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Fuel Loads and Plant Traits as Community-Level Predictors of Emergent Properties of Vulnerability and Resilience to a Changing Fire Regime in Black Spruce Forests of Boreal Alaska

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Abstract Black spruce forest communities in boreal Alaska have undergone self-replacement succession following low-to-moderate severity fires for thousands of years. However, recent intensification of interior Alaska's fire regime, particularly deeper burning of the soil organic layer, is leading to shifts to deciduous-dominated successional pathways, resulting in many socioecological consequences. Both fuel load quantity and quality (or "burnability") influence black spruce plant communities' potential to burn. Even relatively low fuel loads, such as those seen in black spruce forest understory, can be highly influential drivers of fire behavior due to their high flammability. Additionally, black spruce community self-replacement following fire can be largely attributed to the suite of functional and life history traits possessed by the species dominating these communities. We used fuel load (quantity and quality) and amount of within-population plant trait variation (coefficient of variation; CV) as community-level emergent properties to investigate black spruce forest vulnerability and resilience to a changing fire regime across the landscape. Our burn severity potential index (BSPI), calculated from fuel load quantity and quality measurements, indicates that drier, higher elevation stands with thicker active layers were the most vulnerable to fire-induced vegetation shifts under a changing fire regime. Forest resilience to fire-induced vegetation shift, represented by higher CV, was negatively associated with BSPI and greatest in ecoregions dominated by lowland black spruce forests. Together, these analyses provide critical information for determining the likelihood of stand-replacing shifts in dominant vegetation following fire and for implementing appropriate ecosystem management practices.

Plain Language Summary As larger and more severe wildfires occur more often, it is becoming increasingly important to understand the ecological effects of fire and to predict how landscapes may change in the future. To investigate properties of black spruce forest vulnerability and resilience to fire-induced vegetation changes in interior Alaska, we quantified burn severity potential index and plant trait variation for 28 sites using site-level measurements of fuel load (organic biomass) and plant traits, respectively. We assessed which black spruce forests, in terms of their location across the landscape, are likely the most vulnerable versus the most resilient to severe burning. We found that two types of black spruce forest plant communities (dry nonacidic upland black spruce and dry acidic upland black spruce lichen woodlands) are most vulnerable to experiencing postfire vegetation shifts and, notably, ~27% of the landscape in interior Alaska is covered by these forest types. Although more research is necessary to verify that plant trait variation is a broadly useful measure of site resilience to fire, these findings will influence future management practices across interior Alaska's landscapes to minimize the loss of social and ecological values that black spruce forests provide.

Key Points:

- Burn severity potential index was significantly related to burn severity, validating it as an indicator of site vulnerability
- Dry nonacidic upland black spruce and dry acidic upland black spruce lichen woodlands are most vulnerable to fire-induced vegetation shifts
- Site-level coefficient of variation will require further validation as an indicator of forest resilience to severe fire

Supporting Information:

Supporting Information may be found in the online version of this article.

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1. Introduction

The boreal forest biome is regularly disturbed by wildfire, which contributes to the development of a spatiotemporal vegetation mosaic across the landscape and causes forest stands to vary in age, size, and species composition (Payette, 1992). In particular, landscapes in interior Alaska have been affected by regular intervals of low to moderate severity fire disturbances for the past 5,500 years (Lynch et al., 2003), allowing for self-replacement of the dominant black spruce forest type over time (Calef et al., 2008). However, in recent decades, climate change-related shifts in the wildfire regime are causing higher frequencies of large, high severity fires (Kasischke

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& Turetsky, 2006), often extending later into the season and causing deeper burning of the soil organic layer (SOL; Turetsky et al., 2011).

Alterations to the forest's historic wildfire regime, and in particular deeper burning of SOL, are expected to trigger above-average amounts of C losses and to induce shifts in postfire forest succession, leading to altered patterns and rates of C accumulation and storage (Coop et al., 2020; Mack et al., 2021). For example, more severe burning of organic soils and greater exposure of underlying mineral layers has been shown to lead to shifts from black spruce (*Picea mariana*) dominated to deciduous dominated stands due to the competitive advantage fast-growing deciduous tree species have over spruce seedlings on mineral soil beds (Johnstone & Chapin, 2006; Johnstone et al., 2010; Mann et al., 2012). Deciduous dominance following fire is common in early successional stages, eventually transitioning to conifer dominance later in succession as often seen along floodplain forests in interior Alaska (Van Cleve & Viereck, 1981). However, as severe wildfires become more frequent, they are likely to trigger pivotal changes in stand-level biophysical processes causing postfire deciduous dominance to be maintained long-term, possibly through following fire cycles (Kasischke & Johnstone, 2005). Shifts to deciduous dominated forests would change ecosystem services, decrease permafrost stability and ultimately affect postfire C and N storage with implications for the global C cycle (Chapin et al., 2006; Johnstone et al., 2010; Mack et al., 2021).

