RESEARCH ARTICLE

An alternate vegetation type proves resilient and persists for decades following forest conversion in the North American boreal biome

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Abstract

1. Climate change and natural disturbances are catalysing forest transitions to different vegetation types, but whether these new communities are resilient alternate states that will persist for decades to centuries is not known. Here, we test how changing climate, disturbance and biotic interactions shape the long-term fate of a deciduous broadleaf forest type that replaces black spruce after severe wildfires in interior Alaska, USA.

2. We simulated postfire deciduous forest that replaced black spruce after severe fires in 2004 for tens to hundreds of years under different climate scenarios (contemporary, mid 21st century, late 21st century), fire return intervals (11–250 years), distances to seed source (50–1,000 m) and browsing intensities (background, moderate, chronic). We identified combinations of conditions where deciduous forest remained the dominant vegetation type and combinations where it returned to black spruce forest, transitioned to mixed forest (where deciduous species and black spruce co-dominate) or converted to nonforest.

3. Deciduous forest persisted in 86% of simulations and was most resilient if fire return intervals were short (≤50 years). When transitions to another vegetation type occurred, mixed forest was most common, particularly when fire return intervals were long (>50 years) and the nearest seed source was 500 m or farther. Moderate and chronic browsing also reduced deciduous sapling growth and survival, helping black spruce compete if fire return intervals were long and seed source was distant. Dry soils occasionally caused conversion to nonforest following short-interval fire when simulations were forced with a late 21st-century climate scenario that projects warming and increased vapor pressure deficit. Return to black spruce forest almost never occurred.

4. *Synthesis*. Conversion from black spruce to deciduous forest is already underway at regional scales in interior Alaska, and similar transitions have been widely observed throughout the North American boreal biome. We show that this boreal deciduous forest type is likely a resilient alternate state that will persist through the 21st century, which is important, because future vegetation outcomes will shape biophysical feedbacks to regional climate and influence subsequent disturbance regimes.

1 | INTRODUCTION

Changing climate and natural disturbances are catalysing forest conversion to different vegetation types (e.g. new tree species assemblages, grass/shrublands; Bowman, Murphy, Neyland, Williamson, & Prior, 2014; Donato, Harvey, & Turner, 2016; Johnstone, Hollingsworth, Chapin, & Mack, 2010; Odion, Moritz, & DellaSala, 2010; Tiribelli, Kitzberger, & Morales, 2018). Because vegetation structure and composition shapes biogeochemical cycling (Sitch et al., 2008), climate regulation (Bonan, 2008; Swann et al., 2018; Thom, Rammer, & Seidl, 2017) and ecosystem service provision (Seidl, Spies, Peterson, Stephens, & Hicke, 2016; Turner, Donato, & Romme, 2013), determining the long-term fate of these emerging communities is essential for forecasting 21st-century earth system function. However, succession in terrestrial ecosystems unfolds slowly, and it remains poorly resolved whether new vegetation types are transient or will prove to be resilient alternate states that persist for decades to centuries (sensu; Beisner, Haydon, & Cuddington, 2003; Johnstone et al., 2016; May, 1977).

Resilience is the capacity of a system to absorb perturbation while retaining function, structure, and thus, identity (Walker et al., 2006). The long-term resilience of new vegetation types following forest conversion will depend on reinforcing and destabilizing feedbacks (Connell & Sousa, 1983; Petraities & Latham, 1999; Ratajczak et al., 2018). However, feedbacks often develop over years to decades (Hughes, Linares, Dakos, van de Leemput, & van Nes, 2013; Johnstone et al., 2016), and 20th-century forest conversion following disturbance was comparatively rare (e.g. Turner, Braziunas, Hansen, & Harvey, 2019; Wood & Bowman, 2012). Thus, we lack observations of how feedbacks shape long-term outcomes. Further, the magnitude of projected 21st-century climate change means that historical observations may be a poor guide for predicting vegetation responses to future climate (Keane et al., 2018; Seidl, 2017). The rarity of 20th-century forest conversion following disturbance and the prospect of no-analog future climate both limit the utility of empirical approaches for determining whether emerging vegetation types will prove resilient.

Process-based simulation models offer a promising path forward. They describe cause and effect relationships between system variables (Foster et al., 2019; Gustafson, 2013; Miller, Thompson, Tepley, & Anderson-Teixeira, 2018; Serra-Diaz et al., 2018; Tepley et al., 2018), making them useful for tracking feedbacks as ecosystems reorganize and for identifying the underpinning abiotic and biotic drivers (Dietze, 2017; Grimm & Berger, 2016; Seidl, 2017). Process-based models are also well suited to evaluate forest responses to no-analog future climate conditions because they are based on first principles rather than statistical relationships derived from past observations (Keane et al., 2018; Seidl et al., 2011).

The boreal forest of interior Alaska is an excellent system from which to gain generalizable insights regarding the long-term fate of new vegetation types following forest conversion (Johnstone et al., 2016). For much of the Holocene, interior Alaskan forests were dominated by black spruce *Picea mariana*, interspersed with pockets of deciduous broadleaf (hereafter; deciduous) trembling aspen *Populus tremuloides* and Alaskan birch *Betula neoalaskana* (Calef, McGuire, Epstein, Rupp, & Shugart, 2005; Higuera, Brubaker, Anderson, Hu, & Brown, 2009). Wildfire is the dominant disturbance, and black spruce trees are well adapted to the historical fire regime (Higuera et al., 2009; Johnstone, Hollingsworth, et al., 2010). However, temperature in interior Alaska has warmed at nearly twice the global average, increasing the frequency and size of severe fires (Chapin et al., 2010; Hoecker & Higuera, 2019; Kelly et al., 2013; Wolken et al., 2011). Intensifying fire activity now favours postfire establishment and dominance of aspen and birch in stands that were previously comprised of black spruce (Johnstone et al., 2016; Johnstone, Hollingsworth, et al., 2010). Regional transitions from black spruce to deciduous forest after fire are already underway (Beck et al., 2011; Mann, Rupp, Olson, & Duffy, 2012).

