

## SIMULATING THE INFLUENCES OF VARIOUS FIRE REGIMES ON CARIBOU WINTER HABITAT

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**Abstract.** Caribou are an integral component of high-latitude ecosystems and represent a major subsistence food source for many northern people. The availability and quality of winter habitat is critical to sustain these caribou populations. Caribou commonly use older spruce woodlands with adequate terrestrial lichen, a preferred winter forage, in the understory. Changes in climate and fire regime pose a significant threat to the long-term sustainability of this important winter habitat. Computer simulations performed with a spatially explicit vegetation succession model (ALFRESCO) indicate that changes in the frequency and extent of fire in interior Alaska may substantially impact the abundance and quality of winter habitat for caribou. We modeled four different fire scenarios and tracked the frequency, extent, and spatial distribution of the simulated fires and associated changes to vegetation composition and distribution. Our results suggest that shorter fire frequencies (i.e., less time between recurring fires) on the winter range of the Nelchina caribou herd in eastern interior Alaska will result in large decreases of available winter habitat, relative to that currently available, in both the short and long term. A 30% shortening of the fire frequency resulted in a 3.5-fold increase in the area burned annually and an associated 41% decrease in the amount of spruce-lichen forest found on the landscape. More importantly, simulations with more frequent fires produced a relatively immature forest age structure, compared to that which currently exists, with few stands older than 100 years. This age structure is at the lower limits of stand age classes preferred by caribou from the Nelchina herd. Projected changes in fire regime due to climate warming and/or additional prescribed burning could substantially alter the winter habitat of caribou in interior Alaska and lead to changes in winter range use and/or population dynamics.

**Key words:** Alaskan boreal forest; ALFRESCO; caribou; fire regime; global warming; landscape modeling; Rangifer tarandus; spatially explicit; spruce woodlands; succession.

### INTRODUCTION

North American caribou (*Rangifer tarandus*) are a predominant feature of many northern landscapes. Not only a vital subsistence food source for many, caribou are central to a way of life for some indigenous peoples. Increasingly, too, caribou are important for tourism and outdoor recreation.

Caribou generally range in alpine and/or arctic tundra during the summer and in adjacent forested areas during the winter (Klein 1982). Winter forage of caribou is usually composed of a high proportion of fruticose lichens, often dominated by species characteristic of older successional forest stands (Klein 1982, Boertje 1984, Morneau and Payette 1989). Because lichens, and the older spruce forest communities they occur in, are so important to caribou throughout the North American

boreal forest, it is critical to understand the long-term landscape effects of increased fire frequency that is forecasted with climate warming (Price and Rind 1994, Flannigan et al. 2005).

Fire is a natural and pervasive feature of the boreal forest (Van Cleve et al. 1991, Payette 1992). Fire drives secondary succession and is responsible, in part, for the mosaic of vegetation types and stand ages found across the boreal landscape (Zackrisson 1977, Payette 1992). It is this process of post-fire succession—the interaction between biotic and abiotic factors—that primarily determines the composition and structure of the vegetation at any point in time (Viereck 1973, Van Cleve et al. 1991, 1996). Changes in the fire regime (i.e., frequency, severity, and/or extent) may influence post-fire successional trajectories (Mann and Plug 1999, Fastie et al. 2002) and impact landscape level vegetation patterns (Rupp et al. 2002).

Numerous studies have postulated that decreases in past caribou populations were the result of fire-induced winter range depletion (Leopold and Darling 1953,

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Kelsall 1960, Scotter 1965, Thomas 1969). In contrast, other literature suggests that caribou populations were not appreciably impacted by fire (Scotter 1967, Skoog 1968, Bergerud 1974) and in fact are dependent upon fire to improve their winter range (Johnson and Rowe 1975). This debate resulted in several evaluations of fire influences on winter habitat use by caribou (Miller 1976, 1980, Schaefer and Pruitt 1991, Thomas 1991, Thomas et al. 1998, Joly et al. 2003). The consensus was that caribou avoid areas burned within the last 50–60 years because of a lack of adequate lichen abundance, which is likely due to low productivity of burned sites for several decades following fire (Auclair 1985) and slow lichen growth rates (Scotter 1963, Pegau 1968, Ouzilleau and Payette 1975). Although these conclusions suggest a negative effect of burning for several decades, there is also the recognition that fire in the longer term may be a requisite to maintain high lichen productivity at the landscape level (Miller 1980, Klein 1982, Schaefer and Pruitt 1991, Joly et al. 2003). Klein (1982) stated that, given the high preference of caribou for lichens as a primary winter diet component, destruction of significant portions of lichen habitat by fire will likely have short-term detrimental impacts on caribou populations depending on seasonal range use patterns and availability of alternative undisturbed range. At the same time, the long-term maintenance of vegetation diversity, including rejuvenation of climax forest stands may be dependent upon recurring fire (Zackrisson 1977).

Climate is a primary driver of the boreal fire regime (Johnson 1992), however, fuels, ignition agents, and humans also strongly influence fire activity (Swetnam 1993, Flannigan and Wotton 2001, Flannigan et al. 2005). Climate warming (and its impacts on the fire regime) along with increased pressure to initiate prescribed burning will likely increase the annual area burned in interior Alaska's boreal forest (Rupp et al. 2000a, 2002, Chapin et al. 2003, Joly et al. 2003). The implication for caribou in interior Alaska, assuming an increase in area burned, is that there will likely be a reduction in winter foraging habitat (Joly et al. 2003).

In order to assess the potential response of spruce-lichen forest to a changing fire regime, we used a spatially explicit frame-based model called Alaskan Frame-based Ecosystem Code (ALFRESCO; Rupp et al. 2000b). We addressed the following questions: (1) What are the effects of different fire regimes on the abundance and spatial distribution of spruce-lichen habitat? (2) What are the short-term (defined here as <80 years, which represents the period of time following fire where little or no lichen forage is present [W. B. Collins, B. W. Dale, D. E. McElwain, K. Joly, and L. G. Adams, *unpublished manuscript*]) and long-term ( $\geq 80$  years) consequences of habitat changes on the winter range of the Nelchina caribou herd in the eastern interior of Alaska.

## METHODS

### *Study site*

Our study area was located in the eastern interior region of Alaska (141–143°30' W, 63–64° N) and is roughly bounded by the United States–Canada border to the east and the Alaska Highway to the south (Fig. 1). This region constitutes the current wintering grounds of the 31 000 caribou in the Nelchina herd (Joly et al. 2003). The landscape is dominated by open black spruce (*Picea mariana*) woodlands among gently rolling hills. The region also supports smaller stands of open and closed white spruce (*Picea glauca*) forest and hardwood stands composed of trembling aspen (*Populus tremuloides*) and paper birch (*Betula neoalaskana*). Wetlands and shrub communities are present; as is a limited amount of alpine tundra above 1100 m, but these communities represent a small portion of the landscape relative to the black spruce woodlands (Joly et al. 2003). The region experiences a strong continental climate with long, cold winters and warm, dry summers. Snow accumulates throughout winter and reaches maximum depths in late spring. Mean growing season (May–September) temperature for the region (1954–2003) was 10.3°C with a mean total growing season precipitation of 172 mm. This region is characterized by frequent fire—approximately 20% of the region burned in the 50 years ending in 2003; fire ignition is typically by lightning, but human-caused ignitions including prescribed burns do occur (Joly et al. 2003).

