Fire, climate change, and forest resilience in interior Alaska[1]

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Abstract: In the boreal forests of interior Alaska, feedbacks that link forest soils, fire characteristics, and plant traits have supported stable cycles of forest succession for the past 6000 years. This high resilience of forest stands to fire disturbance is supported by two interrelated feedback cycles: (*i*) interactions among disturbance regime and plant–soil–microbial feedbacks that regulate soil organic layer thickness and the cycling of energy and materials, and (*ii*) interactions among soil conditions, plant regeneration traits, and plant effects on the environment that maintain stable cycles of forest community composition. Unusual fire events can disrupt these cycles and trigger a regime shift of forest stands from one stability domain to another (e.g., from conifer to deciduous forest dominance). This may lead to abrupt shifts in forest cover in response to changing climate and fire regime, particularly at sites with intermediate levels of moisture availability where stand-scale feedback cycles are only weakly constrained by environmental conditions. However, the loss of resilience in individual stands may foster resilience at the landscape scale, if changes in the landscape configuration of forest cover types feedback to stabilize regional patterns of fire behavior and climate conditions.

Résumé : Dans la forêt boréale de l’intérieur de l’Alaska, les rétroactions qui relient les sols forestiers, les caractéristiques des incendies et celles de la végétation ont assuré le maintien des cycles de succession forestière pendant les 6000 dernières années. Cette grande résilience des peuplements forestiers face aux perturbations causées par le feu est le résultat de deux cycles interreliés de rétroactions : (*i*) les interactions entre le régime de perturbations et les rétroactions entre les plantes, le sol et les microbes qui contrôlent l’épaisseur de l’horizon organique du sol et le recyclage de l’énergie et des matériaux et (*ii*) les interactions entre les conditions du sol, les caractéristiques de la régénération des plantes et les effets des plantes sur l’environnement qui maintiennent la stabilité des cycles de composition des communautés forestières. Les incendies inhabituels peuvent perturber ces cycles et déclencher un changement de régime des peuplements forestiers d’un domaine de stabilité à un autre (p. ex., d’une forêt dominée par des conifères à une forêt dominée par des feuillus). Cela peut entraîner des changements abrupts dans le couvert forestier en réponse aux changements climatiques et à la modification du régime de feux, particulièrement dans les stations avec un niveau intermédiaire de disponibilité en eau où les cycles de rétroaction à l’échelle du peuplement sont assujettis seulement faiblement aux conditions environnementales. Cependant, la perte de résilience de peuplements particuliers peut favoriser la résilience à l’échelle du paysage si les changements dans la configuration des types de couvert forestier à l’échelle du paysage ont un effet de rétroaction qui stabilise les patrons régionaux du comportement du feu et des conditions climatiques.

[Traduit par la Rédaction]

Introduction

Earth is undergoing pronounced environmental changes that are strongly influenced by human activities. Climate warming in recent decades is particularly pronounced at high latitudes, and past carbon emissions from burning of fossil fuels commit the planet to continued warming over coming decades to centuries (Solomon et al. 2009). Because this high-latitude warming is unprecedented in recorded history (Arctic Climate Impact Assessment 2005), there is considerable uncertainty about how the rate and pattern of climate warming will proceed and interact with ecological and social changes. Resilience theory provides a framework for addressing large uncertain changes (Gunderson and

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Holling 2002; Chapin et al. 2009), such as those already observed in Alaska's boreal forests as climate conditions change from those experienced in recent millennia (Hinzman et al. 2006). Resilience is the capacity of a social–ecological system to absorb a spectrum of perturbations and to sustain its fundamental function, structure, identity, and feedbacks as a result of recovery or reorganization in a new context (Holling 1973; Gunderson and Holling 2002). In ecological systems with multiple stability domains, changes that exceed the process limits of a given domain result in a loss of resilience and a shift to a new domain, from which the probability of return to the previous state is low (Holling 1973).

Rates of resource supply, disturbance regime, functional diversity, and ecosystem feedbacks are key sources of ecological resilience that are changing in the boreal forest (Chapin et al. 2006). Changes in fire regime driven by current and future climate change (e.g., Flannigan et al. 2005; Balshi et al. 2009) have the potential to interact with the heterogeneous physical and biotic environment to alter the structure, functioning, and long-term successional dynamics of ecosystems in complex ways. Within this context, the functional diversity of organisms determines the range of options available for responding to change, and feedbacks influence the likelihood that past ecosystem dynamics will persist or change (Chapin et al. 2009). In this paper, we address changes in these sources of resilience as related to patterns of vegetation succession and soil environmental conditions within the boreal forests of interior Alaska. Resilience theory is used to provide a framework for thinking about not only the expected impacts of changes in fire regime on forest cover but also the interactions among stand-scale versus landscape-scale dynamics.

Forests in interior Alaska are disturbed by large wildfires that have historically burned forests at intervals of about a century (Yarie 1981; Viereck 1983). Although fire disturbance is frequent and widespread in much of the boreal forest, patterns of forest succession often result in forests returning to a composition that is similar to that of the prefire stand, indicating a high level of stand-scale resilience (Van Cleve and Viereck 1981). Over time scales of centuries to millennia, paleoecological records suggest that boreal forests have experienced long periods of relatively stable composition that were punctuated by rapid shifts to a new configuration. These abrupt shifts were often accompanied by a change in fire regime (e.g., Lynch et al. 2003; Tinner et al. 2008), indicating that changes in forest composition and fire often coincide over long ecological time scales (Lloyd et al. 2006; Higuera et al. 2009). However, the factors that contribute to resilience or trigger threshold changes in forest dynamics are poorly known.

