

# Land cover influences boreal-forest fire responses to climate change: geospatial analysis of historical records from Alaska

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## Abstract

**Context** Wildfire activity in boreal forests is projected to increase dramatically in response to anthropogenic climate change. By altering the spatial arrangement of fuels, land-cover configuration may interact with climate change to influence fire-regime dynamics at landscape and regional scales.

**Objectives** We evaluate how land cover interacts with weather conditions to influence boreal-forest burning from 2012 to 2014 in Alaska.

**Methods** Using geospatial fire and land-cover data, we quantify relationships between area burned and land cover, and test whether observed patterns of burning differ from random under varying weather conditions and fire sizes.

**Results** Mean summer moisture index was correlated with annual area burned ( $\rho = -0.78$ ,  $p < 0.01$ ), the total number of fires ( $\rho = -0.68$ ,  $p = 0.01$ ), and the number of large fires ( $>500 \text{ km}^2$ ;  $\rho = -0.58$ ,  $p = 0.04$ ). Area burned was related positively to percent cover of coniferous forest and woody wetlands, and negatively to percent cover of shrub scrub, dwarf scrub, and open water and barren areas. Fires preferentially burned coniferous forest, which represented 50.1 % of the area burned in warmer/drier summers and 40.3 % of area burned in cooler/wetter summers, compared to the 34.5 % ( $\pm 4.2$  %) expected by random selection of land-cover classes. Overall vegetation tended to burn more similarly to random in warmer/drier than cooler/wetter years.

**Conclusions** Land cover exerted greater influences on boreal fire regimes when weather conditions were less favorable for forest burning. Reliable projections of boreal fire-regime change thus require consideration of the interactions between climate and land cover, as well as feedbacks from land-cover change.

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## Introduction

Wildfires are a keystone disturbance in many ecosystems affecting a wide range of ecological processes, including vegetation dynamics, biogeochemical cycles, and water balance (e.g., Bond-Lamberty et al. 2009; Johnstone et al. 2011; Kelly et al. 2015). Fire occurrence and spread are driven by both top-down and bottom-up controls (e.g., Bessie and Johnson 1995; Parisien et al. 2011; Barrett et al. 2013). Regional climate conditions are the top-down control of fire regimes (e.g., Kasischke et al. 2002; Bond and Keeley 2005; Kasischke and Turetsky 2006), with a high probability of ignition, high temperature, and low moisture creating ideal conditions for fire occurrence and spread. For example, >75 % of inter-annual variation in area burned in the boreal forests of Alaska is explained by summer temperature and precipitation (Duffy et al. 2005; Balshi et al. 2009). Bottom-up factors, such as topography and vegetation composition, can strongly affect fire occurrence and spread by changing microclimate, fuel load, and the spatial arrangement of flammable fuels (Heyerdahl et al. 2001). Mosaics of land-cover classes can decrease fire spread across a landscape as a consequence of fires burning out when encountering less flammable fuels or firebreaks such as water bodies (Grimm 1984; Larsen 1997; Lloret et al. 2002; Hellberg et al. 2004). Thus decreased contagion of flammable fuels often leads to fewer and less intense fires when compared with nearby landscapes with homogeneous fuel cover (Dansereau and Bergeron 1993).

Several studies have considered both top-down and bottom-up controls of fire-regime dynamics (e.g., Bessie and Johnson 1995; Parisien et al. 2011). In subalpine forests, daily weather and fuels accounted for 83 and 15 % of the variation in fire intensity, respectively (Bessie and Johnson 1995). In the boreal forests of western Canada, Parisien et al. (2011) found that weather and fuels explained 29.2 and 67.4 %, respectively, of the spatial variation in burn probability. These studies revealed that the relative importance of fire-regime controls varies widely among different ecosystems (Parks et al. 2011). In addition, the importance of bottom-up controls on fires may change through time in response to changing climate (e.g., Heyerdahl et al. 2001; Gedalof et al. 2005; Barrett et al. 2013). For example, Turner and Romme (1994) reviewed the literature on fire behavior in crown-fire ecosystems and found that when climate conditions

were less conducive for fires, landscape features such as the spatial arrangement of fuels strongly influenced fire spread in these systems. However, during periods when climate was more conducive to fires (i.e., low fuel moisture, strong winds, and high probability of ignition), fires spread regardless of fuel connectivity. Similarly, paleoecological analyses based on tree-ring and lake-sediment records suggest that the relative importance of climate and landscape controls of fire regimes has shifted over centennial to millennial timescales during the Holocene (e.g., Heyerdahl et al. 2001; Gavin et al. 2003; Ali et al. 2009; Colombaroli and Gavin 2010).

In the boreal-forest biome, wildfire activity is projected to increase dramatically in response to anthropogenic climate warming in the coming decades (Flannigan et al. 2005; Balshi et al. 2009). These projections are supported by the increased frequency of extreme fire years and unprecedented burning in the Alaskan boreal forest as a result of climate change over the past several decades (Kasischke and Turetsky 2006; Kelly et al. 2013). However, the temporal trajectory of boreal-forest burning is likely to vary at landscape to regional scales (Kasischke et al. 2002), such that in some regions increased precipitation over the next century might result in reduced fire frequency (Flannigan et al. 2009). In addition, boreal ecosystems are characterized by complex land-cover configurations (Hellberg et al. 2004; Barrett et al. 2013) and striking flammability variation among land-cover types (Cumming 2001). These factors may interact with climate change to dictate fire-regime dynamics at landscape and regional scales. Previous studies (Higuera et al. 2009; Barrett et al. 2013; Girardin et al. 2013) have speculated that varying flammability associated with vegetation types played a key role in shaping the spatiotemporal patterns of Holocene fire-regime dynamics in the boreal forests of North America. Increasing abundance of deciduous species as a result of increased forest burning may also diminish the impacts of anthropogenic climate warming on boreal fire regimes in the twenty first century because forests dominated by deciduous species are less flammable than those dominated by coniferous species (Mann et al. 2012). A rigorous assessment is needed to elucidate how land cover interacts with climate to influence boreal fire regimes. Historical observations provide an important means for such assessments.

