Ecosystem feedbacks and cascade processes: understanding their role in the responses of arctic and alpine ecosystems to environmental change

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Abstract

Global environmental change, related to climate change and the deposition of airborne N-containing contaminants, has already resulted in shifts in plant community composition among plant functional types in arctic and temperate alpine regions. In this paper, we review how key ecosystem processes will be altered by these transformations, the complex biological cascades and feedbacks that may result, and some of the potential broader consequences for the earth system. Firstly, we consider how patterns of growth and allocation, and nutrient uptake, will be altered by the shifts in plant dominance. The ways in which these changes may disproportionately affect the consumer communities, and rates of decomposition, are then discussed. We show that the occurrence of a broad spectrum of plant growth forms in these regions (from cryptogams to deciduous and evergreen dwarf shrubs, graminoids and forbs), together with hypothesized low functional redundancy, will mean that shifts in plant dominance result in a complex series of biotic cascades, couplings and feedbacks which are supplemental to the direct responses of ecosystem components to the primary global change drivers. The nature of these complex interactions is highlighted using the example of the climate-driven increase in shrub cover in low arctic tundra, and the contrasting transformations in plant functional composition in mid-latitude alpine systems. Finally, the potential effects of the transformations on ecosystem properties and processes which link with the earth system are reviewed. We conclude that the effects of global change on these ecosystems, and potential climate-change feedbacks, can not be predicted from simple empirical relationships between processes and driving variables. Rather, the effects of changes in species distributions and dominances on key ecosystem processes and properties must also be considered, based upon best estimates of the trajectories of key transformations, their magnitude and rates of change.

Introduction

There is growing evidence of a pan-arctic "greening" in arctic tundra (Myneni *et al.* 1997; Sturm *et al.* 2001; Epstein *et al.* 2004; Chapin *et al.* 2005; Tape *et al.* 2006), and that related changes are occurring in mid-latitude alpine regions (Walther *et al.* 2005; Pauli *et al.* 2007; but see Cannone *et al.* 2007). For the Arctic, this greening has been linked explicitly to a shift in plant community composition, namely an increase in 'shrubbiness' (Sturm *et al.* 2001; Epstein *et al.* 2004; Chapin *et al.* 2005; Tape *et al.* 2006). In alpine[1] regions there are significant shifts in plant community composition, such as the balance of graminoids and forbs (Klein *et al.* 2007; Sebastià 2007), and increased shrubbiness is common both in response to climate warming (Sanz-Elorza *et al.* 2003) and abandonment or extensification of sub-alpine grassland management (Tappeiner & Bayfield 2002). These shifts in plant species distributions and community composition have the potential to substantially alter how arctic and alpine ecosystems respond to, and feedback on, global change.

There are compelling reasons why arctic and alpine ecosystems merit attention. First, they represent a 'bellwether of change'. The argument that organisms close to the limits of their physiological tolerances may be particularly susceptible to environmental change remains robust, and it is well-documented that high latitude and high altitude ecosystems will be especially responsive to rapid climatic changes in the coming decades (Overpeck *et al.* 1997; Serreze *et al.* 2000; Beniston 2005; ACIA 2005; Körner *et al.* 2005; Euskirchen *et al.* 2006; IPCC 2007a,b). Second, recent research has demonstrated powerful coupling between arctic terrestrial ecosystems, surface energy budget, and atmospheric chemistry (Chapin *et al.* 2000), especially CO_2 and CH_4 concentrations. The recognition that substantial feedbacks exist between the biosphere and the climate system has gathered pace since global circulation models explicitly incorporated basic ecosystem properties such as surface roughness and

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[1] Subsequently referred to as 'alpine' only (but excluding low-latitude and equatorial alpine systems)

albedo (see Foley *et al.* 1994). Finally, because arctic and alpine ecosystems contain a broad

spectrum of plant growth forms (cryptogams, deciduous and evergreen dwarf shrubs,

graminoids and forbs) shifts in dominance among these forms potentially represent a

substantial change in ecosystem structural characteristics and functional properties.

Our principal aim here is to review the role of plant species, growth forms and functional

types (PFTs[2]; Lavorel *et al.* (1997)) in determining ecosystem responses to global change in

Arctic and alpine ecosystems. The review takes an integrated approach to above- and below-

ground processes, linking PFTs both with rhizosphere properties and processes, and with soil

microbial processes and populations, as well as with both invertebrate and vertebrate

herbivores. Firstly, we summarize the potential effects of changes in plant functional

composition on patterns of growth and allocation, nutrient uptake, decomposition and

herbivory, as well as feedbacks among them (see Fig. 1). We consider these processes to be

the minimum that must be considered in order to make predictions of the ecosystem-level

response to change that might be initiated by a shift in PFTs. Secondly, we give examples of

on-going transformations[3] in arctic and alpine ecosystems, considering the initial drivers of

change and reviewing what is known of the biotic feedback and cascade[4] processes within the

ecosystems (this section relates to the 'species effects' box within Fig. 1). Finally, we

illustrate how such species-related effects are linked more generally with the earth system

(right-hand box of Fig. 1).

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[2] Plant functional types, including growth form-based classifications and continuous traits, form the focus for a broad spectrum of ecological research attempting to quantify the relationships between ecosystem structure and function (Chapin *et al.* 1996; Lavorel & Garnier 2002; Cornelissen *et al.* 2004, 2007a; Garnier *et al.* 2004; Dorrepaal *et al.* 2005, 2007; Bråthen *et al.* 2007; Díaz *et al.* 2007a) and to make robust generalizations about these relationships (Lavorel *et al.* 2007)

[3] Transformations are defined in this context as shifts in plant community composition among Plant Functional Types

[4] We apply a broader definition to 'cascade' than the 'trophic cascades' discussed by Polis *et al.* (2000). In the present context the term applies both to the trophic and the physico-chemical consequences of shifts in plant community composition. The term cascade is also used to evoke a directional flow (see Swift, Heal & Anderson (1979)) rather than simply biotic and abiotic interactions

Ecosystem processes, plant growth forms and PFTs

Growth and allocation

Because the dominant plant form (*sensu* Chapin *et al.* 1996) in arctic and alpine tundra may
be woody or herbaceous, evergreen or deciduous, aerenchymatous or non-aerenchymatous,
mycorrhizal or non-mycorrhizal, vascular or non-vascular, changes in species composition
play a particularly important role in regulating both responses and feedbacks to change.
These contrasting plant forms differ sharply in the controls on their rates and patterns of
growth, and in their allocation of essential elements among tissues like leaves, stems, below-
ground storage tissues, and roots.