The fate of postfire deciduous forest once dominated by black spruce is not known (though, see Alexander & Mack, 2017; Kurkowski, Mann, Rupp, & Verbyla, 2008). However, climate, disturbance and biotic interactions may all be important for determining whether deciduous forest persists, transitions to forest of mixed species composition, returns to black spruce dominance or converts to nonforest. Tree growth is already limited by soil moisture during hot-dry years (Trugman, Medvigy, Anderegg, & Pacala, 2018), and future water balance remains uncertain because general circulation models (GCMs) vary widely in precipitation and vapor pressure deficit (VPD) projections. Deciduous forest is also less flammable than spruce (Higuera et al., 2009). Yet, it can burn when weather is extreme (Barrett et al., 2016), and short-interval fires might reinforce the resilience of deciduous forest because aspen and birch resprout asexually after burning (Burns & Honkala, 1990; Johnstone, 2005). Further, browsing in the boreal forest occurs at rates sufficient to alter global carbon cycling (Schmitz et al., 2014, 2018). Moose *Alces alces* heavily browse deciduous saplings (Brown et al., 2018; Seaton et al., 2011), while snowshoe hares *Lepus americanus* target understorey black spruce (Olnes, Kielland, Genet, & Ruess, 2019), both of which, might influence successional trajectories following fire.

We conducted a simulation experiment with an individual-based forest-process model, iLand, to ask: *How do changing climate, disturbance characteristics and biotic interactions shape the resilience of postfire deciduous forest previously dominated by black spruce?* We hypothesized (A) that deciduous forest would be resilient under contemporary climate conditions and wetter future climate scenarios, when fire return intervals (FRIs) were short, and when postfire

FIGURE 1 Hypothesis A: The combinations of climate, disturbance characteristics and biotic interactions under which deciduous forest that replaces spruce after severe wildfires will persist in Alaska, USA. Hypotheses B and C: The combinations of conditions under which deciduous forest may transition to mixed forest or return to black spruce forest versus converting to nonforest. FRI stands for fire return interval
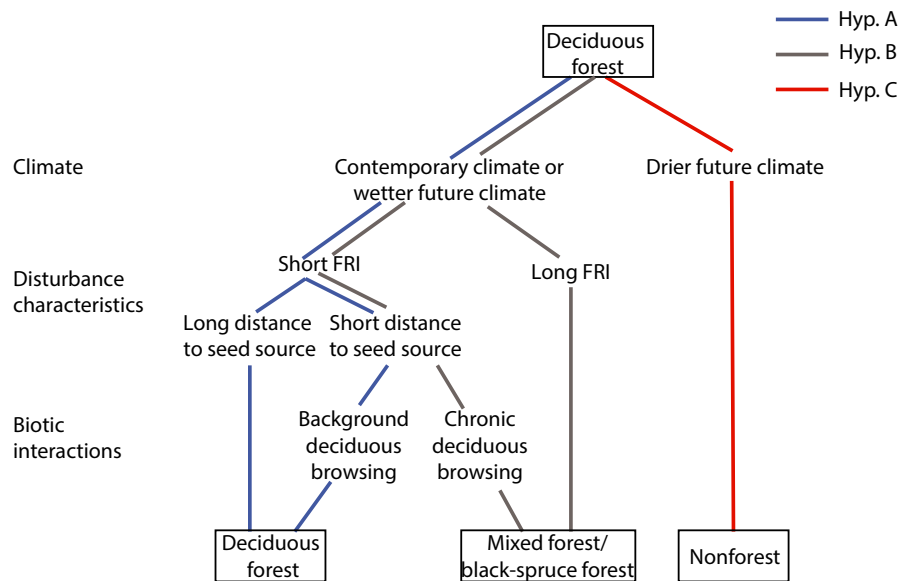
seed source was distant or browsing intensity on aspen and birch was low (Figure 1). We then asked: *When resilience of deciduous forest is exceeded, under what conditions do transitions to mixed forest or black spruce forest occur, rather than transitions to nonforest?* We hypothesized (B) that transitions to mixed forest or black spruce forest would occur under contemporary climate or wetter future climate scenarios, but only when FRIs were long, or postfire seed source was close and deciduous trees were heavily browsed. Finally, we hypothesized (C) that transitions to nonforest would only occur under warmer-drier future climate scenarios.

2 | MATERIALS AND METHODS

2.1 | Study area

The Alaskan boreal forest covers a massive area (~450,000 km^2) south of the Brooks mountain range and north of the Alaska range (Figure S1). Climate is continental (January mean minimum temperature: –27°C, July mean maximum temperature: 23°C, mean annual precipitation: 270 mm; http://climate.gi.alaska.edu/Climate/Normals). Roughly half of the Alaskan boreal forest is underlain by near-surface permafrost (≤1 m deep; Pastick et al., 2015), concentrated in cooler valley bottoms and north-facing slopes (Hinzman, Viereck, & Adams, 2006). Throughout much of the Holocene, black spruce has dominated the Alaskan boreal forest, and is widespread in areas underlain by permafrost (Chapin, Hollingsworth, Murray, Viereck, & Walker, 2006). Deciduous forest is interspersed in warmer uplands and on south-facing slopes. Though not included in this study, white spruce (*Picea glauca*) can be found in well-drained uplands and flood plains (Chapin et al., 2006).

Slow decomposition rates in black spruce forest cause thick layers of surface organic material to accumulate that serve as fuel for wildfires (Boby, Schuur, Mack, Verbyla, & Johnstone, 2010; Kasischke & Johnstone, 2005). Historically, black spruce forest burned in large

fires every 80–250 years (Higuera et al., 2009; Hu et al., 2006; Lynch, Clark, Bigelow, Edwards, & Finney, 2002). Fires were stand replacing (killing the trees), but often, the soil organic layer was not completely consumed (Kasischke & Johnstone, 2005). This ensured postfire self-replacement by black spruce (Johnstone & Kasischke, 2005). Black spruce are the only tree species in the Alaskan boreal forest with seeds that have sufficient carbohydrate reserves to support root growth through the organic layer into mineral soil. Further, black spruce trees produce huge seed crops in semi-serotinous cones (that remain partially closed until heated by fire; Johnstone et al., 2009). However, black spruce trees do not disperse seeds long distances; most fall within 80 m of the source tree (Burns & Honkala, 1990). Thus, the in situ seed supply is a critical determinant of postfire regeneration success (Johnstone et al., 2009).

