Is Alaska's Boreal Forest Now Crossing a Major Ecological Threshold?

Authors: Mann, Daniel H., Scott Rupp, T., Olson, Mark A., and Duffy, Paul A.

Source: Arctic, Antarctic, and Alpine Research, 44(3) : 319-331

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1938-4246-44.3.319

Arctic, Antarctic, and Alpine Research, Vol. 44, No. 3, 2012, pp. 319–331

Is Alaska's Boreal Forest Now Crossing a Major Ecological Threshold?

Daniel H. Mann§*
T. Scott Rupp†
Mark A. Olson† and
Paul A. Duffy‡

*Geography Program, School of Natural Resources and Agricultural Sciences, University of Alaska, Fairbanks, Alaska 99775, U.S.A.
‡Scenarios Network for Alaska and Arctic Planning, School of Natural Resources and Agricultural Sciences, University of Alaska, Fairbanks, Alaska 99775, U.S.A.
‡Neptune and Company, Inc., 8550 West 14th Avenue, Lakewood, CO 80215, U.S.A.
§Corresponding author: dhmann@alaska.edu

Abstract

Many boreal forests grow in regions where climate is now warming rapidly. Changes in these vast, cold forests have the potential to affect global climate because they store huge amounts of carbon and because the relative abundances of their different tree species influence how much solar radiation reflects back to space. Both the carbon cycling and albedo of boreal forests are strongly affected by wildland fires, which in turn are closely controlled by summer climate. Here we use a forest disturbance model in both a retrospective and predictive manner to explore how the forests of Interior Alaska respond to changing climate. Results suggest that a widespread shift from coniferous to deciduous vegetation began around A.D. 1990 and will continue over the next several decades. This ecological regime shift is being driven by old, highly flammable spruce stands encountering a warmer climate conducive to larger and more frequent fires. Increased burning promotes the spread of early successional, deciduous species at the expense of spruce. These striking changes in the vegetation composition and fire regime are predicted to alter the biophysics of Alaska's forests. The ground will warm, and a surge of carbon emission is likely. Our modeling results support previous inferences that Alaska's boreal forest is now shifting to a new ecological state and that positive feedbacks to global warming will accompany this change.

DOI: http://dx.doi.org/10.1657/1938-4246-44.3.319

Introduction

The responses of ecosystems to changing climate can be sudden, nonlinear, and sometimes lead to very different self-sustaining states (Higgins et al., 2002; Scheffer, 2009). Such ecological regime shifts involve sweeping changes in ecosystem structure, function, and species composition that entail changes in chemical and biophysical exchanges with the rest of the biosphere (Scheffer and Carpenter, 2003). Ecological regime shifts are of particular concern when they involve entire biomes and threaten to trigger positive feedbacks to human-caused warming (Lenton et al., 2008).

The circumboreal forest is of special concern in regard to climate change and ecological regime shifts because of the enormous amounts of carbon (C) it stores. Boreal forests cover some 16 million km^2 globally, and every year about 8% of the atmospheric pool of carbon (C) cycles through them (McGuire et al., 2009). Altogether, boreal forests currently contain 10–20% of the world's vegetation C and are underlain by about 30% of the world's soil C (McGuire et al., 2009). This abundant soil C has accumulated in boreal forests because decomposition rates there are low due to the wet, cold soils.

Temperatures are rising rapidly in many boreal forest regions today (Hinzman et al., 2005). As soil temperatures warm and decomposition rates increase, more CO_2 and methane (CH_4) will be released to the atmosphere (Schuur et al., 2009). Wildland fires are the other important recycler of vegetation and soil C in boreal forests (Soja et al., 2006; Boby et al., 2010). By removing shading vegetation, insulating moss, and soil organic horizons, fires can cause soils to warm dramatically (Viereck et al., 2008), which speeds the decomposition of soil organic matter. If the boreal forest ''freezers'' defrost through a combination of rising air and soil temperatures caused by a combination of warmer climate and increased burning, the resulting release of trace gases could trigger significant positive feedback to global warming.

Climate is now changing rapidly in Alaska (Hinzman et al., 2005). Over the last century, mean annual temperature in Interior Alaska rose 1.4 °C, and precipitation decreased by 11% (Wendler and Shulski, 2009; Wendler et al., 2010). Growing season length has increased by about three days per decade since 1970 (Euskirchen et al., 2010). Temperatures in the top meter of the ground have risen in Alaska by 0.7 °C per decade over the last 40 years, and widespread thawing of permafrost seems inevitable if this trend continues (Jorgenson et al., 2010). How stable is Interior Alaska's forest in the face of these rapid changes in climate?

PORTENTS OF IMPENDING CHANGE?

Previous research suggests that boreal forests in general (Soja et al., 2006) and Interior Alaska's forests in particular are approaching a major ecological threshold. White spruce in Interior Alaska is sensitive to temperature-induced drought (Barber et al., 2000), and recent warming has caused reductions in its growth throughout the region (McGuire et al., 2010). Chapin et al. (2004) speculated that white spruce forests in Interior Alaska might be replaced by aspen parkland or grassland with a future temperature rise of just 2 °C. Similarly, Calef et al. (2005) inferred that a combination of warmer drier summers and more frequent fires could cause a significant expansion of deciduous stands at the expense of white spruce and tundra vegetation. Based on a review of the key processes that structure the boreal forest and that are believed to be sensitive to warming temperature (e.g., fire regime, tree regeneration, thermokarst), Chapin et al., (2010) inferred that ''. . .the Alas-

1523-0430/6 $7.00

kan boreal forest is on the cusp of potentially large nonlinear changes in structure and functioning.''

Focusing on the fire regime, Kasischke et al. (2010) suggested Interior Alaska's forest is vulnerable to sweeping ecological changes triggered by two fire effects. The first is a shortened fire-free period that could reduce the opportunity for the recruitment of black spruce seedlings (Johnstone and Chapin, 2006) and so allow an increase in deciduous vegetation. The second is the increased combustion of organic soils, which could significantly alter the soil-legacy effects (Harden et al., 2006) that today favor the self-replacement of black spruce. This might further encourage the spread of short-lived deciduous vegetation at the expense of black spruce (Johnstone et al., 2010). Similarly, Kurkowski et al. (2008) suggested that a warming climate could trigger changes in the relative importance of different post-fire successional pathways in such a way as to cause the widespread replacement of spruce by deciduous trees.

Beck et al. (2011) presented compelling evidence that forest productivity has declined over the last several decades in Interior Alaska as summers have warmed and trees become more drought stressed. Based on this evidence, Beck et al. (2011) warned of an impending ecological regime shift in Interior Alaska. These threads of inference and evidence converge on the conclusion that a sudden shift in the structure and functioning of Interior Alaska's boreal forest is possible as climate continues to warm. What has been missing is a way to combine these different threads into a unified, testable hypothesis of forest function and forest response to climatic drivers.

RESEARCH QUESTIONS AND MODELING APPROACH

Our primary research questions are these: How sensitive is the boreal forest in Interior Alaska to ongoing climate forcing? What key processes mediate this sensitivity? Does an integrative, modeling analysis of this forest substantiate the suggestions that an ecological regime shift is imminent?

To answer these questions, we use the ALFRESCO computer model, a forest-disturbance model that integrates fire, forest succession, and climate change across spatially explicit landscapes of regional extent. By ''spatially explicit'' we mean that the ALFRESCO model tracks the changing vegetation and fire history of a myriad of separate, contiguous sites on real topography through time. Its historical, climate-influenced, and spatially explicit structure endows ALFRESCO with the ability to estimate transient change in albedo, heat fluxes, and carbon budgets on a forested landscape experiencing rapid climate changes.

The main virtue of a computer model is its ability to meld inferences about diverse ecological processes into a single, unified hypothesis about how an entire forest functions and consequently how it might respond to changing climate. The relative simplicity of boreal forests makes modeling their responses to climate change more straightforward than for many other biomes. Many boreal forests still exist in primeval states because of their remoteness from human activities, and a typical boreal forest contains just a handful of tree species. Disturbance-regeneration cycles in these forests are triggered mainly by lightning-ignited fires (Kasischke and Turetsky, 2006; Kasischke et al., 2010) whose frequency and size are controlled by relatively few weather parameters (Duffy et al., 2005). Here we use ALFRESCO in both a retrospective and predictive manner to explore how boreal forests of Interior Alaska respond to changing climate.

Materials and Methods

STUDY AREA

Interior Alaska includes approximately 47 million ha between the Alaska and Brooks Range. The regional topography consists of a series of large tectonic basins separated by low mountain ranges and interconnected by meandering rivers. The combination of a diverse topography with low sun angles in summer sets up a complex mosaic of radiative microclimates (Kurkowski et al., 2008), which give rise to a corresponding mosaic of soil microclimates. These soil microclimates influence both the distribution of permafrost and the thickness of the active layer, which together strongly influence vegetation distribution, decomposition rate, and soil-organic horizon thickness (Harden et al., 2006). Interior Alaska lies within the zone of discontinuous permafrost (Osterkamp and Romanovsky, 1999), and stand-replacing fires are the most frequent forest disturbance (Viereck, 1983). The most abundant tree species in the region is black spruce (*Picea mariana*), which usually grows on the coldest, wettest soils with the thickest organic horizons. Aspen (*Populus tremuloides*) occupies the warmest, driest sites where the organic mat is thin or absent. White spruce (*Picea glauca*) and birch (*Betula neoalaskana*) occupy sites that have microclimates and soil characteristics intermediate between black spruce and aspen. Detailed descriptions of this forest and its physical environment can be found in Chapin et al. (2006). Kasischke et al. (2010) described fire regimes in Alaskan forests, Johnstone et al. (2010) described fire effects on tree regeneration there, and Euskirchen et al. (2010) reviewed forest-climate interactions.

