Resilience of Alaska's boreal forest to climatic change[1]

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Abstract: This paper assesses the resilience of Alaska's boreal forest system to rapid climatic change. Recent warming is associated with reduced growth of dominant tree species, plant disease and insect outbreaks, warming and thawing of permafrost, drying of lakes, increased wildfire extent, increased postfire recruitment of deciduous trees, and reduced safety of hunters traveling on river ice. These changes have modified key structural features, feedbacks, and interactions in the boreal forest, including reduced effects of upland permafrost on regional hydrology, expansion of boreal forest into tundra, and amplification of climate warming because of reduced albedo (shorter winter season) and carbon release from wildfires. Other temperature-sensitive processes for which no trends have been detected include composition of plant and microbial communities, long-term landscape-scale change in carbon stocks, stream discharge, mammalian population dynamics, and river access and subsistence opportunities for rural indigenous communities. Projections of continued warming suggest that Alaska's boreal forest will undergo significant functional and structural changes within the next few decades that are unprecedented in the last 6000 years. The impact of these social–ecological changes will depend in part on the extent of landscape reorganization between uplands and lowlands and on policies regulating subsistence opportunities for rural communities.

Résumé : Cet article évalue la résilience du système forestier boréal de l'Alaska face aux changements rapides du climat. Le réchauffement récent est associé à la réduction de croissance des espèces d'arbre dominantes, aux maladies des plantes et aux épidémies d'insectes, au réchauffement et à la fonte du pergélisol, à l'assèchement des lacs, à l'augmentation de l'étendue des incendies de forêts, au recrutement accru d'espèces feuillues après un feu et à la diminution de la sécurité des chasseurs qui se déplacent sur le lit glacé des rivières. Ces changements ont modifié des caractéristiques structurales, des rétroactions et des interactions fondamentales dans la forêt boréale, incluant la réduction des effets du pergélisol des hautes terres sur l'hydrologie régionale, l'expansion de la forêt boréale vers la toundra et l'amplification du réchauffement climatique à cause de la diminution de l'albédo (saison hivernale plus courte) et des émissions de carbone provenant des incendies de forêt. D'autres processus sensibles à la température pour lesquels aucune tendance n'a été détectée incluent la composition des communautés végétales et microbiennes, les changements à long terme à l'échelle du paysage dans les stocks de carbone, le débit des cours d'eau, la dynamique de population des mammifères ainsi que l'accès aux rivières et les perspectives de subsistance des communautés indigènes rurales. Les projections concernant la poursuite du réchauffement indiquent que la forêt boréale de l'Alaska va subir au cours des prochaines décennies des changements fonctionnels

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[1]This article is one of a selection of papers from The Dynamics of Change in Alaska's Boreal Forests: Resilience and Vulnerability in Response to Climate Warming.
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et structuraux sans précédents depuis les 6000 dernières années. L'impact de ces changements socio-écologiques dépend en partie de l'ampleur de la réorganisation du paysage entre les zones sèches et humides et des politiques qui régissent les perspectives de subsistance des communautés rurales.

[Traduit par la Rédaction]

Introduction

The boreal forest is the northernmost and coldest forested biome. It is underlain by discontinuous permafrost (permanently frozen ground) that governs stand-level biogeochemistry and regional hydrology. The continental climate of interior Alaska results in cold winters (January mean –23 °C), warm summers (July mean 16 °C), and an annual precipitation (mean 287 mm) that is similar to that of midlatitude deserts (Hinzman et al. 2006). Despite low precipitation and warm summer air temperatures, permafrost, where present, results in cold, wet soils during summer that have in the past constrained rates of decomposition, nutrient turnover, and productivity (Van Cleve et al. 1991).

High-latitude amplification of 20th century global warming has caused Alaska's boreal forest to warm twice as rapidly as the global average (Arctic Climate Impact Assessment 2005; Hinzman et al. 2005; Intergovernmental Panel on Climate Change 2007). Mean annual air temperature in interior Alaska has increased by 1.3 °C during the past 50 years (Shulski and Wendler 2007) and is projected by downscaled climate models to increase by an additional 3–7 °C by the end of the 21st century (Walsh et al. 2008; Scenarios Network for Alaska Planning 2010). Precipitation has increased by only 7 mm in the last 50 years (Hinzman et al. 2006). Its projected continued increase will likely be insufficient to offset summer evapotranspiration (Scenarios Network for Alaska Planning 2010), leading to potentially drier soils and lower lake levels.

