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4 Experimental approaches to predicting the future of tundra plant communities

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21 **Abstract**

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

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

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

## 44 **Introduction**

45 Tundra ecosystems are reported to be undergoing pan-arctic changes in community composition  
46 (Myneni et al. 1997; Sturm et al. 2001; Tape et al. 2006), with evidence of related changes in the  
47 mid-latitude Alpine (Grabbherr et al. 1994; Walther et al. 2005; Cannone et al. 2007; Pauli et al.  
48 2007). These changes are being linked to climate warming, and more specifically to earlier snow-  
49 melt and a lengthening growing season. There is a strong consensus among general circulation  
50 models of the earth's climate that climate change at northern high latitudes will accelerate into  
51 the 21<sup>st</sup> Century (ACIA 2005; IPCC 2007). The rate and magnitude of warming in these regions  
52 are predicted to exceed the global average substantially, although regional variations in  
53 precipitation (and hence surface water balance) are much less clear. The tundra biome will,  
54 nonetheless, represent a sensitive indicator of change. Furthermore, the land surface and  
55 atmosphere are strongly coupled in the Arctic, and changes in the structure and functioning of  
56 tundra ecosystems have the potential to impact on global biogeochemistry and the climate system  
57 through changes in surface energy balance, biogenic trace gas fluxes, and regional hydrology  
58 (Chapin et al. 2000, 2005). There is therefore considerable urgency to improve the understanding  
59 and prediction of ecosystem dynamics in response to global change drivers.

60 But climate change is not operating in isolation from other drivers of change in the Arctic:  
61 Environmental change has multiple facets (including direct land-use change). This makes  
62 prediction of ecosystem effects of change a serious intellectual and practical challenge. For  
63 example, increasing concentrations of carbon dioxide (CO<sub>2</sub>) in the atmosphere have a global  
64 dimension (IPCC 2007), and are unequivocally-linked with anthropogenic activity. More variable  
65 regionally, but also with a strong global dimension, is the increased deposition of airborne N-  
66 containing contaminants into remote locations, including arctic and alpine ecosystems.  
67 Furthermore, stratospheric ozone depletion over high latitudes increases fluxes of UV-B radiation

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

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

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

87

### 88 **An experimental approach to understanding global warming and the tundra biome**

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

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

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

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

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

124 Henry and Molau (1997) reviewed and synthesized the results of the early (1-3 yr) site- and  
125 species-specific investigations of vegetative and reproductive growth and phenology without the  
126 benefit of statistical meta-analysis. They concluded that all species measured at that stage  
127 responded to ITEX temperature manipulations, but that they responded largely  
128 individualistically. Although it was difficult to distinguish clear patterns of response related to  
129 growth form, forbs (e.g. *Ranunculus glacialis*) appeared the most responsive group to warming  
130 (Molau 1997) but the range of responses within this group was large. Results also suggested that  
131 plants towards the colder limits of their ranges responded more strongly to warming than plants  
132 of the same species further south (e.g. *Saxifraga oppositifolia* and *Cassiope tetragona*), and there  
133 were indications of stronger responses to experimental warming during ‘colder’ growing seasons  
134 (both of which are consistent with Figure 3). Increases in reproductive growth (seed set, seed  
135 weight, and germinability) also appear to be general responses to warming in the short-term:  
136 Wookey et al. (1995), for example, reported a 141% increase in seed germinability of *Dryas*  
137 *octopetala* at a high arctic polar semi-desert, Svalbard, in association with warming over three  
138 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).

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

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

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

190

### 191 **Limitations with environmental manipulation experiments**

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

198 Experiments which are sophisticated in nature (involving, for example, CO<sub>2</sub>, UV-B or  
199 ‘active’ temperature manipulations - e.g. heating cables or lamps - either singly or in factorial  
200 combination) are usually restricted geographically to a few sites with suitable infrastructure  
201 (Harte and Shaw 1995; Johnson et al. 2002). This carries with it the problem, however, that  
202 results might be difficult to extrapolate to regional, or even local scales (Epstein et al. 2004),  
203 depending on whether or not ‘zonal’, or other more specialized plant communities, were selected  
204 for investigation. A counter-argument in an arctic-alpine context, however, is that micro- or  
205 meso-topographic variations have a disproportionate effect on thermal environment and water-  
206 balance, and for this reason substantial community variability at the local scale (Walker 2000)  
207 can be exploited to make inferences about how ecosystems much further apart would respond to  
208 the same drivers of change. This hypothesis might have some validity, but ‘scaling-up’ to reach  
209 regional conclusions on the basis of results from one or a few sites in the same macro-climatic or