Black spruce forests inherently have greater potential to burn compared to other boreal forest types, due to notably greater fuel loads, particularly belowground, and presence of highly flammable plant species (Cronan et al., 2012; Viereck et al., 1986). As plant biomass or fuel load builds up during postfire succession, the potential for forest fuel loads to support fire also increases (Mack et al., 2008; Schimmel & Granström, 1997). Additionally, the quality or "burnability" of the fuel load will depend on the species composition of the forest plant community and on the abundance of highly flammable plant species. For example, the presence of *Cladonia*-type lichens, feather mosses, and evergreens shrubs has been shown to exert strong effects over fire dynamics (Plucinski & Anderson, 2008; Schwilk & Caprio, 2011; van Altena et al., 2012). Fuel load quantity and quality of black spruce forests vary widely along spatiotemporal gradients (Hollingsworth et al., 2006; Johnston et al., 2015; Mack et al., 2008; Schimmel & Granström, 1997; Thompson et al., 2017) and consequentially cause variability in black spruce forest burning potential over the landscape. However, few studies have linked both fuel load quantity and quality to black spruce plant community composition and environmental variables (but see Hollingsworth et al., 2008). Quantifying community-level variability in quantity and quality of fuel loads will contribute to better understand heterogeneity in black spruce forest burning potential and would help to predict landscape and community vulnerability of black spruce stands to a changing fire regime.

The persistence of black spruce forest communities through repeated fire disturbances can be largely attributed to the suite of functional traits of many species that help promote self-replacement successional pathways and resilience to fire (Bernhardt et al., 2011; Chapin III et al., 1993; Keeley et al., 2011; Nilsson & Wardle, 2005; Roberts, 2004). Black spruce community assemblages are particularly tolerant of low-to-moderate severity fire disturbances due to traits that allow them to be capable of either fire resistance (i.e., species that resist burning) or postfire regeneration (Hollingsworth et al., 2013; Pyne, 2010; Violle et al., 2007), although severe fire disturbances are threatening to alter these relationships. Recent evidence on the benefits of intraspecific trait variation to ecosystem functioning suggests that a greater amount of within-population trait variation increases the probability of a community persisting through variable environmental conditions or disturbance regimes (Cornelisson et al., 2003; Garnier et al., 2007; Helsen et al., 2017; Henn et al., 2018). For example, Anderegg et al. (2018) found that higher variation in hydraulic traits of dominant tree species was associated with slower ecosystem flux during drought or greater resilience to drought in temperate and boreal forests. Therefore, the resilience of black spruce forest communities to fluctuations in the fire regime will be somewhat influenced by the amount of trait variation in plant populations (Violle et al., 2007).

Emergent properties can be defined as whole-ecosystem properties that result from the relationships or interactions of a group of components to produce a measurable effect that cascades through the system (Mayr, 1982; Ponge, 2005). For example, structural characteristics of forests, like spacing and bole diameter of individual trees as well as the interconnectedness of tree crowns, produce whole-ecosystem properties, such as the ability to withstand detrimental crown collisions during windstorms and an albedo effect from the forest canopy, respectively (Ponge, 2005; Rudnicki et al., 2003). Likewise, highly competitive and light demanding plant species that compose forest edge communities together act as a filter against foreign species and impede the expansion of invasive, weedy plant species into the forest core community (Honnay et al., 2002). We suggest that site-level

fuel load characteristics (both quantity and quality) and plant traits together provide information about community-level emergent properties of vulnerability and resilience of black spruce forests to severe burning under a changing fire regime in boreal Alaska.

To investigate these emergent properties of black spruce forests, we first created a site-level burn severity potential index (BSPI) using information about both the quantity and quality of fuel loads and assessed how common environmental variables can be used to predict forest burning potential. Second, we measured the amount of site-level intraspecific trait variation (CV) in two ubiquitous boreal plant species and measured correlations with environmental variables. Together, these analyses provide a better understanding about locations across the black spruce landscape that are most susceptible to fire-induced ecosystem state shifts versus those that may withstand severe burning under a changing fire regime, a critical component in determining the likelihood of stand-replacing shifts in dominant vegetation postfire and thus for the implementation of ecosystem management strategies.

2. Materials and Methods

2.1. Study Area

Our study area spanned three ecoregions, the Ray Mountains (~51,000 km^2), the Yukon-Tanana Uplands (~102,000 km^2), and the Tanana-Kuskokwim Lowlands (~52,000 km^2) that together stretch across interior Alaska from the Alaska Range south to the Brooks Range north (Figure 1). Interior Alaska is characterized by swampy lowlands, gently sloping uplands, rocky tundra, and braided rivers and floodplains. The region is underlain by discontinuous permafrost, which typically occurs on north-facing slopes and in low-lying areas. Interior Alaska has a continental climate and extreme temperatures; average annual temperature in Fairbanks is −2.5°C with mean temperatures in January and July of −23.1°C and 22.8°C, respectively. The region receives an average annual precipitation of 286 mm with approximately 35% falling as snow (Hinzman et al., 2005). Soils show poor morphological development and are typically composed of Inceptisols, Entisols, Histosols, or Gelisols (Ahrens et al., 2004). Summer wildfires are prevalent, typically occurring from May through August, but may also extend from April and into September depending on seasonal precipitation and humidity (de Volder, 1999; Viereck, 1973).

