

RESEARCH REVIEW

# Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change

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## Abstract

Global climate change is already having significant impacts on arctic and alpine ecosystems, and ongoing increases in temperature and altered precipitation patterns will affect the strong seasonal patterns that characterize these temperature-limited systems. The length of the potential growing season in these tundra environments is increasing due to warmer temperatures and earlier spring snow melt. Here, we compare current and projected climate and ecological data from 20 Northern Hemisphere sites to identify how seasonal changes in the physical environment due to climate change will alter the seasonality of arctic and alpine ecosystems. We find that although arctic and alpine ecosystems appear similar under historical climate conditions, climate change will lead to divergent responses, particularly in the spring and fall shoulder seasons. As seasonality changes in the Arctic, plants will advance the timing of spring phenological events, which could increase plant nutrient uptake, production, and ecosystem carbon (C) gain. In alpine regions, photoperiod will constrain spring plant phenology, limiting the extent to which the growing season can lengthen, especially if decreased water availability from earlier snow melt and warmer summer temperatures lead to earlier senescence. The result could be a shorter growing season with decreased production and increased nutrient loss. These contrasting alpine and arctic ecosystem responses will have cascading effects on ecosystems, affecting community structure, biotic interactions, and biogeochemistry.

**Keywords:** C cycle, microbial activity, N mineralization, NDVI, phenology, snowpack, trophic interactions, tundra

Received 17 September 2013 and accepted 28 January 2014

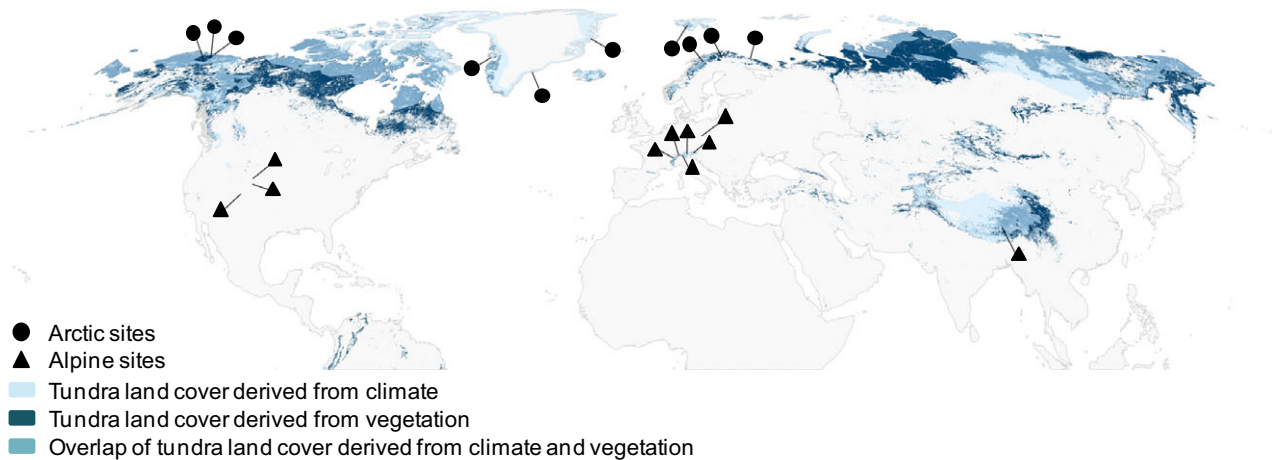
## Introduction

Among the ecosystems, most vulnerable to rapid climate change are those at the coldest margins of life on Earth, including arctic and alpine ecosystems, broadly characterized as the ‘tundra biome’ (Holdridge, 1947; Whittaker, 1975). Estimates of the area covered by tundra range from approximately 15–24% of the terrestrial surface of the Earth (Bliss, 1971; Tarnocai *et al.*, 2009; Zhao & Running, 2010) (Fig. 1). Arctic and alpine tundra share many commonalities, including low temperatures during the growing season that limit vegetation growth and decomposition, resulting in landscapes dominated by low shrubs, herbs, and graminoids. These cold ecosystems are particularly susceptible to the impacts of climate change because biological and chemical processes are more temperature-sensitive in colder environments (Kirschbaum, 1995). Biological consequences of climate warming in tundra ecosystems

include shifts in the seasonal timing of plant and animal life cycles (Arft *et al.*, 1999; Hollinger & Richardson, 2005), altered species composition (Sturm *et al.*, 2005; Walker *et al.*, 2006), and species migration and extinction (Grabherr *et al.*, 1994; Walker *et al.*, 2006; Bryant *et al.*, 2008). In turn, these biological responses can alter biogeochemical cycles and ecosystem services, cause climate feedbacks through increased decomposition of carbon (C) stored in soils and permafrost (Schuur *et al.*, 2008), lead to a loss of biodiversity (Pauli *et al.*, 2012), and affect other organisms through changes in trophic dynamics (Post & Forchhammer, 2008; Post & Pedersen, 2008; Wookey *et al.*, 2009).

Arctic and alpine regions experience differences in seasonal patterns of key environmental factors, such as solar radiation. The spatial distribution of cold ecosystems varies from isolated equatorial and temperate high mountains to the continuous, topographically diverse landscapes of the poles, which include arctic and arctic–alpine ecosystems. As climate change alters the seasonal patterns of temperature and precipitation, plant phenology and the timing of microbial activity

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**Fig. 1** Map of the northern hemisphere depicting the location of arctic (circle) and alpine (triangle) sites for which we compare climate and ecological data. Light shading indicates climates classified as arctic and alpine at 0.5 degree resolution, using the updated Köppen–Geiger climate classification (Kottek *et al.*, 2006). Dark shading indicates regions with arctic and alpine vegetation, based on the Global Land Cover Characteristics Database's Global Ecosystems classification of cold grassland, heath scrub, tundra, and polar and alpine desert. These areas were derived from 1 km Advanced Very High Resolution Radiometer (AVHRR) data (USGS, 2008). Medium shading indicates regions where the tundra climate and vegetation layers overlap.

