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Examining forest resilience to changing fire frequency in a fire-prone region of boreal forest

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Abstract

Future changes in climate are widely anticipated to increase fire frequency, particularly in boreal forests where extreme warming is expected to occur. Feedbacks between vegetation and fire may modify the direct effects of warming on fire activity and shape ecological responses to changing fire frequency. We investigate these interactions using extensive field data from the Boreal Shield of Saskatchewan, Canada, a region where >40% of the forest has burned in the past 30 years. We use geospatial and field data to assess the resistance and resilience of eight common vegetation states to frequent fire by quantifying the occurrence of short-interval fires and their effect on recovery to a similar vegetation state. These empirical relationships are combined with data from published literature to parameterize a spatially explicit, state-and-transition simulation model of fire and forest succession. We use this model to ask if and how: (a) feedbacks between vegetation and wildfire may modify fire activity on the landscape, and (b) more frequent fire may affect landscape forest composition and age structure. Both field and GIS data suggest the probability of fire is low in the initial decades after fire, supporting the hypothesis that fuel accumulation may exert a negative feedback on fire frequency. Field observations of pre- and postfire composition indicate that switches in forest state are more likely in conifer stands that burn at a young age, supporting the hypothesis that resilience is lower in immature stands. Stands dominated by deciduous trees or jack pine were generally resilient to fire, while mixed conifer and well-drained spruce forests were less resilient. However, simulation modeling suggests increased fire activity may result in large changes in forest age structure and composition, despite the feedbacks between vegetation–fire likely to occur with increased fire activity.

KEYWORDS
alternative stable state, black spruce, climate change, immaturity risk, jack pine, resistance, self-regulation, spatially explicit state-and-transition simulation model

1 | INTRODUCTION

Over the past several decades, warm and dry conditions have promoted extensive wildfire in vegetated ecosystems worldwide (Brando et al., 2014; Kasischke & Turetsky 2006; Westerling, Hidalgo, Cayan, & Swetnam, 2006). Future changes in climate are widely anticipated to increase the area burned and frequency of wildfire (Flannigan, Krawchuk, de Groot, Wotton, & Gowman, 2009). Wildfire changes will have cascading consequences for ecosystem services, such as carbon dynamics (Turetsky et al., 2015), water quality (Bladon, Emelko, Silins, & Stone, 2014), habitat availability (Whitman et al., 2017), human health (Liu, Pereira, Uhl, Bravo, & Bell, 2015), and our economies (Hope, McKenney, Pedlar, Stocks, & Gauthier, 2016). In this context, a key challenge is understanding the conditions where ecological resilience, the ability to recover essential structures and functions following disturbance (Holling, 1973), may be compromised. Resilience may be lost when changes in the fire regimes alter disturbance legacies, the biologically derived remnants that persist postfire (Johnstone et al., 2016). Yet for many systems, it is difficult to predict if and when climate change-driven alterations to wildfire regimes may compromise ecological resilience because climate change influences both disturbance and recovery processes (Seidl et al., 2017; Turner, 2010).

Wildfire, climate, and their interactions are key drivers of forest dynamics in boreal forests (Payette, 1992). Across the boreal biome, temperatures are expected to warm by 4–11°C by 2100 (IPCC 2014). Thus, boreal forests may be especially vulnerable to climate change, particularly if feedbacks between disturbance regimes and climate cause systems to cross thresholds (Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015). Changes in climate that affect disturbance regimes and forest resilience have significant global implications, as boreal forests cover ~1.89 billion ha of land (Brandt, Flannigan, Maynard, Thompson, & Volney, 2013), encompass roughly one-third of terrestrial carbon stocks (Pan et al., 2011), and produce more than one-third of the world's lumber (Gauthier et al., 2015).

In the North American boreal forest, stand-replacing wildfire is a key driver of forest composition, structure, and function (Payette, 1992). A central mechanism promoting resilience of conifer forests is the production of aerial seed banks in serotinous cones, which promote rapid postfire establishment of trees such as pine (*Pinus* spp.) and black spruce (*Picea mariana*; Greene et al., 1999). However, recruitment may be hindered when wildfires burn too intensely, consuming seeds or creating postfire seedbeds that confer a competitive advantage to deciduous broadleaf species (Arseneault, 2001; Greene et al., 2007; Johnstone & Chapin, 2006a). Similarly, recruitment failures may occur due to immaturity risk associated with high fire frequency (Keeley, Ne'eman, & Fotheringham, 1999). For instance, black spruce may take more than 50 years to develop a substantial aerial seedbank (Gauthier, Bergeron, & Simon, 1996; Viglas, Brown, & Johnstone, 2013), and thus, repeat burning within a short interval may lead to recruitment failure (Buma, Brown, Donato, Fontaine, & Johnstone., 2013). Conditions that lead to poor regeneration of spruce and pine may promote the establishment of broadleaf deciduous species such as aspen (*Populus tremuloides*) and birch (*Betula* spp.), which produce abundant, light seeds that may disperse great distances (Johnstone, Hollingsworth, Chapin, & Mack, 2010). Once a shift to broadleaf deciduous cover occurs, the subsequent changes in plant–soil feedbacks alter fuels and support low severity fire, promoting the maintenance of the broadleaf forest community. Hence, more frequent or severe fire may compromise conifer forest resilience to wildfire and catalyze shifts to alternative states dominated by functionally different tree communities (Johnstone et al., 2016).

Temperature-driven statistical models suggest future warming may increase the annual area burned in western boreal forests of North America to 3.5–5.5 times that of the current (1991–2000) period by 2100 (Balshi et al., 2009). Yet the effects of future warming on wildfire activity may be moderated by processes of self-regulation, whereby vegetation changes caused by previous fires increase resistance to subsequent fire (Peterson, 2002). Indeed, regional, paleoecological, and landscape studies in the North American boreal forest suggest annual area burned has historically been moderated by a negative feedback exerted through decreased postfire fuel availability in young stands and shifts to less flammable forest composition (Girardin et al., 2013; Héon, Arseneault, & Parisien, 2014; Parisien et al., 2014). Thus, changes in forest vegetation in response to recent or recurring fire may create stabilizing feedbacks that constrain climate-driven increases in fire activity (Boulanger et al., 2017; Erni, Arseneault, Parisien, & Bégin, 2017; Héon et al., 2014).

Here, we study fire and forest dynamics in Saskatchewan's Boreal Shield, where >40% of the forested area has burned in the past 30 years (Kansas, Vargas, Skatter, Balicki, & McCullum, 2016), to better understand interactions between vegetation and fire. This region supports some of the highest rates of lightning-caused fire activity in Canada (Parisien et al., 2014), with large increases expected by end of the 21st century (Balshi et al., 2009; Flannigan, Logan, Amiro, Skinner, & Stocks, 2005). Thus, the Saskatchewan Boreal Shield is an ideal system to study if and how fire return interval regulates fire and vegetation dynamics in the North American boreal forest. Our research design combines extensive field data with existing research and geospatial data to empirically test two specific hypotheses about the potential effects of fire return interval on interactions between vegetation and fire: (a) self-regulation of fire where young, recently burned forest stands have a lower probability of fire than older stands (Peterson, 2002), and (b) immaturity risk, where short-interval fires reduce forest resilience (Keeley, Ne'eman, & Fotheringham, 1999). Empirical relationships between fire interval and forest resistance and resilience were then used to parameterize a spatially explicit, state-and-transition simulation model (STSM) of fire and forest succession (Figure 1). We use this model to perform simulation experiments that explore the effects of fire–vegetation interactions on landscape vegetation and wildfire conditions. Specifically, we examine the following scenarios of fire–vegetation interactions: (a) immaturity risk, where the probability of vegetation returning to its pre-fire state is lower in young stands (*IR*); (b) self-regulation of area burned, where the probability of burning is reduced in stands ≤50 years age (*SR*); and (c) a scenario representing increasing probability of fire consistent with climate change predictions (*IPF*). Comparison of these simulation experiments provides insight into how interactions between fire and vegetation may affect landscape-scale responses of forests to projected changes in fire activity.