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

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

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

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

269

#### 270 **ITEX-specific constraints?**

271 As a 'passive' warming experiment using small plots (i.e. not reliant upon heat inputs requiring  
272 an electrical supply, such as soil heating cables, or above-ground radiators; see Harte and Shaw  
273 (1995)), ITEX is associated with several artefacts. ITEX uses open-topped chambers (OTCs) to  
274 produce a modest net warming of near-surface temperatures (generally around 1.2 – 1.8 °C). The  
275 advantages and disadvantages of this design are discussed by Kennedy (1995), Marion et al.  
276 (1997), Wookey and Robinson (1997), and Hollister and Webber (2000), but in summary most of  
277 the heating is during the day because it is dependent upon incident solar radiation, there is a small  
278 attenuation of light (especially at low solar angles), wind-speeds are generally reduced within the  
279 OTCs, and surface moisture may also be reduced due to exclusion of the precipitation around the  
280 edges of the chambers. In addition, due to lateral heat-sink effects, soil warming may not reach

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

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

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

305 Like other environmental manipulation experiments, ITEX has had to be selective in terms of  
306 the environmental change scenarios it investigates. In this case it is summer warming that has  
307 formed the focus. It must be emphasized, however, that there is a strong consensus among  
308 climate models that the magnitude of warming during the winter will be very significantly greater  
309 in mid- and high-latitudes than the magnitude of summer warming (Overpeck et al. 1997; ACIA  
310 2005), as has been the case over the past 50 years (Serreze et al. 2000); for this reason there is a  
311 growing interest in winter ecology in the tundra biome (both arctic and alpine) (see Callaghan et  
312 al. 2004a). This argument does not, however, invalidate ITEX because the modest warming  
313 produced by the OTCs is consistent with predictions of warming during this season in the coming  
314 decades. ITEX could not, however, incorporate parallel environmental change drivers (e.g.  
315 elevated CO<sub>2</sub> concentrations, or increased fluxes of UV-B radiation at the surface) in a fully  
316 factorial design within the original concept. To do so would have restricted the geographical  
317 coverage of the programme and, arguably, also the time-scales over which it could be maintained.  
318 Callaghan et al. (2004a), as a contribution to ACIA (2005), synthesize the effects of climate  
319 change, UV-B, and other environmental change drivers (e.g. elevated CO<sub>2</sub> concentrations and  
320 deposition of airborne N-containing pollutants) on arctic tundra and polar desert ecosystems, and  
321 their analysis draws from environmental manipulation experiments as well as  
322 palaeoenvironmental and natural gradient studies.

323

#### 324 **Comparison with alternative approaches**

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

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

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

348

## 349 **Conclusion**

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

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

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

370

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376

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552 **Figure legends**

553 **Figure 1.** The International Tundra Experiment (ITEX) was designed to be based upon individual  
554 species responses to a single environmental change driver (specifically climate warming during  
555 the thaw period). The upper box (physico-chemical environment) represents climate, and the left  
556 hand arrow links this with individual 'ITEX species' responses. ITEX syntheses (Arft et al. 1999;  
557 Walker et al. 2006) have sought to examine responses at the species level, and then to determine  
558 if broader generalizations can be made when these are aggregated into several functional types  
559 (FTs) or growth forms (e.g. deciduous and evergreen dwarf shrubs, forbs and graminoids, mosses  
560 and lichens). The return arrows from communities/vegetation and ecosystems/landscape to  
561 individual species identify the possibility that individual species' responses to warming could be  
562 modulated by the communities of which they are part (e.g. via competition). The continuing  
563 upwards arrows are designed to show that community/ecosystem-level changes have the potential  
564 to feedback on the physico-chemical environment through alterations in surface properties and  
565 the exchange of biogenic trace gases (e.g. CH<sub>4</sub>), CO<sub>2</sub> and water vapour between ecosystems and  
566 the atmosphere.

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

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

574 temperatures over a growing season, or as some other metric of thermal energy availability, e.g.  
575 growing degree days (GDDs), or in the case of tundra plants thawing degree days (TDDs),  
576 representing accumulated ‘thermal time’). Increasing temperature in tundra ecosystems will co-  
577 vary with other abiotic factors (e.g. precipitation or depth of the active layer) and also with biotic  
578 factors, such as intensity of competition or herbivory. Intensity of competition (e.g. for light or  
579 soil nutrients) is likely to increase from the extreme polar deserts and alpine fellfields to the more  
580 closed tundras of the Low Arctic and mid- to low alpine (perhaps leading to a skewed NPP curve,  
581 with values dropping more steeply at the warmer end of the distribution due to competition  
582 interactions). Note that, according to this scheme, a given temperature increase ( $\Delta T$ ) could  
583 produce quite different outcomes depending on where in the species’ range the warming occurs,  
584 and on the ecological amplitude and competitiveness of the species concerned (shown by small  
585 arrows within the two areas demarcated by A – B and C – D). Thus warming at the colder end of  
586 the distribution could markedly improve plant performance (but note the contrasting magnitude  
587 of response for the two species), while toward the warmer end of the distribution increased  
588 respiratory demands, or intensity of competition, could reduce NPP to the extent that the species  
589 dies out, or is forced-out, of the community. Note, by contrast, that the NPP of one of the two  
590 species is unaffected in the range C – D, and this might represent a competitive plant functional  
591 type.

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

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

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