### *Model description*

ALFRESCO was originally developed to simulate the response of subarctic vegetation to a changing climate and disturbance regime (Rupp et al. 2000a, b). Previous research has highlighted both direct and indirect (through changes in fire regime) effects of climate on the expansion rate, species composition, and extent of treeline in Alaska (Rupp et al. 2000a, 2001). Additional research, focused on boreal forest vegetation dynamics, has emphasized that fire-frequency changes—both direct (climate-driven or anthropogenic) and indirect (as a result of vegetation succession and species composition)—strongly influence landscape-level vegetation patterns and associated feedbacks to future fire regime (Rupp et al. 2002, Chapin et al. 2003, Turner et al. 2003). A detailed description of ALFRESCO can be obtained from the literature (Rupp et al. 2000a, b, 2001, 2002). For the purposes of our research, we will focus our description on details relevant to this specific model application.

The boreal forest version of ALFRESCO was developed to explore the interactions and feedbacks between fire, climate, and vegetation in interior Alaska (Rupp et al. 2002). ALFRESCO is a state-and-transition model of successional dynamics that explicitly represents the spatial processes of fire and vegetation recruitment across the landscape (Rupp et al. 2000b). ALFRESCO does not model fire behavior, but rather models the

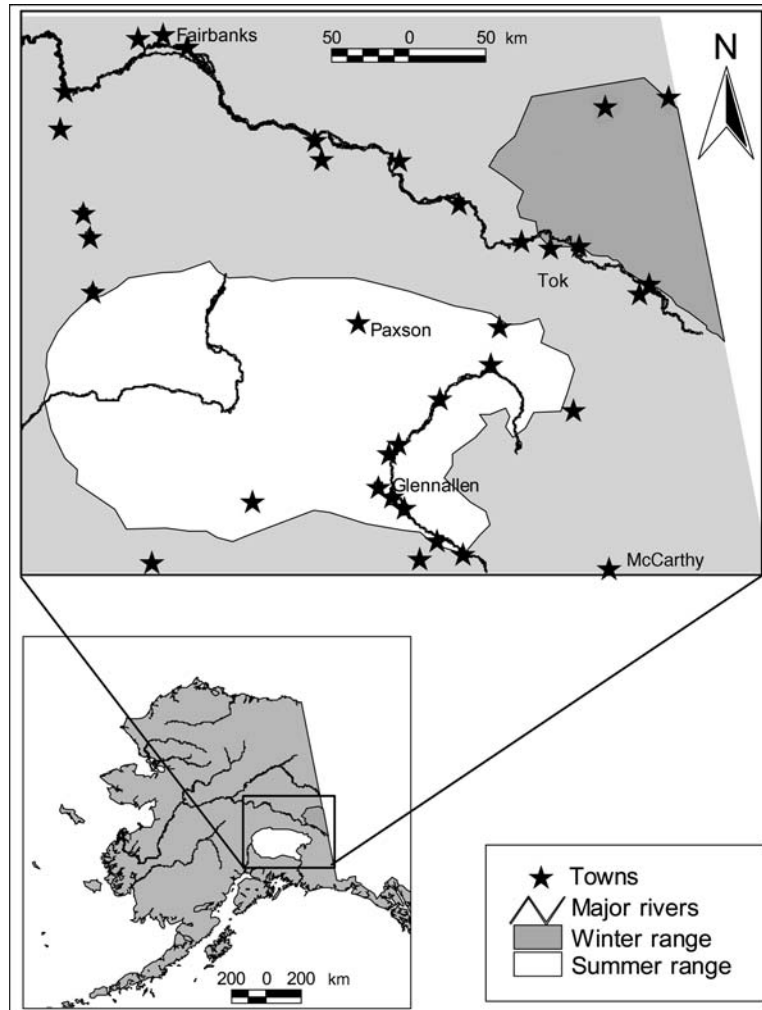


FIG. 1. Location of study region in Alaska and the Nelchina caribou herd's winter (hatched polygon) and summer (open polygon) range. The winter range defines the simulation landscape.

empirical relationship between growing-season climate (e.g., average temperature and total precipitation) and total annual area burned (i.e., the footprint of fire on the landscape). ALFRESCO also models the changes in vegetation flammability that occurs during succession through a flammability coefficient that changes with vegetation type and stand age (Chapin et al. 2003).

The fire regime is simulated stochastically and is driven by climate, vegetation type, and time since last fire (Rupp et al. 2000b). ALFRESCO employs a cellular automaton approach, where an ignited pixel may spread to any of the eight surrounding pixels. "Ignition" of a pixel is determined using a random number generator and as a function of the flammability value of that pixel. Fire "spread" depends on the flammability of the receptor pixel and any effects of natural firebreaks including non-vegetated mountain slopes and large water bodies, which do not burn.

The relative effects of climate on fire were computed using a two-parameter regression analysis similar to

that used by Kasischke et al. (2002). We stratified interior Alaska by ecoregion (Gallant et al. 1995), climate (Fleming et al. 2000), and fire frequency (Kasischke et al. 2002). Fire frequencies and climate variables were computed directly (and respectively) from the Bureau of Land Management, Alaska Fire Service (AFS) large-fire database (Kasischke et al. 2002) and monthly statewide maps of precipitation and temperature (Fleming et al. 2000).

We relied on the literature for computation of the rate at which tundra and deciduous and white and black spruce stands burn (Starfield and Chapin 1996, Cumming 2001). In addition, we utilized stand age data from Yarie (1981), collected in a region of interior Alaska generally representative of our study area. This analysis provided relative burn rates for each vegetation type. A sensitivity analysis of the model revealed that area burned is highly nonlinear with flammability factor (Rupp et al. 2000b). As a result, we performed baseline calibration runs to compute the actual flammability

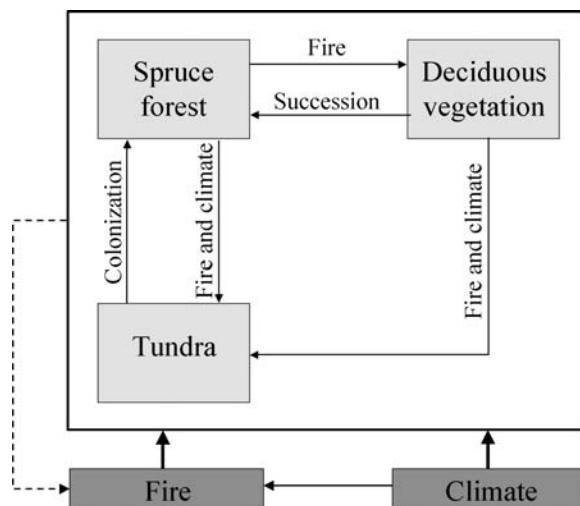


FIG. 2. Conceptual model of frame types (shaded boxes), possible transitions (arrows), and driving processes/factors responsible for the rate and direction of frame transitions (arrow labels).

factors required by the model to produce the computed burn rates for each vegetation type.

