

# Evidence and implications of recent and projected climate change in Alaska's forest ecosystems

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**Abstract.** The structure and function of Alaska's forests have changed significantly in response to a changing climate, including alterations in species composition and climate feedbacks (e.g., carbon, radiation budgets) that have important regional societal consequences and human feedbacks to forest ecosystems. In this paper we present the first comprehensive synthesis of climate-change impacts on all forested ecosystems of Alaska, highlighting changes in the most critical biophysical factors of each region. We developed a conceptual framework describing climate drivers, biophysical factors and types of change to illustrate how the biophysical and social subsystems of Alaskan forests interact and respond directly and indirectly to a changing climate. We then identify the regional and global implications to the climate system and associated socio-economic impacts, as presented in the current literature. Projections of temperature and precipitation suggest wildfire will continue to be the dominant biophysical factor in the Interior-boreal forest, leading to shifts from conifer- to deciduous-dominated forests. Based on existing research, projected increases in temperature in the Southcentral- and Kenai-boreal forests will likely increase the frequency and severity of insect outbreaks and associated wildfires, and increase the probability of establishment by invasive plant species. In the Coastal-temperate forest region snow and ice is regarded as the dominant biophysical factor. With continued warming, hydrologic changes related to more rapidly melting glaciers and rising elevation of the winter snowline will alter discharge in many rivers, which will have important

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consequences for terrestrial and marine ecosystem productivity. These climate-related changes will affect plant species distribution and wildlife habitat, which have regional societal consequences, and trace-gas emissions and radiation budgets, which are globally important. Our conceptual framework facilitates assessment of current and future consequences of a changing climate, emphasizes regional differences in biophysical factors, and points to linkages that may exist but that currently lack supporting research. The framework also serves as a visual tool for resource managers and policy makers to develop regional and global management strategies and to inform policies related to climate mitigation and adaptation.

**Key words:** Alaska; boreal forest; climate change; climate projections; coastal-temperate forest; conceptual framework; disturbance regime; ecosystem services; insects and disease; invasive species; permafrost; wildfire.

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#### INTRODUCTION

Currently, climate changes are significantly impacting Alaska's ecosystems (ACIA 2005). These impacts have been repeatedly synthesized for arctic tundra (ACIA 2005, Hinzman et al. 2005, McGuire et al. 2009) and portions of the boreal forest (Chapin et al. 2006*a*), but there has been no comprehensive review of climate-change impacts on the broad spectrum of Alaskan forests, which is the goal of this review. Changes in high-latitude forests have important implications both regionally and globally. Shifts in the disturbance regimes of Alaska's forests (boreal and coastal-temperate rainforest biomes) at the regional scale directly affect the global climate system through greenhouse gas emissions (Tan et al. 2007) and altered surface-energy budgets (Chapin et al. 2000, Randerson et al. 2006). Climate-related changes in Alaskan forests also have important regional societal consequences, and human responses to these changes may amplify their impact on forest ecosystems. Understanding the current and potential future impacts of contemporary climate change is important not only for regional-level adaptive management, but also for national and international decision- and policy-making related to mitigation and adaptation strategies.

Alaska's forests (Fig. 1A) cover one-third of the state's 172 million ha of land (Parson et al. 2001) and are functionally significant, both regionally

and globally. Ninety percent of the forests are classified as boreal (42 million ha), collectively representing 4% of the world's boreal forests (Shvidenko and Apps 2006); these occur throughout the Interior-, Southcentral- and Kenai-boreal regions (Fig. 1B). Coastal-temperate forests (5 million ha) comprise 10% of Alaska's forests and represent 19% of the world's coastaltemperate forests (NAST 2003). Forests in Alaska play a large role in the economies and livelihoods of people, as a result of their proximity to urban and rural communities, and a diversity of associated ecosystem services (MEA 2005). Changes in forest structure and function will not only directly impact the biological components of these ecosystems, but will also have important consequences for society (Flint 2006, Chapin et al. 2008, Trainor et al. 2009).

Changes in boreal forests have the potential to affect the global climate system for several reasons. First, the boreal biome comprises onethird of the Earth's total forested area (Shvidenko and Apps 2006) and is one of the biomes expected to change most rapidly with future climate change (Christensen et al. 2007). Second, boreal ecosystems contain 40% of the earth's reactive soil organic carbon (McGuire et al. 1995). Third, the age-dependent stand structures and species compositions characteristic of boreal forests modulate high-latitude energy budgets by affecting surface albedo (Euskirchen et al. 2009*a*). And fourth, carbon cycling, albedo, and

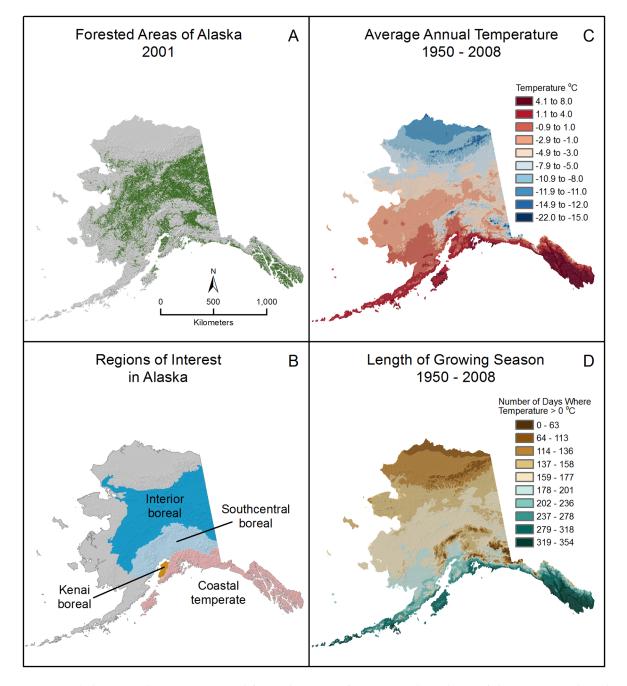


Fig. 1. Alaska maps illustrating (A) total forested area, (B) forest region boundaries of the: (1) Interior-boreal forest that is bounded by the Brooks Range to the north, the Alaska Range to the south, and the Seward Peninsula to the west; (2) Southcentral-boreal forest that includes the forests south of the Alaska Range, west of the Alaska-Yukon border, and east of the Alaska Peninsula; (3) Kenai-boreal forest that includes the western side of the Kenai Peninsula; and (4) Coastal-temperate forest that occurs on the Alaska Panhandle, the eastern portion of the Kenai Peninsula, Prince William Sound, and the islands of the Kodiak archipelago, (C) average annual temperature from 1950–2008, and (D) length of growing season from 1950–2008. Length of growing season values were calculated as the difference between the day of freeze (first Julian date when the temperature was  $<0^{\circ}$ C) and day of thaw (Julian date when the temperature and length of growing season were obtained from the Climatic Research Unit (CRU; http://www.cru.uea.ac.uk/).

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stand structure in the boreal forest are strongly influenced by the frequency and severity of wildfires (Randerson et al. 2006, Euskirchen et al. 2009*a*, Johnstone et al. 2010*a*, Turetsky et al. 2011), and burning is an important disturbance mechanism by which stored carbon is released to the atmosphere (Amiro et al. 2001, Kasischke et al. 2000, 2005).

Changes in coastal-temperate rainforests, although confined to a relatively small footprint (<0.5% of the Earth's total forested area; Ecotrust 1992), also have potential global impacts, due to the importance of coastal margins in global matter and energy budgets and the delivery of dissolved organic carbon to coastal oceans (Muller-Karger et al. 2005). Small-scale natural disturbances (e.g., windthrow, landslides, disease) dominate in these old-growth late-successional forests (Hennon and McClellan 2003). The resulting old-growth forests accumulate carbon for many centuries (Luyssaert et al. 2008), and represent a large carbon pool (Waring and Franklin 1979). Given their small areal coverage, these ecosystems support a disproportionately high diversity of plant and animal species (Schoonmaker et al. 1997), and the adjacent highly productive terrestrial-marine ecotone supports a diversity of fish, bird, and mammal species (Simenstad et al. 1997).

In Alaska, climate change effects have already occurred and, as a result of high-latitude amplification are expected to be greater than at lower latitudes (Shulski and Wendler 2007, Karl et al. 2009). During the 20th century, boreal Alaska has warmed twice as rapidly as the global average (Hinzman et al. 2005, Wendler and Shulski 2009). Mean annual air temperature in the Interior increased by 1.3°C during the past 50 years, with the greatest warming occurring in winter (Hartmann and Wendler 2005, Shulski and Wendler 2007). Air temperature is projected to increase by an additional 3 to 7°C by the end of the 21st century (Walsh et al. 2008, Scenarios Network for Alaska and Arctic Planning [SNAP]; http://www. snap.uaf.edu). Precipitation in this region has increased by only 1.4 mm decade<sup>-1</sup> (Hinzman et al. 2006), thus, projected increases in precipitation will likely be insufficient to offset increases in summer evapotranspiration (Rouse 1998). The Coastal-temperate forest may be particularly sensitive to climate change, as winters have been

warmer since the 1970s (Fig. 1C; average annual temperature  $>0^{\circ}$ C), with more precipitation falling as rain (NAST 2003), and the region is characterized by long growing seasons (Fig. 1D; >240 days year<sup>-1</sup>).

In Alaska, warming since the 1950s appears to be unprecedented in at least the last 400 years (Overpeck et al. 1997, Barber et al. 2004, Kaufman et al. 2009). Melting glaciers and ice fields in Alaska have contributed more to sea level rise over the past 50 years than any other glaciated region measured outside of the Greenland and Antarctic ice sheets (Arendt et al. 2002). In boreal Alaska, water balance has decreased significantly over the past several hundred years (Anderson et al. 2007, Clegg and Hu 2010), causing a consistent decrease in the number and area of closedbasin ponds (Klein et al. 2005, Riordan et al. 2006). Across Alaska, observations indicate significant shifts in vegetation composition and production, including yellow-cedar decline throughout the Coastal-temperate forest region (Hennon et al. 2006), decreased spruce growth in boreal Alaska (Barber et al. 2000, McGuire et al. 2010, Beck et al. 2011), woody vegetation encroachment into wetlands (Berg et al. 2009) and negative productivity throughout forested Alaska (e.g., Goetz et al. 2005, Verbyla 2008, Beck et al. 2011).

Recent changes in major disturbance regimes in Alaska are linked to changes in climate. Wildfire, the dominant driver of ecosystem change in Interior forests, is strongly linked to climate (Duffy et al. 2005). In the last decade, annual area burned in this region has doubled compared to any decade of the previous 40 years (Kasischke et al. 2010). The life histories of damaging insects (e.g., spruce beetle [Dendroctonus rufipennis] and spruce budworm [Choristoneura fumiferan]) are tightly linked to summer temperature (Holsten et al. 1985, Werner and Holsten 1985, Han et al. 2000), and their recent outbreaks have been attributed to climate change (Werner 1994, 1996, Werner et al. 2006). Alaskan forests are becoming increasingly susceptible to non-native plant invasions as the climate warms and the amount of land disturbance (anthropogenic and natural) increases, which could collectively promote the establishment of invasive plant species into remote regions of Alaska (Villano and Mulder 2008). The rate of new introductions of exotic plant taxa has increased from roughly one to three species per year (1941– 1968 and 1968–2006, respectively) (Carlson and Shephard 2007).

This paper presents a comprehensive synthesis of climate-change-related research in Alaskan forests that extends previous synthesis efforts and assesses the effects of climate change within a conceptual framework. Specifically, in this assessment of Alaska's forest regions we: (1) develop a conceptual framework to summarize our current understanding of climate-changerelated research in each region and identify knowledge gaps; (2) summarize the projected changes in key climate and climate-related abiotic characteristics of the environment that control ecosystem processes; (3) evaluate the global implications and feedbacks that may either increase or decrease the rate of climate and ecosystem changes; (4) summarize the key regional societal consequences of climate-change effects; and (5) discuss uncertainties, policy options, and areas of future research.

### **M**ETHODS

### Study area

We broadly delineated Alaska's forested area (Fig. 1A) into either boreal or coastal-temperate forest. The boreal forest was further divided into three regions, designated as the: (1) Interior-boreal forest; (2) Southcentral-boreal forest; and (3) Kenai-boreal forest. The Coastal-temperate forest was designated the fourth forest region (Fig. 1B).

# Climate and abiotic projections for Alaska's forest regions

We present climate projections for two time slices (i.e., 2050 and 2100), as the biological and social implications of these changes vary with the temporal resolution. Many of these projections were developed by SNAP (http://www.snap.uaf. edu) and are based on output from global climate models (GCMs) used by the Intergovernmental Panel on Climate Change (IPCC) to prepare its Fourth Assessment Report (IPCC 2007). The 15 GCMs utilized by the IPCC were evaluated and ranked according to how accurately each model predicted high-latitude mean monthly surface air temperature, precipitation, and air pressure at sea level (Walsh et al. 2008). The SNAP climate projections utilize the intermediate A1B scenario output from the five best performing GCMs (Walsh et al. 2008). The output variables from the GCMs were then downscaled with the delta method (Hay et al. 2000, Hayhoe 2010) using Parameter-Elevation Regressions on Independent Slopes Model (PRISM; http://www.prism. oregonstate.edu/) 1961–1990 climate normals as the baseline climate at 2 km resolution. Where data were available, references for climate projections from sources other than those generated by SNAP are cited.

### Creating a framework to evaluate current and future effects of climate change

To evaluate the impact of climate changes in Alaskan forests, we first identified the primary climate drivers (e.g., wind, surface air temperature, precipitation) and the biophysical factors (e.g., insects, disease, invasive species, permafrost, wildfire) that change in response to these drivers. We then developed a conceptual framework similar to that described by Overpeck et al. (2005) and Francis et al. (2009), to synthesize our current understanding of climate-related changes in Alaskan forests. In our framework, we envision two interacting subsystems-the biophysical and social subsystems (Fig. 2). These two subsystems interact via the consequences of ecosystem changes on the social subsystem and the impacts of the social response to these ecosystem changes on the biophysical subsystem. We identify three elements of the biophysical subsystem: climate drivers, biophysical factors, and types of change (depicted in Fig. 2; defined in Table 1). Our strategy was to concentrate on what we viewed to be the most critical biophysical factors for each forest region given a changing climate. Based on an extensive literature review, we identified the types of change that exert the greatest influence on the structure and function of each forest region; an exhaustive description of all underlying processes is beyond the scope of this review. This literature review provided the information to (1) identify key climate variables that drive changes in each forest region, (2) select biophysical factors that are currently responding to climate changes and exert the greatest influence on the types of change observed, and as such will have the

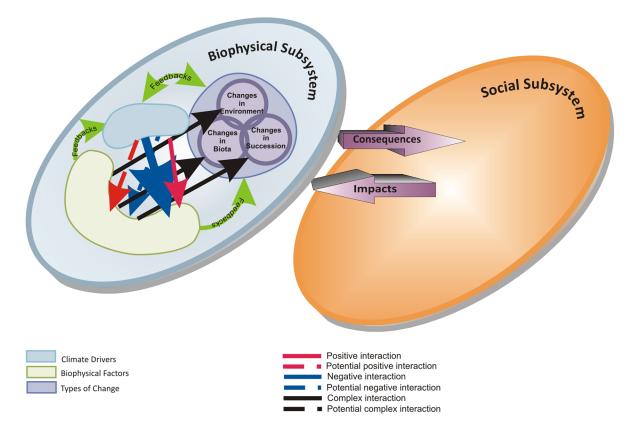


Fig. 2. Conceptual framework of Alaskan forests synthesizing the current understanding of climate-related changes. The framework illustrates the interactions between the biophysical and social subsystems. These subsystems interact via the consequences of ecosystem changes on the social subsystem, and the impacts of the social response to ecosystem changes on the biophysical subsystem. There are interactions (see Fig. 3 for description of arrow color, line type, and thickness) and feedbacks (green labeled arrows) that link the elements of the biophysical subsystem: climate drivers (blue circles), biophysical factors (green circles) and types of change (violet circles) (described in Table 1). The complex interactions occurring between the categories of the types of change (changes in environment, succession and biota) are depicted with overlapping circles.

largest regional and global implications for the social subsystem of our framework, and (3) depict the interactions and feedbacks that link the elements of the biophysical subsystem through the use of arrow size, direction, and color (Fig. 2). Finally, we utilize future projections of climate and abiotic characteristics, as well as suggestions from the literature, to hypothesize specific biophysical factors that will become important under various climate scenarios (Fig. 2). These regional depictions of the effects of climate change were then used to describe the consequences that changes in the biophysical subsystem will have on the social subsystem, to compare regional differences in climate drivers, biophysical factors, and types of change, and to

identify the gaps in our knowledge of climaterelated changes in Alaska's forest regions. We emphasize the major elements (climate drivers, biophysical factors, and types of change) of the biophysical subsystem and the typology of their interconnections (arrows) rather than the mechanisms that underlie each arrow (e.g., temperature effects on enzyme activity, drought, nutrient supply). This emphasis reflects our primary goal (i.e., to describe differences among forest regions), and underscores the fact that biophysical elements are better documented than is the relative importance of underlying mechanisms in most of these forests.