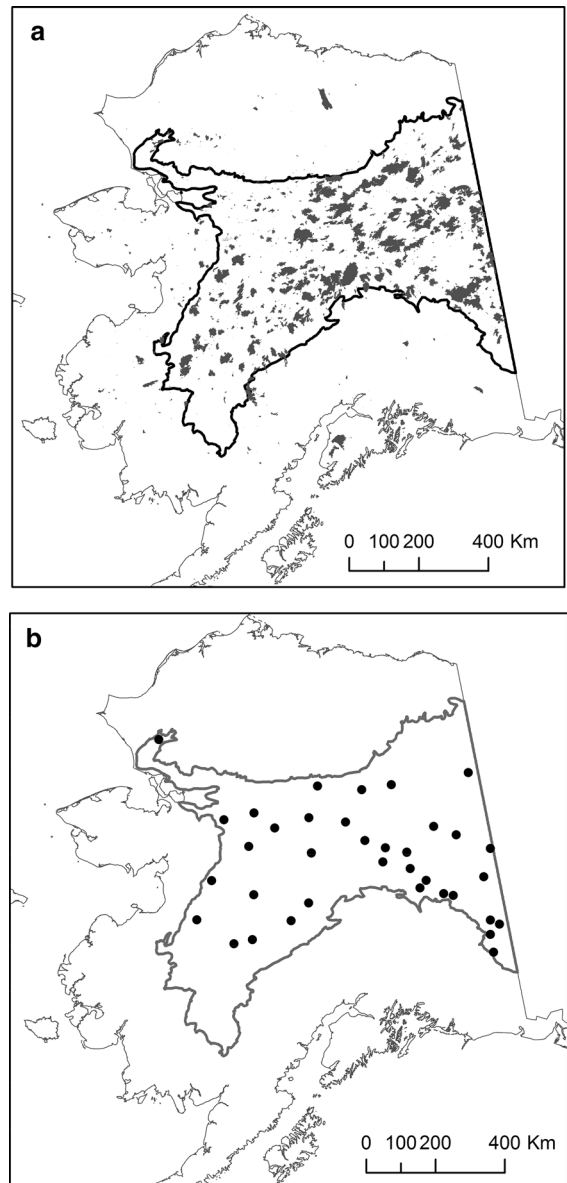
In this study, we investigated how weather, land cover, and their interaction influenced boreal-forest fires in Alaska. First, we compared fire records with summer weather conditions and land-cover composition to assess the effects of these factors individually. We then tested for interactive effects of weather and land cover on fire regimes by comparing the composition of land-cover classes that burned under different weather conditions and in different fire sizes with null models of random burning. Finally, we explored the spatial patterns of burning across different land-cover classes by examining the size and contagion of land-cover patches that burned in large and small fires. These results illuminate the role of land cover in driving boreal fire-regime responses to climate change.

## Methods

This study focused on the period of 2002–2014 because of the availability of reliable land-cover information for this period; the National Land Cover Database files, the raster datasets of land cover in Alaska at 30-m resolution, were derived from satellite imagery collected in 2001 and 2011 (Homer et al. 2007, 2015). Longer time series of fires and weather are available for Alaska; we restricted our analyses to the period of 2002–2014 because previous studies have investigated climate-fire relationships in Alaska over the past several decades (Kasischke et al. 2002; Duffy et al. 2005) and because no reliable land-cover data are available prior to 2001 for assessing the role of land cover in fire-regime responses to weather/climate variation—the primary focus of this study. Land-cover composition may have changed annually as a result of fire occurrence, and thus the lack of yearly land-cover data may compromise our ability to assess the effects of land cover on fire regimes. However, our analyses for the period of 2002–2011 based on the 2001 land cover map (Homer et al. 2007) and the period of 2012–2014 based on the updated 2011 land cover map (Homer et al. 2015) yielded similar results (described below), suggesting that our conclusions are robust to inter-annual variation in land-cover change within our study period.

We used the database of fire perimeters from the Alaska Fire Service (available from the Alaska Interagency Coordinating Center, <http://fire.ak.blm>.

<http://fire.ak.blm>, Kasischke et al. 2002), which includes all fires  $>0.4 \text{ km}^2$  during the study period (Fig. 1a). The dataset likely overestimates the area burned because some of the burn perimeters encompass unburned areas including open water, barren land, and patches of vegetation (Kolden et al. 2012). Using the land-cover classes that existed in 2001 and 2011 allowed us to analyze the approximate percentage of each land-



**Fig. 1** **a** Fires occurring between 2002 and 2014 (dark grey polygons) and interior Alaskan boreal forest (outlined in black). **b** Locations of weather stations used in this analysis

cover class that burned in each fire from 2002 to 2011 and 2012 to 2014, respectively. These land-cover classes include barren land, coniferous forest, deciduous forest, dwarf scrub, herbaceous wetlands, mixed forest, open water, shrub scrub, and woody wetlands. Dwarf scrub is defined as areas dominated by shrubs <20 cm tall with >20 % shrub canopy, and shrub scrub is defined as an area dominated by shrubs <5 m tall with shrub canopy typically >20 % of total vegetation; see Supporting Material Table S1 for the definitions of other land-cover classes. The thematic accuracy of land-cover classification in the 2001 National Land Cover Database was determined to be 76 % for Alaska overall, 84 % for coniferous forest, and 92 % for open water (Selkowitz and Stehman 2011). An accuracy assessment has not yet been performed for the 2011 map. Land-cover classes that are rare have lower classification accuracies, but they do not make up a substantial amount of the area burned. To increase the accuracy of our maps, we excluded land-cover classes that represent <1 % of interior Alaska.

To assess weather conditions during the summers of 2002–2014, we used data from 30 Remote Automated Weather Stations (RAWS; <http://www.raws.dri.edu>). These stations were selected from RAWS that meet the following criteria: (1) the station was within interior Alaska; (2) the station had no missing monthly temperature or precipitation data for June, July, and August of 2002–2014; and (3) the stations were at least 20 km apart to avoid spatial bias from the inclusion of multiple stations from the same area. We augmented the RAWS data with data from six traditional weather stations in the NOAA's Cooperative Observer Network (<http://www.wrcc.dri.edu/>). These six stations were selected with the same criteria as for the RAWS stations. Thus we used a network of 36 weather stations across interior Alaska in this study (Fig. 1b; for a list of the weather stations, see Supporting Material Table S2).