The other component modeled by ALFRESCO is vegetation succession. This model version has three vegetation types: upland tundra, spruce forest (we do not discern between black and white spruce forest types), and deciduous vegetation (Fig. 2). Fire normally causes a transition from spruce forest to early successional deciduous vegetation as a result of fire-induced spruce tree mortality (Rupp et al. 2000a). Deciduous vegetation is well suited for immediately colonizing burned areas via root suckers, basal buds, and prolific seeding from surrounding unburned vegetation (Zasada et al. 1992). The deciduous vegetation type is conceptually an early successional spruce forest stage and naturally succeeds to spruce forest, except in circumstances of repeated burning and climatic extremes (Rupp et al. 2000b). Transitional age ranges were identified from the literature (Vioreck et al. 1986, Van Cleve et al. 1991), and a small stochastic element was included to operate around these estimated transition times. For purposes of this research we do not provide details for tundra as the scenarios in this study assume the treeline ecotone to be static, and tundra constitutes a minor component of our study area.

ALFRESCO maintains climatic information for each individual pixel because the vegetation types in our simulations depend on climatic information to determine their internal variables (Rupp et al. 2000b) and fire is modeled based both on climate and vegetation type (i.e., fuel structure and loading [Rupp et al. 2000a, b]). A map of average climate (i.e., growing-season temperature and precipitation) is stored as the basis for the spatial portion of climate. A temporal offset from the average climate is selected at each time step from a normal deviate for the

entire map (i.e., we assume that climatic variability is constant over the selected study region, but not the spatial average [Rupp et al. 2000b]). The climate in each pixel can then be computed and utilized to drive both the fire routine and vegetation dynamics.

#### Model calibration and simulations

We conducted three distinct phases of modeling tasks. The calibration phase involved performing multiple replicate simulations to define parameter values so that fire frequency and extent, extreme fire events, and stand age distribution were similar to those observed in the study area. The “spin-up” phase allowed us to produce a simulation landscape including patch size and stand age structure similar to the current landscape. The final phase used the calibrated parameters and the “spin-up” landscape to simulate the different fire scenarios.

For model calibration we assumed a quasi-dynamic equilibrium state in that both biotic and abiotic components of the model are relatively static (i.e., no directional changes in climate or fire regime) and the response of the system, while not constant, does not inherently produce a significant change in vegetation composition or distribution over time (Starfield and Chapin 1996, Rupp et al. 2000b). Initial model calibration involved two major components: (1) calibrating the fire regime and (2) calibrating the stand age structure. Analysis of the AFS large-fire database revealed an average of 1.7 fires per year that burned on average 6132 ha for a total of 10 404 ha/yr over the period 1950–1999. The model was calibrated (100 replicated 1000-yr runs) to produce a similar fire regime, i.e., average annual number of ignitions (1.8), average fire size (6480 ha), and total area burned (11 627 ha). Calibration was accomplished by systematically weighting the ignition and spread probability (i.e., pixel flammability values) algorithms (Rupp et al. 2000b, 2002).

In addition to calibrating point estimates of the means, the model was also calibrated with respect to extreme fire events. From fire history and initial runs of the model, we noted that distributions of area burned annually are dominated by infrequent events of disproportionate magnitude (Alvarado et al. 1998). For example, in the AFS database (1950–1999) more than 213 000 ha burned in the 1966 fire season, but the next largest fire season (1999) burned only 101 000 ha. We designed a calibration routine to derive a probability distribution for the return interval of extreme fire events (defined as >80 000 ha burned annually). The calibration resulted in simulated extreme fire events occurring on average every  $84 \pm 28$  years (mean  $\pm$  SE).

The model was then calibrated to species-specific stand age distributions. Simulated stand age distributions were calibrated against field observations for spruce stands having >10% canopy closure (W. B. Collins, B. W. Dale, D. E. McElwain, K. Joly, and L. G. Adams, *unpublished manuscript*). From exploratory data analysis, a three-parameter Weibull distribution was

chosen to model the stand age data. The Weibull distribution has been commonly employed in the fitting of both fire frequency data and time-since-last-fire (TSLF) data (Johnson 1979, 1992, Grissino-Mayer 1999). We used maximum likelihood estimation (MLE) to estimate model parameters. The Anderson-Darling test ( $A^2$ ), modified to account for substituting MLE estimated parameters in place of "theoretical" parameter values, was employed to assess the goodness of fit (Lockhart and Stephens 1994). We tested the hypothesis that the observed stand age data followed a Weibull distribution ( $A^2 = 0.604$ ,  $P = 0.125$ ,  $\alpha = 0.05$ ) and concluded that the three-parameter Weibull provided a plausible fit. MLE parameter estimates were used to compute the distributional median spruce forest age of 74.4 yr. Calibration of ALFRESCO to the observed field data followed and consisted of two parts: (1) MLE estimates were used to parameterize ALFRESCO's initial spruce forest age algorithm; and (2) sensitivity analyses were performed until the sampled TSLF distributional properties matched the observed stand age data.

An 800-yr spin-up simulation was performed that allowed realistic patch size and age-class distributions to be generated over multiple fire cycles. We chose 800 years because that represents four times the length of the longest reported fire frequency for these ecosystem types (30–200 yr; Yarie 1981, Van Cleve et al. 1991, Chapin et al. 2003). The spin-up assured ecologically realistic initial conditions for our scenario simulations. Without this step, the initial distribution and composition of vegetation and their associated ages may not conform to observations or basic ecological principles (Rupp et al. 2000b). The final (year 800) vegetation and age maps from the spin-up served as initial conditions for the various fire scenarios. Comparisons of the initial conditions (derived from the spin-up methodology) with remote sensing and field observations of stand structure (W. B. Collins, B. W. Dale, D. E. McElwain, K. Joly, and L. G. Adams, *unpublished manuscript*) revealed similar conditions: approximately 800 000 ha of spruce-lichen forest >80 years old.