THE ALFRESCO MODEL

Overview

ALFRESCO is a vegetation disturbance model to which biogeochemical fluxes can be appended (http://www.snap.uaf.edu/resource_page.php?resourceid = 11). Because vegetation cover in ALFRESCO is a function of topographic position and time-since-last-fire (TSLF), the overall species composition and stand-age distribution of the study region emerges from the continually changing responses of the overall forest mosaic to local fire histories. In this way the model incorporates both the emergent properties of forests and the crucial role played by climate-fire linkages in structuring them. ALFRESCO's strength lies in its ability to simulate rapid changes in the forest's overall species composition and tree-age distribution, which can then be used to quantify biophysical properties using estimates of the rates and magnitude of heat fluxes, and carbon emissions within specific vegetation types (e.g., 40-year-old aspen *versus* 100-year-old black spruce).

ALFRESCO quantifies interactions among climate, topography, vegetation distribution, post-fire succession, and age-dependent flammability specifically for Interior Alaska's boreal forest (Rupp et al., 2000, 2006, 2007). The model simulates the transient states of vegetation at a spatial scale of 1 × 1 km and at annual time steps in response to climate-driven changes in the fire regime (fire frequency, fire severity, and fire size). The fire regime is simulated stochastically and constrained by climate and vegetation type. Ignition is determined randomly and is a function of pixel flammability. The model uses a cellular automaton approach in which an ignited pixel can spread fire to any neighboring pixel (Brubaker et al., 2009). Fire spread depends on the flammability of the adjacent pixels as modified by the presence of firebreaks such as non-vegetated mountain slopes, rivers, and lakes. Fire-climate rules come from a statistical model (Duffy et al., 2005) that explains 79% of the interannual variability in area burned in Interior Alaska as a function of monthly climate parameters over the period 1950–2005. Post-fire successional pathways are determined by the burn severity in each pixel, which is modeled as a function of fire size and topography (Duffy et al., 2007).

We used the age structure, species composition, and fire regime of the present-day forest to establish model rules and to calibrate ALFRESCO within reasonable values of observed parameters taken from the extensive literature on post-fire succession and its relation to topography and pre-fire stand type in Interior Alaska (Chapin et al., 2006; Kurkowski et al., 2008; Johnstone et al, 2010). For more details on model calibration, the reader is referred to the model's user manual (http://www.snap.uaf.edu/resource page.php?resourceid = 11). We estimated annual area burned back to A.D. 1860 using the climate-area burned relationship of Duffy et al. (2005) in conjunction with reconstructed and downscaled data sets of monthly temperature and precipitation. Climate reconstructions for 1860–1900 are from the Potsdam Institute for Climate Impact Research (Leemans and Cramer, 1991); spatially interpolated, observational climate data for 1901–2002 are from the Climate Research Unit (Mitchell and Jones, 2005). Further details on the climate inputs to the model are given below.

We tuned ALFRESCO's pixel-scale rules governing flammability, fire spread, and hence annual area burned using estimates of annual area burned from two sources. For 1950–2007, we used fire management records (Kasischke et al., 2002, 2010; Bureau of Land Management–Alaska Fire Service, 2008). For 1860–1949, we used back-casts of annual area burned made using the fire-climate relationship (Duffy et al., 2005). We assessed model accuracy by iteratively running the model forward from 1860 and comparing the simulated fire-regime metrics and vegetation composition with the back-cast fire history (1860–1949), with the observed fire history (1950–2007), with regional forest composition in 2001 (Homer et al., 2004), and with comparisons between observed and modeled power law exponents. Power-law exponents, β, are a sensitive metric useful in characterizing fire regimes across multiple spatial and temporal scales (Malamud et al., 2005; Song et al., 2006; Pueyo, 2007). We applied ALFRESCO to the future by inputting the downscaled climate predictions of the five global circulation models found to work best over Alaska (Walsh et al., 2008).

ALFRESCO Vegetation

The model uses the minimum number of vegetation types needed to realistically depict the stand mosaic that comprises the boreal forest of Interior Alaska today. The vegetation data used in model spin-up were reclassified from the 1990 AVHRR vegetation classification of Interior Alaska (http://agdcftp1.wr.usgs.gov/pub/projects/fhm/vegcls.tar.gz) and the 2001 National Land Cover Database vegetation classification (http://www.mrlc.gov) (Homer et al., 2004) into tundra, black spruce, white spruce, or deciduous vegetation. Deciduous vegetation includes aspen, cottonwood (*Populus balsamifera*), and birch. In the first few decades after a fire, deciduous vegetation includes seedlings and saplings of the above-mentioned tree species plus herbaceous species like grass, sedge, horsetail (*Equisetum* spp.), and fireweed (*Epilobium angustifolium*) (Mann and Plug, 2002; Johnstone and Chapin, 2006). Remote sensing is unable to distinguish black spruce from white spruce (Kurkowski et al., 2008), so ALFRESCO uses aspect and topographic position as a predictor of spruce species, with black spruce located on north-facing slopes, poorly drained flats, and toe slopes. These are all sites where organic soils are common, so in this way the model incorporates the role that soil organic matter plays in maintaining ecological inertia on this landscape (Harden et al., 2006).

ALFRESCO Climate

Two spatially explicit (0.5° × 0.5°) data sets provide ALFRESCO with monthly averages of temperature and monthly totals of precipitation between A.D. 1860 and 2002. The Potsdam Institute for Climate Impact Research (PIK) data set is a modified version of that presented in Leemans and Cramer (1991) (McGuire et al., 2001). We used PIK data for the years 1860–1900 and CRU data (http://www.cru.uea.ac.uk/~timm/grid/CRU_TS_2_0.html) for the years 1901–2002. Predictions of future climate come from the general circulation models (GCMs) that best match historical weather records in Alaska (Walsh et al., 2008). These five are the MPI_ECHAM5, the GFDL_CM2_1, MIROCC3_2_MEDRES, UKMO_HADCM3, and CCCMA_CGCM3_1. We used the mid-range emission scenario (A1B) with each of these models. To span the several years missing between the CRU and GCM-predicted weather data, we used output of whichever of the five models best predicted the observed area burned in Interior Alaska in that year. Details about how we down-scaled GCM-predicted climate to the 1 × 1 km scale used in ALFRESCO can be found at http://www.snap.uaf.edu/.

Inputting Climate and Calibrating Flammability

Climate data are used in ALFRESCO to define the flammability coefficient of each pixel. Pixel flammability also varies according to its vegetation cover, which depends on TSLF and topographic position. Monthly fields of average temperature and total precipitation at a 1 × 1 km scale are superimposed over vegetation mapped at the same scale. The flammability coefficients of different vegetation types under varying climatic conditions are iteratively tuned within ecologically realistic bounds so that the model's output matches the observational records of several key parameters (http://www.snap.uaf.edu/resource_page.php?resourceid = 11). The first of these is annual area burned as recorded by the Alaska Fire Service of the Bureau of Land Management (http://afsmaps.blm.gov/) (Kasischke et al., 2002; Kasischke and Turetsky, 2006). These historical records provide a target for tuning ALFRESCO's flammability coefficients between 1950 and 2007. We extended the annual area burned record into the past by using the climate-area burned relationship inferred by Duffy et al. (2005) in conjunc-

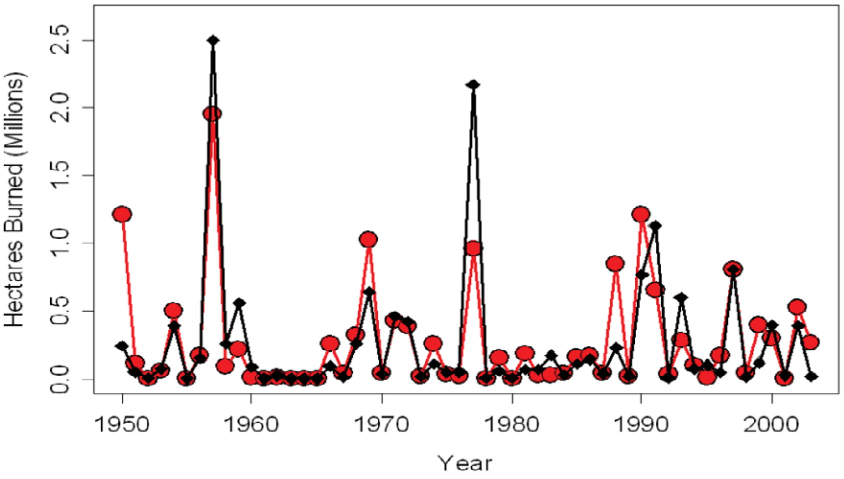

FIGURE 1. Predicted and observed annual area burned in Interior Alaska, 1950–2002. Observed values are red circles. Black diamonds are values predicted by the ALFRESCO model using the climate-area burned relationship of Duffy et al. (2005).

tion with the CRU and PIK climate data sets to back-cast annual area burned between 1860 and 1949. While comparing ALFRESCO's simulated annual area burned to these historical and back-cast estimates of area burned, we iteratively adjusted the rules governing pixel flammability within ecologically reasonable limits until the model yielded predictions of annual area burned that were consistent with observed and back-cast values (Fig. 1).

Biophysical Effects in ALFRESCO

Landscape-scale changes in vegetation and fire regime strongly influence surface radiation budgets and C cycling in Alaskan forests (McGuire et al., 2006; Balshi et al., 2007; Chapin et al., 2009; Euskirchen et al., 2009, 2010). By combining ALFRESCO's predictions with published estimates of the effects of TSLF and vegetation type on various biophysical parameters, we can predict the effects of changes in the Alaskan boreal forest at local, regional, and global scales. We used the measurements of Randerson et al. (2006) to define a TSLF-albedo function. Similar trends in albedo change over time result from using the TSLF-albedo estimates of Amiro et al. (2006), Lyons et al. (2008), and Euskirchen et al., (2007, 2010). We based estimates of net solar radiation, latent heat flux, ground heat flux, and sensible heat flux on the chronosequence data of Liu et al. (2005) and Liu and Randerson (2008). To estimate C emissions from burning boreal forests, we mainly followed Turquety et al. (2007). Estimates of the amount of C in dry matter come from Harden et al. (2000) and Soja et al. (2004).