In response to a gradual Holocene cooling and moistening of climate, black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) assumed regional dominance 5000–7000 years ago, producing a landscape mosaic whose pollen and charcoal abundances were similar to those of today (Lloyd et al. 2006). People have occupied this region for at least the last 8000 years (Aigner 1986) and have therefore been part of the modern boreal forest since its inception. This boreal system has persisted relatively unchanged, within the detection capabilities of paleoecological indicators, for the past 6000 years, despite substantial climatic fluctuations such as the Medieval Warm Period and Little Ice Age (Mann et al. 2009). This suggests substantial historical resilience of the boreal forest to climatic change. However, warming since the 1950s appears to be unprecedented in at least the last 2000 years (Overpeck et al. 1997; Kaufman et al. 2009). In this paper, we synthesize and integrate the findings of the Bonanza Creek Long-Term Ecological Research (LTER) program, as detailed in other papers in this special issue. We conclude that the Alaskan boreal system remains quite resilient but is undergoing changes in ecosystem and landscape structure, feedbacks, and interactions that, with continued warming, will likely cause reor-

ganization or potential transformation to a fundamentally different system.

Conceptual background and framework

We view the boreal forest as a coupled social–ecological system in which social and ecological components interact in ways that govern the structure, functioning, and feedbacks of the system as a whole; a conceptual framework developed by the US LTER Network (Collins et al. 2007). Increases in the global human population and its use of resources and technology drive changes in Alaska that include climate warming, extraction of fossil fuels, and human immigration (Fig. 1). These changes in regional drivers, in turn, alter the natural disturbance regimes that govern the structure and functioning of ecosystems. Climate warming, for example, has modified ecosystem process rates through a variety of "press" perturbations (gradual changes) (Collins et al. 2007), including increased frequency of drought and lake drying (Fig. 1). In addition, warming modifies the frequency and severity of "pulse" perturbations (events), such as fires, floods, and thermokarst (ground depressions related to thawing permafrost). Climate warming and regional economic and demographic changes also influence social systems directly, thereby altering human effects on ecosystems, such as fire suppression, hunting, and land-use change.

The changes in press and pulse perturbations alter ecosystem structure and functioning in ways that affect "ecosystem services", the benefits that society derives from ecosystems (Fig. 1). Ecosystem services include food, fiber, and water (provisioning services); regulation of climate, disturbance regime, and hydrologic flows (regulatory services); and cultural, aesthetic, and recreational ties to the land (cultural services) (Millennium Ecosystem Assessment 2005). Ecosystem services, in turn, alter human behavior such as hunting patterns, food sharing, and demographic shifts, yielding human outcomes such as village structure, cultural integrity, land ethic, and hunting regulations (Fig. 1). The effect of ecosystem services on human behavior depends strongly on culture and human values. Although people have interacted with the boreal forest throughout its history, these interactions have changed substantially in the past century (Kofinas et al. 2010).

Vulnerability and resilience are conceptual frameworks that facilitate assessment of the long-term consequences of these changes. "Vulnerability" is the degree to which a system is likely to change due to exposure and sensitivity to a specified hazard or stress (Fig. 2, left side). Vulnerability also depends on a system's adaptive capacity to respond to the stress (Turner et al. 2003; Adger 2006). Adapting to climate change requires coping with current changes, learning the ecological and social consequences of change, innovating, and adapting to these changes. The boreal forest is ex-