Our simulations were generated by increasing or decreasing, relative to the control simulation, the average individual fire size by 50% using a constant weighting factor. In this manner, we were able to force the model to produce four different fire regime scenarios without explicitly modeling any changes in climate or human influences. Each scenario therefore represents a change in fire frequency, which we define as the time period between recurring fires at a given location (i.e., pixel), for a particular vegetation type, and/or the entire simulation landscape. The scenario that lengthened fire frequency (scenario 1, reduced fire [RF], 95 years between fires) represented the potential effect of increased fire suppression on the number and/or size of fires and the resulting changes in vegetation (Chapin et al. 2003). The scenario that simulated the current fire

regime served as a control (scenario 2, current fire [CF], 82 years between fires). The scenarios that shortened fire frequency (scenarios 3 and 4, increased fire 1 [IF1] with 75 years between fires and increased fire 2 [IF2] with 67 years between fires) represented possible increased human ignitions (including prescribed fire) and/or ecological and environmental changes caused by a continuation of recent warming trends (Keyser et al. 2000, Chapin et al. 2003). The driving climate data was randomly generated based on average growing-season temperature and precipitation for the period 1960–1990; interannual variability was based on this same time period (Fleming et al. 2000). The same driving climate data was used for all replicates and across all scenarios to minimize stochastic effects. This methodology provides for realistic simulation of interannual variability in climate and associated fire activity without the confounding issues involved with climate change scenarios. All model simulations were conducted on the same initial landscape ( $174 \times 160$  km, 27 840 km<sup>2</sup>) and ran at an annual time step for a 200-yr period with a  $2 \times 2$  km pixel resolution. Results across five replicates were then combined to produce multi-replicate averages to identify long-term trends. We analyzed individual replicate runs from each scenario to investigate variability among replicates and to better understand the possible interactions between fire and resultant vegetation. In addition, we performed 1000-yr simulations for each fire frequency scenario and developed representative ( $n = 1$ ) fire history maps (i.e., maps of TSLF) to investigate the spatial pattern of fire across the landscape.

Available caribou winter habitat (i.e., mature spruce-lichen forest) in our simulations was quantified by determining both the distribution of spruce forest stand ages across the landscape and through time, and by calculating the areal extent of spruce forest >80 years old, or those stands that are most likely to include adequate forage lichens in their understories to be utilized by caribou (Morneau and Payette 1989; W. B. Collins, B. W. Dale, D. E. McElwain, K. Joly, and L. G. Adams, *unpublished manuscript*).

## RESULTS

### *Simulated fire regimes*

The average annual number of fire ignitions did not change substantially over the range of fire frequency scenarios we simulated (12% increase; Table 1). However, the average annual area burned increased 3.5-fold (Table 1, Fig. 3). In addition, the number of extreme fire events (years with >80 000 ha burned) increased substantially in the IF1 and IF2 scenarios (Table 1, Fig. 3). Interestingly, the RF scenario produced one extreme fire event where the CF scenario produced no extreme events. We attribute this result to the stochastic nature of the model and the relatively small number of within scenario replicates ( $n = 5$ ). The changes in fire sizes, not ignitions, are realistic simulations of how fire regimes might change under reduced fire suppression,

TABLE 1. Simulated fire regime components for each fire frequency scenario.

Parameter	Fire frequency scenarios			
	Reduced	Current	Increased 1	Increased 2
No. fires per year				
Mean	1.7	1.8	1.8	1.9
Median	1.0	2.0	2.0	2.0
SD	1.4	1.4	1.3	1.4
Minimum	0.0	0.0	0.0	0.0
Maximum	7.0	9.0	7.0	7.0
Extreme events	1.0	0.0	5.0	15.0
Area burned in each fire (ha)				
Mean	2832	4373	6480	9880
Median	1120	1200	1400	1600
SD	6678	10 142	18 985	39 171
Minimum	0	0	0	0
Maximum	120 800	93 200	258 200	804 800
Area burned per year (ha)				
Mean	6631	10 182	17 054	23 575
Median	2000	2400	2800	3200
SD	22 368	23 567	63 682	77 506
Minimum	0	0	0	0
Maximum	604 000	255 200	1 291 000	876 500
Spruce fire frequency (yr)				
Mean	95	82	75	67
Median	87	73	67	56
SD	37	32	29	26
Minimum	40	39	39	39
Maximum	196	195	198	199

*Notes:* The results indicate shorter fire frequencies as you move from the reduced scenario to the increased 2 scenario, based on five replicate runs of 200 years for each scenario. See *Methods: Model calibration and simulations* for a description of the scenarios.

the institution of large prescribed fires, and/or the influence of a warmer and dryer climate (Chapin et al. 2003, Flannigan et al. 2005).

#### *Effects of fire frequency on vegetation*

Fire frequencies for the spruce forest type (i.e., the average time between simulated recurring fires in pixels composed of spruce forest) only ranged from an average of approximately 95 yr in RF to approximately 67 yr in the IF2: a 30% difference (Table 1). The total amount of the relatively flammable spruce forest type on the study landscape declined markedly with increased fire frequency (Fig. 4a), ranging from 1 456 000 ha in the longest fire frequency scenario (RF) to 858 000 ha in the shortest frequency scenario (IF2): a 41% difference (Table 2). An associated increase in deciduous vegetation occurred with decreasing fire frequencies (Fig. 4b) as fire-killed spruce forest was recolonized by early successional deciduous vegetation.

The interactions between fire and vegetation across the landscape are highlighted in an example of IF1 (Fig. 5). Substantial decreases in spruce forest in years 3, 57, and 159 are the direct result of large fire years (267 504, 102 416, and 186 736 ha burned, respectively). The post-fire recolonization by deciduous vegetation resulted in concurrent increases in deciduous forest abundance in the landscape. Likewise, secondary succession of these burned areas can be seen in the transient distribution of

spruce forest on the landscape. The pulses of spruce forest shown in Fig. 5 represent the successional maturation of previously burned areas, which in turn provides an increased fuel load on the landscape. Therefore, the temporal fluctuations in the relative amount of spruce forest are the result of climate driven fire events (i.e., abnormally warm and dry fire seasons) and adequate availability of fuels (Rupp et al. 2000a, Chapin et al. 2003, Turner et al. 2003).

#### *Variability of model replicates*

In addition to the clear trends indicated from averaging replicate simulations, we also explored the variability among replicates. Although clear trends are apparent in the scenario averages (Table 2, Fig. 4a and 4b), individual replicates produce different results (Fig. 6) because of the unique history of fire-vegetation-climate interactions over the 200-yr simulation for each replicate. Although long-term management decisions may not be affected by this variability (i.e., a decreasing trend in spruce forest distribution is apparent), the short-term management strategies will be highly impacted by the unique trajectory taken that could be represented by any replicate (Fig. 6).