Approximately 40% of Interior Alaska is classified as poorly drained and is covered by thick (>25 cm), often water-saturated, organic soil horizons (Harden et al., 2001). Because water content controls the maximum amount of biomass combusted during a fire (Soja et al., 2004; French et al., 2004; Turquety et al., 2007), carbon release from organic soils is strongly affected by seasonal variations in water-table height. To depict this in the model, we added rules that scaled C output from burning to seasonal changes in moisture. The seasonal pattern of soil moisture is fairly predictable in Interior Alaska. Fires occurring early in the summer typically encounter relatively high water tables in areas of thick organic soils, while the rare late summer fires usually encounter low water tables.

Thus for the 40% of the annual area burned that is underlain by thick organic deposits (peat), if a fire occurs before July 1:

$$\frac{\textit{Biomass}}{\textit{Consumed}} = \frac{\textit{Total Area}}{\textit{Burned}} * 6.4 \text{ kg Dry Matter m}^{-2} * \textit{0.7}, \quad (1)$$

where 0.7 is a scaling factor applying to burning at times of high water tables. If a fire occurs between July 1 and August 1:

$$\frac{\textit{Biomass}}{\textit{Consumed}} = \frac{\textit{Total Area}}{\textit{Burned}} * \textit{6.4 kg Dry Matter m}^{-2} * \textit{1.0}, \quad (2)$$

where 1.0 is the scaling factor depicting the ''average'' height of the water table. If a fire occurs after August 1, conditions are deemed unusually dry, so:

$$\frac{\textit{Biomass}}{\textit{Consumed}} = \frac{\textit{Total Area}}{\textit{Burned}} * \textit{6.4 kg Dry Matter m}^{-2} * \textit{1.5}, \quad (3)$$

*w*here 1.5 is the scaling factor accounting for unusually low water tables in organic soils. All the above estimates are divided by 2 to convert dry matter to C. For the other 60% of the landscape that burns and is not peatland, we assumed that 3.7 kg of Dry Matter m^{-2} (1.85 kg of C m^{-2}) is combusted regardless of the forest successional stage or the preceding fire history.

Model Spin-Up

To establish realistic initial conditions for the model, we performed spin-ups that were >10× the length of a typical fire cycle in Interior Alaska, which is estimated at 105 years since A.D. 1920 (Kasischke et al., 2010). For the first 1000 years of each spin-up, pairs of temperature and precipitation values were chosen at random from the CRU-PIK–derived maps of monthly mean temperature and precipitation during summers between A.D. 1860 and 1990. This was followed by a 392-year additional spin-up that used 1860–1990 repeated in order three times. To check for possible ''sequencing'' artifacts, we compared these results against the result of a single 392-year, randomized climate scenario drawn from the same climate data and found no difference. The resultant stand-age, vegetation, and burn-severity maps were then used as the model's depiction of the region's forested landscape in the year A.D. 1860. To assess the model's sensitivity to initial conditions, we made multiple model runs using a variety of flammability coefficients. Spin-up under conditions of heightened flammability resulted in an 1860 forest with approximately equal spruce and deciduous trees. Reducing flammability resulted in more spruce trees. Regardless of initial flammability, the modeled vegetation converged towards the spruce/deciduous ratio actually observed in the region in 2001 (See **Results** section), demonstrating that ALFRESCO's behavior after A.D. 1860 is quite robust with respect to initial conditions.

Model Verification

After calibrating the model to agree with observed and back-cast estimates of annual area burned, we assessed its performance in two ways. First, we used ALFRESCO to predict the age structure of the present-day forest and then compared this prediction to the age structure inferred from 4800 tree ages obtained along an east-west transect across the region (Mann, Rupp, and Duffy, unpublished data). The close agreement of observed and predicted age structures demonstrates that the model accurately simulates the interactions among climate, fire, and post-fire succession that underlie the age structure of the present-day forest (Fig. 2).

The second way we checked the model's realism was by comparing the exponents of the power-law relationships between frequency and magnitude of annual area burned. As mentioned above, power-law exponents, β, are a sensitive metric for characterizing fire regimes across multiple spatial and temporal scales. ALFRESCO produces estimates of β that are statistically similar to those estimated from the observed and back-cast data between 1988 and 2007 (Fig. 3). We did not use the observed area-burned data collected prior to 1988 in these calculations because of irregularities in the way fire records were kept in those years (Lyons et al., 2008).

Results

FIRE REGIME

ALFRESCO predicts that the annual area burned in Interior Alaska will increase markedly after 2010 compared to the annual areas burned between 1860 and 2010 that are estimated from historical records and from our back-casts of annual area burned (Fig. 4). This steepening occurs under all five GCMs we used as predictors of future climate. In the model, a region-wide increase in burning started around 1990 (Fig. 4), and is predicted to continue until at least 2040. Much of the increase in annual area burned is caused by more frequent mega-fire seasons like those occurring in 2004 and 2005 when >15,000 km^2 burned each summer.

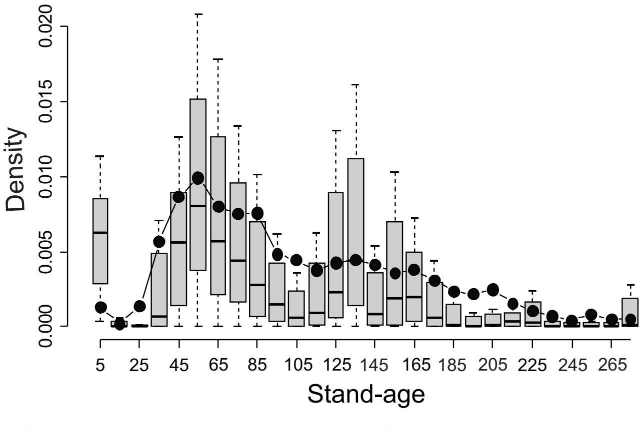

FIGURE 2. The observed distribution of stand ages is represented by the dots with connecting lines. ALFRESCO's predictions are the box plots for each decade. Shaded portions of each box represent the interquartile range, and horizontal bars represent the median.

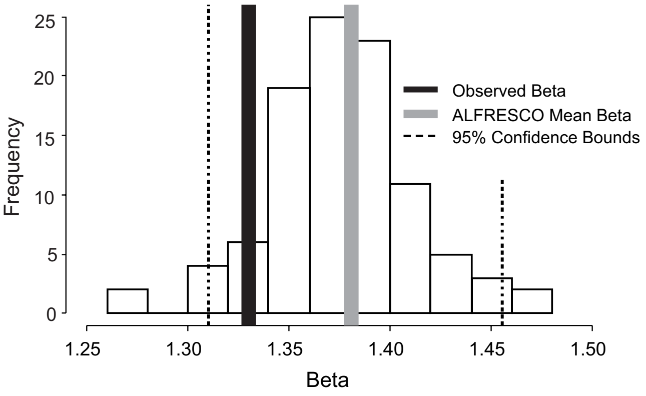

FIGURE 3. Power law exponents (β) for annual area burned, 1988–2007, in Interior Alaska. Observed value of β comes from Alaska Fire Service records and the simulated estimate from 100 ALFRESCO runs covering this same time period.

As annual area burned increases, other aspects of the fire regime are predicted to change as well. Mean fire size will increase, continuing a trend that started in the 1990s (Fig. 5, part a). An increased frequency of sporadic, mega-fire summers like those in 2004 and 2005 will probably typify Interior Alaska's fire regime over the next 40 years. ALFRESCO also predicts that the variance in the annual area burned will increase until ca. 2020 when the forest begins to stabilize under its new fire regime (Fig. 5, part b).

FOREST STRUCTURE AND COMPOSITION

According to the ALFRESCO model, climate-driven changes in the fire regime are causing striking changes in the structure of Alaska's forests already today, and these changes are predicted to continue over the next 30 years. Increased burning is removing old-aged stands, which is causing a decline in both the mean stand age and the spatial variability of stand ages across the landscape (Fig. 6). In 2001, white and black spruce together comprised more than half of all forest stands in Interior Alaska (Homer et al., 2004). Our retrospective modeling suggests spruce were even more abundant between 1920 and 1990 when they comprised roughly two-thirds of all stands (Fig. 7). Looking ahead, ALFRESCO predicts that changes in the fire regime will cause deciduous plants (aspen, birch, willow, and herbaceous taxa) to replace spruce at many sites. In the model, the magnitude of fire-conducive climatic changes predicted by the GCMs overwhelms the potential, negative feedback between the increased spatial coverage of less flammable, deciduous vegetation and annual area burned. The replacement of spruce by deciduous species is predicted to slow by ca. 2020, by which time deciduous vegetation cover is predicted to be nearly twice as abundant as spruce.