We calculated the climate moisture index (CMI) as the difference between precipitation and potential evapotranspiration (PET) (Hogg 1997). Lower CMI values indicate warmer and drier conditions. PET was determined with the Hamon equation, which is based on daytime length and saturation vapor pressure (Allen et al. 1998; Lu et al. 2005). Most fires occurred between June and August; thus we calculated CMI, PET, precipitation, and temperature as the overall

mean of the station means determined from June, July, and August values for each year. As an additional measure of data-quality control, we excluded station means that were >3 standard deviations from the overall mean during the same summer and recalculated the overall mean. We then compared mean summer CMI, PET, precipitation, and temperature with annual area burned and total number of fires using Spearman's rank correlation analysis.

To test if land-cover class influenced the probability of burning, we created a lattice of sampling points that were 36.5 km apart, yielding an area around each point 100 times larger than the median fire size to minimize spatial autocorrelation. Within a 13 km radius around each point, which represents an area 50 times larger than the median fire size, we calculated the percentages of area burned and each major land-cover type in the 2001 NLCD dataset. A Spearman's rank correlation analysis was performed to quantify the relationship between area burned and land cover.

We also compared the observed percentage of each land-cover class that was burned from 2002 to 2014 with a null model of random burning, which minimized the confounding effects of climate variation in our assessment of land-cover impacts on fire probability. The null model was created by randomly sampling areas of interior Alaska equivalent to the average size of observed fires from the 2001 and 2011 National Land Cover Database maps. This process was repeated 1000 times through Monte Carlo replicate model runs. We sampled the 2001 and 2011 maps 850 and 150 times, respectively, in proportion to the percent areas that burned in 2002–2011 and 2012–2014. We then calculated the mean percent cover and 95 % confidence interval of each land-cover class burned by chance under the null model in the 1000 Monte Carlo simulations. If the observed percentage of a burned land-cover class fell outside the 95 % confidence interval estimated from the null model, we interpreted this as evidence of a significant difference at that  $\alpha = 0.05$  level. We also examined how patterns of observed land-cover burning under different weather conditions and fire sizes differed from chance by creating two null models for each of the following comparisons: (1) summers with higher versus lower mean CMI, partitioned with a k-means cluster analysis, (2) large (>500 km<sup>2</sup>) versus small (<1 km<sup>2</sup>) fires in all summers, and (3) large versus small fires in the summer of 2004, an extreme

fire season with the lowest mean CMI and largest area burned. The 500 km<sup>2</sup> threshold for defining large fires was chosen following Kasischke and Turetsky (2006), and the 1 km<sup>2</sup> threshold for small fires represents the smallest quartile of fires recorded in interior Alaska from 2002 to 2014. We used t-tests to evaluate differences between the observed patterns of burning within each land-cover class for each of the above comparisons. To further evaluate how land cover and weather interact to control fires, we calculated the squared chord distance, a dissimilarity index (Overpeck et al. 1985), to quantify the difference in land-cover composition between observed fire and random burning along a CMI gradient.

Finally, to quantify the effects of land-cover composition on the spatial patterns of burning, we calculated the largest patch index (McGarigal et al. 2002) in large and small fires, which is defined as: (area of the largest burned patch of a given land-cover class  $\times$  100/total burned area of that land cover). Contagion was also measured for all burns ( $n = 875$ ) by calculating the average adjacency of each grid cell to cells of its own class or other classes within each burn perimeter (McGarigal et al. 2002). A null model of contagion in interior Alaska was created by repeating this analysis for a set of 875 randomly selected areas drawn from the distribution of fire sizes that occurred from 2002 to 2014. To examine the relationship between fire size and contagion, we performed a regression analysis, which was repeated for the null model.

Differences were considered statistically significant at the  $\alpha = 0.05$  level. However, we applied a Bonferroni correction when comparing all nine major land-cover classes. Thus for such comparisons statistical significance is inferred at  $\alpha = 0.005$ . Spatial analyses were performed in Mathwork's Matlab version 2010b, R version 2.15.1, ESRI's ArcMap version 9.3, FRAGSTATS (McGarigal et al. 2002), and Hawth's Analysis Tools in ArcGIS (Beyer 2004). All statistical analyses were conducted in Mathwork's Matlab version 2010b.

## Results

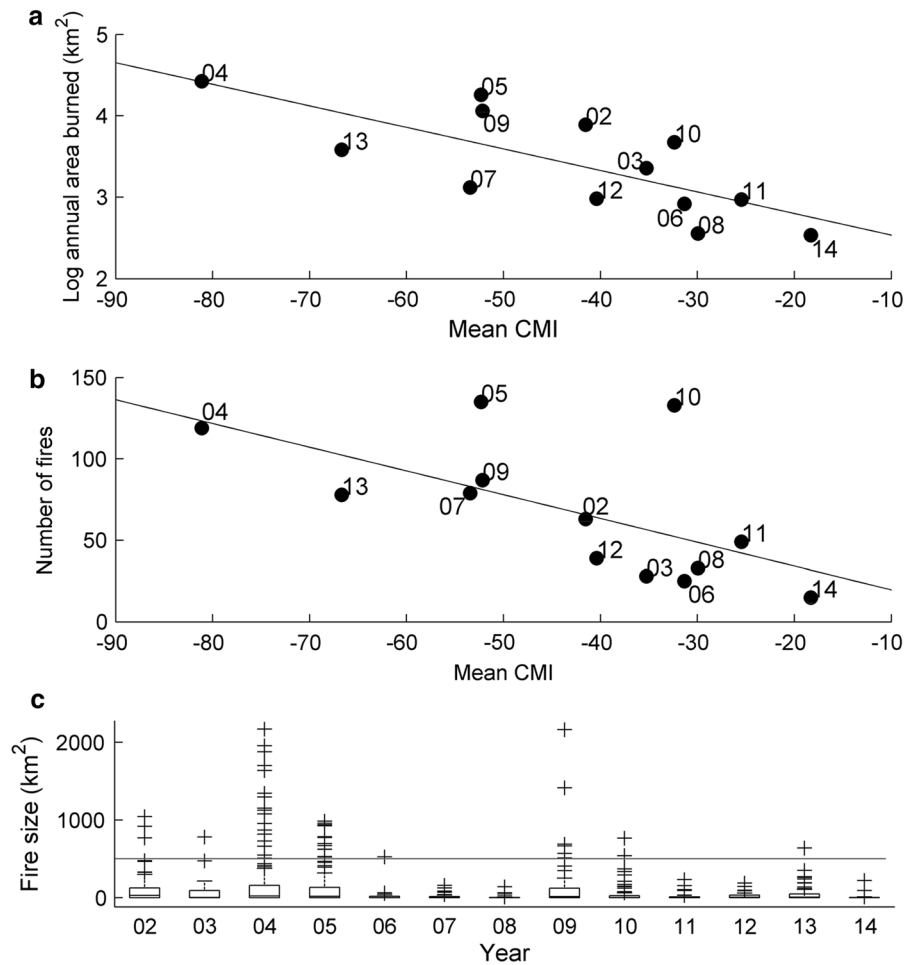
During the period of 2002–2014, mean summer CMI is negatively correlated with annual area burned ( $\rho = -0.78$ ,  $p < 0.01$ , Fig. 2a) and with the number