2.2. Field Sampling

During the summer of 2019, we sampled 28 black spruce-dominated sites that were previously established by the Bonanza Creek Long Term Ecological Research (BNZ-LTER) program (Figure 1). These sites were chosen because they span a gradient of stand age (time since fire) and site moisture, which have been identified as two major influences on fuel loads (Thompson et al., 2017) and were easily accessible. Upon establishment of these sites in 2011, the BNZ-LTER measured environmental characteristics (stand age, moisture, elevation, slope, aspect, active layer depth, topographic position, soil pH, and surficial geology) and annually measure active layer depth at each site. The BNZ-LTER conducts regular sampling of understory vegetation and tree species DBH and density within each plot and regularly inventories tree seedlings and tall deciduous shrubs on two 2-m-wide transects along the 50 and 60 m edges of the sites. All sampling methods and data sets can be found at http://www.lter.uaf.edu/data/data-catalog/. The sites included young (0–15 years since fire), intermediate (40–60 years), and mature (>80 years) stands and ranged in site moisture (Table S1 in Supporting Information S1). Site moisture classes from driest to wettest include xeric, subxeric, subxeric/mesic, mesic, mesic/subhygric, and subhygric. Study sites ranged in active layer depth (depth to permafrost) from 25 to 92 cm and in elevation from 128 to 770 m above sea level (Table S1 in Supporting Information S1). Burn severity from last fire of young sites ranged from low to high (based on metrics of above and belowground residual fuels). Mature and intermediate sites were the representatives of black spruce community subtypes common to the interior Alaskan region (Hollingsworth et al., 2006). Prior to the last fire, all sites were forests dominated by black spruce.

2.3. Quantifying Fuel Loads

We sampled understory plant fuels (consisting of live biomass and litter), organic soil biomass, and dead downed wood at each site along two 30 m transects. The two transects ran approximately perpendicular to each other in order to sample along two directional orientations and to reduce directional bias, although directional