Although replicates differ, the general trends (median age and overall distribution) remain unchanged within scenarios (Fig. 7). The amount of ideal-aged spruce habitat (i.e.,  $\geq 80$  yr) varied both over time and across

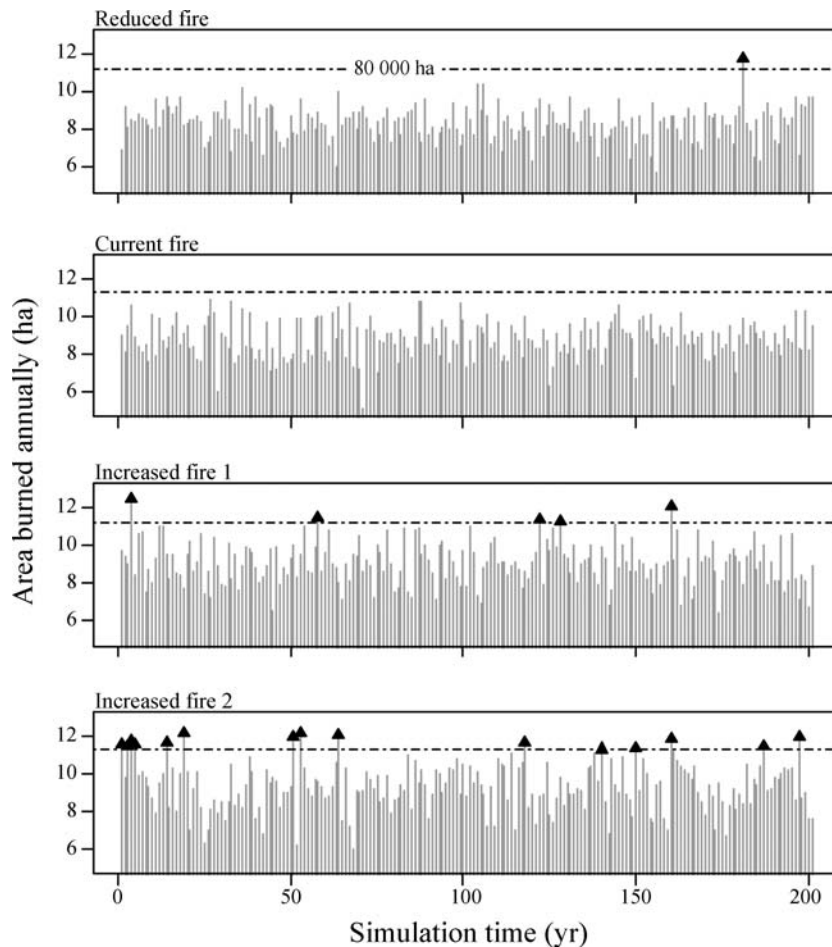


FIG. 3. Time series of area burned annually (log-transformed) for each fire frequency scenario. The dot-dashed line indicates the threshold for extreme fire years (i.e., >80 000 ha burned), which are identified by triangles. Data are based on five replicates of 200 years for each scenario. Spruce forest fire frequency equals 95, 82, 75, and 67 yr for the reduced, current, increased 1, and increased 2 fire scenarios, respectively.

scenarios (Fig. 8). The IF1 and IF2 scenarios exhibited more variability (i.e., more pulses) across the 200-yr simulation period than the RF and CF scenarios, due mainly to the impacts of the fire regime. Moreover, IF1 and IF2 scenarios resulted in substantially less spruce habitat >80 yr than is currently available on the landscape. The reduction over time varies from 4% to 66% between scenarios, with the IF2 scenario exhibiting consistent reductions of at least 25%. The RF and CF scenarios consistently showed increasing abundance of spruce-lichen habitat after the first 10 years of the simulations, although these projections must be considered within the context of the assumptions of the model.

#### *Simulated spatial patterns*

Assuming most boreal forest fires are stand replacing (Johnson 1992), the simulated TSLF maps provide general age class information for the study area. Substantial differences in the spatial pattern of stand age over the range of simulated fire scenarios were

identified (Fig. 9). The RF scenario yielded relatively long TSLF values: there were very few pixels with TSLF <161 yr and the majority of the landscape was >240 yr or did not burn at all. In contrast, IF2 had TSLF values as short as 1–80 yr with the majority of the landscape burning at <161 yr.

## DISCUSSION

### *Model simulations: comparison of scenarios*

Our simulations suggest that more frequent and larger fires will result in less of the spruce-lichen forest habitats preferred by caribou on the landscape. ALFRESCO simulated substantial reductions (4–66%) in the amount of older spruce-lichen stands (Fig. 8). This relationship between fire and spruce forest abundance has been documented in the literature (Scotter 1967, Maikawa and Kershaw 1976, Kershaw 1977, Morneau and Payette 1989). Our modeling also suggests that more frequent large fires will result in a shift in the spruce-lichen forest age structure towards younger stands,

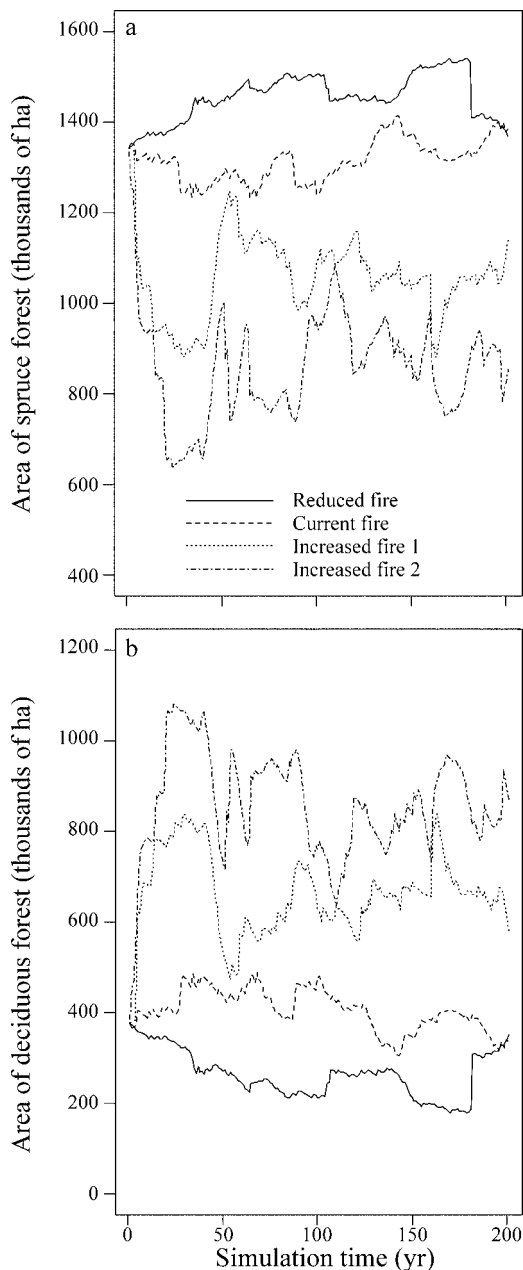


FIG. 4. Time series of the average amount of (a) spruce forest and (b) deciduous vegetation on the landscape for each fire frequency scenario from five replicates for each scenario. Spruce forest fire frequency equals 95, 82, 75, and 67 yr for the reduced, control, increased 1, and increased 2 fire scenarios, respectively.

which may not support adequate forage lichen biomass. Based on the simulated median age and overall distribution of stand ages, RF and CF produced a more ideal stand-age structure, for caribou winter habitat. In contrast, IF1 and IF2, which produced large increases in area burned and shorter spruce fire frequencies, resulted in a relatively immature age structure with few forest stands older than 100 yr. The transient nature of

foraging habitat abundance for the shorter fire frequency simulations (IF1 and IF2) would likely have strong implications for both short- and long-term caribou population dynamics (Klein 1982). Some preferred lichen species such as *Cladina rangiferina* are rarely even present prior to 100 years following fire (Thomas and Kiliaan 1998; W. B. Collins, B. W. Dale, D. E. McElwain, K. Joly, and L. G. Adams, unpublished manuscript).