1. Element use efficiencies, and allocation among tissues (root, rhizome, stem, leaf, and
inflorescence): Typically, growth of arctic and alpine plants is limited strongly by availability
of essential elements such as nitrogen (N) or phosphorus (P), or both (Bliss *et al.* 1984;
Shaver *et al.* 1992; Güsewell 2004; Olofsson *et al.* 2004; Weintraub & Schimel 2005;
Soudzilovskaia *et al.* 2007). Differences in use of limiting elements are closely related to
differences in chemical composition and the physical properties of individual tissues. The N
concentrations of leaves, for example, vary consistently among growth forms; evergreen
leaves typically have lower N concentrations than deciduous leaves (Antunez *et al.* 2001;
Díaz *et al.* 2004; Wright *et al.* 2004; but see Villar *et al.* (2006)). This applies also to arctic
species (Hobbie and Gough 2002; Hobbie *et al.* 2005), but these differences are not usually
maintained in litter because of more efficient withdrawal of N from senescing leaves by
deciduous plants (Quested *et al.* 2003). Leaves have greater concentrations of N than woody
stems (Shaver *et al.* 2001) because of the greater concentration of rubisco in leaves and lignin

in stems, so the overall concentration of N in above-ground biomass reflects the relative abundance of leaf versus stem tissues (van Wijk *et al.* 2005). Furthermore, because the total amount of plant biomass and primary production per unit of N varies greatly among plant tissue types and with the relative amount of each tissue type, species can differ greatly in the amount of production or biomass accumulation per unit of N (see final section; Links with the earth system). Although, on average, inflorescences make up only a small portion of plant biomass and production in arctic and alpine vegetation, in some species and in some years inflorescence production can be a significant proportion of a species' total production (Fabbro & Körner 2004). Furthermore, reproductive tissues often have contrasting chemical composition from vegetative parts (Buxton & Marten 1989), leading to markedly faster decomposition and nutrient release, with repercussions for nutrient cycling and patchiness. Finally, differences in allocation among above and below-ground plant parts also determine differences in the location of litter inputs to the decomposer community (Fig. 1).

2. <u>Morphological and genetic constraints on growth rates:</u> Many arctic and alpine species are limited in the amount of growth that they can achieve in each year by the number and characteristics of the perennating buds (i.e. those surviving from the previous year) and the number and size of leaves associated with a single meristem (Shaver & Chapin 1986; Shaver & Laundre 1997; Bret-Harte *et al.* 2001). Most species of deciduous and evergreen shrubs, for example, and many forbs, can take up and store resources, but are limited in their ability to increase their extension growth in the short-term because they must first form new buds, containing new leaves and stems (Shaver & Chapin 1986; Bowman & Conant 1994; Diggle 1997). Graminoids, by contrast, often respond more rapidly to changes in resource availability because their leaves grow from basal, intercalary meristems, and are less limited in the size of the leaves that can be produced (Shaver & Laundre 1997). A second set of

controls relates to the total population of meristems available for growth. The deciduous dwarf shrub *Betula nana*, for example, maintains a large population of short shoots that normally produce only 2-3 leaves with very short internodes. When resource availability is increased, these short shoots can elongate rapidly, producing more leaves, each with an axillary meristem that can produce another shoot (Plate 1a,b). As a result, *B. nana* can branch much more rapidly than other shrub species, creating new sinks for resources and more rapid growth (Bret-Harte *et al.* 2001). The response of species also depends on genetic constraints. Sørenson (1941) distinguished two phenological patterns in tundra plants: periodic species, characterized by a fixed growing period controlled by genetic constraints; and aperiodic species, for which both growth and the production of new leaves are maintained until conditions become unfavorable. Consequently, in the event of a lengthened growing season, periodic species, such as *Polygonum bistorta* in the Arctic (Starr *et al.* 2000) and *P. viviparum* or *Carex foetida* in alpine meadows (Diggle 1997; Baptist *et al.* unpublished), may be disadvantaged compared to aperiodic species such as *Dryas octopetala* (Welker *et al.* 1997) or *Ranunculus adoneus* (Galen & Stanton 1993).

3. <u>Controls on plant height and canopy structure</u>: Often, changes in community composition are related to the inherent potential of some species to grow taller than others. To do this requires the ability to produce erect stems, which is a major reason why woody species are more abundant in more productive vegetation with larger standing biomass. Because of the growth of such shrubs, the entire community's canopy may increase in height with warming (Wahren *et al.* 2005). The N requirements for the production of woody stems are less than for leaf production (per unit mass) because most of the costs are for structural components rather than metabolically active systems with high protein requirements (Chapin 1989; Shaver *et al.* 2001). Generally there are fewer mosses and lichens when the vegetation is taller and more

productive because of shading (Cornelissen *et al.* 2001; Klanderud & Totland 2005; Jägerbrand *et al.* 2006; Olofsson 2006; Walker *et al.* 2006). However, it has been noted that decreasing productivity, as a result of warming-related soil water deficits, promotes short rosette forbs at the expense of taller grasses in sub-alpine grassland (Sebastià 2007).

4. Belowground allocation and interactions with the rhizosphere: Allocation of resources below-ground as root and rhizome growth, exudation of labile C into the rhizosphere, and the costs and benefits of mycorrhizal associations, are some of the least well-understood, but potentially important aspects of plant growth and allocation in arctic and alpine ecosystems. In general, arctic and alpine plants have a high proportion of their biomass below-ground relative to plants in other biomes (Jackson *et al.* 1996; Körner 1999). Most arctic and alpine vascular plants are mycorrhizal (Cripps & Eddington 2005), and recent estimates suggest that, at least for ectomycorrhizal species (e.g. of the genera *Salix* and *Betula*), symbiotic fungi may receive 10-30% of net C fixation (Read *et al.* 2004) with allocation patterns potentially dependent on soil nutrient availability (Högberg *et al.* 2003). Whilst exudation of C-rich compounds from roots influences soil biomass and microbial activity, and other soil processes such as C and nutrient dynamics (Nguyen 2003), little is known about their role in cold biomes. However, patterns of root exudation are known to vary markedly between plant species, leading to substantial differences in the composition and activity of rhizosphere microbial communities (Wardle *et al.* 2004), and, in wet tundra, root exudation plays a potentially important role through the promotion of methanogenesis and hence soil C fluxes (Ström *et al.* 2003, 2005). These different pathways of C input below-ground are important because they vary among species and have different feedbacks on element cycling.

Nutrient uptake

Here we document the ways in which contrasting plant species and PFTs differ in acquisition of nutrients, in terms of the chemical forms of the compounds used, the types of mycorrhizal symbioses that exist, as well as the location and timing of uptake.