Elements of conceptual framework	Definition	Variables/categories	Factors impacting the effect of this element
Climate drivers	Climate variables that directly or indirectly affect the biophysical factors and types of change within the biophysical subsystem	Surface air temperature, precipitation, wind, cloud cover	Implicit within the climate drivers are the interactions that occur among individual climate variables (e.g., interactions between surface air temperature and precipitation)
Biophysical factors	The primary categories of disturbances and surface characteristics in Alaskan forests that have large cascading and long-term effects on the climate drivers and/or types of change	Wildfire, permafrost thaw, insects and diseases, invasive species, snow and ice cover	A biophysical factor may change directly as a result of changes in climate, but may also interact with another biophysical factor to influence the types of change observed (e.g., interactions between permafrost thaw and wildfire)
Types of change	The categories of changes that occur over different time scales and levels of complexity that apply to all Alaskan forests (though their relative importance may differ among regions)	(1) Changes in environment associated with permafrost thaw, increased growing- season length, and seasonal timing of soil moisture recharge; (2) Changes in succession associated with changes in wildfire, glacier melt and insect/disease outbreaks; and (3) Changes in biota associated with migration, altered species composition and abundance, and plant growth rates and phenology.	Within the types of change are the complex interactions that occur between the three categories that are critical to understanding how forest ecosystems are responding to changes in climate. For example, changes in environment and biota interact reciprocally to affect plant phenological events (within- year response) and succession (multi-year response)

Table 1. Definitions of the elements in the biophysical subsystem of the conceptual framework of climate-related changes in Alaskan forests (see Figs. 2 and 3).

## Results

#### Types of change in Alaskan forests

The types of change are the categories of change (changes in environment, succession, and biota) that occur in all forests (Fig. 3A–D). The fact that some of the material could be presented under multiple types of change categories emphasizes the complex interactions occurring between the categories of change (Fig. 2).

Interior-boreal forest. -

1. Changes in environment.—In Interior Alaska, local conditions that affect ground insulation, such as snow depth, incident solar radiation, vegetation cover, and depth of surface organic soils, in part determine the distribution of permafrost (Jorgenson et al. 2010). Variation in topography, disturbance history, and ecosystem and hydrological processes can lead to a spectrum of permafrost responses to climate warming in this region (Jorgenson et al. 2010). Disturbance to permafrost structure and distribution can occur as a gradual change, such as a thickening of the seasonally thawed active layer that can eventually lead to the development of a talik, the bottom of the deepened active layer that does not refreeze during winter, or it can occur abruptly in the form of catastrophic ground subsidence (thermokarst) (Schuur et al. 2008). One primary factor controlling ecosystem responses to permafrost degradation is the hydrologic regime following thaw, particularly because permafrost restricts drainage and can control surface hydrology (Hinzman et al. 1998). Permafrost degradation can change surface hydrology substantially, resulting locally in poorly drained wetlands and/ or thaw lakes (Smith et al. 2005). Alternately, permafrost thaw can result in well-drained ecosystems, where steeper slopes or more permeable soils and geologic substrates allow for deeper flowpaths and better surface drainage.

Observational studies demonstrate some of the disparate effects of permafrost thaw and their implications for hydrology and biogeochemical

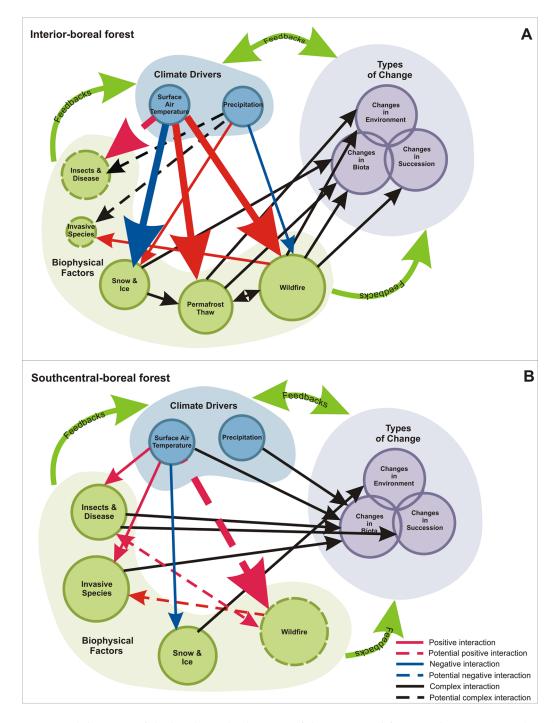


Fig. 3. Regional diagrams of the biophysical subsystem of the conceptual framework (see Fig. 2 and *Methods: Creating a framework to evaluate current and future effects of climate change*) depicting climate change impacts in the (A) Interior-boreal; (B) Southcentral-boreal; (C) Kenai-boreal; and (D) Coastal-temperate forest regions of Alaska. Interactions between elements within the biophysical subsystem (defined in Table 1) are supported by research and may be positive (red arrows), negative (blue arrows), or complex (black arrows; i.e., the change in one variable is contingent on the magnitude of change in the other variable).

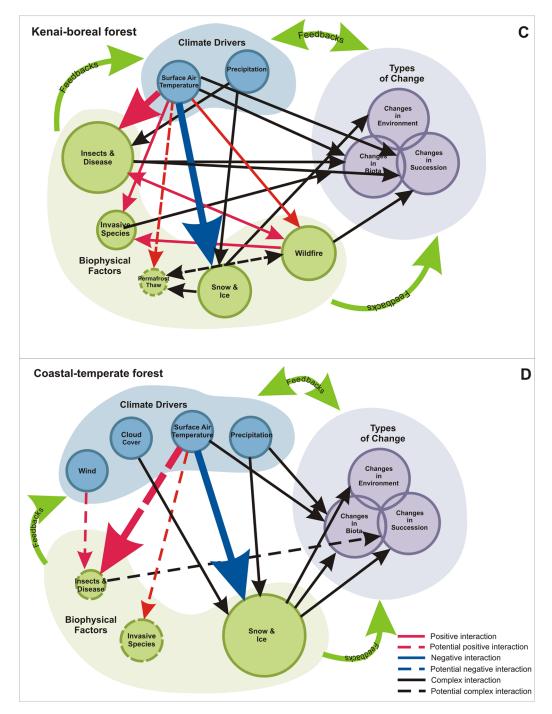


Fig. 3. Continued. The framework includes both current (solid-line circles) and potential (dashed-line circles) biophysical factors, with larger circles influencing change more than smaller circles. Interaction arrows (either red, blue or black) involving a potential biophysical factor are represented with dashed-line arrows. Where multiple climate drivers interact with a biophysical factor the dominant climate driver is identified with a thicker arrow (either red, blue or black, and solid or dashed). The conceptual framework depicts the complex interactions that occur between the three categories of types of change (changes in environment, succession, and biota) that are critical to understanding how forest ecosystems are responding to changes in climate (described in Table 1) as overlapping circles.

cycling. Creation of thermokarst wetlands and open water can lead to increased methane emissions and increased carbon uptake and sequestration under anaerobic conditions (Myers-Smith et al. 2007). In contrast, in lowlands underlain by gravel, high-ice permafrost is less common, and climate warming causes drying of lakes due to increased evapotranspiration, and in some situations, loss of permafrost and internal drainage (Yoshikawa and Hinzman 2003, Riordan et al. 2006, Jorgenson et al. 2010). With future permafrost thaw, drainage of lakes during the winter will likely increase (Brabets and Walvoord 2009). The eventual (decadal- to century-scale) hydrological outcome is expected to be an overall drying in this region, because permafrost restricts surface drainage in many locations on the landscape (Christensen et al. 2007).

Changes in surface hydrology will amplify the direct effects of permafrost thaw on biogeochemical cycles. In particular, large pools of carbon previously stored in frozen soil are subject to increased decomposition as permafrost thaws, with regional and ecosystem effects on gross primary productivity (Vogel et al. 2009) and species composition (Schuur et al. 2007), leading to feedbacks to the global carbon cycle (Schuur et al. 2008). Permafrost thaw and ground subsidence in uplands can have complex effects, as initially increased carbon uptake by plants may offset increased ecosystem respiration, creating a carbon sink (Schuur et al. 2009, Vogel et al. 2009, Lee et al. 2010) but eventually result in a net source of carbon to the atmosphere as increased old soil carbon losses offset increased carbon uptake (Vogel et al. 2009).

Interactions between wildfire and permafrost thaw impact soil organic dynamics (O'Donnell et al. 2010). A distinguishing characteristic of much of the boreal forest is the presence of a thick continuous moss layer. This moss layer controls many ecosystem processes (Turetsky et al. 2010). For example, thermal properties of soil organic layers mediate the effects of climate warming (O'Donnell et al. 2009). The high water retention of hummock-forming *Sphagnum* species may reduce wildfire severity (Shetler et al. 2008) through the maintenance of poor drainage conditions that keep permafrost soils cool (Harden et al. 2006). Following wildfire, permafrost degradation or aggradation is determined by the thickness of the soil organic layer (Yoshikawa et al. 2003). Permafrost is maintained by the positive feedbacks between cold temperature, poor drainage, and the resistance of moss layers to decomposition, resulting in the accumulation of thick organic layers (Harden et al. 2006). However, projected warming and/or an increase in wildfire will increase permafrost thaw postfire, as wildfire is the dominant biophysical factor in the Interior-boreal (Myers-Smith et al. 2008).

Research during the 1970s and 1980s determined that biogeochemical processes in the Interior-boreal forest were largely limited by temperature and nutrients (Van Cleve et al. 1986, 1991). However, more recent studies indicate that nutrient limitations on tree growth only occur during early spring when soils are cold. As a result, moisture availability is now considered the primary factor limiting forest production late in the growing season when precipitation and temperature interact to reduce available soil moisture (Yarie and Van Cleve 2010).

2. Changes in succession.-Changes in fire regime create opportunities for rapid plant community reorganization (Chapin et al. 2006a). Historically, black spruce forests burned during stand-replacing fires every 70-130 years; low severity wildfires in combination with plant traits of black spruce and associated understory species led to a resilient forest type in the Interior-boreal forest (Johnstone et al. 2010a). However, changes in the fire regime with climate warming that are mediated by biogeochemical and life-history feedbacks have the potential to drive shifts in successional trajectories and break the legacy lock of black spruce regeneration (Johnstone et al. 2010b). Three of the largest wildfire years in Alaska occurred in the last decade (Kasischke et al. 2010). Warm dry summers allow fires to continue burning late into the summer, when soils are deeply thawed and have lower soil moisture, and therefore burn more deeply (Kasischke and Johnstone 2005), creating a radically different soil environment for seedling establishment (Epting and Verbyla 2005, Johnstone and Kasischke 2005, Harden et al. 2006). Post-fire succession has shifted towards deciduous-dominated forests with the recent

increase in mineral soil seedbeds following highseverity wildfires (Johnstone and Kasischke 2005, Kasischke and Johnstone 2005, Johnstone and Chapin 2006) and reduction in fire return interval (Johnstone et al. 2010*a*, *b*, Bernhardt et al. 2011).

Interactions between wildfire, permafrost, and soil organic layers also affect post-fire successional trajectories (Johnstone et al. 2010a). An increase in the frequency and severity of wildfire will likely decrease Sphagnum moss species, while favoring feather moss species (Turetsky et al. 2010). The low bulk density and susceptibility of feather mosses to drying could increase wildfire and permafrost degradation (Johnstone et al. 2010a). In addition, depth of post-fire organic layers acts as a threshold for deciduous germination potential (Johnstone et al. 2010a). As wildfire severity increases, we expect the depth of the soil organic layer and permafrost to decrease, creating a landscape susceptible to large changes in successional trajectories.

3. Changes in biota.-Climate change effects on vegetation growth and composition will have variable effects on wildlife species in the Interior. Predicted increases in wildfires (Kasischke et al. 2006) will increase the recruitment of deciduous trees from seed on severely burned sites (Johnstone et al. 2010b), producing benefits to mammalian herbivores and secondary benefits to numerous bird species. However, most moose (Alces alces) populations in the Interior are controlled by predation (Boertje et al. 2010) and are thus unlikely to increase on account of more abundant forage alone. For moose, a transition from a largely coniferous landscape to one dominated by deciduous trees is not a long-term benefit unless disturbance is frequent and widespread enough to maintain a large component of young forest. Rather, the relative strengths exerted by changing summer versus winter conditions are likely to greatly influence the population-level responses of numerous wildlife species that stay active year-round. Moreover, several wildlife species (e.g., red squirrels, spruce grouse, cavity-nesting species, caribou) show distinct preferences for forest types that are predicted to decrease greatly (Pastor et al. 1996, Rupp et al. 2006).

Adaptations of wildlife species in the Interior are closely governed by the strong seasonality of the environment, both in terms of climate and resource availability. The observed temporal shifts in snow accumulation and melt are likely to have immediate effects on species whose change of pelt color is tied to photoperiod (e.g., ptarmigan, the smaller mustelids, snowshoe hares). Shallow or dense snow or mid-winter icing could reduce the survival of small mammals and gallinaceous birds that burrow into low-density snow for thermoregulation during extreme cold. Although some species are buffered by changes in winter conditions per se (e.g., hibernating sciurids, bears, beavers), most species are likely to benefit, at least temporarily, from a longer growing season and greater primary productivity.

In the Interior-boreal forest, there is a strong coupling of spring temperatures with ice breakup and budburst of deciduous trees. The date of first frost in autumn is later and spring start is earlier, increasing the growing season length by >30 days over the past century (Wendler and Shulski 2009). Temperature-dependent phenological events are likely to occur earlier with warmer springs. Earlier ice-out and warmer summer water temperatures can lead to higher zooplankton densities and increased growth of juvenile salmon in lakes (Schindler et al. 2005). Spring warming may enhance carbon uptake by Interior-boreal forests, but this may vary by forest type, as net carbon uptake increased by 40% at a deciduous stand and only 9% at a black spruce stand during a warm growing season (Welp et al. 2007).

Because of the association between warming temperatures and increasing drought, most tree species in the Interior exhibit negative growth responses to warming (Juday et al. 2005, McGuire et al. 2010, Beck et al. 2011), a pattern that is consistent with declines in greenness detected by remote sensing since 1990 (Goetz et al. 2005, Lloyd and Bunn 2007, Verbyla 2008). Dendrochronological, population-level, and experimental rainfall exclusion studies show that individual white spruce trees exhibit a spectrum of growth responses to warming and rainfall, ranging from positive to negative; however, negative growth responses to increased temperatures predominate (McGuire et al. 2010). Even in cool environments such as at treeline, white spruce are susceptible to drought-stress (Sullivan and Sveinbjörnsson 2011), and a large proportion of trees exhibited decreased growth in response to climate warming over the last 50 years (Wilmking et al. 2004).

The recent increase of alder dieback and mortality in Interior Alaska (Table 2) has been linked to both the direct and indirect effects of climate change. During the 1990s, thinleaf alder (Alnus incana subsp. tenuifolia) expanded in both old- and young-successional stands along the Tanana River (Hollingsworth et al. 2010, Nossov et al. 2011). However, in the last decade a large increase in alder dieback and mortality has been attributed to the canker-causing fungus Valsa *melanodiscus* (anamorph *Cytospora umbrina*) (Lamb and Winton 2010). Although little is known about the cyclic dynamics of canker infection, the increased presence of alder canker in the last decade is likely related to alder's susceptibility to canker in drought years (Ruess et al. 2009). In combination with the sensitivity of alder to temperature, precipitation, and riverlevel (Nossov et al. 2010), alder growth and abundance may decline rapidly in the future. The reductions in alder growth and nitrogen fixation associated with alder canker are ecologically important, as a result of alder's role in nitrogen accumulation during floodplain succession (Van Cleve et al. 1971, Ruess et al. 2006, 2009). Green alder (Alnus crispa) in uplands also interacts with drought-mediated diseases (Mulder et al. 2008), which has important implications for post-fire nitrogen dynamics (Anderson et al. 2004, Mitchell and Ruess 2009).

