



Increasing fire and the decline of fire adapted black spruce in the boreal forest

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Intensifying wildfire activity and climate change can drive rapid forest compositional shifts. In boreal North America, black spruce shapes forest flammability and depends on fire for regeneration. This relationship has helped black spruce maintain its dominance through much of the Holocene. However, with climate change and more frequent and severe fires, shifts away from black spruce dominance to broadleaf or pine species are emerging, with implications for ecosystem functions including carbon sequestration, water and energy fluxes, and wildlife habitat. Here, we predict that such reductions in black spruce after fire may already be widespread given current trends in climate and fire. To test this, we synthesize data from 1,538 field sites across boreal North America to evaluate compositional changes in tree species following 58 recent fires (1989 to 2014). While black spruce was resilient following most fires (62%), loss of resilience was common, and spruce regeneration failed completely in 18% of 1,140 black spruce sites. In contrast, postfire regeneration never failed in forests dominated by jack pine, which also possesses an aerial seed bank, or broad-leaved trees. More complete combustion of the soil organic layer, which often occurs in better-drained landscape positions and in dryer duff, promoted compositional changes throughout boreal North America. Forests in western North America, however, were more vulnerable to change due to greater long-term climate moisture deficits. While we find considerable remaining resilience in black spruce forests, predicted increases in climate moisture deficits and fire activity will erode this resilience, pushing the system toward a tipping point that has not been crossed in several thousand years.

wildfire | ecological state change | resilience | climate change | tree regeneration

Disturbances can be powerful catalysts of state changes in ecosystems, first by disrupting the inertia that site occupancy confers on long-lived, sessile organisms like trees and second by affecting the biophysical conditions that influence patterns of vegetation recovery (1). Disturbances may be particularly disruptive when they depart from the historical regimes experienced by an ecosystem, altering postdisturbance regeneration outcomes and stimulating rapid reorganization of the system into a new ecological state, often referred to as a

loss of resilience (2, 3). In boreal North America, climate change is leading to warmer, drier conditions with more lightning strikes in many regions (4), altering fire activity (5, 6) and modifying postfire regeneration conditions. These changes affect which species' traits promote successful postfire recruitment and may disrupt forest regeneration entirely, creating substantial uncertainty in the prediction of future forest composition (1, 7). Forecasting changes in boreal forest

Significance

Black spruce is the dominant tree species in boreal North America and has shaped forest flammability, carbon storage, and other landscape processes over the last several thousand years. However, climate warming and increases in wildfire activity may be undermining its ability to maintain dominance, shifting forests toward alternative forested and nonforested states. Using data from across North America, we evaluate whether loss of black spruce resilience is already widespread. Resilience was the most common outcome, but drier climatic conditions and more severe fires consistently undermine resilience, often resulting in complete regeneration failure. Although black spruce forests are currently moderately resilient, ongoing warming and drying may alter this trajectory, with large potential consequences for the functioning of this globally important biome.

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composition is further complicated by regional differences that shape the local biophysical context (e.g., species pools, soil organic layer thickness, and climate). To date, large-scale patterns in regeneration dynamics have been precluded by the vastness of the boreal biome and lack of biome-wide recruitment information.

Currently, much of boreal North America is dominated by evergreen conifers, most notably, black spruce (*Picea mariana*), which over the Holocene has repeatedly self-replaced via seedling establishment from aerial seedbanks, demonstrating the high resilience of this species to stand-replacing fire (8–10). In this region, where fires typically occur at intervals shorter than the life span of the postfire cohort of trees (i.e., <100 to 150 y) (8, 11), initial patterns of tree regeneration and relative growth rates determine the trajectory of future forest composition until the next fire (12, 13). Consequently, seedling recruitment in the initial years after fire is the critical determinant of mature forest stand composition for boreal tree species (8, 9, 12, 14, 15). Recent studies have indicated that fires of unusually high severity and/or short return intervals can disrupt the successful regeneration strategy of black spruce, stimulating shifts to alternative states dominated by deciduous broadleaf trees or jack pine (*Pinus banksiana*) (16–18) or even nonforest (19, 20), changes indicative of reduced black spruce resilience. As a dominant species, large areas of the North American boreal forest are shaped by the flammability of black spruce (21) and also its role in creating wildlife habitat for important species, such as caribou (22), and supporting the sequestration of large quantities of belowground carbon (23) while being one of the most economically important boreal tree species (24); as such, reduced recovery of black spruce forest postfire has wide-ranging implications.

Fire can trigger state changes away from black spruce dominance, and although we do not know how common these changes are, rapid rates of warming and fire activity intensification in boreal North America would suggest that such state changes are already widespread. Previous research has shown that black spruce self-replacement is supported in sites where thicker soil organic layers persist following fire (16, 25), whereas shortening fire return intervals and postfire drought conditions may undermine regeneration processes (19, 20). Indeed, complete regeneration failure has been observed at 9% of sites experiencing short-interval fires simply because reproductive maturity was not yet attained (26). Given these findings, we expected widespread reductions in black spruce resilience and that previously demonstrated drivers of population dynamics (e.g., residual soil organic layer thickness and fire return interval) would be consistently important at the continental scale. However, we also expected regional differences in the frequency of state changes given climatic gradients from east to west that may affect burning (5) and/or create more stressful regeneration conditions (19) leading to more frequent loss of resilience and the most extreme manifestation—a complete absence of recruitment—in the drier, western regions of boreal North America.