Here we discuss how interactions among boreal forest soils, fire characteristics, and species traits reinforce one another to support stable patterns of forest composition and succession across fire cycles. First we present a brief background on the biophysical setting of boreal forests in interior Alaska. We then describe two interrelated feedback cycles that we believe explain the long-term resilience of boreal forests in Alaska: (*i*) feedbacks among abiotic soil conditions, decomposition rates, plant and moss growth, and fire regime that determine soil organic layer thickness; and (*ii*) feedbacks among soil conditions, plant regeneration traits, and plant effects on the environment that maintain stable cycles of forest community composition. We discuss how unusual fire events may trigger a regime shift in boreal forest stands from one stable domain of attraction to another, particularly at sites with intermediate moisture availability. We hypothesize that forest landscape responses to directional environmental change, such as climate warming, will be strongly influenced by disturbance events that trigger shifts from one feedback cycle to another. In particular, fire events that cause substantial changes in soil organic layer depths or plant regeneration may lead to abrupt shifts in stand-scale forest cover that are then likely to persist through future fire cycles. We further hypothesize that the loss of stand-scale resilience may contribute to landscape- and regional-scale resilience, as a shift in the landscape configuration of current forest systems may feedback to influence future fire and climate regimes. Our conceptual synthesis identifies several key processes at stand and landscape scales that require further investigation to improve our ability to predict the future dynamics of Alaskan boreal forests.

Background

Interior Alaska is bounded by the Alaska Range (~63°N) to the south and the Brooks Range (~67°N) to the north. The region is an intermontane plateau dissected by the Yukon, Tanana, and Kuskokwim river valleys. It is characterized by isolated mountain ranges, large areas of gently sloping uplands, flat lowlands, and braided rivers with broad floodplains (Van Cleve et al. 1983). Soils show relatively little morphological development and are typically classed as Inceptisols, Histosols, or Gelisols (Ping et al. 2006). Quaternary deposits show that soils have been formed through alternating periods of deposition and erosion of silt and gravel (Van Cleve et al. 1983; Ping et al. 2006). In uplands, silt caps developed from wind-blown loess intergrade with soils derived from the underlying, predominantly schist bedrock. Because of their fine texture, the distribution of loess strongly influences surface hydrology (Van Cleve et al. 1983; Ping et al. 2006).

Interior Alaska has a continental climate, with extreme temperatures ranging from –70 to +35 °C. Annual precipitation averages 286 mm, of which about 35% falls as snow (Hinzman et al. 2006). The region is within the discontinuous permafrost zone, with approximately 75%–80% of the ground underlain by permafrost (Osterkamp and Romanovsky 1999). Permafrost temperatures range from –0.1 to –3.5 °C and are influenced by topography, soil properties, hydrology, and ground vegetation (Osterkamp and Romanovsky 1999; Jorgenson et al. 2010). North-facing and toe-slope forests receive less solar energy than do south-facing slopes and, therefore, are cooler and wetter and more likely to contain permafrost (Hinzman et al. 2006). Recent climate warming has increased permafrost temperatures in interior Alaska and many locations are now within a degree of thawing (Osterkamp and Romanovsky 1999; Hinzman et al. 2006).

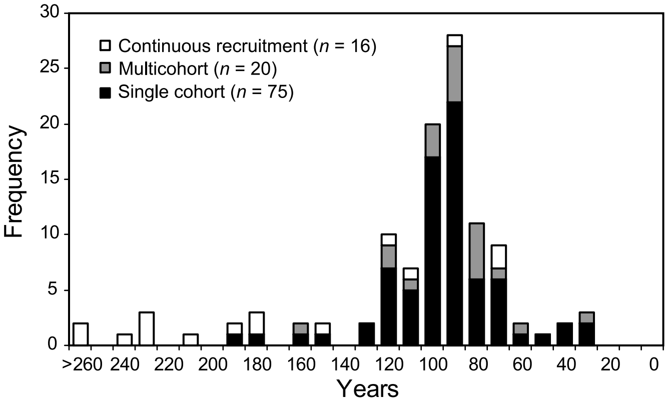
Black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) is the most widespread forest type in interior

Alaska and covers about 40% of boreal Alaska (Van Cleve et al. 1983). Black spruce tolerates a wide range of soil moisture and nutrient conditions and can be dominant in both drier upland and wetter lowland ecosystems. Despite its prevalence, black spruce is a relatively recent colonizer of central Alaska. In the early Holocene (13 000 – 10 000 years BP), interior Alaska was dominated by open woodlands of broadleaf deciduous species, such as aspen or poplar (*Populus* L.; Edwards et al. 2005). White spruce (*Picea glauca* (Moench) Voss) was the first conifer to expand in interior Alaska and it dominated forests for much of the mid-Holocene (10 000 – 5 000 years BP; Edwards et al. 2005). Following a gradual shift to a moister, cooler climate at approximately 5000 years BP, black spruce increased in abundance throughout interior Alaska, accompanied by an increase in fire frequency (Lynch et al. 2003; Higuera et al. 2009). This history suggests that Alaskan boreal forests have undergone punctuated changes in forest types from deciduous to white spruce to black spruce dominance at regional scales. Nevertheless, the current black spruce period has been resilient to substantial climatic shifts (e.g., medieval warm period and Little Ice Age) during the past ~5000 years (Lloyd et al. 2006).

Interior Alaska also supports widespread forest communities dominated by deciduous broadleaf trees, such as trembling aspen (*Populus tremuloides* Michx.), Alaskan paper birch (*Betula neoalaskana* Sarg.), and balsam poplar (*Populus balsamifera* L.; Van Cleve et al. 1983). Broadleaf forests commonly occur in warmer portions of the landscape not underlain by permafrost, such as river floodplains and south-facing slopes (Van Cleve et al. 1983; Kurkowski et al. 2008). These deciduous stands are often considered to be an early stage in the successional pathway to white spruce forest (Van Cleve and Viereck 1981). However, several empirical studies suggest that broadleaf dominance can persist in Alaskan stands for at least 100–200 years (Fastie et al. 2003; Kurkowski et al. 2008). Recent evidence suggests that deciduous broadleaves may be able to replace black spruce as the dominant species when severe fires alter soil conditions (Johnstone and Kasischke 2005; Johnstone et al. 2010).