Conversely, aspen and birch produce small light seeds that do not germinate well on thick surface organic layers (Johnstone, Chapin, et al., 2010) but can travel in the wind for kilometres from the source tree (Burns & Honkala, 1990). Both species also resprout asexually after fire. Warming, combined with increased lightning frequency, is causing more frequent and larger fires (Sanford, Wang, & Kenward, 2015; Veraverbeke et al., 2017) that burn deep into the surface organic layer (Johnstone et al., 2016; Walker et al., 2019). Where postfire surface organic layers are thin or mineral soil has been exposed, faster growing aspen and birch can establish, outcompete spruce and dominate the overstorey (Johnstone, Hollingsworth, et al., 2010). Larger and more frequent fires also may favour deciduous tree seedling establishment due to differences in effective dispersal distance and the ability of aspen and birch to resprout.

2.2 | Model overview

To determine how climate, disturbance and biotic interactions will shape the future of postfire deciduous forest in Alaska, we conducted a simulation experiment with the individual-based forest-process

model, iLand (Seidl, Rammer, Scheller, & Spies, 2012; online documentation: http://iland.boku.ac.at). iLand simulates individual trees in a hierarchical framework where broader-scale forest dynamics emerge from interactions among individuals (Seidl, Rammer, et al., 2012). Tree growth, mortality and competition are modelled as functions of canopy light interception, radiation, temperature, soil moisture and nutrient limitation. Climate and soils are modelled as spatially homogeneous within a stand (1 ha). However, individual trees determine light availability at a 2 m × 2 m horizontal resolution within each stand.

The model explicitly represents seed dispersal using a two-part exponential equation that accounts for both short (e.g. wind-based) and long distance (e.g. animal-based) dispersal (Seidl, Rammer, et al., 2012). Dispersal probability declines with distance from seed source. Effects of climate on seed germination and seedling establishment are also accounted for (Seidl, Spies, et al., 2012). The model simulates serotinous seed dispersal (Hansen, Braziunas, Rammer, Seidl, & Turner, 2018; Hansen, Abendroth, Rammer, Seidl, & Turner, 2020) and asexual resprouting. It also represents natural disturbances, including wildfire (Hansen, Abendroth, et al., 2020; Seidl, Rammer, & Spies, 2014). In the model, a user-defined species-specific probability of animal browsing can be applied. This determines what percentage of seedlings and saplings are browsed each year. If a seedling or sapling is browsed, annual biomass production does not occur (i.e. stems do not grow and leaves are not produced). This causes stress to build, as carbon reserves are reduced, which may eventually kill the simulated seedling or sapling.

iLand can simulate forest landscapes or independent forest stands in parallel where neighbouring stands do not influence one another. When run in this mode, iLand simulates each stand as if they are 'wrapped' where trees on one side of the stand influence trees on the other side, eliminating edge effects. The model has been well tested in landscape and stand modes and used extensively in the western United States (Braziunas, Hansen, Seidl, Rammer, & Turner, 2018; Hansen, Abendroth, et al., 2020; Hansen et al., 2018; Seidl, Rammer, et al., 2012; Seidl et al., 2014; Seidl, Spies, et al., 2012) and Europe (Albrich, Rammer, & Seidl, 2020; Albrich, Rammer, Thom, & Seidl, 2018; Silva Pedro, Rammer, & Seidl, 2015; Thom, Rammer, Dirnböck, et al., 2017). We used stand mode in this application.

2.3 | Model parameterization and benchmarking

We parameterized iLand for black spruce, trembling aspen and Alaskan birch. Parameters were identified through extensive literature review (Appendix S1). We benchmarked the model with long-term field data using a pattern-oriented approach (i.e. Grimm et al., 2005). First, we evaluated whether iLand could simulate trajectories of forest structure in monospecific stands of each species (Appendix S2). We then evaluated postfire tree regeneration in the model as a function of distance to seed source (Appendix S3). Finally, we tested whether the model could simulate historical

successional trajectories of forest structure and composition when species were mixed (Appendix S4). Modest parameter calibration was necessary based on benchmarking exercises (Appendix S1), but the model generally agreed well with independent field observations (Malone, Liang, & Packee, 2009; Ruess, Hollingsworth, & Johnstone, 2018).

2.4 | Initial forest structure and topoedaphic conditions

We initialized iLand based on field surveys of forest stands that burned across much of interior Alaska during the large fire season of 2004 (Johnstone et al., 2020; Johnstone, Hollingsworth, et al., 2010; Figure S1). Black spruce was the dominant tree species in stands before burning in 2004, accounting for 90 ± 3.8% (mean ± standard error; *SE*) of prefire density. Stands then transitioned to deciduous dominance after the 2004 fires. Postfire species composition was 81 ± 2% deciduous seedlings and 19 ± 2% black spruce seedlings when sampled in 2017.

For each stand in the experiment, we extracted geographically corresponding soil characteristics including percent sand, silt, clay and effective soil depth, derived from the Alaska STATSGO database (NRCS, 2019). Relative soil fertility (expressed as plant available nitrogen; Braziunas et al., 2018) was set at 45 kg ha^{-1} year^{-1}, loosely based on field measurements of plant available nitrogen in mixed and deciduous forest of interior Alaska (Melvin et al., 2015). We kept relative fertility spatially constant (no variation across stands in the experiment) because there is a lack of reliable gridded soil nitrogen data for interior Alaska. Remote sensing indicated that most of the stands (~75%) are currently not underlain by near-surface permafrost (Pastick et al., 2015). Further, the extent of permafrost is expected to markedly decrease in coming decades (Schuur & Mack, 2018). Thus, we assumed permafrost was not present in simulations.