*Model simulations: spatial patterns and implications*

More-frequent and large fires will also affect the spatial pattern of spruce-lichen stands across the landscape including patch size and continuity. We did not directly quantify patch size or patch continuity in this study. However, given the general characteristics of fires in boreal North America—most of the area burned is burned by few very large fires (Stocks et al. 2002) and fires in the boreal forest tend to be stand replacing (Johnson 1992)—we can make some broad inferences regarding our simulations. The spatial distribution of fire perimeters reveals a fairly homogenous landscape for both the longest and shortest fire frequency scenarios, but with substantially different consequences

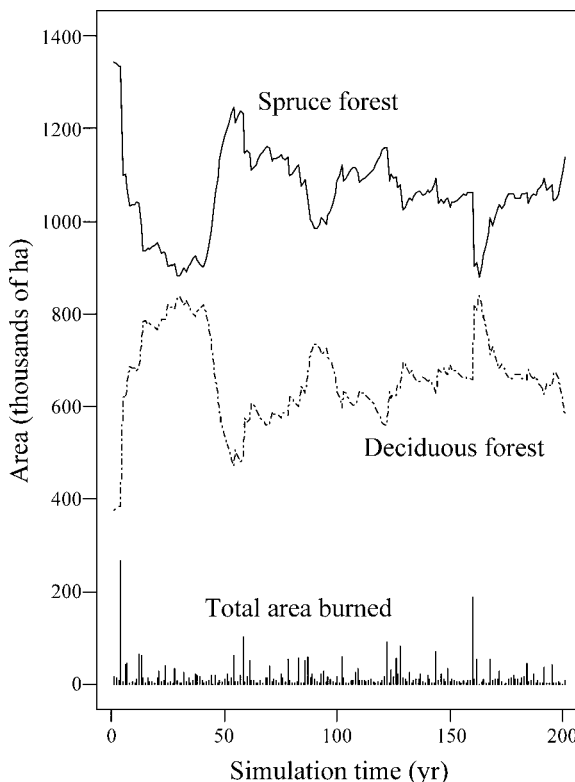


FIG. 5. Dynamics of early-successional deciduous vegetation (dot-dashed line) and late-successional spruce forest (solid line) in relation to fire events (i.e., total area burned, represented by bars) simulated in increased fire 1 scenario.

TABLE 2. Simulated vegetation distribution for each fire frequency scenario.

Parameter	Fire frequency scenarios			
	Reduced	Current	Increased 1	Increased 2
Total area of spruce (ha)				
Mean	1 456 000	1 314 000	1 058 000	858 300
Median	1 478 000	1 321 000	1 082 000	873 600
SD	115 331	93 381	225 017	236 032
Minimum	883 600	1 048 000	298 000	348 000
Maximum	1 612 000	1 539 000	1 518 000	1 505 000
Area of spruce >80 yr old (ha)				
Mean	1 187 000	977 300	656 100	587 800
Median	1 243 000	972 500	652 700	579 600
SD	123 240	62 182	52 401	55 790
Minimum	863 600	843 100	558 000	504 600
Maximum	1 305 000	1 096 000	868 600	868 600
Area of deciduous trees (ha)				
Mean	263 000	405 600	661 200	861 200
Median	241 200	397 600	637 200	845 600
SD	115 305	93 357	225 157	236 146
Minimum	107 600	180 800	201 200	214 400
Maximum	836 800	670 400	1 422 000	1 372 000

Notes: Fire frequencies shorten from the reduced scenario to the increased 2 scenario (Table 1). Results are based on five replicates of 200 years for each scenario. See *Methods: Model calibration and simulations* for a description of the scenarios.

in terms of the age distribution of forested stands. Both the CF and IF1 scenarios produced a more heterogeneous landscape, which may be important for overall landscape-level habitat diversity (Miller 1980, Schaefer and Pruitt 1991). Although the RF scenario provides the most ideal-aged habitat, the complexity (or in this case lack of complexity) could exert substantial negative impacts from an ecosystem/community diversity perspective. In general, as we shorten the fire frequency we produce larger patches of like-aged vegetation. This also reduces spatial heterogeneity (see Fig. 9) and creates a long-term positive feedback to the fire regime and future fires (i.e., legacies of large continuous fuel patches that pulse on and off the landscape over time due to fire and its effects; Turner et al. 2003).

There is little information regarding the importance of patch size to foraging strategies or dynamics of caribou populations. However, Nelchina caribou using the current winter range selected strongly for the interiors of older forest stands while using the 500 m wide perimeters of those stands more or less in proportion to availability (Joly et al. 2003). Thus, caribou did not seek out edges or their hypothetical beneficial effects. From these observations, we might infer that caribou select for larger patches because the proportion of the patch with neutral selection (i.e., the 500 m wide perimeter) is reduced. Large stands may provide reduced costs of movement among forage patches or reduced predation risk. Large patches may allow use by larger numbers of caribou that can reduce predation risk through increased vigilance, predator dilution (prey swamping), or increased predator search time (Bergerud 1980, Dale et al. 1994). Under this scenario, some of the costs of shorter fire frequencies, in terms of decreased lichen

availability, may be mitigated to some degree by larger patch size. Although there will be less total lichen available with shorter fire frequencies, the suitable patches will likely be larger. If our speculation that

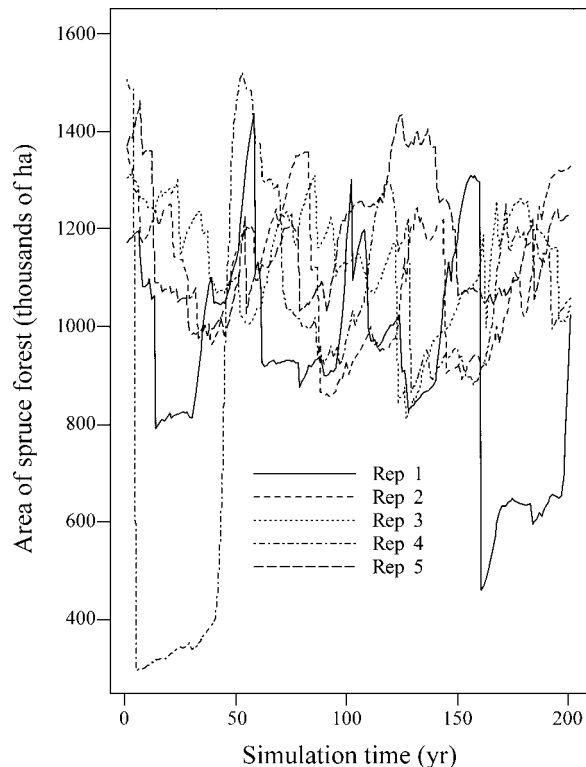


FIG. 6. Extent of spruce forest on the landscape for each of the five replicates (Rep) simulated under the increased fire 1 scenario.