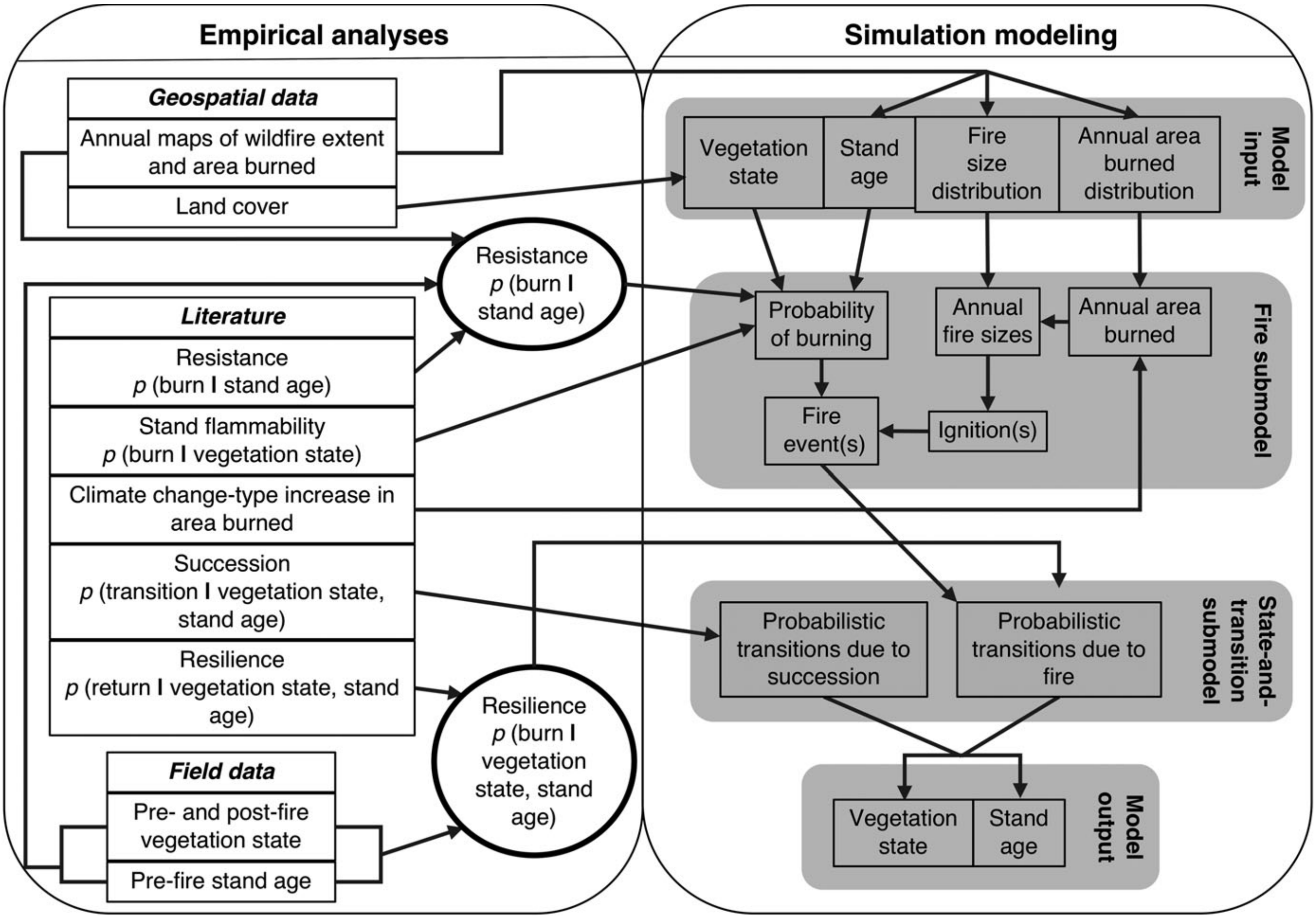

FIGURE 1 Flowchart of the data products used to quantify resilience and resistance to fire and simulate fire and forest succession

2 | MATERIALS AND METHODS

2.1 | Study area

Saskatchewan's Boreal Shield ecozone covers an area of 183,435 km^2 in western Canada that extends from 54.5°N to 59.5°N (Figure 2). While elevation varies only minimally across the region (<850 m), the landscape is characterized by a complex undulating terrain with many water bodies. Saskatchewan's Boreal Shield experiences a continental climate with average annual (1950–2000) daily temperatures of −2.4°C and average annual precipitation of 465 mm (WorldClim climate data; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

Wildfire is the most important disturbance affecting Saskatchewan's boreal forest (Dix & Swan, 1971; Heinselman, 1981; Swan & Dix, 1966). Most fires are estimated to be of small to moderate size (<50,000 ha; Figure 2c); however, the majority of the area burns in large fires (>50,000 ha; Parisien, Hirsch, Lavoie, Todd, & Kafka, 2004). Large fire events occur during periods of warm and dry weather that are driven by broadscale ocean–atmosphere teleconnections (Macias-Fauria & Johnson, 2008) with most of the area burning in years with extreme fire weather. Thus, interannual variability in area burned is high (Figure 2b). Stand-replacing wildfire is relatively frequent in Saskatchewan's Boreal Shield; Parisien et al. (2004) estimated the fire cycle to be about 100 years. In contrast to many other North American forests, the fire regime of Saskatchewan's Boreal Shield has experienced relatively little anthropogenic modification; fires are predominately caused by lightning strikes, with only 6.1% of fires being human-caused (Parisien et al., 2004). The region has little active forest management and a low density of human communities and infrastructure, with limited fire suppression activity (Magnussen & Taylor, 2012).

Forests across Saskatchewan's Boreal Shield are dominated by black spruce and jack pine (*Pinus banksiana*); also present but rarely dominant are deciduous broadleaf species, such as trembling aspen and white birch (*Betula papyrifera*), and nonserotinous conifers, such as white spruce (*Picea glauca*) and eastern larch (*Larix laricina*). In these forests, fire is frequent enough that disturbance-independent succession (e.g., stand break-up) plays only a minor role in driving forest composition and structure. Late-successional, shade-tolerant species such as balsam fire (*Abies balsamifera*) are notably absent from the system (Dix & Swan, 1971). However, as in other parts of the North American boreal forest, long-lived, shade-tolerant black spruce may replace short-lived, shade intolerant species like aspen and jack pine during fire-free intervals >70 years (Belleau, Leduc,