The model was initialized with tree species composition and stem densities that matched field measurements in 2017. Seedling heights were not available from most of the field surveys. Thus, we fit species-specific distributions (gamma for aspen and spruce, Weibull for birch) to seedling-height data collected in a subset of the sampled fires (Conway & Johnstone, 2017) and assigned initial heights to simulated seedlings and saplings by randomly drawing from these distributions. Because stand density, species composition and tree heights came from different field surveys conducted in different years, we set initial tree ages to 11 years, which also helps account for any infilling of seedlings in the stands since 2004.

2.5 | Simulation experiment

We conducted a simulation experiment to evaluate how climate, fire return interval, postfire distance to seed source and browsing

intensity affect the resilience of deciduous forest (Table 1). Stands were simulated with contemporary and future climate forcing until they were scheduled to burn in a second severe fire. After the second fire, simulations continued for another 50 years as if the nearest live spruce and deciduous seed sources were different distances away. The intensity of browsing on spruce and deciduous seedlings and saplings was also varied.

We represented effects of current and future climate on simulated stands by forcing the model under three climate periods: contemporary (1971–2000), mid 21st century (2031–2060) and late 21st century (2071–2100). iLand ingests daily climate (minimum and maximum temperature, sum of precipitation, sum of shortwave radiation and mean vapour pressure deficit). For each climate period, we used daily meteorological data from three GCMs that represent historical climate well in Alaska (Walsh et al., 2018) and span the range of projected 21st-century conditions (Figure 2). The GCMs were the MRI-CGCM3, IPSL-CM5A-LR and CCSM4 GCMs (Dufresne et al., 2013; Gent et al., 2011; Yukimoto et al., 2012). Runs of each GCM were carried out as part of the fifth phase of the Coupled Model Intercomparison Project (Taylor, Stouffer, & Meehl, 2012). Future GCM runs were forced with the RCP 8.5 emissions scenario (van Vuuren et al., 2011). Modelled daily meteorological grids were statistically downscaled to a 1-km spatial resolution using quantile matching (Appendix S5).

Each stand was simulated until scheduled to burn at 11, 50, 125 and 250 years after the initial 2004 fire. This spans the observed range of FRIs from very short-interval fires to long FRIs observed during the Holocene (Higuera et al., 2009). Fire ignition and spread were not simulated explicitly. Instead, we represented effects of stand-replacing fires by prescribing 100% mortality to the prefire trees, saplings and seedlings in each burned stand.

The stands used to initialize the experiment each burned at high severity in the 2004 fires and 76 ± 3.6% of the surface organic layer was consumed on average. Surface organic material accumulates slowly in deciduous and mixed forest compared to
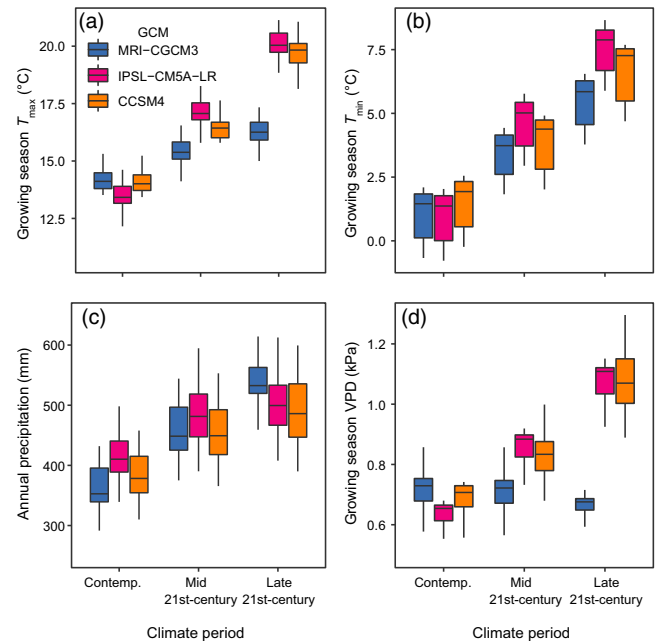

FIGURE 2 (a) April–September mean daily maximum temperature (T_{max}), (b) April–September mean daily minimum temperature (T_{min}), (c) annual total precipitation, and (d) April–September mean daily vapour pressure deficit (VPD) for simulated stands, by climate period and GCM. All GCMs were forced with the RCP 8.5 emissions scenario. Contemp., contemporary; GCM, general circulation model

monospecific black spruce stands because litter quality is higher, decomposition rates are faster and moss cannot establish as well (Melvin et al., 2015). Thus, we did not explicitly represent surface organic layer accumulation during simulations. Instead, we assumed that simulated fires completely consumed any surface organic layer that would have accumulated since the initial 2004 fires.

Following fire, the probability of deciduous and black spruce seeds arriving in each burned stand differed as if the nearest unburned forest was 50, 500 or 1,000 m away, based on species-specific dispersal kernels. Treatments were chosen to reflect distances to live seed source commonly measured in the field surveys used to initialize the simulation experiment (Johnstone, Hollingsworth, et al., 2010). Black spruce trees that burned also served as an in situ seed source because of their semi-serotinous cones. Deciduous trees that burned could resprout asexually.

Species parameters that determine seedling establishment and sapling growth are derived from field measurements, where at least some individuals have been browsed. Thus, we assumed that seedlings and saplings in the model are always influenced by a low background probability of browsing, which was set at 20% for deciduous individuals <2 m tall and 1.5% for black spruce <2 m tall, based on field surveys (Lord & Kielland, 2015; Olnes et al., 2019). To evaluate effects of more intense browsing, we compared stands with background levels of browsing to stands that experienced medium browsing intensities (45% and 15% of deciduous and black spruce individuals <2 m tall) and chronic browsing (60% and

TABLE 1 Experimental factors and treatment levels

Factor	Levels
Climate period	Contemporary (1971–2000) Mid 21st-century (2031–2060) Late 21st-century (2071–2100)
GCM	MRI-CGCM3 IPSL-CM5A-LR CCSM4
Fire return interval	11, 50, 125, 250 years postfire
Postfire distance to seed source	50, 500 1,000 m from seed source
Deciduous browsing intensity	Background (20% probability) Moderate (45% probability) Chronic (60% probability)
Black spruce browsing intensity	Background (1.5% probability) Moderate (15% probability) Chronic (25% probability)

25% of deciduous and black spruce individuals <2 m tall; Lord & Kielland, 2015; Olnes et al., 2019).