1. Chemical form of compounds used: The ability of vascular plants in arctic ecosystems to utilize organic forms of nutrients is well established (Lipson & Näsholm 2001; Weintraub & Schimel 2005), irrespective of mycorrhizal status (Chapin *et al.* 1993; Lipson & Monson 1998; McKane *et al.* 2002), and there is evidence that organic N can form a significant component of the nitrogen budget of arctic cryptogams (Kielland 1997). However, differences in the relative importance of contrasting inorganic versus organic sources are currently difficult to evaluate within a PFT context, although even among graminoids, differences in uptake of organic and inorganic forms of N are pronounced (McKane *et al.* 2002; Weigelt *et al.* 2005), and are often as large as between PFTs. Furthermore, free amino acids in soil solution are both very labile and readily scavenged by both free-living and symbiotic microorganisms (Kielland *et al.* 2007), and this further confounds any quantitative assessment of the relative significance of inorganic versus organic nutrient uptake. Similarly, in bryophytes there appear to be species-specific differences in the uptake of contrasting N-containing compounds (Kielland *et al.* 1997; Paulissen *et al.* 2004; Forsum *et al.* 2006; Krab *et al.* 2008). Environmental change-induced alterations in the relative abundances of these compounds thus potentially alter competition among plants, and between plants and soil microbes, and the consequences of such feedbacks and cascades remain poorly understood.

2. Mycorrhizal symbioses: Although sedges such as *Eriophorum vaginatum* are predominantly non-mycorrhizal, many other graminoids and forbs form arbuscular mycorrhizal (AM) associations, and dwarf shrubs usually have either ecto-mycorrhizal

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(ECM) or ericoid mycorrhizal (ERM) symbioses (Read *et al.* 2004). There is also evidence of liverworts and hornworts forming fungal symbioses, but no evidence for such symbioses with mosses (Read *et al.* 2000; Cornelissen *et al.* 2007b). Ecto-mycorrhizal and ERM fungi are considered to be more effective at N capture than AM fungi (Leake *et al*. 2004), and may be responsible for between 60 and 90% of the N uptake in nutrient-limited systems (Hobbie & Hobbie 2006). Furthermore, mycorrhizal fungi differ in their ability to play a direct role in the breakdown of soil organic matter (SOM). Certain ECM species have highly-developed proteolytic capacities, although these may still be less than in many ERM and saprotrophic groups (Read *et al.* 2004). It also appears that the fungi with the greatest proteolytic capacities may be prevalent in the most N-limited ecosystems (Lilleskov *et al*. 2002). Whilst AM fungi may also stimulate decomposition (Hodge *et al*. 2001), there seems to be less evidence of them producing the amounts of extra-cellular enzymes required to increase SOM breakdown (Leake *et al*. 2004). By playing a direct role in decomposition processes, and actively taking up simple organic forms of N, ERM and ECM fungi allow their plant partners (trees and shrubs) to by-pass the conventional N-cycle and out-compete other groups of plants in nutrient-limited conditions.

3.   Location of uptake: Differences in root architecture between species appear to affect the depth in the soil at which the majority of nutrients are acquired (McKane *et al.* 2002). Rooting depth may vary substantially within (Shaver & Billings 1975) and between PFTs (Jackson *et al.* 1996), and it is altered by ecosystem warming and changes in active layer[5] depth (Walsh *et al.* 2005). However, the response to warming may be mediated more through changes in species composition rather than through changes in rooting depth per se (Björk *et al.* 2007; but see Sullivan *et al.* (2007)).

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[5] The active layer is the seasonally thawed layer overlying
Permafrost (Walsh *et al.* 2005)

4. Timing of uptake: There are also phenological differences in root development and activity between species, PFTs and communities (McKane *et al.* 2002; Weintraub & Schimel 2005). Bilbrough *et al.* (2000) indicated, for example, that N uptake by alpine species during snowmelt was 7 to 12% of the whole season's uptake, depending upon growth form, compared with only 0.1% for arctic species. In addition, changes in climate and the timing of snow cover may alter seasonal availability of different nutrients (Schimel *et al.* 2004), and therefore competition between different plant species and microbes (Lipson *et al.* 1999; Bardgett *et al.* 2005).

5. N-fixation: N-fixation by cyanobacteria growing in lichens (Weiss *et al.* 2005; see references in Cornelissen *et al.* (2007b)) or epiphytically on bryophytes (Basilier *et al.* 1978; Solheim *et al.* 1996; Zackrisson *et al.* 2004), may represent an important component of the N-cycle in the Arctic, especially in highly N-limited systems where nodulated plants are rare (Hobara *et al.* 2006). Weiss *et al.* (2005) found that the abundance of the N-fixing lichens *Peltigera aphthosa* and *Peltigera polydactyla* differed between two common Alaskan low arctic communities, so that despite no difference in 'per biomass' fixation rates, overall inputs of N to the two communities differed. At the nearby Imnavait Creek watershed, Hobara *et al.* (2006) estimated N-fixation of 0.8 to 1.31 kg N ha^{-1} yr^{-1}, representing 85 to 90% of total watershed N inputs. N-fixation was also observed, in laboratory incubations, to be highly sensitive to moisture, temperature and light intensity, both in soils sampled from Imnavait Creek (Hobara *et al.* 2006) and from high arctic sites in Svalbard (Zielke *et al.* 2002). In addition, any change in the distribution of alder species (Tape *et al.* 2006), or direct effect of temperature (Uliassi *et al.* 2002) and elevated CO_2 (Vogel *et al.* 1997) on N-fixation rates,

will have the potential to alter N-availability in the low Arctic. Alder is significant because it is a widely distributed N-fixing tree/shrub in low arctic regions.

In alpine ecosystems, symbiotic N-fixation may also be an important component of the N cycle. For example, at Niwot Ridge, Colorado, *Trifolium* spp. with their symbiont *Rhizobium* spp. are responsible for 4.9 kg N fixation ha^{-1} yr^{-1} (Bowman *et al.* 1996), which represents ca. 1-13% of the annual N assimilation by plants (Fisk & Schmidt 1995) in these communities. It is thought, however, that N fixation may be of benefit principally to the legumes, as production of other plants was similar in *Trifolium* patches to that in the surrounding tundra (Thomas & Bowman 1998). Although not tested in alpine regions, increased dominance of legumes over grasses, which has been observed in grasslands subject to elevated atmospheric carbon dioxide concentrations (Hanley *et al.* 2004), could induce a positive feedback on microbial activity and carbon mineralization due to enhanced soil nutrient availability and decomposition of nutrient-rich litter.

Decomposition

The rate and pathway of litter decomposition is controlled by a hierarchy of factors, with climate (temperature and moisture), litter quality, and the soil food web being the most important (Swift *et al.* 1979; Lavelle *et al.* 1993; Aerts 2006). Chemical composition and physical properties of leaf litter differ consistently and significantly among PFTs (Hobbie 1996; Aerts & Chapin 2000; Quested *et al.* 2003; Dorrepaal *et al.* 2005, 2007), with a number of studies demonstrating that mosses (especially *Sphagnum* spp.) decompose very slowly (Hobbie *et al.* 2000), and that differences exist between vascular PFTs, with rates of breakdown varying in the order: forbs > graminoids ≥ deciduous shrubs > evergreen shrubs (Cornelissen 1996; Quested *et al.* 2003; Dorrepaal *et al.* 2005; Cornelissen *et al.* 2007a). For

high-latitude peatlands, however, climatic and nutritional constraints may promote convergence towards nutrient-efficient plant traits, resulting in rather similar decomposition rates among the vascular PFTs, despite their contrasting litter composition (Dorrepaal *et al.* 2005). This suggests that, in these ecosystems, overall rates of decomposition are determined mainly by the litter mass ratio between mosses and vascular plants (*cf.* Dorrepaal 2007). Thus any shifts in the cover and biomass of these two growth forms will not only affect decomposition directly, but also indirectly, via altered energy and water balance (Cornelissen *et al.* 2007b; Douma *et al.* 2007; Gornall *et al.* 2007).