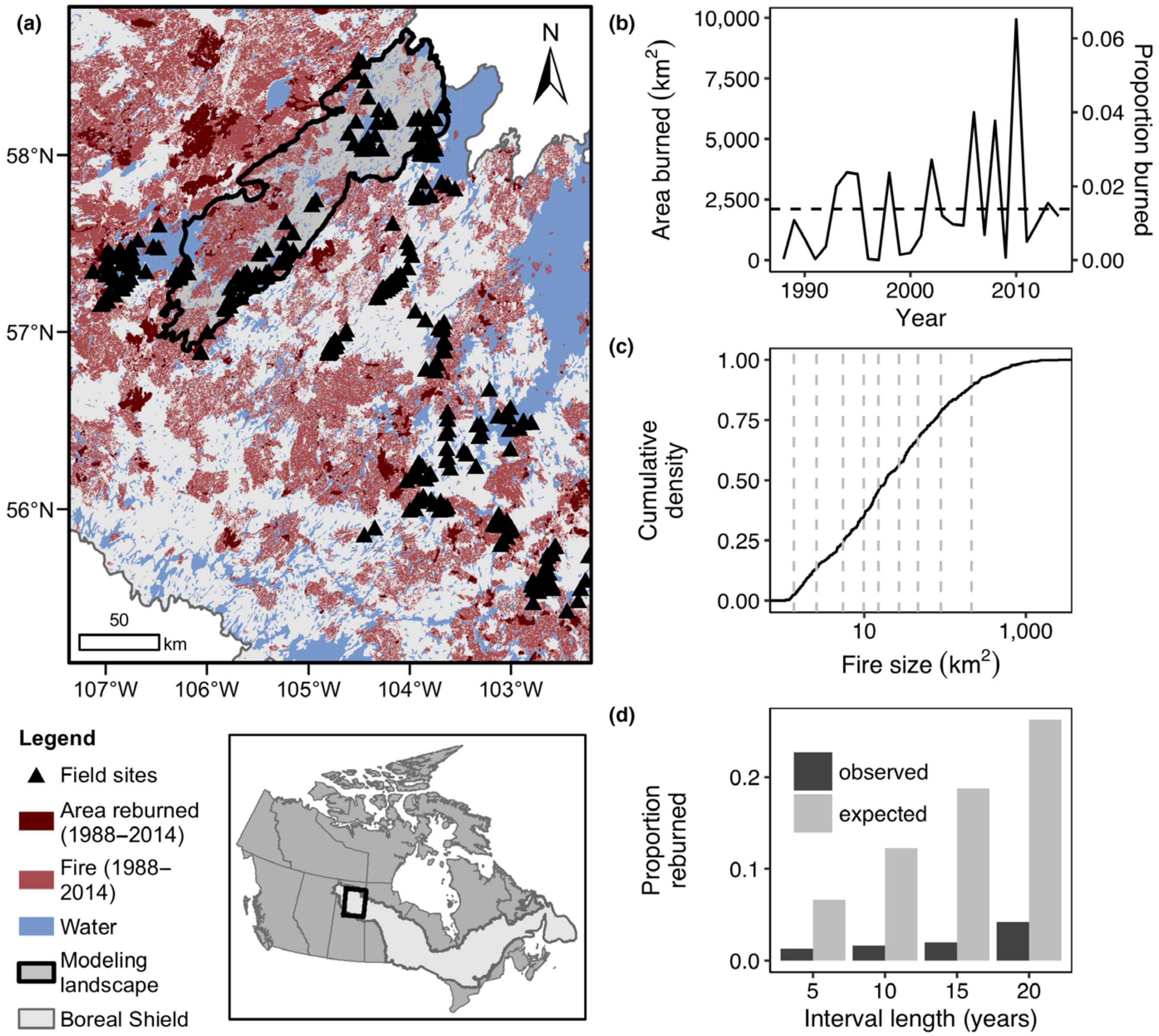

FIGURE 2 The study area (a) in the Boreal Shield of Saskatchewan in Canada (inset map) and wildfire history statistics for Saskatchewan's Boreal Shield (b–d), derived from a Landsat-based classification of the area burned in individual wildfire events for the 1988–2014 period (Kansas et al., 2016). In a, burned areas are mapped as having burned once (red) or twice (dark red) during the 1988–2014 period. Triangles indicate locations of field sites and the modeling landscape is outlined in black. In b, the solid line shows the annual area burned within the ecoregion, and the mean is given by the dashed horizontal line. In c, the cumulative density of fires is plotted, and dashed vertical lines show the empirical deciles. In d, bars represent the observed and expected (assuming no self-regulation) proportions of area reburned at increasing interval lengths of ≤5, ≤10, ≤15, ≤20 years within the 1988–2014 period (for methodological details, see Materials and Methods: *Quantifying resistance to short-interval fire*). [Colour figure can be viewed at wileyonlinelibrary.com]

Lecomte, & Bergeron, 2011; Caroll & Bliss, 1982; Lesieur, Gauthier, & Bergeron, 2002).

2.2 | Field data collection

During the summers of 2014–2016, we sampled stand composition and structure, environmental conditions, and fire history at 150 sites burned since 1964 (i.e., <50 years old) across Saskatchewan's Boreal Shield (Figure 2a). Sites were selected using a stratified random design, where strata were defined by time since fire using the Forest Fire Chronology of Saskatchewan (Parisien et al., 2004) and dominant species. To reduce travel time and increase sampling efficiency, all sites were located >100 m and ≤1.0 km of a road or accessible water body. All sites were separated by >300 m.

At each site, we established a 10 × 10 m plot following protocols developed for Saskatchewan's ecosite classification system (McLaughlan, Wright, & Jiricka, 2010). For each plot, we recorded the slope, aspect, elevation, latitude and longitude, and terrain shape (concave, flat, convex, or undulating). We also collected soil data from two cores, each 2 m outside of the northeast and southwest plot corners. We recorded the effective texture (the finest soil texture within the top 50 cm) for each core using a texture-by-feel approach, along with the thickness of the organic layer, the depth to the water table and/or frost line, and the moisture regime class (Supporting Information Table S1-1; McLaughlan et al., 2010).

To characterize stand structure and composition, we recorded the species, diameter at breast height (DBH), and status (live, fire-killed, post-fire-killed, or unknown) for each tree (>5 cm DBH) in the plot. Within four 2 × 2 m subplots located in the plot corners, we recorded the species and DBH of all saplings (height > 1.3 m and DBH ≤ 5 cm) and seedlings (height ≤ 1.3 m). When the density of either seedlings or saplings was <0.5 individuals/m^2 in the subplots, we recorded abundance in the entire plot. Given the difficulty in differentiating between white and black spruce seedlings, they were only classified to the genus level. However, the vast majority of identified spruce trees at the study sites were black spruce, and white spruce was relatively uncommon on the landscape. Where charring prevented the identification of tree genus, stems were classified as either broadleaf deciduous or conifer.

2.3 | Dendroecology methods

To characterize fire history, we collected tree cores at the root collar from four living trees of both the dominant and subdominant species within each plot. We also collected cross sections from four seedlings and four saplings of the dominant and subdominant species. Ring counts from the live trees, saplings, and seedlings were used to estimate when the stand last burned, based on the assumption that most postfire tree recruitment occurs 5–10 years after fire (Gutsell & Johnson, 2002). We also collected tree cores from the base of four fire-killed trees of both the dominant and subdominant species to estimate stand age at the time of fire.

Tree cores and cross sections were processed using standard dendrochronological approaches (Stokes & Smiley, 1996). For each sample, we counted the number of growth rings using a high-resolution scanner and the WinDendro computer program (Regent Instruments,2015) or a standard light microscope for samples with narrow rings (Speer, 2010). Fire history, including fire severity as stand-replacing (lethal) or non-stand-replacing, was determined for each site using tree-core data. Stand-replacing events (lethal) were recognized by a postfire tree cohort (≥2 trees) where the oldest trees established over a relatively short period of time (mean age of trees in the cohort ±10 years). Non-stand-replacing events were recognized by the synchronous establishment of two or more trees along with older surviving trees. For both non-stand-replacing and stand-replacing events, the maximum age count of the fire cohort was assigned as the event year.

2.4 | Characterizing vegetation state

We classified vegetation states based on tree density and time since fire, further stratified where necessary by site moisture (Table 1; McLaughlan et al., 2010). First, stands were divided into forest and non-forest strata where the forest stratum was defined by a live basal area ≥1 cm^2/m^2 for older stands (≥20 years since last stand-replacing fire) or stem density (the total of seedling, sapling, and tree density) ≥0.5 individuals/m^2 for young stands (<20 years since last stand-replacing fire). The forest stratum was further divided into (a) deciduous-, pine-, or spruce-dominated states, stands where ≥66% of the tree density was the focal tree group; (b) a mixed conifer state, stands where neither jack pine nor spruce were dominant but together were ≥66% of the tree density; or (c) mixed deciduous–conifer, stands where neither deciduous trees nor conifer trees dominated the stand (e.g., <66% deciduous and <66% conifer). Tree species dominance was determined using the relative live basal area unless time since fire was <20 years, when stem density was used instead. Finally, two vegetation states that occurred over a broad range of moisture conditions (non-forested and spruce-dominated stands) were further subdivided based on drainage, where sites were classified as poorly drained when two or more of the following conditions were met: (a) thickness of the organic layer >40 cm, (b) depth to the water table ≤50 cm, (c) depth to frost ≤60 cm, and (d) moisture regime classed as very moist or wetter (McLaughlan et al., 2010).

TABLE 1 Characteristics of forest states defined for Saskatchewan's Boreal Shield ecozone and the number of sample sites within each state (see Materials and Methods for more details)

					Sample size	
State	Forested	Drainage	Tree species dominance	Annual prob. of fire	Pre-fire	Postfire
Poorly drained non-forest	Non-forest	Poor	NA	0.0075	2	5
Well-drained non-forest	Non-forest	Well	NA	0.0075	1	8
Deciduous	Forest		≥66% broadleaf deciduous species	0.0063	2	3
Conifer mix	Forest		<66% spruce or jack pine but ≥2/3 conifer	0.10	8	7
Deciduous–conifer mix	Forest		<66% broadleaf deciduous species and <66% conifer	0.0086	3	11
Jack pine	Forest		≥66% jack pine	0.01	46	49
Poorly drained spruce	Forest	Poor	≥66% spruce	0.0092	7	3
Well-drained spruce	Forest	Well	≥66% spruce	0.11	31	14

2.5 | Quantifying resistance to short-interval fire

Resistance to fire was quantified by calculating the frequency of short-interval fire. Here, we characterize a short-interval fire as a repeat occurrence of stand-replacing fire within 50 years. This age threshold represents a plausible maximum stand age likely to significantly reduce fire risk based on field studies of wildfire in Canadian boreal forests (Beverly, 2017; Erni et al., 2017; Héon et al., 2014), while capturing a reasonable range of ages for effects of immaturity risk (Johnstone & Chapin, 2006b; Johnstone, Hollingsworth et al., 2010; Viglas et al., 2013). If short-interval fire is rare, then forests may be resistant to high burn rates, consistent with the hypothesis of self-regulation of fire at the landscape scale. We used field data to tabulate the number of field sites that were ≤50 years of age at the time of the most recent fire (Figure 1) Additionally, we used spatial overlay analysis (O'Sullivan & Unwin, 2010) to quantify the area of wildfire that occurred in areas that had recently experienced fire. To this end, we first acquired geospatial data depicting the annual area burned 1988–2014 (Kansas et al., 2016). Polygon data were converted to a 250 × 250 m raster by listing all pixels that intersected the polygon as burned and all other pixels as unburned. We then masked all urban and water areas using land-cover data from Beaudoin et al. (2014). Next, we created maps of the cumulative area burned prior to each year. To test if and how long previous fires affected subsequent fires, we created maps of the total area previously burned during four different moving time windows: ≤5, ≤10, ≤15, and ≤20 years prior to the focal year. Longer intervals could not be assessed due to the length of the geospatial fire record.