Each of the 31 stands in the experiment were run with all combinations of climate period (three levels), GCM (three levels), FRI (four levels), distance to seed source (three levels), deciduous browsing intensity (three levels) and black spruce browsing intensity (three levels). Because we did not want the order of the climate records to influence results, we also ran five replicates of each stand and combination of experimental treatments where the temporal order of the climate forcing was rearranged with replacement. This yielded a total of 150,660 simulations.

2.6 | Model outputs and data analysis

We quantified the mean percentage of replicate stands that remained deciduous forest 50 years after simulated fire, and the mean percentage that transitioned to mixed forest (co-dominance of deciduous species and spruce), black spruce forest or nonforest using importance values (IV). IV is a measure of stand dominance that considers the relative proportions of species or plant functional type density and basal area. Values range from zero to two. Larger values indicate the species or plant functional type is more dominant in the stand. Based on all trees with a DBH ≥ 2.5 cm, stands were considered deciduous forest if the deciduous IV was above 1.5. Stands were considered mixed forest when deciduous IV ranged from 0.5 to 1.5, and they were considered black spruce forest if deciduous IV was below 0.5. Stands were classified as nonforest if fewer than 50 stems/ha remained (Hansen et al., 2018). The percentage of stands ± the SE among replicates is presented in the text.

We used random forest classification to quantify how the dominant vegetation type (deciduous forest, mixed forest, black spruce forest, nonforest) at the end of simulations differed across combinations of the experimental treatments and varied by replicate. Random forest is a powerful machine learning algorithm for analysing complex datasets that do not meet traditional statistical assumptions. It is useful for analysing simulation experiments where large sample sizes can artificially inflate statistical significance derived from parametric approaches (Lucash, Ruckert, Nicholas, Scheller, & Smithwick, 2019). In random forest, a user-defined number of classification trees (in this study, $n = 500$) are fit to bootstrapped subsamples of the dataset (Cutler et al., 2007). Classification trees partition observations into homogenous groups (in this analysis, final vegetation type) based on explanatory variables. At each node, only a few randomly selected variables are available for observation partitioning (in this study, $n = 2$). For each classification tree, observations from the dataset that are not included among the bootstrapped samples are used to evaluate model accuracy. Then, explanatory variables are randomly permuted, and the difference in classification accuracies between the two models provides a normalized metric of variable importance (mean decrease in accuracy), reported as a percentage (Cutler et al., 2007).

3 | RESULTS

Stand densities (trees with DBH ≥ 2.5 cm) ranged widely (3–8,251 stems/ha, mean = 1,370 stems/ha) 50 years after simulated fire. Deciduous tree densities were between 3 and 7,198 stems/ha (mean = 1,122 stems/ha), and black spruce densities varied from 0 to 7,925 stems/ha (mean = 248 stems/ha). Simulated stand composition and densities aligned well with independent field observations collected across interior Alaska (Malone et al., 2009; Ruess et al., 2018; see Appendix S2 for descriptions of these datasets).

Most stands (86 ± 0.04%) remained deciduous forest across all combinations of GCMs, climate periods, FRIs, distances to seed source and browsing intensities. When transitions to another vegetation type occurred, mixed forest was the most likely outcome (13.7 ± 0.05% of stands), and was 85 times more common than return to black spruce forest or conversion to nonforest. Transition to nonforest was rare (0.32 ± 0.015% of stands) and stands almost never returned to black spruce forest (0.001 ± 0.0008%).

3.1 | Determinants of deciduous forest resilience

FRI, distance to seed source and deciduous browsing intensity jointly determined whether deciduous stands were resilient or transitioned to another vegetation type 50 years after simulated fire (Figure 3a). Nearly 1.3 times more stands remained deciduous forest when FRIs were short (11 or 50 years; 97 ± 0.04% of stands) versus long (125 or 250 years; 75 ± 0.16% of stands; Figure 3b). However, when FRIs were 125 or 250 years, stands were most likely to remain deciduous forest if seed source was close and deciduous browsing intensity was low (Figure 3c). For instance, when FRIs were long, nearly three times more stands remained deciduous forest if the nearest seed source was 50 m away with background levels of deciduous browsing (99.9 ± 0.04% of stands), compared to stands where seed source was 1,000 m away and deciduous browsing intensity was chronic (34.4 ± 0.4% of stands). Climate period, GCM, spruce browse intensity and replicate had little to no influence on whether deciduous forest persisted (Figure 3a).

3.2 | Determinants of transitions to other vegetation types

For the simulated stands that did transition from deciduous forest to another vegetation type, FRI most strongly determined whether mixed forest or nonforest was most likely (Figure 4a). Nearly two and a half times more stands transitioned to mixed forest, rather than to nonforest, when FRIs were 125 or 250 years (99.6 ± 0.05% of stands) versus when FRIs were 11 or 50 years (41.4 ± 0.35% of stands; Figure 4b). Climate period and GCM also had small effects on whether stands transitioned to mixed forest or nonforest (Figure 4a).