of fires ( $\rho = -0.68$ ,  $p = 0.01$ , Fig. 2b). Annual area burned and the number of fires are also strongly correlated with June–August mean precipitation ( $\rho = -0.79$ ,  $p < 0.01$ ;  $\rho = -0.75$ ,  $p < 0.01$ , respectively), mean PET ( $\rho = 0.68$ ,  $p = 0.01$ ;  $\rho = 0.73$ ,  $p < 0.01$ , respectively), and mean temperature ( $\rho = 0.62$ ,  $p = 0.03$ ;  $\rho = 0.72$ ,  $p < 0.01$ , respectively). We focus on CMI in this study because it integrates all of these weather metrics. Total area burned is approximately 79 times higher in the lowest CMI summer (2004) than in the highest CMI summer (2014) during 2002–2014. Fire size is not normally distributed and is skewed by large fire events (statistical outliers) (Fig. 2c). Large fires ( $>500$  km<sup>2</sup>) constitute 5.1 % of the number of fires but account for 53.8 % of the total area burned, and they occur more often as mean summer CMI decreases ( $\rho = -0.58$ ,  $p = 0.04$ ).

As summer CMI decreases, the area burned in each major land-cover class tends to increase ( $\rho = -0.81$  to  $-0.60$ ,  $p = 0.001$ – $0.03$ , Fig. 3), except for barren areas and herbaceous wetlands ( $\rho = 0.45$ ,  $p = 0.13$  and  $\rho = -0.47$ ,  $p = 0.11$ , respectively). Land-cover composition significantly affects area burned. Percent area burned is correlated positively with the percent cover of coniferous forest ( $\rho = 0.25$ ,  $p < 0.001$ ) and woody wetlands ( $\rho = 0.21$ ,  $p < 0.001$ ), and negatively with percent cover of dwarf shrub ( $\rho = -0.22$ ,  $p < 0.001$ ), shrub scrub ( $\rho = -0.12$ ,  $p = 0.06$ ), and fuel-free areas (open water and barren,  $\rho = -0.12$ ,  $p = 0.07$ ; Table 1). Compared with the null model, percent area burned is larger for coniferous forest and woody wetlands, and smaller for dwarf shrub, shrub scrub, deciduous forest, and herbaceous wetlands ( $p < 0.05$ , Fig. 4a). Water and barren areas comprise a lower proportion within the burn perimeters than expected by chance ( $p < 0.05$ , Fig. 4a). The largest deviation between the observed burning and the null model is for coniferous forest, which comprises 48.1 % of the actual area burned but only 34.5 % ( $\pm 4.2$  %) of the area burned in the null model.

In terms of the direction (positive or negative) of land-cover effects, results from comparisons with the null models for both lower (2004, 2005, 2007, 2009, and 2013) and higher (2002, 2003, 2006, 2008, 2010, 2011, 2012, and 2014) CMI summers are broadly similar to those for all summers (Fig. 4). Percent area burned is significantly greater during lower than higher CMI summers for coniferous forest (50.1 vs 40.3 %). In contrast, percent area burned is significantly smaller

**Fig. 2** **a** Log annual area burned ( $\text{km}^2$ ) in relation to mean summer climate moisture index (CMI,  $\rho = -0.78$ ,  $p < 0.01$ ) for the period 2002–2014. **b** Number of fires in relation to mean summer CMI ( $\rho = -0.68$ ,  $p < 0.01$ ) for the period of 2002–2014. **c** Box plots of fire sizes for the period 2002–2014. On each box, the central mark represents the median and + symbols represent outliers. The horizontal black line is at  $500 \text{ km}^2$



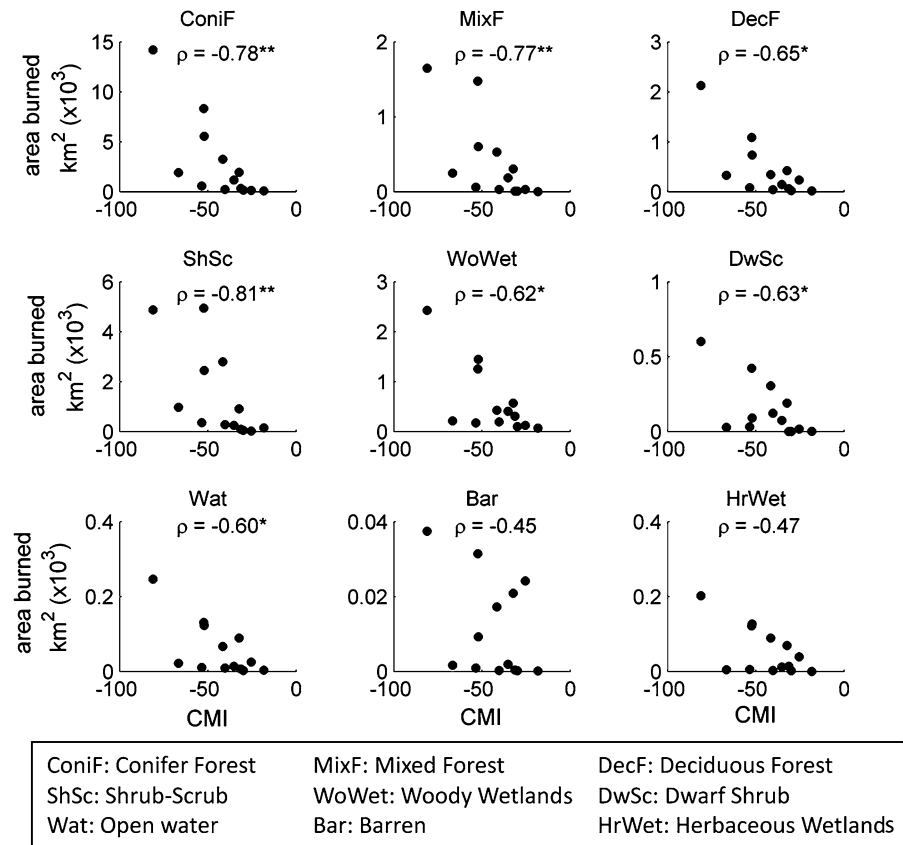
during lower than higher CMI summers for shrub scrub (22.3 vs 25.2 %). Although more absolute area is burned in all major land cover classes in lower CMI summers than in higher CMI summers, total area burned is significantly higher for coniferous forest, mixed-forests, deciduous forest, and shrub scrub in each fire in lower CMI summers ( $t(873) > 3.2$ ,  $p < 0.005$ ). Dissimilarity analysis further reveals that the land-cover composition within the fire perimeters tends to differ more from random during higher than lower CMI summers ( $t(11) = -1.87$ ,  $p = 0.09$ , Fig. 5).