Fig. 1. Diagram of the Alaskan boreal social-ecological system, based on the framework and concepts developed by the US Long-Term Ecological Research network (Collins et al. 2007). Global-scale drivers of change influence the regional drivers that directly perturb the boreal system through effects on social and ecological subsystems and the disturbance regime that links these subsystems. The resulting changes in dynamics alter ecosystem services, which modify human behavior and outcomes. Modified from Collins et al. (2007).
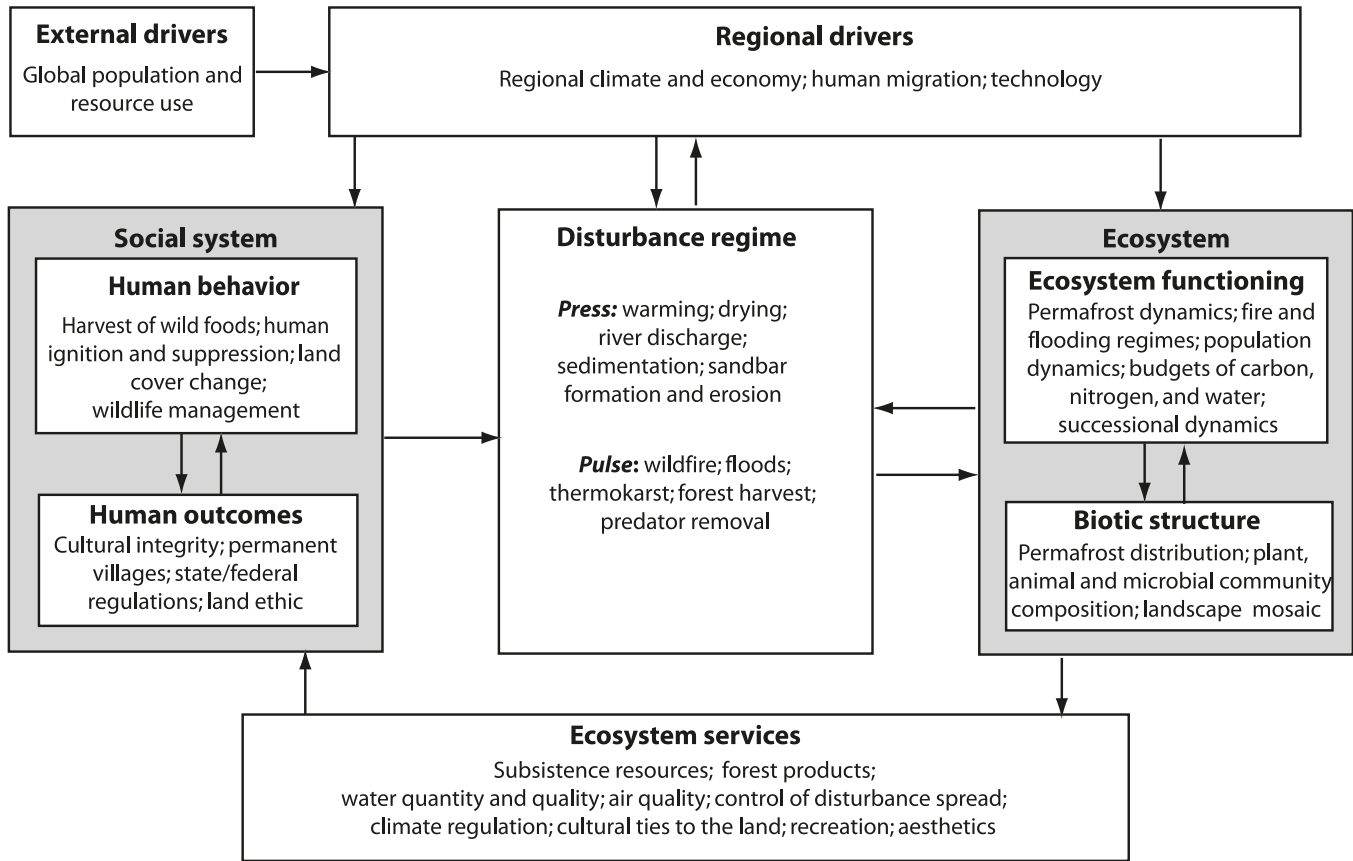
posed to a greater degree of climate warming than most places on Earth. This special issue documents the sensitivity and adaptive responses of the boreal system to climate warming with the aim of assessing the vulnerability of boreal forests to recent climate forcing.

"Resilience" is the capacity of the system to sustain its fundamental function, structure, and feedbacks when confronted with perturbations such as unprecedented warming (Walker et al. 2004; Folke 2006; Chapin et al. 2009a) (Fig. 2, right side). Resilience depends on the diversity of options available, the capacity to adapt to change, and the human capacity to adjust governance to implement new solutions. The boreal forest has properties that convey both *specific resilience* to particular perturbations (e.g., the semi-serotinous cones of black spruce that disperse seeds after fire) and *general resilience* (e.g., a diversity of species, successional trajectories, and patch dynamics that permit flexible response to a wide variety of expected and unforeseen perturbations) (Chapin et al. 2009a). Exceeding the resilience of the system may cause it to transform to some new state that has different system properties, that is sustained by different feedbacks, and that becomes resilient within this new domain of attraction (Fig. 2). The difference between persistence of a system (its resilience) or its transformation often depends on the balance between negative (stabilizing) feedbacks that tend to maintain the system in its current

state and positive (amplifying) feedbacks that tend to push the system toward some new state (Chapin et al. 2009a). We assume that the boreal forest, like all ecosystems, has a suite of stabilizing feedbacks associated with competition, trophic dynamics, and successional cycles that sustain its characteristics over time. We hypothesize that certain climate-driven changes could initiate amplifying feedbacks that might transform the boreal forest to a new state (Fig. 2). Triggers for change might include the following:

- changes in soil moisture and hydrology associated with loss of permafrost, increased growing-season length, and seasonal timing of soil moisture recharge;
- changes in successional trajectory and biogeochemistry associated with changes in fire, flooding, or insect and (or) pathogen outbreaks;
- changes in abundance of keystone species (i.e., those that are disproportionately important relative to their biomass) or dominant species, including white spruce, alder, *Sphagnum* mosses, and snowshoe hares; and
- changes in human use of landscapes.

In this paper, we describe sources of boreal resilience. We also ask whether there have been changes that have the potential to trigger transformation and whether these transformations have begun to occur. A final consideration, about which we can only speculate, is the permanence or reversibility of ongoing or potential transformations.