FIGURE 3 (a) Variable importance plot of experimental treatments used in random forest classification to predict which simulated stands were most likely to remain deciduous forest 50 years after simulated stand-replacing fire. Values show the decrease in classification accuracy when variables are permuted in random forest classification. Larger values indicate the variable is more important to the classification. (b) Percent of stands that remained deciduous forest or transitioned to another vegetation type (i.e. mixed forest, black spruce forest or nonforest) 50 years after simulated stand-replacing fire as a function of fire return interval. (c) For the subset of simulated stands that burned in long fire return intervals (125 or 250 years; *n* = 75,330), percent of stands that remained deciduous forest or transitioned to another vegetation type as a function of distance to seed source and deciduous browsing intensity. In plots (b) and (c), standard errors across simulation replicates were too small to visualize
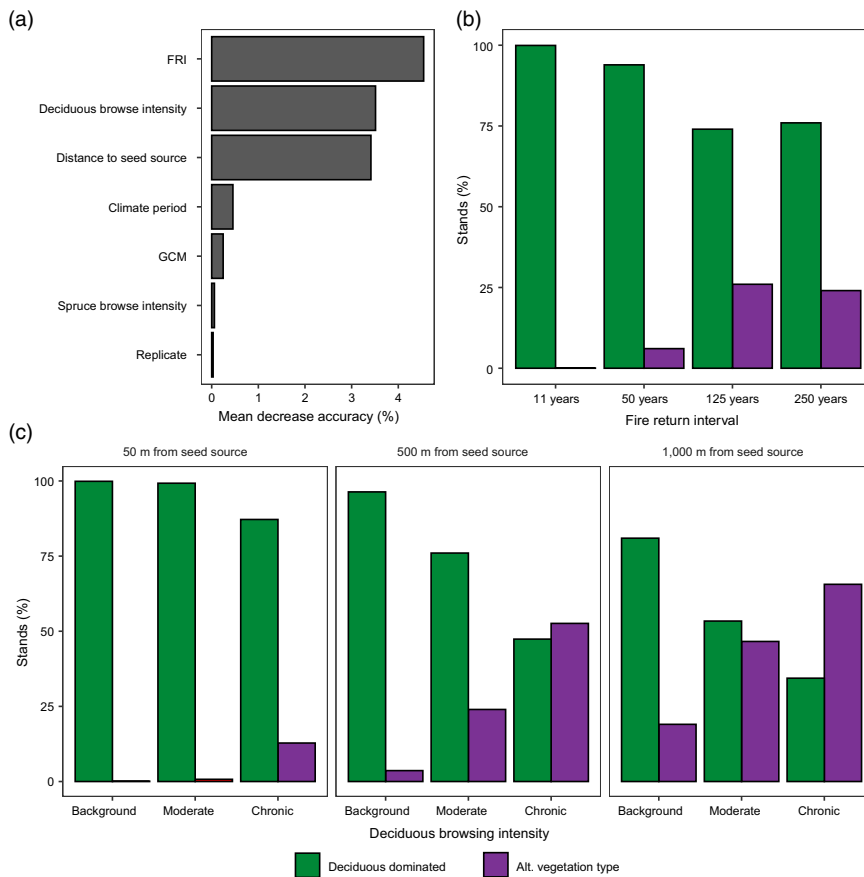

FIGURE 4 (a) Variable importance plot of experimental treatments used in random forest classification to predict whether stands converted to mixed forest or nonforest for the subset (*n* = 21,154) of simulated stands that transitioned from deciduous forest to an another vegetation type 50 years after simulated stand-replacing fire. Values show the decrease in classification accuracy when variables are permuted in random forest classification. Larger values suggest the variable is more important to the classification. (b) For a subset of simulated stands that transitioned to another vegetation type (*n* = 21,154), percent of stands classified as mixed forest or nonforest as a function of fire return interval. (c) For a subset of simulated stands that transitioned to another vegetation type and burned in short fire return intervals (11 or 50 years; *n* = 10,557), percent of stands that transitioned to mixed forest or nonforest as a function of GCM and climate period. In plots (b) and (c), standard errors across simulation replicates were too small to visualize. Contemp., contemporary; GCM, general circulation model
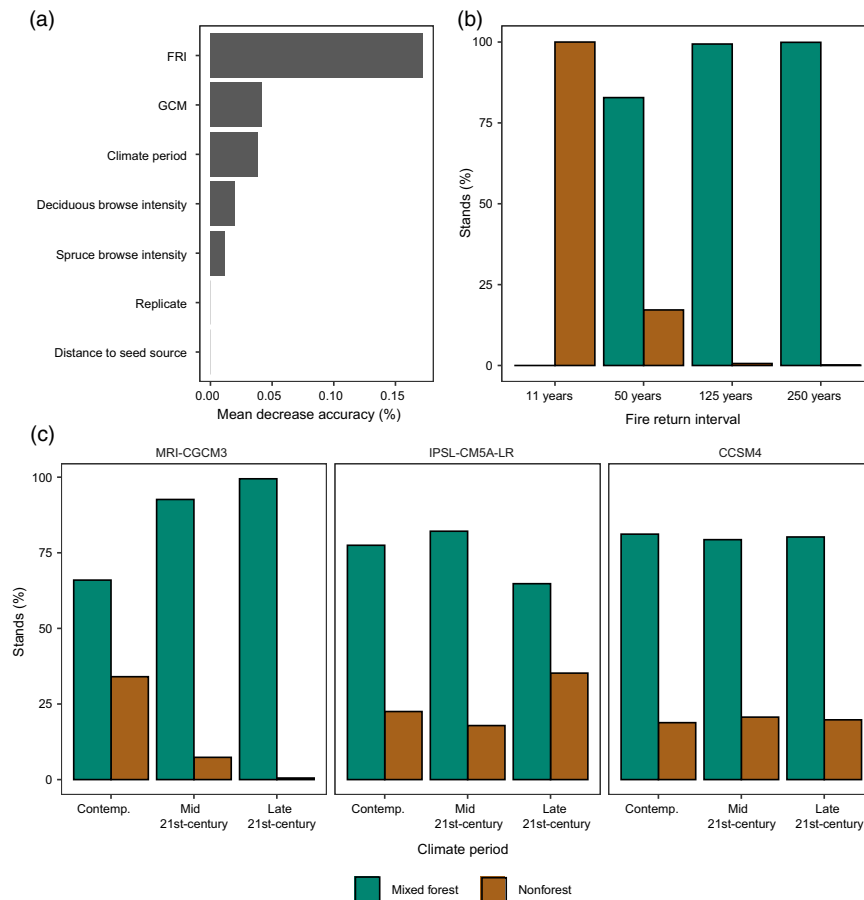
When FRIs were short, transitions to nonforest were more likely to occur in the late 21st-century climate period (35 ± 2.5% of stands) than the contemporary period (from 23 ± 2.5%) under the IPSL-CM5A-LR GCM (warmest with highest VPD; Figure 2; Figure 4c). Conversely, if simulations were forced with climate from the MRI-CGCM3 GCM (largest precipitation increases with lowest VPD; Figure 2) transitions to nonforest were less likely to occur under late 21st-century climate compared with the contemporary period (Figure 4c).