We performed spatial overlays for each year and window combination separately. Thus, for each year and window combination, we first calculated the observed area burned in areas with and without recent fire. These observed areas were compared to an expected area, calculated as the proportion of the landscape occupied by recent burns multiplied by the area burned in that year. For each time window, we summed the observed areas burned across all years and compared it to the sum of expected area burned to summarize the effect of prior burning on subsequent fire area. Observed and expected areas were then converted to proportions to allow for comparison among the different time windows. Because our spatial overlay approach assesses entire populations and not samples, we interpret all deviations between observed and expected proportions as real differences. All spatial analyses were performed in *R* (R Core Team,2017) using the *raster* package (Hijmans, 2016).

2.6 | Quantifying resilience to short-interval fire

Here, we define resilience as the probability of each state returning to the same state following stand-replacing wildfire (Figure 1). In our study area, canopy dominance is largely a function of initial postfire density and relative growth rate (Ilisson & Chen, 2009; Gutsell & Johnson, 2002; Dix & Swan, 1971), thus initial postfire tree communities can be used to quantify forest resilience (Johnstone, Hollingsworth et al., 2010). If short-interval fire (i.e., repeat occurrence of stand-replacing fire within 50 years) promotes greater differences between pre- and postfire composition than long-interval fire, then forests may be less resilient to high burn rates, consistent with the hypothesis of immaturity risk. We quantified resilience using a Bayesian statistical approach that incorporates prior knowledge from existing empirical research and expert opinion with new field observations for improved parameter estimation. Bayesian analyses are particularly useful when sample sizes are small or limited in their representativeness of the system (Choy, O'Leary, & Mengersen, 2009). Here, we assume resilience, θ, is a random variable described by a beta distribution:

$$f(\theta) = \frac{\theta^{a-1}(1-\theta)^{b-1}}{\beta(a,b)}$$

where: a and b are the prior estimates of returning to the same and switching states, respectively, and $\beta(a,b)$ is the beta function, which normalizes the beta distribution and ensures the function sums to one. The spread of the distribution is related to the concentration of the distribution (k), which is defined by the sum of a and b shape parameters. When k is large, the distribution becomes narrower and more observations are needed to shift the posterior distribution toward the likelihood (Kruschke, 2014).

We first calculated resilience independent of time since fire (*all fire* events). We assigned a prior distribution with a mode (m) of 0.975 to all states based on existing research that shows self-replacement is the dominant trajectory of forest recovery (Greene et al., 1999; Ilisson & Chen, 2009). We set k to be weakly informative (k = 10). Next, given immature stands may be more likely to shift to alternative states (Johnstone & Chapin, 2006b; Lavoie & Sirois, 1998), we calculated resilience for *short-interval fires*, here sites that reburned within 50 years, and *long-interval fires*, sites that had not burned in the past 50 years. The prior distributions for long-interval fire were the same as the all fire approach (i.e., m = 0.975 and k = 10). Given that conifers are expected to experience greater immaturity risk (Johnstone & Chapin, 2006b), prior distributions for short-interval fire in states with conifers were assigned a prior mode equal to half of the long-interval mode (m = 0.488). In contrast, deciduous species are able to resprout after a short interval (Johnstone & Chapin, 2006b); thus, the prior distribution was unchanged for short-interval fire in deciduous, well-drained non-forest, and poorly drained non-forest (i.e., m = 0.975 and k = 10). Prior distributions were then mathematically updated using the field observations (Supporting Information Appendix S3) and compared prior distributions for different time-since-fire intervals.

2.7 | Simulation model description and implementation

To explore how climate change-driven alterations to the fire frequency may affect forest composition in the study area, we developed a spatially explicit state-and-transition model (STSM; Daniel, Frid, Sleeter, & Fortin, 2016) using ST-Sim software (Figure 1; ApexRMS, 2016). Possible states in the model include the eight states identified in the field data (and water) and transitions between states occur due to wildfire or disturbance-independent succession (e.g., stand break-up or relay succession; Ilisson & Chen, 2009; Figure 3). To reduce computation time, we ran our simulations on a smaller modeling landscape, the 7,398,000 ha Athabasca Plains ecoregion (ecodistrict no. 386; Ecological Stratification Working Group, 1995; Figure 2a). State type was initialized using maps of forest attributes from Natural Resources Canada (Beaudoin et al., 2014; CCRS, 2008), for further details see Supporting Information Appendix S1. Stand age was initialized using Landsat-based maps of area burned for the 1988–2014 period (Kansas et al., 2016) and fire perimeter data for the 1945–1987 period using data from the FFCS (Naelapea, 1997), for further details see Supporting Information Appendix S2. All simulations were run for 100 years with an annual time step and a spatial grain of 250 × 250 m. Simulations were repeated for 100 Monte Carlo realizations.

In our model, disturbance-independent successional transitions between states occur stochastically, where the probability of succession driving a transition from state i to state j for a given cell depends on the state type and stand age (Figure 1). Succession transition probabilities were based on data from Belleau et al. (2011) for the Boreal Shield in northwestern Quebec and northeastern Ontario (Supporting Information Table S3-2). It is worth noting that the high fire frequencies in our study area mean that stands are likely to burn before sufficient time has elapsed for stand break-up or relay succession to occur, precluding the realization of potential successional transitions (Dix & Swan, 1971; Gutsell & Johnson, 2002). Wildfire was modeled as a stochastic process where the probability of fire (W_{ct} for cell c and timestep t) depends on an aspatial model of wildfire occurrence (Z_{ct}) and a spatially dependent model of fire spread