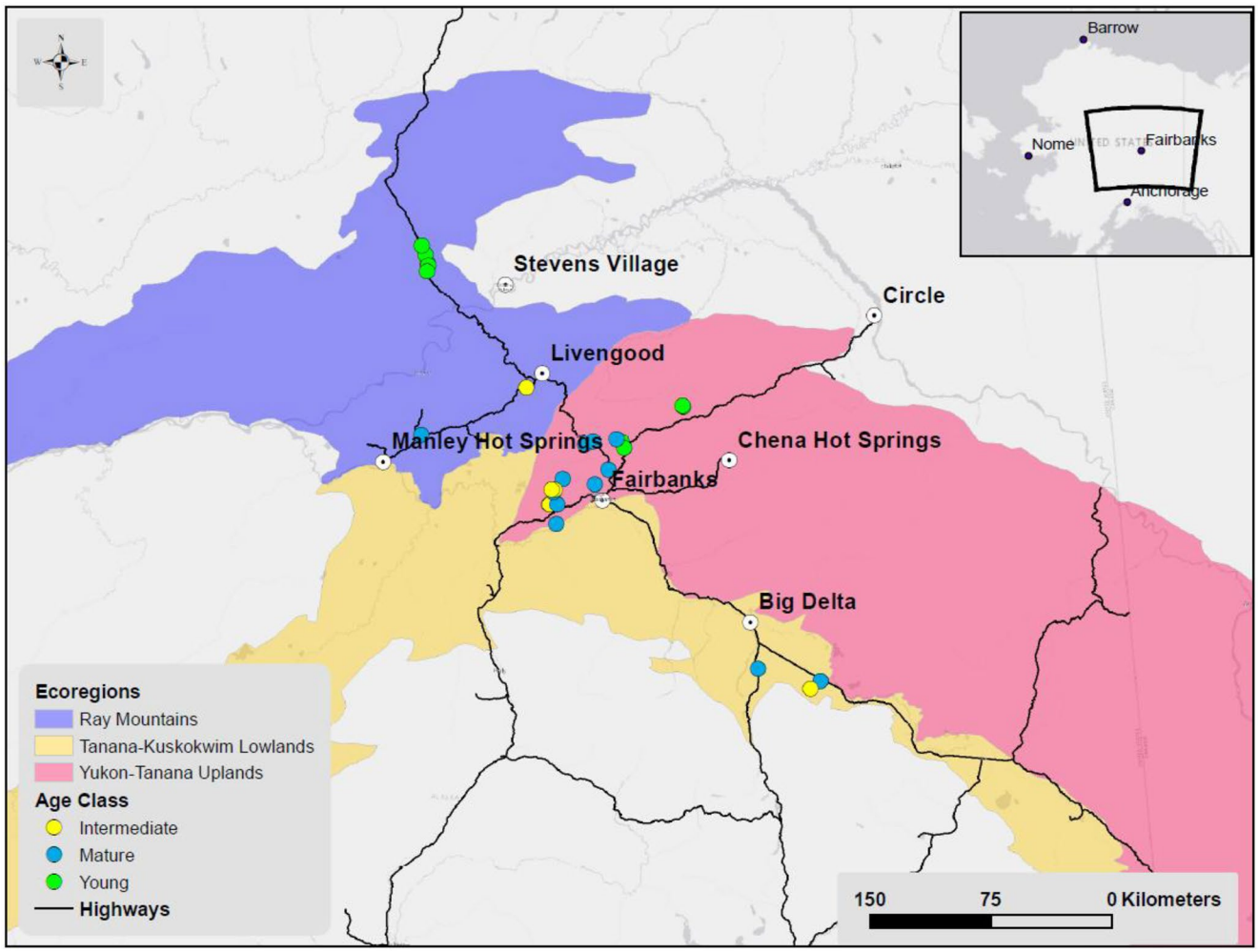

Figure 1. Map of the study region within interior Alaska, USA, with ecoregions indicated in shaded areas (Ray Mountains = blue, Tanana-Kuskokwim Lowlands = yellow, Yukon-Tanana Uplands = red). Circles indicate the locations of 28 young (0–15 years postfire; green circles), intermediate (40–60 years postfire; yellow), and mature (>80 years postfire; blue) aged black spruce-dominated study sites. Major highways are denoted by black lines. Map courtesy of Jamie Hollingsworth, site manager of the Bonanza Creek Long-Term Ecological Research program.

heterogeneity in plant fuels was not evident at any of the sites. We quantified the following fuel load classes: (a) understory plant fuels (vascular and nonvascular vegetation below 1 m in height), (b) organic soil biomass and dead downed wood, (c) tall shrubs (above 1 m in height), tree seedlings (less than 1 m in height and tree saplings greater than 1 m in height and less than 2 inches in diameter at breast height), and (d) trees (greater than or equal to 2 inches diameter at breast height).

Understory plants and organic soils were measured and collected by destructively sampling three 20 × 20 cm plots at 10 m intervals along each transect on alternating sides, yielding six plots per site. The maximum height of each vascular plant type was measured and then all vascular plant biomass was clipped and bagged. We measured nonvascular understory plant and organic soil biomass by extracting a volume (or cube) of biomass that extended from the moss/lichen layer down to the mineral soil layer, encompassing the entire organic soil layer. We measured the height of moss/lichen, fibric, mesic, and humic (soil horizon below mesic) layers, as well as the depth to the mineral soil layer or permafrost (if mineral soil could not be reached). Subsamples of the moss/lichen layer were collected together and subsamples of fibric and mesic layers were collected separately from the cube of biomass and dimensions of subsamples (length, width, and height) were recorded. All samples were brought to the lab and stored at 4°C.

Understory plant samples, both vascular and nonvascular, were sorted by plant functional types, dried at 60°C and then weighed. The mass of vascular understory plants was divided by the area of the sampling plot (0.04 m^2) to determine the fuel load ($kg \cdot m^{-2}$). Nonvascular understory and organic soil sample dry weights were divided by sample volume to determine bulk density of the sample ($kg \cdot m^{-3}$), then bulk density was multiplied by the overall height of the fuel layer, measured in the field, to determine fuel load. Site-level understory and organic soil fuel loads were then determined by taking the mean fuel load of the six plots for each plant or soil type.

Dead downed woody debris was inventoried along each transect using the line intersect method (van Wagner, 1968). The diameters of dead downed wood <7.0 cm were sorted into appropriate dead downed wood size classes (van Wagner, 1982) and then quantified by using the counts of intersecting pieces in each class and the equation and multiplier values found in Nalder et al. (1997). Fuel load for dead downed wood ≥7.0 cm in diameter was quantified using the equation Fuel Load = $\sum d^2$ G/8L (where d is wood diameter, G is specific gravity, and L is the length of the transect (Alexander et al., 2004), along with the value for specific gravity, 0.427 g/cm^3 (Johnston et al., 2015; Ter-mikaelian et al., 2008). Site-level dead downed wood fuel load was taken as the average fuel load from the two transects.

To quantify tall deciduous shrub (>1 m tall), tree seedling, and tree fuel loads, we used inventory data collected by the BNZ-LTER (https://www.lter.uaf.edu/data/data-detail/id/530, https://www.lter.uaf.edu/data/data-detail/id/320). For tall shrubs and tree seedlings, we used median values (cm) of basal diameter size classes (size classes 1–14 correspond to basal dimeters 0–0.99 cm, 1–1.99 cm, 2–2.99 cm, etc. and correspond to median values 0.5 cm, 1.5 cm, 2.5 cm, etc., respectively) to estimate biomass. Allometric equations for tall shrubs (Berner et al., 2015) and tree seedlings (Alexander et al., 2012) were used and multiplied by the count number of individuals/ramets of that species in each basal diameter size class and then summed. Fuel load was determined by dividing the summed biomass by sampling area and then site-level fuel load was determined as the mean fuel load of the two sampling areas. For trees, we used diameter at breast height (DBH; diameter [cm] at 1.37 m) to estimate total aboveground biomass using allometric equations developed for white spruce, black spruce, and Alaska paper birch (Yarie et al., 2007), for quaking aspen (Alexander et al., 2012), and for larch (Carpenter, 1983). Biomass was summed for trees in each plot and fuel load was determined by dividing the summed tree biomass by plot area, then site-level fuel load was determined as the average of all plots.