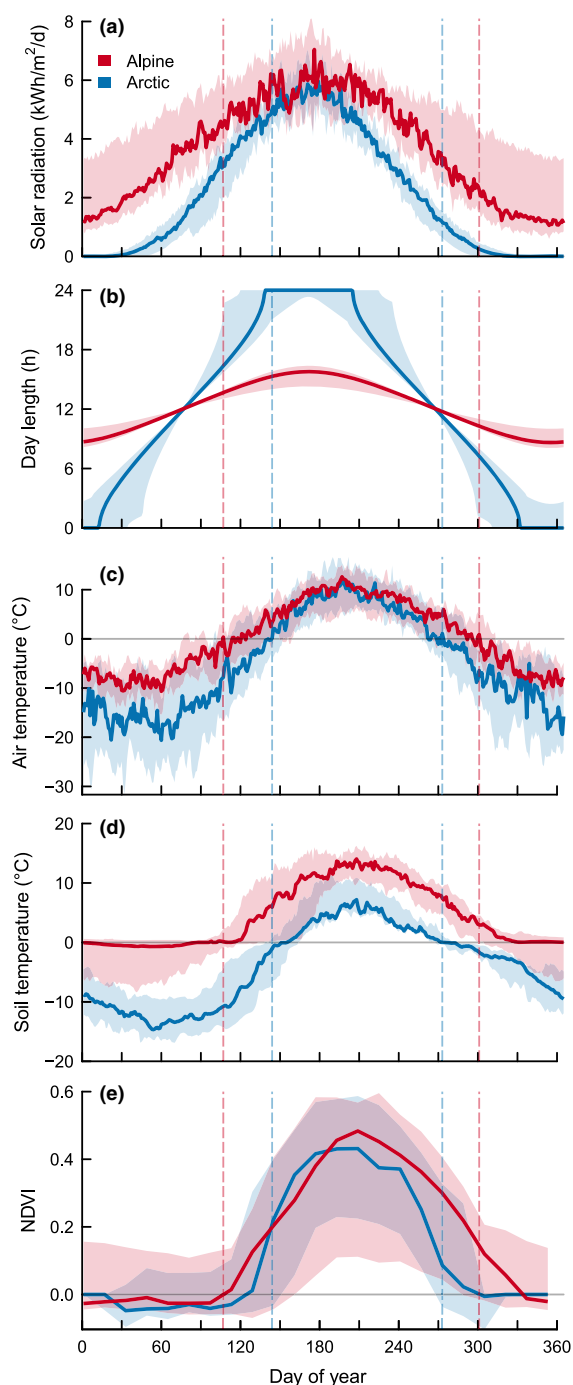
and nutrient cycling may be affected differently in arctic and alpine ecosystems. The ways in which ecosystem processes respond to the changes in the seasonal timing and synchrony of events, or seasonality, are central to understanding and predicting ecosystem responses to global change.

Our objective was to identify similarities and differences in arctic and alpine seasonality, and to examine the potential for divergence in the ecology of these environments as a result of climate-induced alterations to seasonality. To do so, we compared the seasonality of abiotic and biotic factors between arctic and alpine sites. We compiled data on daily radiation, day length, air temperature, soil temperature, and normalized difference vegetation index (NDVI) from 20 Northern Hemisphere research sites and monitoring stations to determine the effect of physical drivers on the seasonality of arctic and alpine tundra biomes. We also reviewed biological studies from these sites to compare arctic and alpine ecosystems (Fig. 1, Table S1). We focused on sites within the Northern Hemisphere because the areal coverage of its tundra biome is over three times greater than in the Southern Hemisphere (USGS, 2008), and the seasonality of tundra ecosystems in the tropics differs from the Northern Hemisphere. This comparative review provides novel insights into how arctic and alpine ecosystem responses to climate change may diverge, which will help to inform global climate and ecosystem models, estimates of future biogeochemical cycling, and our understanding of cascading effects across trophic levels.

### Seasonality of the physical environment

Arctic and alpine tundra systems share cold, short growing seasons (Billings, 1973), but they differ in the timing of onset and duration of the growing season. In the spring, the start of the growing season is cued by increases in incoming solar radiation and air and soil temperatures (Fig. 2a, c, d), all of which occur earlier in alpine systems, leading to earlier plant growth (Fig. 2e). These factors also induce snow melt and soil thaw; greater topographic heterogeneity in alpine systems and in mountainous parts of the Arctic causes more intra-site variability in snow-free date. While arctic and alpine ecosystems receive similar amounts of daily incoming solar radiation over the course of the growing season (Fig. 2a), this energy is delivered over a full 24-h period during summer in the Arctic (Fig. 2b). Arctic and alpine ecosystems receive different amounts of incident solar radiation on an annual basis, with total yearly solar radiation decreasing toward the poles. These seasonal patterns of solar radiation and temperature are fundamental drivers of ecosystem structure and function.

Colder winter temperatures in arctic relative to alpine ecosystems are driven by the seasonal cycle of incoming solar radiation (Fig. 2c). For 20 arctic and alpine sites (Table S1), mean winter air temperatures are about 6 degrees colder in arctic than alpine sites. In addition, the difference is greater when northern European arctic sites are excluded, since their air temperatures are moderated by the Gulf Stream. Additionally, the transition of air temperature from below to above



**Fig. 2** Abiotic drivers of seasonality and NDVI for the 20 sites in Table S1. (a) Average daily incoming solar radiation from 1985 to 2004 (NASA, 2010), (b) day length in hours from 2005 (USNO, 2010), (c) average daily air temperature (years listed in Table S1) (d) average daily soil temperature at 10 cm depth (years listed in Table S1), and (e) average normalized difference vegetation index (NDVI), an index of canopy greenness, at 250 m resolution between 2000 and 2012 (ORNL DAAC, 2012). Solid lines and shaded areas represent across-site averages and 95% confidence intervals for alpine (red) and arctic (blue) ecosystems. Vertical lines indicate when air temperatures cross 0 °C

