

Global Change and the Boreal Forest: Thresholds, Shifting States or Gradual Change?

Changes in boreal climate of the magnitude projected for the 21st century have always caused vegetation changes large enough to be societally important. However, the rates and patterns of vegetation change are difficult to predict. We review evidence suggesting that these vegetation changes may be gradual at the northern forest limit or where seed dispersal limits species distribution. However, forest composition may be quite resilient to climate change in the central portions of a species range until some threshold is surpassed. At this point, changes can be rapid and unexpected, often causing a switch to very different ecosystem types. Many of these triggers for change are amenable to management, suggesting that our choice of policies in the coming decades will substantially influence the ecological and societal consequences of current climatic change.

INTRODUCTION

The prevailing paradigm among ecologists is that vegetation responds gradually to climatic change. Each species is believed to migrate according to its own unique environmental requirements. As climate changes, a species therefore moves into areas where it remains within its range of climatic tolerance and zone of competitive dominance. Both the current distribution of vegetation and its pollen record are consistent with this concept. Under conditions of a relatively stable climate, each species tends to have a unique pattern of distribution along spatial gradients in environment rather than being grouped into discrete communities (1). Moreover, reconstruction of the vegetation history of the last 10 000 years from the pollen record shows that, as species migrate in response to climatic change, they have changed their associations through time, resulting in new species assemblages as environmental conditions change (2, 3). However, at time scales that are relevant to policy (decades to millennia), vegetation assemblages are often quite resilient and maintain a stable composition, despite substantial variability in climate.

In some cases, resilience reflects the long-lived nature of the dominant plant species. For example, mountain birch in Fennoscandia is a tree whose individual trunks and branches generally live for a few decades. However, an individual rootstock can continue to produce new stems indefinitely, so individual plants persist for very long periods of time. This longevity engenders resilience, because the persistence of long-lived individuals reduces the potential for invasion of new species.

Species adaptations to disturbance generate additional resilience. After fire and other natural disturbances, for example, the successional sequence of vegetation is often similar to that which preceded the disturbance. This occurs in part because of

“historical legacies” that tend to maintain existing vegetation through cycles of predictable disturbance and succession. For example, many conifer trees that dominate fire-prone ecosystems, such as lodgepole pine (*Pinus contorta*), jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and Siberian larch (*Larix siberica*), produce cones that open after the intense heat of a fire (serotinous cones), releasing abundant seed onto the post-fire soil and ensuring regeneration of the same species. Early successional species such as willow (*Salix*), aspen (*Populus*), and birch (*Betula*) resprout from roots or belowground stems to regenerate predictably after disturbance (4). Some herbaceous species produce seeds that remain dormant in the soil for decades until the heat of a fire or post-fire nutrient flush triggers their germination (5). These and other adaptations reinforce repeated cycles of the same successional sequences and create a resilience of vegetation composition, even though post-disturbance regeneration may occur under a wide range of weather conditions.

Given these sources of vegetation resilience, how does vegetation change occur? How do new species migrate and gain dominance in response to climatic change? Does this happen gradually over millennia or suddenly, when some threshold is exceeded? These questions are important to policy makers and the public because the species composition and productivity of the boreal forest strongly influences the well-being of its human residents. Ecological resilience in the face of recent environmental change leads policy makers and the public to expect the current vegetation to persist indefinitely into the future, or, if it changes, to do so slowly, allowing time for economic adjustment and social adaptation. Our goal in this paper is to summarize the nature of past and current changes in the boreal forest, as a framework for future planning.

Temporal and spatial scales also influence our perceptions of whether changes are gradual or abrupt. Changes that appear abrupt in the pollen record may have occurred over a few centuries—a change that would be considered gradual to human observers of current processes. Similarly, ecosystems often exist as mosaics of patches. At the scale of an individual patch, transitions may appear abrupt, due to the sudden loss of a key species. On the other hand, at a landscape scale, abrupt patch transitions may be distributed over time and space, leading to the impression of ‘gradual’ change (6).

Based on patterns described in this paper, we suggest that gradual changes in species composition are most likely at the northern/high-elevation limits of species ranges, such as at the treeline, where competitive interactions are less important and species distributions may respond directly to changes in the physical environment. Gradual vegetation change may also occur when dispersal, rather than climate, limits a species distribution. This can occur when new species are introduced or extant species are released from climatic limitation. In contrast, we suggest that, within central portions of the boreal forest, the

resilience of boreal vegetation to change may cause vegetation to remain stable for long periods followed by abrupt changes to a new state. If these dynamics of change are common in the north, a continuation of recent climate warming trends and/or intensification of forest management could lead to rapid irreversible vegetation changes within boreal forests that are not readily predicted from our observations of their current dynamics.