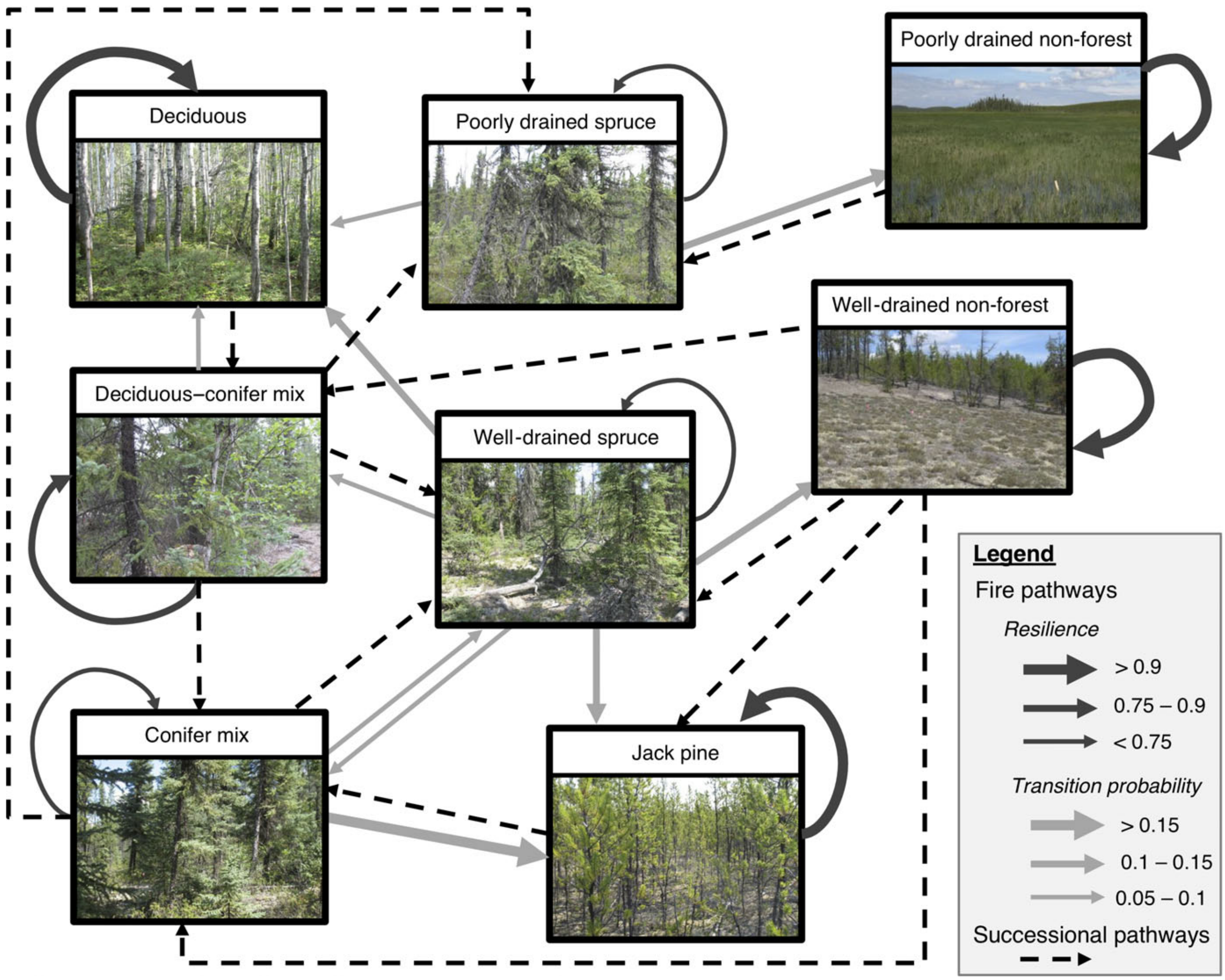

FIGURE 3 State-and-transition diagram illustrating the dominant transition pathways for the study area. The resilience and transition probabilities illustrated were quantified using observations of pre- and postfire composition from all 100 field sites and do not incorporate any potential effects of fire interval. Note transition probabilities <0.05 are not shown for simplification (see Supporting Information Table S3-1 for more details). [Colour figure can be viewed at wileyonlinelibrary.com]

(Daniel et al., 2016). Briefly, aspatial wildfire occurrence was first determined by calculating $Z_{ct} = M_{ct}\ V_t\ S_c\ I_t$, where V_t is a temporal variability multiplier (sensu Daniel et al., 2016), which accounts for annual variability in area burned, S_c is a spatial multiplier that accounts for dependence of wildfire on topographic factors, and I_t is a temporal trend multiplier (sensu Daniel et al., 2016), which allows for a change in the mean probability of fire through time. In recognition that the probability of fire depends on the forest type (Cumming, 2001), M_{ct} was defined as the probability of fire given the state of cell c at time t.

State-specific annual probabilities of fire were based on species-specific burn rates estimated at the landscape scale for northern Alberta from Cumming (2001). We expanded Cumming's (2001) five-state classification, which consisted of deciduous, white spruce, black spruce, jack pine, and other (non-forested) states, to match our 8-state classification by simply assigning a probability equal to the midpoint between the two closest states present in Cumming's (2001) classification. For instance, the conifer mix state was assigned a probability of fire equal to the average of the jack pine and black spruce burn rates. To account for the fact that burn rates are higher in Saskatchewan's Boreal Shield, burn rates from Cumming (2001) were linearly increased such the fire rotation for the modeling landscape was equal to historical fire rotation (99 years; Parisien et al., 2004). The temporal variability in the annual area burned, V_t, was defined by the empirical distribution of the ratio of annual area burned to average annual area burned, calculated from GIS data of the area burned over the 1988–2014 period (Figure 2a). Because the probability of fire depends on topography, particularly the distance to large water bodies (Nielsen, DeLancey, Reinhardt, & Parisien, 2016), S_c was defined as the likelihood of wildfire given the presence of islands and amount, distance, direction, and shape of nearby lakes using data for the study area from Nielsen et al. (2016). Accounting for the effects of topography on the probability of fire allows for fire refugia to emerge in our modeling, consistent with patterns of stand age across the boreal forest (Erni et al., 2017).

Next, to account for spatial dependence of fire we used all wildfire events (1988–2014) to define empirical deciles of wildfire size (Figure 2b). Wildfire was initialized on the landscape by first defining the aspatial expectation for total area burned (from Z_{ct}), and then dividing this area into discrete fire events based on the empirical deciles. For each fire event, ignition was simulated randomly and fire spread to the surrounding eight cells based on Z_{ct}. In our model, fires stop spreading once the simulated fire size has been reached or it runs out of neighboring cells—in which $Z_{ct} > 0$ (Daniel et al., 2016).

We modeled vegetation and wildfire conditions that might result from the interaction of the presence/absence of three conditions: (a) immaturity risk (*IR*), (b) self-regulation of area burned (the probability of fire occurring depends on stand age) (SR), and (c) increasing probability of fire concordant with predictions under climate change (IPF). In all scenarios, transitions in vegetation state following fire occur stochastically. In scenarios with no IR, the probability of wildfire driving a transition from state i to state j depends only on the state type (Figure 3). Postfire return probabilities were defined using the posterior mode of resilience for the all fire interval condition. In scenarios with IR, transitions following fire depend on both the state type and stand age. Here, return probabilities were defined using posterior mode of resilience for the short fire interval condition for stands <50 years and the long fire interval condition for stands >50 years. The probability of transitioning to each of the different states was then defined using field observations and mechanisms presented in the literature (Supporting Information Table S3-1). In scenarios with SR, we used a simple threshold model to describe the effect of time since fire on the probability of fire. Specifically, we assumed the probability of fire was 50% lower in stands <50 years of age (Erni et al., 2017; Héon et al., 2014). In the IPF scenarios, the probability of fire was set to linearly increase such that by the end of the simulation period, the probability of fire was 3.5 times greater than the 1988–2014 period. This scenario reflects a conservative estimate of the potential increase in area burned in western North America (Balshi et al., 2009). Conditions were combined in a full factorial design, resulting in eight different scenarios (Supporting Information Table S3-3).

3 | RESULTS

Of the 150 sites sampled, 26 sites exhibited evidence of non-stand-replacing fire and 1 site exhibited evidence of disturbance other than wildfire. Non-stand-replacing fire occurred predominantly in jack pine (n = 9), well-drained black spruce (n = 7), and conifer mix (n = 5) sites. At 26 sites, the pre-fire tree community could only be classified to conifer. We based our calculations on data from the 100 sites in our sample with evidence of only stand-replacing fire and where pre- and postfire state could be assigned. Of these sites, pre-fire composition was dominated by jack pine (n = 46; Table 1) and well-drained black spruce (n = 31; Table 1), while postfire composition exhibited notably fewer well-drained black spruce sites (n = 14; Table 1).

3.1 | Resistance to frequent wildfire

The fire interval could be determined at two-thirds of sites (68/100 sites). We found 28% of sites had burned twice in a period <50 years (19/68 sites). Most short-interval fire occurred in stands that had not experienced fire in a few decades; however, three sites burned twice in <5 years. About half of the short-interval fire occurred in stands dominated by jack pine (10/19 sites), and the remainder in well-drained spruce (4/19 sites), conifer mix stands (3/19 sites), deciduous–conifer mix stands (1/19 sites), and poorly drained spruce stands (1/19 sites). More than a third of stands that experienced short-interval fire burned in 2010, an extreme fire year that burned >6.5% of the Saskatchewan Boreal Shield (994,175 ha; Figure 2d). While the proportion of short-interval fires in our limited field data suggest short-interval fire is relatively common, geospatial data suggest that of the 39% of vegetated area in the Saskatchewan Boreal Shield that burned in 1988–2014 (5,599,945 ha), only 6% of that area burned more than once (326,427 ha; Figure 2a). Consistent with the hypothesis of fire self-regulation, spatial overlay analyses showed that far less area burned in young postfire stands (<20 years since fire) than would be expected by chance (Figure 2c). This effect of previous burning on subsequent fire appeared to persist for at least 20 years.

3.2 | Resilience to frequent wildfire

Most (approximately two-thirds) of field sites were classified as returning to the same vegetation state following fire (Figure 3, Supporting Information Table S3-1). Resilience was lowest where spruce was a sizeable component (i.e., conifer mix and well-drained or poorly drained spruce states; Figure 3). Our field data were not able to substantially inform estimates of resilience for deciduous and non-forest types due to low sample sizes (Table 1). Consistent with the hypothesis of immaturity risk, we found that field sites classed as conifer mix, jack pine, and poorly drained spruce prior to burning were less likely to return to the same state when the interval between fires was <50 years (Figure 4). Well-drained spruce sites commonly transitioned to alternative states regardless of fire interval; that is, the posterior mode of resilience for well-drained spruce was nearly the same for long and short fire-free intervals, 0.56 and 0.54, respectively (Figure 4g; Supporting Information Table S3-1). Jack pine stands showed high resilience following long fire-free intervals, and higher than expected resilience following short fire-free intervals (Figure 4d).