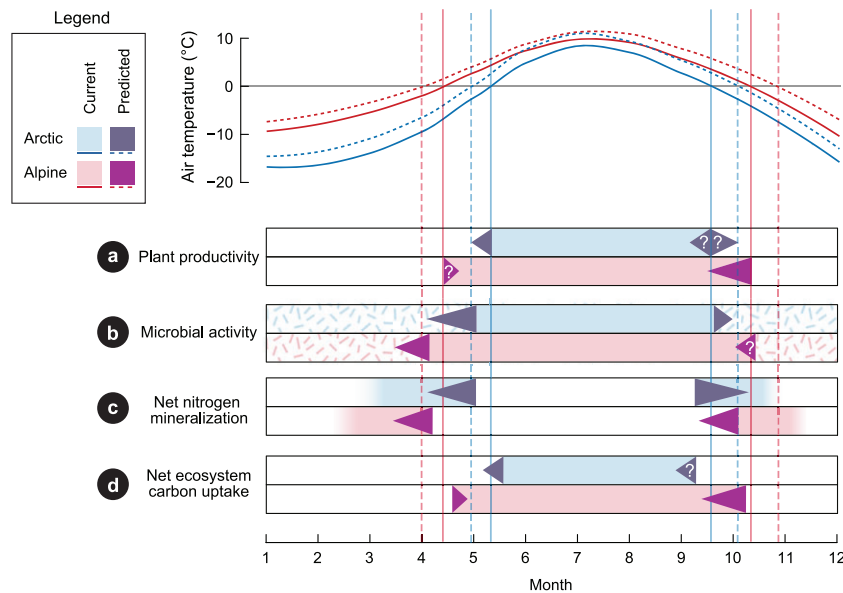
freezing occurs earlier in alpine regions than the Arctic. The seasonal patterns of air temperature drive activity and functioning of organisms living in these ecosystems, as well as acting as an environmental filter to dictate which species can survive and thrive.

For plant roots and the organisms inhabiting soils, soil temperature rather than air temperature is the primary driver of their metabolic activities. Soil temperatures generally reflect air temperature and incoming solar radiation, but soil temperatures are consistently higher in alpine than in arctic ecosystems (Fig. 2d), despite air temperature convergence during the growing season (Fig. 2c). Colder winter temperatures and a delay in spring soil warming in arctic relative to alpine ecosystems could partially explain this discrepancy. The insulating properties of more consistent alpine snow cover and the predominance of permafrost in arctic ecosystems, and its relative rarity in alpine ecosystems, may also drive warmer alpine soil temperatures.

Climate warming in the tundra biome is already happening at rates significantly above the global average, and temperatures will continue rising throughout the 21st century (Christensen *et al.*, 2013). At 20 arctic and alpine sites, the number of days with above-freezing air temperatures is projected to increase by over a month by the year 2070, with more warming in winter than in summer for both the Arctic and alpine (Christensen *et al.*, 2013; WorldClim, 2013; Fig. 3). These changes will lengthen the potential growing season, extending it slightly longer into the fall shoulder season than the spring at both the arctic and alpine sites (WorldClim, 2013). On average, arctic sites are projected to warm more than alpine sites [2.6 °C vs. 2.0 °C increase by 2070, calculated as the difference between current measurements (Table S1) and the CCSM4 model output for 20 sites (Fig. 3)]. A significant increase in precipitation is also projected for the Arctic, with a 25% increase in winter and 15% increase in summer (Christensen *et al.*, 2013). Generalized projections for how precipitation will change across alpine ecosystems, including arctic-alpine regions, are more difficult to make due to the topographic complexity in mountain regions and variation in their position relative to atmospheric circulation patterns, as well as the higher uncertainty in modeling precipitation than temperature. These seasonal changes will alter the timing and strength of biotic processes and interactions, and impact ecosystem function particularly during the spring and fall shoulder seasons across the tundra biome (Fig. 3).

### Seasonality of arctic and alpine plant phenology

The physical environment constrains the duration of arctic and alpine growing seasons, which can be as



**Fig. 3** Current and predicted changes in the timing of seasonal events in the Arctic (blue shades) and in alpine environments (red shades). Projected climate data for 20 arctic and alpine sites were obtained from downscaled climate projections from the National Center for Atmospheric Research's CCSM4 model for the year 2070, with Representative Concentration Pathway 6 at 30-s spatial resolution (Hijmans *et al.*, 2005; WorldClim, 2013). Vertical lines indicate when air temperatures cross 0 °C for the air temperature panel, and are intended merely as a point of reference for (a)–(d). Arrows in (a)–(d) indicate directional shifts that we predict will occur with climate change, and question marks denote predictions that have less certainty. Plant productivity (a) is constrained by both light and temperature. We predict that climate change-induced increases in temperature will cause the potential plant growing season to begin earlier, but light limitation may prevent alpine plants from taking advantage of earlier snow melt, and predicted drying in alpine environments may cause earlier plant senescence. Soil microbial activity (b) continues year-round in these environments, even after soils freeze, but rates are highest when soils thawed. We predict that this period of higher activity will occur earlier in both environments, following the advanced timing of soil thawing. Microbial activity during the winter contributes to net N mineralization in both environments (c). As a result, available N accumulates over the winter, but crashes at spring thaw in synchrony with microbial and plant uptake. We predict that the timing of this crash will advance earlier in the spring in both environments. This will make N availability fall out of sync with plants in alpine environments since they will be dormant during this period, resulting in increased microbial N immobilization. Conversely, the synchrony of arctic plants with the N pulse will increase. Finally, we predict that in the Arctic net C uptake (d) will begin earlier in the year, driven by advanced plant phenology. In alpine environments, net C uptake will occur later since microbial activity will increase earlier in the year, but plant productivity will not.

short as 30–90 days (Bliss, 1956; Billings, 1973). Since the growing season is short, the timing of plant phenological events is critical in both arctic and alpine tundra. As climate has changed in recent decades, the potential growing season has lengthened in polar regions (Myrnes *et al.*, 1997; Stockli & Vidale, 2004; Kim *et al.*, 2012), which could lead to greater plant production (Billings & Bliss, 1959; Walker *et al.*, 1993; Jonas *et al.*, 2008). However, we expect responses to alterations in the growing season length to differ between arctic and alpine systems because of inherent differences in their physical environments and evolutionary differences between their vegetation.

The timing and rates of seasonal events such as green-up and senescence, as characterized by remote sensing of the normalized difference vegetation index (NDVI), vary between arctic and alpine ecosystems (Fig. 2e). Early-emerging species begin growth soon

after snow melt. Their growth, as well as ongoing leaf expansion by later-emerging species, contributes to rapid early-season increases in NDVI. Although green-up occurs later on average in the Arctic than in alpine regions, the rate of greening is faster in the Arctic (Fig. 2e). This difference could partially be explained by faster rates of snow melt in the Arctic due to the 24-h photoperiod that leads to warmer nights than in alpine ecosystems (Walker *et al.*, 1999). While growth patterns derived from NDVI tend to represent the landscape well, these patterns are highly variable among individual species and communities (Steltzer & Post, 2009).