To test these predictions, we conducted a continent-wide examination of regeneration success by synthesizing field data from wildfires that occurred between 1989 and 2014 (SI Appendix, Table S1) across boreal North America [637 million ha of forested land and 37% of the boreal biome (27)]. We compared prefire tree species composition and relative density with postfire establishment of tree seedlings (measured from 2 to 13 y following fire, depending on the study). This recruitment window measures an initial cohort of trees that grow to dominate the canopy (13), providing a good predictor of forest composition during preceding decades (12, 15) and the one to two centuries that follow (13, 28). Most sites were dominated by conifers before fire (1,400 of 1,538 sites; 91%), and more

specifically by black spruce (1,140 sites; 74%), approximating the proportion of forest types that burn in boreal North America (21) (SI Appendix, Table S1). We define resilience as the ability of a stand to quickly recover its basic structure and function following disturbance (29) and expect that recent changes in climate and fire activity may have altered regeneration conditions sufficiently to erode resilience to varying degrees following fire, ranging from loss of dominance to regeneration failure. To address this, we evaluated the frequency of losses of conifer resilience (i.e., conifer regeneration failure or a shift toward broadleaf dominance) and black spruce resilience (i.e., black spruce regeneration failure or a shift toward broadleaf or pine dominance) using a postfire trajectory metric based on changes in stem density and species dominance (Fig. 1; see Materials and Methods). We considered two groups: dominant (locally most common) and subordinate (locally less common) species in the canopy at the time of burning (Fig. 1). For dominants, we evaluated forest responses in two ways: all conifers combined (to evaluate the conifer-to-broadleaf transition) or black spruce only (to evaluate changes in this historically dominant species). For prefire dominants, postfire regeneration could lead to two resilient outcomes (Fig. 1A): self-replacement or density reduction; in both, relative dominance is maintained or increased but absolute density responses differ. Three outcomes associated with loss of dominance reflect decreasing postfire resilience: competition (absolute density of prefire dominant is maintained or increased concurrent with strong recruitment of other taxa; regeneration outcome is dictated by relative competitive abilities), poor establishment (decreased absolute density), or regeneration failure (postfire density of the prefire dominant is zero). For common prefire subordinate taxa, we again evaluated forest response in two ways: broadleaf taxa combined (to evaluate the potential for broadleaf taxa to replace conifers postfire) and jack pine only (to evaluate conifer-to-conifer transitions between black spruce and jack pine). For prefire subordinates, expansion and competition categories indicate reduced resilience of the prefire dominant (conifer or black spruce) (Fig. 1B).

We used this framework to address two questions: 1) How often does the prefire dominant species show decreased resilience (i.e., ecological state change) to recent fires in boreal North America? and 2) Is the magnitude and direction of change consistent among regions? Finally, to address whether there are consistent drivers across boreal North America that promote postfire ecological state change, we assessed several factors related to fire and seedbed conditions considered important in determining the postfire regeneration outcomes outlined in Fig. 1. Evidence of common drivers suggests the intensification of wildfire activity will affect boreal North America in predictable ways.

Results and Discussion

The most common regeneration outcome for black spruce stands across North America was self-replacement; resilient outcomes (self-replacement and density reduction) occurred in approximately two thirds (62%) of black spruce stands that burned between 1989 and 2014 (Fig. 2). When considering all conifers combined, resilience was even more common, occurring at 74% of sites (SI Appendix, Fig. S1). This difference in regeneration outcomes is because within conifer-dominated forests, conifer-to-conifer shifts in dominance were common, notably the replacement of black spruce by jack pine (Fig. 2) within its range east of the Rocky Mountains.

Resilience to fire varied geographically across our broad study region. Individual ecozones varied significantly in the proportion of sites that maintained dominance of black spruce (39 to 78%; evidenced by self-replacement and density reduction;

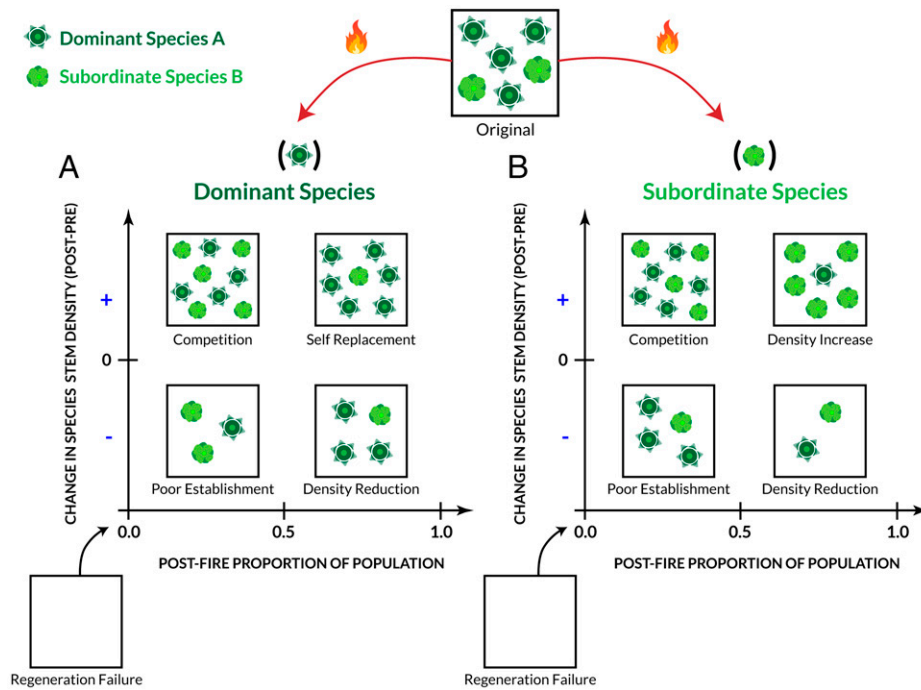


Fig. 1. A framework to evaluate the potential for state changes following fire. *A* represents possible trajectories for Species A, a prefire dominant taxon (Species A comprises $\geq 50\%$ of prefire stem density). Resilience is the most likely outcome in the self-replacement panel, in which the prefire dominant taxon continues to dominate after fire and sufficient seedlings have established to at least maintain, or possibly increase, species-specific prefire stem densities; density reduction was also considered to be a more stable or resilient outcome than the other outcomes. We considered that the competition, poor establishment, and regeneration failure categories would all likely lead to state change. *B* represents possible trajectories for Species B, a prefire subordinate taxon (Species B comprises $< 50\%$ stem density), and we were interested in understanding the potential for expansion (i.e., postfire increase in dominance and maintenance or increase in stem density) of Species B. In this case, postfire state change (i.e., loss of resilience of the prefire dominant) is most likely in the expansion category. However, in our study, given the greater competitive abilities of the prefire subordinates in question (i.e., broadleaf taxa and jack pine) compared to black spruce (the most common prefire dominant in our dataset), the competition category will also likely lead to loss of resilience when the prefire dominant is black spruce. Poor establishment and density reduction categories in *B* were never observed in our dataset. In boreal North America, fires typically occur at intervals shorter than the lifespan of the postfire cohort of trees (< 100 y); therefore, the pulse of seedling establishment immediately postfire typically determines the trajectory of future forest composition until the next fire.