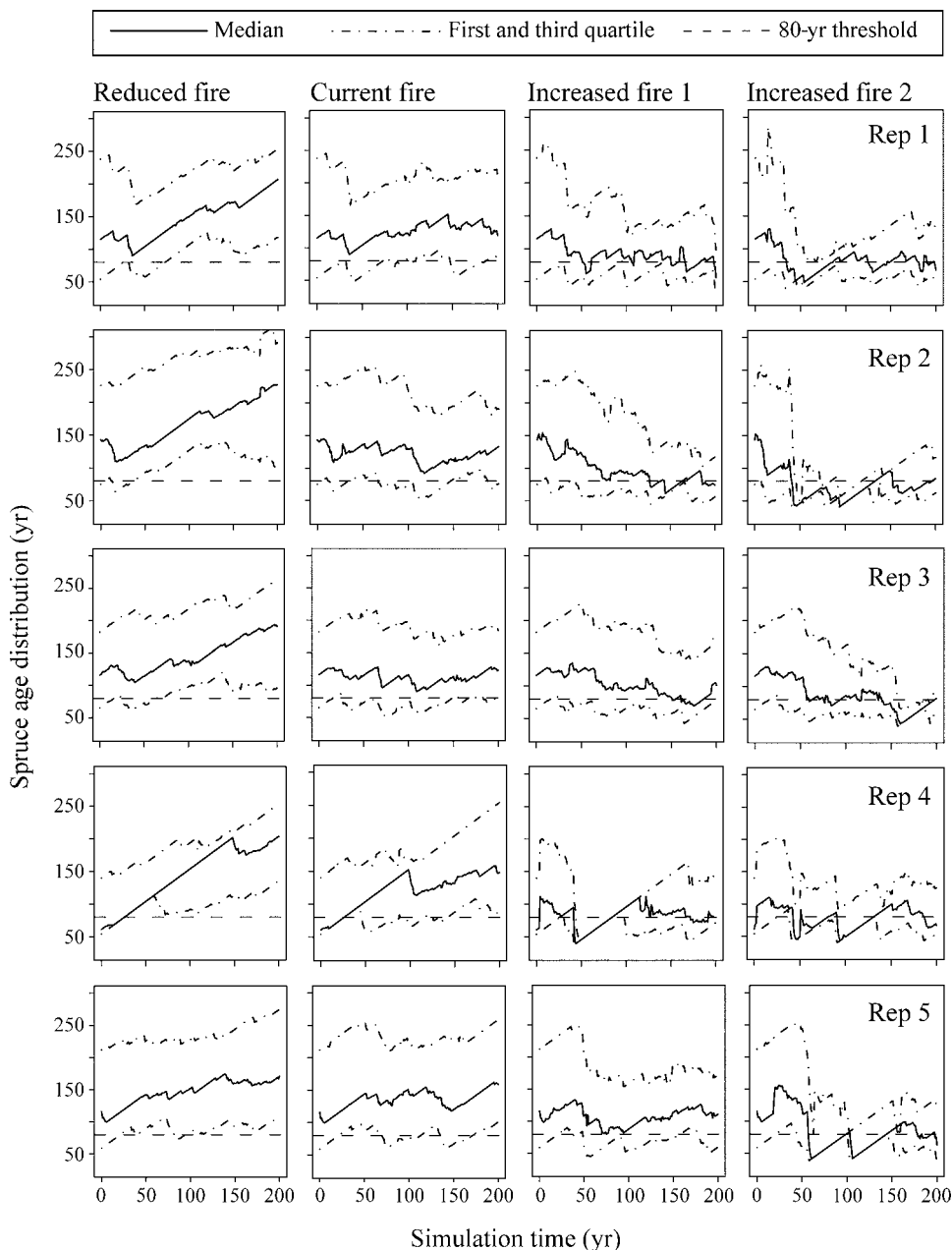


FIG. 7. Time series showing the median, 25th percentile, and 75th percentile of spruce forest age distribution across the simulation landscape for each fire frequency scenario, for replicates (Rep) 1–5. The dashed line indicates the lower (80-yr) threshold of preferred spruce-lichen habitat (see *Results* and *Discussion* sections).

larger patches have population benefits is valid, then costs of lower overall food availability (e.g., decreased forage productivity) may be partially offset for the population by those benefits (e.g., increased survival rates due to reduced predator risk). Similarly, the benefits of longer fire frequencies, in terms of increased lichen availability, may be partially offset by increased predation risk due to smaller suitable patch size, although these patches will comprise a minor component, relative to the overall homogenous vegetation

pattern of the RF simulation landscape. Given these assumptions regarding caribou and our general interpretation of the model simulation results, we suggest that further investigation into caribou foraging behavior relative to patch size may be warranted.

*The role of extreme fire events*

Our simulation studies suggest that the likelihood of extreme fire years will increase under scenarios of shorter fire frequencies (Figs. 3 and 8). This represents the worst-

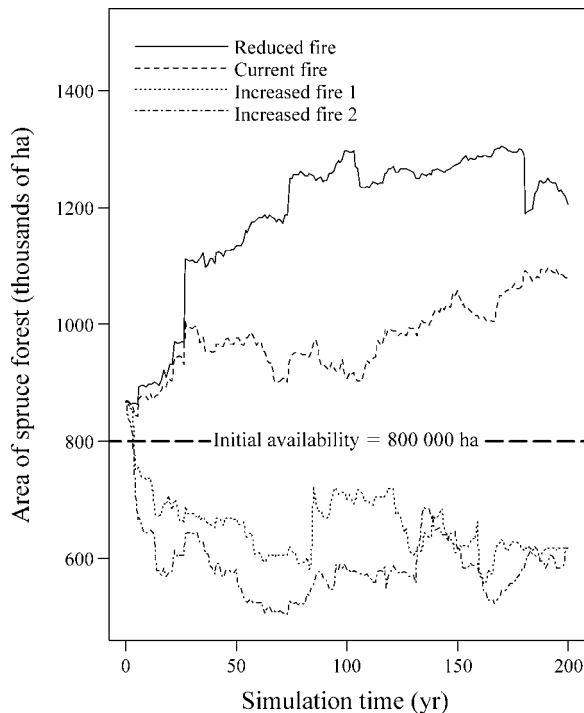


FIG. 8. Time series showing the average amount of spruce forest on the landscape >80 yr old for each fire frequency scenario. Results are from five replicates per scenario. The thick horizontal dashed line (800 000 ha) represents the amount of spruce-lichen forest initially available on the landscape.