Within regions, variation in topography, wind, snow depth, and melt date produce asynchrony in the timing of plant phenological events across the landscape (Bliss, 1956; Billings & Bliss, 1959; Jonas *et al.*, 2008). Topographic variation and snowfall tend to be greater in alpine ecosystems than the Arctic, which causes greater



variation over short distances in the timing of alpine plant phenological events (Walker *et al.*, 1995, 1999). Communities with intermediate growing season lengths and abundant water resources (e.g., moist or wet tundra) are the most productive (Shaver & Chapin, 1991; Walker *et al.*, 1994; Bay, 1998; Fisk *et al.*, 1998; Elberling *et al.*, 2004; Schuur *et al.*, 2007; Arndal *et al.*, 2009; Nagy, 2009). Using NDVI as a surrogate measure for productivity, the mean vegetation production for 20 tundra sites (Table S1) is higher on average and also slightly more variable within the alpine sites than in the Arctic (Fig. 2e).

Although plants use multiple cues to determine the timing of growth and flowering (Körner & Basler, 2010), snow melt date explains much of the variation in plant phenology across sites (Walker *et al.*, 1995; Hollister *et al.*, 2005; Molau *et al.*, 2005; Wahren *et al.*, 2005; Börner *et al.*, 2008; Ellebjerg *et al.*, 2008; Jonas *et al.*, 2008; Steltzer *et al.*, 2009; Wipf & Rixen, 2010). Some tundra species are physiologically active under snow and maintain green leaves throughout winter (Bilbrough *et al.*, 2000; Starr & Oberbauer, 2003). For these winter-active species, temperature, particularly belowground, may be more important than snow melt for cueing spring phenology (van Wijk *et al.*, 2003).

Secondary controls on the timing of spring events, such as photoperiod and temperature, also constrain growth after snow melts (Hollister *et al.*, 2005; Hülber *et al.*, 2006, 2010; Steltzer *et al.*, 2009) to reduce risks associated with early or late development (Forrest & Miller-Rushing, 2010; Pau *et al.*, 2011). These cues interact to prevent plants from initiating growth in response to sudden snow melt, when temperatures are cold and the risk of freezing damage is high. Under current climate conditions, above-freezing air temperatures are well synchronized with the start of plant growth in alpine ecosystems (Fig. 2c, e). Plant growth does not commence immediately upon release from snow if temperature remains low, which may happen, for example, with an advance in snow-free date due to below-average winter snowfall or experimentally accelerated snow melt (Walker *et al.*, 1995; Molau *et al.*, 2005; Wahren *et al.*, 2005; Jonas *et al.*, 2008; Steltzer *et al.*, 2009). Over half of 23 species studied from an alpine meadow were sensitive to photoperiod as a developmental cue, yet they showed greater sensitivity to temperature early in the season when photoperiod was short (Keller & Körner, 2003). Similarly, photoperiod constrains plant phenology on alpine ridge tops that are snow-free earlier more than at other topographical positions where snow melts later (Hülber *et al.*, 2010).

As climate change alters some of the abiotic factors that cue spring growth initiation, such as temperature

and snow melt date, arctic and alpine plants' ability to respond to these changes will likely differ. At snow melt, day length is shorter in alpine regions, which may have led to the evolution of greater photoperiod sensitivity. As climate warms, this will constrain alpine plant life cycles more than those in the Arctic since day length is unaffected by climate change. Conversely, in the Arctic, colder winter soil temperatures cause later soil thawing than in alpine soils (Fig. 2d), which delays the onset of root growth and nutrient uptake (Callaghan, 1991). Because air temperature and light availability in the Arctic are high while the ground is still frozen, the onset of above- and belowground phenological cues can be separated temporally (Fig. 2a, c–e) (Chapin & Shaver, 1985; Shaver & Kummerow, 1992; Pop *et al.*, 2000). Release from belowground temperature limitation may therefore partially explain why arctic plants more consistently advance the timing of spring events than do alpine plants in response to warming (Welker *et al.*, 1997; Arft *et al.*, 1999; Walker *et al.*, 1999; Hollister *et al.*, 2005; Smith *et al.*, 2012). Therefore, photoperiod is likely a more important spring phenological cue for alpine plants, and soil temperature more important in the Arctic.

Some species require a specific duration of cold winter temperatures, a chilling requirement, before they can initiate growth and flowering. This may have a greater effect on alpine plant phenology (Shimono & Kudo, 2005) because in the Arctic, colder temperatures well exceed species' chilling requirements, which are often met in early fall (Pop *et al.*, 2000). This could lead to further divergence between arctic and alpine responses to climate change if warming leads to insufficient chilling durations, and therefore delayed growth initiation, for alpine plants. This difference may be further amplified by slightly greater winter warming in alpine regions than in the Arctic, as is suggested by temperature projections for 20 Arctic and alpine sites (Fig. 3).

In the Arctic and alpine, a decoupling of snow melt from the onset of growth and flowering due to environmental changes will also alter the timing of plants' access to key nutrients and water. A reduction in soil nutrient availability would affect arctic more than alpine plants because nutrient availability is already exceptionally low in the Arctic due to abundant soil C that fuels microbial growth and nutrient uptake by soil microbes (Weintraub & Schimel, 2003). In alpine ecosystems, reduced water rather than nutrient availability is more likely to alter the timing of plant life cycles and productivity. Alpine plants typically depend on snow melt water (Fisk *et al.*, 1998; Jonas *et al.*, 2008), which may increasingly limit growth as the growing season lengthens (Berdanier & Klein, 2011). In the Arctic, water resources from melting permafrost may sustain plant

growth during peak season even when snow melts early.

In arctic and alpine environments, the timing of seed set, cessation of root growth, and senescence is more conservative than the onset of growth (Shaver & Billings, 1977; Körner, 2003; Körner *et al.*, 2003). In an Arctic–alpine reciprocal transplant experiment, origin effects were greater for the timing of flowering and senescence than for leaf expansion, which changed in response to environmental cues at the transplant site (Prock & Körner, 1996). Across the landscape within a region, senescence is often more synchronous than the onset of growth or flowering. Even when soil and air temperatures are favorable and soil moisture is sufficient, senescence often continues unabated (Bliss, 1971; Starr *et al.*, 2000; Borner *et al.*, 2008), indicating that it is cued by a factor that is constant across the landscape, such as photoperiod. However, some arctic and alpine species senesce earlier if they green earlier in response to warmer springs, and low soil moisture can also cue early senescence for alpine plants (Arft *et al.*, 1999; Hollister *et al.*, 2005; Post *et al.*, 2008). Since warmer growing season temperatures may drive greater reductions in soil moisture in alpine systems than in the Arctic, where soil moisture tends to increase in response to warming (Xu *et al.*, 2013), we predict that earlier senescence will be more common in alpine ecosystems under climate change.

