and respiration may respond almost instantaneously to changing environmental conditions, others, such as allocation patterns (Björk et al. 2007), or alterations in quantity and quality of litterfall, plant and decomposer community composition, may take months to decades. Figure 4 illustrates the approximate maximum longevity of on-going environmental manipulation experiments, and extrapolation beyond a decade is problematic based on existing results. Indeed Chapin et al. (1995) noted that “short-term (3-yr) responses were poor predictors of longer term (9-yr) changes in community composition” in response to light, temperature and nutrient manipulations near Toolik Lake. Furthermore, Rinnan et al. (2007) observed that 15 years of nutrient additions were needed before a significant response could be observed in soil microbial biomass and community composition in experiments near Abisko in Swedish Lapland. It is possible that nutrient addition experiments may suffer more from changing trajectories of response through time than more subtle temperature manipulation experiments such as ITEX, but this has not been tested systematically. In any case, most nutrient addition experiments fail to simulate the increasing soil mineral nutrient availability that might result from more rapid decomposition in warmer and/or drier soils: The doses of nutrients applied are generally far too high. Furthermore, ITEX meta-analyses only span the period up to Synthesis II (Walker et al. 2006), and experimental data relating to warming beyond 6-7 years have not been subjected to similar analysis thus far.

Clearly, in interpreting the results of environmental manipulation experiments it is important that their spatial and temporal context is considered explicitly (Epstein et al. 2004). How applicable are conclusions across an array of contrasting community and ecosystem types, and how useful are the results for making predictions for the future? These are overarching issues superimposed upon the more practical considerations of experimental artefacts, or indeed whether or not appropriate environmental change scenarios are being simulated. On a more positive note, some unintentional artefacts associated with manipulation experiments might actually represent a reasonable simulation of a future scenario. Warming experiments which result in surface drying, for example, may be realistic if future climate warming occurs with no parallel increase in precipitation. Interpreting the results must, however, be based upon sound monitoring data on appropriate physical environmental parameters in both manipulated and control plots (Marion et al. 1997; Hollister and Webber 2000).

ITEX-specific constraints?

As a 'passive' warming experiment using small plots (i.e. not reliant upon heat inputs requiring an electrical supply, such as soil heating cables, or above-ground radiators; see Harte and Shaw (1995)), ITEX is associated with several artefacts. ITEX uses open-topped chambers (OTCs) to produce a modest net warming of near-surface temperatures (generally around 1.2 – 1.8 °C). The advantages and disadvantages of this design are discussed by Kennedy (1995), Marion et al. (1997), Wookey and Robinson (1997), and Hollister and Webber (2000), but in summary most of the heating is during the day because it is dependent upon incident solar radiation, there is a small attenuation of light (especially at low solar angles), wind-speeds are generally reduced within the OTCs, and surface moisture may also be reduced due to exclusion of the precipitation around the edges of the chambers. In addition, due to lateral heat-sink effects, soil warming may not reach

the magnitude expected, and snow cover and duration may also be affected due to altered drifting patterns within and around the OTCs.

Nonetheless, Hollister and Webber (2000) have conducted a 'biotic validation' of the ITEX OTCs in wet meadow tundra in Alaska in which they compare plant development and phenology in two summers with highly contrasting heat sums. This fortuitous contrast enabled them to compare plant responses in 'control' (unwarmed) plots during a relatively warm summer (1995) with responses in a warmed (OTC) plot during a colder summer (1996) (Fig. 5). Significantly, plant development was very similar in both situations (which had similar growing season cumulative heat sums) suggesting that OTCs are successful at simulating the effects of warming. ITEX community-level responses to OTCs (Walker et al. 2007) are also consistent with on-going observations of increased shrubiness in part of the arctic tundra (Tape et al. 2006), and this further supports the conclusions.

But another experimental artefact of ITEX (and other passive warming experiments involving relatively small plots) is that the OTCs potentially act as a physical barrier to herbivores (both vertebrate and invertebrate) and pollinators (although see Richardson et al. 2002). It could be argued that contrasting ecosystem components may become uncoupled from each other, and thus trophic and other interactions are altered or weakened (den Herder et al. 2004). This is undoubtedly the case for large herbivores, although lemmings and voles will not be excluded from OTCs, and reduced pollination has not been identified as a problem to date. The exclusion of large herbivores from OTC plots and not from control plots is an experimental artefact which is likely to become cumulatively more important as experiments progress (see Grellmann 2002; Olofsson et al. 2004; Bråthen et al. 2007; Ims et al. 2007). An uncoupling between the magnitudes of air and soil warming is also likely to have cumulative effects on plant-soil interactions (Bardgett et al. 2005), nutrient recycling and ecosystem C flux.