Fig. 2. System perspective on the vulnerability and resilience of the Alaskan boreal forest, showing how changes in drivers (left side) modify the system to produce resilient or transformational outcomes (right side). The arrows at the bottom show the range of processes associated with vulnerability, adaptability, resilience, and transformability. Multiple external stresses (climate warming and resource development) interact to increase the extent and severity of wildfire. This, in turn, creates impacts (permafrost loss and habitat change). Social learning (learning, coping, innovating, and adapting) in response to these impacts has the potential to alter social–ecological interactions and various forms of capital of the system, which in turn, influence sensitivity to future events. Social learning also governs the relative likelihood of three potential outcomes: persistence of the existing system through resilience; actively navigated transformation to a new, potentially more beneficial trajectory through transformation; or unintended degradation to a new state due to vulnerability and failure to adapt or transform. Modified from Chapin et al. (2009*a*).
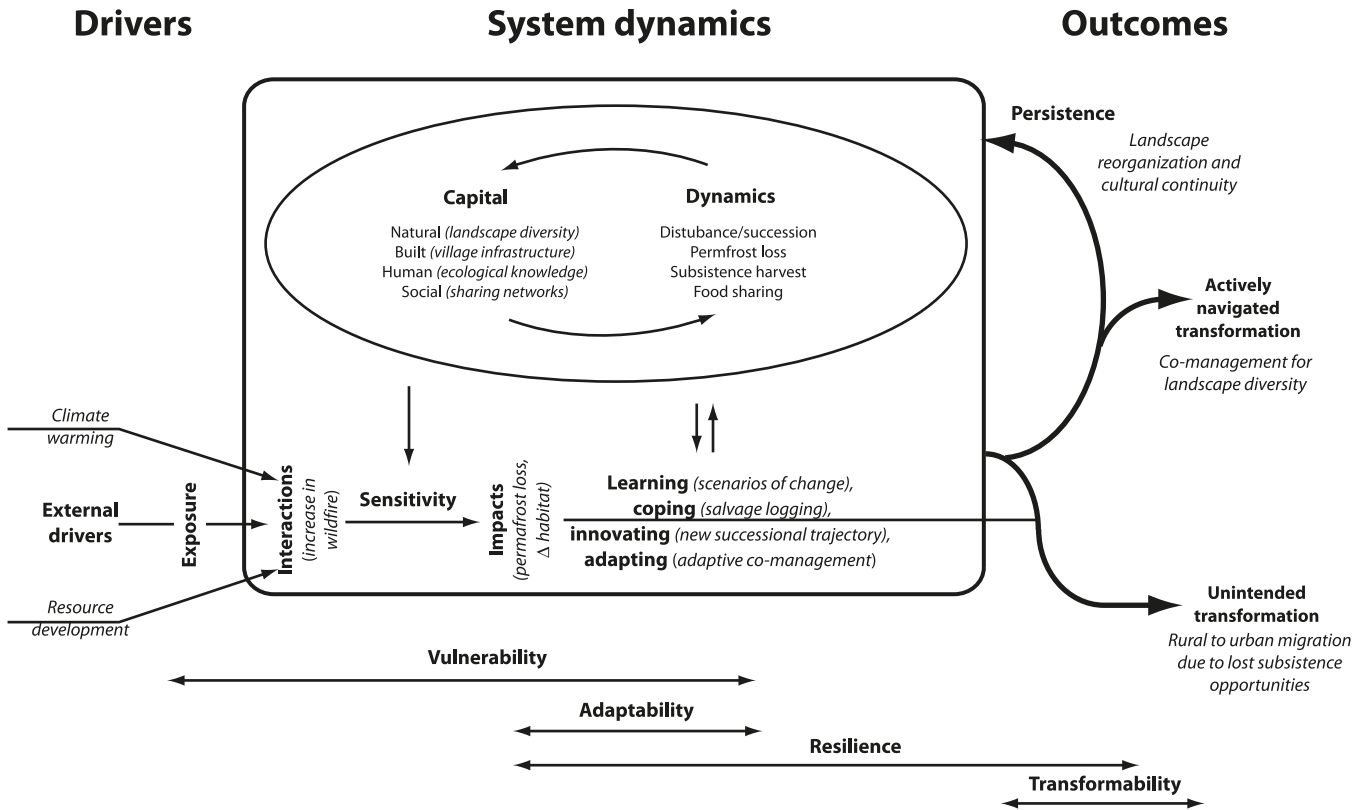
Climate sensitivity

Changes in uplands and well-drained sites

In contrast to the continuous permafrost zone of the Arctic, changes in discontinuous permafrost of the boreal forest are driven primarily by changes in ecosystems rather than by climatic change (Jorgenson et al. 2010). In interior Alaska, for example, changes in the insulative properties of snow, surface water, and vegetation and in the surface organic layer have altered permafrost integrity more than have changes in air temperature. Consequently, topographic and successional variations in these ecosystem properties lead to a spectrum of permafrost responses to climate warming (Jorgenson et al. 2010). In north-facing uplands, where there is no impoundment of surface water, gradual warming of permafrost has not greatly altered permafrost integrity except through occasional gully formation, whereas accumulation of surface water in thawing ice-rich lowlands or loss of organic insulation after severe fires leads to rapid permafrost loss.

Upland hydrology has also been relatively resilient to Alaska's long-term warming trend (Jones and Rinehart 2010). Although there is generally less discharge in warm years than in cool years, presumably due to greater evapotranspiration, there has been no detectable temporal trend in base flow or total summer discharge over the past forty years. Winter flow appears to be increasing in regions of the larger Yukon River Basin where permafrost is discontinuous (Walvoord and Striegl 2007). These results suggest that upland soils might continue to dry, and headwater streams could become ephemeral, if warming continues (Jones and Rinehart 2010).