Fire events at our field sites led to multiple transition pathways for most states with >2 samples (Table 1). Conifer mix sites were commonly observed switching to a different state; 50% of conifer mix sites transitioned to jack pine following fire (4/8 sites; Figure 4, Supporting Information Table S3-1). Transitions from conifer mix to jack pine occurred when the interval between fires was <40 years and also when comparatively thick (≥4 cm) organic layers remained after fire. Jack pine states typically returned to jack pine (41/46 sites), but switches to well-drained non-forest and conifer mix were also observed (Supporting Information Table S3-1). Well-drained spruce exhibited a range of transition pathways following stand-replacing wildfire, most frequently recovering to the pre-fire type (13/31 sites) or transitioning to a deciduous–conifer mix (8/31 sites, Supporting Information Table S3-1). Following stand-replacing fire in well-drained spruce, the relative abundance of deciduous trees increased when pre-fire basal area of spruce was low or postfire organic layer depth was thin, suggesting a severe fire. Transitions from well-drained spruce to a non-forested state occurred when the residual organic layer was relatively thick (>6 cm) or when the interval between fires was <50 years.

3.3 | Simulating interactions between vegetation and wildfire

In our simulation modeling, the SR scenario representing negative feedbacks on area burned exerted by fuel depletion and shifts to less flammable deciduous forest moderated but did not mitigate the

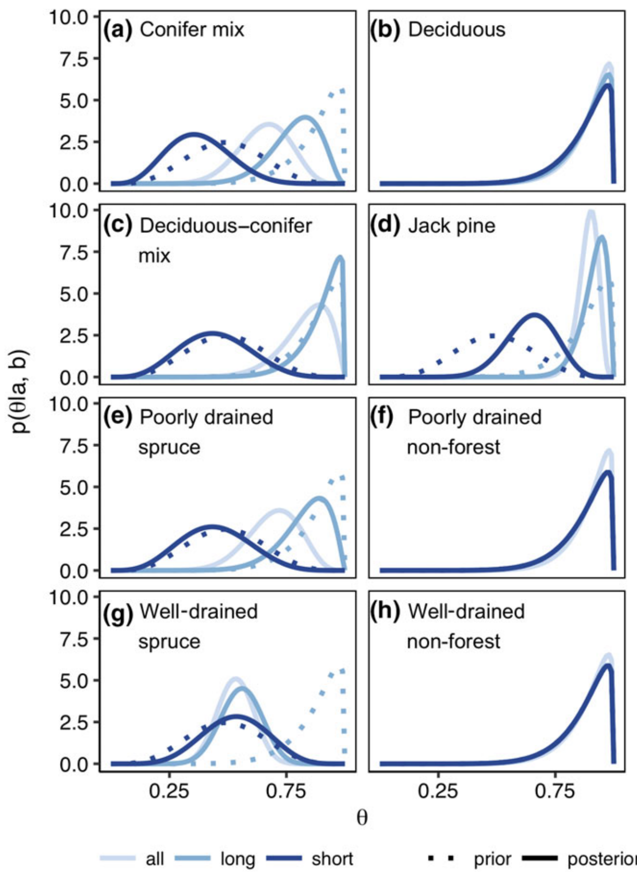

FIGURE 4 Distributions of prior (dotted lines) and posterior (solid lines) resilience for eight stand types in the Saskatchewan Boreal Shield: conifer mix (a), deciduous (b), deciduous–conifer mix (c), jack pine (d), poorly drained spruce (e), poorly drained non-forest (f), well-drained spruce (g), and well-drained non-forest (h). Line colors differentiate resilience distributions following short (<50 years, dark blue), long (>50 year, medium blue), and all (light blue) fire-free intervals. Where only posterior distributions are visible, prior distributions are equal to posterior distributions. Sample size for each stand type is given in Table 1. [Colour figure can be viewed at wileyonlinelibrary.com]

effect of a climate change-type increase in the probability of fire (Figure 5). Simulations where fire was self-regulating were characterized by lower average annual area burned at the end of the simulation period than scenarios where fire was not self-regulating (mean annual proportion burned = 0.031 for both the *IR & no SR & IPF and no IR & no SR & IPF* scenarios, vs. 0.026 for both the *no IR & SR & IPF* and *IR & SR & IPF* scenarios). Scenarios with immaturity risk had little effect on annual area burned in the model.

Simulation models showed changes in the proportion of the landscape occupied by different vegetation states even under the null scenario of no IR, no SR, and no IPF (Figure 6). The greatest vegetation change was simulated when the area burned increased over the simulation period (IPF scenarios). The magnitude of change depended on state type, with only minor effects of scenarios representing immaturity risk and self-regulation of fire. Under all scenarios, the proportion of well-drained spruce decreased over the 100-year simulation period. The largest decreases occurred in IPF scenarios, where well-drained spruce

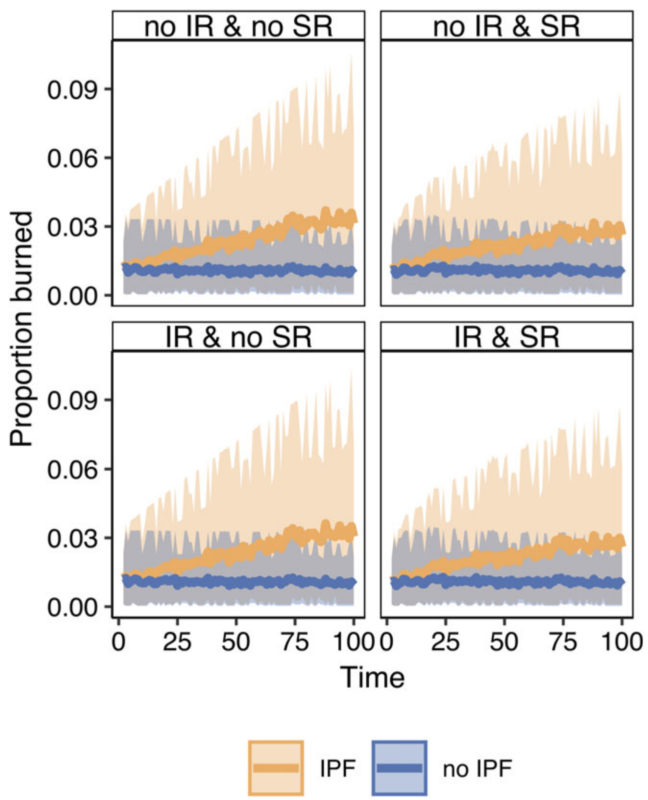

FIGURE 5 Change in proportion of the forested area burned for eight different scenarios. Scenarios are combinations of the presence/absence of: IR (immaturity risk), SR (self-regulation of area burned), and IPF (increasing probability of fire). Lines illustrate the mean of the 100 simulations. Shaded areas indicate the 95% confidence interval. [Colour figure can be viewed at wileyonlinelibrary.com]

was lost from >20% of the landscape by the end of the simulation period. In contrast, the proportion of well-drained non-forest generally decreased when area burned was constant but increased when the probability of fire increased and postfire resilience was age-dependent. The abundance of poorly drained spruce, poorly drained non-forest, jack pine, and conifer mix states was relatively stable under all scenarios (i.e., changes in landscape proportion ±5% initial conditions by the end of the simulation period). Conifer mix and poorly drained spruce became more abundant when the probability of fire was constant but decreased with increasing area burned. Jack pine cover increased by 4% of the landscape area when more area burned annually and postfire recovery was not age-dependent. The proportion of deciduous and deciduous–conifer cover increased under all scenarios, with increases of at least 10% and 7%, respectively, of the landscape when the probability of fire increased over the simulation period (Figure 6).

The mean age of vegetation states in our model was not stationary under any scenario (Figure 7). Simulation modeling suggested that the mean age of states was most strongly affected by scenarios with increased probability of fire, with limited effects of scenarios of self-regulation or immaturity risk (Figure 7). Under historical burning conditions, mean stand age generally decreased. However, the mean stand age for conifer mix, poorly drained spruce, and well-drained spruce increased, largely due to successional transitions (Figure 3). The deciduous state was initially very rare (Figure 6) and characterized by a mean landscape age of 52 years (range of 22–150 years). Over the simulation period, the mean landscape age of the deciduous state first decreased as rare stands were burned and then quickly increased (Figure 7) as the area of deciduous cover increased due to fire-driven transitions. The higher probability of fire in deciduous–conifer versus deciduous states (Table 1) led to a gradual decline in age of deciduous–conifer mixed states, while deciduous states increased in mean age. When the area burned increased over the simulation period, mean stand ages generally declined. Under these conditions, mean ages of conifer mix and jack pine states decreased by >26 and >28 years, respectively, by the end of the simulation period (Figure 7).