ENERGY FLUXES

Because ALFRESCO is spatially explicit and tracks fire history and successional stages, we can quantify the biophysical ef-

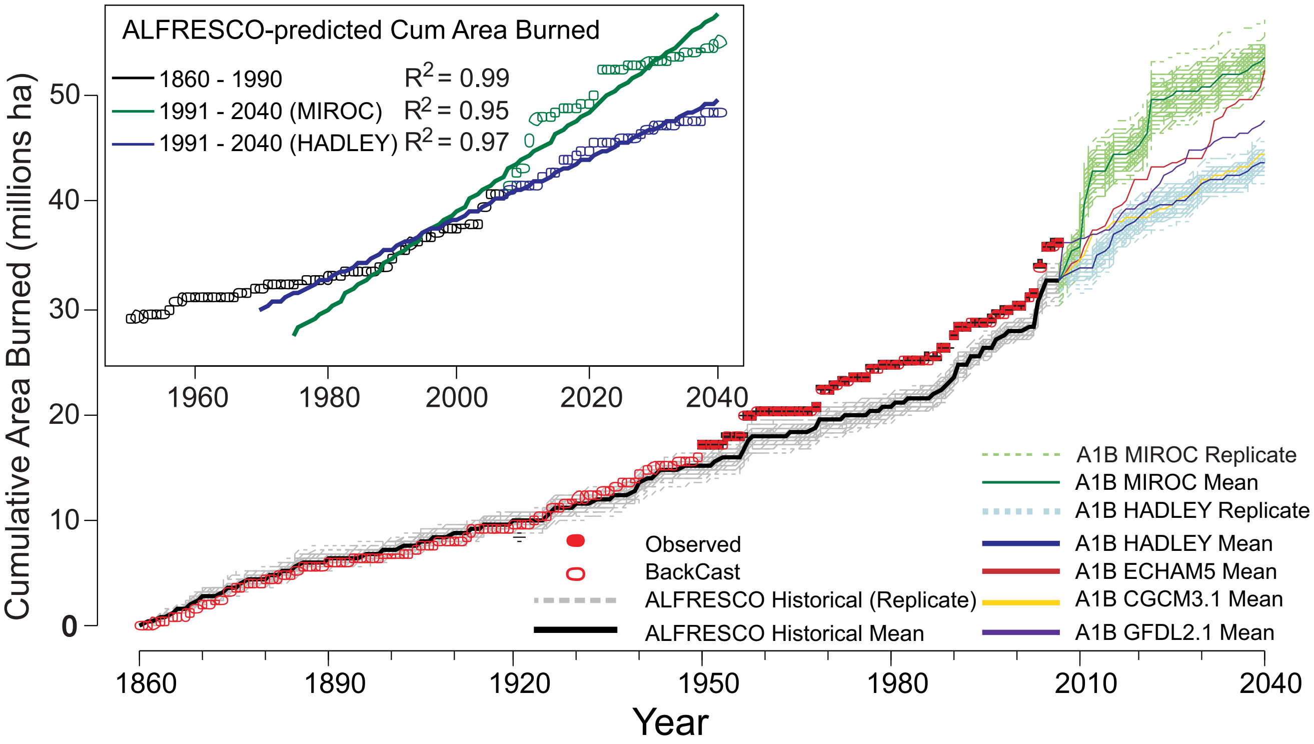

FIGURE 4. Cumulative annual area burned in interior Alaska, A.D. 1860–2040. Annual area burned is described from historical records, from back-casts based on a climate–area burned statistical relationship, and from our modeling results utilizing climate predictions from the five global circulation models that best apply in Alaska. For the period 1950–2007, model estimates of area burned differ from the observed because fire managers' estimates ignore unburned inclusions within overall fire perimeters. The inset details change in the slope of cumulative area burned.

fects of the predicted changes in fire regime and forest composition across the entire shifting mosaic of fires and post-fire vegetation that covers Interior Alaska (Fig. 8). The predicted net increase in summertime albedo caused by the proliferation of deciduous vegetation at the expense of spruce across Interior Alaska could lower net solar radiation in summer by 3–5 W m^{-2} by 2020 (Fig. 8, part a), a decline of 6–8% from present values. This albedo modification is comparable in magnitude (though opposite in sign) to the estimated effects of earlier snowmelt in springtime (Euskirchen et al., 2009). In response to changes in summertime albedo, ALFRESCO predicts that sensible heat fluxes will decline (Fig. 8, part b). Note that these results do not address how changes in vegetation cover could affect snow-season albedos and energy fluxes (Euskirchen et al., 2010). In contrast to net radiation, summertime fluxes of latent heat are predicted to increase because deciduous leaves have higher evapotranspiration rates than conifer needles (Beringer et al., 2005; Amiro et al., 2006) (Fig. 8, part c). An increase in burned-over, blackened ground will likely cause a transient increase of 3–6% in heat flux into the ground in summer (Fig. 8, part d).

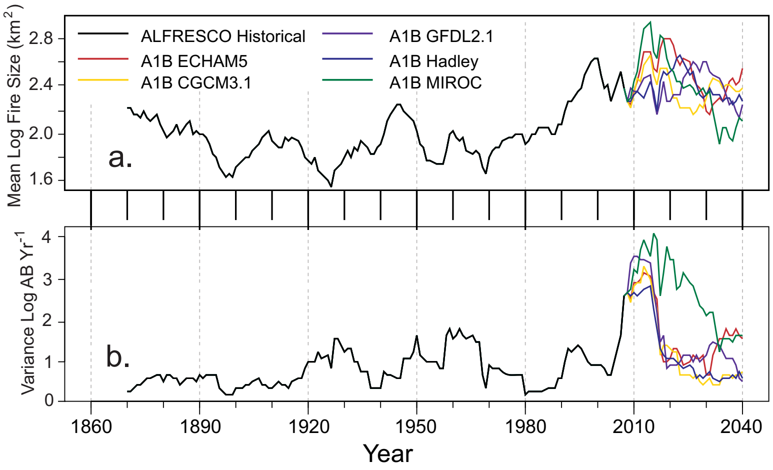

FIGURE 5. Impacts of the changing fire regime on (a) mean fire size and on (b) variance in annual area burned.

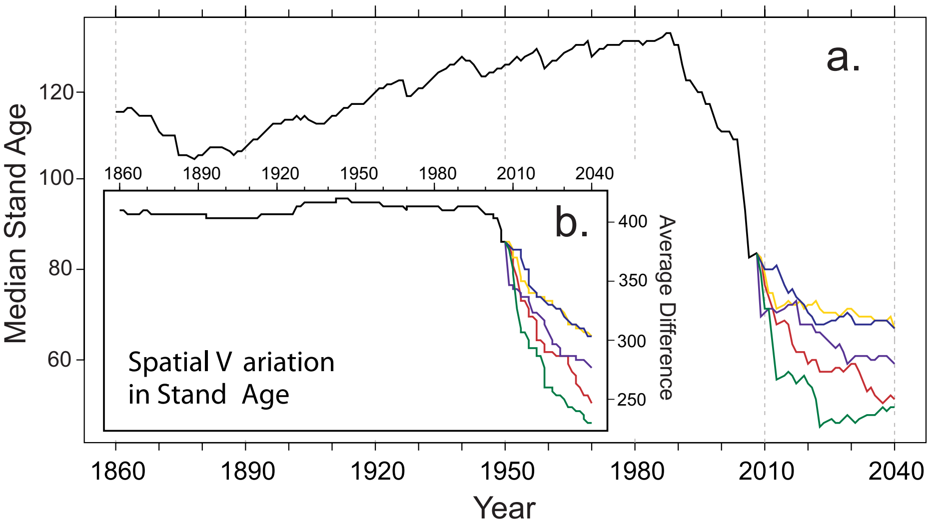

FIGURE 6. Impacts of the changing fire regime on median stand age. Inset shows spatial variability in stand ages expressed as average difference between the 90th-percent quantile and the 10th-percent quantile of time-since-last-fire in all pixels on the model landscape in a given year. Colored lines represent the same GCM scenarios as in Figure 4.

CARBON EMISSIONS

The altered fire regime and vegetation cover that ALFRESCO predicts could have dramatic effects on the carbon balance of Interior Alaska's forest. Burning releases an immediate pulse of C to the atmosphere, followed by a decade of declining C emission from decaying vegetation (Welp et al., 2006) (Fig. 9). C sequestration occurs most rapidly in the first 10–40 years after a fire during the initial stages of revegetation (O'Neill et al., 2003; Welp et al., 2006). By integrating C emission and sequestration across the disturbance/recovery mosaic of the entire forest, ALFRESCO is able to estimate the net impacts of changes in fire regime and vegetation composition on C balance (Fig. 9). Results suggest that starting ca. 1990, Interior Alaska became a net source of C to the atmosphere. This was accentuated in the mega-fire years of 2004 and 2005, and Interior Alaska is predicted to continue to be a C source until sometime after 2020 (Fig. 9). This predicted 25- to 50-year pulse of heightened C emissions results from the release of C that accumulated in Interior Alaska's vegetation and soils over preceding centuries when the climate was less favorable for burning.

Discussion

These modeling results support previous inferences based on assessments of ecological sensitivities (Chapin et al., 2004) and on tree-growth responses (Beck et al., 2011) that a critical ecological threshold is now being crossed in Interior Alaska's boreal forest. The key processes that have created this threshold event can be inferred from the interactions between fire, forest succession, and climate change depicted in the ALFRESCO model. As previously suggested by Duffy et al. (2005) and Kasischke et al. (2010) and others, the first and largest impact of changing climate in Interior Alaska is occurring through the climate-fire linkage. This is happening because slight changes in summer weather are capable of triggering large changes in the fire regime. Specifically, annual area burned increases nonlinearly as summer weather becomes warmer and drier.

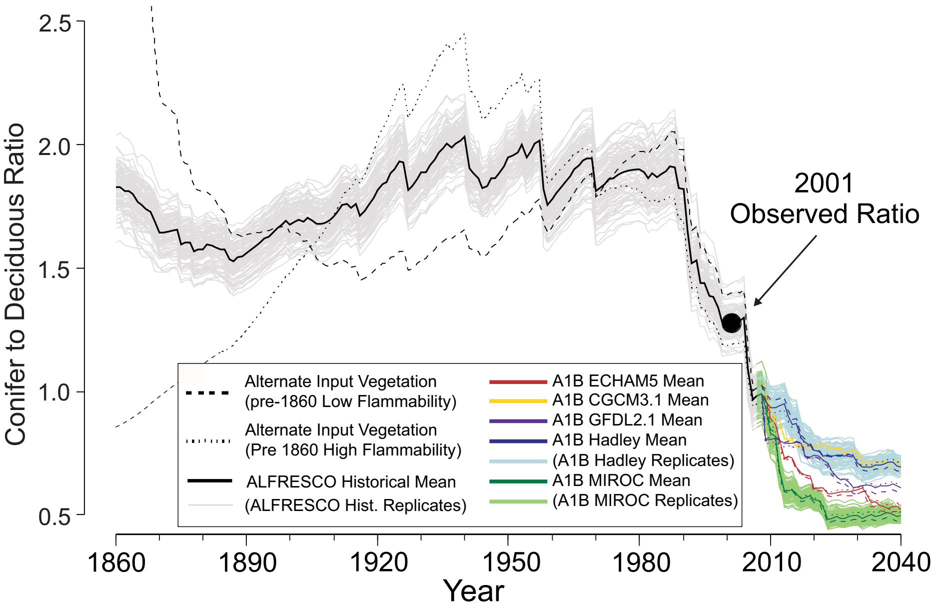

FIGURE 7. Observed, reconstructed, and predicted ratios of spruce to deciduous species. Black dot indicates the spruce/deciduous ratio in 2001 that was estimated by satellite mapping of vegetation (Homer et al., 2004). Different model spin-up trajectories are shown as dashed lines that rapidly converge, illustrating the model's robustness under different starting conditions.