Fire is widespread in interior Alaska. Current fire cycles (the number of years required to burn an area equal in size to the study area) reconstructed from stand age distributions are estimated at ~100 years for black spruce forests in Alaska and western Canada (Yarie 1981; Larsen 1997). This fire cycle estimate is supported by prefire stand ages calculated from tree rings for burned black spruce stands in interior Alaska (Johnstone and Kasischke 2005; Johnstone et al. 2010), which show a peak in observed fire return intervals between 70 and 130 years (Fig. 1). Similar fire cycle estimates have been developed for boreal peatlands in western Canada, based on remote sensing of fire and peatland distributions (Turetsky et al. 2004). Fire cycles are generally estimated to be shorter for broadleaf than black spruce stands (Yarie 1981; Larsen 1997), but these estimates are confounded by successional relationships and the nonrandom distribution of broadleaf stands on a landscape (Larsen 1997; Mann and Plug 1999). If all else were equal, broadleaf stands appear to have a lower potential for fire initiation (Krawchuk et al. 2006) and spread (Cumming 2001; Hély et al. 2000), suggesting that fire cycles would be longer for broadleaf than black spruce stands in a uniform, nonsuccessional landscape.

Fig. 1. Frequency histogram of prefire stand ages (in years) from stands of black spruce that burned in 1994 (n = 21 stands in one fire; Johnstone and Kasischke 2005) or 2004 (n = 90 stands in three fires; Johnstone et al. 2010). Stand ages were estimated from tree-ring counts sampled near the tree base from trees that were alive when the stand burned (n = 5–10 trees/stand). Most stands showed an age structure indicative of a single cohort (black bars) or two cohorts (grey bars) of trees, as tree ages clustered closely into one or two groups, respectively. We assumed the youngest cohort represented the most recent cycle of postfire recruitment and estimated the age of these stands as the age of the oldest tree in the youngest cohort. Stands that showed no clustering of tree ages appeared to have experienced continuous recruitment since the last fire (white bars), and stand age was estimated from the oldest sampled tree.

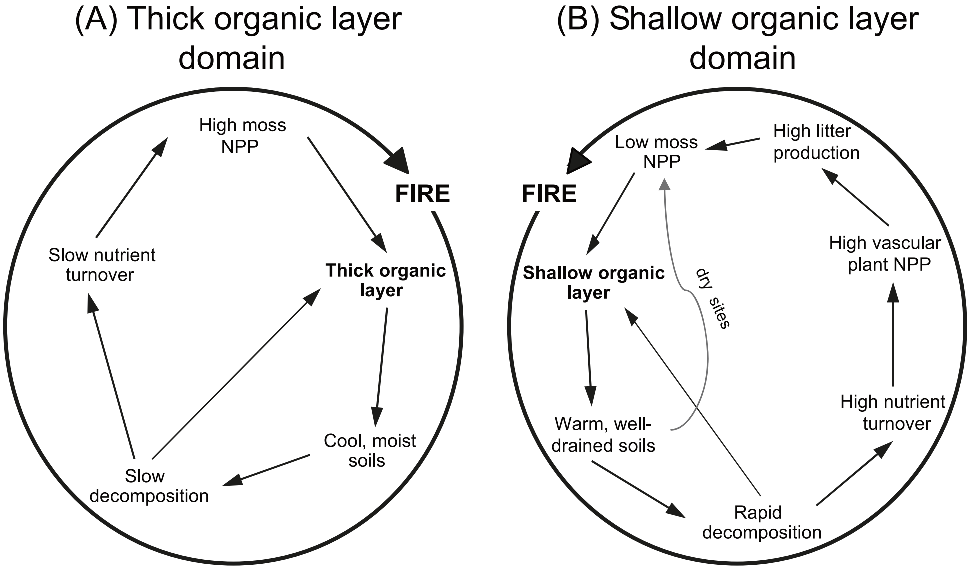


Feedback cycles — soil organic layers

The soil organic layers of boreal forests store carbon, harbor a diverse assemblage of microbes, supply nutrients to plants, regulate hydrology and energy exchange, and insulate permafrost. Across forest types in boreal Alaska, the depth of the soil organic layer is controlled by two factors: (*i*) the balance between the production and decomposition of plant litter, which determines the accumulation of organic matter between fires, and (*ii*) the amount of soil organic matter that escapes fire combustion and accumulates across multiple fire cycles (Harden et al. 2000). These factors interact strongly to generate negative (stabilizing) feedback cycles that maintain ecosystem structure and function over multiple fire cycles, i.e., maintain the ecological resilience (Holling 1973). Here we identify two stability domains of organic matter accumulation in interior Alaskan forests: a thick organic layer cycle characteristic of black spruce stands across a wide range of drainage conditions, and a shallow organic layer cycle characteristic of aspen and birch stands on well-drained upland soils (Fig. 2).

Organic layers in mature black spruce forests range in thickness from ~7 to 40 cm in upland forests (Hollingsworth et al. 2006; Boby et al. 2010) to many metres in forested bogs and poor fens (Vitt et al. 2000). Organic matter accumulation is strongly tied to soil moisture, and the thickest organic layers often occur in lowlands or valley bottoms where moisture accumulates (Van Cleve and Viereck 1981).