Like other environmental manipulation experiments, ITEX has had to be selective in terms of the environmental change scenarios it investigates. In this case it is summer warming that has formed the focus. It must be emphasized, however, that there is a strong consensus among climate models that the magnitude of warming during the winter will be very significantly greater in mid- and high-latitudes than the magnitude of summer warming (Overpeck et al. 1997; ACIA 2005), as has been the case over the past 50 years (Serreze et al. 2000); for this reason there is a growing interest in winter ecology in the tundra biome (both arctic and alpine) (see Callaghan et al. 2004a). This argument does not, however, invalidate ITEX because the modest warming produced by the OTCs is consistent with predictions of warming during this season in the coming decades. ITEX could not, however, incorporate parallel environmental change drivers (e.g. elevated CO₂ concentrations, or increased fluxes of UV-B radiation at the surface) in a fully factorial design within the original concept. To do so would have restricted the geographical coverage of the programme and, arguably, also the time-scales over which it could be maintained. Callaghan et al. (2004a), as a contribution to ACIA (2005), synthesize the effects of climate change, UV-B, and other environmental change drivers (e.g. elevated CO₂ concentrations and deposition of airborne N-containing pollutants) on arctic tundra and polar desert ecosystems, and their analysis draws from environmental manipulation experiments as well as palaeoenvironmental and natural gradient studies.

Comparison with alternative approaches

The use of transects and gradients (so-called ‘space-for-time’ substitution) is potentially useful for indicating ‘end-points’ of change (Epstein et al. 2004), but in the context of rapid and multifaceted change it is unclear the extent to which trajectories of response towards a notional fixed ‘target’ are relevant (it can be said that the ‘goal posts’ are likely to shift). Other issues

which must be considered are whether or not contemporary systems are at ‘equilibrium’ with present environment (if not then constructing precise and reliable bioclimatic envelopes for existing organisms or communities is problematic), and the extent to which space-for-time approaches are influenced by interspecific interactions and dispersal ability (Brooker et al. 2007). Linked with this, space-for-time substitution and bioclimatic envelope approaches give no information about rates of change of contrasting ecosystem components.

Although multi-proxy palaeoenvironmental approaches (see e.g. Dalton et al. 2005) are now enabling the effects of past climate change to be teased-apart from other changes (e.g. acid deposition or landscape developmental processes) they cannot provide information on future environmental scenarios for which no past analogues exist. Furthermore, superimposed upon the global change drivers there are direct human activities (e.g. the development of transport and industrial infrastructure) which are altering the dispersal capabilities of organisms, including invasive species. Palaeoenvironmental approaches are, nonetheless, extremely valuable in improving understanding of the linkages between biosphere, global biogeochemical cycles and the climate system of the past (Kutzbach et al. 1996), as well as for providing information on past environmental variability (rates and magnitudes of change) against which future change can be assessed (Callaghan et al. 2004b). As stated earlier in this paper, however, we cannot consider the past as *the* key to the future, but as *a* key to the future (as noted by Adams and Woodward back in 1992).

Conclusion

Environmental manipulation experiments clearly fail to address biological processes and their responsiveness to change on evolutionary timescales. The key constraints concern treatment artefacts, restricted spatial and temporal coverage, and limited incorporation of multiple

environmental change drivers. They do, however, provide valuable information on short- to medium-term (seasonal through decadal) phenological, growth, reproduction, and ecosystem responses which have a direct bearing on ecosystem-atmosphere interactions (through changes in surface roughness and albedo, and net exchange of greenhouse gases), species interactions, and, potentially, trophic cascades (with careful design; see Gough et al. 2007). They are also relevant for quantifying and understanding the provision of ecosystem products and services. Arguably, they provide the linchpin linking palaeoenvironmental proxies and transect (space-for-time substitution) approaches because they provide information on the dynamics of contrasting ecosystem components in response to change across timescales of direct relevance to Humankind. They also enable specific hypotheses to be tested directly.