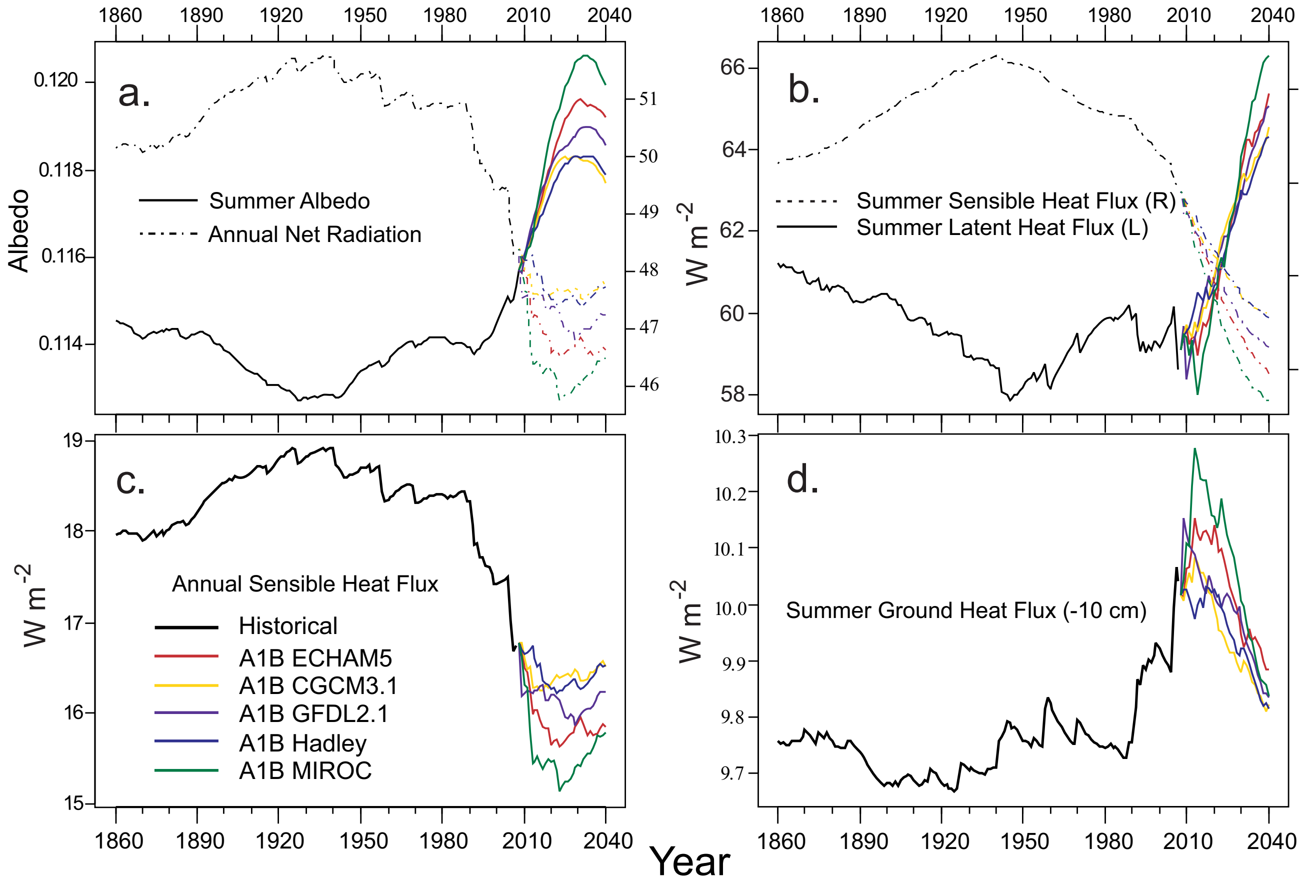

FIGURE 8. Predicted biophysical impacts in the Alaskan boreal forest. Previous observations of how biophysical parameters change along post-fire chronosequences in Alaska are integrated with simulations of burning and forest succession to infer changes in (a) summertime albedo and annual net solar radiation, (b) annual sensible heat flux, (c) summertime fluxes of sensible heat and latent heat, and (d) summertime heat flux into the ground.

Another important threshold that emerges from the ALFRESCO model is the outcome of interactions between fire frequency and post-fire succession. Increasing annual area burned shortens the temporal window available for post-fire succession, which favors plant species with shorter juvenile periods. Once the time between successive fires drops below a threshold of 60–80 years, spruce trees are increasingly excluded from this forest. Fires intervene before the slower growing, longer-lived spruce can replace the faster growing deciduous species in the forest canopy (Kurkowski et al., 2008).

The impacts of both the climate-area burned relationship and its domino effect on forest succession are accentuated by the ecological legacy of fuels accumulated under preceding fire regimes that were characterized by less frequent and smaller fires. The more fuel that is available, the greater is the surge in burning that occurs as climate warms, and the less likely it is that a spruce canopy will have time to develop. According to the ALFRESCO model, the ecological threshold now being crossed in Interior Alaska is the result of a fuel-load legacy encountering rapid summertime warming, which together are triggering the nonlinear climate-fire and fire-succession processes just described.

Why doesn't a negative feedback kick in to reduce flammability as deciduous vegetation becomes more widespread on the landscape? As every firefighter knows, deciduous plants tend to be less flammable than spruce trees. In the ALFRESCO model, the scenarios of future climate are so warm and dry that they overwhelm the potential negative feedback caused by increases in deciduous vegetation cover. This result is not surprising given that much of the increase in burning is predicted to occur during extreme fire seasons like those of 2004 and 2005 when fires were able to burn spruce and deciduous stands at similar frequencies (Kasischke et al., 2010).

WARNING SIGNS OF IMPENDING THRESHOLDS?

Our results identify several warning signs that might prove useful for detecting ecological regime shifts elsewhere. The predicted shift to a deciduous state in Interior Alaska was preceded by decades of accumulation of old (>100 years) conifer stands on the landscape. This created high levels of spatial variation in stand ages (Fig. 6, part b). Because of their heightened flammabilities, the presence of these old stands predisposed the forest to extensive fires and lowered its overall resistance (the capacity of a system to absorb stresses and continue functioning) to climate-induced perturbations to its fire regime. When combined with the ongoing climate trend, the 1990 age structure of this forest was unstable because annual area burned inevitably increased as summers became warmer and drier. Old spruce stands were first to burn because of their higher flammability, and their loss increased the coverage of younger stands, which caused the spatial variability of stand ages to decline. Based on these results, we speculate that in ecosystems where the probability of stand-replacing disturbances increases with stand age, heightened variability in stand age is a warning sign of lowered resistance and an impending threshold.

Increasing variance sometimes precedes ecological transitions (Carpenter and Brock, 2006; Contamin and Ellison, 2009). In Interior Alaska, interannual variance in area burned appears to be peaking now as the forest shifts towards a new, deciduous-dominated state (Fig. 5, part b). This is happening because fires characteristic of both the old and the new fire regime occur. In effect, the forest is now straddling two different attractor basins as it transits into a new disturbance regime.

EXISTING ANALOGS TO THE FUTURE FOREST?

The future forest predicted by the ALFRESCO model has both prehistoric and present-day analogs. A poplar-dominated, parkland vegetation was widespread in Interior Alaska during the early Holocene (Higuera et al., 2009) when a precession-driven summer insolation anomaly caused summertime temperatures 1–2 °C higher than today (Kaufman et al., 2004).

A present-day analogue for Alaska's future forests may be the boreal mixedwoods of south-central Canada (Hogg and Hurdle, 1995; Cumming, 2001; Schneider et al., 2009) that grow under a climate slightly warmer and drier than Interior Alaska is today. Aspen dominates the boreal mixedwoods, white spruce is restricted to mesic sites (Alberta Natural Regions Committee, 2006), and lightning-caused fires are common (Weir et al., 2000).

How close is the analogy between Alberta's mixedwoods and Interior Alaska's future forests? To address this question we compared the power-law exponents describing the frequency-magnitude relationships of predicted fires in Interior Alaska and recent fires in the boreal mixedwoods (Fig. 10). ALFRESCO predicts that the β exponent declines rapidly in Interior Alaska after 1990, falling to values between 1.4 and 1.5 by 2030. In the mixedwoods of northern Alberta between 1961 and 2007, β was 1.48 ($r^2 = 0.99$) for all fires >0.5 km^2 in size (Government of Alberta Sustainable Resources Development Wildfire Information, 2009). Alaska's declining β is the result of an increase in the relative frequency of larger fires, which is consistent with both a predicted increase in fire size (Fig. 5) and with the trajectory of the historical fire data (Kasischke et al., 2010). The close match between the frequency-magnitude relationship of fires in Alberta's boreal mixedwoods between 1961 and 2007 and that predicted by ALFRESCO for Interior Alaska between 2010 and 2040 supports the idea that Interior Alaska's forest and its fire regime are changing to resemble Alberta's present mixedwoods.