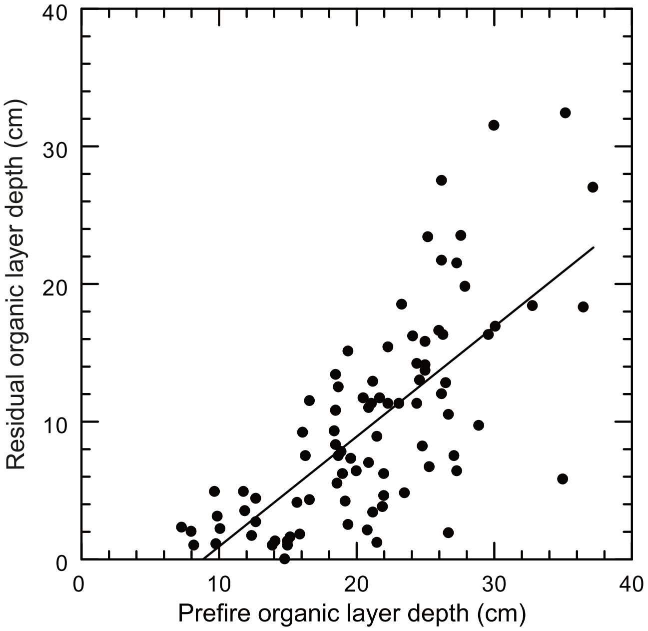
Fig. 2. Soil organic layer dynamics across fire and successional cycles representing alternative stability domains. In the thick organic layer domain (A), the accumulation of soil organic layers in mesic-to-moist sites is associated with feedbacks among cool, moist soils; low rates of decomposition and nutrient cycling; and high moss productivity (net primary productivity, or NPP). Alternatively in the shallow organic layer domain (B), shallow organic layers in mesic-to-dry sites are associated with feedbacks among warm, dry soils; high rates of decomposition; and high vascular plant productivity that smothers mosses with deciduous leaf fall. Shallow organic layers are also maintained at dry sites by direct moisture limitation of moss productivity (curved grey line in Fig. 2B).



However, plant–environment feedbacks are also important in regulating soil moisture. In many black spruce forests and peatlands, soils are moist because (*i*) unproductive black spruce forests have low rates of evapotranspiration (Bonan 1991; Liu et al. 2005); (*ii*) the ecohydrological traits of mosses, especially *Sphagnum* species, promote high water retention (Turetsky et al. 2010); and (*iii*) permafrost prevents deep drainage (Jorgenson et al. 2010). The insulative and hydraulic properties of moss and organic soils and the presence of permafrost maintain cool, moist forest-floor environments where decomposition and nutrient turnover are slow, further contributing to the accumulation of moss and surface organic layers over time (Fenton et al. 2005; Fig. 2A). These feedbacks between vegetation and soil properties create a stability domain characterized by cool, moist organic-dominated soils that is highly resilient to spatial or temporal changes in climate (e.g., Camill and Clark 2000; Fenton et al. 2005).

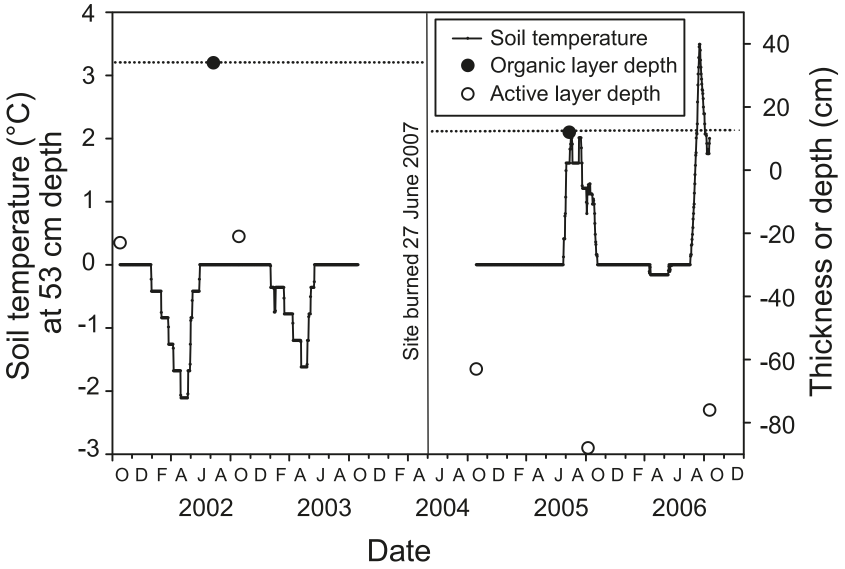
Although moss-dominated spruce forests accumulate large amounts of ground-layer fuel, the high moisture content of the moss and organic layers inhibits deep burning under all but the most severe fire-weather conditions (Dyrness and Norum 1983; Shetler et al. 2008). Because moisture content increases with depth (Miyanishi and Johnson 2002), prefire soil organic layer depth is a strong predictor of postfire organic layer depth across a range of landscape positions (Kane et al. 2007; Boby et al. 2010). For example, in a study of 90 black spruce forests that burned in the 2004 fires, prefire soil organic layer depth accounted for about half of the variation in postfire residual organic layer depth (Fig. 3). The resistance of the thick organic layer to deep burning appears to be weakened by late-season fire activity, when deep thawing of the active layer allows increased drainage and drying of the organic layer (Kane et al. 2007).

Fig. 3. Prefire versus postfire organic layer depth (cm) measured in 90 sites arrayed across three 2004 fire complexes in interior Alaska. Prefire organic layer depth was estimated after fire with an adventitious root method described in Johnstone and Kasischke (2005) and Boby et al. (2010).



The degree of fire consumption of organic soils represents an important resilience threshold for maintaining sites in domains characterized by deep versus shallow organic soils because postfire organic layer depth has important effects on soil temperature, moisture, and future organic layer accumulation (Yoshikawa et al. 2003; Fenton et al. 2005). Fires that consume organic material alter the energy balance of the

Fig. 4. Prefire and postfire soil temperature and organic and active layer depths in a permafrost site at Nome Creek in interior Alaska (S. Marchenko, V. Romanovsky, and T. Hollingsworth, unpublished data). Soil temperature was taken in mineral soil at a depth of 0.53 m from the organic soil surface both before (left panel) and after fire (right panel). For ease of interpretation, organic and active layers are presented as thickness (in cm; filled and open circles, respectively). The active layer is the layer of soil that thaws each summer.



soil, and for many years after fire, the soil thaws more deeply, and permafrost may disappear from the upper few metres of soil (Fig. 4, Yoshikawa et al. 2003). Ecosystem resilience of thick organic layers is maintained after low-severity burns by rapid moss recolonization on partially consumed organic material (Benscoter 2006; Turetsky et al. 2010). Long-term measurements in black spruce forests in interior Alaska indicate that permafrost returns, the forest floor begins to develop, and mosses regain dominance within 2–3 decades after low-severity fire (Viereck et al. 2008; Bernhardt et al. 2010).