PAST VEGETATION CHANGES

A careful analysis of the paleorecord in boreal regions suggests that many past vegetation changes involved relatively abrupt changes in state, although the limited temporal resolution of this record makes it difficult to specify the time scale. For example, in Siberia the vegetation changed at the Pleistocene-Holocene boundary from a mosaic in which productive steppe grassland was widespread to a mosaic in which less productive moss/shrub tundra predominated (7). The steppe grassland supported a megafauna of mammoths, bison, horses, caribou, moose, etc. These animals in turn disturbed and fertilized the ground sufficiently to maintain productive steppe grassland (8, 9) that functioned much like the current grazing systems of Africa (10). The Pleistocene climate was highly continental because the lowered sea level and extensive sea ice sharply reduced marine influences. This resulted in warm summers, making a high productivity possible, and cold dry winters, which minimized snow cover, making the dead grasses available to animals during winter. At the Pleistocene-Holocene boundary, when temperatures became warm enough to support northward migration of people with an effective hunting technology (microblades), the megafauna disappeared, and the vegetation changed from steppe-grassland to moss-shrub tundra. Zimov et al. (9) argue that there are two alternative stable states in the north; a productive grazing system maintained by animal disturbance and an unproductive moss-shrub system in the absence of disturbance by grazers. The cause of the sudden disappearance of the megafauna is actively debated, but probably involved some combination of change in climate, human hunting, diseases, and other factors. What is important in the context of this paper is that the change in vegetation and megafauna represented a threshold change in the properties of the ecosystem, rather than a gradual transition in abundances of individual species. This contrasted with the persistence and resilience of steppe grassland through many previous glacial-interglacial cycles of climatic change. If human hunting was indeed a contributor to this change, it suggests that human activities combined with climatic change can precipitate ecological changes of much greater magnitude than would be expected from climatic changes alone.

Changes in the abundance of a single species can sometimes trigger massive alterations in the properties of a system, leading to a new stable state. This has occurred repeatedly in modern times as a result of introduction of exotic species—for example, the invasion of a nitrogen-fixing tree in Hawaii, European annual grasses in California, and deep-rooted trees that tap groundwater in deserts (11). A similar event may have occurred through the natural migration of black spruce into interior Alaska. About 9000 BP (years before present) the climate of Alaska was warmer than at any time since the end of the Pleistocene ice ages and was dominated by poplar (*Populus balsamifera*) forests. Climate then became gradually wetter and cooler (12), leading to the replacement of poplar forests by white spruce and subsequently by black spruce forests. Black spruce is a keystone species that promotes fire through both its

own flammability and that of the understory feathermosses and evergreen shrubs (13). The expansion of black spruce coincided with a threshold *increase* in fire frequency 6000 BP, despite cooler, moister climate, suggesting that vegetation rather than climate drove long-term trends in fire regime (12, 14). The change in disturbance regime in turn promoted persistence of fire-adapted black spruce with its serotinous cones and capacity to re-seed quickly after fire.

In the boreal forests of eastern Canada, fire frequency was high 10 000–7500 BP and low 7500–2500 BP and has increased subsequently (15). These changes in fire regime have triggered vegetation shifts that lead, in many cases, to an imbalance between observed vegetation and current climate. For example, subarctic forest tundra covers a large area of the Precambrian shelf between the boreal forest and arctic tundra in northern Canada. This large zone was previously covered by forest that was later disrupted by lack of post-fire regeneration (16). A similar process currently occurs further south as weak regeneration after fire is gradually eroding closed-canopy black spruce forests and transforming them to Jack pine or spruce lichen woodlands (17). Although gradual at the regional scale, the phenomenon is locally abrupt, occurring, for example, after severe fires 2500 BP (18). It is the cumulative effects of these local events that explain the current forest mosaic. Because the present situation has not yet reached a balance, it is difficult to forecast future vegetation patterns and species distributions without a better knowledge of the complex interactions between disturbance regimes and their specific controls over forest mosaics.