LOCAL IMPLICATIONS

Besides the prospect of more mega-fire seasons like those in 2004 and 2005, one of the most troubling implications of our modeling results concerns the predicted increase of heat flux into the ground (Fig. 8, part d). The transient spike that is predicted in ground heat flux during summer implies an increase in thermokarsting throughout the region. Thermokarst is the alteration of existing topography by the thawing of underlying permafrost. In Interior Alaska, thermokarsting often occurs after fires because burning removes organic matter that previously shaded or insulated the ground (Jorgenson and Osterkamp, 2005; Jorgenson et al., 2010). Thermokarst may continue for decades to a century after a fire (Viereck et al., 2008) and it can increase trace gas emissions by thawing organic-rich sediment and disrupting stream networks (Schuur et al., 2008, 2009). Thermokarsting can also enhance Hg-methylation rates by creating waterlogged conditions (Grigal, 2003; Turetsky et al., 2006).

GLOBAL IMPLICATIONS

Our results suggest that Interior Alaska switched from being a C sink to a C source starting ca. 1990 accompanied by a 20- to 30-year pulse of heightened C emissions (Fig. 9). These findings are consistent with the results of other studies using different models that suggest boreal North America shifted from being a carbon sink to a source at the end of the 20th century (Balshi et al., 2007, 2009; McGuire et al., 2009). If boreal forests in other parts of the subarctic undergo similarly radical shifts in their fire and successional processes, a significant positive effect on global warming seems likely, especially if these changes in fire regimes and vegetation composition are accompanied by decreases in annually averaged albedo caused by lengthening of the snow-free season (Euskirchen et al., 2010). We have resisted applying our regionally summed estimates of future C emissions, albedo, and heat fluxes to estimating Alaska's contributions to global radiative forcing. While interesting, these back-of-the-envelope calculations have enormous error terms. For example, Randerson et al. (2006) estimated the total forcing derived from a fire in Interior Alaska to be 18 ± 42 W m^{-2} in the year following the fire and -2.4 ± 2.3 W m^{-2} during years 0–80 post-fire.

HOW GOOD IS ALFRESCO?

Models are deliberate abstractions of reality. A good model is one that quantifies what we think we know about how a natural system works in the simplest possible manner leading to meaningful results. Meaningful results either expose major gaps in our current understanding and/or make plausible predictions about what could happen to the system in the future. One can add realistic embellishments to a model *ad infinitum* without improving on these two main purposes.

The ALFRESCO model has several strengths and several weaknesses. Its greatest strength is its ability to synthesize the ecological states of myriads of separate, post-fire successional disturbance patches across a vegetation mosaic of regional extent. ALFRESCO's other strength is its ability to depict climate-fire-vegetation interactions, including feedbacks caused by the vegetation mosaic's changing flammability due to successional stage.

ALFRESCO has two possible weaknesses at present. The first one involves the stationarity of the relationship between summer climate and annual area burned as deduced by Duffy et al. (2005). This relationship may change in the future as the region's vegetation and climate both change. Twenty years hence it is possible that snowmelt may have advanced a month, June mean temperature may be significantly warmer, and the onset of summer rains may

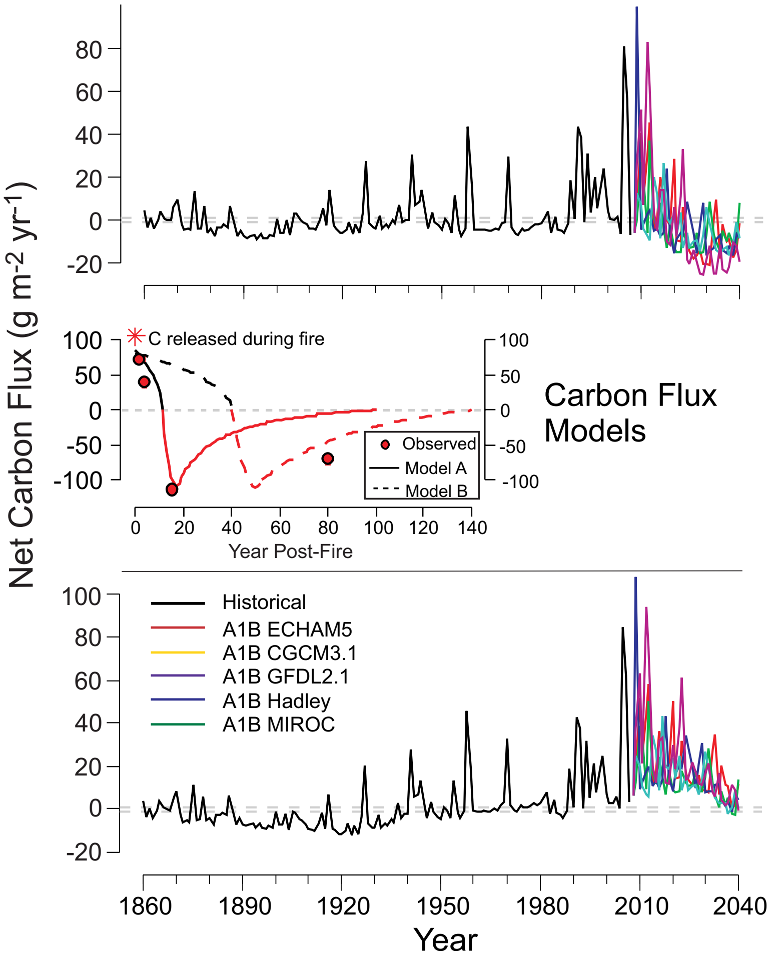

FIGURE 9. Net C emissions from Interior Alaska. Inset shows two limiting estimates of the C budget in the aftermath of fires taken from studies of post-fire chronosequences in Interior Alaska (O'Neill et al., 2003; Welp et al., 2006). Negative values of C flux reflect net sequestration in living and dead biomass, and positive values represent net release of C to the atmosphere by burning and by decay during the first several decades after a fire. In both scenarios there is a transient spike in C emitted to the atmosphere from Interior Alaska beginning ca. 1990 and tailing off ca. 2040.

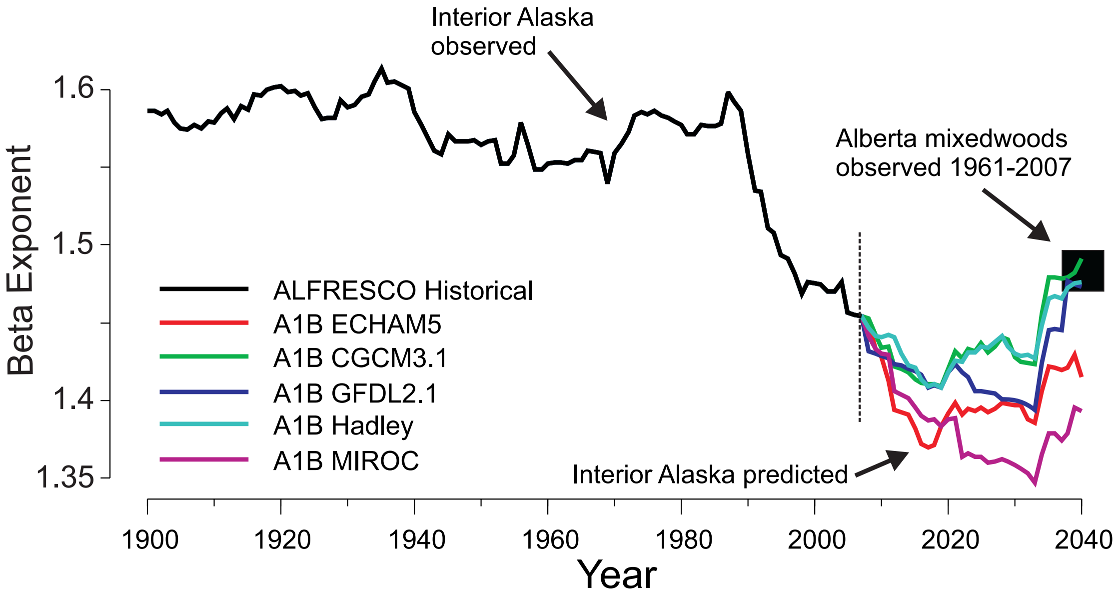

FIGURE 10. Simulated changes in the power law relationship between frequency and size of annual area burned in Alaska. β's are estimated from ALFRESCO reconstructions of annual area burned in the years prior to 2008 and from predicted areas burned after 2008. Each β in the time series is derived across the fire size distribution formed by the current year plus the 29 years prior. The 30-year moving window of β in Alaska declines rapidly after 1990 and is predicted to stabilize ca. 2040 at values between 1.4 and 1.55. Recent fires in the mixedwoods of northern Alberta, a modern analog for the future forests of interior Alaska, have a β of 1.48.

routinely be delayed into September. Sizable changes in the climate of Interior Alaska are indicated by tree-ring studies that cover the last 200 years (Barber et al., 2004). Such changes could alter how ALFRESCO now predicts annual area burned from climate parameters.

ALFRESCO's second potential weakness involves the way it depicts post-fire succession. The model now assumes that all vegetated sites, regardless of their pre-fire vegetation cover, undergo ''species-dominance relay'' in which all plants establish within a few decades after a fire. The faster growing, deciduous species then dominate the canopy until either the next fire destroys them or spruce trees slowly emerge from the understory. Recent work by Kurkowski et al. (2008) and Johnstone et al. (2010) shows that another successional pathway, self-replacement, is important in certain settings. One such setting is hilly terrain where low summer sun angles cause steep gradients in incoming solar radiation and so create persistent safe sites for species possessing different physiological tolerances (Kurkowski et al., 2008). Another setting where self-replacement may be important is peatland where fires are unable to alter the pre-existing soil and drainage conditions, and thus black spruce communities immediately reestablish (Johnstone et al., 2010). In these two settings, it could be that more frequent and severe fires will have little impact on the landscape's overall conifer/deciduous ratio. It is possible that incorporating a self-replacement pathway of post-fire succession into the ALFRESCO model will reveal a larger inertia in the response of vegetation to climate change. This might reduce the speed and magnitude of the ecological changes predicted here.