Table 2 summarizes the damage and ecological implications of climate changes on insects and diseases significantly impacting Interior-boreal forests. Several invasive plant species invade recently burned areas in the Interior-boreal forest (Table 3; Villano and Mulder 2008, Cortés-Burns et al. 2008); therefore, invasive plants may increase in areal extent with the projected increase in the frequency and severity of wildfire in the Interior by facilitating the spread of nonnative plants into areas not adjacent to roads (Villano and Mulder 2008).

Southcentral-boreal forest.—

1. Changes in environment.—Despite differences in climate between Southcentral- and Interiorboreal forests, increasing temperatures are giving rise to similar trends. For example, Southcentralboreal forest lakes and wetlands are exhibiting a drying trend, consistent with more extensive observations in the Interior-boreal forest (see Interior-boreal forest: 1. Changes in environment) and the Kenai lowlands (see Kenai-boreal forest: 1. Changes in environment) (Riordan et al. 2006). However, the Southcentral region experiences warmer winters with greater snowfall and cooler summers with greater rainfall than the Interior and as a consequence growth of dominant tree species, such as white spruce, tends to be greater (Sveinbjörnsson et al. 2010). Although there is some evidence of water limitation on southfacing aspects near treeline (Dial et al. 2007), drought stress is generally less common in the Southcentral. The direct effects of rising temperatures could potentially lead to greater tree growth, provided that water availability remains sufficient; however, the indirect effects on water and nutrient availability will likely determine the future productivity of trees in the Southcentral. Soil carbon sequestration and release are also likely to be driven by the indirect effects of rising temperatures such as snowpack depth. Recent work demonstrates that belowground respiration in Southcentral-boreal forests increases strongly with soil temperature and is largely unrestricted by soil water availability over its current range of variability (Sullivan et al. 2010). During the winter months, ecosystems that maintain relatively deep snowpacks lose proportionately more carbon than those with shallow snowpacks (Sullivan et al. 2010). If the winter snowpack is retained and summer water availability remains sufficient, warming temperatures will lead to increased soil respiration.

2. Changes in succession.-Insects are significantly impacting forests in the Southcentralboreal (Table 2), changing succession through direct impacts on vegetation and associated shifts in the frequency and severity of wildfires (Berg et al. 2006). In recent decades, warmer temperatures contributed to the spruce beetle outbreaks in the Southcentral- and Kenai-boreal forests (Werner 1996) in part due to a reduction of the beetle life cycle from 2 years to 1 year (Berg et al. 2006, Werner et al. 2006). This has led to white spruce and Lutz spruce mortality throughout 1.2 million ha between 1990-2000 (Werner 1996, Werner et al. 2006). In some watersheds of the Copper River Basin, spruce bark beetles have killed nearly every living mature white spruce Table 2. Insects (native and non-native) and diseases in Alaska's forest regions, and associated damage and ecological implications of changes in climate.

Common name	Latin name	Hosts	Region	Damage and ecological implications	Source
Native insects Spruce budworm	Choristoneura fumiferana	White, Sitka and Lutz spruce	IB, SB	Reduces tree growth and density; life cycle events affected by temperature; outbreaks in the late-1990s and mid-1980s attributed to warming that increased the rate of larval development; projected increases in temperature will likely increase the occurrence and extent of outbreaks	1, 2, 3, 4, 5
Spruce beetle	Dendroctonus rufipennis	White, Sitka and Lutz spruce	SB, KB	See Results: Types of change in Alaskan forests: Southcentral- boreal forest and Kenai-boreal forest: 2. Changes in succession	
Aspen leaf miner Non-native insects	Phyllocnistis populiella	Aspen	IB	Prolonged outbreak since 2003; conspicuous mines reduce photosynthetic area and reduce tree growth (especially during drought); should drought become the prevailing condition this insect could cause large-scale landscape change through its effects on tree growth and mortality	5, 6, 7
Green alder sawfly	Monsoma pulveratum	Thinleaf alder	IB, SB, KB	Native of Europe and North Africa; significantly defoliates alder; coupled with extensive dieback and mortality from alder canker [see <i>Types of</i> <i>Change in Alaskan Forests:</i> <i>Interior-boreal forest—Changes in</i> <i>biota</i> ], riparian areas that are dependent on nitrogen fixed by alder may be threatened	8
Woolly alder sawfly	Eriocampa ovata	Thinleaf alder	SB, KB	by alder may be threatened Native of Europe; damage and implications are the same as for green alder sawfly	9
Diseases Hemlock dwarf mistletoe	Arceuthobium tsugense	Western hemlock	СТ	Parasitic higher plant causing growth loss and tree mortality; climate currently limits the reproduction and dispersal of the parasite; longer growing seasons and reduced snow will favor both the host and parasite; competitive advantages offered by climate changes will likely be mitigated by the disease	10, 11
Alder canker	Valsa melanodiscus	Thinleaf alder	IB	See Results: Types of Change in Alaskan Forests: Interior-boreal forest: 3. Changes in biota	
Noninfectious diseases Yellow-cedar decline		Yellow-cedar	СТ	See Results: Types of Change in Alaskan Forests: Coastal- temperate forest: 2. Changes in biota	

*Notes*: Abbreviations are: IB, Interior-boreal forest; SB, Southcentral-boreal forest; KB, Kenai-boreal forest; and CT, Coastal-temperate forest. Sources are: 1, Swaine (1928); 2, Werner (1994); 3, Han et al. (2000); 4, Gray (2008); 5, http://agdc.usgs.gov/data/projects/fhm/; 6, Krishnan et al. (2006); 7, Wagner et al. (2008); 8, Kruse et al. (2010); 9, Lamb and Wurtz (2009); 10, Hennon et al. (2011); 11, Muir and Hennon (2007).

Invasive plant	Latin name	Region	Ecological implication	Source
Garlic mustard	Alliaria petiolata	СТ	Invades urban forest understory; could eliminate native species through competition and/or allelopathy	1, 2, 3
Siberian peashrub	Caragana arborescens	IB, SB	Spreads aggressively on burned soil adjacent to roads; has spread into undisturbed forests away from ornamental plantings	4, 5, 6
Narrowleaf hawksbeard	Crepis tectorum	IB	Spreads aggressively on burned soil adjacent to roads; invades lightly to moderately burned forest soils	6
Knotweed complex	Fallopia spp.	СТ	Found along roadsides, stream banks, and beach meadows; reduces nutrient quality of litter input to aquatic habitats; could depress cover and density of native species and change forest structure and function of riparian forests and aquatic habitats	3, 7
Orange hawkweed	Hieracium aurantiacum	SB, CT	Spreads vegetatively and by seed; forms monospecific stands and displaces native vegetation; currently spreading into meadows and open areas where it has escaped cultivation	4, 8
Narrowleaf hawkweed	Hieracium umbulatum	IB	Spreads aggressively on burned soil	6
Purple loosestrife	Lythrum salicaria	SB	adjacent to roads Widely planted as an ornamental; forms monospecific stands; could displace native vegetation in wetlands	9
White sweetclover	Melilotus alba	IB, SB, CT	Spreads aggressively; invades heavily burned areas; decreases survival and pollination of native plants; alters primary succession on glacial floodplains by modifying nitrogen status	6, 10, 11, 12
Reed canarygrass	Phalaris arundinacea	KB, CT	Planted along forestry roads; invades wetlands and stream banks; out- competes native vegetation; limits riparian tree regeneration; spread could alter riparian forest regeneration and salmon habitat	3, 9, 13, 14
European bird cherry	Prunus padus	SB	Escaped ornamental plantings; replacing native trees in riparian forests; foliage supports lower biomass and taxa richness than native species	9, 15, 16
European mountain ash	Sorbus aucuparia	СТ	Escaped from ornamental plantings; now a dominant species of coastal rainforest plant communities	17, 18
Bird vetch	Viccia cracca	IB, SB	Spreads aggressively on burned soil adjacent to roads; invades aspen and south-facing bluff communities; could change forest structure through competition and/or altered soil nitrogen	6, 19

Table 3. Invasive plant species in Alaska's forest regions and ecological implications expected to increase with projected changes in climate.

Notes: Abbreviations are: IB, Interior-boreal forest; SB, Southcentral-boreal forest; KB, Kenai-boreal forest; and CT, Coastaltemperate forest. Sources are: 1, Meekins and McCarthy (1999); 2, Prati and Bossdorf (2004); 3, Lamb and Shepard (2007); 4, Lapina and Carlson (2004); 5, Viereck and Little (2007); 6, Cortés-Burns et al. (2008); 7, Urgenson et al. (2009); 8, IWAC (2006); 9, Carlson et al. (2008); 10, Conn et al. (2008); 11, Spellman (2008); 12, Villano and Mulder (2008); 13, Lavergne and Molfsky (2004); 14, Spellman (2009); 15, Cortés-Burns and Flagstad (2010); 16, Roon et al. (2010); 17, Dickinson and Campbell (1991); 18, Rapp (2006); 19, Conn et al. (2007). tree (P. F. Sullivan, personal communication). Although the outbreak is within the historic geographic range, the outbreak during the 1990s exhibits greater spatio-temporal synchrony (i.e., more sites record high-severity infestations) than at any other time in the last  $\sim$ 250 years (Sherriff et al. 2011). The mortality of mature white spruce in beetle-killed areas of the Southcentral-boreal has impacted succession by reducing the structural complexity of stands to earlier successional stages dominated by a more homogeneous overstory composition (Allen et al. 2006).

In contrast to the spruce beetle outbreak in the Kenai-boreal where the size and density of spruce regeneration were reduced by competition from bluejoint grass (Calamagrostis canadensis) and fireweed (Chamerion angustifolium) (see Kenai-boreal forest: 2. Changes in succession), spruce regeneration in the Southcentral-boreal appears to be reduced by the low soil temperatures associated with the abundance of moss cover in the forest understory in this region (Allen et al. 2006). Spruce regeneration could be increased in this region by applying high-intensity prescribed burning (Goodman and Hungate 2006), which reduces the moss layer thickness, resulting in soil temperatures that are favorable for spruce regeneration (Allen et al. 2006).

3. Changes in biota.—Changes in vegetation composition and productivity created by climate changes could affect wildlife reproduction. For example, moose have exhibited greater reproductive success in Denali National Park and Preserve than in the Nelchina Basin, due to nutritional differences in forage (McArt et al. 2009). Forage quality (e.g., content of crude protein, indigestible fiber) is likely to be sensitive to climate changes, and changes in these factors can affect growth and fecundity of Alaskan ungulates (Lenart et al. 2002, McArt et al. 2009).

Changing seasonality will be especially difficult for wildlife species that initiate life-history events based on non-climatic cues (e.g., photoperiod), as such changes ultimately create 'climate-phenology mismatches' (Stenseth and Mysterud 2002). For example, caribou herds that utilize forests in the Southcentral-boreal are in decline. Around the world, caribou and reindeer (both *Rangifer tarandus*) herds are declining synchronously, coincident with increasing temperatures and precipitation. In turn, these climatic trends, in combination with increased anthropogenic landscape change, create changes in phenology, spatio-temporal changes in species overlap, and higher frequencies of extremeweather events (Vors and Boyce 2009). Another concern for wildlife species in this and other forest regions is the increased frequency of freeze-thaw events during winter, which make low-lying vegetation effectively inaccessible to ungulates and other herbivores (Morrison and Hik 2007).

The majority of goods are shipped to Alaska via ports in the Southcentral region, thus invasive plant species (Table 3) are an important biophysical factor in these forests. As the frequency and severity of wildfire on the landscape is projected to increase in this region with a warming climate, this can increase the numerous invasive plant species known to establish on recently burned sites (Table 3).

### Kenai-boreal forest. -

1. Changes in environment.—The Kenai-boreal region is generally considered to be permafrost-free in the lowlands, but isolated permafrost does exist (Hopkins et al. 1955). This permafrost is typically overlain by an active layer >2 m (Berg 2009) and underlies small islands of black spruce forest within a larger peatland complex. These permafrost pockets occupy a very small fraction of the landscape and might be expected to follow similar trajectories as described for the Interior-boreal forest through changes in the environment and potential interactions with wildfire (see *Interior-boreal forest: 1. Changes in environment*).

In the Kenai lowlands, evidence from historic aerial photography and dendrochronology demonstrate that a significant number of water bodies experienced shrinkage and subsequent invasion of woody vegetation (largely Betula nana and *P. mariana*) since the 1950s (Klein et al. 2005). Additional evidence suggests the process of woody vegetation invasion has recently accelerated, with a 56% decline in water balance since 1968, and a subsequent increase in woody invasion of lowland wetlands in the Kenai-boreal forest region (Berg et al. 2009). Recent work along a hydrologic gradient in the Kenai lowlands demonstrated that the combined effects of wetland drying and vegetation succession have turned wetlands from strong carbon sinks to weak carbon sources, particularly in years with warm and dry summers (Ives et al., *unpublished manuscript*).

2. Changes in succession.-Insect outbreaks in the Kenai-boreal region are impacting forest succession (Table 2). Warm temperatures were an important element of the spruce beetle outbreaks (1971-1996) in the Kenai-boreal forest (Berg et al. 2006) (see Southcentral-boreal forest: 2. *Changes in succession*). This massive outbreak removed all suitable host trees from the landscape allowing little chance of a repeat for many decades. However, with projected warming, endemic levels of spruce beetles will likely be high enough to perennially thin the forests as trees reach susceptible size (Berg et al. 2006). The outbreaks in the Kenai have impacted postdisturbance succession by reducing both plant diversity and the size and density of spruce, as a result of competition from bluejoint grass and fireweed (Holsten et al. 1995, Werner et al. 2006).

Changes in vegetation composition associated with the spruce bark beetle outbreak in the Kenai-boreal vary with the geographic location (Boucher and Mead 2006). Forests in the southern Kenai Lowland demonstrated the greatest change in composition, with high white spruce mortality (87% reduction in basal area) and an increase in the percent cover of early successional species. In contrast, forests in the northern Kenai Lowland exhibited low levels of spruce mortality (28% reduction in basal area), as white spruce in this area was a secondary canopy species to paper birch, black spruce, and aspen (Boucher and Mead 2006).

Until recently, wildfire in the Kenai-boreal was primarily restricted to poorly drained lowland areas of black spruce, where the average fire return interval was approximately 90 years (De Volder 1999). Black spruce stands are the dominant vegetation type in the northwest icefree areas of the region and are currently expanding in the area due to encroachment into wetlands (Berg et al. 2009). Wildfire is anticipated to increase in this region with the increase in black spruce area, combined with the increased fuel load resulting from beetle kill in white, Lutz and Sitka spruce and projected increases in summer temperature (Berg and Anderson 2006, Berg et al. 2009). As a consequence, earlier successional stages are anticipated to become more prevalent in this region (Berg et al. 2006).

3. Changes in biota.-Fish and wildlife species within the Kenai-boreal forest will be affected by climate-related changes in the composition and structure of forests. Modeling associated with the ALCES (Alaska Landscape Cumulative Effects www.kenaiwatershed.org/alces.html) Model; project in the Kenai National Wildlife Refuge suggests that the distribution of salmonids, which constitute an important resource for people throughout Alaska's coastal areas (see Coastal-temperate forest: 3. Changes in biota and Discussion: Regional societal consequences: Coastaltemperate forest), will likely be sensitive to rising stream temperatures in the Kenai-boreal forest. Additionally, many indirect effects of climate changes on wildlife species in the Kenai-boreal appear to be a function of recent insect outbreaks.

Invasive species will likely increase in importance in the Kenai-boreal with projected climate changes. Alder may become more susceptible to damage caused by the green and woolly alder sawflies (Table 2), as a result of the recent dieback and mortality associated with alder canker (see *Interior-boreal forest: 3. Changes in biota*). Invasive plant species (Table 3) may also increase with the confluence of increasing human population, wildfire potential following the spruce bark beetle outbreaks and the increased likelihood of invasive plants establishing in recently burned areas.