While high-latitude warming associated with climate change has the potential to accelerate leaf litter breakdown rates, concurrent changes in PFT distributions may modify the magnitude or sign of this response. It should also be borne in mind, however, that the volume of soil in which decomposer metabolism is significant will depend on the depth of the active layer (Walsh *et al.* 2005) in permafrost regions. In arctic tundra it is conceivable that the temperature-driven increase in litter decomposition rates might be counteracted to some extent by the observed shrub expansion, because leaf litter decomposition of shrubs is slower than that of the forbs and the graminoids that they replace (Cornelissen *et al.* 2007a). It is not yet known how this negative effect on decomposition compares in magnitude with changes in decomposition (potentially both positive or negative) mediated by changes in snow cover (Chapin *et al.* 2005; Sturm *et al.* 2005a,b; Weintraub & Schimel 2005, see below) or depth of the active layer (Schuur *et al.* 2007). Also, since tundra shrubs tend to have shallower root systems than graminoids (Mack *et al.* 2004) decomposition of their root litter may be enhanced by warming upper soil horizons. Conversely, decreased water availability, as a consequence of summer warming and/or reduced snow depth and longevity, could lead to a decrease in rates of decomposition (Bryant *et al.* 1998; Sjögersten & Wookey 2002

A full account of feedbacks from PFTs can only be given when we include litter production and decomposability not only of the leaves but also of the other plant parts of contrasting PFTs (note that the below-ground parts of vascular plants very often contribute more than 50% to plant litter production (Scheffer & Aerts 2000; Scheffer et al. 2001)). Central to this, the lignin content of plant residues is a major determinant of litter breakdown, because of its structural stability and biochemical recalcitrance, with the result that decomposition of plant materials can usually be related to the lignin-to-N ratio, or other similar quality indices which are also relevant to digestion by animals (Swift et al. 1979; Cadisch & Giller 1997; Cornelissen et al. 2004). Any changes in vegetation that result in a change in the relative abundance of woody material will likely be accompanied by a change in the amount of lignin in soil and litter. But substantial uncertainties regarding lignin concentrations and distribution in plants, allocation of biomass between above and belowground parts, root lignin concentrations, and decomposition processes in general for roots, limit our understanding of the absolute effect of more lignin (see e.g. Personeni & Loiseau (2005)).

Finally, differences in microbial community composition between communities dominated by different PFTs (see e.g., Wallenstein et al. 2007) may also affect decomposition rates (J.C. Moore, unpublished). The presence of an active rhizosphere alters decomposition rates in a number of ecosystems (Fontaine & Barot 2005; Subke et al. 2004; Trueman & Gonzalez-Meler 2005), and these "priming" effects could be altered by soil nutrient status (Kuzyakov 2002; Fontaine & Barot 2005), and potentially by the exact makeup of the plant community and changes in relationships between free-living and root-associated soil microbes. Furthermore, enhanced UV-B fluxes at the surface also appear to exert significant effects on microbial C:N ratios, bacterial growth rate and community structure via UVB-induced changes in the plant photosynthate allocation and potential changes in root exudation (Johnson et al. 2002; Rinnan et al. 2008). Getting inside the "black box" to determine species

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and food-web effects on decomposition rates remains a major challenge for ecosystem ecologists.

Herbivory

Climate change-induced shifts in the functional composition of vegetation could affect herbivore populations via several mechanisms. First, large-scale shifts in vegetation productivity, phenology and composition will substantially alter the quantity, quality and temporal availability of herbivore diet, thereby affecting their performance and behavior. Second, climate-induced alteration of growth and allocation patterns in individual PFTs, for example in terms of secondary metabolite production and allocation to foliage, will alter the quality and quantity of forage (Coley *et al.* 1985). Third, the potential direct effects of climate change, together with changes mediated by shifts in vegetation composition, will influence soil biological properties that regulate the availability of nutrients to plants, thereby creating a potential feedback on plant productivity and forage supply (Bardgett & Wardle 2003; Olofsson *et al.* 2004). Finally, changes in vegetation composition will modify habitat availability and architecture, and spatial arrangement, with potential effects for herbivores and fauna that use plants for habitat, such as rodents, insects and birds.

   Such indirect effects of climate change on herbivore performance and behavior will in turn feedback to the plant community, acting as inhibitors or facilitators of vegetation change (Niemela *et al.* 2001; Gough *et al.* 2007). The potential for grazers to cause shifts in vegetation composition is well established: heavy reindeer grazing in Scandinavian tundra has substantially reduced the cover of lichens in inland districts, with serious consequences for reindeer husbandry (Moen and Danell 2003); reindeer at high density in north Norway have effectively homogenized the biomass of palatable plants across environmental productivity gradients at the scale of 1000s of km^2 (Bråthen *et al.* 2007); and spring grazing by increasing

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numbers of lesser snow geese at Hudson and James bays, Canada, has resulted in destruction of salt-marsh swards and the exposure of bare sediments at sites along the 2000-km coastline where the geese breed or stage (Srivastava and Jefferies 1996; Jefferies *et al.* 2006). Grazing by large herbivores, and the feedback mechanisms that result from this, have been proposed as a major driver of shifts between moss and grass dominated tundra (Zimov *et al.* 1995; van der Wal and Brooker 2004), an idea that is currently being tested in the 'Pleistocene Park'[6] (Zimov 2005); and even shrub encroachment can be affected by large herbivores, for example by suppression of shrub growth by selective feeding (Bardgett *et al.* 2001; den Herder *et al.* 2004; Bråthen *et al.* 2007; Ims *et al.* 2007) or trampling (Plate 1c). Potentially, changes in grazing pressure locally and regionally could be more important as a driver of vegetation change and ecosystem processes than climate change (at least over decadal timescales). As noted by Gough *et al.* (2007), however, almost all studies used to predict changes in vegetation community structure and ecosystem function in response to climate warming have not explicitly considered interactions with herbivores, thus the role of herbivores as drivers of vegetation change under climate warming is largely unknown (see also Díaz *et al.* 2007a).