Conclusions

Results of the ALFRESCO forest-disturbance model support previous suggestions that a major ecological regime shift is now underway in Interior Alaska. The formerly spruce-dominated vegetation seems to be responding to rapid climate warming by shifting back towards its early Holocene state, which was similar to the boreal mixedwoods now growing in southern Canada. Interior Alaska's forest started across this ecological threshold ca. 1990, and the transition is predicted to be completed by 2040. Our modeling results suggest that larger and more frequent wildland fires are an important driver of this ecological regime shift. The changing fire regime is the result of the intersection of warming summer climate with the legacy of fuel accumulated over preceding decades of less frequent fires. Crossing the ecological threshold between conifer forest and boreal mixedwoods will have large impacts on the biophysical properties of Interior Alaska, including its heat fluxes and carbon budget, with possible positive feedbacks to global warming.

Acknowledgments

Partial funding came from National Science Foundation grant ARC-0902169. We thank Randy Jandt, Jane Wolken, Chris Fastie, Pieter Beck, Glenn Juday, and Janet Wilmshurst for useful discussions in the course of this project.

References Cited

Alberta Natural Regions Committee, 2006: *Natural Regions and Subregions of Alberta*. Compiled by D. J. Downing and W. W. Pettapiece. Government of Alberta Publication Number T/852.

Amiro, B. D., Orchansky, A. L., Barr, A. G., Black, T. A., and Chambers, S. D., 2006: The effect of post-fire stand age on the boreal forest energy balance. *Agricultural and Forestry Meteorology*, 140: 41–50.

Balshi, M. S., McGuire, A. D., Zhuang, Q., Melillo, J., and Kicklighter, D. W., 2007: The role historical fire disturbance in the carbon dynamics of the pan-boreal region: a process-based analysis. *Journal of Geophysical Research*, 112: G02029, http://dx.doi.org/10.1029/2006JG000380.

Balshi, M. S., McGuire, A. D., Duffy, P., Flannigan, M., Kicklighter, D. W., and Melillo, J., 2009: Vulnerability of carbon storage in North American boreal forests to wildfires during the 21st century. *Global Change Biology*, 15: 1491–1510, http://dx.doi.org/10.1111/j.1365-2486.2009.01877.x.

Barber, V. A., Juday, G. P., and Finney, B. P., 2000: Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. *Nature*, 405: 668–673.

Barber, V. A., Juday, G. P., Finney, B. P., and Wilmking, M., 2004: Reconstruction of summer temperatures in Interior Alaska from tree-ring proxies: evidence for changing synoptic climate regimes. *Climatic Change*, 63: 91–120.

Beck, P. S. A., Juday, G. P., Alix, C., Barber, V. A., Wonslow, S. E., Sousa, E. E., Heiser, P. A., Herriges, J. D., and Goetz, S. J., 2011: Changes in forest productivity across Alaska consistent with biome shift. *Ecological Research Letters*, http://dx.doi.org/10.1111/j.1461-0248.2011.01598.x.

Beringer, J., Chapin, F. S., III, Thompson, C. C., and McGuire, A. D., 2005: Surface energy exchanges along a tundra-forest transition and feedbacks to climate. *Agricultural and Forestry Meteorology*, 131: 143–161.

Boby, L. A., Schuur, E. A. G., Mack, M. C., Verbyla, D., and Johnstone, J. F., 2010: Quantifying fire severity, carbon, and nitrogen emissions in Alaska's boreal forest. *Ecological Applications*, 20(6): 1633–1647.

Brubaker, L. B., Higuera, P. E., Rupp, T. S., Olson, M. A., and Anderson, P. M., 2009: Linking sediment-charcoal records and ecological modeling to understand causes of fire-regime change in boreal forests. *Ecology*, 90: 1788–1801.

Bureau of Land Management–Alaska Fire Service, 2008: Large Fire Database: http://agdc.usgs.gov/data/blm/fire/. (access date 9/2009).

Calef, M. P., McGuire, A. D., Epstein, H. E., Rupp, T. S., and Shugart, H. H., 2005: Analysis of vegetation distribution in Interior Alaska and sensitivity to climate change using a logistic regression approach. *Journal of Biogeography*, 32: 863–878.

Carpenter, S. R., and Brock, W. A., 2006: Rising variance: a leading indicator of ecological transition. *Ecology Letters*, 9: 311–318.

Chapin, F. S., III, Callaghan, T. V., Bergeron, Y., Fukuda, M., Johnstone, J. F., Juday, G., and Zimov, S. A., 2004: Global change and the boreal forest: thresholds, shifting states or gradual change? *Ambio*, 33: 361–365.

Chapin, F. S., III, Oswood, M. W., and Van Cleve, K., 2006: *Alaska's Changing Boreal Forest*. New York: Oxford University Press.

Chapin, F. S., III, McFarland, J., McGuire, A. D., Euskirchen, E. S., and Ruess, R. W., 2009: The changing global carbon cycle: linking plant–soil carbon dynamics to global consequences. *Journal of Ecology*, 97: 840–850.

Chapin, F. S., III, McGuire, A. D., Ruess, R. W., Hollingsworth, T. N., Mack, M. C., Johnstone, J. F., Kasischke, E. S., Euskirchen, E. S., Jones, J. B., Jorgenson, M. T., Kielland, K., Kofinas, G. P., Turetsky, M. R., Yarie, J., Lloyd, A. H., and Taylor, D. L., 2010: Resilience of Alaska's boreal forest to climatic change. *Canadian Journal of Forest Research*, 40: 1360–1370.

Contamin, R., and Ellison, A. M., 2009: Indicators of regime shifts in ecological systems: what do we need to know and when do we need to know it? *Ecological Applications*, 19: 799–816.

Cumming, S. G., 2001: Forest type and wildfire in the Alberta boreal mixedwood: what do fires burn? *Ecological Applications*, 11: 97–110.

Duffy, P. A., Walsh, J. E., Graham, J. M., Mann, D. H., and Rupp, T. S., 2005: Impacts of large-scale atmospheric-ocean variability on Alaskan fire season severity. *Ecological Applications*, 15: 1317–1330.

Duffy, P. A., Epting, J., Graham, J. M., Rupp, T. S., and McGuire, A. D., 2007: Analysis of burn severity patterns using remotely sensed data. *International Journal of Wildland Fire*, 16: 277–284.

Euskirchen, E. S., McGuire, A. D., and Chapin, F. S., III, 2007: Energy feedbacks of northern high-latitude ecosystems to the climate system due to reduced snow cover during 20th century warming. *Global Change Biology*, 13: 2425–2438, http://dx.doi.org/10.1111/j.13652486.2007.01450.x.

Euskirchen, E. S., McGuire, A. D., Chapin, F. S., III, and Thompson, C. C., 2009: 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., McGuire, A. D., Chapin, F. S., III, and Rupp, T. S., 2010. The changing effects of Alaska boreal forests on the climate system. *Canadian Journal of Forest Research*, 40: 1336–1346.

French, N. H. F., Goovaerts, P., and Kasischke, E. S., 2004: Uncertainty in estimating carbon emissions from boreal forest fires. *Journal of Geophysical Research*, 109: D14S08, http://dx.doi.org/10.1029/2003JD003635.

Government of Alberta Sustainable Resource Development Wildfire Information, 2009: http://www.srd.alberta.ca/UpdatesFireAlerts/WildfireStatus/HistoricalWildfireInformation/ (access date 9/2009).

Grigal, D. F., 2003: Mercury sequestration in forests and peatlands: a review. *Journal of Environmental Quality*, 32: 393–405.

Harden, J. W., Trumbore, S. E., Stocks, B. J., Hirch, A., Gower, S. T., O'Neill, K. P., and Kasischke, E. S., 2000: The role of fire in the boreal carbon budget. *Global Change Biology*, 6: 174–184.

Harden, J. W., Meier, R., Silapaswan, C., Swanson, D. K., and McGuire, A. D., 2001: Soil drainage and its potential for influencing wildfires in Alaska. *In* Galloway, J. P. (ed.), *Studies by the U.S. Geological Survey in Alaska. U.S. Geological Survey Professional Paper*, 1687: 139–144.

Harden, J. W., Manies, K. L., Turetsky, M. R., and Neff, J. C., 2006: Effects of wildfire and permafrost on soil organic matter and soil climate in Interior Alaska. *Global Change Biology*, 12: 2391–2403.

Higgins, P., Mastrandea, M. D., and Schneider, S. H., 2002: Dynamics of climate and ecosystem coupling and multiple equilibria. *Philosophical Transactions of the Royal Society of London*, 357B: 647–655.

Higuera, P. E., Brubaker, L. B., Anderson, P. M., Hu, F. S., and Brown, T. A., 2009: Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs*, 79: 201–219.

Hinzman, L. D., Bettez, N. D., Bolton, W. R., Chapin, F. S., and Dyurgerov, M. B., 2005: Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climate Change*, 72: 251–298.

Hogg, E. H., and Hurdle, P. A., 1995: The aspen parkland in western Canada: a dry-climate analogue for the future boreal forest? *Water, Air, and Soil Pollution*, 82: 391–400.

Homer, C., Huang, C., Yang, L., Wylie, B., and Coan, M., 2004: Development of a 2001 national land-cover database for the United States. *Photogrammetric Engineering and Remote Sensing*, 70: 829–840.

Johnstone, J. F., and Chapin, F. S., III, 2006: Fire interval effects on successional trajectory in boreal forests of northwest Canada. *Ecosystems*, 9: 268–277.

Johnstone, J. F., Hollingsworth, T. N., Chapin, F. S., III, and Mack, M. C., 2010: Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, 16: 1281–1295.

Jorgenson, M. T., and Osterkamp, T. E., 2005: Response of boreal ecosystems to varying modes of permafrost degradation. *Canadian Journal of Forest Research*, 35: 2100–2111.

Jorgenson, M. T., Romanovsky, V., Harden, J., Shur, Y., O'Donnell, J., Schuur, E. A. G., Kanevskiy, M., and Marchenko, S., 2010: Resilience and vulnerability of permafrost to climate change. *Canadian Journal of Forest Research*, 40: 1219–1236.