Earlier snowmelt and later freezeup in interior Alaska (Euskirchen et al. 2010; Juday et al. 2005) have lengthened the growing season, causing trees to leaf out earlier in spring (Robin et al. 2008). Earlier spring leaf out enhances both photosynthesis and ecosystem respiration and, in moist systems, might increase carbon sequestration (Welp et al. 2007; Richardson et al. 2009). However, the functional consequences of longer and warmer growing seasons for water, carbon, and nutrient balance of Alaskan boreal ecosystems vary with soil moisture (McGuire et al. 2009), whose temporal trends depend on landscape position.

Fertilization and moisture exclusion studies show that moisture is now the primary factor limiting production of Alaskan boreal trees (Yarie and Van Cleve 2010). Nutrient

responses occur primarily early in the season when soils are cold, in cool moist sites, or in wet years. These recent findings of strong drought effects contrast with earlier research, conducted when climate was cooler, which showed widespread nutrient limitation of forest production at our LTER sites (Van Cleve et al. 1986, 1991).

Because of the widespread occurrence of drought, most tree species in interior Alaska exhibit negative growth responses to warming (Juday et al. 2005; McGuire et al. 2010), a pattern that is consistent with declines since 1990 in greenness indices measured by satellites (Goetz et al. 2005; Lloyd and Bunn 2007; Verbyla 2008). Reductions in tree growth have been examined most thoroughly in white spruce (*Picea glauca* (Moench) Voss), the late-successional tree that dominates warm south-facing uplands and lowland floodplain forests. In this species dendrochronological, population, and experimental rainfall exclusion studies show that individual trees show a spectrum of growth responses to warming and rainfall, ranging from positive to negative. Negative responses of growth to temperature predominate over positive responses in this species (McGuire et al. 2010). White spruce is most negatively affected by warming in warm regions and in floodplain landscape positions where river levels are dropping. Even in cool environments such as tree line, formerly positive responses of tree growth to warming are now changing to growth reductions in many locations (Wilmking et al. 2004).

Recent extensive insect outbreaks on white spruce, aspen (*Populus tremuloides* Michx.), and larch (*Larix laricina* (Du Roi) K. Koch) might be both a response and contributor to reductions in tree growth. In the Kenai Peninsula of southern Alaska, extensive stand-level mortality of white–Sitka (*Picea sitchensis* (Bong.) Carrière) spruce hybrids, associated with warming and drying, led to dense growth of the grass *Calamagrostis canadensis* (Michx.) P. Beauv. and very poor spruce regeneration, suggesting a switch from forest to grassland (Berg et al. 2006). In interior Alaska, upland white spruce has dispersed into adjacent black spruce habitat after fire, producing seedling densities sufficient to generate fully stocked white spruce stands (Wirth et al. 2008). Together these studies suggest a low stand-level resilience of white spruce and perhaps other forest types, but the possibility of landscape-level resilience, if upland species shift into landscape positions that are currently dominated by black spruce. This landscape reorganization might occur extensively if wildland fire continues to increase in extent and severity in black spruce forests, as described later.

Changes in lowlands and poorly drained sites

In some poorly drained lowlands, permafrost shows low resilience to climate warming. Here thawing of high-ice-content permafrost, formed during the Little Ice Age, has in recent decades, caused surface subsidence and conversion of forests to ponds or wetlands, which absorb more radiation due to the low albedo (short-wave reflectance) of the wet surface, thereby accelerating the rates of thaw and landscape change (Jorgenson et al. 2010).

In lowlands underlain by gravel, high-ice permafrost is less common, and climate warming causes drying of lakes because of increased evapotranspiration and, in some situations, loss of permafrost and internal drainage (Jorgenson et

al. 2010; Riordan et al. 2006). Willows, which colonize drained lake basins, have high rates of evapotranspiration, causing further drying. Lake drainage and wetland drying currently predominate over paludification in interior Alaska (Riordan et al. 2006).

In many peatlands and black spruce forests, the most widespread forest type in interior Alaska (Calef et al. 2005), permafrost has been relatively resilient. In these systems, water table depth and plant species composition strongly influence biogeochemical dynamics. *Sphagnum* and other mosses are keystone boreal taxa that account for 20% and 48% of production in uplands and wetlands, respectively (Turetsky et al. 2010). These mosses have tended to increase in abundance in late-successional stands, perhaps in response to insect-induced canopy reduction (Hollingsworth et al. 2010; Turetsky et al. 2010). The effective thermal insulation and low litter quality of mosses, especially *Sphagnum*, lead to cold, permafrost-dominated, nutrient-poor soils that constrain rates of decomposition, nutrient cycling rates, and therefore forest productivity (Turetsky et al. 2010). These conditions lead to carbon sequestration (Ping et al. 2005; Hollingsworth et al. 2008). Despite slow rates of overall carbon and nitrogen cycling, small pools of dissolved organic nitrogen (DON) cycle rapidly, with rates that are controlled by root and (or) mycorrhizal turnover (Ruess et al. 2006) and by competition for DON between plants (and their mycorrhizal fungi) and decomposers (Kielland et al. 2007; Chapin et al. 2009*b*). The stabilizing (negative) biogeochemical feedbacks associated with cold, wet soils contribute to the resilience of black spruce forests in landscape positions with stable permafrost (Johnstone et al. 2010*a*).