The ecosystems of Scandinavia have also been characterized by periods of both vegetation stability and rapid change. Forest vegetation colonized rapidly in northern Sweden following deglaciation about 9000 BP (19–21). This was probably facilitated by a landscape and climate that were out of synchrony and therefore had little resilience to change. As glaciers retreated, they left a landscape with little vegetative cover that was colonized by vegetation that has no present-day analogue. An early dominant was sea buckthorn *Hippophaë*, a warmth-demanding shrub with low competitive ability currently found in southern Norway (19). In central Scandinavia, where climate was continental, pine reached its highest treeline position for the entire Holocene within less than a thousand years. In northern Norway and Finnish Lapland, where the climate was more oceanic, birch forests developed within about 700 years and persisted as an open subarctic birch woodland-tundra until about 5500 BP. This woodland was similar to that of today except that its understory had more meadow species and fewer heath species. Between 5500 and 3400 BP, when the climate probably became more continental and variable, pine reached its maximum latitudinal and altitudinal extent. Pine-birch woods occurred on dry soils and birch-alder-willow woodlands on damp soils. Meadows became less frequent, heaths expanded, and spruce reached its northernmost extent. From 3400 BP until the present, the area has regressed to the earlier subarctic birch woodland tundra reflecting a cooler, more oceanic climate. In summary, the initial post-glacial vegetation showed low resilience and changed rapidly to subarctic birch forests that have been highly resilient to subsequent climatic variations. Birch coexisted with pine during dry periods. Its understory has ranged from meadow species in dry times that persist today on south-facing slopes to heath species in cooler moister times and locations.

CURRENT PROCESSES

Alaska: Shifting Mosaics of Alternative Stable States

The uplands of interior Alaska exhibit a predictable topographic pattern of forest dominance and succession after wildfire. In general, self-replacement predominates in extreme environments. Black spruce replaces itself directly after fire in cold permafrost-dominated sites. Similarly, aspen replaces itself directly after fire in warm dry sites without other intervening tree species. On intermediate sites, however, there is a predictable replacement sequence of deciduous species (aspen on south-facing slopes or birch on cooler east- or west-facing slopes), followed by white spruce after about 100 years (Fig. 1) (22–24). These repeatable patterns of succession are a consequence of competitive interactions over multiple fire cycles that have sorted species into those environments where they grow most successfully (25).

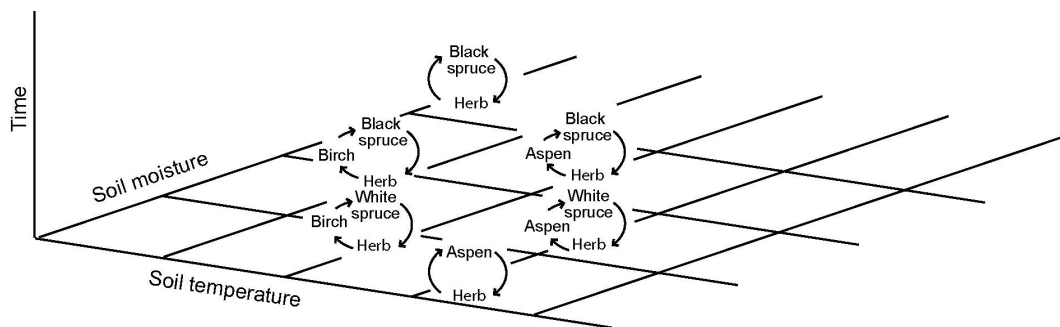


Figure 1. Representative successional trajectories on upland sites in interior Alaska, arrayed along gradients of soil temperature and soil moisture. Upward arrows indicate successional changes in community composition; downward arrows indicate vegetation change caused by fire. Changes in environment, disturbance regime, or post-disturbance seed availability can shift a stand to a new successional trajectory, but in the absence of these changes, succession tends to repeat the same successional trajectory following each disturbance event.

The mosaic of successional patterns in interior Alaska are then maintained by strong legacies that provide a high probability that the same successional trajectories will be repeated after each fire. Deciduous species regenerate vegetatively by root or stump sprouts. Large belowground reserves enable these resprouts to grow quickly and attain canopy dominance after fire. Black spruce, with its semiserotinous cones also regenerates effectively after fire. White spruce is the most vulnerable tree species to being lost from a site after fire, because it must regenerate from seeds that disperse into the burn area from adjacent unburned trees. All species in each of these successional sequences establish within two decades after fire, and their changes in relative abundance reflect differences in growth rate and longevity rather than differences in establishment time (26, 27). Therefore successional trajectories can shift only as a result of an event that causes a gain or loss of species during the post-fire establishment phase.