Sites with shallow organic layers and little moss cover have minimal year-round insulation of mineral soils and, consequently, warm and dry more rapidly during summer (Fig. 2B). Permafrost is absent because of warmer soil temperatures in summer, allowing surface moisture to drain freely into deeper soil layers during summer. These sites tend to be dominated by aspen and birch, and high rates of evapotranspiration from broadleaf trees in midsummer helps to maintain drier soils (Bonan 1991; Liu et al. 2005). Litter and nutrients turn over faster in broadleaf stands than in black spruce stands (Flanagan and Van Cleve 1983; Vance and Chapin 2001), and organic layer depths are generally <10 cm (Van Cleve et al. 1983). Vascular productivity is high, and relatively little light penetrates to the understory, where low soil moisture and shading by broadleaf litter restrict moss growth (Van Cleve and Viereck 1981; Startsev et al. 2008). Because the organic layer at these sites is dry and shallow, fires typically consume much of the organic layer, maintaining the resilience of the shallow organic layer domain.

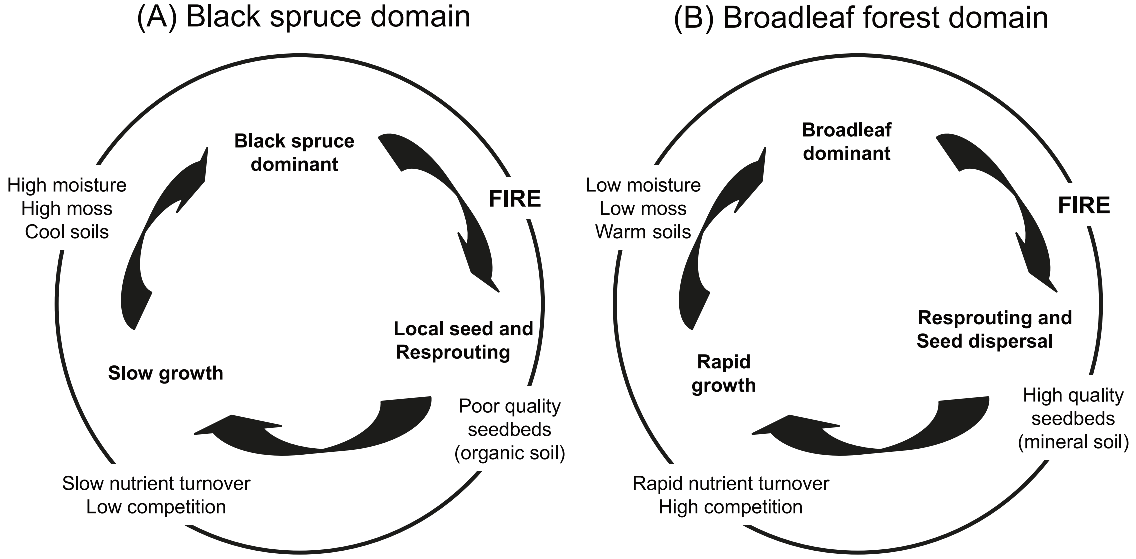
Feedback cycles — plant communities

In boreal ecosystems, fire consumption of surface organic layers is often more important in controlling vegetation recovery than are other aspects of fire behavior, such as fire intensity (Schimmel and Granström 1996). Postfire seedbeds in burned spruce forests are usually dominated by singed or partially combusted surface organic layers (Dyrness and Norum 1983; Greene et al. 2007). These are generally poor seedbeds because their dark color and high porosity favors heating and drying events that desiccate and kill small seedlings (Johnstone and Chapin 2006*a*).

Black spruce overcomes the limitations of low recruitment success on organic seedbeds by producing large amounts of seed from an aerial seed bank stored in semiserotinous cones (Fig. 5). These cones release a high density of seedfall after fire, ensuring that some seeds find favorable microsites for postfire regeneration (Viereck 1983). In addition, the carbohydrate reserves provided in the relatively large seeds of black spruce enable rapid root growth and allow seedlings to tap dependable soil moisture relatively quickly. Consequently, black spruce and other serotinous conifers are highly resilient to fire across a wide range of fire severities and rapidly recolonize a site during the postfire reorganization phase (Greene and Johnson 1999). In contrast, species that colonize organic seedbeds after fire from off-site seed sources are usually at a disadvantage because of the typically low densities of dispersed seed. This disadvantage is particularly severe if a species has small seeds, such as many broadleaf species, because small seed reserves lead to substantially lower recruitment success on organic seedbeds (Johnstone and Chapin 2006*a*; Greene et al. 2007).

Low-severity fires also favor the regeneration of the same understory plant community because many understory species can regenerate asexually after fire from belowground tissues, resulting in little long-term change in species composition (Fig. 5; Schimmel and Granström 1996; Bernhardt et al. 2010). Most of the dominant understory plants in black spruce forests, such as sedges (*Carex* and *Eriophorum*), horsetails (*Equisetum*), evergreen shrubs (*Ledum*, *Vaccinium*), and deciduous shrubs (*Salix*), resprout from roots

Fig. 5. A conceptual diagram of plant dominance cycles in alternative stability domains dominated by (A) black spruce and (B) broadleaf forests. The plant communities that characterize each stability domain have regeneration strategies that strongly favor self-replacement and dominance after fire (inner bold text). Functional traits of the dominant vegetation further reinforce environmental conditions that help maintain their dominance during the fire-free period (outer plain text).