Comparisons between large ( $>500 \text{ km}^2$ ) and small ( $<1 \text{ km}^2$ ) fires show that coniferous forest accounts for 48.5 % of the area burned in large fires, and only 34.2 % in the small fires and accounts for a significantly greater area burned in large fires ( $t(270) = -2.9$ ,  $p < 0.004$ , Fig. 6a, b). Compared with the null model, large fires burn a higher percentage of coniferous forest

and lower percentages of open dwarf scrub, and shrub scrub ( $p < 0.05$ , Fig. 6b). Small fires differ from the null model by burning a higher percentage of woody wetlands and lower percentages of deciduous forest and mixed forest ( $p < 0.05$ , Fig. 6a). Similar patterns exist in the summer of 2004 (Fig. 6c, d), which features the lowest mean CMI and numerous large fires in interior Alaska within our study period.

We used the largest patch index to infer how large and small fires spread across land-cover classes (Fig. 7). In large fires, the largest burned patches occur in only three land-cover classes: coniferous forest, shrub scrub, and woody wetlands, with coniferous forest as the dominant class (68.2 %, Fig. 7b). In small fires, the largest burned patches are distributed across several land-cover classes: 34.1 % coniferous forest, 24.9 % shrub scrub, 14.4 % woody wetlands, and  $\sim 1.5$ –10 % each of the remaining classes (Fig. 7a). The largest

**Fig. 3** Relationship between mean summer climate moisture index (CMI) and area burned (km<sup>2</sup>) in each land-cover class for the period of 2002–2014. The  $\rho$  values are based on Spearman’s rank correlation (significance is indicated by \* $p \leq 0.05$  or \*\* $p \leq 0.005$ )



**Table 1** Spearman rank correlations between percent area burned and percent of each major land-cover class measured in a survey of areas of Alaska. The fuel-free classification includes open water and barren land cover

Land-cover class	Spearman’s rho	p value
Coniferous forest	0.25	<b>&lt;0.001</b>
Woody wetlands	0.21	<b>&lt;0.001</b>
Deciduous forest	0.08	0.19
Herbaceous wetlands	0.05	0.41
Mixed forest	0.03	0.62
Fuel-free	-0.12	0.07
Shrub scrub	-0.18	0.06
Dwarf scrub	-0.22	<b>&lt;0.001</b>

Bold values indicate P-values <0.001

Italic values indicate P-values <0.10 but >0.001

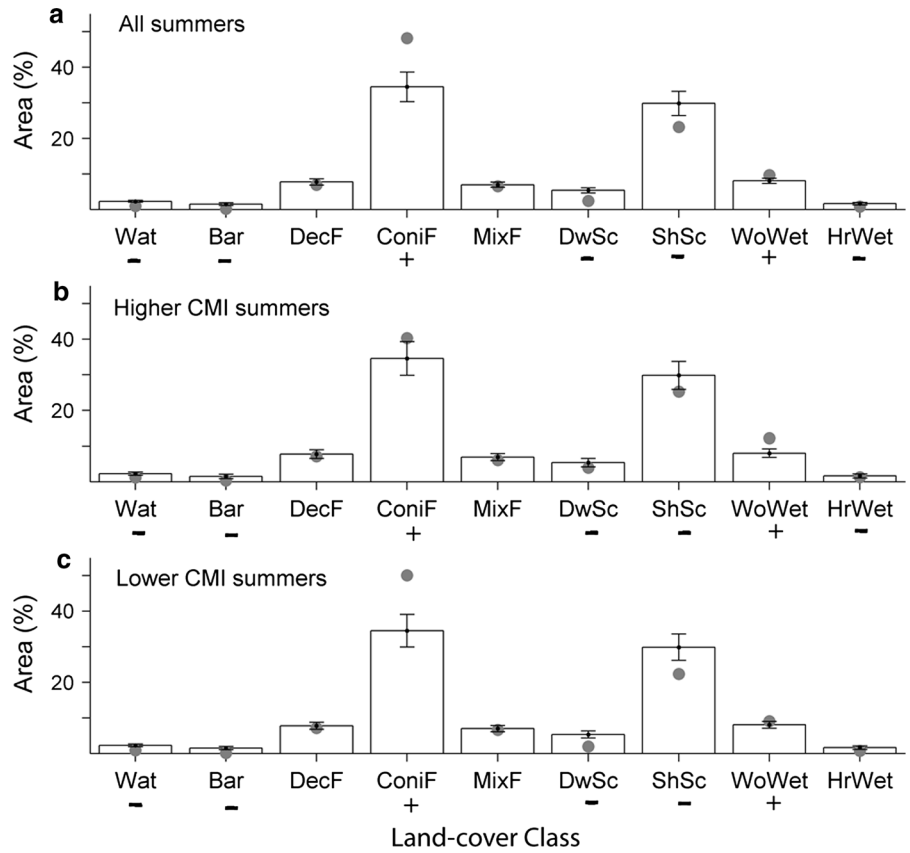
burned patch in coniferous forest is usually <10 % of the total area burned in small fires (Fig. 7c) but is often greater in large fires (Fig. 7d). Additionally, analysis of all burned areas in 2002–2014 indicates that land-cover contagion increases modestly with area burned

( $\rho = 0.25$ ,  $p < 0.01$ ). Although larger areas tend to have greater contagion even under the null model, observed fires show a significantly stronger relationship between contagion and area burned than by chance ( $t(1746) = -2.79$ ,  $p < 0.01$ ,  $t$  test comparing regression slopes of null vs observed dataset).