Total site-level aboveground fuel loads were calculated as:

$\sum$ site-level understory fuel load + site-level dead downed wood fuel load + site-level tree seedling/sapling fuel load + site-level tall deciduous shrub fuel load + site-level tree fuel load

Total site-level belowground fuel loads were calculated as:

$\sum$ site-level fibric fuel load + site-level mesic fuel load

2.4. Fuel Load Quality

Specific leaf area (SLA) is a trait known to be highly associated with plant flammability across many plant functional types and ecosystems (Murray et al., 2013; Schwilk & Caprio, 2011; van Altena et al., 2012). Therefore, fuel load quality was determined by obtaining mean SLA values for each aboveground fuel type (excluding dead downed wood) using measurements for 45 different plant species found in our sites from the literature (Aerts et al., 1992; Bond-Lamberty & Gower, 2007; Michel et al., 2012; Sylvester & Wein, 1981; van Altena et al., 2012). Each SLA value was converted to the units $m^2 \cdot kg^{-1}$ and grouped into one of the understory or tree fuel types based on the species' plant type and mean SLA values were then determined for each plant functional type (Figure S1 in Supporting Information S1).

2.5. Trait Selection and Sample Collection

We measured plant functional traits for *Hylocomium splendens* (splendid feather moss) and *Vaccinium uliginosum* (bog blueberry), the most ubiquitous nonvascular and vascular understory plant species across our study sites. Plant traits measured can be linked to the individual species' response to fire. These traits fall along "fire adaptability" and "fire resistance" gradients (Figure 2). For *H. splendens* samples, we measured traits related to size: vertical length, horizontal width, surface area, and moisture content at maximum capacity, all known to

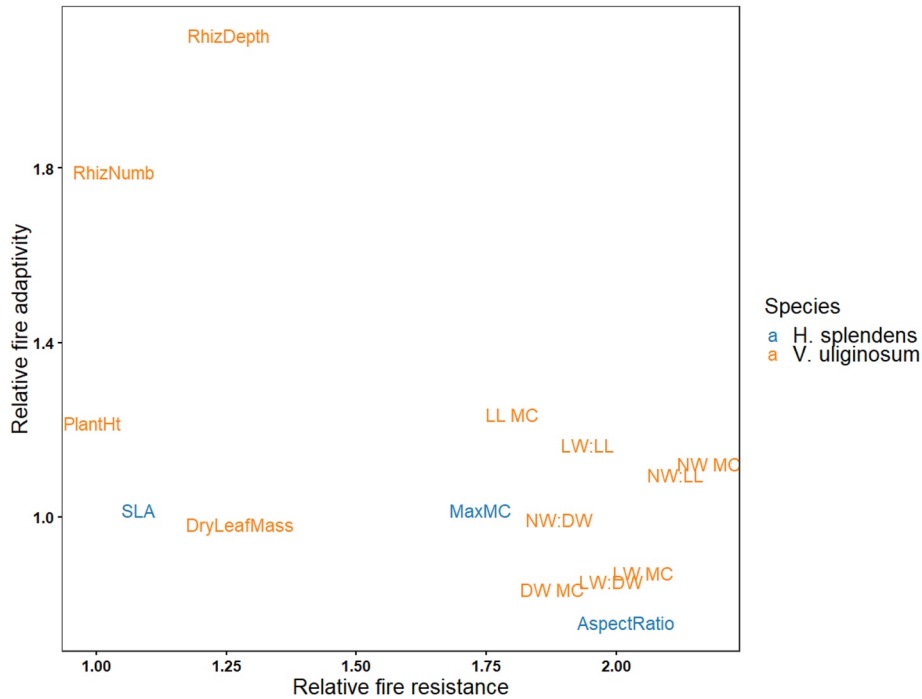

Figure 2. Plant growth traits of *H. splendens* (SLA = specific leaf area; MaxMC = moisture content % at maximum capacity; AspectRatio = aspect ratio or width to length ratio) in blue, and *V. uliginosum* (RhizDepth = rhizome depth; RhizNumb = number of rhizomes; PlantHt = plant height; DryLeafMass = dry leaf mass; LW MC = live wood moisture content %; NW MC = new wood moisture content %; DW MC = dead wood moisture content %; LL MC = leaf moisture content %; LW:DW = live wood to dead wood ratio; LW:LL = live wood to leaf ratio; NW:DW = new wood to dead wood ratio; NW:LL = new wood to leaf ratio), in orange, with respect to their relative fire resistance (flammability) and fire adaptivity (postfire regeneration ability). Based on reports in the literature of these species' traits responses to fire, traits were categorized as either 1.00 or 2.00 on fire resistance and fire adaptivity gradients, which are arbitrary values meant to qualitatively depict a trait's relatively low or high fire resistance and fire adaptivity. When plotted, traits were positioned with a slight "jitter" so that observations did not overlap for visual clarity.