As in most forested ecosystems, Alaskan microbial communities are dominated by fungi, especially by ectomycorrhizal and ericoid mycorrhizal fungi (Taylor et al. 2010). Fungal diversity is at least 10-fold greater than plant diversity in the same sites. Fungal community composition is determined primarily by forest type, soil horizon, and time of year but does not differ among years. These observations suggest extreme fungal specialization to ecosystem structure and seasonality but low sensitivity to interannual variation in climate. We therefore hypothesize that changes in microbial communities and the biogeochemical processes mediated by them will be more sensitive to climatically driven changes in disturbance and vegetation than to the direct effects of climate warming.

Changes in floodplains

In river floodplains, successional pathways have changed in ways that might have important functional consequences. Thinleaf alder (*Alnus incana* (L.) Moench subsp. *tenuifolia* (Nutt.) Breitung) is a keystone nitrogen-fixing species that expanded in both old and young successional stands along the Tanana River during the 1990s (Hollingsworth et al. 2010; Nossov 2008). The alder expansion in older stands may reflect improved light availability associated with canopy reduction of white spruce by insect outbreaks (response to warmer summers) and ice storms (warmer winters) and of poplar by expanding beaver populations (unknown cause). Increased seed input from alder expansion in mature sites might explain recent increases in alder recruitment in early successional sites. In addition, moose, which have increased

in abundance in the Tanana River lowlands due to predator control (see below), browse heavily on willows, releasing early successional alder recruits and invasive plants from competition. Modeling of the functional responses of these interactions between plant competition and herbivory (Feng et al. 2009) suggests that climate warming and predator control are facilitating invasion of exotic nitrogen fixers (Wurtz et al. 2008) and reducing carrying capacity for moose (reduced forage biomass and palatability) (Kielland et al. 2006). These changes indirectly reduce recruitment of white spruce (Angell and Kielland 2009). Although the data record is too short and the connections to climate too unclear to assess long-term persistence of these trends, the patterns suggest that forest resilience in floodplains depends on stand renewal through historically important successional pathways after river disturbance, but the long-term consequences of novel successional pathways characteristic of warmer drier conditions are less certain. The relative frequency of historical versus novel successional pathways will likely depend on changes in climate, herbivory by moose (a function of predator control and wildfire extent) (Kielland et al. 2006), and alder canker, an expanding forest pathogen that reduces alder abundance and its rates of nitrogen fixation and seed production (Ruess et al. 2009).

The reduction in alder growth and nitrogen fixation by alder canker is important because of alder's keystone role in nitrogen accumulation during floodplain succession (Ruess et al. 2009). Alder canker is most widespread in dry sites and dry years, suggesting a climate link to its spread. Green alder in the uplands also interacts with drought-mediated diseases (Mulder et al. 2008), with important implications for postfire nitrogen economy (Mitchell and Ruess 2009).

In summary, recent research suggests a high sensitivity of the Alaskan boreal forest to changes in moisture availability and to new species interactions (e.g., with insects and pathogens) that are emerging. This research suggests that controls over boreal forest dynamics are shifting from temperature and nutrient limitation, which were well documented in the 1970s and 1980s (Van Cleve et al. 1986, 1991), to more frequent limitation by drought.

Landscape consequences and societal implications

Fire and permafrost

Long-term studies by the Bonanza Creek LTER suggest that boreal forest stands show a mixture of sensitivity and resilience of different functional components in response to climatic change and that the net effect of these changes depends, in part, on reorganization of landscape patterns. We briefly summarize the landscape consequences of the changes described above and discuss their implications for society.

In the past decade, an increase in the number of years with extensive fires has doubled the annual area burned in interior Alaska compared with any decade of the previous 40 years and is 50% higher than any decade since 1940 (Kasischke et al. 2010). The area burned during late-growing season fires in the 2000s was three times higher than in any previous decade since 1950. Warmer and drier summers allow fires to continue burning in late summer,

when soils are deeply thawed and have lower soil moisture, and therefore burn more deeply, creating a radically different soil environment for seedling establishment. These severe fires have disrupted conditions for black spruce regeneration that sustained black spruce dominance for thousands of years (Johnstone et al. 2010b; Turetsky et al. 2010). Stabilizing feedbacks that have sustained the resilience of black spruce forests include biogeochemical feedbacks (thermal insulation by mosses, presence of permafrost, moist soils, and low fire severity) and life-history feedbacks (high availability of black spruce seeds from on-site semiserotinous cones and effective establishment on organic seedbeds). The recent increase in mineral soil seedbeds and the reduction in fire interval have generated new successional trajectories dominated by deciduous tree seedlings (Johnstone et al. 2010b; Kasischke et al. 2010). In extremely dry sites, no tree recruitment may occur after fire (Kasischke et al. 2007; Johnstone et al. 2010a).