Whether transitions to nonforest after short-interval fire were more or less likely in the late 21st century depended on differences in simulated soil moisture between GCMs. Soils in the late 21st-century climate period were approximately one percentage point drier than in the contemporary period when simulations were forced by the IPSL-CM5-LR GCM. In contrast, soil moisture increased from 13.4 ± 0.02% during the contemporary period to 15.9 ± 0.002% during the late 21st-century period with the MRI-CGCM3 GCM. Deciduous and spruce browsing intensity, replicate and distance to seed source had little influence on whether stands transitioned to mixed forest or nonforest (Figure 4a).

4 | DISCUSSION

Changing climate and disturbances are catalysing forest transitions to new vegetation types in many biomes (Bowman et al., 2014; Enright, Fontaine, Bowman, Bradstock, & Williams, 2015; Johnstone et al., 2016; van Nes et al., 2018; Turetsky et al., 2017). Determining the long-term fate of these vegetation types is essential for understanding how earth system function will change during this century. Across interior Alaska, more frequent and larger severe fires have initiated widespread conversion from black spruce to deciduous forest (Johnstone, Chapin, et al., 2010; Mann et al., 2012). Our simulations indicate that this forest type is likely a resilient alternate state that could persist for decades to centuries under a wide range of plausible future conditions. iLand does not yet represent permafrost, an important process in lowland areas of interior Alaska. Even now, however, near-surface permafrost underlies only approximately half of the Alaskan boreal forest, and its spatial extent is expected to decline over the next few decades (Pastick et al., 2015). Our findings resolve critical uncertainties regarding postfire successional trajectories in vast areas of boreal forest not underlain by permafrost. This is important, as future vegetation outcomes will shape biophysical feedbacks to regional climate and influence subsequent disturbance regimes (Chapin et al., 2000).

4.1 | The fate of an alternate vegetation type

Deciduous forest that replaced spruce after severe fires in 2004 often persisted for decades to centuries in our simulations. Consistent with hypotheses (Figure 1), short FRIs reinforced the deciduous state. Most stands (97%) remained deciduous forest

when FRIs were 11 or 50 years. Once established from seed, trembling aspen and Alaskan birch resprout asexually following severe fire, whereas, black spruce are obligate re-seeders (Johnstone & Chapin, 2006). Thus, when FRIs are shorter than ~75 years, black spruce seedling establishment is reduced because prefire trees have not produced sufficient cones to ensure self-replacement (Brown & Johnstone, 2012; Johnstone, Hollingsworth, et al., 2010; Whitman, Parisien, Thompson, & Flannigan, 2019). However, even if spruce seed is present, deciduous trees may capitalize on belowground carbohydrate reserves to fuel prolific resprouting and rapid stem growth, providing a competitive advantage (Johnstone, 2005; Pausas et al., 2016). In this study we did not consider CO_2 fertilization in future climate scenarios, which could alter competitive dynamics between deciduous species and black spruce. However, effects of increasing atmospheric CO_2 concentrations on tree regeneration and interspecific competition remain uncertain (D'Arrigo & Jacoby, 1993; Dusenge, Duarte, & Way, 2019; Girardin et al., 2016; Johnson, McCulloh, & Reinhard, 2011), and thus, problematic to incorporate into models.

This study highlights how resprouting could be a valuable functional trait in forests where climate change causes disturbance regimes to intensify (e.g. subalpine forests of Yellowstone National Park; Hansen, Romme, Ba, & Turner, 2016). Yet, the influence of resprouting on forest resilience is context dependent. In mixed eucalypt forests of Australia, for instance, extremely short FRIs now occur that exceed the resilience of even resprouting tree species (Fairman, Bennett, & Nitschke, 2019). Understanding how postfire regeneration strategies, like resprouting, may interact with expected changes in climate and disturbance regimes will be important for predicting 21st-century successional trajectories in forests globally (Turner, 2010).

Under long FRIs, deciduous forest persisted if postfire seed source was close. When deciduous seed source was distant, however, some stands transitioned to mixed forest (spruce and deciduous trees co-dominated). By 125–250 years, black spruce trees have developed large aerial seedbanks held in semi-serotinous cones (Viglas, Brown, & Johnstone, 2013). Once heated by fire, seeds are released, which decouples postfire spruce seedling density from distance to unburned forest (Johnstone et al., 2009). In contrast, aspen and birch are short lived; mature stems start to senesce after 125 years in interior Alaska (Alexander & Mack, 2017; Viereck, Dyrness, Van Cleve, & Foote, 1983). Both species also resprout with less vigour as they age (Burns & Honkala, 1990; Johnstone, 2005), which increases the importance of postfire distance to unburned deciduous seed source under long FRIs. It is worth noting that black spruce initially colonized interior Alaska and eventually replaced preceding deciduous woodland during the early-to mid-Holocene when FRIs were longer because conditions were cooler and wetter (Higuera et al., 2009). This palaeoecological context highlights how feedbacks that link deciduous and spruce forest to environmental drivers, like climate and fire, reinforce each as resilient alternate states.