Coastal-temperate forest. -

1. Changes in environment.-The Coastal-temperate forest exhibits two distinct watershed types: glacial-fed watersheds and non-glacial watersheds supplied by annual precipitation (predominantly snowpack), with both varying in seasonality of discharge, chemistry, and temperature (Hood et al. 2009). Glacial-fed watersheds have permanent ice fields and discharge patterns closely tied to surface air temperature and cloud cover (IPCC 2007). At present, approximately 47% of the water discharged into the Gulf of Alaska comes from glaciers and ice fields (Neal et al. 2010). The loss of glacial inputs and changes in the timing of surface runoff associated with changes in the snowpack and snow/rain ratios are expected to impact stream habitats and the annual pattern of carbon and nutrient inputs to the freshwater and marine systems (Hood and Berner 2009, Hood et al. 2009). In contrast, non-glacial watersheds have discharge patterns that are affected by both

surface air temperature, and melting snow and rainfall patterns (Edwards et al., *in press*). These watersheds have peak discharge in the spring during snow melt and during the fall rainy season. Potential climate-associated changes will shift non-glacial watersheds to rainfall-dominated discharge, and glacial-fed watersheds to snowfall-driven discharge. These hydrological changes have important consequences for fish and wildlife habitat quality, distribution, and access by altering the temporal balance of freshwater discharge.

The high soil moisture conditions of Coastaltemperate forests lead to the limitation of forest productivity on sites and the accumulation of soil organic material (Neiland 1971). Although warmer temperatures promote greater decomposition and associated forest growth (Davidson et al. 2006), the impact of temperature increases also depends on the soil moisture, and quality of the organic material (Giardina and Ryan 2000, Martin and Bolstad 2005, Davidson and Janssens 2006). Increasing temperatures must be associated with adequate soil moisture for tree roots to access available nutrients (Litton et al. 2007). However, the quality of the organic matter mitigates the effects of temperature increases, as recalcitrant compounds may not easily break down, leading to a negative feedback to forest growth (Heimann and Reichstein 2008).

2. Changes in succession.-The areal extent of sites undergoing primary succession in the Coastal-temperate forest region has changed with the accelerated rate of glacier recession observed since the mid 19th century following advance during the Little Ice Age. Although glacial advances were observed over the latter part of the 20th century (Pelto and Miller 1990, Hall et al. 1995, Miller et al. 2003), the termini of most major glaciers extending from Glacier Bay and the Juneau ice field have receded several kilometers since 1750 (Motyka et al. 2002, Larsen et al. 2005). The vegetation composition following the exposure of glacial till and outwash is related to the conditions present at the onset of colonization (Fastie 1995), which ultimately impacts forest succession.

Climate change may indirectly alter the structure and composition of Coastal-temperate forests via its effects on the interaction between wind disturbances and stem decay fungi. Windstorms are a major disturbance force that shapes the age, structure, and function of forests in this region (Nowacki and Kramer 1998). Widespread, stand-replacing events occur at 100-year intervals, with exposure to the prevailing southeast storms increasing the likelihood of catastrophic wind disturbance. Although the frequency and intensity of windstorms are difficult to predict, wind-protected landscapes support old-growth stands with multi-aged structures where stem decays and other disease agents produce finescale disturbances involving the death of individual or small groups of trees (Hennon 1995, Hennon and McClellan 2003). Currently, stemdecay fungi consume an estimated 31% of the volume of live trees (Farr et al. 1976). Projected increases in temperature and growing-season length will increase growth rates of these fungi, which combined with the susceptibility of decayed trees to wind-breakage, could increase the proportion of early-successional tree species.

3. Changes in biota.-Climate-change effects on wildlife in Coastal-temperate forests will be driven primarily by changes in snowpack and growing season length. Snow depth and duration exert major effects on habitat for animals, burying forage for herbivores such as blacktailed deer (Odocoileus hemionus), moose, and mountain goat (Oreamnos americanus), and providing protective cover for subnivean mammals such as the Northwestern deermouse (Peromyscus keeni), long-tailed vole (Microtus longicaudus), and common shrew (Sorex cinereus), and insulation to denning black and brown bears (Ursus americanus and U. arctos). Longer growing seasons could benefit wildlife species such as blacktailed deer by increasing the total area of snowfree winter range, increasing winter energy availability, decreasing winter energy expenditures, and increasing the availability of high quality foods in spring at a critical time of the annual nutritional cycle (Parker et al. 1999), thereby decreasing winter mortality. Increasing populations of deer, on the other hand, are likely to exert significant browsing pressure on the vegetation of their habitat, changing vegetation composition and structure (Hanley 1987). Deer, vegetation, and wolves (*Canis lupus*) are likely to interact in complex patterns in relation to a changing climate, principally mediated through snow regime; populations may grow during successive mild winters but crash more severely during periodic cold winters.

The sharp elevational gradients characteristic of the Coastal-temperate forest influence the effect of climate changes on fish and wildlife species. Warmer, wetter winters may mean less snow at low-elevations, but may translate into more snow at higher elevations. High-elevation snowpack will affect some animals directly, such as mountain goats (Oreannos americanus). However, it will affect a wide range of low-elevation animals indirectly through effects on stream-flow and the production and availability of salmon (Oncorhynchus gorbuscha, O. keta, O. kisutch, O. nerka, and O. tshawytscha), which are a major summer food resource for a diverse group of mammals, birds, and insects (Gende et al. 2002). Salmon play a critical role in body size, population density, and productivity of brown bear (Ursus americanus; Hilderbrand et al. 1999), nesting success and productivity of bald eagle (Haliaeetus leucocephalus; Hansen 1987), timing and success of reproduction in mink (Ben-David 1997, Ben-David et al. 1997a), and body condition and survival of American marten (Martes americana; Ben-David et al. 1997b). Due to the complex life cycles of salmon, the difficulty of establishing quantitative relationships between the supporting services of river systems and salmon returns has been noted (Chittenden et al. 2009). In the Coastal-temperate forest, as in other regions, the responses of anadromous salmonids to climate change differs among fish species and depends on their life cycle in fresh water and at sea (Bryant 2009).

Earlier snowmelt and later freeze-up (Juday et al. 2005) resulting from climate change have important implications for yellow-cedar decline. The culturally and economically important yellow-cedar has been dying on over 200, 000 ha of pristine forests for the past 100 years in this region (Hennon et al. 2006). The onset of decline in 1880 corresponds with the end of the Little Ice Age (Hennon et al. 1990). The cause is complex and includes a number of cascading landscape, site, and stand factors (Hennon et al. 2008) that interact with the physiological susceptibility of yellow-cedar's fine roots to spring freezing injury (Schaberg et al. 2008). Although yellow-cedar trees are tolerant of cold temperatures in fall and early winter (Schaberg et al. 2005), its roots are

dehardened in late winter and early spring, at which time soil temperatures below  $-5^{\circ}$ C are lethal (Schaberg et al. 2008). When snow is present, this temperature threshold is not crossed (Hennon et al. 2010), due to the insulative effect of snow. Warmer winters and reduced snow-pack, but persistent early spring freezing events throughout the 1900s were necessary conditions for yellow-cedar decline (Beier et al. 2008). Thus, a trend of continued yellow-cedar decline is expected with projected warming temperatures.

Diseases and invasive plant species are projected to become important *biophysical factors* in Coastal-temperate forests. Table 2 summarizes the damage and ecological implications resulting from hemlock dwarf mistletoe and yellow-cedar decline in this forest region. Additionally, several invasive plant species (Table 3) in this region could reduce the growth and density of native species via competition and alter forest structure and function, and salmon habitat.

# Projections of changes in key climate and climate-related abiotic characteristics

Climate changes are projected to continue throughout Alaskan forests. We present projections of key climate and climate related abiotic characteristics of the environment which control ecosystem processes (Table 4). Although aquatic systems may appear peripherally related to the impact of climate changes on forest ecosystems, we include sea level and length of ice-free season for rivers and lakes in our climate projections (Table 4), as three of our four forest regions have an intimate relationship with the ocean and streams (Fig. 1B).

In Alaska, increases in surface air temperature, growing season length as a result of later autumn freeze-up and shorter snow season, length of icefree rivers and lakes, and river and stream temperatures are expected in Alaska's forest regions (Table 4). In the Interior-boreal, the area of permafrost degradation is projected to increase, and in the Coastal-temperate forest region, glacial coverage is expected to continue to decrease.

# Summary of regional conceptual framework diagrams

Although surface air temperature is the predominant climate driver in Alaskan forests (Fig.

Climate/ecosystem variable	General change expected	Specific change expected and reference period	Patterns of change	Source
Temperature	Increase	<b>2050:</b> $+2.5^{\circ}C \pm 1.5^{\circ}C$ (IB); +2.0°C $\pm 1.5^{\circ}C$ (SB, KB); +1.5°C $\pm 1^{\circ}C$ (CT); <b>2100:</b> +4.0°C $\pm 2.0^{\circ}C$ (IB, SB, KB); +3.5°C $\pm 1.5^{\circ}C$ (CT)	More pronounced in autumn- winter	1, 2
Snow	Increased rate of snowfall in winter, but shorter snow season (nearly zero snow in some areas of CT)	2050: 10–25% (IB); Winter snowfall (IB, SB, KB, CT); 2100: 20–50% (IB); Winter snowfall (IB, SB, KB, CT)	Cold season snow will increase, but increased percent of precipitation in spring/fall will be rain. Mean April temperature above freezing in Fairbanks by 2050; mean October temperature above freezing by 2100 (IB); increased precipitation will fall as rain. Mean monthly temperatures above freezing for March and November in Anchorage by 2100 (SB); increased precipitation will fall as rain. Mean monthly temperatures above freezing for all months in Homer by 2100 (KB); snow still expected in mountains, but snowline will occur at higher elevations. Mean monthly temperatures above freezing in Juneau for all months by 2100 (CT)	2, 3
Length of ice-free season for rivers and lakes	Increase	<b>2050:</b> ~10 d (IB); 7–10 d (SB); 10–15 d (KB); <b>2100:</b> ~20 d (IB); 14–21 d (SB); variable, with some areas freezing only sporadically (KB, CT)	Continuation of recent changes (IB); large increase near coasts where sea ice retreats, open water season lengthens (SB, KB); mostly ice-free at lower and mid elevations by 2100 (CT)	1, 2
River and stream temperatures	Increase	<b>2050:</b> 1–3°C (IB, SB, KB, CT); <b>2100:</b> 2–4°C (IB, SB, KB, CT)	Consistent with earlier breakup and higher temperatures (IB, SB, KB, CT)	4
Growing season length	Increase	<b>2050</b> : 10–20 d (IB, SB, CT); ~10 d (KB); <b>2100</b> : 20–40 d (IB, SB, CT); ~20 d (KB)	(IB); largest increase near coasts (SB, KB, CT)	1, 2
Sea level	Increase (SB, KB); Uncertain due to isostatic rebound (CT)	<b>2050:</b> 8–61 cm (SB, KB); <b>2100:</b> 18–183 cm (SB, KB)	Large uncertainties, especially at the upper end of the range (SB, KB); glacier melt may offset sea level rise during this period (CT)	1
Permafrost	Increased area of permafrost degradation (IB)	<b>2100:</b> Mean annual ground temperature >0°C at 2 m (except isolated areas at high elevation)	Permafrost degradation throughout the region (IB); greatest changes in mean annual ground temperatures at 2 m depth by 2050 and 2100; increase in active layer thickness by 2050 and 2100	2, 5
Glaciers and ice caps	Continued shrinkage of glaciers and ice caps (CT)	<b>2100:</b> 0.026 ± 0.007 m sea- level equivalent	Continuation of volume losses (CT)	6

Table 4. Projected changes in key climate and climate-related abiotic characteristics of the environment which control ecosystem processes in Alaska's forest regions for 2050 and 2100.

*Notes*: Abbreviations are: IB, Interior-boreal forest; SB, Southcentral-boreal forest; KB, Kenai-boreal forest; and CT, Coastal-temperate forest. Projected changes are for the mid-range greenhouse emission scenario (A1B). Sources are: 1, Field and Mortsch (2007); 2, SNAP (see *Methods: Climate and abiotic projections for Alaska forest regions*); 3, AMAP (*in press*); 4, Kyle and Brabets (2001); 5, Marchenko et al. (2008); 6, Radić and Hock (2011).

3), the response of the biophysical factors impacted by warming differs for each forest region. The regional diagrams provide a framework for assessing current and future consequences of a changing climate, and emphasize regional differences in biophysical factors and point to linkages that may exist but have not been studied in a particular region.

The Interior-boreal has the richest research history of the four forest regions and as a result, has a more detailed summary of climate-change effects (Fig. 3A). Forecasted changes in future climate may affect the stability of boreal forest ecosystems directly, by warming permafrost in undisturbed ecosystems, and indirectly, through an increase in fire size and severity (Kasischke and Turetsky 2006). While permafrost thaw may occur directly as a result of changes in regional and global climate, it is particularly prominent following disturbance to the organic soil layer by wildfire.

The Southcentral-boreal is the least studied of the forest regions, and as a consequence, is the region where we have the greatest gaps in our understanding of the interactions governing the types of change. Continued warming could result in more extensive and more frequent spruce beetle outbreaks than have been observed in the Copper River area where larger white spruce are present (Snyder et al. 2007). With the primary entry of goods shipped to Alaska occurring via ports in this region, the increase in the potential for wildfire on the landscape following the spruce beetle outbreaks and the occurrence of invasive plant species in burned areas (Table 3), we regard invasive species as an increasingly important biophysical factor (Fig. 3B).

Although the Kenai-boreal contains only a small fraction of Alaska's forests, this region may be particularly sensitive to climate changes, as all of the biophysical factors play significant roles on the landscape (Fig. 3C). The interaction of insect disturbance with wildfire potential is particularly important in this region given the confluence of human population growth and changing biophysical factors.

The Coastal-temperate forest region is topographically complex. Snow and ice is regarded as the dominant biophysical factor (Fig. 3D), as elevation and slope influences the form of precipitation received and the accumulation and distribution of soil moisture. Temperature increases have impacted forests in this region via changes in hydrology resulting from melting glaciers and lower levels of snow precipitation.

## Discussion

### Global implications and feedbacks

Climate-related changes in Alaskan forests have the potential to influence the global climate system through numerous feedbacks. Currently, Alaskan forests provide climate regulation as an ecosystem service, but we do not yet understand whether the net effect of the climate feedbacks would enhance or mitigate warming (Euskirchen et al. 2010). The largest and most rapid climate feedbacks are positive feedbacks to warming associated with earlier snowmelt in Alaska (Euskirchen et al. 2009b, 2010). The subsequent slower changes caused by changes in trace gas fluxes, permafrost, fire regimes, and vegetation constitute a complex mixture of positive and negative feedbacks, whose net effects are uncertain.

Climate feedbacks associated with carbon dioxide (CO<sub>2</sub>) and methane (CH<sub>4</sub>) releases from microbial decomposition related to permafrost thaw are likely substantial and could potentially impact the global climate system (Zhuang et al. 2007). Future changes in ecosystem carbon storage in lowlands are likely to be a balance of increased soil carbon storage at the surface that may, in part, offset deep carbon losses from newly thawed permafrost. In addition, extremely warm, dry years with more extensive or severe wildfires are also years when more permafrost thaws than normal. This combination of thawing and wildfires may expose and rapidly transfer large amounts of carbon to the atmosphere, exacerbating this positive climate feedback. Permafrost thaw can also result in forests being replaced by peatlands, bogs, and fens (Jorgenson et al. 2001) that may accumulate more carbon, but emit more CH<sub>4</sub> compared to the forest.

In areas where forests remain, the  $CO_2$  released from permafrost thaw and resulting positive climate feedback is likely to be only slightly compensated for by the negative climate feedback associated with an increased growing season and greater  $CO_2$  uptake by these forests (Schuur et al. 2008). Likewise, some research in

Alaska demonstrates that warmer conditions and longer growing seasons favor treeline advance, either in latitude or elevation (e.g., Lloyd et al. 2002). This replacement of tundra with boreal forest may result in greater carbon uptake during the growing season, acting as a negative feedback to climate. However, forest ecosystems lose more carbon during winter than adjacent tundra (Sullivan 2010) and advance of the treeline will likely reduce albedo, causing greater heat absorption, and a stronger positive feedback to warming (Beringer et al. 2005). Nevertheless, latitudinal treeline advance in Alaska may proceed quite slowly due to limitations related to seed dispersal and establishment, and physical barriers (Rupp et al. 2001). Consequently, we cannot rely on the negative climate feedback related to potential future increases in vegetation biomass of Alaskan forests to counteract the potentially large positive feedback to climate due to releases of carbon from permafrost thaw.