Understanding how the arctic and alpine flora will change in response to global change drivers will require much more than a sound appreciation of their evolutionary history and genetics. This is, of course, essential, alongside robust biogeographical information linking distributions with bio-climatic envelopes. But the multifaceted nature of on-going changes, their lack of past analogues, and the dramatic rates of change, all mean that, even acknowledging their weaknesses, environmental manipulation experiments remain a key tool for understanding and predicting the effects of environmental change on terrestrial ecosystems.

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Figure legends

Figure 1. The International Tundra Experiment (ITEX) was designed to be based upon individual species responses to a single environmental change driver (specifically climate warming during the thaw period). The upper box (physico-chemical environment) represents climate, and the left hand arrow links this with individual ‘ITEX species’ responses. ITEX syntheses (Arft et al. 1999; Walker et al. 2006) have sought to examine responses at the species level, and then to determine if broader generalizations can be made when these are aggregated into several functional types (FTs) or growth forms (e.g. deciduous and evergreen dwarf shrubs, forbs and graminoids, mosses and lichens). The return arrows from communities/vegetation and ecosystems/landscape to individual species identify the possibility that individual species’ responses to warming could be modulated by the communities of which they are part (e.g. via competition). The continuing upwards arrows are designed to show that community/ecosystem-level changes have the potential to feedback on the physico-chemical environment through alterations in surface properties and the exchange of biogenic trace gases (e.g. CH₄), CO₂ and water vapour between ecosystems and the atmosphere.

Figure 2. Schematic diagram to illustrate that plant community responses to change (e.g. warming) only occur via individual species’ responses (thus communities, as an entity, cannot respond to change). The magnitude and rate of species’ and community responses to change will also be affected by both abiotic (e.g. nutrient availability; depth of thaw; disturbance) and biotic ‘modifiers’ (e.g. herbivory).

Figure 3. This schematic diagram illustrates the performance of two plant species (in terms of net primary productivity, NPP) across a gradient of temperature (which could be expressed as mean

temperatures over a growing season, or as some other metric of thermal energy availability, e.g. growing degree days (GDDs), or in the case of tundra plants thawing degree days (TDDs), representing accumulated ‘thermal time’). Increasing temperature in tundra ecosystems will co-vary with other abiotic factors (e.g. precipitation or depth of the active layer) and also with biotic factors, such as intensity of competition or herbivory. Intensity of competition (e.g. for light or soil nutrients) is likely to increase from the extreme polar deserts and alpine fellfields to the more closed tundras of the Low Arctic and mid- to low alpine (perhaps leading to a skewed NPP curve, with values dropping more steeply at the warmer end of the distribution due to competition interactions). Note that, according to this scheme, a given temperature increase (ΔT) could produce quite different outcomes depending on where in the species’ range the warming occurs, and on the ecological amplitude and competitiveness of the species concerned (shown by small arrows within the two areas demarcated by A – B and C – D). Thus warming at the colder end of the distribution could markedly improve plant performance (but note the contrasting magnitude of response for the two species), while toward the warmer end of the distribution increased respiratory demands, or intensity of competition, could reduce NPP to the extent that the species dies out, or is forced-out, of the community. Note, by contrast, that the NPP of one of the two species is unaffected in the range C – D, and this might represent a competitive plant functional type.

Figure 4. Time scales of response to temperature change by various ecosystem processes and components. Each of the processes or components shown in the figure affect net ecosystem production either directly or indirectly. For convenience, they are grouped into categories: vegetation, soils, and other. The intent is to show how different processes and components respond to temperature change at different rates; hence, the overall ecosystem response (the result

of the individual responses and their interactions) may be very different in the long-term versus the short-term. The arrow at the top identifies (approximately) the longest environmental manipulation experiments: Extrapolation of conclusions beyond this must necessarily be done with caution, and with reference to other approaches (e.g. palaeoenvironmental or gradient-based). Many other processes and components could be added to this figure. (Ps, photosynthesis; Rs, respiration; SOM, soil organic matter.) [modified from Shaver et al. 2000]

Figure 5. [permission from authors must be sought] Thawing degree day accumulation (TDD_{sm}) from snow-melt for the 1995 and 1996 thaw periods at ITEX wet meadow tundra plots near Barrow, Alaska. The mean (thick line) and range (thin line), based on $n \geq 7$ plots, are shown for control (unwarmed) and OTC (warmed) plots. Note that the warmed plots in 1995 have a lower TDD_{sm} than unwarmed plots in 1996 due to interannual variability in weather conditions. Plant phenology and growth in these two situations was very similar in the contrasting years, providing a biotic validation of ITEX OTCs.