case scenario for caribou and caribou managers. The occurrence of years with >80 000 hectares burned is rare for the RF and CF scenarios; however they become relatively frequent in the shortest fire frequency scenario (IF2). Large fire seasons burning 80 000 hectares or more represented a 10% or greater reduction in the current amount of older spruce-lichen stands. This result is all the more significant following the record 2004 fire season experienced in Alaska where more than 2.6 million hectares burned in the eastern interior, including approximately 0.5 million hectares, or approximately 40% of the spruce-lichen habitats, in and around the winter range of the Nelchina Caribou Herd. The ALFRESCO simulations indicate several 30–50% reductions in spruce-lichen habitat due to extreme fire years in the IF1 and IF2 scenarios (Fig. 8). A relatively high caribou population during those extreme events would potentially be a recipe for disaster. Caribou would either be forced to go elsewhere, which would affect current herd management paradigms, or they may not have adequate winter range, which could influence winter nutritional condition resulting in starvation at the extreme to varying degrees of higher predation mortality, reduced overall survival, reduced productivity and subsequent recruitment (Ferguson et al. 2001, Hemming 1971).

#### *Application and model assumptions*

Our model results and previous research (see review by Klein [1982]) suggest that at the landscape-level the

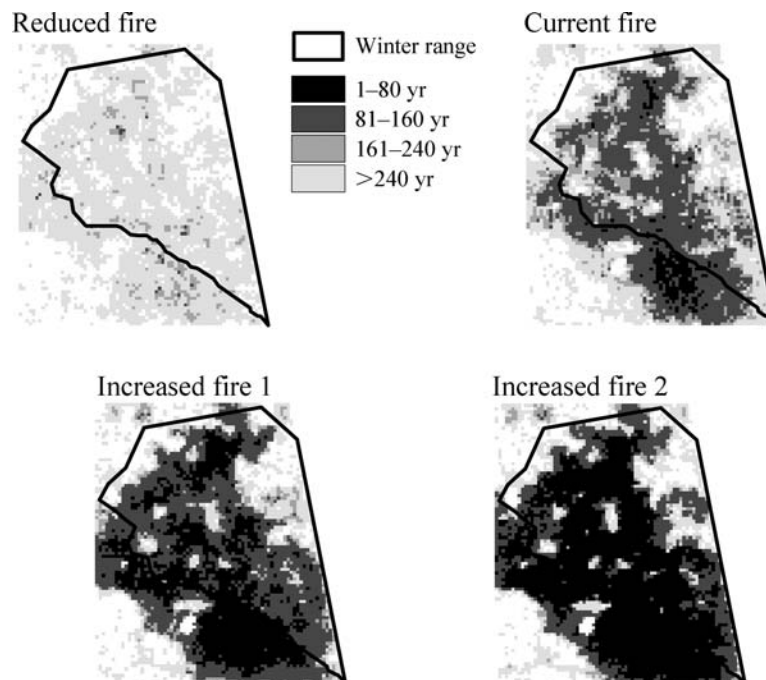


FIG. 9. Simulated fire history maps for each fire frequency scenario. The maps depict the time since the last fire simulated by a 1000-yr single (representative) replicate run. Average spruce forest fire frequency equals 95, 82, 75, and 67 yr for the reduced, current, increased 1, and increased 2 fire scenarios, respectively.

relationship between fire, vegetation, and caribou habitat are quite complex. Most large, migratory populations leave the tundra and migrate long distances to forested winter ranges because of the energy-rich lichen-based diets they can consume there (Russell and Martell 1984). Energy is probably the compelling nutritional requirement for caribou in winter (Boertje 1981), and lichen is a highly digestible, energy-rich forage that caribou prefer if it is available (Russell and Martell 1984). Therefore, at least over short time periods (e.g., <50 yr; Klein 1982), forecasted changes in future fire frequencies need to be addressed because of the importance of lichen in the winter diet of North American caribou and the fact that lichen abundance is strongly tied to succession (i.e., stand age/vegetation development; Maikawa and Kershaw 1976, Black and Bliss 1978). In fact, a balance must exist between fire frequency and extent that provides both a specific forest age-structure across the landscape and an abundance of forest habitat within specific age classes (Joly et al. 2003).

We know of no other research that has looked specifically at the interaction between fire and caribou habitat in a spatially explicit manner (see Bunnell et al. [1975] for nonspatial computer simulations). There have been similar modeling studies that have looked at the interactions between disturbance and large ungulates, specifically moose in the boreal forest (Pastor et al. 1998). Our modeling work is unique because we are able to address transient ecosystem responses to a changing fire regime on a geographically defined landscape. This approach allows us to simulate contagion processes (i.e., wildfire) and directly assess the consequences in terms of stand structure, specifically, stand age distribution and its relationship to caribou winter forage preference.

Several model assumptions must be considered with respect to this discussion. First, the model assumes that spruce-lichen forest >80 yr old will indeed support lichen biomass at levels preferred by caribou and does not account for possible decreases in lichen biomass from grazing pressure. Second, the model assumes that drivers (i.e., climate warming) of change in fire regime do not impact fire severity, which may lead to alternative successional pathways and the permanent loss of lichen habitat. These assumptions suggest our simulation results likely represent overestimates of available caribou habitat through time under a changing fire regime. Currently, model application is limited to manipulations of the fire regime in seclusion to other transient dynamics occurring across the landscape. Further model development would allow for more realistic and complex simulations of vegetation response to global climate change. For example, it would be useful to have the ability to simulate the interactions between a warmer/drier climate and an increase in anthropogenic influences (e.g., prescribed fire, human-caused ignitions, land-use change), and to identify the associated impacts on fire and caribou.

The results of our model simulations suggest that increases in the annual area burned within the current winter range of the Nelchina caribou herd could pose both short- and long-term challenges. More frequent fires will likely result in sustained low levels of mature spruce-lichen forest (>80 yr) relative to the amount of this forest type currently found on the landscape. It appears that maintenance of the current fire regime should perpetuate a stand structure and abundance favorable to caribou, assuming our model assumptions are valid. The recent and projected future trends in increased air temperatures (Chapman and Walsh 1993, Serreze et al. 2000, Arctic Climate Impacts Assessment Secretariat 2004) and the associated reduced growth rates of spruce forest (Barber et al. 2000), and projected increased acreage burned in wildfires (Kasischke et al. 1999) will likely make it very difficult for land managers to sustain the current fire regime. Understanding the potential response of the landscape to global climate change and the impact on caribou habitat throughout the North American boreal forest will provide managers with more complete information to develop strategies to adapt to changing habitat conditions and caribou population dynamics.

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