be involved in the regulation of water retention in many nonvascular species (Bond-Lamberty & Gower, 2007; Busby et al., 1978; Michel et al., 2012). Greater depth of rhizomatous roots as well as greater number of rhizomes of *V. uliginosum* result in greater postfire regeneration success; thus, we measured these two traits because of their relevance to the fire-adaptivity of *V. uliginosum* (Figure 2; Lutz, 1956; Maillette, 1988; Schimmel & Granstrom, 1996; Viereck, 1983). We also measured plant height, dry leaf mass, moisture content % of plant tissues (live wood, new wood [current year's growth], dead wood and leaf) and dry mass ratios of high moisture-retaining to low moisture-retaining tissues (live wood to dead wood, live wood to leaf, new wood to dead wood, and new wood to leaf) because of their relevance to fire resistance of *V. uliginosum* (Figure 2; Granstrom & Schimmel, 1993; Norum & Miller, 1984; Papio & Trabaud, 1991; Pausas et al., 2012).

Samples of *H. splendens* and *V. uliginosum* were collected at 22 and 25 sites, respectively, of the 28 sites initially sampled for fuel load (Table S1 in the Supporting Information S1). By destructively sampling along one transect at each site, we collected five cushions of *H. splendens* and five individuals of *V. uliginosum*. Transects extended at least 20 m in length or more, which allowed for samples to be collected every 5 m or more to prevent the sampling of subsequent clonal individuals along the transect, as the literature has reported *V. uliginosum* clones covering areas of 5 m^2 (Jacquemart, 1996).

H. splendens samples were hand-collected and included both the live and dead moss cushion. *V. uliginosum* samples were cut at the base of the stem and included the entire aboveground portion of the individual. Prior to collection of *V. uliginosum* samples, we measured maximum aboveground plant height, the number of belowground rhizomes and the depth to the deepest rhizome below the surface of the ground for each individual sample. All samples of *H. splendens* and *V. uliginosum* were brought to the lab and stored at 4°C.

2.6. Measuring Plant Functional Traits

For each *H. splendens* moss cushion sample, up to six intact individuals from a single cushion sample were selected; all living and dead portions of the individual attached to the main stem were considered as part of the intact individual. We did not use individuals that appeared damaged or to be missing portions of its stem, branches, etc. Moss individuals were washed thoroughly with deionized water to remove any foreign, non-moss particles, such as soil, other plants, and invertebrates. Moss individuals were allowed to fully hydrate by submerging them in deionized water overnight (at least 12 hr) to achieve consistent water status for all samples.

Following rehydration, moss individuals were separated into live and dead tissue portions using established criteria (Bond-Lamberty & Gower, 2007; Williams & Flanagan, 1998). The wet weight of individuals was recorded first by lightly shaking off excess water and then measuring the weight of live and dead parts, separately. Next, vertical length (*L*) was measured for live and dead parts from the tip of the individual to the bottom of its main stem using digital calipers. The horizontal width (*W*) was measured for live and dead parts at the widest point on the individual using digital calipers. Lastly, surface area was measured for live and dead parts (Bond-Lamberty & Gower, 2007) with an Epson Perfection V800 Photo flatbed scanner. Scanned images were digitized (400 dpi) to determine leaf area (cm^2) using the leaf area scanner function in the Easy Leaf Area software package. Projected leaf area (PLA) was calculated as the final image pixel count divided by the scan resolution. PLA is assumed to be equal to hemi-surface leaf area (HSLA) for flat-leaved moss species, such as *H. splendens* (Bond-Lamberty & Gower, 2007). Lastly, live and dead moss parts were placed in a drying oven at 60°C for 72 hr or until a constant mass was reached and weighed immediately upon removal from the oven to obtain dry mass (g). Finally, we calculated specific surface leaf area (SLA) by dividing HSLA (cm^2) by dry leaf mass (g) and aspect ratio (W/L) for each live and dead moss sample.

For each *V. uliginosum* individual, aboveground biomass was separated into live wood, dead wood, new growth (i.e., current annual wood growth), and leaves (including live leaves and dead leaves that were attached to the plant upon sample collection). We measured the wet weight of these four tissue types, then placed tissues into a drying oven at 60°C for 72 hr or until a constant mass was reached, and then measured the dry weight of the materials. Using these measurements, we quantified the moisture content ((wet weight – dry weight)/dry weight) × 100% of each plant material as well as the dry mass ratios of live wood to dead wood, live wood to leaves, new wood to dead wood, and new wood to leaves.

2.7. Data Analysis

All statistical analyses were performed in R, version 3.5.2 (R Core Team, 2014). We condensed site moisture into three classes (dry = xeric and subxeric, moderate = subxeric/mesic and mesic, and wet = mesic/subhygric and subhygric) for the following analyses.