Fig. 2) or conifers (35 to 93%; *SI Appendix, Fig. S1*) after fire. Two main regional patterns emerged. First, there was a clear east–west divide in postfire regeneration. Sites in northwestern North America were more likely to experience decreased black spruce resilience, conifer regeneration failure, and the expansion of broadleaf taxa (*SI Appendix, Fig. S1*). Second, where black spruce lost resilience, resulting state changes varied across eozones and included replacement with aspen and balsam poplar (*Populus tremuloides* and *Populus balsamifera*; Alaska Boreal Interior, Western Plains), birch (*Betula papyrifera* and *Betula neoalaskana*; Cordillera, Western Shield), and jack pine (Western and Eastern Plains, Eastern Shield) as well as total regeneration failure (all ecoregions to varying degrees) (Fig. 2 and *SI Appendix, Fig. S2*). Much of the variation in these outcomes seems at least in part contingent on biogeography; east of the Rocky Mountains, jack pine made gains where black spruce lost resilience, whereas beyond the range of jack pine, in the west, broadleaf dominance was the primary outcome. The notable exception to this is in the Western Shield, where jack pine rarely replaced black spruce and, instead, paper birch was the most common alternate trajectory (Fig. 2). In this ecozone, there is much less overlap in the local distributions of jack pine (dry, rocky sites) and black spruce (lower-lying peatlands), whereas birch is more ubiquitous. The fact that the highest instances of total regeneration failure (i.e., no postfire regeneration of any tree species; Fig. 2) were in the Alaskan Interior and Cordillera regions is perhaps not surprising given the general absence of an alternate species possessing an aerial seedbank. Black spruce density reduction was the most common

outcome in eastern North America but relatively infrequent elsewhere; here, short interval fires limit seed availability and promote transitions from closed-crown forest to open lichen woodlands (20, 26). There are functional implications of such changes and, if considered a state change, this paints a very different picture for the resilience of black spruce forests in eastern North America.

Black spruce resilience was lost at 38% of sites, and this loss was not counterbalanced by gains in dominance elsewhere in its range. For sites where black spruce was present but not dominant prefire (121 sites mainly dominated by jack pine or broadleaf taxa), it seldom expanded ($< 10\%$ of sites). Detailed paleoecological studies of boreal forest vegetation during the Holocene indicate a high resilience of black spruce-dominated stands to frequent fire (30–32), consistent with early contemporary studies of postfire regeneration (33–35); this suggests that the loss of resilience documented here is a shift from the historic norm. On average, spruce regeneration failed (i.e., no spruce recruitment) in 18% of sites (range: 10 to 25%) across North America (Fig. 2); most regions greatly exceeded previously documented or projected levels of postfire regeneration failure in spruce stands (20, 26). Such high regeneration failure in a fire-adapted species is unusual and has been previously attributed to short interval fires and reproductive immaturity (19, 36, 37) or postfire climate (7, 19), factors we explore further below.

In contrast, where broadleaf taxa or jack pine were dominant prefire (173 sites), regeneration failure never occurred and self-replacement and density reduction were the most common