Plant productivity may not necessarily increase due to differences in the physical environments and evolutionary differences between arctic and alpine vegetation, but changes in plant population and community structure are likely. Species composition in the Arctic is changing, notably through increasing shrub cover, including the establishment of new individuals and increased growth of established individuals (Chapin *et al.*, 1995; Tape *et al.*, 2006; Myers-Smith *et al.*, 2011; Elmendorf *et al.*, 2012). In alpine ecosystems, species composition is changing through shifts in the production of extant species, establishment of subalpine species, and increasing species richness (Grabherr *et al.*, 1994; Pauli *et al.*, 2012). The rate of immigration of lower elevation species into alpine regions is more likely to keep pace with the rate of climate warming, whereas lower latitude species must disperse across much greater distances to reach the Arctic (Loarie *et al.*, 2009). The projected loss of species from arctic and alpine plant communities is difficult to confirm, since species are long-lived and do not produce leaves and flowers in all years. However, some alpine species declines have already been documented (Gottfried *et al.*, 2012). Changes in plant phenology, such as early senescence or decreased flowering in response to warming (Dorji *et al.*, 2013), are indicative

of species likely to decline as a consequence of climate change.

Climate warming will likely continue to extend the potential growing season duration in both regions (Fig. 3). We expect that some species will advance the timing of phenological events in spring and some will end growth later in the fall, but individual site characteristics and specific climatic changes in particular locations will modify these general phenological patterns. Overall, we predict that climatic and evolutionary differences may lead to delays in the timing of spring phenological development for some alpine plants in relation to the timing of snow melt, greater advances in the timing of phenological events in the spring in the Arctic, and earlier senescence in the fall in alpine ecosystems, altering the growing season length through different mechanisms in both systems (Fig. 3).

### The seasonality of microbes and belowground processes

Tundra soils host a diverse community of microorganisms (bacteria, archaea, and fungi) and fauna that interact through complex food webs (Moore *et al.*, 2004; Bardgett *et al.*, 2005). These soil organisms are responsible for ecosystem functions including nutrient mineralization, decomposition, and trace gas production. The rates of these functions are controlled by a suite of abiotic factors, including soil temperature and moisture (Clein & Schimel, 1995), snowpack dynamics (Buckner & Grogan, 2008), and substrate quality and availability (Schimel & Mikan, 2005; Schmidt *et al.*, 2007; Wallenstein *et al.*, 2007). Arctic and alpine microbial Community composition shifts seasonally resulting in a phenology in their structure, affecting biogeochemical cycling. These seasonal patterns in microbial activity appear somewhat decoupled from plant activities.

Unlike plants, microbes remain active throughout the year in tundra soils (Fig. 3) (Mikan *et al.*, 2002; Elberling & Brandt, 2003; Bardgett *et al.*, 2005; Monson *et al.*, 2006; Steven *et al.*, 2007). Fungi dominate the winter microbial communities and bacteria dominate summer communities (Bardgett *et al.*, 2005; Björk *et al.*, 2008; Buckeridge *et al.*, 2013), although both bacteria and fungi are active throughout the year. Microbial biomass in arctic and alpine soils is at its lowest in the summer and reaches its annual maximum during the snow-covered season (Brooks *et al.*, 1998; Lipson *et al.*, 2002; Edwards *et al.*, 2006; Schmidt *et al.*, 2007), consistent with evidence that microbes are capable of growth in frozen soils (McMahon *et al.*, 2009; Drotz *et al.*, 2010).

The transition period of spring thaw is a critical time in the annual cycle of tundra ecosystems (Edwards

*et al.*, 2006). Microbial communities are poised to take advantage of the moist conditions driven by snow melt following a long winter of slow growth, enzyme production (Lipson *et al.*, 1999; Wallenstein *et al.*, 2009), decomposition (Monson *et al.*, 2006), and nitrogen (N) mineralization. However, soil microbial biomass crashes in both arctic and alpine ecosystems before soil temperatures consistently rise above 0 °C (Brooks *et al.*, 1998; Jaeger *et al.*, 1999; Edwards *et al.*, 2006; Buckeridge & Grogan, 2010). The prevalent hypothesis to explain this crash is that soil freeze-thaw cycles induce stress, lowering microbial biomass and reducing the ability of the microbial community to compete for nutrients at the start of the growing season (Brooks *et al.*, 1998; Jaeger *et al.*, 1999). The decline in microbial biomass has also been attributed to the release of intracellular antifreeze and antidesiccation osmolytes needed for winter survival (Schimel *et al.*, 2007), starvation due to reduced availability of soluble C (Lipson *et al.*, 2000), and plant competition for N (Lipson *et al.*, 1999). However, Buckeridge & Grogan (2010) and Buckeridge *et al.* (2010) did not find support for any of these mechanisms and proposed that increased predation by soil fauna could result in this decline. Jefferies *et al.* (2010) proposed that climate strongly controls the microbial community and causes turnover due to an emerging temperature regime inhospitable to the winter microbial community, further suggesting that the seasonality of tundra climates plays a strong role in the phenology and function of microbial communities in tundra ecosystems.

Although the summer microbial communities in both arctic and alpine ecosystems are bacterially dominated (Bardgett *et al.*, 2005; Björk *et al.*, 2008; Buckeridge *et al.*, 2013), the two systems exhibit finer scale differences. Alpine microbial community composition is more dynamic (Schmidt *et al.*, 2007; Björk *et al.*, 2008), with multiple communities emerging and turning over during the plant growing season, whereas arctic microbial community structure is more stable (Männistö *et al.*, 2006; Wallenstein *et al.*, 2007; Buckeridge *et al.*, 2013). This distinction is important because whereas arctic microbial communities may be able to respond rapidly to seasonal shifts in substrate availability (Schimel & Mikan, 2005; Sturm *et al.*, 2005) and perturbations in climate because most taxa are present throughout the year, though likely in a dormant state, alpine microbial populations would require a turnover of the community before they could respond to environmental changes, resulting in a lagged response.

In contrast to the volume of research that has attempted to understand belowground spring-thaw processes, the fall–winter transition has only recently been examined. The timing of soil freezing in relation

to the development of an insulating snowpack has persistent effects on ecosystem function because early snowfall buffers winter soil temperatures in both arctic and alpine ecosystems resulting in increased microbial activity and C release over the winter (Brooks & Williams, 1999; Grogan & Chapin, 1999). For example, when snow accumulated early at an alpine site, microbial biomass increased through the winter and continued to increase at snow melt (Brooks & Williams, 1999). When cold temperatures arrived before significant snowfall, soil temperatures dropped and remained cold, limiting microbial activity throughout the winter.