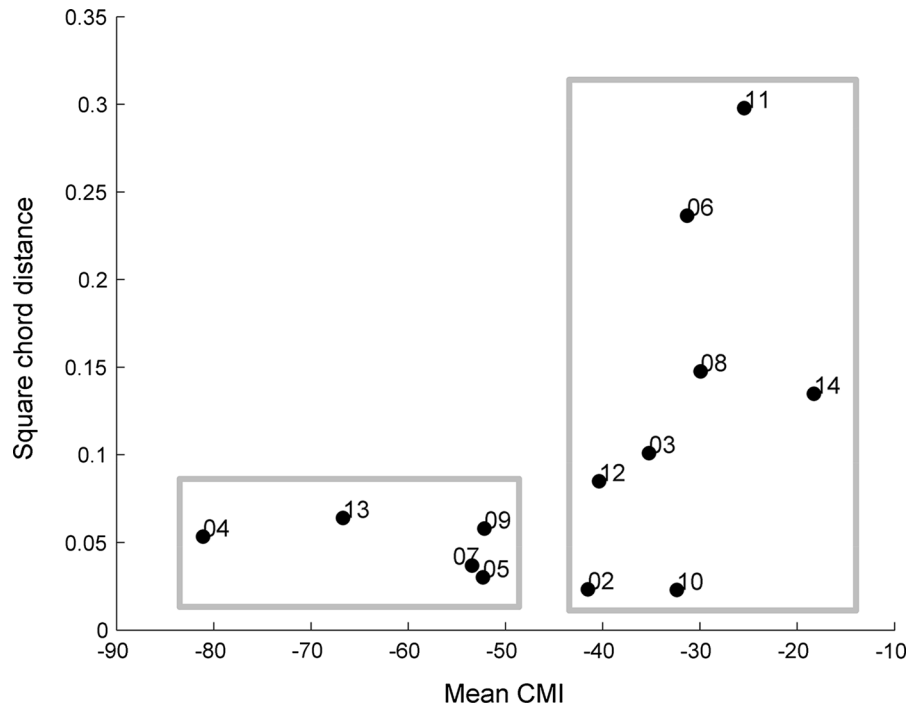
### Discussion

Recent studies have projected that wildfire activity in boreal forests will increase dramatically in response to anthropogenic climate change, possibly leading to a regime shift in the twenty first century (Balshi et al. 2009; Mann et al. 2012; Kelly et al. 2013). At landscape to regional scales, the temporal trajectory of fire activity is influenced by the composition and spatial configuration of land-cover classes with contrasting flammability and fuel loads (Turner and Romme 1994; Barrett et al. 2013). Understanding how land cover influences fire-regime responses to climate change is thus essential for projecting changes

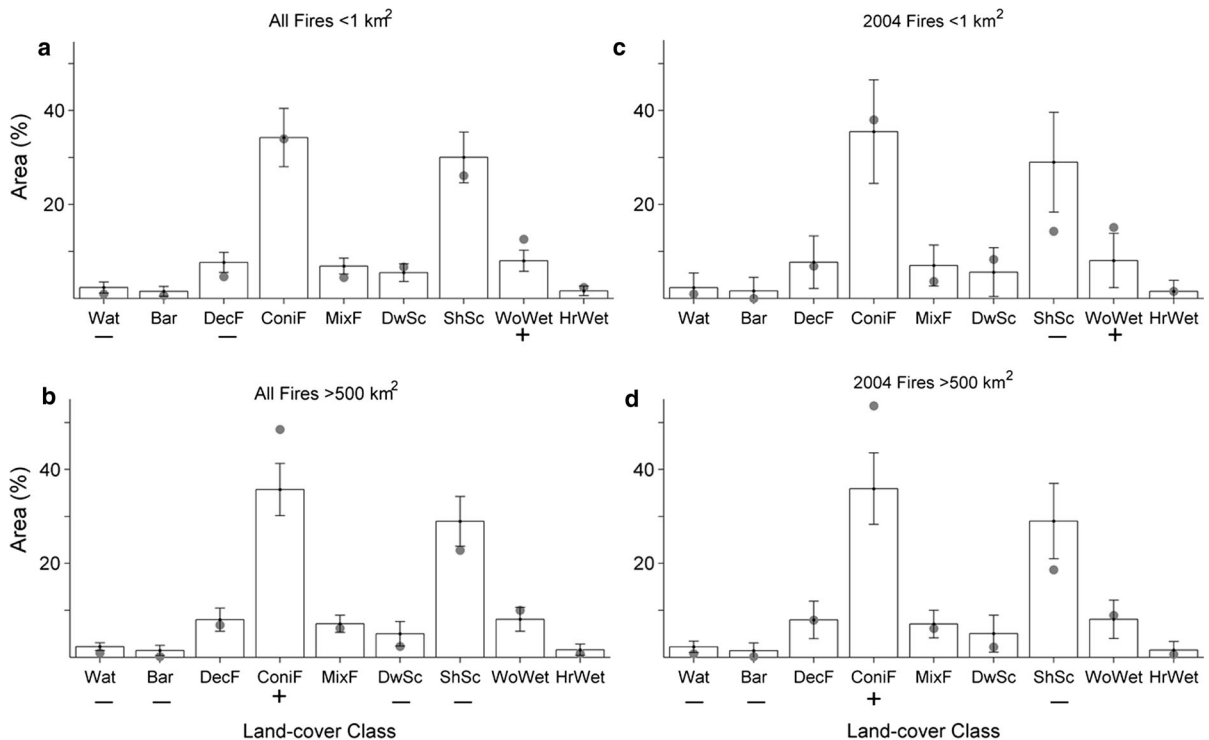
**Fig. 4** Comparison of the actual percentage of observed area burned (grey circles) with null models of Alaskan land cover (bars) in **a** all summers from 2002 to 2014, **b** the years with higher mean summer climate moisture index (CMI), and **c** the years with lower CMI. Percent area burned above and below the 95 % confidence interval of the null model is indicated by + and −, respectively. See Fig. 3 for explanation of abbreviated land-cover names