4 | DISCUSSION

Field surveys and fire mapping in the fire-prone Boreal Shield of Saskatchewan provided empirical evidence that the interval between fires affects both postfire recovery and patterns of area burned. Forest stands dominated or codominated by conifers were in general more likely to return to the same state following long fire-free intervals than short intervals, consistent with the immaturity risk hypothesis, which states that resilience of vegetation communities in fire-prone ecosystems is affected by fire interval length (Keeley, Ne'eman, & Fotheringham., 1999). Yet most wildfire occurred following long fire-free intervals, supporting the self-regulation hypothesis, which states that recently burned areas are less likely to burn (Peterson, 2002). Interactions between vegetation and fire that depended on fire interval affected the vegetation transitions simulated in response to a climate change-type increase in the probability of fire. Nevertheless, modeled scenarios representing age-dependent patterns of stand resistance or resilience to fire had relatively weak effects on the simulated responses of the forest landscape to increased fire activity.

We found substantial evidence of forest resilience to fire in our study region, and self-replacement was the dominant postfire trajectory. However, multiple alternative trajectories were observed in association with unusual fire characteristics, and some vegetation types appeared more vulnerable to state changes. For example, jack pine stands exhibited high resilience to fire across a broad range of conditions, while well-drained states dominated or codominated by black spruce exhibited particularly low resilience, as documented for boreal forests in Alaska (Johnstone, Chapin et al., 2010) and Quebec (Lavoie & Sirois, 1998). Decreases in the relative abundance of spruce and increases in the relative abundance of deciduous trees were observed at sites where burning was severe enough to remove the organic layer and expose mineral soils, which favors the establishment of deciduous species (Greene et al., 2007; Johnstone & Chapin, 2006a). However, not all shifts toward increased deciduous tree abundance occurred in severely burned stands, suggesting a role of additional (unknown) factors in driving these state changes.

When both jack pine and black spruce were dominant components of the pre-fire community, our field data indicated that

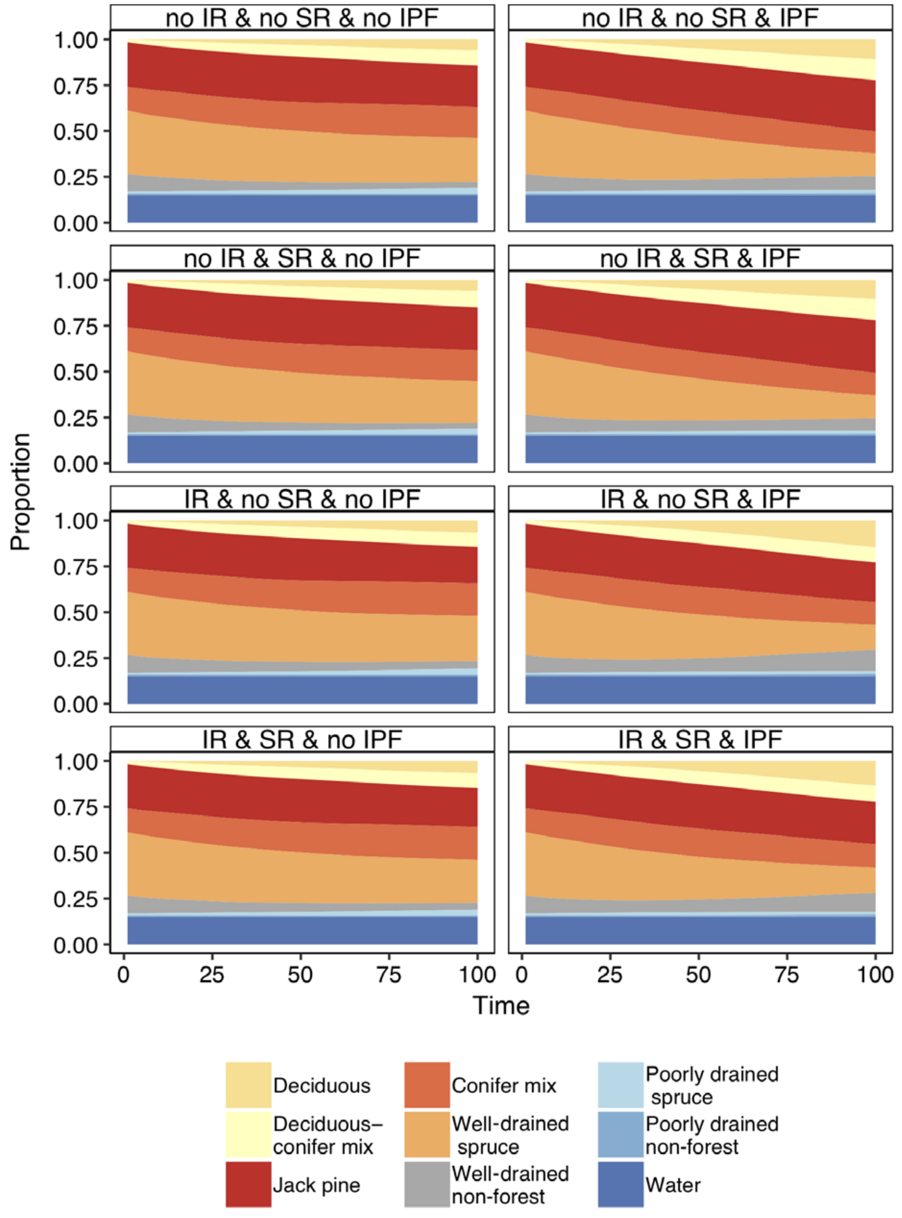

FIGURE 6 Change in landscape species composition (proportion of landscape cover by vegetation state) for eight different scenarios. The panel in the upper left corner represents the null scenario for evaluating scenario effects. [Colour figure can be viewed at wileyonlinelibrary.com]

decreases in the relative abundance of spruce were often offset by increases in the relative abundance of pine. Jack pine reaches maximum seed production earlier (~5 years; Eyre & LeBarron, 1944; Viereck, 1983) and has higher cone serotiny than does black spruce, which may confer an advantage when burning is particularly severe or occurs in young stands (Greene & Johnson, 1999; Lavoie & Sirois, 1998). Further, the seeds of jack pine are almost 4-times larger than are those of black spruce (0.0045 g for jack pine and 0.0012 g for black spruce; Burns & Honkala, 1990), which promotes greater initial root growth and may allow for establishment on thicker organic soils (Johnstone & Chapin, 2006a). The lower resilience observed for well-drained black spruce and conifer mix states was incorporated into our simulation model and led to dramatic decreases in the abundance of well-drained spruce forest under all simulations. These results are consistent with simulation modeling from Québec, which suggested more frequent stand-replacing fire favors jack pine over black spruce (Le Goff & Sirois, 2004).

We hypothesized that fire return interval is an important factor regulating fire and vegetation dynamics in the Saskatchewan Boreal Shield, where the frequency of fire activity is among the highest in Canada (Parisien et al., 2014). The empirical data presented here provide support for two hypothesized forms of fire–vegetation interactions: (a) fire self-regulation due to resistance to burning in young postfire stands, and (b) immaturity risk, where forest resilience to fire is reduced after short-interval fires. Field data showed that although short-interval burns do occur, most sites burned following a fire-free interval of >50 years. GIS overlay analysis indicated that very little burning has occurred in stands <20 years old during recent decades. Self-regulation of fire, where young stands burn less frequently than expected, arises from fuel limitations in early successional vegetation that inhibit ignition (Krawchuk, Cumming, Flannigan, & Wein, 2006)