Temperature and the timing and amount of snowfall are tightly linked with microbial activity, so projected differences in climate change may cause divergent patterns in arctic and alpine microbial communities. Climate change scenarios suggest that the Arctic will experience warmer winters with increased precipitation, which could create more favorable belowground conditions to drive higher rates of microbial activity during the snow-covered period (Fig. 3). However, a longer summer season could reduce the duration of the fungally dominated, winter-active community in the Arctic and lead to a longer period of faster nutrient cycling by the bacterially dominated food web. This could result in more N availability for arctic plants. If alpine snowpack declines with warmer winter temperatures and altered precipitation regimes, the belowground community could be less buffered from colder soil temperatures, which could limit microbial activity (Brooks & Williams, 1999; Fig. 3). Additionally, warmer temperatures during the summer and shoulder seasons in both arctic and alpine ecosystems will warm seasonally frozen ground and increase the thickness of the active layer in areas with permafrost, making more organic C available for microbial decomposition. Given the short length of the fall and spring shoulder seasons, shifts in seasonality due to climate change are likely to have strong effects on soil microbial communities and ecosystem functions, such as decomposition and nutrient mineralization and retention (Fig. 3).

### Seasonality of biotic interactions

Changes in the seasonal patterns of abiotic drivers have the potential to induce complex feedbacks in the structure and function of arctic and alpine ecosystems due to the interactions of animals, plants, soil fauna, and microbes. For example, physiological and phenological responses of plants and changes in plant species composition may alter the quantity and quality of forage for aboveground herbivores (Jefferies *et al.*, 1992), as well as the detritus that forms the substrate for the belowground detrital food web (Moore *et al.*, 2004;

Cornelissen *et al.*, 2007). In turn, the composition of the active detrital community can shift, for example, from a fungal-dominated food web that cycles nutrients more slowly to a bacterially dominated food web (van der Heijden *et al.*, 1998; Wardle *et al.*, 2004). The resulting shifts in the timing and quantity of nutrient inputs from microbial processes, as well as herbivores, further affect vegetation production.

The timing of spring snow melt and soil thaw, when the N mineralized over the winter is released in a pulse, relative to the onset of plant activity can determine plant–microbe competition for the nutrient pulse that accompanies the thaw. Thus, it is an important determinant of N retention and loss from snow-covered ecosystems. In both arctic and alpine ecosystems, low N availability limits net primary productivity (Bowman *et al.*, 1993; Shaver *et al.*, 2001). In alpine systems, the pulse of organic N that occurs at spring snow melt is rapidly assimilated into microbial biomass, resulting in a period of rapid microbial growth (Brooks *et al.*, 1998; Hiltbrunner *et al.*, 2005). However, this period is short-lived, as plants quickly begin to compete with microorganisms for N. Under current climate conditions, alpine plants are successful N competitors (Bilbrough *et al.*, 2000), but in the Arctic, soil thaw and plant bud-burst can be separated temporally by a few weeks, and this pulse of N can be immobilized by microbes or lost from the ecosystem (Bilbrough *et al.*, 2000; Buckeridge & Grogan, 2010).

Future climate changes could cause arctic and alpine plant–microbe competition to increase through greater synchrony or decrease through greater asynchrony. In alpine ecosystems, projected increases in air and soil temperatures during the spring shoulder season could result in microbial N immobilization or ecosystem loss through leaching and denitrification if dependence on photoperiodic cues prevents plant growth initiation from advancing at the same rate as snow melt and microbial processes (Fig. 3). Alpine plants' reduced ability to access early-season N could reduce aboveground production throughout the growing season. Furthermore, plant species with stronger photoperiodic cues and later growth initiation may have a competitive disadvantage within the plant community, leading to shifts toward greater dominance of species with earlier growth initiation. Arctic plants can initiate growth earlier in response to warmer early-season temperatures and advanced soil thaw, and could increasingly capitalize on N mineralized over winter (Fig. 3). This would increase aboveground biomass and give arctic plant species that are successful early-season N competitors an advantage for growth and reproduction, and have long-term implications for shifts in plant community composition.

One of the most dramatic shifts predicted for tundra communities is the northward and upward expansion of shrubs, resulting in a change in plant community composition commonly attributed to warming (Sturm *et al.*, 2005). Due to their growth form and stature, shrubs alter their microclimate; in the summer, they shade the soil, and in the winter, they trap snow, which leads to warmer winter soil temperatures, later soil thaw and increased soil moisture. Increasing shrub abundance also alters litter chemistry, which reduces decomposition rates and soil respiration (Cornelissen *et al.*, 2007). In addition, increasing abundance of shrub vegetation results in a reduction in forage quality and quantity for large ungulate grazers, such as caribou (Sturm *et al.*, 2005). Grazers can mitigate the effects of warming on changes in aboveground community composition by placing top-down pressure on shrubs, thereby keeping their abundance in check (Post & Pedersen, 2008).

The spring shoulder season is particularly important for maintaining reproduction and nutrition of tundra animals, and there is a tight coupling between the timing of animals' emergence from winter and the initiation of the plant growing season. Grazers forage on early spring growth to support their increasing metabolic demands after overwintering. The synchrony of animals' reproductive cycles with green-up is also critical for survival of newborns (Bronson, 2009). In turn, plants from moderately to heavily grazed tundra systems rely on nutrient inputs from grazers to fuel their early-season green-up (Jefferies *et al.*, 1992).