These observations suggest potential shifts in the relative abundance of forest types that currently dominate the Alaskan boreal forest: a decline in abundance of black spruce, which has dominated the lowland landscape and north-facing slopes for the last 6000 years; a potential increase of deciduous forests in former black spruce habitat; and a conversion to grasslands or shrublands on dry sites (Johnstone et al. 2010a). Deciduous forests, until now, have been largely restricted to south-facing uplands and floodplain corridors and have acted as a stabilizing feedback to fire probability and spread because of their high leaf moisture content and low flammability. As climate warms, however, vegetation effects on flammability decline, weakening this stabilizing feedback, so the areal extent of fire is projected to continue increasing with climate warming despite the shift to deciduous vegetation (Kasischke et al. 2010). Hardwoods accumulate less soil organic matter than spruce ecosystems (Van Cleve et al. 1983; Mack et al. 2008), so increased hardwood dominance might reduce carbon sequestration at landscape scales.

Historically, the high latent heat content of ice-rich permafrost enabled permafrost to persist after fire until moss-dominated black spruce communities fostered permafrost recovery (Jorgenson et al. 2010). With a switch to deciduous-dominated vegetation, the thick moss and organic layers are unlikely to rebuild, and permafrost will probably continue to degrade (Johnstone et al. 2010b; Jorgenson et al. 2010; Turetsky et al. 2010). We hypothesize that declines in stand-level resilience in community composition in both uplands (due to climatic sensitivity to drought) and lowlands (due to changes in successional feedbacks) convey substantial resilience of species composition at landscape-to-regional scales as a result of potential redistribution of stand types across the landscape. Long-term observations are required to test this hypothesis.

Landscape changes in the boreal forest alter its role in the global climate system. The most dramatic of these feedbacks is earlier snowmelt, which amplifies climate warming as a result of reduced albedo (Euskirchen et al. 2010). This is slightly offset by an increase in area burned, which increases albedo in winter (less forest cover to obscure the snow) (Liu et al. 2005; Randerson et al. 2006) and in summer (shift to a lower-albedo deciduous forest trajectory) (Euskirchen et al.

2010). Changes in trace gas (mainly CO_2 and CH_4) feedbacks from the boreal forest are less clear. Greater areal extent and depth of burning and insect outbreaks reduce carbon sequestration (McGuire et al. 2009), but the consequences of the hydrologic reorganization of landscapes are more complex. Sites that are drying generally show reduced rates of carbon, nitrogen, and water cycling, with greater declines in photosynthesis than in ecosystem respiration (and therefore a decline in carbon sequestration); sites that are getting wetter show the opposite trends (Euskirchen et al. 2010). Methane efflux also declines with drier conditions.

Mammals

Observed and projected changes in environment and vegetation will influence the responses of mammals to climate warming. In general, small mammals such as microtine rodents are more sensitive to interannual variations in weather than are large mammals such as moose and caribou that respond more strongly to variations in food supply and predation (Kielland et al. 2006). Snowshoe hares are quite sensitive to all of these factors (Kielland et al. 2010). Snow depth, rain-on-snow events, floods, and other climate-related events that are difficult to predict are projected to become more variable (Intergovernmental Panel on Climate Change 2007) and are likely to exert stronger effects on most mammals than will warming per se. Habitat changes resulting from warming-induced increases in floods, insect outbreaks, and wildfires could also strongly affect mammal distributions. In general, we hypothesize that most mammalian communities will show low resilience, with some species declining in abundance (e.g., lichen-dependent caribou), others increasing (e.g., fire-dependent moose and snowshoe hares), and others changing in species composition and distribution (e.g., microtine rodents that are sensitive to extreme events but some of which are favored by grasslands). These changes, if they occur, would substantially restructure the mammalian communities of interior Alaska.

Human communities

Changes in environment, ecosystems, and subsistence resources have important implications for Alaskan boreal communities, particularly those in rural areas where indigenous people have historically led a subsistence lifestyle as hunters and gatherers (Fig. 2). Warming directly affects communities as a result of thinner river ice and therefore reduced safety of winter travel and access to hunting grounds. Increased evapotranspiration and declining river discharge also reduce opportunities for barge delivery of fuel and increase the cost of living and therefore the dependence on subsistence harvesting (Kofinas et al. 2010). Now that communities are permanently situated rather than seminomadic, increased wildfire risk constitutes the major pathway by which warming influences rural communities. Wildfire constitutes a risk to life and property, reduces access to the land, threatens cultural resources, and reduces moose and caribou abundances for one to several decades (Maier et al. 2005; Chapin et al. 2008; Kofinas et al. 2010). Sources of resilience to address these changes include traditional sharing networks that maintain community identity while sustaining food supplies to the most vulnerable households and allowing hunters to borrow hunting equipment. As the abundance and distribution of subsistence resources change and access to hunting areas is modified, hunters will likely shift their hunting effort to those species that increase in availability and (or) accessibility. Development of community gardens or changes in hunting regulations to constrain competition from urban hunters could enhance resilience (Kofinas et al. 2010; Loring and Gerlach 2010). Changes in economic conditions, such as employment in rural and urban communities, will undoubtedly interact with the effects of climatic change, affecting human migration patterns and the overall resilience of villages. In summary, climate warming and socioeconomic changes challenge the resilience of rural indigenous communities, but indigenous culture has proven relatively resilient to even greater threats over the past century.