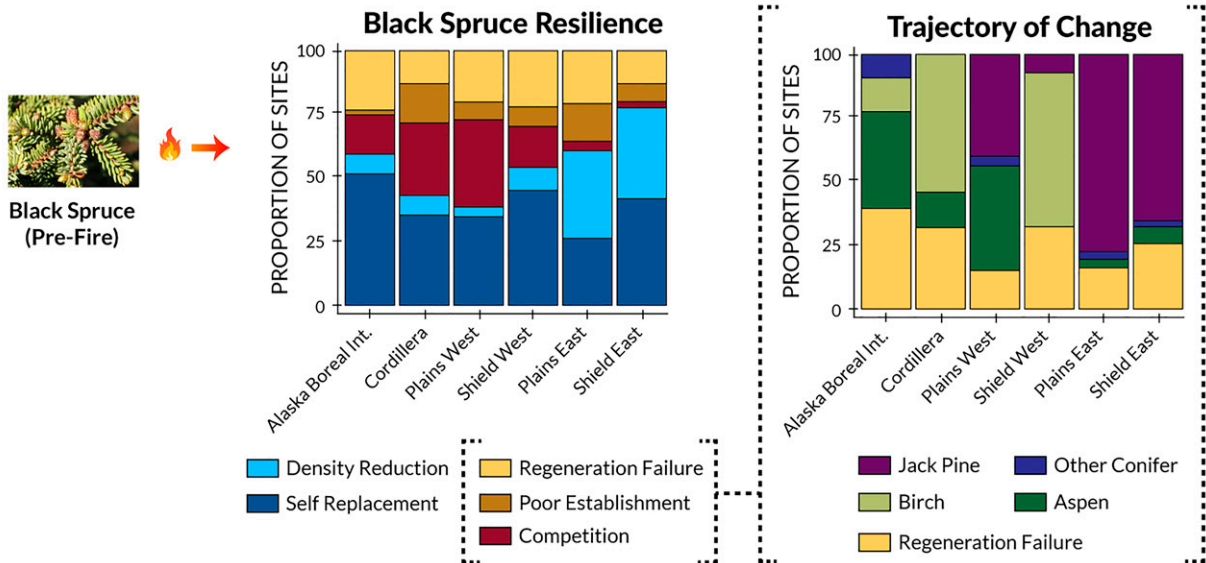
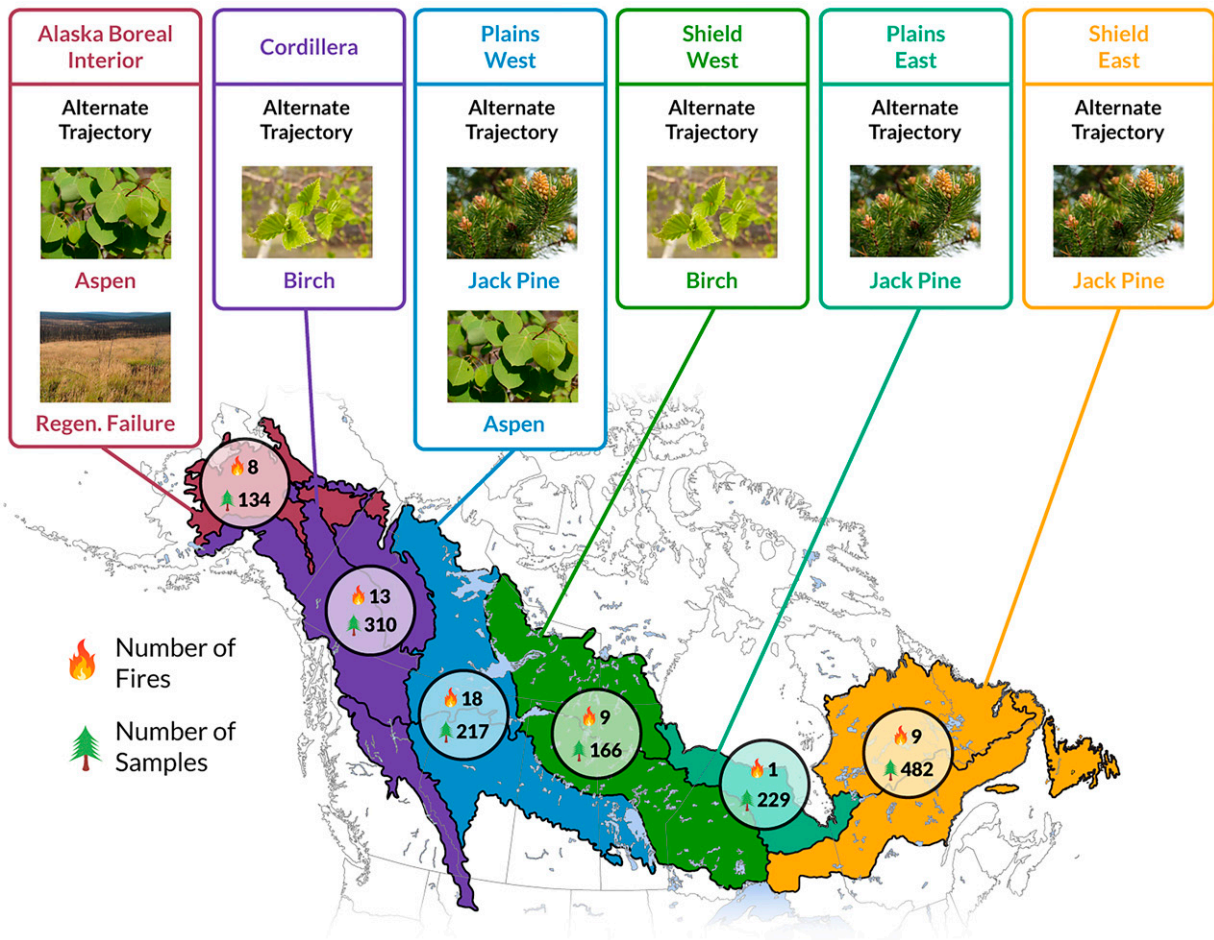


Fig. 2. Characterizing black spruce resilience and state changes represented by alternative trajectories of postfire recovery across boreal North America for fires that burned from 1989 to 2014. Sample sizes of fires and individual sites with postfire seedling counts are overlain on ecoregions. For all analyses, ecoregions were pooled as depicted by the colored regions on the map, based on biophysical similarities. Across ecoregions, black spruce was the most common prefire stand dominant (1,140 of 1,538 sites). The fire-free interval for these stands ranged from 8 to 322 y; the range of stand ages was largely comparable across ecoregions (*SI Appendix, Table S1*). Categories of change in the “Black Spruce Resilience” panel are defined in Fig. 1A. Where loss of resilience is expected (Regeneration Failure [$n = 187$], Poor Establishment [$n = 106$], and Competition [$n = 144$]), we quantified the likely outcome of state changes in the “Trajectory of Change” panel. The main alternative trajectories are depicted above the map for each pooled ecoregion. Images showing landscape perspectives of these alternative trajectories are provided in *SI Appendix, Fig. S2*. *SI Appendix, Table S1* provides details of individual studies included in this synthesis.

outcomes (137 of 173 sites, 79%). Black spruce, a modestly shade-tolerant species, could potentially replace its more intolerant competitors through succession at sites where it has a small initial number of recruits; however, in the northern and western boreal forests of North America, the fire return interval is often too short (e.g., mean fire return interval of 77 y across our study sites; *SI Appendix, Figs. S3 and S4*) for this to occur (8, 13). These findings of net losses of black spruce forest are corroborated by remote sensing and modeling studies of land cover changes in boreal North America. Across 31 y of Landsat records for northwestern North America, broadleaf forest area increased by nearly 15% at the expense of conifer forests (38). Ecosystem modeling suggests that even more extreme shifts away from conifer forests are possible, even in areas with jack pine as an alternate conifer tree species, with some scenarios projecting a more than doubling of broadleaf forest area (17, 39, 40). Succession from broadleaf to conifer species has been more common in boreal forests of eastern North America, where mean fire return intervals are longer (>150 y) (28); however, because climate change decreases fire return intervals across boreal North America (41), opportunities for relay succession are also likely to diminish in eastern forests. Indeed, cumulative effects of warming and increased wildfire resulted in the near-complete replacement of spruce forests with pine and broadleaf taxa between 19,000 and 8,000 y ago in the southern Great Lakes region of North America (42).