Abiotic cues, such as photoperiod and air temperature, as well as vegetation conditions, are the primary seasonal factors affecting reproductive cycles and grazing behavior of mammalian herbivores. Larger, longer lived herbivores, such as caribou, tend to synchronize their reproduction with photoperiodic cues, while small mammals with shorter generation times, such as voles and lemmings, are able to adjust their reproductive cycles more dynamically in response to changes in forage availability (Bronson, 2009). Thus, small mammals will be better able to adapt their reproductive cycles in response to shifts in seasonality and plant phenology (Bronson, 2009), whereas large herbivores that are dependent on fixed photoperiodic cues may face a decoupling of the timing of the birth of offspring and the supply of nutrient dense foliage at plant green-up, thereby leading to increased mortality of offspring (Post & Forchhammer, 2008). Alpine marmots emerge from hibernation in response to spring temperatures. Those that ramp up their metabolic rates in response to warmer spring air temperatures while plants are still snow-covered and inaccessible are susceptible to starvation (Inouye *et al.*, 2000). Yet, even if alpine spring



snowpack decreases with climate warming and altered winter precipitation patterns, we predict that alpine plants may be too constrained by photoperiodic cues and chilling requirements to advance their growth in synchrony with small mammals' activity in the spring shoulder season. Projections of deeper and more persistent snow cover in the Arctic will also prevent some grazers from reaching forage. Muskoxen are not well adapted for travel and foraging in deeper snow, so increases in winter precipitation may lower their energy balance, increase winter mortality, and reduce rates of reproduction (Jefferies *et al.*, 1992). Greater oscillations or declines in the population numbers of large and small mammals with climate change will have cascading effects to lower and higher trophic levels, as well as to biogeochemical cycles.

Although trophic interactions of arctic and alpine plants with microbes and herbivores at individual sites are currently relatively well understood, climate change-induced perturbations in these interactions will be difficult to predict (Walther *et al.*, 2002; Wookey *et al.*, 2009). The variation in the responses to a changing climate will be tied to the seasonality of the abiotic drivers of plant production and microbial processes, as well as with those of the organisms at higher trophic levels with which they interact.

### Seasonality of ecosystem carbon balance

The carbon (C) cycles of arctic and alpine ecosystems have similar seasonality because whether an ecosystem is acting as a C sink or source is largely driven by abiotic conditions, such as air temperature, daily solar radiation, and soil temperature and moisture. During the growing season, net ecosystem production (NEP) is typically positive, with photosynthesis driving net sequestration of C in plant biomass and soil (Rennermalm *et al.*, 2005; Freeman *et al.*, 2009). Ecosystem respiration releases C back to the atmosphere throughout the year in arctic and alpine ecosystems, but during the spring and fall shoulder seasons, as well as during the snow-covered period, respiration drives the tundra biome to become a net C source (Zimov *et al.*, 1993). Thus, the timing of the onset and end of the growing season is a major control on whether arctic and alpine ecosystems function as C sinks or sources to the atmosphere (Fig. 3).

Abiotic drivers, such as temperature and soil moisture, have the potential to directly affect C source and sink strength by controlling autotrophic and heterotrophic metabolism rates (Lupascu *et al.*, 2013). In the European alpine, air temperature was found to be the most important variable controlling ecosystem respiration (Wohlfahrt *et al.*, 2008). Similarly, Oechel *et al.*

(2000) found that increases in growing season temperature as small as 0.5 °C caused Alaskan arctic tundra to become a C source. Microbial responses to temperature are likely more plastic and able to take advantage of warming in arctic and alpine ecosystems than plant responses, which are constrained by other abiotic cues. Thus, increased warming in the summer, the snow-covered period, or both would increase microbial decomposition and respiration. Although the small increase in temperature may only alter the rate of microbial decomposition slightly, this can have a large impact on the annual C balance. For example, Clein & Schimel (1995) estimated that up to 30% of the C flux from Toolik Lake occurs during the 'frozen' season, so projected winter warming could substantially affect the net annual C sink strength of these systems (Christensen *et al.*, 2013).

Abiotic drivers can also affect ecosystem C balance indirectly by changing the length of the growing season. In particular, shifting seasonality that extends or reduces the number of growing season days will cause an ecosystem to become more of a net C sink or source, respectively, by altering the photosynthetically active period for plants. Earlier, we suggested that arctic plants are more likely than alpine plants to advance their photosynthetically active season in the spring. Additionally, we expect that alpine plants are less likely to extend their growing season later into the fall due to resource limitation. Therefore, arctic ecosystems may be more likely to increase their C sink strength (Ueyama *et al.*, 2013) than alpine sites (Fig. 3).

Indeed, a circumpolar study of NDVI trends and CO<sub>2</sub> fluxes north of 45°N latitude found that the timing when northern systems switch from a net CO<sub>2</sub> source to a sink has advanced by 5.7 days on average since 1972, concurrent with advances in the growing season of 3.3 days from 1982 to 2011 (Barichivich *et al.*, 2013). However, the switch from net sink to source at the end of the growing season also advanced by 6.3 days on average, offsetting the early-season gains in C, despite an extension of the growing season by 2.9 days (Barichivich *et al.*, 2013). Although Barichivich *et al.* included areas south of the Arctic, another study using NDVI measurements in arctic tundra to track phenological change from 2000 to 2010 confirms the changes in growing season length (Zeng *et al.*, 2011). Thus, across the tundra biome, warming-induced resource limitation at the end of the growing season may constrain ecosystems' ability to sequester C under a warmer climate that is otherwise favorable for photosynthesis. For example, although the C sink strength appears to increase with warming in the low Arctic (Ueyama *et al.*, 2013), Lupascu *et al.* (2013) found that at a site in the high Arctic, warming had to be

accompanied by precipitation treatments to sequester more C. Earlier senescence would allow litter-fall and decomposition to occur at warmer temperatures, thereby increasing the decomposition rate and decreasing net C sink strength in the Arctic (Fig. 3). However, decomposition rates in alpine ecosystems may not remain high during earlier vegetation senescence if soil moisture is limiting to both plant growth and microbial activity, thus reducing both C efflux and uptake during the fall shoulder season.

Changing above- and belowground species composition in response to warming will also affect C uptake and efflux processes in the Arctic and alpine. For example, warming-induced shrub expansion across the tundra biome could lead to greater C sequestration via slower decomposition of more recalcitrant litter (Cornelissen *et al.*, 2007); however warmer winter soil temperatures under shrub tundra could increase decomposition rates (Sturm *et al.*, 2005). Although we have predicted that alpine C sink strength will decrease with a shortening of the alpine plant growing season, changing species composition, driven in part by an immigration of species from lower elevations, may produce compensatory effects for ecosystem processes, which in the long term could increase the alpine C sink strength (Fig. 3).

Warmer temperatures will contribute to greater permafrost thaw in the Arctic, which will release C from the soil, altering the regional C balance of these systems more dramatically than in alpine systems (Schuur *et al.*, 2008). Whether C release from permafrost will be offset by increased plant productivity is under debate, although recent work indicates that C efflux will be greater than the effect of stimulating vegetation (Schuur *et al.*, 2009; Natali *et al.*, 2014). Additionally, heat generated by greater microbial activity could drive further permafrost thaw (Khvorostyanov *et al.*, 2008; Ciais *et al.*, 2013). Therefore, increased summer and winter arctic temperatures may lead to year-round net C efflux.