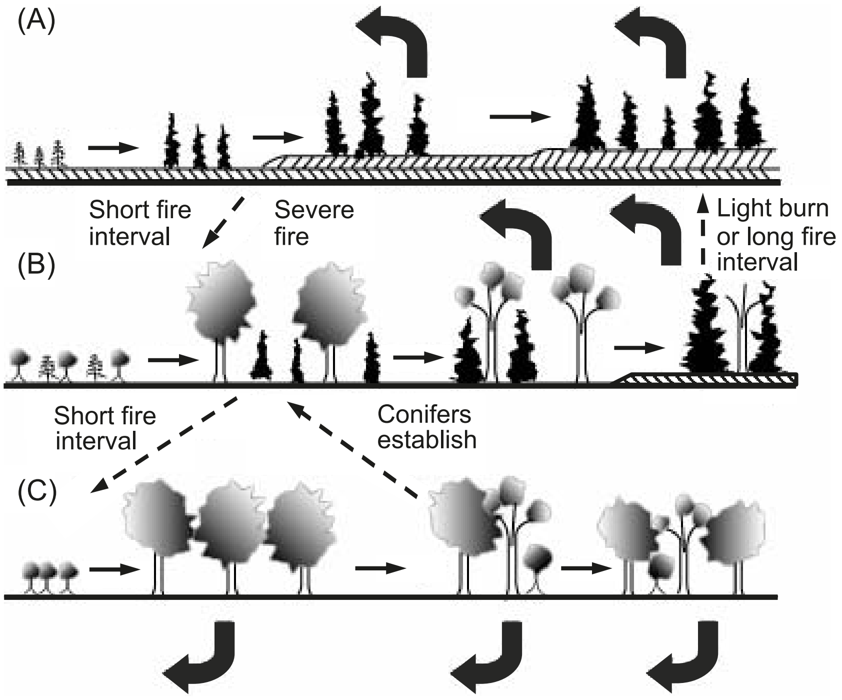
and rhizomes in the soil organic layer that survive low-severity fires (e.g., Schimmel and Granström 1996). In black spruce forests with thick moss layers, the mineral soil is often frozen for much of the growing season, and the bulk of belowground plant tissue is found in the surface organic layers or at the interface between the mineral and organic soil layers (Van Cleve et al. 1983). The potential for asexual regeneration is therefore highest when there is minimal combustion of the soil organic layer and declines as more of the organic soil, and the roots and rhizomes within it, are consumed by fire (Schimmel and Granström 1996). The composition of the postfire understory community is therefore most similar to that of the prefire community in sites with low-severity burns (Rydgren et al. 2004), and composition recovers substantially within 2–3 decades (Bernhardt et al. 2010).

The ecophysiological traits of plants influence soil conditions and community composition, creating feedbacks that stabilize successional cycles and support the resilience of alternate stability domains characterized by spruce–moss versus broadleaf forests (Fig. 5). As discussed above, the poor litter quality of black spruce and understory evergreen shrubs supports slow rates of decomposition and nutrient turnover, further favoring the conservative growth strategies of these species and the development of the moss layer (Van Cleve and Viereck 1981). Rapid growth of feather mosses or *Sphagnum* moss, both of which can be common in black spruce forests, contributes large amounts of low-quality organic litter to the forest floor, which decomposes slowly and accumulates as a surface organic layer. As discussed above, the ecophysiological traits of moss species, particularly *Sphagnum* mosses, help to maintain moist organic soils and limit the potential for fire consumption of the organic layer (Shetler et al. 2008).

A high resilience of broadleaf-dominated forests is also maintained across fire cycles by a combination of fire characteristics, plant regeneration cycles, and plant–soil interactions (Fig. 5). Low fuel loads on the forest floor and the high water content of the canopy fuels generally lead to fires that may kill aboveground tissue but are rarely intense enough to kill roots and rhizomes within the mineral soil (Mann and Plug 1999). Deciduous broadleaf trees such as trembling aspen are able to resprout abundantly from belowground roots and use belowground carbohydrate reserves to regrow rapidly and quickly reestablish a deciduous canopy (Greene and Johnson 1999). Mineral soils exposed by fire also provide high-quality seedbeds to support off-site colonizers such as white spruce, which often co-dominate with broadleaf trees later in succession (Van Cleve and Viereck 1981). As succession proceeds, the functional traits of dominant broadleaf species reinforce environmental effects on decomposition by producing high litter quality that favors rapid turnover of organic matter and nutrients (Flanagan and Van Cleve 1983). High rates of nutrient cycling support high vascular plant productivity, and the abundant deciduous litterfall inhibits the growth of understory mosses (Startsev et al. 2008), further promoting the dominance of vascular species over mosses (Fig. 5).

Interactions among plant communities, rates of element cycling and organic matter turnover, and fire characteristics act as negative, stabilizing feedbacks that constrain ecosystem responses to environmental change and maintain ecological resilience. Strong interactions among prefire plant composition, disturbance severity, and regeneration strategies are particularly important in generating the “positive neighbor effects” that support stable domains of forest community composition across disturbance cycles (Frelich and Reich 1999). Nevertheless, unusual disturbance events and directional environmental change can interrupt these feedback cycles and generate rapid shifts in forest ecosystems from one stability domain to another (Frelich and Reich 1999; Gunderson and Holling 2002). Below, we discuss how changes in fire or climate regimes can lead to a loss of stand-scale forest resilience and to shifts to alternate stability domains.

Fig. 6. Successional trajectories in Alaskan boreal forests, showing key phases of development from initial recruitment (far left), through stand maturity (center), and later phases of canopy break-up and infilling (far right). Depending on initial recruitment and survival, stands may develop along (A) conifer-dominated, (B) mixed conifer – broadleaf, or (C) broadleaf-dominated trajectories. Conifer-dominated trajectories typically accumulate organic material (hatched layer in A) over time, while this is delayed until late in succession in mixed forests (B) and is unlikely to occur in deciduous forests (C). Fires that occur under typical conditions usually act to restart succession on the same trajectory (curved bold arrows). However, unusual fire events (dashed arrows) can disrupt these stable cycles and cause a switch to an alternative trajectory. Figure is modified from Chapin et al. (2004).