Importantly, climate-induced changes in vegetation composition (and gross primary productivity; see Oksanen *et al.* (1981)) will potentially have cascading effects on other trophic groups (Fig. 1) ultimately influencing trophic complexity. For example, as discussed above, changes in forage availability resulting from climate change will likely affect herbivore densities, with consequences to their predators. Changes in predator numbers or behavior will, in turn, have cascading effects on ecosystem properties by further modulating herbivore effects on vegetation change and resulting feedback mechanisms (Post *et al.* 1999; Beyer *et al.* 2007). A growing number of studies propose that predators strongly modulate

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[6] Pleistocene Park is a 160 km^2 scientific nature reserve in Sakha (Yakutia) region, northern Siberia, in which Sergey Zimov and colleagues are attempting to reconstitute the ecosystem of the Pleistocene epoch that supported vast populations of large animals including mammoths, horses, reindeer, bison, wolves, and other large predators.

herbivore numbers (Terborgh *et al.* 2001; Creel *et al.* 2005; Gunn *et al.* 2007) with

consequences for vegetation (Beyer *et al.* 2007) and other ecosystem properties (Croll *et al.*

2005), as well as for land-use decisions (Höchtl *et al.* 2005). Below-ground food webs may

also be affected, depending, for example, on the response of root-feeding nematodes to

vegetation changes (J.C. Moore, unpublished). However, the potential trophic cascades

resulting from the influence of climate change on shrub encroachment and other shifts in

vegetation are not known.

Transformations, internal feedback processes, and trajectories of change

The following section considers some on-going transformations as case studies, and focuses

on internal and external biotic drivers (Fig. 1).

Case studies illustrating key PFT transformations

Examples from arctic ecosystems

We identify two, intimately linked PFT transformations that are occurring in arctic regions,

and illustrate the feedbacks and cascading responses involved. Following a brief outline of the

key points, they are considered together (Fig. 2).

1. Increase in (deciduous) shrubs: *Betula nana* (Alaskan tundra, Plate 1a,b) has become more

   dominant over the past few decades, especially in tussock tundra (Hobbie & Chapin 1998;

   Sturm *et al.* 2001; Stow *et al.* 2004; Walker *et al.* 2006), with some additional indications

   that *Betula glandulosa*, alder (specifically *Alnus crispa*) and shrub willow species (*Salix*

   alaxsensis, S. pulchra, and *S. glauca*) have also increased at a regional level (Tape *et al.*

   2006). Generally, the increase of *B. nana* leads to a reduction of the biomass of the

   graminoid *Eriophorum vaginatum* (see Fig. 2; also visible in Plate 1a). So far, there is

   less documentation of similar changes going on in the rest of the Arctic. Nevertheless, the

data available do confirm that shrub encroachment is also taking place in some tundra plant communities in the Russian Arctic and in northern Canada (Sturm *et al*. 2005a,b). Most researchers attribute increased shrubbiness in the Arctic to global warming, possibly commencing as early as the close of the Little Ice Age (*ca*. mid-19th Century), and continuing with accelerating warming in the latter half of the 20th Century (Tape *et al*. 2006). The increase in shrubbiness has been linked with to a lengthening of the growing season, caused by earlier snow melt (Silapaswan *et al*. 2001; Chapin *et al*. 2005; Goetz *et al*. 2005; Euskirchen *et al*. 2006), having a disproportionate effect on deciduous shrubs compared with other PFTs (see Growth and Allocation section). However, there remains uncertainty as to the exact cause of the increase in shrub cover and the extent to which species are responding directly to global change versus alterations in soil nutrient availability caused by changes in decomposition rates.

2. Decline of cryptogams (mosses and lichens): Warming experiments and natural gradients show a decline of cryptogams in response to warming (Cornelissen *et al*. 2001; Walker *et al*. 2006), although accentuated surface drying as an artefact of warming may be partially responsible for a decrease in lichen performance. This decline is most clearly manifested in low-Arctic sites, where the vascular plant responses are the strongest in terms of cover and canopy height. Increased vascular plant biomass and canopy cover reduce light penetration to the ground surface to such an extent that the shade-intolerant cryptogams are out-competed by the vascular plants (Fig. 2). As this leads to less nutrients taken up by the cryptogams, total nutrient supply to the vascular plants increases, possibly promoting further vascular plant dominance. This positive feedback loop may be augmented by die-back of cryptogams, with their subsequent decomposition and nutrient release However, N-fixation rates of cyanobacteria in the moss layer may be reduced.

The canopy properties of *B. nana* form the basis of a positive feedback loop (Fig. 2) that connects ameliorating snow cover and soil conditions in such a way that the spread of *B. nana* is further promoted (Weintraub & Schimel, 2005). This is superimposed upon the direct effects of longer or warmer growing seasons on shrub growth and soil nutrient availability (Sturm *et al.* 2005a,b). As shrubs trap and hold snow, the soil beneath them is better insulated in winter (Körner 1999; Elberling 2007; Goetz *et al.* 2007). As a result, temperatures in the active layer are elevated to such an extent that there can be significant increases in microbial activity due to an increase in the volume of unfrozen soil (Sturm *et al.* 2005a,b; Walsh *et al.* 2005). This, in turn, leads to greater rates of N mineralization in winter and early spring (Schimel *et al.* 2004; Bardgett *et al.* 2005; Schimel *et al.* 2006), which may promote further shrub encroachment because part of the *Betula* canopy is above the snow layer and bud-burst/photosynthesis may occur ahead of other, low-stature species. Due to the larger canopy, more snow will be trapped in subsequent winters, causing greater winter and early spring N mineralization, further accelerating shrub encroachment and so on. However, at a landscape and regional scale (see Walker (2000) for discussion of landscape position and vegetation community type in the Arctic), it is not known if the shrub-snow feedback might be constrained by overall winter precipitation and thus total supplies of snow. Snow packs may, however, be less dense within a developing *Betula* canopy, potentially allowing for some increase in mean regional snow depths, but this needs to be set against an on-going potential decrease in regional snowfall and duration of snow-cover in low arctic regions in the future (Walsh *et al.* 2005). In addition, the canopy expansion of *Betula* will result in a deteriorated light climate for low-stature, shade-intolerant species beneath. The C to N stoichiometry of woody shrubs further contributes to the positive feedback loop that promotes shrub encroachment. Replacement of graminoids and herbaceous species with low C:N ratios compared to the woody shrubs with much greater C:N ratios, results in a greater amount of

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biomass produced per unit available N. This leads to more above-ground biomass, more snow insulation, more shading of lower-statured species, greater biomass of the shrubs and so on.

In contrast with warmer soils during the winter period, taller canopies with greater leaf area reduce the energy incident on the soil surface during the snow free period, potentially leading to cooler soils and low rates of decomposition (Goetz *et al.* 2007). Taller canopies are, however, often linked with decreases in moss and lichen cover (Cornelissen *et al.* 2001) which, because of their low thermal conductivity, act as insulators to reduce the transfer of energy from the surface into the soil (Gornall *et al.* 2007). This may therefore tend to compensate, but is unlikely to cancel-out, the reduced energy incident beneath taller shrub canopies.