Another negative climate feedback may occur due to the increase in deciduous stands across the landscape under changes in wildfire frequency, severity and area. This increase in distribution leads to an overall increase in albedo and a decrease in heating relative to coniferous stands. This negative feedback to atmospheric heating (Randerson et al. 2006) has been shown to be larger than the positive feedback from fire emitted greenhouse gases over the course of an 80-year fire cycle in boreal Alaska (Randerson et al. 2006). However, the strength of this negative feedback may be reduced if late-season burning increases, resulting in greater fire C emissions (Turetsky et al. 2011). It may also be reduced if lightly burned stands with a greater proportion of spruce dominate the landscape (Barrett et al. 2011, Shenoy et al. 2011). Another study shows that taking into account changes in successional dynamics associated with a change in the future fire regime (2003-2100) results in a decrease in atmospheric heating due to an increase in early successional stands with a greater albedo in the boreal forests of Alaska and western Canada (Euskirchen et al. 2009b). These results underline a generally greater significance of changes in albedo on climate feedbacks in Alaska than those associated with changes in trace gases and biogeochemistry, although, as discussed above, the thawing of permafrost may, in the future

represent a strong positive feedback to warming.

Smoke and haze aerosols from boreal forest fires in Alaska may also feedback to the climate in other regions. While the impacts of aerosols on climate are not well understood, it is generally accepted that smoke cools the surface, acting as a negative feedback to climate. During the summer of 2004, large quantities of smoke from wildfires in Alaska and northwestern Canada were dispersed throughout the Northern Hemisphere. This smoke had a cooling effect in regions outside of boreal Alaska, although this effect was partially dampened by the absorption of solar radiation by black carbon fire aerosols, and by the greenhouse gas emissions from the fires (Pfister et al. 2008, Stone et al. 2008).

### Regional societal consequences

Our conceptual framework recognizes the strong interaction between the biophysical and social subsystems (Fig. 2). While we acknowledge the complexity and dynamic interactions within the social subsystem, the main focus of this paper is on the biophysical subsystem. The details of the interactions and feedbacks within the social subsystem are therefore not elaborated here. Alaskan forests will be impacted by landuse, resource management, and evolving forest policy. By 2030, the overall state population is expected to increase by 25% relative to 2006, with the greatest increase anticipated in Anchorage (Southcentral-boreal forest), and a slight decrease in the Coastal-temperate forest region. Migration from rural communities to urban centers is the most significant component of population change and is highly variable with changing economic opportunity (Huntsinger et al. 2007). These population changes will likely lead to both an increase in the wildland-urban interface (and associated increased wildfire risk in relevant regions), and an increase in demand for timber and non-timber forest products. We expect climate-related changes in Alaskan forests will continue to have consequences for people, economies and livelihoods through changing ecosystem services, changing forest structure and composition and related cascading events. Here we synthesize societal consequences of changes in the key biophysical factors for each forest region.

Interior-boreal forest. - Changes in environment,

ecosystems, and subsistence resources have important implications for rural communities throughout the state, where indigenous people have historically led a subsistence lifestyle as hunters and gatherers (Chapin et al. 2006b, Kofinas et al. 2010). The three most prominent social consequences of climate change in Interiorboreal forests are related to changes in seasonality, permafrost thaw, and wildfire. In this region, temperatures are warming most dramatically in the winter, and growing season length has increased. This poses safety hazards and challenges for winter travel on frozen rivers. Unpredictable ice conditions increase risk and decrease safety for winter travel. Increased evapotranspiration and declining river discharge also reduce opportunities for barge delivery of fuel and increase the cost of living in remote villages (Chapin et al. 2008, Fresco and Chapin 2009). The ecological and hydrological changes related to permafrost degradation will likely impact the migration and distribution of subsistence and recreational fishing and hunting species. In addition, warming air and permafrost temperatures have the potential to impact transportation, water and sewer, and other public infrastructure (Nelson et al. 2002, Larsen et al. 2008).

The frequency and severity of wildfire in the Interior are expected to increase with climate change and will likely result in increased fire suppression activity near communities. This may involve economic opportunities for both rural communities and for Fairbanks as the regional population hub with emergency fire fighting crew deployment (Trainor 2006), equipment rental, and other fire suppression activities. However, increased severity and annual extent of area burned will increase risk to life and property, decrease hunting opportunities, and likely increase both physical and mental health effects from wildfire smoke (Chapin et al. 2008). Increased wildfire in Alaska may also have cascading repercussions for wildfire suppression in other parts of the United States, as fire-fighting resources are shared nation-wide (Trainor et al. 2009). Focus on structure protection rather than fire suppression per se and adaptive land and resource management that anticipates ecological changes are two possibilities for adaptive responses in fire suppression and land management. Potential exists for rural communities to

simultaneously decrease wildfire risk and increase energy independence by utilizing hazard fuels for heating and electrical power generation (Chapin et al. 2008).

Southcentral-boreal and Kenai-boreal forests.—The majority of Alaskan residents live in the Southcentral- and Kenai-boreal forest regions. Spruce bark beetle infestation in these regions has increased wildfire risk and raised concern about its consequences for recreation and aesthetic values (Ross et al. 2001) and associated impacts on humans (Berg and Anderson 2006). Flint (2006) examined community perceptions regarding the spruce beetle impact on selected social, economic, and ecological parameters. This study found a diverse array of perceived impacts and risks across communities, which in some cases varied with the stage of the outbreak near a particular community. Concerns included immediate risk to life and property as well as broader concern about community and ecological wellbeing (Flint 2006). In addition to increased risk of wildfire, bark beetle mortality has implications for management of federal lands, and additional consequences may be experienced in the tourism and recreation sectors.

The diverse landscape of the Southcentral- and Kenai-boreal forests supports ecosystem services that extend beyond the boundaries of these regions. These include commercial endeavors related to oil and gas production and transportation (largest), and commercial fishing, timber harvesting, and tourism (fastest growing) (Kenai Peninsula Borough Council 2011). Ecosystem services also support non-commercial values such as aesthetic, biological, cultural, economic, future, historic, intrinsic, learning, life sustaining, recreational, spiritual, subsistence, therapeutic, and wilderness values (Alessa et al. 2008). Climate changes will influence human-land use choices and therefore also affect the forest presence and successional trajectory. Agriculture (via increased growing season and maximum daily temperature) is anticipated to be favored by temperature increases, especially in coastal areas (Juday et al. 2005). Land use and permafrost changes upstream are anticipated to impact the timing and quality of surface water runoff (Juday et al. 1997). Nutrient loads, sedimentation and turbidity affects the ability of the freshwater, near-shore, and off-shore aquatic ecosystems to support a diversity and abundance of larval, juvenile, and adult fish populations (Bryant et al. 2009). Salmonid populations in particular have life history strategies such as timing of emergence, run timing, and residence time in freshwater uniquely adapted to localized conditions. The response of anadromous salmonids to climate-driven changes depends upon their life cycle in freshwater and will differ among species (Bryant 2009).

Coastal-temperate forest.-Rapid glacial melt, vellow-cedar decline and vulnerabilities to salmon and other important food resources, such as deer (Brinkman et al. 2007) have been identified as the most significant social consequences of climate change in the Coastal-temperate forest region. Climate variability influences snowpack, and in turn, community energy availability to the extent that hydropower is a prominent energy source in many communities (REAP 2009; Cherry et al., unpublished manuscript). Research in other parts of the Pacific Northwest document observed sensitivity of water resources, salmon, and forests to climate variability as well as continued consequences of projected climate change requiring societal adaptation (Mote et al. 2003). Salmon populations originating from Coastal-temperate forests provide the foundation for most Alaskan economies in this region, via tourism, commercial fishing, processing stations, and hatcheries. Climate change impacts on salmon habitat, salmon associated species, water abundance and seasonality, and the resulting challenges for management, may therefore have large repercussions for commercial, sport, subsistence, and Native and local culture (C. Brown, ADF&G, subsistence division, personal communication).

The decline in yellow-cedar reported in many areas of the Coastal-temperate forest has both market and non-market provisioning ecosystem service impacts. Alaskan yellow-cedar is typically the highest valued commercial timber species exported from the region (Robertson and Brooks 2001). This tree is also highly valued by Native Alaskans for carving ceremonial and functional items. Documented subsistence uses include fuel, wood articles, clothing, baskets, bows, tea, and medicine (Schroeder and Kookesh 1990, Pojar and MacKinnon 1994).

# Uncertainties, policy options and future research

In addition to uncertainties inherent in climate projections, there are uncertainties in determining how changes in climate will affect Alaskan forests. There are numerous examples of these uncertainties. First, whether the future fire regime of the Southcentral-boreal will shift into the frequent fire regime currently observed in the Interior-boreal forest is unknown. The outcome depends on whether precipitation, and particularly summer precipitation, increases enough to offset temperature increases. Second, the ability to evaluate the role that stochastic disturbances such as spruce beetles have played in changing forests in the Southcentral- and Kenai-boreal in recent decades, and the potential of future outbreaks in the Interior-boreal is uncertain. The occurrence of such disturbances suggests predictions of future outbreaks should be made cautiously (Berg et al. 2009, Klein et al. 2005). Third, it is difficult to predict altered distributions of wildlife. The most fundamental manner in which animals may be affected by climate change is via altered species distributions, across gradients of latitude, elevation, precipitation, or temperature, often mediated by soil differences (Post et al. 2009) and wildfire (Rupp et al. 2006). However, the ability to predict altered spatial distributions varies dramatically by species (Poyry et al. 2008, Sekercioglu et al. 2008, Baselga and Araujo 2009); this variability poses challenges in developing and implementing blanket policies that mitigate the effects of climate changes on wildlife. Fourth, it is difficult to quantify how widespread various reported insect infestations were in the past. Records of insect outbreaks in Alaska have been intermittent in time and space. For example, spruce beetle records date back only to 1920 (Holsten 1990), and the spruce budworm has only been surveyed in Alaska since the early 1950s (McCambridge 1954; Furniss, unpublished report). The accessibility to field sites in Alaska and specimen collection also limits the examination of insect population dynamics. Finally, increased use of a transcontinental shipping route through the Arctic Ocean and ocean- and road-based tourism may affect invasive species (i.e., insects, diseases, plants) expansion in unpredictable ways, resulting in a large delay between detection of exotic species and implementation of effective management strategies.

Numerous opportunities exist to implement policies that will mitigate the ecological and societal impacts and consequences of climate change (Chapin et al. 2004). The following regional issues illustrate how state and federal resource managers can plan for future conditions and implement climate mitigation and adaptation policies. First, post-fire plant communities provide ideal moose habitat, but concomitantly result in a loss of winter habitat for caribou. Both moose and caribou are important food sources for many Alaskan Native peoples, and subsistence living is culturally important for many non-Native Alaskan residents. Land-use and wildlife policies could include guidelines for managing wildfire in a manner that provides moose habitat, yet preserves long-term winter habitat for caribou. Second, the increased potential for invasive species establishment, especially in the Southcentral- and Kenai-boreal forests, suggests that policies governing the import of goods shipped to Alaska need to afford flexibility to land managers to implement new prevention, detection and management strategies. Third, yellowcedar decline in the Coastal-temperate forest region is most prevalent at low elevations. The overall health and competitiveness of yellowcedar could be promoted in areas where it is not declining to ensure that this culturally and economically important tree species remains a part of Alaskan forests.

Future research is required to address the gaps in our knowledge of climate-related changes in Alaskan forests. Continued detection and monitoring of invasive species is required in all forest regions, in order to more effectively understand the role of this biophysical factor in altering the structure and function of Alaskan forests as the climate changes. Research in the Interior-boreal forest has been more extensive than in the other regions, which is evident by comparing the regional diagrams (Fig. 3A–D). In fact, we would argue, as presented, the conceptual framework for the Interior-boreal is the most complete, based on our current state of knowledge. Although the effects of wildfire and permafrost on forests are well documented, interactions of these biophysical factors on global carbon and energy budgets and the associated consequences

for society are not fully understood. Additionally, the degree to which recent changes in the fire regime have altered forest composition in the Interior-boreal is unknown (Barrett et al. 2011) and requires further study. In contrast, one defining feature of the Southcentral-boreal forest is the lack of links between the biophysical factors and types of change, which we attribute to a lack of research in this region, rather than to a lack of relationship. Hence, the greatest research need in the Southcentral-boreal is to initiate long-term monitoring of the mechanisms underlying the structure and function of representative mixed-species forest stands. Such research and monitoring would enable assessment of the current state of these forests and their trajectory of change. The Kenai-boreal forest has received greater research attention than the Southcentral, but less than the Interior. Here, all of the biophysical factors described in our conceptual framework are currently altering the structure and function of forest ecosystems. These changes will likely be amplified by the confluence of population growth and changing biophysical factors in this region. We hypothesize that, because this small region is experiencing such a variety of biophysical factors, it could potentially act as a 'canary in the coal mine' over the next two decades, representing the Alaska forest region where the greatest ecological changes will occur in a relatively short period of time. In addition, important issues such as insect outbreaks, wildfire, land-surface drying, and invasive species have often been addressed separately. We suggest that the interactions among these biophysical factors need to be more explicitly addressed, along with their implications for wildlife, salmon, and human habitation. In the Coastal-temperate forest, climate-change effects on glacier melt and elevation of the snowline are well-documented. The conceptual diagram of the Coastal-temperate forest suggests that this strong link between water, forests, and people makes it the region where continued research is required to address the cascading effects of the associated changes in hydrology on salmon and wildlife species and subsistence harvesting.

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The conceptual framework we present provides a means of summarizing our current understanding of the climate drivers and the current and potential biophysical factors, and to discuss how the feedbacks and interactions within our framework affect the rate and types of change in Alaska's forest ecosystems. Within each region, biophysical factors have the potential to alter forest composition and biogeochemical cycles. In the Interior-boreal forest, changes in the fire regime and thawing permafrost are currently the most important biophysical factors. An increase in the frequency of wildfires will result in changes in forest composition and structure, and continued and rapid thawing of permafrost will significantly alter the soil moisture, hydrology, and biogeochemical cycles of forest ecosystems in this region. We regard the increase in the frequency of insect outbreaks and associated wildfire and potential increase in invasive plant species establishment to be the most important biophysical factors in the Southcentral- and Kenai-boreal forests; changes in these biophysical factors will alter forest composition and biogeochemical cycles. Finally, in the Coastal-temperate forest region, we view changes in snow and ice associated with melting glaciers and changes in the elevation of the snow line as the dominant biophysical factor. Future changes in snow and ice will have cascading effects on the composition and soil nutrient cycling of Coastal-temperate forests.

Climate changes have impacted Alaskan forests and are projected to increase over the next 50 to 100 years. These changes have important consequences for Alaskan residents through the socio-economic impacts associated with alterations in fish and wildlife habitat and for the global climate system via effects on carbon and radiation budgets. The regional diagrams presented here provide a visual tool for resource managers and policy makers to foster understanding of the complex interactions and feedbacks occurring within Alaska's forested ecosystems. This knowledge of the underlying processes and interactions is required to develop regional and global management strategies and to inform policies related to mitigation and adaptation under changing climatic conditions.

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### LITERATURE CITED

- ACIA. 2005. Impacts of a warming climate: arctic climate impact assessment. Cambridge University Press, Cambridge, UK.
- Allen, J. L., S. Wesser, C. J. Markon, and K. C. Winterberger. 2006. Stand and landscape level effects of a major outbreak of spruce beetles on forest vegetation in the Copper River Basin, Alaska. Forest Ecology and Management 227:257–266.
- Alessa, L., A. Kliskey, and G. Brown. 2008. Socialecological hotspots mapping: a spatial approach for identifying coupled social-ecological space. Landscape and Urban Planning 85:27–39.
- AMAP. In press. SWIPA (snow, water, ice and permafrost in the Arctic) layman's report. Cambridge University Press, Cambridge, UK.
- Amiro, B. D., J. B. Todd, B. M. Wotton, K. A. Logan, M. D. Flannigan, B. J. Stocks, J. A. Mason, D. L. Martell, and K. G. Hirsch. 2001. Direct carbon emissions from Canadian forest fires, 1959-1999. Canadian Journal of Forest Research 31:512–525.
- Anderson, M. D., R. W. Ruess, D. D. Uliassi, and J. S. Mitchell. 2004. Estimating N<sub>2</sub> fixation in two species of *Alnus* in interior Alaska using acetylene reduction and <sup>15</sup>N<sub>2</sub> uptake. Ecoscience 11:102–112.
- Anderson, L., M. B. Abbott, B. P. Finney, and S. J. Burns. 2007. Late Holocene moisture balance variability in the southwest Yukon territory, Canada. Quaternary Science Reviews 26:130–141.
- Arendt, A. A., K. A. Echelmeyer, W. D. Harrison, C. S. Lingle, and V. B. Valentine. 2002. Rapid wastage of Alaska glaciers and their contribution to rising sea level. Science 297:382–386.
- Barber, V. A., G. P. Juday, and B. P. Finney. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature 405:668–673.