The ability of the tundra biome to store C will be affected by climate warming and shifts in seasonality that induce cascading effects on growing season length, species composition, and the physiological processes that control ecosystem C fluxes. Evidence of how these ecosystems are responding to changes in abiotic drivers leads us to postulate that alpine C sink strength will decrease (Fig. 3). Conversely, arctic tundra might increase its ability to act as a C sink with earlier initiation of plant growth, but advancing senescence and increased decomposition of permafrost C may offset these gains in C uptake (Fig. 3). Because of the complex ways in which ecosystem C balance is governed by the activity and interactions of autotrophs and heterotrophs,

as well as their responses to changes in the seasonality of abiotic drivers, ecosystem C balance can be viewed as an aggregator of the responses of many other ecosystem properties to changes in seasonality.

## Conclusions

The common attributes of short and cold growing seasons in arctic and alpine ecosystems have resulted in the widespread view that these systems are also similar in structure and function. These systems may, however, respond differently to global climate change. There is strong evidence that temperatures will rise significantly by the end of the 21st century, extending the number of above-zero days into the shoulder seasons across arctic and alpine systems (Fig. 3). Projections of future precipitation patterns are less certain across the tundra biome, particularly for alpine ecosystems. The Arctic is expected to receive more winter snowfall, while alpine systems are projected to receive reduced precipitation. Latitude explains many ecosystem processes across the tundra biome by affecting day length in relation to the timing of snow melt, evolved cues for plant phenology, and winter temperatures. Changes in climate will lead to biological asynchronies if above- and belowground communities respond differently to higher temperatures and altered precipitation regimes, with cascading effects across trophic levels.

This review contributes a novel synthesis of predicted ecological responses of below- and aboveground communities, processes, and their interactions in response to global climate change across the tundra biome. Predictions of whole-system responses are based on logical inferences of current knowledge of ecosystem components and their responses to global change experiments and observations to date. We have primarily presented situations where alpine and arctic ecosystems respond differently to changes in seasonality produced by global climate change.

We predict that differences in photoperiod, cues for plant phenological development, persistence of snow cover, and resource availability will trigger divergent responses between alpine and arctic ecosystems (Fig. 3), with alpine ecosystems emerging as potentially more vulnerable to climate change than the Arctic. Although warmer air temperatures are extending the potential growing season in both arctic and alpine ecosystems, constraints on alpine plants prevent them from realizing a longer growing season. We expect delays in spring phenological development for some alpine plants, and earlier senescence in the fall in alpine ecosystems. Microorganisms and belowground biogeochemistry, however, are temperature dependent, so changing seasonality in alpine ecosystems will extend

their period of activity unless declines in the alpine snowpack result in less-buffered soil temperatures and lower soil moisture, which limit microbial activity (Brooks & Williams, 1999; Fig. 3). N availability to alpine plants may decrease if increased air and soil temperatures during the spring shoulder season drive asynchronies in the timing of plant growth and microbial turnover. This could reduce aboveground production throughout the growing season. The result of a shortened growing season and a decline in aboveground biomass will result in a decreased alpine C sink (Fig. 3). Herbivores will be affected by the asynchrony between spring temperatures and plant green-up, as well as by declines in biomass, unless changing plant species composition alters the ability of plants to respond to changing seasonality.

Unlike the response for alpine plants, we predict that arctic spring phenological events will be able to advance their timing, thereby lengthening the arctic growing season. Warmer temperatures also result in a longer period with a bacterially dominated belowground food web, resulting in more N availability for arctic plants due to rapid nutrient cycling. Higher N availability in turn is expected to increase plant biomass and increase the C sink strength in the Arctic. However, warmer winters with more snowpack will increase winter soil temperatures, driving higher rates of microbial activity during the snow-covered period (Fig. 3), which could negate growing season C gains. In addition, the impacts of increased temperatures on decomposition of C from thawing permafrost remain uncertain. Increased snowpack might also limit herbivores' access to forage resources, thereby reducing their populations and altering nutrient cycles and trophic interactions.

We have highlighted the importance of seasonal transitions, particularly the spring and fall 'shoulder seasons,' for understanding how arctic and alpine regions will respond to climate change. Many important transitions in arctic and alpine ecosystems occur during the shoulder seasons, including the release of inorganic N at soil thaw, the turnover of microbial communities from winter-active to summer-active, and the transition from C sink to source, and *vice versa* (Fig. 3). Continuous monitoring programs in many arctic and alpine ecosystems worldwide are now providing detailed climate data for these critical periods, yet few studies have investigated the biology of arctic and alpine systems during the shoulder seasons. Future studies should focus on how C and N cycling during these periods contribute to annual process rates to better predict the functioning of these ecosystems under future climate conditions. In addition, future research should target a more definitive estimate of the spatial extent of

the tundra biome to enable our ability to scale up predictions regionally and globally. This estimate should include the location and identity of vegetation types within it and at its margins, as these are the possible immigrant pool to the tundra biome as it warms. Given the complex interactions between abiotic drivers and biotic processes, an integrated systems approach will be required to unravel the cascade of effects that will accompany changes in seasonality in arctic and alpine environments.

## Acknowledgements

Fellowships from the Department of Energy Global Change Education Program and the National Science Foundation Graduate Research Fellowship Program supported JE, the latter of which also supported KH and AB. Award number 0902030 from the National Science Foundation Office of Polar Programs supported MW and HS. MW was also supported by an NSF CAREER award (#1255228) and a grant from the Office of Science (BER), U.S. Department of Energy. Thanks to Kate Buckenridge and Anthony Darrouzet-Nardi for comments on the manuscript, and to three anonymous reviewers whose comments significantly improved the manuscript. Thank you to the field stations and research programs that provide online access to their climate data, and to the individuals who provided data. Additional acknowledgements for data sharing are in Table S1. We are very grateful to those who generously supplied data for our analyses, including data for temperature projections in 2070.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** List of research stations/sites, as well as site characteristics, years of air and soil temperature data used for the synthesis, and acknowledgements for data sharing. To calculate averages for air and soil temperature, we generally used data from 2001 to 2006, unless these dates were unavailable and then we used the closest data possible. The details are within the table. When multiple measures of a variable were given for a site, we used an average of the values.