The expansion of ECM deciduous shrubs, coupled with the potential response of extra-radical hyphae to increasing temperatures (Clemmensen *et al*. 2006) and elevated CO_2 (Alberton *et al.* 2005), is likely to increase the amount of ECM fungal tissue in these soils. If the range expansion in ECM shrubs is in direct response to changes in the abiotic environment, rather than mediated through changes in soil N availability, this will likely result in a greater competition between mycorrhizal fungi and free-living soil microbes (Högberg *et al*. 2003). Such competition may increase the proportion of available nutrients immobilized in ECM plant and fungal tissue and reduce soil N availability making conditions even more favorable for ECM and ERM shrubs at the expense of AM and non-mycorrhizal plants (Fig. 2). Long-lived ECM hyphae, which can survive low winter temperatures (Tibbett & Cairney 2007), may allow plants to cope with potential changes in the seasonal timing of nutrient availability linked to climate change and plant community effects on snow dynamics (Sturm *et al*. 2001;

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Euskirchen *et al*. 2007), supporting the earlier bud break, development and photosynthesis observed in some shrub communities (Weintraub & Schimel, 2005). Furthermore, leaf litter derived from shrubs is likely to be more recalcitrant than that derived from graminoids (Cornelissen *et al.* 2007a), and increases in the abundance of woody residues are also likely to reduce rates of nutrient cycling and nutrient availability (see decomposition section above).

In summary, the net effects of this transformation for soil nutrient availability are complex and difficult to predict when changes in the quantity and quality of litter inputs, root exudation, and mycorrhizal associations are superimposed upon changes in snow conditions and the soil physical environment (see Fig. 2). However, in balance it appears that changes nutrient availability are likely to favor ECM and ERM shrubs further, potentially setting up a positive feedback loop.

Examples from alpine ecosystems

1. Increase in graminoids in response to nitrogen deposition: Airborne N deposition ranges from 2 to 12 kg N ha^{-1} yr^{-1} in North America to 60 kg N ha^{-1} yr^{-1} in parts of Europe. This N deposition can have both direct effects on plant physiology and soil biogeochemistry, but also indirect effects mediated via changes in plant species composition (Manning *et al.* 2006). Because alpine ecosystems are strongly N limited, deposition-induced changes in N availability have substantial consequences for community composition, production, and the interaction between plants and insect herbivores. Both experimental studies and general vegetation survey at Niwot Ridge, Colorado (Bowman *et al.* 1993, 1995) have indicated community shifts in favor of graminoids (e.g. the grass *Deschampsia caespitosa* and sedge *Carex rupestris*) in response to N-deposition. Similarly, N deposition in the central Alps and northern Caucasus caused large changes in dry matter production and

community composition toward greater abundance of sedges (especially *Carex* spp.) (Bassin *et al.* 2007; Soudzilovskaia & Onipchenko 2005). Thus, these studies have consistently found graminoids to benefit more from N deposition than forbs, as a result of a greater photosynthetic nutrient use efficiency (Bowman *et al.* 1995) and a potentially greater capacity to limit nutrient losses (Aerts 1999; Bassin *et al.* 2007).

In addition, increased N availability also leads to increased leaf N-content, especially in the form of proteins, concomitant with a reduction in C-based secondary compounds such as phenolics (lignin, tannins) and terpenes (see Throop & Lerdau (2004) for a review). This N deposition-induced shift in nutrient storage above-ground may affect herbivory because a strong relationship has been documented between leaf N concentration, palatability to invertebrates (Díaz *et al.* 2004), and insect growth, development and survival. The increased biomass production in response to moderate deposition may also lead to greater performance of invertebrate herbivore populations (Bowman 2000), but growth of herbivore populations could become a controlling mechanism able to stabilize and/or limit leaf development. Thus, N deposition and grazing do not operate independently and may amplify community composition shifts. For example, in an experimental study in the Scottish Highlands, van der Wal *et al.* (2003) illustrated that N deposition, in combination with heavy grazing pressure, can result in the replacement of moss-dominated (*Racomitrium lanuginosum*) habitat by grasses and sedges. This is a feedback loop whereby N deposition both encourages the growth of grasses and sedges, but is potentially toxic to the *Racomitrium*. The improved growth of grasses and sedges both attracts herbivores and also shades the *Racomitrium*. Finally, the increased grazing pressure causes direct physical damage to the *Racomitrium* via trampling.

2. <u>Increase in graminoids and shrubs in response to abandonment:</u> Cessation of traditional

    grassland management practices in alpine and sub-alpine grasslands leads to their

    dominance by tall and/or tough graminoids and shrubs (Plate 1e,f) (Quétier *et al.* 2007;

    Tasser & Tappeiner 2002). This change in predominant growth form is accompanied by

    the increased prevalence among graminoids of species with a conservative nutrient

    economy, high dry matter, fiber and especially lignin contents, and low tissue N and P

    concentrations (Quétier *et al.* 2007). These changes in functional composition decelerate

    biogeochemical cycles due to reduced rates of litter decomposition (Fortunel *et al.*

    submitted), resulting in litter accumulation, decreased primary productivity and nutrient

    availability, and increased accumulation of nutrients in pools in the soil (Zeller *et al.*

    2000, 2001; Bardgett *et al.* 2001; Díaz *et al.* 2007b; Quétier *et al.* 2007; Robson *et al.*

    2007). These changes are associated with modifications of microbial community

    composition and activities (Bardgett *et al.* 2001; Robson *et al.* 2007; Zeller *et al.* 2001).

    Invertebrate herbivore and bird diversity also decrease (Theurillat & Guisan 2001;

    Bolliger *et al.* 2007), but consequences for herbivory and their effects on N cycling have

    not been quantified. Finally, Quétier *et al.* (2007) also identify a link between plant traits,

    environmental risk and hydrology in these systems: The physical structure of senescent

    Festuca paniculata (Plate 1e) in un-mown meadows may provide a glide-plane for the

    snow-pack and thus increase the risk of avalanche.

Links with the earth system

C and N cycling

Carbon sequestration potential in many cold ecosystems may be constrained by low N

availability. In the low Arctic, unless there are major changes in the rates of N-fixation

(driven by, for example, alder expansion, or loss of symbiotic N fixation in the cryptogam

layer) or anthropogenic N input, C sequestration is likely to be determined by differences in the C:N ratios between encroaching plant species and those species that they are replacing (see above). Shaver and Chapin (1991), for example, compared four tundra communities dominated by different PFTs in Northern Alaska, and found that evergreen-dominated heath tundra produced and accumulated, respectively, ~ 23 and 25% more above-ground biomass per unit of N than graminoid-dominated wet sedge tundra. This difference was largely explained by the greater allocation to woody tissues with low N concentrations in the heath tundra. A parallel example from the alpine (see section above) is the herbaceous dicotyledonous plant *Acomastylis rossii* versus the grass *Deschampsia caespitosa* at Niwot Ridge (Suding *et al.* 2004; Steltzer and Bowman 2005). In addition, due to the greater C:N ratios of encroaching species compared with soil organic matter, increased decomposition rates may, counter-intuitively, increase C sequestration if much of the mineralized N is immobilized in plant biomass (Shaver *et al.* 1992; but see Mack *et al.* 2004). Alternatively, greater rates of mineralization in winter under the deeper snow in shrub communities, may both increase nutrient losses through leaching during spring melt, and enhance respiratory C losses.