Many of the changes described above (e.g., wildfire risk and thawing permafrost) also affect larger communities and cities along the road network. However, urban areas are buffered by alternative income sources (jobs) and transportation options (roads) that reduce vulnerability. Rural-to-urban migration links villages with cities, putting pressure on public services (especially schools) in the cities but extends social networks of villages to tap urban employment opportunities (Kofinas et al. 2010).

Conclusions, uncertainties, and policy options

Although the Alaskan boreal forest and its people have been quite resilient to past warming, recent changes in structure and functioning suggest that the limits of this resilience have been approached and in some cases exceeded (Fig. 2). Disturbances (permafrost thaw, wildfire, insect outbreaks, disease, and drying of lakes and streams) are more extensive than at any time in the historical record, and the stabilizing (negative) feedbacks that previously constrained the magnitude of these changes or fostered recovery have been substantially weakened by warming. This suggests that the Alaskan boreal forest is on the cusp of potentially large nonlinear changes in structure and functioning. The major uncertainties concern the rates of change in disturbance and the extent to which these changes might be compensated at regional scales by redistribution of stand types across the landscape or by policies affecting rural–urban interactions. Current evidence from long-term studies at the Bonanza Creek LTER suggests the following.

- Permafrost will remain relatively resilient to continued warming except in high-ice-content lowlands and in areas burned by severe wildfires. The greatest sources of uncertainty are changes in snow cover, which will influence the rate at which these changes occur, and the extensiveness of severe wildfires and wetland formation that will likely trigger permafrost loss. In lowland areas, permafrost degradation causes a radical shift from black spruce ecosystems to *Sphagnum* bogs and herbaceous fens, whereas loss of permafrost and increased drainage in upland areas promotes replacement of black spruce by deciduous forests.

- New successional trajectories contribute to the variability of floodplain forests, with the long-term functional conse-

quences (e.g., nitrogen accumulation and suitability for wildlife) being uncertain.

- Increasingly extensive and severe wildfires are triggering a landscape transformation with potential expansion of deciduous forests from uplands to lowlands and north-facing slopes and perhaps the development of shrublands, grasslands, agriculture, or other novel ecosystem types in south-facing uplands and in lowlands. The future nature of upland ecosystems and the rates of transformation of lowland ecosystems are highly uncertain. These transitions and associated permafrost change will likely dominate changes in regional hydrology.

- The current mammalian fauna of interior Alaska will likely persist but reorganize into new patterns of distribution and abundance in response to both direct effects of climate and changes in habitat. The low degree of habitat fragmentation by human activities in Alaska provides greater opportunities for species migration and community reorganization in Alaska (and therefore regional resilience) than in most regions of the world. The net effect of these changes on subsistence opportunities for rural indigenous communities will depend on the rates and patterns of change, both of which are uncertain. Over the long term, resilience of both the animal and human communities may depend on policy decisions about the management of wildfire and human disturbances and the allocation of hunting opportunities between rural and urban hunters.

Global anthropogenic carbon emissions commit the planet to centuries of elevated CO_2 concentration in the atmosphere (Solomon et al. 2009). Actions taken globally to reduce emissions will influence the future magnitude and rate of change but are unlikely to prevent a continued warming trend (Fig. 1). Given the high certainty of continued warming in the Alaskan boreal forest, there are few policy options available at local-to-regional scales that could prevent the changes we have projected. However, local actions can influence the impacts of warming on ecosystems and society. For example,

- Agricultural and resource management policies will likely affect land-cover type, landscape connectivity, and species migration, and therefore, the trajectory of ecosystem change, particularly the rate of tree migration from south-facing uplands to lowlands and north-facing uplands.

- Fire management adjacent to human communities may influence the size, frequency, and configuration of future fires and therefore fire risk to these communities. In more remote areas, climate-driven changes in flammability will likely be more important than fire management in driving changes in fire regime and landscape heterogeneity.

- Development and resource management policies will influence the human exploitation of renewable and nonrenewable resources, the food and energy security of rural communities, and therefore, the integrity of the boreal forest as a coupled social–ecological system.

Continued research by the Bonanza Creek LTER has the opportunity to inform these policy choices and therefore the regional resilience of the Alaskan boreal forest.

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