The capacity of Alaskan aspen and birch trees to resprout may decline faster as they age than in other portions of their ranges. In

the absence of fire, resprouting is rare in mature aspen forest across interior Alaska (Alexander & Mack, 2017). However, aspen stands in Yellowstone National Park have persisted for millennia through asexual reproduction, even without burning (Romme, Turner, Wallace, & Walker, 1995). Exploring the environmental and genetic underpinnings of intraspecific variation in resprouting across species' distributions may elucidate how local populations will fare under 21st-century climate and fire. Chronic moose browsing further limited deciduous dominance over spruce when FRIs were long and seed source was distant. Compounded consequences of disturbance and browsing remain an underappreciated determinant of high-latitude forest structure and function (Conway & Johnstone, 2017; Schmitz et al., 2014).

We also expected transitions from deciduous forest to nonforest might be more likely in simulations forced with hotter-drier future climate scenarios because aspen, birch and black spruce are already stressed by drought during some growing seasons (Johnstone, McIntire, Pedersen, King, & Pisaric, 2010; Trugman et al., 2018; Walker, Mack, & Johnstone, 2016). In our study, soil moisture influenced vegetation outcomes when FRIs were short, but not when FRIs were long. Following short-interval fire, conversion to nonforest was 55% more common in the late 21st century, compared with the contemporary climate period, if the model was forced with the warmest and driest GCM (IPSL-CM5A-LR). Drought-induced reductions in seedling density have also been documented following short-interval fires in boreal forest of Alberta (Whitman et al., 2019). While moisture stress was only modestly influential in this study, tree seedling establishment in a warmer-drier future will almost certainly be a resilience lynchpin of forest recovery from disturbance globally (Clark et al., 2016; Davis et al., 2019; Hansen & Turner, 2019; Martínez-Vilalta & Lloret, 2016). The interactive effects of changing disturbance regimes and climate on tree seedling establishment warrant further investigation (Hansen et al., 2018).

4.2 | Future stand composition and feedbacks in the Alaskan boreal forest

Deciduous forest persisted in simulations under a wide range of plausible future climate and fire conditions across interior Alaska. However, conversion to other vegetation types was possible, and how 21st-century climate and fire trajectories will actually play out remains poorly resolved (Balshi et al., 2009; Kitzberger, Falk, Westerling, & Swetnam, 2017; Mann et al., 2012). Most GCMs project strong warming-induced declines in soil moisture (Cook et al., 2020). In conjunction with more lightning (Veraverbeke et al., 2017), drying may cause continued increases in fire frequency, size and severity (Flannigan et al., 2016). Yet, some GCMs project sufficient increases in precipitation to offset expected warming (Dufresne et al., 2013; Gent et al., 2011; Yukimoto et al., 2012). Thus, it is plausible that fuel moisture will increase in the future, reducing fire activity.

Whether and how vegetation feeds back to further alter fire trajectories is another key uncertainty. Deciduous forest is less flammable than black spruce in interior Alaska, often burning only when summer fire weather is extreme (Barrett et al., 2016) or during spring and fall before and after leaf-out (Alexander, 2010). When fire does occur in deciduous forest, it usually burns at lower severity than spruce (Epting & Verbyla, 2005), which we did not consider in this study. Thus, differences in fire behavior and effects may reduce subsequent burned area regionally as deciduous forest increases in prevalence (Johnstone, Rupp, Olson, & Verbyla, 2011).

If fire activity does increase, our results indicate that deciduous forest expansion will likely continue, consistent with results from other modelling studies (Euskirchen et al., 2016; Foster et al., 2019; Johnstone et al., 2011; Mekonnen, Riley, Randerson, Grant, & Rogers, 2019). This could increase landscape heterogeneity, with upland positions becoming more deciduous dominated and lowland sites remaining black spruce forest, particularly where permafrost persists. Expanding deciduous forest will drive biophysical feedbacks to regional climate (Chapin et al., 2000). Latent heat fluxes and albedo are higher in deciduous forest than spruce forest, causing a negative forcing on regional temperature (Baldocchi, Kelliher, Black, & Jarvis, 2000; Randerson et al., 2006; Rogers, Randerson, & Bonan, 2013). While other studies have quantified these climate feedbacks (e.g. Mann et al., 2012), they have not resolved stand composition beyond deciduous and spruce plant functional types. We found that spruce trees were often widespread in the understorey of deciduous-dominated stands, and some deciduous stands (~15%) transitioned to mixed forest. By not accounting for mixed species composition, past modelling studies probably overestimated the net cooling effect of expanding deciduous forest. Further, the presence of spruce in deciduous stands may increase flammability, counteracting the negative feedback of deciduous forest on subsequent burned area.

4.3 | Gaining mechanistic insights across the North American boreal biome

Just as in interior Alaska, warming and drying have caused fire activity to increase across the North American boreal biome (Balshi et al., 2009; Kitzberger et al., 2017; Krawchuk, Cumming, & Flannigan, 2009; Wotton, Flannigan, & Marshall, 2017). Aspen and birch are also replacing black spruce after severe fires, and the fate of postfire deciduous forest will almost certainly be determined by similar abiotic and biotic drivers to those studied here. In other parts of the North American boreal biome, lodgepole pine and jack pine trees are now becoming dominant over black spruce after fire (Jean, Pinno, & Nielsen, 2020; Johnstone & Chapin, 2003; Searle & Chen, 2017; Whitman, Parisien, Thompson, & Flannigan, 2018; Whitman et al., 2019). We must evaluate whether and how feedbacks will form that determine the long-term fate of these emerging vegetation types. Factorial experiments with individual-based simulation models, such as the one conducted here, show promise for determining plausible outcomes across a wide range of potential future conditions in the North American boreal biome.

AUTHORS' CONTRIBUTIONS

W.D.H. and R.F. designed the study; W.D.H. parameterized the model and W.D.H. and R.F. conducted the simulation experiment; A.P.W. downscaled the climate projections; J.O. provided browsing data; W.D.H. wrote the paper and all co-authors contributed.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Cary Institute of Ecosystem Studies Digital Repository https://doi.org/10.25390/caryinstitute.12412910 (Hansen et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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