Environmental change, fire, and forest resilience

Strong feedbacks between soil conditions and plant traits in the boreal forests of Alaska lead to plant communities that are highly resilient to fire disturbance, as described in the previous two sections. Postfire communities therefore tend to reassemble on successional trajectories similar to those of the prefire community (Fig. 6). Under stable climate and fire regimes, these cycles of vegetation composition are likely to be highly stable on a landscape. Even under directional changes in climate, feedbacks among organic layer depths, soil temperature and moisture, and plant growth can constrain boreal ecosystems from responding in equilibrium with climate (Camill and Clark 2000). However, unusual fire or other disturbance events can weaken the processes that maintain a given feedback cycle and can exceed the resilience of the system, permitting abrupt changes in community composition (Fig. 6; Gunderson and Holling 2002). Such changes are particularly likely when climate or other environmental conditions have undergone directional change since the last phase of community reorganization. Fire disturbance may thus act to catalyze community responses to climate change, by temporarily weakening the plant and soil feedbacks that account for stand-scale resilience, and to drive ecological change through changes in disturbance regime.

The stimulus provided by fire or other disturbances will interact with directional changes in environmental conditions to determine the potential of a system to switch to an altered cycle of feedbacks, i.e., to switch to a new stability domain. For example, climate changes that affect the hydrological or permafrost regime could strongly affect the potential for forests to tip from one feedback cycle to another. Winter and spring temperatures in interior Alaska have warmed substantially over the last 30 years (Hinzman et al. 2006), which is likely responsible for observed warming of permafrost (Osterkamp and Romanovsky 1999; Hinzman et al. 2006). Degradation of permafrost within uplands and well-drained slopes will increase soil drainage and drying of surface soils (Yoshikawa et al. 2003; Jorgenson et al. 2010). In low-lying areas with poor hydrological drainage, permafrost thaw may lead to surface subsidence and increased soil moisture and moss proliferation. Thus, the sensitivity of permafrost to long-term (multidecadal and longer) changes in climate may destabilize soil feedback cycles by causing slow changes in soil moisture that influence rates of organic soil accumulation and the potential for organic layer consumption by fire. These changes will alter ecosystem resilience by influencing both fire behavior and plant regeneration patterns, so that when the system burns it may rapidly reorganize in a new stability domain (Fig. 6).

Changes in the fire regime or unusual fire events may directly destabilize feedback cycles and cause sites to shift to new successional trajectories or stability domains (Fig. 6; Frelich and Reich 1999). For example, regeneration of black spruce communities is disrupted when severe fires consume thick organic layers and create mineral soil seedbeds that favor the establishment of competitively superior species. Under such situations, deciduous trees can recruit at high densities (Greene et al. 2007; Johnstone et al. 2010), and warmer soil conditions associated with shallow organic layers may allow them to rapidly dominate the forest canopy (Fig. 5; Johnstone and Kasischke 2005). Severe fires also destroy plant roots and rhizomes within the soil organic layer, reducing the potential for asexual regeneration of understory plants from the prefire community (Schimmel and Granström 1996). Climate warming may directly influence the potential for severe fires to occur by increasing the duration and extent of fire activity (Flannigan et al. 2005; Balshi et al. 2009) and indirectly by altering soil thermal regime and moisture drainage.

Unusually short fire return intervals may also disrupt stable domains of conifer dominance and favor conversion to broadleaf-dominated forest or nonforested communities (Fig. 6). Black spruce and other boreal conifers, such as lodgepole and jack pine, rely on an aerial seed bank stored in serotinous cones to ensure ample postfire regeneration (Greene and Johnson 1999). Several decades of growth are required before young trees accumulate a sufficient store of viable seed in the canopy to supply adequate seed after a fire. Stands that experience repeated disturbances, separated by only a short recovery interval, may shift to a deciduous stability domain because of seed constraints on conifer regeneration. For example, in boreal forests of western North America, stands dominated by black spruce and lodgepole pine that burned twice within a 30-year interval experienced a very low regeneration of conifers and developed into broadleaf-dominated stands instead (Johnstone and Chapin 2006*b*). Similarly, studies of boreal forests in eastern North America have shown that fires that follow recent outbreaks of defoliating insects reduce black spruce regeneration and stimulate the formation of open, lichen-dominated spruce woodlands (Jasinski and Payette 2005). Repeated fires are also likely to increase the consumption of the soil organic layer (Johnstone 2006), interrupting the soil cycles that support black spruce resilience (Fig. 6).

Alternatively, increases in the length of the fire-free interval or multidecadal cooling could promote the transition of broadleaf-dominated sites with shallow organic layers to alternative stable domains characterized by conifers and thick organic layers (Fig. 6). Broadleaf stands that experience fire-free intervals longer than 100–200 years are likely to undergo successional changes in canopy dominance, since mortality of shorter-lived deciduous trees opens gaps in the canopy for understory conifers (Fig. 6; Van Cleve and Viereck 1981; Bergeron 2000). Successional transitions to conifer dominance promote the spread of moss in the understory and eventual accumulation of thick organic soils (Van Cleve and Viereck 1981; Fig. 6). Within a stand, successional transitions from deciduous to conifer dominance may be accelerated by autogenic or multidecadal climatic changes that reduce soil temperatures, enhance soil moisture, slow rates of decomposition and nutrient turnover, or enhance moss growth.