Barber, V. A., G. P. Juday, B. P. Finney, and M.

Wilmking. 2004. Reconstruction of summer temperatures in interior Alaska from tree-ring proxies: Evidence for changing synoptic climate regimes. Climatic Change 63:91–121.

- Barrett, K., A. D. McGuire, E. E. Hoy, and E. S. Kasischke. 2011. Potential shifts in dominant forest cover in interior Alaska driven by variations in fire severity. Ecological Applications. [doi: 10.1890/ 10-0896.1]
- Baselga, A., and M. B. Araujo. 2009. Individualistic vs community modelling of species distributions under climate change. Ecography 32:55–65.
- Beck, P. S. A., G. P. Juday, C. Alix, V. A. Barber, S. E. Winslow, E. E. Sousa, P. Heiser, J. D. Herriges, and S. J. Goetz. 2011. Changes in forest productivity across Alaska consistent with biome shift. Ecology Letters [doi: 10.1111/j.1461-0248.2011.01598.x]
- Beier, C. M., S. E. Sink, P. E. Hennon, D. V. D'Amore, and G. P. Juday. 2008. Twentieth-century warming and the dendroclimatology of declining yellowcedar forests in southeastern Alaska. Canadian Journal of Forest Research 38:1319–1334.
- Ben-David, M. 1997. Timing of reproduction in wild mink: The influence of spawning Pacific salmon. Canadian Journal of Zoology 75:376–382.
- Ben-David, M., T. A. Hanley, D. R. Klein, and D. M. Schell. 1997a. Seasonal changes in diets of coastal and riverine mink: The role of spawning Pacific salmon. Canadian Journal of Zoology 75:803–811.
- Ben-David, M., R. W. Flynn, and D. M. Schell. 1997b. Annual and seasonal changes in diets of martens: Evidence from stable isotope analysis. Oecologia 111:280–291.
- Berg, E. E., and R. S. Anderson. 2006. Fire history of white and Lutz spruce forests on the Kenai Peninsula, Alaska over the last two millennia as determined by soil charcoal. Forest Ecology and Management 227:275–283.
- Berg, E. E., J. D. Henry, C. L. Fastie, A. D. De Volder, and S. M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. Forest Ecology and Management 227:219–232.
- Berg, E. E., K. M. Hillman, R. Dial, and A. DeRuwe. 2009. Recent woody invasion of wetlands on the Kenai Peninsula Lowlands, south-central Alaska: a major regime shift after 18 000 years of wet Sphagnum-sedge peat recruitment. Canadian Journal of Forest Research 39:2033–2046.
- Berg, E. 2009. Permafrost on the Kenai lowlands. US Fish and Wildlife Service Kenai National Wildlife Refuge, Refuge Notebook November 13, 2009. http://kenai.fws.gov/overview/notebook/2009/ november/13nov2009.htm
- Beringer, J., F. S. Chapin III, C. C. Thompson, and A. D.

McGuire. 2005. Surface energy exchanges along a tundra-forest transition and feedbacks to climate. Agricultural and Forest Meteorology 131:141–161.

- Bernhardt, E. L., T. N. Hollingsworth, and F. S. Chapin III. 2011. Fire mediates climate-driven shifts in understorey community composition of black spruce stands of interior Alaska. Journal of Vegetation Science 22:32–44.
- Boertje, R. D., M. A. Keech, and T. F. Paragi. 2010. Science and values influencing predator control for Alaska moose management. Journal of Wildlife Management 74:917–928.
- Boucher, T. V., and B. R. Mead. 2006. Vegetation change and forest regeneration on the Kenai Peninsula, Alaska following a spruce beetle outbreak, 1987-2000. Forest Ecology and Management 227:233–246.
- Brabets, T. P., and M. A. Walvoord. 2009. Trends in streamflow in the Yukon River Basin from 1944 to 2005 and the influence of the Pacific Decadal Oscillation. Journal of Hydrology 371:108–119.
- Brinkman, T. J., G. Kofinas, F. S. Chapin III, and D. K. Person. 2007. Influence of hunter adaptability on resilience of subsistence hunting systems. Journal of Ecological Antrhopology 11:58–63.
- Bryant, M. D. 2009. Global climate change and potential effects on Pacific salmonids in freshwater ecosystems of southeast Alaska. Climatic Change 95:169–193.
- Bryant, M. D., M. D. Lukey, J. P. McDonell, R. A. Gubernick, and R. S. Aho. 2009. Seasonal movement of Dolly Varden and cutthroat trout with respect to stream discharge in a second-order stream in southeast Alaska. North American Journal of Fisheries Management 29:1728–1742.
- Carlson, M. L., and M. Shephard. 2007. Is the spread of non-native plants in Alaska accelerating? Pages 117–133 in T. B. Harrington and S. H. Reichard, editors. Meeting the challenge: invasive plants in Pacific Northwest ecosystems. General Technical Report PNW-GTR-694. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Carlson, M. L., I. V. Lapina, M. Shephard, J. S. Conn, R. Densmore, P. Spencer, J. Heys, J. Riley, and J. Nielson. 2008. Invasiveness ranking system for non-native plants of Alaska. Technical Paper R10-TP-143. USDA Forest Service, Alaska Region.
- Chapin, F. S., III et al. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. Global Change Biology 6:211–223.
- Chapin, F. S., III et al. 2004. Resilience and vulnerability of northern regions to social and environmental change. Ambio 33:344–349.
- Chapin, F. S., III., L. A. Viereck, P. Adams, K. Van Cleve, C. L. Fastie, R. A. Ott, D. H. Mann, and J. F.

Johnstone. 2006a. Successional processes in the Alaskan boreal forest. Pages 100–120 *in* F. S. Chapin III, M. Oswood, K. Van Cleve, L. A. Viereck, and D. Verbyla, editors. Alaska's changing boreal forest. Oxford University Press, New York, New York, USA.

- Chapin, F. S., III, M. D. Robards, H. P. Huntington, J. F. Johnstone, S. F. Trainor, G. P. Kofinas, R. W. Ruess, N. Fresco, D. C. Natcher, and R. L. Naylor. 2006b. Resilience of Athabascan subsistence systems to interior Alaska's changing climate. American Naturalist 168:S36–S49.
- Chapin, F. S., III et al. 2008. Increasing wildfire in the boreal forest: causes, consequences, and pathways to the potential solutions of a wicked problem. BioScience 58:531–540.
- Chittenden, C. M., R. J. Beamish, and R. S. McKinley. 2009. A critical review of Pacific salmon marine research relating to climate. ICES Journal of Marine Science 66:2195–2204.
- Christensen, J. H., et al. 2007. Regional climate projections. Pages 847–940 *in* S. Solomon et al., editors. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA.
- Clegg, B. F., and F. S. Hu. 2010. An oxygen-isotope record of Holocene climate change in the southcentral Brooks Range, Alaska. Quaternary Science Reviews 29:928–939.
- Conn, J. S., N. R. Werdin-Pfisterer, Z. Behr, and K. Mohrmann. 2007. Susceptibility of Alaska plant communities to invasion by bird vetch (*Viccia cracca* L). Annual Alaska Committee for Noxious Plant Management Workshop November 14–15, Fairbanks, Alaska, USA.
- Conn, J. S., K. L. Beattie, M. A. Shephard, M. L. Carlson, I. Lapina, M. Hebert, R. Gronquist, R. Densmore, and M. Rasy. 2008. Alaska *Melilotus* invasions: Distribution, origin, and susceptibility of plant communities. Arctic Antarctic and Alpine Research 40:298–308.
- Cortés-Burns, H., I. Lapina, S. C. Klein, M. L. Carlson, and L. Flagstad. 2008. Invasive plant species monitoring and control: areas impacted by 2004 and 2005 fires in interior Alaska: A survey of Alaska BLM lands along the Dalton, Steese, and Taylor Highways. Bureau of Land Management, Alaska State Office, Anchorage, Alaska, USA.
- Cortés-Burns, H., and L. Flagstad. 2010. Invasive plant inventory and bird cherry control trials. Phase II: bird cherry distribution, demography and reproduction biology along the Chester and Campbell Creek trails, Anchorage, Alaska. The Alaska Natural Heritage Program for the Municipality of Anchorage and The Anchorage Parks Foundation,

Anchorage, Alaska, USA.

- Davidson, E. A., and I. A. Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173.
- Davidson, E. A., I. A. Janssens, and Y. Q. Luo. 2006. On the variability of respiration in terrestrial ecosystems: moving beyond Q10. Global Change Biology 12:154–164.
- De Volder, A. 1999. Fire and climate history of lowland black spruce forests, Kenai National Wildlife Refuge, Alaska. Thesis. Northern Arizona University, Flagstaff, Arizona, USA.
- Dial, R. J., E. E. Berg, K. Timm, A. McMahon, and J. Geck. 2007. Changes in the alpine forest-tundra ecotone commensurate with recent warming in southcentral Alaska: Evidence from orthophotos and field plots. Journal of Geophysical Research: Biogeosciences 112:G04015.
- Dickinson, T. A., and C. S. Campbell. 1991. Population structure and reproductive ecology in the Maloideae (Rosaceae). Systematic Botany 16:350–362.
- Duffy, P. A., J. E. Walsh, J. M. Graham, D. H. Mann, and T. S. Rupp. 2005. Impacts of large-scale atmospheric-ocean variability on Alaskan fire season severity. Ecological Applications 15:1317– 1330.
- Ecotrust. 1992. Coastal temperate rainforests: ecological characteristics and distribution worldwide. Occasional Paper Series. Ecotrust and Conservation International, Portland, Oregon, USA.
- Edwards, R. T., D. V. D'Amore, E. Norberg, and F. E. Biles. In press. Riparian ecology, climate change, and management in North Pacific Coastal Rainforests. *In*: Ecology and conservation of North Pacific rainforests.
- Epting, J., and D. L. Verbyla. 2005. Landscape-level interactions of prefire vegetation, burn severity, and postfire vegetation over a 16-year period in interior Alaska. Canadian Journal of Forest Research 35:1–11.
- Euskirchen, E. S., A. D. McGuire, T. S. Rupp, F. S. Chapin, and J. E. Walsh. 2009a. Projected changes in atmospheric heating due to changes in fire disturbance and the snow season in the western Arctic, 2003-2100. Journal of Geophysical Research: Biogeosciences 114:G04022.
- Euskirchen, E. S., A. D. McGuire, F. S. Chapin III, S. Yi, and C. C. Thompson. 2009b. Changes in vegetation in northern Alaska under scenarios of climate change, 2003-2100: Implications for climate feedbacks. Ecological Applications 19:1022–1043.
- Euskirchen, E. S., A. D. McGuire, F. S. Chapin, and T. S. Rupp. 2010. The changing effects of Alaska's boreal forests on the climate system. Canadian Journal of Forest Research 40:1336–1346.
- Farr, W. A., V. J. LaBau, and T. H. Laurent. 1976. Estimation of decay in old-growth western hem-

lock and Sitka spruce in southeast Alaska. Research Paper PNW-204. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.

- Fastie, C. L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. Ecology 76:1899–1916.
- Field, C. B., and L. D. Mortsch. 2007. North America. Pages 617–652 *in* M. L. Parry, J. P. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hansen, editors. Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Flint, C. G. 2006. Community perspectives on spruce beetle impacts on the Kenai Peninsula, Alaska. Forest Ecology and Management 227:207–218.
- Francis, J. A., D. M. White, J. J. Cassano, W. J. Gutowski, Jr., L. D. Hinzman, M. M. Holland, M. A. Steele, and C. J. Vörösmarty. 2009. An arctic hydrologic system in transition: Feedbacks and impacts on terrestrial, marine, and human life. Journal of Geophysical Research: Biogeosciences 114:G04019.
- Fresco, N., and F. S. Chapin III. 2009. Assessing the potential for conversion of biomass fuels in Interior Alaska. Research Paper. USDA Forest Service, Pacific Northwest Experiment Station, Portland, Oregon, USA.
- Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52:917–928.
- Giardina, C. P., and M. G. Ryan. 2000. Evidence that temperature does not influence decomposition or organic carbon in forest mineral soils. Nature 404:858–861.
- Goetz, S. J., A. G. Bunn, G. J. Fiske, R. A. Houghton, and G. M. Woodwell. 2005. Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. Proceedings of the National Academy of Sciences of the United States of America 102:13521–13525.
- Goodman, L. F., and B. A. Hungate. 2006. Managing forests infested by spruce beetles in south-central Alaska: effects on nitrogen availability, understory biomass, and spruce regeneration. Forest Ecology and Management 227:267–274.
- Gray, D. R. 2008. The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. Climatic Change 87:361–383.
- Hall, D. K., C. S. Benson, and W. O. Field. 1995. Changes of glaciers in Glacier Bay, Alaska, using ground and satellite measurements. Physical Geography 16:27–41.
- Han, E. N., E. Bauce, and F. Trempe-Bertrand. 2000. Development of the first-instar spruce budworm

(Lepidoptera : Tortricidae). Annals of the Entomological Society of America 93:536–540.

- Hanley, T. A. 1987. Physical and chemical response of understory vegetation to deer use in Southeastern Alaska. Canadian Journal of Forest Research 17:195–199.
- Hansen, A. J. 1987. Regulation of bald eagle reproductive rates in Southeast Alaska. Ecology 68:1387– 1392.
- Harden, J. W., K. L. Manies, J. C. Neff, and M. R. Turetsky. 2006. Effects of wildfire and permafrost on soil organic matter and soil climate in interior Alaska. Global Change Biology 12:1–13.
- Hartmann, B., and G. Wendler. 2005. The significance of the 1976 Pacific climate shift in the climatology of Alaska. Journal of Climate 18:4824–4839.
- Hay, L. E., R. L. Wilby, and G. H. Leavesley. 2000. A comparison of delta change and downscaled GCM scenarios for three mountainous basins in the United States. Journal of the American Water Resources Association 363:387–397.
- Hayhoe, K. A. 2010. A standardized framework for evaluating the skill of regional climate downscaled techniques. Dissertation. University of Illinois, Urbana-Champaign, Illinois, USA.
- Heimann, M., and M. Reichstein. 2008. Terrestrial ecosystem carbon dynamics and climate feedbacks. Nature 451:289–292.
- Hennon, P. E., C. G. Shaw, and E. M. Hansen. 1990. Dating decline and mortality of *Chamaecyparis nootkatensis* in Southeast Alaska. Forest Science 36:502–515.
- Hennon, P. E. 1995. Are heart rot fungi major factors of disturbance in gap-dynamic forests? Northwest Science 69:284–293.
- Hennon, P. E., and M. H. McClellan. 2003. Tree mortality and forest structure in the temperate rain forests of southeast Alaska. Canadian Journal of Forest Research 33:1621–1634.
- Hennon, P. E., D. D'Amore, D. Wittwer, A. Johnson, P. Schaberg, G. Hawley, C. Beier, S. Sink, and G. Juday. 2006. Climate warming, reduced snow, and freezing injury could explain the demise of yellowcedar in southeast Alaska, USA. World Resource Review 18:427–450.
- Hennon, P. E., D. V. D'Amore, D. Wittwer, and J. Caouette. 2008. Yellow-cedar decline: Conserving a climate-sensitive tree species as Alaska warms. Pages 233–245 *in* R. Deal, editor. Integrated restoration of forested ecosystems to achieve multiresource benefits: Proceedings of the 2007 national silviculture workshop. U.S. Department of Agrictulture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Hennon, P. E., D. V. D'Amore, D. T. Wittwer, and M. B. Lamb. 2010. Influence of forest canopy and snow on microclimate in a declining yellow-cedar forest

of Southeast Alaska. Northwest Science 84:74-87.