Kasischke, E. S., and Turetsky, M. R., 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, http://dx.doi.org/10.1029/2006GL025677.

Kasischke, E. S., Williams, D., and Barry, D., 2002: Analysis of the patterns of large fires in the boreal forest region of Alaska. *International Journal of Wildland Fire*, 11: 131–144.

Kasischke, E. S., Verbyla, D. L., Rupp, T. S., McGuire, A. D., Murphy, K. A., Jandt, R., Allen, J. L., Hoy, E. E., Duffy, P. A., Calef, M., and Turetsky, M. R., 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., Ager, T. A., Anderson, N. J., Anderson, P. M., Andrews, J. T., Bartlein, P. J., Brubaker, L. B., Coats, L. L., Cwynar, L. C., Duvall, M. L., Dyke, A. S., Edwards, M. E., Eisner, W. R., Gajewski, K., Geirsdóttir, A., Hu, F. S., Jennings, A. E., Kaplan, M. R., Kerwin, M. W., Lozhkin, A. V., MacDonald, G. M., Miller, G. H., Mock, C. J., Oswald, W. W., Otto-Bliesner, B. L., Porinchu, D. F., Rühland, K., Smol, J. P., Steig, E. J., and Wolfe, B. B., 2004: Holocene thermal maximum in the western Arctic (0–180°W). *Quaternary Science Reviews*, 23: 529–560.

Kurkowski, T. A., Mann, D. H., Rupp, T. S., and Verbyla, D. L., 2008: Relative importance of different secondary successional pathways in an Alaskan boreal forest. *Canadian Journal of Forest Research*, 38: 1911–1923.

Leemans, R., and Cramer, W. P., 1991: The IIASA database for mean monthly values of temperature, precipitation, and cloudiness on a global terrestrial grid. Laxenburg, Austria: International Institute for Applied Systems Analysis, Report No. RR-91-18.

Lenton, T. M., Held, H., Kriegler, E., Hall, J. W., and Lucht, W., 2008: Tipping elements in the Earth's climate system. *Proceedings of the National Academy of Sciences of the USA*, 105: 1786–1793.

Liu, H., and Randerson, J. T., 2008. Interannual variability of surface energy exchange depends on stand age in a boreal forest fire chronosequence. *Journal of Geophysical Research*, 113: G01006, http://dx.doi.org/10.1029/2007JG000483.

Liu, H., Randerson, J. T., Linfords, J., and Chapin, F. S., III, 2005: Changes in the surface energy budget after fire in boreal ecosystems of Interior Alaska: an annual perspective. *Journal of Geophysical Research*, 110: D13101, http://dx.doi.org/10.1029/2004JD005158.

Lyons, E. A., Jin, Y., and Randerson, J. T., 2008: Changes in surface albedo after fire in boreal forest ecosystems of Interior Alaska assessed using MODIS satellite observations. *Journal of Geophysical Research*, 113: G02012, http://dx.doi.org/10.1029/2007JG000606.

Malamud, B. D., Millington, J. D. A., and Perry, G. L. W., 2005: Characterizing wildfire regimes in the United States. *Proceedings of the National Academy of Sciences of the USA*, 102: 4694–4699.

Mann, D. H., and Plug, L. J., 1999: Vegetation and soil development at an upland taiga site, Alaska. *Ecoscience*, 6: 272–285.

McGuire, A. D., Stich, S., Clein, J. S., Daragaville, R., and Esser, G., 2001: Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO_2, climate and land-use effects with four process-based ecosystem models. *Global Biogeochemical Cycles*, 15: 183–206.

McGuire, A. D., Chapin, F. S., Walsh, J. E., and Wirth, C., 2006: Integrated regional changes in arctic climate feedbacks: implications for the global climate system. *Annual Review of Environment and Resources*, 31: 61–91.

McGuire, A. D., Anderson, L. G., Christensen, T. R., Dallimore, S., Guo, L., Hayes, D. J., Hemiann, M., Lorenson, T. D., MacDonald, R. W., and Roulet, N. T., 2009: Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs*, 79: 523–555, http://dx.doi.org/10.1890/08-2025.1.

Mitchell, T. D., and Jones, M. D., 2005: An improved method of constructing a database of monthly climate observations and associated high resolution grids. *International Journal of Climatology*, 25: 693–712.

O'Neill, K. P., Kasischke, E. S., and Richter, D. D., 2003: Seasonal and decadal patterns of soil carbon uptake and emission along an age sequence of burned black spruce stands in Interior Alaska. *Journal of Geophysical Research*, 108(D1): 8155, http://dx.doi.org/10.1029/2001JD000443.

Osterkamp, T. E., and Romanovsky, V. E., 1999: Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes*, 10(1): 17–37, http://dx.doi.org/10.1002/(SICI)1099-1530(199901/03)10:1<17::AID-PPP303>3.0.CO;2-4.

Pueyo, S., 2007: Self-organized criticality and the response of wildland fires to climate change. *Climatic Change*, 82: 131–161.

Randerson, J. T., Liu, H., Flanner, M. G., Chambers, S. D., and Jin, Y., 2006: The impact of boreal forest fire on climate warming. *Science*, 314: 1130–1132.

Rupp, T. S., Chapin, F. S., III, and Starfield, A. M., 2000: Response of subarctic vegetation to transient climatic change on the Seward Peninsula in north-west Alaska. *Global Change Biology*, 6: 541–555.

Rupp, T. S., Olson, M., Adams, L. G., Dale, B. W., and Joly, K., 2006: Simulating the influences of various fire regimes on caribou winter habitat. *Ecological Applications*, 16: 1730–1743.

Rupp, T. S., Chen, X., and Olson, M., 2007: Sensitivity of simulated boreal fire dynamics to uncertainties in climate drivers. *Earth Interactions*, 11: 1–21.

Scheffer, M., 2009: *Critical Transitions in Nature and Society*. Princeton, New Jersey: Princeton University Press, 384 pp.

Scheffer, M., and Carpenter, S., 2003: Catastrophic regime shifts in ecosystems: linking theory to observations. *Trends in Ecology and Evolution*, 18: 648–656.

Schneider, R. R., Hamann, A., Farr, D., Wang, X., and Boutin, S., 2009: Potential effects of climate change on ecosystem distribution in Alberta. *Canadian Journal of Forest Research*, 39: 1001–1010.

Schuur, E. A. G., Bockheim, J., Canadell, J., Euskirchen, E. S., Field, C., Goryachkin, S., Hagemann, S., Kuhry, P., Lafleur, P., Lee, H., Mazhitova, G., Nelson, F., Rinke, A., Romanovsky, V., Shiklomanov, N., Tarnocai, C., Venevsky, S., Vogel, J. G., and Zimov, S. A., 2008: The vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *Bioscience*, 58(8): 701–714, http://dx.doi.org/10.1641/B580807.

Schuur, E. A. G., Vogel, J. G., Crummer, K. G., Lee, H., Sickman, J. O., and Osterkamp, T. E., 2009: The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature*, 459: 556–559.

Soja, A. J., Cofer, W. R., Shugart, H. H., Sukhinin, A. I., and Stackhouse, P. W., 2004: Estimating fire emissions and disparities in boreal Siberia (1998–2002). *Journal of Geophysical Research*, 109: D14S06, http://dx.doi.org/10.1029/2004JD004570.

Soja, A. J., Tchebakova, N. M., French, N. H. F., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E. I., Chapin, F. S., and Stackhouse, P. W., 2006: Climate-induced boreal forest change: predictions versus current observations. *Global and Planetary Change*, 56: 274–296.

Song, W., Wang, J., Satoh, K., and Fan, W., 2006: Three types of power-law distribution of forest fires in Japan. *Ecological Modelling*, 196: 527–532.

Turetsky, M. R., Harden, J. W., Friedli, H. R., Flannigan, M., and Payne, N., 2006: Wildfires threaten mercury stocks in northern soils. *Geophysical Research Letters*, 33: L16403, http://dx.doi.org/10.1029/2005GL025595.

Turquety, S., Logan, J. A., Jacob, D. J., Hudman, R. C., and Leung, F. K., 2007: Inventory of boreal fire emissions for North America in 2004: importance of peat burning and pyroconvective injection. *Journal of Geophysical Research*, 112: D12S03, http://dx.doi.org/10.1029/2006JD00728.

Viereck, L. A., 1983: The effects of fire in black spruce ecosystems of Alaska and northern Canada. *In* Wein, R. W., and MacLean, D. A. (EDS.), *The Role of Fire in Northern Circumpolar Ecosystems*. Chichester, U.K.: Wiley, 201–220.

Viereck, L. A., Werdin-Pfisterer, N. R., Adams, P. A., and Yoshikawa, K., 2008: Effect of wildfire and fireline construction on the annual depth of thaw in a black spruce permafrost forest in Interior Alaska: a 36-year record of recovery. *In* Proceedings of the Ninth International Conference on Permafrost, University of Alaska Fairbanks, Fairbanks, Alaska, 29 June–3 July 2008, 1845–1850.

Walsh, J. E., Chapman, W. L., Romanovsky, V., Christensen, J. H., and Stendel, M., 2008: Global climate model performance over Alaska and Greenland. *Journal of Climate*, 21: 6156–6174.

Weir, J. M. H., Johnson, E. A., and Miyanishi, K., 2000: Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. *Ecological Applications*, 10: 1162–1177.

Welp, L. R., Randerson, J. T., and Liu, H. P., 2006: Seasonal exchange of CO_2 and $\delta^{18}O$-CO_2 varies with postfire succession in boreal forest ecosystems. *Journal of Geophysical Research*, 111: G03007, http://dx.doi.org/10.1029/2005JG000126.

Wendler, G., and Shulski, M., 2009: A century of climate change for Fairbanks, Alaska. *Arctic*, 62: 295–300.

Wendler, G., Shulski, M., and Moore, B., 2010: Changes in the climate of the Alaskan North Slope and the ice concentration of the adjacent Beaufort Sea. *Theoretical and Applied Climatology*, 99: 67–74.

MS accepted April 2012