To evaluate whether the intensification of wildfire regimes will affect boreal North America in predictable ways, we must first understand whether there are consistent drivers of state change. To this end, we assessed the importance of fire return interval (18, 43), prefire basal area of focal species (10, 44), seedbed condition [represented by residual soil organic layer depth, which is influenced by soil combustion (25, 45)], canopy combustion severity (44, 46), and climate conditions following fire (7, 19) in determining the postfire regeneration outcomes outlined in Fig. 1. Using a subset of sites for which these predictors were available (see sample sizes in *Materials and Methods, Fig. 3, and SI Appendix, Table S1*), we employed a random forest analysis to evaluate drivers of postfire state changes and corroborated these findings with a formal meta-analysis across studies. Although our studies spanned nearly 30 y, there was no systematic temporal variation in the previously mentioned predictor variables, suggesting that our results are capturing spatial variability in postfire conditions rather than temporal trends (*SI Appendix, Fig. S4*). Residual soil organic layer thickness, a crucial determinant of the regeneration success of small-seeded boreal tree species (25), had the greatest influence in determining conifer resilience and, conversely, the potential for broadleaf tree expansion (Fig. 3). Results of our meta-analysis also identified this as the most significant predictor of state change in black spruce stands, with deeper residual soil organic layers resulting in more resilient outcomes (*SI Appendix, Table S2 and Figs. S5 and S6*). Previous research has shown that in better drained locations, severe fires can reduce the depth of the residual soil organic layer sufficiently to promote successful establishment of fast-growing, small-seeded species such as aspen and birch, thus favoring high relative recruitment of broadleaf taxa over black spruce (16, 25, 45). Further, drier sites are more likely to have exposed mineral or shallow organic soils after fire simply because the prefire soil organic layer was thinner (25, 47). Such sites also typically host mixtures of black spruce and other species prior to disturbance, further facilitating regeneration by alternate species. Our results show that these processes are influential across boreal North America; thin organic soil layers after fire are strongly associated with state changes caused by low relative densities of black spruce and enhanced competition with expanding broadleaf or pine trees, which are likely to outcompete much-slower-growing black spruce (Fig. 3 and *SI Appendix, Fig. S5*). Because early patterns

of recruitment and competitive outcomes determine canopy composition for subsequent decades (9, 15), successional return to black spruce canopy dominance requires long fire-free intervals (>100 y) likely to become increasingly rare across North America (41). Both paleoecological studies of fire–vegetation dynamics (42, 48, 49) and contemporary remote sensing and modeling studies (38, 39) in boreal North America suggest that such reversals of dominance will become less frequent in the future. Further declines in the resilience of black spruce following fire are likely if continued climate warming results in soil drying due to permafrost thaw (50) or increased climatic moisture deficits and more frequent and severe burning (6, 51). However, the importance of drainage class in conifer and black spruce resilience is also noteworthy (Fig. 3 and *SI Appendix, Figs. S6 and S12*). Landscape positions that accumulate moisture may serve as refugia for black spruce in the face of changing fire and climate via maintenance of thicker residual soil organic layers (23, 52), although these sites may also have lower future regeneration potential and slower growth (53).

Our results support the expectation that warmer/drier regions show lower resilience following fire (*SI Appendix, Fig. S7*). The 30-y (1981 to 2010) normal climate moisture deficit (CMD_{normal}) was consistently a more important variable than $CMD_{postfire}$ anomalies following fire ($CMD_{postfire}$; Fig. 3). CMD_{normal} was also a marginally significant predictor of state change in our meta-analysis, with greater CMD_{normal} leading to more frequent state change away from black spruce (*SI Appendix, Table S2 and Fig. S8*); it is noteworthy that our partial dependence plots suggest that this result is largely attributable to east–west differences in CMD_{normal} (*SI Appendix, Figs. S3, S11, and S13*). CMD_{normal} was more extreme in western regions, where we more frequently observed decreased resilience for all conifers and black spruce alone, indicating as expected that environments with consistently lower availability of moisture for plants enhance the likelihood of postfire state change (Fig. 2 and *SI Appendix, Figs. S1, S7, and S8*). Likewise, expansion of both jack pine and broadleaf taxa was more frequent in drier, western regions (*SI Appendix, Figs. S1 and S7*). This relationship is consistent with recent findings that larger annual moisture deficits promote tree regeneration failure (7, 19). Our findings support the idea that wetter, eastern parts of boreal North America are more resilient to warming and may serve as important continental-scale refugia for conifer- and black spruce-dominated forests (52, 54). However, projections suggest that both eastern and western North America will experience climate warming and drying (55) with implications for the longevity of this refugia potential.

Reductions in black spruce recruitment following fire and associated decreases in basal area may worsen losses of black spruce resilience in subsequent fires. For black spruce only, prefire basal area was the most important predictor of regeneration outcomes in the random forest analysis (Fig. 3), with higher prefire black spruce basal area increasing the likelihood of resilience, although this effect diminishes at basal areas $>15 \text{ m}^2 \cdot \text{ha}^{-1}$ (*SI Appendix, Fig. S11*). Black spruce basal area is a strong determinant of postfire seed density (10, 44). Although we considered density reduction without loss of dominance to be a resilient outcome, for black spruce, this will reduce contributions to regeneration following the next fire, reinforcing the trajectory of change and leading to increasingly open woodlands, which could be considered state change in and of itself (26).

Our synthesis provides a continental-scale evaluation of disturbance-driven ecological state change and underlying mechanisms for the largest terrestrial biome on the planet. Across boreal North America, black spruce forests generally showed resilience in the face of fire despite rapid warming and fire activity intensification. However, stands dominated by black