- Hennon, P. E., T. M. Barrett, and D. Wittwer. 2011. The distribution of hemlock dwarf mistletoe suggests influences of climate. Pages 74–77 *in* Forests of southeast and south-central Alaska, 2004-2008. General Technical Report PNW-GTR-835. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology 77:132–138.
- Hinzman, L. D., D. J. Goering, and D. L. Kane. 1998. A distributed thermal model for calculating soil temperature profiles and depth of thaw in permafrost regions. Journal of Geophysical Research: Atmospheres 103:28975–28991.
- Hinzman, L. D., et al. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. Climatic Change 72:251–298.
- Hinzman, L. D., L. A. Viereck, P. C. Adams, V. E. Romanovsky, and K. Yoshikawa. 2006. Climate and permafrost dynamics of the Alaskan boreal forest. Pages 39–61 *in* F. S. Chapin III, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla, editors. Alaska's changing boreal forest. Oxford University Press, New York, New York, USA.
- Hollingsworth, T. N., A. H. Lloyd, D. R. Nossov, R. W. Ruess, B. A. Charlton, and K. Kielland. 2010. Twenty-five years of vegetation change along a putative successional chronosequence on the Tanana River, Alaska. Canadian Journal of Forest Research 40:1273–1287.
- Holsten, E. H., P. E. Hennon, and R. A. Werner. 1985. Insects and diseases of Alaska forests. Report No. 181. USDA Forest Service, Alaska Region, State and Private Forestry, Forest Pest Management, Juneau, Alaska, USA.
- Holsten, E. H. 1990. Spruce beetle activity in Alaska: 1920-1989. Technical Report R10-90-18. USDA Forest Service, Alaska Region, Forest Pest Management, State and Private Forestry, Anchorage, Alaska, USA.
- Holsten, E. H., R. A. Werner, and R. L. Develice. 1995. Effects of a spruce beetle (Coleoptera: Scolytidae) outbreak and fire on Lutz spruce in Alaska. Environmental Entomology 24:1539–1547.
- Hood, E., and L. Berner. 2009. Effects of changing glacial coverage on the physical and biogeochemical properties of coastal streams in southeastern Alaska. Journal of Geophysical Research: Biogeosciences 114:G03001.
- Hood, E., J. Fellman, R. G. M. Spencer, P. J. Hernes, R. Edwards, D. D'Amore, and D. Scott. 2009. Glaciers as a source of ancient and labile organic matter to

the marine environment. Nature 462:1044-1047.

- Hopkins, D. M., T. N. V. Karlstrom, R. F. Black, J. R. Williams, T. L. Péwé, A. T. Fernald, and E. H. Muller. 1955. Permafrost and ground water in Alaska. Geological Survey Professional Paper 264-F. United States Department of the Interior, Geological Survey, Washington, D.C., USA.
- Huntsinger, E., N. Fried, and D. Robinson. 2007. Alaska economic trends. Alaska Department of Labor and Workforce Development, Juneau, Alaska, USA.
- IPCC [Intergovernmental Panel on Climate Change]. 2007. Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA.
- IWAC [Invasive Weed Awareness Coalition]. 2006. Ousting orange hawkweed in Kodiak National Wildlife Refuge. Invasive Weed Awareness Coalition. http://www.fws.gov/invasives/volunteerstrainingmodule/ pdf/bigpicture/AK\_Kodiak.pdf
- Johnstone, J. F., and E. S. Kasischke. 2005. Stand-level effects of soil burn severity on post-fire regeneration in a recently-burned black spruce forest. Canadian Journal of Forest Research 35:2151–2163.
- Johnstone, J., and F. Chapin. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9:14–31.
- Johnstone, J. F., F. S. Chapin III, T. N. Hollingsworth, M. C. Mack, V. Romanovsky, and M. Turetsky. 2010a. Fire, climate change, and forest resilience in Interior Alaska. Canadian Journal of Forest Research 40:1302–1312.
- Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010b. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology 16:1281–1295.
- Jorgenson, M. T., C. H. Racine, J. C. Walters, and T. E. Osterkamp. 2001. Permafrost degradation and ecological changes associated with a warming climate in central Alaska. Climatic Change 48:551–579.
- Jorgenson, M. T., V. Romanovsky, J. Harden, Y. Shur, J. O'Donnell, E. A. G. Schuur, M. Kanevskiy, and S. Marchenko. 2010. Resilience and vulnerability of permafrost to climate change. Canadian Journal of Forest Research 40:1219–1236.
- Juday, G. P., R. A. Ott, D. W. Valentine, and V. A. Barber. 1997. Assessment of actual and potential global warming effects on forests of Alaska. New England Regional Climate Change Impacts Workshop Summary Report, September 3–5. http:// www.necci.sr.unh.edu/necci-report/juday.pdf
- Juday, G. P., et al. 2005. Forests, land management, agriculture. Pages 781–862 *in* Arctic climate impact

assessment. Cambridge University Press, New York, New York, USA.

- Karl, T. R. et al. 2009. Global climate change impacts in the United States, A State of Knowledge Report. New York, New York, USA.
- Kasischke, E. S., K. P. O'Neill, N. H. F. French, and L. L. Bourgeau-Chavez. 2000. Controls on patterns of biomass burning in Alaskan boreal forests. Pages 173–196 *in* E. S. Kasischke, and B. J. Stocks, editors. Fire, climate change, and carbon cycling in the boreal forest. Ecological Studies. Springer-Verlag, New York, New York, USA.
- Kasischke, E. S., and J. F. Johnstone. 2005. Variation in ground-layer surface fuel consumption and its effects on site characteristics in a *Picea mariana* forest complex in Interior Alaska. Canadian Journal of Forest Research 35:2164–2177.
- Kasischke, E. S., E. J. Hyer, P. C. Novelli, L. P. Bruhwiler, N. H. F. French, A. I. Sukhinin, J. H. Hewson, and B. J. Stocks. 2005. Influences of boreal fire emissions on Northern Hemisphere atmospheric carbon and carbon monoxide. Global Biogeochemical Cycles 19:GB1012.
- Kasischke, E. S., T. S. Rupp, and D. L. Verbyla. 2006. Fire trends in the Alaskan boreal forest. Pages 285– 301 *in* F. S. Chapin, M. W. Oswood, K. Van Cleve, L. Viereck, and D. Verbyla, editors. Alaska's changing boreal forest. Oxford University Press, New York, New York, USA.
- Kasischke, E. S., and M. R. Turetsky. 2006. Recent changes in the fire regime across the North American boreal region—spatial and temporal patterns of burning across Canada and Alaska. Geophysical Research Letters 33:L09703.
- Kasischke, E. S. et al. 2010. Alaska's changing fire regime: implications for the vulnerability of its boreal forests. Canadian Journal of Forest Research 40:1313–1324.
- Kaufman, D. S. et al. 2009. Recent warming reverses long-term Arctic cooling. Science 325:1236–1239.
- Kenai Peninsula Borough Council. 2011. Our economy. http://www.borough.kenai.ak.us/econ01.htm
- Klein, E., E. Berg, and R. Dial. 2005. Wetland drying and succession across the Kenai Peninsula lowlands, south-central Alaska. Canadian Journal of Forest Research 35:1931–1941.
- Kofinas, G. P., F. S. Chapin III, S. BurnSilver, J. I. Schmidt, N. L. Fresco, K. Kielland, S. Martin, A. Springsteen, and T. S. Rupp. 2010. Resilience of Athabascan subsistence systems to interior Alaska's changing climate. Canadian Journal of Forest Research 40:1347–1359.
- Krishnan, P., T. A. Black, N. J. Grant, A. G. Barr, E. T. H. Hogg, R. S. Jassal, and K. Morgenstern. 2006. Impact of changing soil moisture distribution on net ecosystem productivity of a boreal aspen forest during and following drought. Agricultural and

Forest Meteorology 139:208-223.

- Kruse, J. J., D. R. Smith, and N. M. Schiff. 2010. Monosoma pulveratum (Retzius) (Hymenoptera: Tenthredinidae: Allantinae), a palaearctic sawfly defoliator of alder in Alaska and new to the United States. Proceedings of the Entomological Society of Washington 112:332–335.
- Kyle, R., and T. Brabets. 2001. Water temperature of streams in Cook Inlet Basin, Alaska, and implication of climate change. Water-Resources Investigations Report 01-4109. National Water-Quality Assessment Program Report. Anchorage, Alaska, USA.
- Lamb, M., and M. Shephard. 2007. A snapshot of spread: locations of invasive plants in Southeast Alaska. Alaska Region R10-MB-597. USDA Forest Service, Forest Health Protection, State and Private Forestry, Juneau, Alaska, USA.
- Lamb, M., and T. Wurtz. 2009. Forest health conditions in Alaska 2008. R10-PR-20. USDA Forest Service, Forest Health Protection, Juneau, Alaska, USA.
- Lamb, M., and L. Winton. 2010. Forest health conditions in Alaska: 2009. Protection Report R10-PR-21. USDA Forest Service, Alaska Region, Forest Health Protection, Juneau, Alaska, USA.
- Lapina, I., and M. L. Carlson. 2004. Non-native plant species of Susitna, Matanuska, and Copper River Basins: Summary of survey findings and recommendations for control actions. USDA Forest Service, State and Private Forestry, Anchorage, Alaska, USA.
- Larsen, C. F., R. J. Motyka, J. T. Freymueller, K. A. Echelmeyer, and E. R. Ivins. 2005. Rapid viscoelastic uplift in southeast Alaska caused by post-Little Ice Age glacial retreat. Earth and Planetary Science Letters 237:548–560.
- Larsen, P. H., S. Goldsmith, O. Smith, M. L. Wilson, K. Strzepek, P. Chinowski, and B. Saylor. 2008. Estimating future costs of Alaska public infrastructure at risk from climate change. Global Environmental Change 18:422–457.
- Lavergne, S., and J. Molofsky. 2004. Reed canary grass (*Phalaris arundinacea*) as a biological model of plant invasions. Critical Reviews of Plant Science 23:415– 429.
- Lee, H., E. A. G. Schuur, and J. G. Vogel. 2010. Soil CO<sub>2</sub> production in upland tundra where permafrost is thawing. Journal of Geophysical Research: Biogeosciences 115:G01009.
- Lenart, E. A., R. T. Bowyer, J. Ver Hoef, and R. W. Ruess. 2002. Climate change and caribou: effects of summer weather on forage. Canadian Journal of Zoology 80:664–678.
- Litton, C. M., J. W. Raich, and M. G. Ryan. 2007. Carbon allocation in forest ecosystems. Global Change Biology 13:2089–2109.
- Lloyd, A. H., T. S. Rupp, C. L. Fastie, and A. M.

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Starfield. 2002. Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska. Journal of Geophysical Research: Atmospheres 107:8161.

- Lloyd, A. H., and A. G. Bunn. 2007. Response of the circumpolar boreal forest to 20th century climate variability. Environmental Research Letters 2:045013.
- Luyssaert, S., E. D. Schulze, A. Börner, A. Knohl, D. Hessenmöller, B. E. Law, P. Ciais, and J. Grace. 2008. Old-growth forests as global carbon sinks. Nature 455:213–215.
- Marchenko, S., V. Romanovsky, and G. Tipenko. 2008.
  Numerical modeling of spatial permafrost dynamics in Alaska. Pages 1125–1130 *in* Proceedings of the Ninth International Conference on Permafrost, 29 June–3 July. Volume 2. Institute of Northern Engineering, Fairbanks, Alaska, USA.
- Martin, J. G., and X. Bolstad. 2005. Annual soil respiration in broadleaf forests of northern Wisconsin: influence of moisture and site biological, chemical, and physical characteristics. Biogeochemistry 73:149–182.
- McArt, S. H., D. E. Spalinger, W. B. Collins, T. Stevenson, and M. Bucho. 2009. Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. Ecology 90:1400–1411.
- McCambridge, W. F. 1954. A summary statement of forest insect conditions in Alaska: Season of 1954. USDA Forest Service, Alaska Forest Research Center, Juneau, Alaska, USA.
- McGuire, A. D., J. M. Melillo, D. W. Kicklighter, and L. A. Joyce. 1995. Equilibrium responses of soil carbon to climate change: Empirical and processbased estimates. Journal of Biogeography 22:785– 796.
- McGuire, A. D., L. G. Anderson, T. R. Christensen, S. Dallimore, L. Guo, D. J. Hayes, M. Hemiann, T. D. Lorenson, R. W. MacDonald, and N. T. Roulet. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. Ecological Monographs 79:523– 555.
- McGuire, A. D., R. W. Ruess, A. Lloyd, J. Yarie, J. S. Clein, and G. P. Juday. 2010. Vulnerability of white spruce tree growth in interior Alaska in response to climate variability: dendrochronological, demographic, and experimental perspectives. Canadian Journal of Forest Research 40:1197–1209.
- MEA [Millenium Ecosystem Assessment]. 2005. Ecosystems and human well-being: synthesis. Island Press, Washington, D.C., USA.
- Meekins, J. F., and B. C. McCarthy. 1999. Competitive ability of *Alliara petiolata* (garlic mustard, Brassicaceae), an invasive nonindigenous forest herb. Journal of Plant Science 160:743–752.
- Miller, M. M., B. F. Molnia, G. W. Adema, S. McGee, J. W. Wilson, and A. H. Clough. 2003. Alaska's

Taku glacier reveals accelerated advance-a signal of global warming. Geological Society of America 35:481.

- Mitchell, J. S., and R. W. Ruess. 2009. N2-fixing alder (*Alnus viridis* ssp. *fruticosa*) effects on soil properties across a secondary successional chronosequence in interior Alaska. Biogeochemistry 95:215–229.
- Morrison, S. F., and D. S. Hik. 2007. Demographic analysis of a declining pika *Ochotona collaris* population: linking survival to broad-scale climate patterns via spring snowmelt patterns. Journal of Animal Ecology 76:899–907.
- Mote, P. W., E. A. Parson, A. F. Hamlet, W. S. Keeton, D. Lettenmaier, N. Mantua, E. L. Miles, D. W. Peterson, D. L. Peterson, R. Slaughter, and A. K. Snover. 2003. Preparing for climate change: the water, salmon, and forests of the Pacific Northwest. Climatic Change 61:45–88.
- Motyka, R. J., S. O'Neel, C. L. Connor, and K. A. Echelmeyer. 2002. Twentieth century thinning of Mendenhall Glacier, Alaska, and its relationship to climate, lake calving, and glacier run-off. Global and Planetary Change 35:93–112.
- Muir, J. A., and P. E. Hennon. 2007. A synthesis of the literature on the biology, ecology, and management of western hemlock dwarf mistletoe. General Technical Report PNW-GTR-718. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Mulder, C. P. H., B. A. Roy, and S. Gusewell. 2008. Herbivores and pathogens on *Alnus viridis* subsp. *fruticosa* in Interior Alaska: effects of leaf, tree, and neighbour characteristics on damage levels. Botany 86:408–421.
- Muller-Karger, F. E., R. Varela, R. Thunell, R. Luerssen, C. Hu, and J. J. Walsh. 2005. The importance of continental margins in the global carbon cycle. Geophysical Research Letters 32:L01602.
- Myers-Smith, I. H., A. D. McGuire, J. W. Harden, and F. S. Chapin III. 2007. Influence of disturbance on carbon exchange in a permafrost collapse and adjacent burned forest. Journal of Geophysical Research: Biogeosciences 112:G04017.
- Myers-Smith, I. H., J. W. Harden, M. Wilmking, C. C. Fuller, A. D. McGuire, and F. S. Chapin III. 2008. Wetland succession in a permafrost collapse: interactions between fire and thermakarst. Biogeosciences 5:1273–1286.
- NAST [National Assessment Synthesis Team]. 2003. United States national assessment of the potential consequences of climate variability and change educational resources regional paper: Alaska. National Assessment Synthesis Team http://www. usgcrp.gov/usgcrp/nacc/education/alaska/default. htm
- Neal, E. G., E. Hood, and K. Smikrud. 2010. Contributions of glacier runoff to freshwater

discharge into the Gulf of Alaska. Geophysical Research Letters 37:L06404.