2.7.1. Describing Fuel Load Quantity

To investigate the differences in fuel load quantity among fuel load classes, we performed an analysis of variance (ANOVA) on plot-level fuel load measurements among tree canopy, understory (both vascular and nonvascular) and organic soil fuel load classes. All fuel load data were log + 1 transformed to achieve normality of residuals.

2.7.2. Creating a Burn Severity Potential Index

We calculated a site-level BSPI to represent both fuel load quantity (biomass) and quality (SLA) of a given site as

$$\mathrm{BSPI} = \left(\sum \mathrm{SLAj} * \mathrm{AFLj}\right) \div \mathrm{OSFL}$$

where SLA = Mean SLA of aboveground fuel types (j), AFL = Site-level fuel load of aboveground fuel types (j), and OSFL = Total site-level organic soil fuel load. The burn severity of a site is largely dependent on the extent of organic soil fuel loads, where greater prefire SOL is associated with greater postfire SOL and lower burn severity (Johnstone et al., 2020). Greater quantity and flammability of aboveground fuels and most importantly, lower quantities of organic soil fuel loads will therefore increase the likelihood of a fire that will burn down to mineral soil, resulting in a severe burn. Thus, we divided the numerator, a measure of aboveground fuel load quantity and quality, by total organic soil fuel load within a site because these are two opposing factors that inherently affect a site's burning potential (E. Miller, personal communication, 11 December 2020). Understandably, other external

factors, such as fire weather, fuel moisture conditions, and so on, play an important role in dictating fire patterns; however, BSPI is intended to illustrate the inherent potential of a site to burn severely, given its fuel load quantity and quality.

2.7.3. Verifying BSPI

Prior to investigating the relationship of BSPI with environmental variables, we verified that BSPI aligned with observed postfire burn severity and served as a reliable indicator of burn severity potential. We calculated BSPI for 15 recently burned black spruce sites (verification sites distinct from our original study sites) for which prefire fuel load was modeled and postfire burn severity was known (Bernhardt et al., 2011; Butler et al., 2013). From here on, BSPI values calculated for these verification sites will be denoted by subscript "m" (i.e., $BSPI_m$) to distinguish that these values are based on modeled prefire fuel load. Verification sites were located within one of our three ecoregions and were between 66 and 176 years old when they burned.

To predict prefire fuel loads in our 15 verification sites, we developed linear mixed-effects (LMER) models for each fuel load class using the *lme4* package (Bates et al., 2015) with measured fuel load quantities from our study sites. We first tested between two random effects structures of site and plot nested within site using Akaike's Information Criterion (AIC). For each model, site alone was used as the random effect structure because it resulted in the best AIC. With separate models for each fuel load class, we then tested whether six fixed environmental factors that were not significantly correlated to each other (Pearson's *r*; stand age, site moisture, average active layer depth, elevation, topographic position, and surficial geology) were important in predicting black spruce forest fuel load quantities. Active layer depth, elevation, slope, and aspect were scaled to account for differences in units and magnitude of values. For each fuel load class, we tested between models that included all combinations of the fixed variables as well as biologically relevant interactions between the fixed variables. Based on prior knowledge of the system, we determined biologically relevant fixed variable interactions to be stand age*active layer depth and elevation*moisture. Fixed effect structures were then selected based on AIC and the most parsimonious parameter number (K value) for each model. Plant functional type was included in final models as a fixed variable so that fuel load could be calculated for individual fuel types.

Prefire fuel loads for each of the 15 verification sites were modeled using the LMER models we developed and known prefire environmental data for the sites (i.e., stand age, site moisture, elevation, and average active layer; Table S4 in Supporting Information S1). Uncertainty associated with the modeled prefire fuel loads was estimated by statistically propagating the standard error of each parameter in the LMER models. The modeled fuel load data were then used to calculate $BSPI_m$ and standard errors associated with the modeled fuel load data were further propagated through the calculation of $BSPI_m$ (Table S4 in Supporting Information S1). Lastly, for each verification site, $BSPI_m$ was regressed and plotted with measured burn severity of that site to determine if a significant relationship existed between prefire $BSPI_m$ and postfire burn severity. The regression analysis was conducted using the *metafor* package in R, allowing for the propagation of $BSPI_m$'s known uncertainty into the calculation of model parameters and associated standard error.

2.7.4. Investigating Environmental Predictors of BSPI

We investigated the relationship of BSPI with environmental variables first with regression analysis (average active layer, elevation, site moisture, soil pH, stand age, and topographic position) and then regression tree analysis to provide a tree-like classification and associated dichotomous key to predict unknown BSPI as a function of five environmental variables (stand age, site moisture, elevation, soil pH, and surficial geology (categories 1–6 correspond to basin colluvium and organic deposits, glacial tills, glaciofluvial deposits, loess, residuum, and stabilized alluvium, respectively)). We chose these variables because they represent variables that are tightly linked to plant community composition and ecosystem function (Hollingsworth et al., 2006, 2008). A Pearson's r correlation matrix indicated that site moisture, topographic position, and average active layer thickness were highly correlated; thus, we only included site moisture in the analysis. The five variables ultimately used in the analysis all had $r < 0.39$. We included surficial geology, a categorical variable, in the analysis as regression trees uniquely allow for both categorical and continuous variables together.