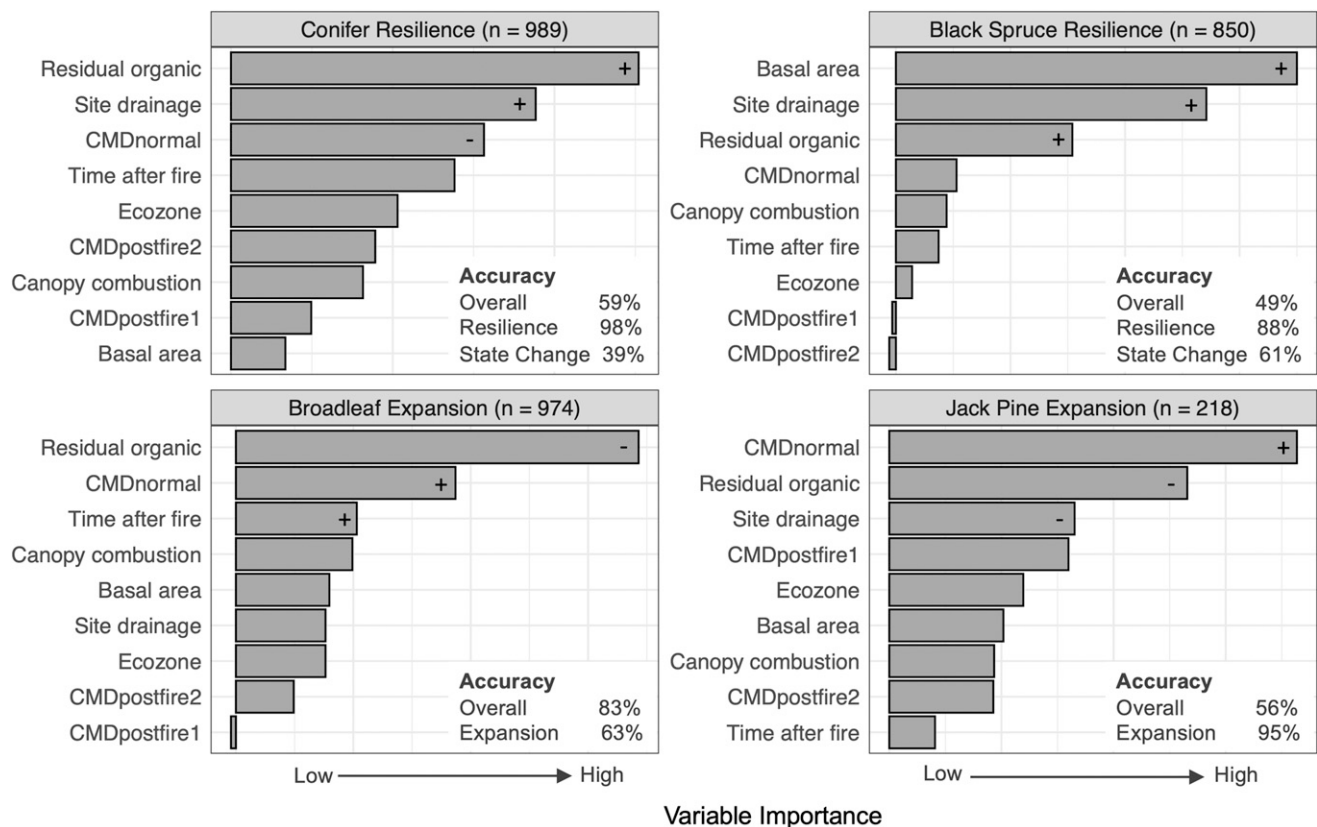


Fig. 3. Relative importance of predictors of conifer and black spruce resilience and broadleaf and jack pine expansion from random forest analyses. Hargreaves' CMD (millimeters) predictors included 30-y (1981 to 2010) normals (CMD_{normal}) and the difference between CMD_{normal} and CMD in years 1 and 2 after fire (CMD_{postfire1} and CMD_{postfire2}, respectively). Other predictors include residual soil organic layer thickness (centimeters, Residual organic), site drainage classes (dry, moist, wet; Site drainage), fire-free interval (years, Time after fire), canopy combustion severity (ordinal scale from 0 to 3; Canopy combustion), prefire basal area for the species or taxa under consideration (m² · ha⁻¹; Basal area), and pooled ecozone (Ecozone). Text in the bottom right of each panel indicates the accuracy of the overall random forest model as well as resilience (self-replacement and density reduction) versus state change (regeneration failure, poor establishment, and competition) categories for black spruce and conifer models or expansion categories (expansion and competition) for broadleaf and jack pine. Model accuracy is based on out-of-bag error estimates. Sample sizes for each dataset are provided in the panels; details of sample size by pooled ecozone can be found in *Materials and Methods* and in *SI Appendix, Table S1*. The direction of the relationship between each variable and resilience (conifer and black spruce) or expansion (broadleaf and jack pine) is given for the three most important variables for each analysis. Relationships between common important variables and regeneration outcomes are also shown in *SI Appendix, Figs. S5–S8*, and partial dependence plots are provided in *SI Appendix, Figs. S11–S14*.

spruce also demonstrated substantial vulnerability to state change after fire, transitions that are likely to become more common in the future despite the long history of spruce coexistence with wildfire over millennia in boreal North America. With continued increases in growing season moisture deficits and associated fire activity, we expect more frequent and widespread reductions in black spruce density and dominance. There was significant continental-scale variation in both the frequency and outcomes of such transitions, suggesting that the patterns and implications of losses of black spruce resilience will vary regionally. For example, state changes from black spruce to deciduous broadleaf dominance occurring more frequently in western North America may have greater impacts on carbon and nutrient cycling, climate forcing, soil conditions, and future fire behavior than shifts from spruce to pine that predominate in the east (17, 56–59). This synthesis provides the framework necessary to anticipate the functional implications of fire-induced ecological state change across boreal North America.

Materials and Methods

Description of Datasets. We obtained data from 1,538 sites across 58 fire perimeters encompassing 4.52 Mha of forest (~1% of boreal North America)

and all major boreal ecozones in North America (Fig. 2 and *SI Appendix, Table S1*). Site selection and sampling methods differed between studies (see references within *SI Appendix, Table S1*). To be included in our synthesis, a site had to contain information on species-specific postfire seedling densities (*SI Appendix, Fig. S3*). This included sites where seedlings had been counted 2 to 13 y postfire, a time frame over which we find little change in relative dominance of species densities (15). Birch, aspen, and poplar can all reproduce both vegetatively (suckers) and sexually (seedlings); for these taxa, seedling and sucker counts were combined, as not all studies differentiated these forms of regeneration.