The low nutrient stocks in many high arctic and alpine systems (e.g. polar desert and semi-desert) may delay the encroachment of species able to survive in new climatic conditions until such a time as stocks have increased sufficiently (through, for example, N-fixation) to support the new community (see Bliss *et al.* (1984) for the Canadian High Arctic, and Caccianiga *et al.* (2006) for glacial moraine sequences in the Italian Alps). This may result in a large discrepancy between climate envelopes and plant species distributions at high latitudes and altitudes (but see Parolo & Rossi (2008)). Nonetheless, a 'greening' in high arctic and high alpine ecosystems can be anticipated to result in net C sequestration in vegetation and soils, in parallel with a gradual build-up of mineral nutrients.

In alpine ecosystems, increased abundance of graminoids, along with potential changes in plant-herbivore relationships, will also affect ecosystem processes. Increasing biomass production by species with smaller C:N ratio litter accelerates N recycling (Bowman 2000) and potentially limits long-term storage of N (Bowman *et al.* 2006). Greater herbivore densities in response to more palatable tissues may affect N pools in SOM (Bowman *et al.* 2006). Also, by stimulating plant production, moderate N deposition has been hypothesized to increase C sequestration in montane ecosystems (Xu *et al.* 2004; Bassin *et al.* 2007; Soudzilovskaia and Onipchenko 2005; but see Bowman *et al.* 2006). However, Neff *et al.* (2002) demonstrated that, in addition to increased productivity, decomposition of the light fraction of SOM increased, resulting in no statistically significant changes in SOM pools. Further, in Alaskan tussock tundra long-term fertilization caused a net ecosystem loss of almost 2 kg C m^{-2} over 20 years (Mack *et al.* 2004), due to greater stimulation of decomposition than plant production.

In summary, due to the tight regulation of nutrient cycles in many arctic and alpine ecosystems, to model and predict rates of C sequestration we must understand how global change will affect nutrient inputs and outputs, and the C:N ratios of all ecosystem C pools, taking into account differences between PFTs (Saleska *et al.* 2002). A pragmatic approach to modeling is to focus on likely scenarios of community change in response to global change drivers (Epstein *et al.* 2004; Chapin *et al.* 2005), with subsequent analysis of the possible implications for internal cascades and feedbacks which link with the earth system. Changes in plant species distribution also have the potential to alter fluxes of the key greenhouse gas methane (see Ström *et al.* (2003 & 2005)), although further consideration of this topic is beyond the scope of this review (but see Johansson *et al.* (2006) and Heimann & Reichstein (2008)).

Snow cover, energy and water exchange

Changes in species composition will affect surface energy and water balance, leading to both positive and negative feedbacks on climate change (Eugster *et al.* 2000; Beringer *et al.* 2005), further species responses (McFadden *et al.* 2001; Chapin *et al.* 2005), and changes in the magnitude, timing and chemistry of surface run-off (McCartney *et al.* 2006). The changes in energy balance will differ with season and will involve interactions between vegetation and snow cover, as well as changes in canopy and soil microclimate during the snow-free season (Walker *et al.* 2003). Changes in vegetation height and stem density will affect the accumulation and insulative properties of snow within the canopy (Grogan & Jonasson 2006; Sturm *et al.* 2001), while the influence of contrasting albedo and surface roughness of contrasting vegetation types on summer energy balance is well established (Chapin *et al.* 2000a,b; Eugster *et al.* 2000; Chapin *et al.* 2005). With regards to the latter, the results of the modeling study by Chapin *et al.* (2000b) indicate that a change from tussock tundra to shrub tundra could result in a ~3.4 W m^{-2} increase in summertime sensible heat flux. This figure is comparable to the radiative forcing of 4.4 W m^{-2} predicted as a consequence of a doubling of atmospheric CO_2 concentration.

The effect of changes in vegetation canopy structure on sensible heat exchange with the atmosphere during late winter and spring must also be considered if taller species emerge above the snow surface (Bonan *et al.* 1992; Foley *et al.* 1994; Sturm *et al.* 2005a,b). At this time, in particular, darker stems and foliage absorb more radiation than the highly reflective snow, leading to a significant increase in net radiation input and warmer canopy and snow surface temperatures (Eugster *et al.* 2000). As a result, there is an increase in sensible heat loss to the atmosphere (rather than direct reflection and loss of incident radiation). On a regional scale, this change in surface energy balance may lead to significant increases in air

temperature, as well as more rapid snowmelt, thus acting as a strong positive feedback on climatic warming (Chapin *et al.* 2005). Comparative studies of energy balance among contrasting vegetation communities have, however, tended to focus on thaw season conditions (Chapin *et al.* 2000; Beringer *et al.* 2005; Chapin *et al.* 2005) while data for the important 'shoulder season' periods (spring melt and autumn freeze) is sparse (Eugster *et al.* 2000).

Changes in energy balance are intimately linked with changes in active layer depth (in permafrost regions), and water balance. Both active layer depth and water balance respond directly to climate and also to changes in vegetation composition (Anisimov & Reneva 2006; Schur and Jorgenson 2007). Schuur *et al.* (2007) applied a gradient approach to understanding the potential effects of thermokarst (ground subsidence related to melting of permafrost) on plant communities, soil thermal and hydrological conditions, and biological processes. Interestingly, vascular plant biomass shifted from graminoid-dominated tundra at the least disturbed site to shrub-dominated tundra at the oldest, most subsided site (which was also warmest, and with highest soil N availability). The implication here is that permafrost melting, as an indirect facet of climate change, could also contribute to shrub encroachment.

Fire

The historical and potential future extent, effects and feedbacks of wild-fires are poorly known for arctic tundra ecosystems compared with boreal forest (Chambers *et al.* 2005; Goetz *et al.* 2007; Liljedahl *et al.* 2007) but it has long been hypothesized (Racine *et al.* 1987, and references therein) that fire may play a substantial role in ecosystem energy and water exchange, C balance and plant community composition. Ongoing climatic and vegetation change are likely to increase the frequency and possibly the intensity of fires in tundra regions, and paleoenvironmental reconstruction of fire frequency in north central Alaska between 14,000-10,000 years ago suggests that birch tundra burned on average every 144

years (Higuera *et al.* 2008). Clearly the potential exists for fire and increasing shrub dominance to interact in the future; global change simultaneously increasing both fire frequency and shrub dominance, with vegetation composition modulating the intensity and spread of fires, and fire impacts, in their turn, affecting contrasting growth forms differentially (Racine *et al.* 1987). Worthy of note here is the 2007 Anaktuvuk River fire on the North Slope of Alaska which burned ~ 100,000 ha over 10 weeks during the warmest and driest year in two decades.