Landscape position and patterns of resilience

The potential for changes in fire and environmental conditions to alter stand resilience and drive shifts between alternative stability domains of community composition will be strongly affected by the degree to which slow-changing abiotic factors constrain soil conditions (Van Cleve et al. 1991). Sites at the extreme ends of landscape moisture gradients, such as well-drained ridge tops or poorly drained valley bottoms, are likely to experience stable dry or moist soil conditions, respectively, and are less likely to vary in the degree of organic layer consumption across fire cycles. In contrast, intermediate positions along moisture gradients are more likely to experience fire-driven changes in soil conditions (Johnstone and Chapin 2006*a*) and thus may be more vulnerable to a fire-initiated loss of resilience. Topographically, these sites often correspond to side slopes or well-drained lowlands. At such sites, feedbacks between plant species traits and soil conditions may be very important in maintaining stable cycles of plant composition. Unusual fire events that interrupt these feedbacks will cause a weakening of ecosystem resilience and thus have a high potential to cause sudden and dramatic shifts in vegetation communities (Fig. 6).

A shift from stand-scale to regional resilience

Loss of resilience at local scales may enhance resilience at the landscape scale (Holling 1973; Gunderson and Holling 2002). In boreal forests, a shift from extensive stands of black spruce to more equal proportions of black spruce and deciduous forest cover could enhance ecological resilience through landscape interactions. Deciduous forests have lower rates of fire spread than black spruce forests because of their higher leaf water content, low biomass of mosses and surface organic matter, and lack of ladder fuels that carry fire to the canopy (Hély et al. 2000). These forests are therefore ignited less frequently (Krawchuk et al. 2006) and can act as fuel breaks that reduce the likelihood of the extensive fires characteristic of many black spruce forests (Cumming 2001; Hély et al. 2000). Thus an increase in deciduous forest cover may reduce overall landscape flammability and the likelihood of high-severity fires that are necessary for the spruce-to-deciduous conversion, thereby stabilizing landscape and regional vegetation composition (Bergeron et al. 2004). The widespread establishment of deciduous tree seedlings in black spruce forests that burned severely in 2004 (Johnstone et al. 2010) and establishment of abundant white spruce in black spruce burns within a kilometre of upland seed sources (Wirth et al. 2008) suggests that these landscape shifts have already begun in interior Alaska.

A shift to a larger proportion of deciduous vegetation may also enhance resilience of the boreal forest through feedbacks to regional climate (Euskirchen et al. 2010). Deciduous forests absorb less radiation (higher albedo) year round and have greater evaporative cooling (higher evapotranspiration rates) in summer than do black spruce forests and therefore have a cooling effect on regional climate (Liu et al. 2005). This cooling effect over deciduous forests could partially offset regional warming trends. The strength of these climate feedbacks depends on the regional extent of vegetation change.

Conclusions and future research

Feedbacks among the soil physical environment, plant traits, and fire behavior act to generate high resilience of plant community types to fire disturbance in the boreal forests of interior Alaska. However, if fire regimes shift in response to changing climate conditions, fires may interrupt these feedback cycles and cause abrupt shifts in community composition. These changes are most likely to occur in portions of the landscape where community composition is not tightly constrained by slow-changing abiotic factors, such as in areas of intermediate moisture drainage. Nevertheless, a reduction in resilience at the stand scale may increase resilience at the regional scale, as with increased broadleaf forest cover causing a decrease in overall landscape flammability.

Evergreen and broadleaf forest cover types offer distinct patterns of ecosystem services for the boreal region, and changes in forest cover have important implications for landscape processes, wildlife populations, and human society (Kofinas et al. 2010). For example, differences in permafrost distribution and summer evapotranspiration between spruce and broadleaf forests may affect patterns of water runoff at a time when climate warming has already led to wetland drying and reductions in river flow (Riordan et al. 2006). Drying of wetlands restricts habitat for waterfowl, and declining river levels reduce accessibility of rural villages for delivery of fuel oil and other supplies.

Spruce forests are also important habitat for many furbearers and provide predator protection for moose and winter habitat for caribou (Nelson et al. 2008). In addition, spruce forests are important sites for berry production (especially *Vaccinium* spp.). Deciduous broadleaf forests offer summer and winter food sources for moose. Many animals use conifer–deciduous edges, where they have ready access to both deciduous (food) and conifer (predator protection) habitats. Both the berries and animals that are harvested and the aesthetic qualities and stories associated with each forest type provide important cultural services to rural indigenous residents (Nelson et al. 2008). A mixed forest landscape that includes multiple forest community types reduces the distance that rural residents must travel to access subsistence resources and could engender support for policies of fire management that sustain such habitat mosaics.

The synthesis presented in this paper builds heavily off the ideas and research that were developed early on in the Bonanza Creek Long Term Ecological Research program (e.g., Van Cleve and Viereck 1981; Van Cleve et al. 1983). Since that time, we have greatly increased our understanding of the feedbacks among plants, soil, disturbance, and climate that shape the successional dynamics and resilience of boreal forests. However, much of this knowledge is based on process studies undertaken at the stand scale, and we still know relatively little about dynamic changes in boreal forest ecosystems at broader landscape scales. Given the many changes that are currently being observed at landscape scales in boreal forests (Arctic Climate Impact Assessment 2005; Soja et al. 2007) and the expectations of further climate and land-use change, understanding and predicting landscape dynamics is a critical research area.

We have presented several qualitative hypotheses in this paper of key factors that are likely to drive changes in boreal forest dynamics at stand and landscape scales. Future research should test and quantify these relationships so that we can develop a stronger mechanistic basis for predicting landscape changes in resilience. We suggest targeting research at a few key areas: (*i*) quantifying the extent of change in organic layer thickness and early successional plant composition that result in domain shifts at the stand scale; (*ii*) testing and mapping topographic controls on stand resilience to predict landscape patterns of resilience; and (*iii*) quantifying feedbacks of forest cover change to key regional processes such as carbon storage, fire behavior, and climate conditions. Advancement in each of these research areas will help us to anticipate and manage changes in resilience of Alaska's boreal forests as we move forward in a century of rapid environmental change.

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