The recent expansion of lodgepole pine at the northern limit of its range in western Canada shows how a species addition during the establishment phase can alter successional trajectory (28). At this range limit, pre-fire forests are dominated by white and/or black spruce and go through an aspen phase before returning to spruce. However, the presence of even a few lodgepole pine trees frequently triggers the abundant recruitment of this species after fire. In such cases, successional trajectories can shift from spruce to pine dominance, within a single fire cycle (Fig. 2). In contrast, in the center of the northern range of lodgepole pine, spruce stands regenerate to spruce, and pine stands regenerate to pine with predictable patterns of self-replacement. Recent warming combined with chance dis-

persal events may be the factors that have triggered the shift in successional trajectory at the northern range limit of lodgepole pine. Once pine attains dominance, its thick layer of needles and high density of flammable trees promote fire, which favors persistence of the pine-dominated state.

Radial growth and reproduction of white spruce in interior Alaska change the nature of their response to climate, depending on whether the summer climate regime is predominantly cool-moist or hot-dry, conditions that persist for multi-decadal time periods (29). Productive upland stands of white spruce in interior Alaska generally occur on warm south-facing, permafrost-free slopes. Annual total precipitation in the region is quite low, usually between 300 and 450 mm. As a result, radial growth of white spruce on such sites is limited by temperature-induced drought stress (30, 31). Cool-moist summer climate regimes are periods of optimum climate for growth, and hot-dry summer climate regimes are characterized by reduced radial growth and high stress on trees (29). One or two

years of stress from hot-dry conditions physiologically induces cone crops, which are produced only irregularly. A hot and dry summer also increases the probability that large landscape-level fires will occur. As a result, large white spruce seeds crops are synchronized for release into landscapes in which fires are likely to have occurred (31). White spruce is well adapted to take environmental cues from this climate system and persist.

However, further climate

warming is likely to shift this productive forest system to an alternate condition. The best climate predictor of white spruce radial growth is mean temperature of May through August. Late 20th century warming represented the hottest and driest summer temperatures, and poorest growth, in the last 200 years (29). Further warming of about 2°C would represent summer temperatures empirically associated with extreme levels of stress and/or an empirically predicted level of zero growth. Based on the current mosaic of ecosystem cover types, productive white spruce forests would probably be replaced by aspen parkland or grassland, in other words a shift to a new biome type.

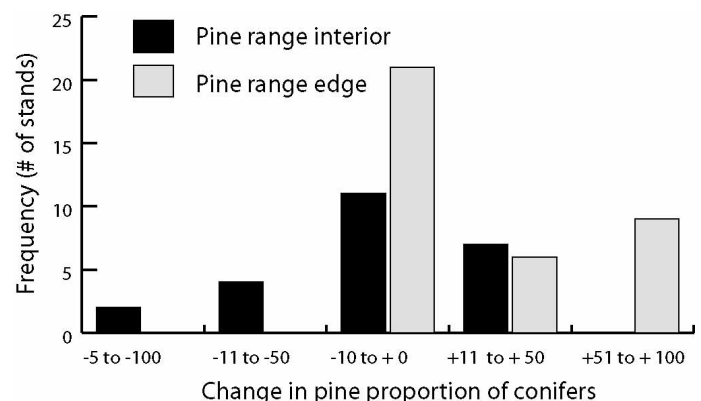


Figure 2. Histogram showing changes in the proportion of pine relative to total conifers after fire. Changes are shown in the center of the range of lodgepole pine and at its northern distributional limit (28).

Fennoscandia: Climate-ecosystem Interactions

Rapid irreversible state changes can occur when multiple environmental changes reduce the resilience of long-established disturbance-recovery regimes. In the mountain birch forests of northern Fennoscandia, disturbance is generated by more or less cyclical outbreaks of defoliating insects such as the autumn moth (*Epirrita autumnata*). Outbreaks occur about every 10 years, creating a mosaic of open woodland within the forest. In 1955, for example, 6000 to 7000 ha of birch forest were defoliated in the Abisko area (32). Under normal conditions, the birch forest regenerates, although this can take up to 70 years. Under some circumstances, however, the regeneration cycle is prevented. In northern Finland, for example, caterpillar defoliation of the birch forest followed by intense reindeer browsing on regenerating sprouts caused a shift from subalpine birch forests to subalpine heaths with little potential for future forest development (33, 34). This long-term shift of state could have been triggered within only one or two growing seasons. Outbreaks of defoliating caterpillars are to some extent limited by low winter temperatures that kill eggs. As temperatures increase and the threshold for egg survival is exceeded (most eggs of the autumn moth freeze after 16 hours at -33°C), outbreaks may become more extensive (35), and new pests might become problematic (32). If climate continues to change, as expected, it is unclear whether the resilience of the forest cyclical succession will be exceeded and, if so, what changes will take place. Extreme results could be a natural succession from birch to pine as seen in the past (19) or degradation of the birch forest to "pseudotundra" with intense human activity and/or pollution, as is seen surrounding the nickel extracting factories in the Kola Peninsula (36).