- Neiland, B. J. 1971. The forest-bog complex of southeast Alaska. Plant Ecology 22:1–64.
- Nelson, F. E., O. A. Anisimov, and N. I. Shiklomanov. 2002. Climate change and hazard zonation in the Circum-Arctic permafrost regions. Natural Hazards 26:203–225.
- Nossov, D. R., R. W. Ruess, and T. N. Hollingsworth. 2010. Climate sensitivity of thinleaf alder on an interior Alaskan floodplain. Ecoscience 17:1–9.
- Nossov, D. R., T. N. Hollingsworth, R. W. Ruess, and K. Kielland. 2011. Development of *Alnus tenuifolia* stands on an Alaskan floodplain: Patterns of recruitment, disease, and succession. Journal of Ecology 99:621–633.
- Nowacki, G. J., and M. G. Kramer. 1998. The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. General Technical Report PNW-GTR-421. USDA Forest Service, Pacific Northwest Station, Portland, Oregon, USA.
- O'Donnell, J. A., V. E. Romanovsky, J. W. Harden, and A. D. McGuire. 2009. The effect of moisture content on the thermal conductivity of moss and organic soil horizons from black spruce ecosystems in Interior Alaska. Soil Science 174:646–651.
- O'Donnell, J. A., J. W. Harden, A. D. McGuire, and V. E. Romanovsky. 2010. Exploring the sensitivity of soil carbon dynamics to climate change, fire disturbance and permafrost thaw in a black spruce ecosystem. Biogeosciences Discussions 7:8853– 8893.
- Overpeck, J. T. et al. 1997. Arctic environmental change of the last four centuries. Science 278:1251–1256.
- Overpeck, J. T. et al. 2005. Arctic system on trajectory to new, seasonally ice-free state. EOS, Transactions American Geophysical Union 86:309–316.
- Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1999. Energy and protein balance of freeranging black-tailed deer in a natural forest environment. Wildlife Monographs 143.
- Parson, E. A., L. Carter, P. Anderson, B. Wang, and G. Weller. 2001. Potential consequences and change for Alaska. Pages 283–312 *in* Climate change impacts on the United States, Foundation Report. Cambridge University Press, Cambridge, UK.
- Pastor, J., D. J. Mladenoff, J. Haila, J. Bryant, and S. Payette. 1996. Biodiversity and ecosystem processes in boreal regions. Pages 33–69 in H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala, and E.-D. Schulze, editors. Functional roles of biodiversity: a global perspective. SCOPE report 55. John Wiley and Sons, New York, New York, USA.
- Pelto, M. S., and M. M. Miller. 1990. Mass balance of the Taku glacier, Alaska from 1946 to 1986. Northwest Science 64:121–130.

- Pfister, G. G., P. G. Hess, L. K. Emmons, P. J. Rasch, and F. M. Vitt. 2008. Impact of the summer 2004 Alaska fires on top of the atmosphere clear-sky radiation fluxes. Journal of Geophysical Research: Atmospheres 113:D02204.
- Pojar, J., and A. MacKinnon. 1994. Plants of the Pacific Northwest Coast: Washington, Oregon, British Columbia, and Alaska. Lone Pine Publishing, Redmond, Washington, USA.
- Post, E. et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325:1355–1358.
- Poyry, J., M. Luoto, R. K. Heikkinen, and K. Saarinen. 2008. Species traits are associated with the quality of bioclimatic models. Global Ecology and Biogeography 17:403–414.
- Prati, D., and O. Brossdorf. 2004. Allelopathic inhibition of germination by *Alliaria petiolata* (Brassicaceae). American Journal of Botany 91:285–288.
- Radić, V., and R. Hock. 2011. Regionally differentiated contribution of mountain glaciers and ice caps to future sea-level rise. Nature Geoscience 4:91–94.
- Randerson, J. T. et al. 2006. The impact of boreal forest fire on climate warming. Science 314:1130–1132.
- Rapp, W. 2006. Exotic plant management in Sitka National Historical Park Sitka, Alaska. Summer 2006 Field Season Report. National Park Service, Glacier Bay National Park, Gustavus, Alaska, USA.
- REAP [Renewable Energy Alaska Project]. 2009. Renewable energy atlas of Alaska. Renewable Energy Alaska Project, Anchorage, Alaska, USA.
- Riordan, B., D. Verbyla, and A. D. McGuire. 2006. Shrinking ponds in subarctic Alaska based on 1950-2002 remotely sense images. Journal of Geophysical Research: Biogeosciences 3:G04002.
- Robertson, G., and D. Brooks. 2001. Assessment of the competitive position of the forest products sector in southeast Alaska, 1985-94. General Technical Report PNW-GTR-504. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Roon, D. A., M. S. Wipfli, T. L. Wurtz, and P. Anupma. 2010. Ecological effects of introduced European bird cherry in Anchorage streams and riparian forests. The Committee for Noxious and Invasive Plant Management (CNIPM) and Alaska Invasive Working Group (AISWG) 2010 Speaker Abstracts. http://alaskainvasivespeciesconference.wikispaces. com/file/view/CNIPM\_2010\_speakers+Abstracts. pdf
- Ross, D. W., G. E. Daterman, J. L. Boughton, and T. M. Quigley. 2001. Forest health restoration in Southcentral Alaska: a problem analysis. General Technical Report PNW-GTR-523. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Rouse, W. R. 1998. A water balance model for a

subarctic sedge fen and its application to climatic change. Climatic Change 38:207–234.

- Ruess, R. W., M. D. Anderson, J. S. Mitchell, and J. W. McFarland. 2006. Effects of defoliation on growth and N fixation in *Alnus tenuifolia*: Consequences for changing disturbance regimes at high latitudes. Ecoscience 13:404–412.
- Ruess, R. W., J. M. McFarland, L. M. Trummer, and J. K. Rohrs-Richey. 2009. Disease-mediated declines in N-fixation inputs by *Alnus tenuifolia* to earlysuccessional floodplains in interior and southcentral Alaska. Ecosystems 12:489–502.
- Rupp, T. S., F. S. Chapin, and A. M. Starfield. 2001. Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in northwestern Alaska. Climatic Change 48:399–416.
- Rupp, T. S., M. Olson, L. G. Adams, B. W. Dale, K. Joly, J. Henkelman, W. B. Collins, and A. M. Starfield. 2006. Simulating the influences of various fire regimes on caribou winter habitat. Ecological Applications 16:1730–1743.
- Schaberg, P. G., P. E. Hennon, D. V. D'Amore, G. J. Hawley, and C. H. Borer. 2005. Seasonal differences in freezing tolerance of yellow-cedar and western hemlock trees at a site affected by yellow-cedar decline. Canadian Journal of Forest Research 35:2065–2070.
- Schaberg, P. G., P. E. Hennon, D. V. D'Amore, and G. J. Hawley. 2008. Influence of simulated snow cover on the cold tolerance and freezing injury of yellowcedar seedlings. Global Change Biology 14:1282– 1293.
- Schindler, D. E., D. E. Rogers, M. D. Scheuerell, and C. A. Abrey. 2005. Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. Ecology 86:198–209.
- Schoonmaker, P. K., B. von Hage, and E. C. Wolf. 1997. Introduction. Pages 1–6 *in* P. K. Schoonmaker, B. von Hage, and E. C. Wolf, editors. The rain forests of home: profile of a North American bioregion. Island Press, Washington, D.C., USA.
- Schroeder, R. F., and M. Kookesh. 1990. Subsistence harvest and use of fish and wildlife resources and the effects of forest management in Hoonah, Alaska. Technical Paper 142. Alaska Department of Fish and Game, Division of Subsistence, Juneau, Alaska, USA.
- Schuur, E. A. G., K. G. Crummer, J. G. Vogel, and M. C. Mack. 2007. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. Ecosystems 10:280–292.
- Schuur, E. A. G. et al. 2008. Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle. BioScience 58:701–714.
- Schuur, E. A. G., J. G. Vogel, K. G. Crummer, H. Lee, J. O. Sickman, and T. E. Osterkamp. 2009. The effect of permafrost thaw on old carbon release and net

carbon exchange from tundra. Nature 459:556-559.

- Sekercioglu, C. H., S. H. Schneider, J. P. Fay, and S. R. Loarie. 2008. Climate change, elevational range shifts, and bird extinctions. Conservation Biology 22:140–150.
- Sherriff, R. L., E. E. Berg, and A. E. Miller. 2011. Climate variability and spruce beetle (*Dentroctonus rufipennis*) outbreaks in south-central and south-west Alaska. Ecology 92:1459–1470.
- Shenoy, A., J. F. Johnstone, E. S. Kasischke, and K. Kielland. 2011. Persistent effect of fire severity on early successional forests in interior Alaska. Forest Ecology and Management 261:381–390.
- Shetler, G., M. R. Turetsky, E. Kane, and E. Kasischke. 2008. Sphagnum mosses limit total carbon consumption during fire in Alaskan black spruce forests. Canadian Journal of Forest Research 38:2328–2336.
- Shulski, M., and G. Wendler. 2007. The Climate of Alaska. University of Alaska Press, Fairbanks, Alaska, USA.
- Shvidenko, A., and M. Apps. 2006. The international boreal forest research association: understanding boreal forests and forestry in a changing world. Mitigation and Adaptation Strategies for Global Change 11:5–32.
- Simenstad, C. A., M. Dethier, C. Levings, and D. Hay. 1997. The Terrestrial/Marine Ecotone. Pages 149– 187 in P. K. Schoonmaker, B. von Hage, and E. C. Wolf, editors. The rain forests of home: a profile of a North American bioregion. Island Press, Washington, D.C., USA.
- Smith, L. C., Y. Sheng, G. M. MacDonald, and L. D. Hinzman. 2005. Disappearing arctic lakes. Science 308:1429–1429.
- Snyder, C., M. E. Schultz, and J. Lundquist. 2007. Forest health conditions in Alaska-2007. Protection Report R10-PR18. USDA Forest Service, Alaska Region, Anchorage, Alaska, USA.
- Spellman, B. T. 2008. The impact of invasive sweetclover (*Melilotus alba*) in early-successional floodplain habitats of Alaska. Thesis. University of Alaska, Fairbanks, Alaska, USA.
- Spellman, B. T. 2009. Managing reed canarygrass on the Kenai Peninsula. Committee for Noxious and Invasive Plants Management, 2009 CNIPM Conference. http://www.kenaiweeds.org/user\_images/ Blaine%20RCG%20talk%20-%20CNIPM%2009.pdf
- Stenseth, N. C., and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: Nonlinearity and match-mismatch to the environment. Proceedings of the National Academy of Sciences of the United States of America 99:13379– 13381.
- Stone, R. S., G. P. Anderson, E. P. Shettle, E. Andrews, K. Loukachine, E. G. Dutton, C. Schaaf, and M. O. Roman. 2008. Radiative impact of boreal smoke in

the Arctic: Observed and modeled. Journal of Geophysical Research: Atmospheres 113:D14S16.

- Sullivan, P. F. 2010. Snow distribution, soil temperature and late winter CO<sub>2</sub> efflux from soils near the Arctic treeline in northwest Alaska. Biogeochemistry 99:65–77.
- Sullivan, P. F., S. J. T. Aren, B. Sveinbjörnsson, and J. M. Welker. 2010. Modeling the seasonality of belowground respiration along an elevation gradient in the western Chugach Mountains, Alaska. Biogeochemistry 101:61–75.
- Sullivan, P. F., and B. Sveinbjörnsson. 2011. Environmental controls on needle gas exchange and growth of white spruce (*Picea glauca*) on a riverside terrace near the Arctic treeline. Arctic, Antarctic and Alpine Research 43:279–288.
- Sveinbjörnsson, B., M. Smith, T. Traustason, R. W. Ruess, and P. F. Sullivan. 2010. Variation in carbohydrate source-sink relations of forest and treeline white spruce in southern, interior and northern Alaska. Oecologia Aquatica 163:833–843.
- Swaine, J. M. 1928. Forest entomology and its development in Canada. Pamphlet No. 97. Canadian Department of Agriculture.
- Tan, Z., L. L. Tieszen, Z. Zhu, S. Liu, and S. M. Howard. 2007. An estimate of carbon emissions from 200 wildfires across Alaskan Yukon River Basin. Carbon Balance and Management 2:12.
- Trainor, S. F. 2006. Emergency fire fighting crew management study report to the Operations Committee of the Alaska Fire Coordinating Group (AWFCG). University of Alaska, Fairbanks, Alaska, USA.
- Trainor, S. F. et al. 2009. Vulnerability and adaptation to climate-related fire impacts in rural and urban interior Alaska. Polar Research 28:100–118.
- Turetsky, M. R., M. C. Mack, T. N. Hollingsworth, and J. W. Harden. 2010. The role of mosses in ecosystem succession and function in Alaska's boreal forest. Canadian Journal of Forest Research 40:1237–1264.
- Turetsky, M. R., E. S. Kane, J. W. Harden, R. D. Ottmar, K. L. Manies, E. Hoy, and E. S. Kasischke. 2011. Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. Nature Geoscience 4:27–31.
- Urgenson, L. S., S. H. Reichard, and C. B. Halpern. 2009. Community and ecosystem consequences of giant knotweed (*Polygonum sachalinense*) invasion into riparian forests of western Washington, USA. Biological Conservation 142:1536–1541.
- Van Cleve, K., L. A. Viereck, and R. Schlentner. 1971. Acummulation of nitrogen in alder (*Alnus*) ecosystems near Fairbanks, Alaska. Arctic and Alpine Research 3:101–114.
- Van Cleve, K., F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, editors. 1986. Forest ecosystems in the Alaskan taiga: A synthesis of

structure and function. Springer-Verlag, New York, New York, USA.

- Verbyla, D. 2008. The greening and browing of Alaska based on 1982-2003 satellite data. Global Ecology and Biogeography 17:547–555.
- Viereck, L. A., and E. L. Little, Jr. 2007. Alaska trees and shrubs. University of Alaska Press, Fairbanks, Alaska, USA.
- Villano, K. L., and C. P. H. Mulder. 2008. Invasive plant spread in burned lands of interior Alaska. Final Report for National Park Service Alaska Region and National Aeronautics and Space Administration. Fairbanks, Alaska, USA.
- Vogel, J., E. A. G. Schuur, C. Trucco, and H. Lee. 2009. Response of CO<sub>2</sub> exchange in a tussock tundra ecosystem to permafrost thaw and thermokarst development. Journal of Geophysical Research: Biogeosciences 114:G04018.
- Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15:2626–2633.
- Wagner, D., L. DeFoliart, P. Doak, and J. Schneiderheinze. 2008. Impact of epidermal leaf mining by the aspen leaf miner (*Phyllocnistis populiella*) on the growth, physiology, and leaf longevity of quaking aspen. Oecologia 157:259–267.
- Walsh, J. E., W. L. Chapman, V. Romanovsky, J. H. Christensen, and M. Stendel. 2008. Global climate model performance over Alaska and Greenland. Journal of Climate 21:6156–6174.
- Waring, R. H., and J. F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. Science 204:1380–1386.
- Welp, L. R., J. T. Randerson, and H. P. Liu. 2007. The sensitivity of carbon fluxes to spring warming and summer drought depends on plant functional type in boreal forest ecosystems. Agricultural and Forest Meteorology 147:172–185.
- Wendler, G., and M. Shulski. 2009. A century of climate change for Fairbanks, Alaska. Arctic 62:295–300.
- Werner, R. A., and E. H. Holsten. 1985. Factors influencing generation times of spruce beetles in Alaska. Canadian Journal of Forest Research 15:438–443.
- Werner, R. A. 1994. Forest insect research in boreal forests of Alaska. Entomology (Trends in Agricultural Science) 2:35–46.
- Werner, R. A. 1996. Forest health in boreal ecosystems of Alaska. Forestry Chronicle 72:43–46.
- Werner, R. A., E. H. Holsten, S. M. Matsuoka, and R. E. Burnside. 2006. Spruce beetles and forest ecosystems in south-central Alaska: A review of 30 years of research. Forest Ecology and Management 227:195–206.
- Wilmking, M., G. P. Juday, V. Barber, and H. Zald. 2004. Recent climate warming forces contrasting

growth responses of white spruce at treeline in Alaska through temperature thresholds. Global Change Biology 10:1–13.

- Yarie, J., and K. Van Cleve. 2010. Long-term monitoring of climatic and nutritional effects on tree growth in interior Alaska. Canadian Journal of Forest Research 40:1325–1335.
- Yoshikawa, K., and L. Hinzman. 2003. Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost. Permafrost and Periglacial Processes 14:151–160.
- Yoshikawa, K., W. R. Bolton, V. E. Romanovsky, M. Fukuda, and L. D. Hinzman. 2003. Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska. Journal of Geophysical Research 108:8148.
- Zhuang, Q., J. M. Melillo, A. D. McGuire, D. W. Kicklighter, R. G. Prinn, P. A. Steudler, B. S. Felzer, and S. Hu. 2007. Net emissions of CH<sub>4</sub> and CO<sub>2</sub> in Alaska: Implications for the region's greenhouse gas budget. Ecological Applications 17:203–212.