**Fig. 5** Relationship of mean climate moisture index (CMI) and a dissimilarity index describing differences in land-cover distribution between observed burned areas and a null model of random burning for the period of 2002–2014. The boxes indicate which years are considered higher and lower CMI summers as determined by the k-means cluster analysis







**Fig. 6** Comparison of observed percent area burned in **a** small fires (<1 km<sup>2</sup>) and **b** large fires (>500 km<sup>2</sup>) in 2002–2014, indicated by grey dots, with null models of Alaskan land cover (bars). Percent area burned above and below the 95 %

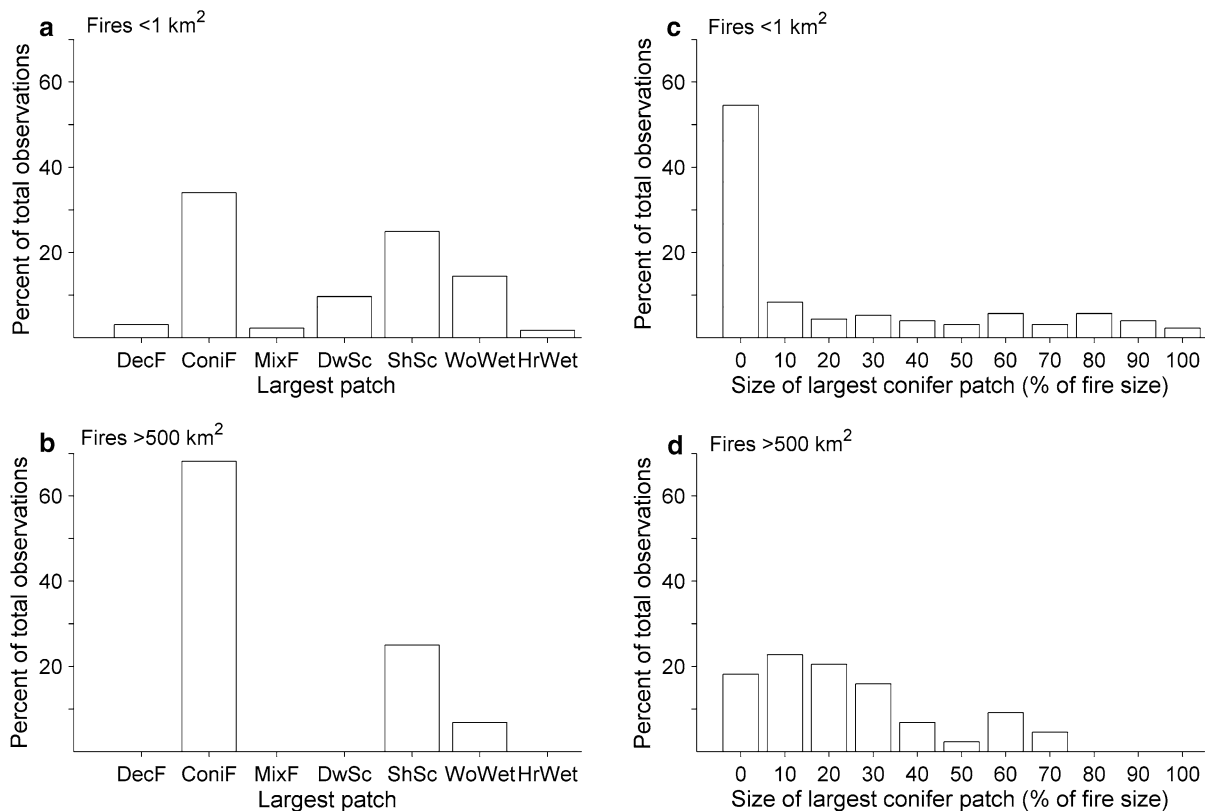
confidence interval of the null model is indicated by + and –, respectively. This analysis was repeated for 2004 (**c**, **d**), the year with the lowest climate moisture index (CMI). See Fig. 3 for explanation of abbreviated land-cover names

at the spatial and temporal scales relevant to fire management and resource planning. Our results contribute to elucidating the roles of climate, land cover, and their interactions in driving fire-regime changes in boreal forests.

Our analyses of the weather and fire data for the period of 2002–2014 show that increases in summer temperature and aridity (low CMI) led to increases in annual area burned and number of fires (Fig. 2). The number of large fires (>500 km<sup>2</sup>) also increased during lower CMI summers. These large fires represented only 5.1 % of all fires but accounted for 53.8 % of the area burned from 2002 to 2014. Similarly, Kasischke and Turetsky (2006) found that the frequency of large fires increased with temperature between 1959 and 1999 and that fires >500 km<sup>2</sup> represented approximately one half of the area burned in Alaska. Together, these data suggest that climate exerts a dominant top-down control on boreal-forest wildfires, and that area burned and extreme fire events will increase with increasing temperature and

moisture deficit in the coming decades (Duffy et al. 2005; Balshi et al. 2009).

Our analyses reveal that area burned was significantly higher during warmer and drier summers in all major land-cover classes, including those considered to have low flammability, such as deciduous forest (Cumming 2001). However, land cover significantly influenced boreal-forest burning. For example, coniferous forest and woody wetlands exhibited larger percent areas burned than expected by chance (Fig. 4a; Table 1). These land-cover classes are likely dominated by *Picea glauca* and/or *P. mariana* in Alaska, and have a relatively high biomass. Although the land-cover data do not allow us to distinguish between the *Picea* species, these two land-cover classes likely contain abundant *P. mariana*, a major constituent of Alaskan coniferous forests and boggy muskeg habitats (Lutz 1956; Yarie 1981; Rupp et al. 2002). *P. mariana* stands are highly flammable because of the high resin content in foliage and a lattice of dry twigs and branches (Johnson 1992).