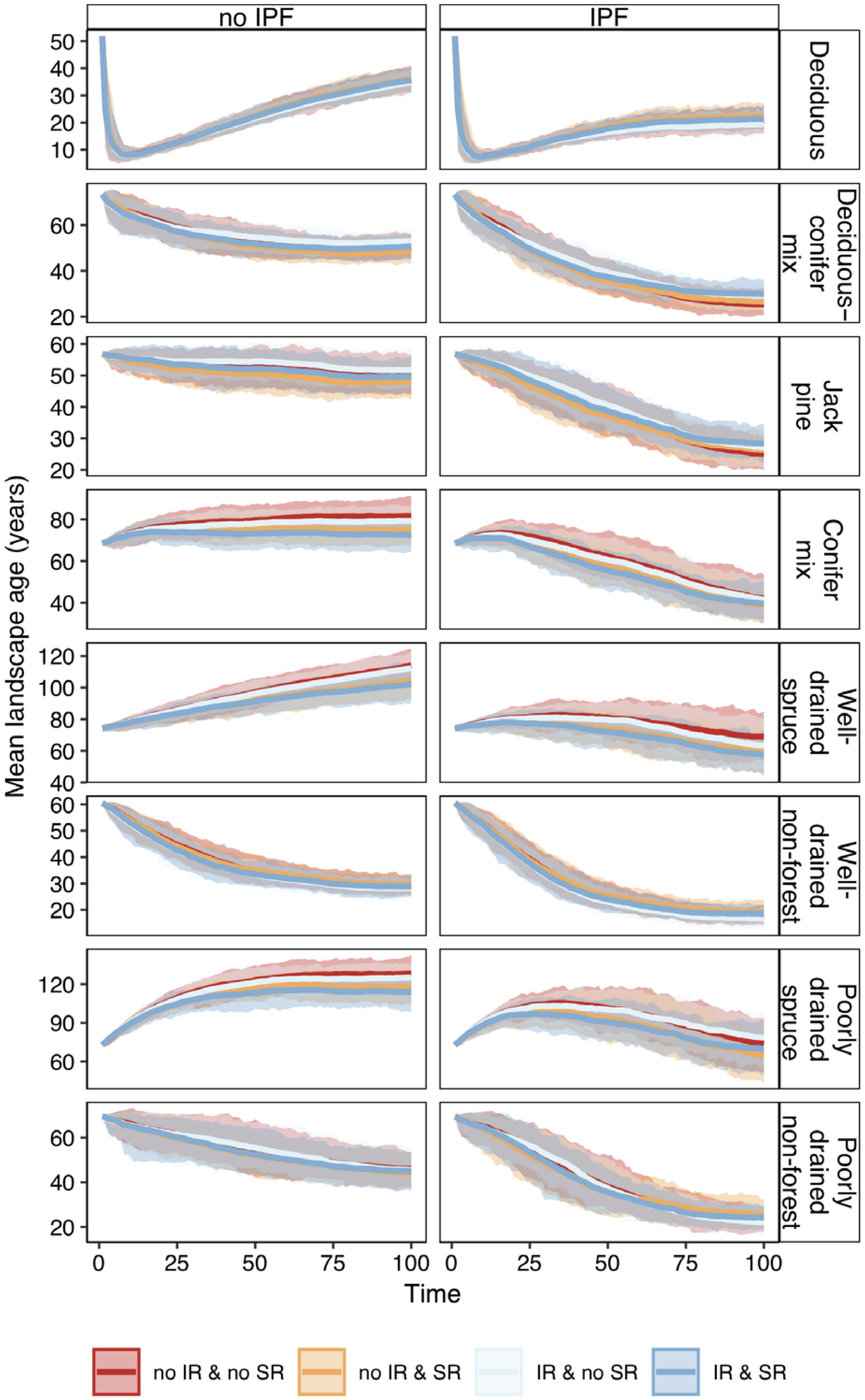

FIGURE 7 Projected change in stand age for eight different modeling scenarios and eight vegetation states. Lines illustrate the mean age of a stand type across the landscape across the 100 simulations, and shaded polygons indicate the 95% confidence interval. Note *y*-axes span different ranges. [Colour figure can be viewed at wileyonlinelibrary.com]

and fire spread into recently burned landscapes (Collins et al., 2009; Parks, Holsinger, Miller, & Nelson, 2015). When short-interval burns did occur, our field observations indicated that several types of conifer forests were less likely to recover to the same state. Thus, the resilience of the system to wildfire depends not only on the average fire frequency, but also on the frequency of short-interval fire events (Buma et al., 2013).

We used a set of simple simulation experiments to explore the potential implications of the fire and vegetation interactions quantified from our empirical data for forest landscapes in northern Saskatchewan. To evaluate the potential effects of self-regulation of area burned, we examined scenarios where flammability was 2-times greater in stands older than 50 years than younger stands, consistent with empirical evidence in support of the self-regulation hypothesis from results herein and research from Quebec (Erni et al., 2017; Héon et al., 2014) and Alberta (Beverly, 2017). The negative effect of time since fire on fire likely decreases as stands accumulate fuels over the 50 years following fire (Beverly, 2017; Parks, Parisien, Miller, Holsinger, & Baggett, 2018), and the scenario used here should estimate the maximum potential effect of self-regulation on area burned. Nevertheless, our modeling results suggest this negative feedback was not great enough to counteract the effect of a climate change-type increase in the probability of fire. In other forests systems, structural or compositional changes that occur as stand ages can promote saturating or nonmonotonic associations between time since fire and stand flammability (Blackhall, Raffaele, & Veblen, 2012; Kitzberger, Aráoz, Gowda, Mermoz, & Morales, 2012; Perry, Wilmshurst, & McGlone, 2014; Tepley et al., 2018). Yet in the North American boreal forest, there is little support for decreased burn rates in older stands (Bernier et al., 2016; Beverly, 2017). In our study area, intermediate and older stands may be equally likely to burn due to the limited role of relay succession (Dix & Swan, 1971; Ilisson & Chen, 2009) and/or the dominant influence of fire weather on fire behavior (Bessie & Johnston 1995). Older stands in this fire-prone landscape likely emerge as a function of landscape position (e.g., proximity to lakes or other fire breaks; Nielsen et al., 2016) rather than age-related changes in flammability (Erni et al., 2017), a mechanism that was incorporated into our simulation modeling.

Model simulations also explored the consequences of scenarios that assumed an immaturity risk due to increased fire frequency, which could reduce fire risk by stimulating shifts to less flammable deciduous forest. We found that the IR scenarios did not mitigate the climate change-type increase in the probability of fire simulated in our model. Our empirical data suggested that jack pine is highly resilient to fire and rarely transitioned to deciduous forest, while well-drained spruce and mixed conifer stands frequently transitioned to jack pine forest following fire. Thus, in landscapes with pine, as in our simulation model, low probabilities of state transitions from pine to deciduous forest and increasing dominance of pine will limit the degree to which deciduous forest can expand and cause a decline in landscape flammability. Landscapes composed of predominantly spruce and deciduous forests may experience stronger negative feedbacks to fire than pine-dominated landscapes.

We based our simulation of fire and forest recovery in the Boreal Shield region of Saskatchewan on our most up-to-date knowledge of this system, combining new empirical data on forest state changes and landscape fire probabilities with published estimates of processes from similar boreal forests. Nevertheless, the simulated landscape composition of forest states and age in our landscape did not suggest equilibrium conditions under simulations designed to mimic recent historical conditions. This non-stationarity in our model may arise from: (a) errors in the initial landscape map, along with the lack of historical data that would allow us to calibrate outcomes against recent changes in forest composition; (b) errors in the model, arising from over-simplification of model assumptions (e.g., the absence of other disturbances) or errors in parameterization; and (c) true non-stationarity in fire and vegetation dynamics in boreal forests. Limitations caused by errors in (a) and (b) above are common to virtually all simulation models and are difficult to address without long time series or model intercomparisons (Bowman, Perry, & Marston, 2015). However, in the process of this study we have become acutely aware that non-stationarity in the system is worthy of serious consideration. For example, the low resilience observed in our field sample of well-drained black spruce suggests the current configurations of forest composition are not currently at an equilibrium. If fire–climate–vegetation interactions in the boreal forest represent a dynamic system of internal feedbacks and nonlinear state changes, as some paleoecological studies suggest (Higuera, Abatzoglou, Littell, & Morgan 2015; Senici, Chen, Bergeron, & Cyr, 2010), then calibrating a model to produce a stable historical landscape is misleading. In this situation, scenario-based modeling that explores the relative effects of different drivers, combined with empirical observations of current dynamics, may be our best approach to anticipating future responses to global change (Bowman et al., 2015).

While much research has emphasized the potential for altered fire regimes to change tree species composition across the North American boreal forest (Johnstone et al., 2010; Krawchuk & Cumming, 2011; Le Goff & Sirois, 2004), our simulation modeling also highlights the effect of increasing area burned on the stand age composition of forest landscapes. Such shifts could have important consequences for species that depend on older forest, including threatened boreal woodland caribou (Schaefer & Pruitt, 1991; Whitman et al., 2017), and thus, compound the effects of more obvious changes in forest cover. For example, declines in stand age of jack pine and mixed conifer forests due to shorter fire intervals are likely to translate into decreased availability of lichen forage and loss of preferred habitat for caribou (Metsaranta, 2007). More focused models that couple scenarios of fire and vegetation interactions with ecosystem services, such as wildlife habitat, would provide additional scope for estimating the consequences of interacting climate, fire, and vegetation for issues of management concern.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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