Conclusions

- Substantial shifts in community composition (and PFTs) in response to global change drivers (including climate and deposition of airborne N-containing contaminants) have already been documented in arctic and temperate alpine regions.

- The occurrence of a broad spectrum of PFTs in these regions, together with hypothesized low functional redundancy, mean that shifts in plant communities will result in a complex series of biotic cascades and feedbacks which are supplemental to the direct responses of ecosystem components to the primary global change drivers. On a regional basis, other drivers of change (such as heavy grazing pressure from ungulates) are superimposed upon global change drivers, and may assume primary significance for plant species composition. Interactions between climate change, and changing grazing regimes, have rarely been studied.

- Biotic cascades and feedbacks in the soil sub-system are complex and very poorly understood. Biodiversity and food-web structure below-ground will be affected substantially by changes in PFTs and by associated changes in soil physical conditions; but these changes will feed-forward on plant nutrient availability and rhizosphere processes.

- At a landscape and regional scale, the shrub-snow feedback highlighted here might be constrained by overall winter precipitation and thus total supplies of snow. Local-scale landscape heterogeneity (*sensu* Walker 2000) might, however, be substantially affected by changing distribution of snow.

- Changes in ecosystem structure and function are strongly coupled with the broader earth system, and have the potential to feedback substantially on further environmental change (e.g. alterations of surface energy budget or net exchange of radiatively forcing gases between ecosystems, soils and the atmosphere).

- The rate of change in ecosystem and soil C partitioning and pools has the potential to be rapid in many low arctic and sub- to mid-alpine ecosystems, due to the presence of a substantial existing mineral nutrient reservoir to support C fluxes. Conversely, high arctic and alpine ecosystems may respond to change more slowly due to the time required for nutrient stocks to accumulate (e.g. through N-fixation, weathering, or aeolian transport) in order to support increased productivity. High arctic and alpine systems may, however, be subjected to rapid relative increases in biodiversity with global warming, even if total biomass remains low initially.

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Figure/plate legends

Figure 1

A conceptual framework for considering the internal linkages and feedbacks associated with a shift in plant functional types (PFTs) on ecosystem-level properties. Changes in PFTs (left-hand major box in Fig. 1, 'Species Effects') will feed forward to affect consumers (both herbivores and decomposers) through changes in the quality, quantity and timing of food availability, as well as changing habitat physical characteristics, for example shelter for small herbivores (e.g. invertebrates, microtines and birds). Where feedbacks occur between two components of the ecosystem they are indicated by bi-directional arrows. Herbivores feedback on vegetation composition, growth and allocation, both through direct browsing effects and also through their influence on processes of decomposition and nutrient recycling, through the spatial and temporal dimensions of the way they use the landscape, and through physical effects such as trampling on sensitive PFTs. In the decomposition subsystem feedbacks are also exerted through potential shifts in the magnitude, timing and location (e.g. in the rhizosphere versus at the soil surface or the interface of dead roots) of nutrient mineralization, alterations in mycorrhizal associations, and competition between decomposers and autotrophs for nutrients. Changes in the composition of PFTs, and in plant growth and allocation patterns, interface directly with the earth system by influencing ecological properties and processes that affect energy and water exchange, soil fertility and physical structure, or susceptibility to fire, while whole-ecosystem metabolism across trophic levels affects carbon fluxes (both gaseous and aqueous).

Figure 2

Ecosystem cascades and feedbacks resulting in an increase in deciduous shrubs and a decline in both graminoids and cryptogams (mosses and lichens) in response to increasing warmth

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and duration of the growing-season in arctic tundra. Note that stronger responses to climate drivers among deciduous shrub species (denoted by the thicker line from 'Global Change Drivers' to shrubs than to graminoids and cryptogams) result in a positive feedback between increasing height and leaf area index (LAI) and increased trapping of snow. Changes in the depth, duration, and both physical properties and chemical composition of the snow-pack can have either positive or negative impacts on N availability through altering soil thermal and moisture regime. Increased height and LAI of shrubs will likely have a negative impact on graminoids and cryptogams through shading effects. Furthermore, increased prevalence of species with ecto-mycorrhizas (ECM) or ericoid mycorrhizas (ERC) will likely decrease nutrient availability to other species, with further negative consequences. Increases in the proportion of low-N, but high lignin, woody litter (leaf and stem litter of woody species associated with increasing shrub dominance) will also tend to reduce N availability. For clarity the figure does not address herbivory directly; this is discussed in the text.

Plate 1

1a Moist acidic tundra at Toolik Lake, Alaska is composed of a mix of plant functional types including tussock-forming and rhizomatous sedges (*Eriophorum vaginatum* and *Carex bigelowii*), deciduous shrubs (*Betula nana*; note senescence), evergreens (*Empetrum nigrum*, *Vacciniuum vitis-idaea, Ledum palustre*), and moss species (*Sphagnum, Hylacomium, Aulacomnium*).

1b Fertilized plots in moist acidic tundra become dominated by *Betula nana* after 3-6 years, as in this photo of a 10 year old fertilized plot at Toolik Lake (Toolik Field Station in background and other greenhouse warming and shade plots in the distance).

1c Summer grazing grounds (left) separated by fence from spring and autumn grazing grounds (right) of reindeer at Ifjordfjellet, Finnmark, Northern Norway (70°26'N, 27°23'N, approx. 300 m a.s.l.). Reindeer trampling on the summer side of the fence causes disturbance that shifts the plant composition. Note especially the shift from tall *Salix* thickets to graminoid-rich lawns.

1d Polar desert/semi-desert at Daudmansodden, Svalbard, Norway. Substantial increases in C sequestration in these systems must be underpinned by increasing mineral nutrient availability. This contrasts with low arctic systems (see 1a,b above) where redistribution of substantial existing nutrient pools in soils and vegetation can result in significant changes in C sequestration over shorter time-scales.

1e Cessation of mowing in sub-alpine grasslands promotes dominance by large cespitous grasses with tough and nutrient-poor leaves such as *Festuca paniculata* (pictured here). This has major effects on ecosystem processes through drastic reduction in palatability (the picture shows a pasture dominated by *F. paniculata* shortly after grazing) and accumulation of poorly degradable litter. The study site is located on the south facing aspect of the upper valley of the Romanche River, central French Alps (ca. 2058 m a.s.l.); "la Meije" mountain (3982 m) in the background.

1f Land use changes have differing effects depending on aspect. This picture contrasts increased dominance by large tussock grasses (foreground) on south-facing slopes with colonization by woody species (here alder, *Alnus viridis*, in the background). Subsequent effects on nutrient cycling are dramatic, with a slowing of nutrient cycles on south-facing vs. increased nitrogen fixation on north facing pastures. There are strong cascading effects on habitat quality for both domestic herbivores and wildlife. Same location as 1e.