Forests face different challenges at the northern edges of their range. At the forest boundary, localized vegetation changes occur even under a constant climate because of tree demography, i.e. births and deaths, and sometimes changes in growth form from low "shrub" to tree. Future environments are likely to alter the balance among these processes, leading to advance, retreat or a new dynamic equilibrium at the treeline. In flat areas or areas with a more oceanic climate, paludification processes may favor bog growth over forest development (37, 38). In contrast, under continued warming and adequate drainage, the forest may migrate northwards in a warming climate so long as soil moisture does not limit tree growth. Alternatively, under prolonged warming in continental areas, soil moisture deficits may cause forest to be displaced by steppe communities analogous to those existing in the early Holocene (7). Evidence for this scenario comes from lack of response of trees to warming in continental areas of Alaska (30) and Fennoscandia (39). Increased land use (36), grazing/browsing, fire frequency/size, and insect pest outbreaks can also lead to the southern retreat of the treeline in a warming climate. Thus, different changes in state can occur under the same warming trend, depending on topography and interactions with other processes.

Canada: Management-driven Change in Forest Structure

In Canada, short-rotation forest harvest has created even-aged forests that differ profoundly from those that were previously controlled by fire (40). After one complete rotation in a region, there will be no stands older than this rotation age. This contrasts with the natural mosaic in which almost 50% of forests are older than the industrial rotation (40). The exclusive use of even-age management regime therefore eliminates old-growth forests, often judged to be essential for the maintenance of biodiversity (41). Forest management also alters the size and

distribution of patches on the landscape. Although it is primarily the large fires (those over 1000 ha) that are responsible for the natural regeneration of the forest and that permeate a given age structure and configuration (42), harvest units are generally limited to few hundred hectares and constitute a wave that moves from south to north. Finally, the inherent differences between fire and logging can alter the composition of plant communities (43). Although the overall effects of these changes on ecosystem sustainability and possible thresholds of change are difficult to predict, it would be prudent to move toward a natural disturbance-based management that decreases the differences between natural and managed landscapes (44, 45).

Eastern Siberia: Climate-Fire-Human Interactions and the Retreat of Forests

One of the most widely held expectations of vegetation response to warming is that latitudinal treeline will move northward, causing tundra to be replaced by forests (46). Indeed, this change appears to be occurring in maritime regions of western Alaska (47). In eastern Siberia, however, the combination of warmer, drier conditions and reduced capacity for fire suppression promoted the spread of anthropogenic fire near the treeline. This led to a net conversion of 50 million ha of forest to treeless vegetation, causing the treeline to move southward (36, 48).

In central Siberia, there are extensive areas of ice-rich loess sediments (yedoma). When these thaw, they produce thermokarst lakes surrounded by meadows (alases), creating a mosaic of forest and meadow. The combination of grazing by horses and cattle, competition from grasses, and the accumulation of salts left behind by surface evaporation inhibits the reforestation of these meadows. Warming, forest harvest, and fire all promote the formation of new alases. In addition, warming increases surface evaporation and salinization and shifts the competition between trees and grasses in favor of grasses. The net effect of these changes is to convert forest to grassland so that what has been scattered alases in a matrix of forest may become a savanna with scattered forest patches.

In both the treeline retreat and alase formation, the interaction of climatic change and human activities causes a vegetation change that would not have been expected from either of these changes acting in isolation.

CONCLUSIONS

The dynamics of change in the boreal forest vary tremendously from time to time and place to place, making simple generalizations and predictions impossible. Nonetheless, certain patterns of change have recurred frequently enough to provide a basis for future planning. First, changes in climate of the magnitude projected for the 21st century (49) have always caused substantial vegetation change, so it is prudent to expect that the current dynamics of northern forests may change within the timeframe of concern to resource managers. At the northern and upper elevational limits of a species, these changes may be gradual, as the climatic limitations to growth, reproduction, and establishment are gradually relaxed. In central portions of a species range, however, vegetation may remain quite resilient to substantial variations in climate. It is often the *interaction* of human-induced changes with climatic change that triggers large changes in the state of these systems. These potential human triggers of change include introductions or elimination of ecologically important species, changes in grazing, fire regime, and atmospheric deposition of nitrogen or heavy metals. All of these changes are amenable to management, suggesting that

our choice of policies in the coming decades will substantially influence the ecological and societal consequences of current climatic change.

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