Framework for Postfire State Change Variable. We considered two central components of postfire regeneration necessary to understand the potential for state change: stem density and species dominance. We considered different postfire regeneration outcomes by combining these metrics, comparing prefire tree and postfire seedling measurements of absolute stem density, and assigning species dominance based on relative density (Fig. 1 and *SI Appendix, Fig. S9*). Our definition emphasizes absolute and relative density because these factors shape patterns of forest dominance during the first 100 to 150 y of succession (9, 12, 13), a time frame prior to senescence of fast-growing trees and encompassing a period when many stands may burn again (8), especially under predictions of increased fire frequency (5, 41). For analyses, the dataset was divided by species dominance. Sites where a species was dominant prior to a fire (comprising ≥50% stem density) had five possible regeneration outcomes (Fig. 1A). Self-replacement represents the strongest indication of forest resilience, in which stands are expected to quickly recover

their basic structure and function following disturbance (29), whereas regeneration failure is the most extreme state change. Classification of the postfire state into these five categories was as follows: 1) Self-replacement: the prefire dominant taxa maintained or increased both relative and absolute stem density; 2) Density reduction: the prefire dominant maintained or increased relative stem density, but absolute stem density decreased; 3) Competition: the prefire dominant lost dominance (i.e., relative density <50%), but absolute stem density increased, indicating that at least one other taxa also showed strong recruitment, thereby reducing the relative stem density of the prefire dominant; 4) Poor regeneration: the prefire dominant lost dominance and absolute stem density decreased; and 5) Regeneration failure: There was no recruitment of the prefire dominant.

Regeneration outcomes in conifer- (all conifers, $n = 1,400$; predominantly black spruce and jack pine with infrequent occurrences of larch [*Larix laricina*], white spruce [*Picea glauca*], and balsam fir [*Abies balsamea*]) and black spruce-dominated (black spruce only, $n = 1,140$) subsets of the data were categorized based on Fig. 1A, given the dominance of these forest types in our dataset and boreal North America. We considered regeneration failure and poor establishment to be indicative of state change (low resilience). For black-spruce-only stands, we also considered competition to be indicative of state change, given traits that make it a poor competitor early in succession (60); however, we acknowledge that this is the most uncertain of our low-resilience categories. The outcome of competition for conifer stands is less clear, given the fast growth rates and early reproductive maturity of jack pine (61), the most common conifer after black spruce. While density reduction also has the potential to represent state change (26), we took the conservative view that maintenance of focal species dominance should support the retention of associated plant community assemblages and related ecosystem functions. Lagged seedling establishment can occur several years after fire (62); however, the vast majority of recruitment occurs in the first 2 y postfire (14, 15), suggesting that such lagged responses are infrequent and will not dramatically alter the postfire trajectory. Indeed, we found no influence of the number of years postfire that seedling counts were conducted on the resulting regeneration outcomes (SI Appendix, Fig. S10 and Table S3). Where the fire return interval is sufficiently long, relay successional processes may unfold; however, successional replacement of the postfire cohort is typically initiated 100 to 150 y following fire (13, 28, 33), a much longer time frame than the average fire return interval of 77 y in the present study (SI Appendix, Fig. S3). We did not have information on the survival of adult trees following fire for many studies, and our analysis assumes stand-replacing fires, a frequent outcome in boreal North America and particularly in black spruce stands (21, 63). However, postfire survival can occur, especially in pine stands, and not accounting for survival of adult trees could overestimate the frequency of postfire state changes away from conifer dominance. Postfire survival of individual trees is most likely to have affected our estimates of regeneration failure; however, less than 3% of sites had both low site-level canopy combustion in which some trees might be expected to survive intact (site level canopy combustion < 1) and conifer regeneration failure. Although eastern North American sites more frequently had low canopy combustion, regeneration failure was least common in this region (SI Appendix, Fig. S1).

For species that were not dominant prefire (<50% stem density; prefire subordinate), sites were categorized into five outcomes following Fig. 1B: 1) Expansion: the prefire subordinate increased in absolute density and became dominant (i.e., relative density $\geq 50\%$), allowing it to expand into parts of the landscape where it was either absent or present in low densities prefire; 2) Density reduction: the prefire subordinate became dominant postfire while the absolute density decreased. This suggests poor recruitment of all taxa but with a decline in the prefire dominant that was greater than that of the prefire subordinate; 3) Competition: the prefire subordinate did not achieve dominance (i.e., relative density stayed below 50%), but its absolute density increased, indicating strong regeneration by multiple species; 4) Poor establishment: the prefire subordinate did not achieve dominance and experienced decreased absolute density; 5) Regeneration failure: there was no recruitment of the prefire subordinate. We characterized the main shifts that have been documented previously: expansion of broadleaf taxa (aspen, poplar, or birch) or jack pine. For broadleaf taxa, long-distance aerial seed dispersal means that the species need not be present at the site to contribute to postfire regeneration; as such, we considered all stands where broadleaf taxa were not dominant prefire ($n = 1,392$). Compared to aspen or birch, the larger seeds of jack pine limit its dispersal distance, so for this data subset, we considered any site where jack pine was present but not dominant (>0% and <50% prefire stem density; $n = 248$). For Fig. 1B, we consider that both expansion and competition categories indicate lower resilience of the prefire dominant, given the strong competitive abilities of broadleaf taxa and jack pine when compared to black spruce. Outcomes of poor establishment and density

reduction for the prefire subordinate were never observed in our data, so they are not considered here, but jack pine can recruit poorly if fire returns before reproductive maturity is reached in the stand (19).

Evaluating the Frequency and Direction of State Change. All sites that included species-specific data on both pre- and postfire stem densities were used to evaluate the frequency and direction of state change (SI Appendix, Table S1; see Fig. 3 for sample size by grouping). We assumed that postfire maintenance of stem density required at least as many recruits as there were prefire adult trees (7), a conservative assumption given the higher level of juvenile compared to adult mortality. To ensure adequate replication within biogeographic regions, we collapsed true ecoregions into biogeographically similar regions (Fig. 2). Sample sizes available for determination of the frequency and direction of state change by pooled ecoregion were as follows: Alaska Interior, $n = 107$; Cordillera, $n = 241$; Plains West, $n = 190$; Shield West, $n = 154$; Plains East, $n = 229$; Shield East, $n = 479$ (total $n = 1,400$); the subset of sites across ecoregions available for analysis for each taxon is provided in Fig. 3. All analyses were conducted using R statistical software (version 4.0.3) (64).