**Fig. 7** The distribution of land-cover classes comprising the largest burned patch in **a** small and **b** large fires, and the size distribution of largest conifer patches in **c** small and **d** large fires. See Fig. 3 for explanation of abbreviated land-cover names

Paleoecological studies have shown that the middle-Holocene expansion of *P. mariana* in Alaska dramatically increased fire frequency and area burned (Hu et al. 2006; Higuera et al. 2009; Kelly et al. 2013). Likewise, ecosystem modeling shows that the expansion of this species on the boreal-forest landscape increases fire occurrence (Rupp et al. 2002; Brubaker et al. 2009). Together with these previous studies, our new results highlight the importance of land-cover composition and associated fuel type and flammability as major bottom-up controls of boreal fire-regime dynamics at annual to millennial timescales.

In contrast to coniferous forest and woody wetlands, percent area burned in shrub scrub and dwarf scrub was lower than expected by chance (Fig. 4a; Table 1). In boreal ecosystems, shrub-scrub and dwarf-scrub vegetation may represent early-successional communities in recently burned areas, and they are not as flammable as coniferous forests (Cumming 2001) in part because of relatively low fuel loads.

Moreover, shrub communities in interior Alaska tend to occur at higher elevations relative to forests, and experience lower lightning densities (Dissing and Verbyla 2003) and climate conditions less conducive to burning. Herbaceous wetlands also burned less than expected by chance (Fig. 4a) because they have low amounts of flammable fuel and are periodically saturated with water, which makes these communities unlikely to burn. As expected, open water and barren, fuel-free, areas were also negatively related with burning (Fig. 4a; Table 1). A number of previous studies suggest that fire occurrence decreases as the mean distance to water bodies decreases (e.g., Larsen 1997; Hellberg et al. 2004; Senici et al. 2010; Barrett et al. 2013), because fuel moisture increases around water bodies and because water bodies act as physical barriers to fire spread (Senici et al. 2010). Barren areas may also act as firebreaks because of their lack of fuels.

Land cover interacted with changing weather conditions to affect area burned in our study region

during the period of 2002–2014. Our dissimilarity analysis reveals that the land-cover composition of burned areas tended to be more similar to the null model under warmer and drier conditions (Fig. 5). Under cooler and wetter conditions, the land cover that burned was highly variable and tended to be more dissimilar from the null model (Fig. 5). Thus land cover appears to have played a more important role in controlling boreal fires when weather conditions were less conducive to burning.

Turner and Romme (1994) provided a conceptual framework for understanding the interactive effects of top-down and bottom-up controls of fire-regime dynamics. They suggested that the influence of bottom-up controls on fire (such as physiography, fuel type, and spatial arrangement of fuels) is less important under climate conditions that are favorable to fire occurrence and spread. In support of this hypothesis, model simulations (Miller and Urban 2000) and observational data (Gedalof et al. 2005) showed that in the American West, the spatial arrangement of fuels had a diminished effect on fire spread when conditions were extremely arid. Miller and Urban (2000) also showed that as fuel moisture decreased and vegetation flammability increased, the functional connectivity of fuels increased to facilitate fire spread. Our results provide partial support for the framework of Turner and Romme (1994), which has not been tested in boreal-forest ecosystems by previous studies. In particular, more area burned in interior Alaska under warmer/drier conditions, and the land-cover composition of the burned areas was more similar to the overall composition of the landscape under such conditions (Fig. 5). Thus under climate conditions conducive to burning, climate tends to overwhelm the effects of land cover as a fire control.

However, our results show strikingly high proportions of coniferous forest within the burned perimeters, especially during warm and dry summers (Fig. 4c). While coniferous forest in interior Alaska represents ~34.5 % of the land cover in both null models, it constituted 50.1 and 40.3 % of the actual area burned in warmer/drier and cooler/wetter summers, respectively (Fig. 4b, c). In the extreme fire year of 2004, when the CMI was lowest (warmest/driest) and area burned highest, coniferous forest constituted 53.6 % of area burned (Fig. 6d). These data suggest that the flammability of coniferous forests increases disproportionately with elevated temperature and

aridity. This finding is broadly applicable to the boreal-forest biome in North America where the dominant conifers are flammable and fire-adapted. However, the influence of land-cover classes in boreal fire-regime responses to climate/weather conditions is probably less strong in Eurasia than in North America because the dominant species in the former region are fire “avoiders” that are less flammable (Rogers et al. 2015).

Our results also show coniferous forest burned more in large *versus* small fires (48.5 and 34.0 %, respectively; Fig. 6a, b). Large fires may have spread selectively from their point of ignition through coniferous forests with flammable fuels, whereas small fires probably burned the areas adjacent to their ignition source and did not spread further when fuel loads and/or fuel flammability became insufficient. Consistent with this interpretation, the largest patch within a large fire was most often coniferous forest (Fig. 7b). In contrast, the largest patch within small fires occurred in any of the major vegetated land-cover classes (Fig. 7a) that were likely the closest to the location of fire ignition. Land-cover contagion of burned areas also increased with fire size, suggesting that larger fires burned through more homogeneous landscapes. These results support model simulations showing that landscapes with large patches of highly flammable fuel enable fires to spread more easily, resulting in larger total area burned (Moritz et al. 2005).

Our results have important implications for future fire-regime changes in boreal-forest ecosystems. Extreme disturbance events are becoming more prevalent as a result of anthropogenic climate change (IPCC 2013). The strong negative correlation of area burned with CMI suggests that large fires will become more prevalent with increases in temperature and aridity (Soja et al. 2007; Kasischke et al. 2010). These fires will likely result in substantial changes in the composition and spatial patterning of land cover in coming decades (Rupp et al. 2000; Mann et al. 2012). In particular, large fires will disproportionately spread through coniferous forest, resulting in a proportional increase in vegetation dominated by shrubs and deciduous species. Because of the lower flammability of the early-successional deciduous forests, an increase of their abundance on the landscape may lead to a decrease in fire frequency and spread (Johnstone et al. 2011; Kelly et al. 2013). Consequently, disturbance-induced changes in vegetation

have the potential to mitigate the influence of increased temperatures on burning (Rupp et al. 2000; Johnstone et al. 2011). However, this potential is limited as our results show that early-successional shrub communities and deciduous forests increased in area burned with decreasing summer CMI. These results suggest that projecting spatiotemporal dynamics of boreal fire regimes in response to future climate change requires that we consider both top-down and bottom-up controls, their interactions, and the potential feedbacks from land-cover changes.

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