χ^2 tests [*chisq.test* in package MASS (65)] were used to assess differences in the expected versus observed frequencies of different state changes by combined ecoregion. In this analysis, an expected distribution of sites into the regeneration categories is generated for each ecoregion based on data across all ecoregions. This is then compared to the observed value within that ecoregion to determine whether regeneration outcomes vary across ecoregions.

Determining the Drivers of State Change. Predictors of state changes were selected based on variables previously shown to affect postfire seedling recruitment. A subset of studies ($n = 1,046$) included data on these hypothesized drivers. Sample sizes available for the evaluation of predictors of state change by pooled ecoregion were as follows: Alaska Interior, $n = 39$; Cordillera, $n = 110$; Plains West, $n = 167$; Shield West, $n = 95$; Plains East, $n = 204$; Shield East, $n = 431$. Stand age (years since postdisturbance establishment and a metric of fire return interval) was determined based on dendroecological assessment of basal cookies and/or cores taken from 2 to 12 trees at each site. Site drainage was determined using topoedaphic characteristics (e.g., refs. 66 and 67) but for analysis was reduced to an ordinal variable with three levels (1 = dry, 2 = moist, 3 = wet). Residual soil organic layer thickness was measured as the depth to mineral soil, bedrock, or permafrost in small soil pits at multiple locations at each site; as soil combustion estimates were not available for many studies, we used residual organic soil layer thickness to represent integrated effects of prefire organic soil depth and fire severity on postfire seedbed quality (47). Within quadrats or transects, the diameter at breast height and identity of all woody stems was recorded, allowing the calculation of species-specific prefire stem density (trees $\cdot m^{-2}$) and basal area ($m^2 \cdot ha^{-1}$). Estimates of canopy combustion were based on either combustion of structural classes resulting in an ordinal variable ranging from 0 (canopy survived fire [i.e., live canopy]) to 3 (all fine fuels and branches combusted) or canopy composite burn index, which is a similar metric that quantifies the level of consumption of canopy foliage and stems on a scale of 0 (canopy survived fire) to 3 (all needles and branches consumed) (68). For sites where both measures of canopy combustion were available, type II regression indicated a significant positive relationship ($r^2 = 0.57$; $P < 0.0001$) that did not differ from unity ($P = 0.9577$) [function *sma* in package *smart* (69)], supporting the combination of these metrics. Growing season Hargreaves' climate moisture deficit was generated with the ClimateNA version 5.60 software package (70) for the 2 y following fire for each site and the 1981 to 2010 normal (CMD_{normal}). We used the difference between CMD following fire and CMD_{normal} to reflect climate anomalies in the 2 y following fire (CMD_{postfire}) with the expectation that anomalies relative to the climate normal would be more relevant than absolute CMD_{postfire} values given the substantial climatic variation across North America. Most seedling recruitment occurs in the first 2 y following stand-replacing fire (15), guiding our inclusion of climate anomalies in years 1 and 2 postfire.

We evaluated whether a common set of drivers predicted observed state changes after fire using random forest machine learning. Random forest constructs many classification trees using combinations of the predictor variables of interest (71). The importance of these variables in correctly predicting the response variable is determined based on consensus across trees. We evaluated the relative importance of these predictors in determining the patterns of state change defined in Fig. 1 with random forest analysis using the *party* package (72), which is an implementation of conditional inference trees. We used this package because it handles mixed variables (categorical and continuous) in an unbiased way (73). It also deals well with correlated variables, as it allows for conditional permutation, which examines the importance of each variable in the absence of its correlations with other variables. This provides ranks of

variables in terms of their importance in correctly classifying the postfire regeneration outcomes defined in Fig. 1. Separate analyses were conducted for stands dominated ($\geq 50\%$ prefire stem density) by black spruce ($n = 850$) and all conifers ($n = 989$). We used the same approach to assess which conditions lead to jack pine ($n = 218$) and broadleaf taxa ($n = 974$) expansion where they were not dominant ($< 50\%$ prefire stem density for broadleaf; $< 50\%$ and $> 0\%$ for jack pine). Confusion matrices and model error statistics were assessed using the *caret* package (74). Model accuracy (the number of correctly classified observations in a classification) ranged from 49 to 83%. Confusion matrices indicated that most of the misclassification arose within our broader resilience and state change groupings. For example, misclassification in black spruce stands most commonly occurred between the self-replacement and density reduction categories. Grouping these reduced confusion and increased classification accuracy from 49 to 88% (Fig. 3). Classification accuracy was relatively low (39%) in the case of conifer state change, which is attributable to the fact that one conifer species (jack pine) replaces another (black spruce) under conditions that also promote broadleaf expansion, making accurate prediction difficult (Fig. 3). Partial dependence plots (*SI Appendix, Figs. S11–S14*) were produced using the package *pdp* (75); these plots provide a visualization of the relationship between response and predictor while taking into account the average effect of other predictors in the model.

Synthesized data from existing studies with unbalanced sample sizes could cause studies or regions with larger samples to have a disproportionate influence on the results (*SI Appendix, Table S1*). To address this, we augmented the random forest analysis with a formal meta-analysis of drivers of postfire state

change across studies in stands dominated ($\geq 50\%$ of stems) by black spruce before fire. Our response variable was categorical (Fig. 1); therefore, we used an approach that converts χ^2 statistics into effect sizes for meta-analysis (76). This approach is fully described in *SI Appendix, Extended Methods*. Results of this analysis corroborated those of the random forest analysis (*SI Appendix, Figs. S6 and S8 and Table S2*).

Data Availability. The raw data used for analysis is available through the Oak Ridge National Laboratory Distributed Active Archive Center at <https://doi.org/10.3334/ORNLDAAC/1955> (77). No custom code was used during analysis and all R code used is available upon request from the authors. R packages used are referenced in the *Methods*.

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