A regression tree analysis is a machine learning technique that builds a decision tree by iteratively partitioning data into smaller branches or nodes that explain the greatest amount of deviance in the data based on explanatory variables (Breiman et al., 1984). The model algorithm first considers all observations that are present in a parent node and examines splits in the data by each independent variable and then ultimately considers the split that

maximizes the deviance between a parent node and daughter node (Poor & Ullman, 2010). The model continues this process until a terminal node reaches its predetermined minimum node size or until the data can no longer be split. We selected the number of splits in the model that minimized the cross-validation error and we further pruned the model using a complexity parameter (the amount by which each split must improve model fit) of 0.08 and a minimum node size of 3.

One outlier site, MDI4, a highly dense mixed tree site with low SOL, was removed when conducting these analyses because its BSPI value was approximately five times greater in magnitude than other BSPI values on average. Regression tree analyses are not sensitive to outliers, but nevertheless this data point was removed in order to maintain the same data set between the regressions and regression tree analyses.

2.7.5. Investigating Predictors of Intraspecific Plant Trait Variability

We conducted ANOVA to determine if *H. splendens* plant trait attributes differed between live and dead tissues. There was no significant difference in traits, except SLA (ANOVA $F = 5.38$, $p = 0.02$); therefore, we used the following six traits for *H. splendens*: moisture content (MC), length, width, aspect ratio, live SLA, and dead SLA. We used 12 *V. uliginosum* traits (rhizome depth, rhizome number, plant height, live wood moisture content [LW MC], dead wood moisture content [DW MC], new wood moisture content [NW MC], leaf moisture content [LL MC], dry leaf mass, live wood to dead wood ratio [LW:DW], live wood to leaf ratio [LW:LL], new wood to dead wood ratio [NW:DW], and new wood to leaf ratio [NW:LL]). We also conducted correlation matrices (Pearson's *r*) of each species' traits to determine if any traits were correlated with each other and if highly correlated variables could be represented by a single trait in future studies investigating this topic.

To determine the amount of intraspecific variation in traits of *H. splendens* and *V. uliginosum* within each site, we calculated a coefficient of variation (CV = Standard Deviation/Mean × 100) from biomass-weighted trait values. Mean biomass values for *H. splendens* and *V. uliginosum* for each site were derived from the mean fuel loads for feather moss and deciduous shrub plant types, respectively, which were then multiplied by trait values to determine biomass-weighted traits. Trait CVs were summed to determine an overall CV for each species ($\sum$ CV) and then an integrated or site-level CV was calculated by summing $\sum$ CV of both species for all sites where both species were measured ($n = 21$; Table S1 in Supporting Information S1). $\sum$ CV of each species and site-level CV was then regressed with BSPI (three outlier sites were removed from these analyses), as well as with environmental variables (stand age, site moisture, soil pH, elevations, average active layer, and topographic position), and was analyzed using ANOVA with ecoregion, a categorical variable. We then modeled site-level CV using regression tree analysis as a function of five environmental variables: stand age, site moisture, soil pH, elevation, and surficial geology (the same five variables used in the regression tree analysis of BSPI). To prevent overfitting the data, we selected a complexity parameter of 0.1 and a minimum node size of 2 or approximately 10% of our total sample size (Buja et al., 2001; Poor & Ullman, 2010).

3. Results

3.1. Variation in Fuel Load Quantity and Quality

We found that organic soil fuel loads (8.07 ± 0.81 kg·m^{-2}) were significantly greater than both tree canopy (1.95 ± 0.51 kg·m^{-2}) and understory (1.19 ± 0.07 kg·m^{-2}) fuel loads (ANOVA $F_{2,81} = 67.07$, $p < 0.001$). Organic soil fuel loads ranged from 2.93 ± 1.87 to 20.22 ± 7.31 kg·m^{-2} across all sites and constituted 36% to 97% of the total fuel load at sites (Figure S1 and Table S2 in Supporting Information S1). Tree fuel loads comprised 0%–60% of the total fuel load across sites and ranged from 0 to 11.83 ± 2.51 kg·m^{-2} (Figure S1 and Table S2 in Supporting Information S1). Tree fuels constituted the greatest portion of the aboveground fuel load in intermediate and mature sites but contributed minimally or not at all to the aboveground fuel load in young sites, which was expected because young stands would not have had enough time for substantial tree growth (Figure S1 and Table S2 in Supporting Information S1). Understory fuel loads ranged from 0.42 ± 0.28 to 1.90 ± 0.26 kg·m^{-2} across all sites and constituted the lowest portion of total fuel loads at sites, making up 3%–26% of the total fuel load. They were significantly lower than organic soil fuel loads (ANOVA $F_{1,54} = 231.9$, $p < 0.001$), but were not significantly different from tree canopy fuel loads (ANOVA $F_{1,52} = 0.081$, $p > 0.05$). On average, nonvascular understory fuel loads constituted 4 ± 0.01% of the total and vascular understory fuel loads constituted 8 ± 0.01% of the total.

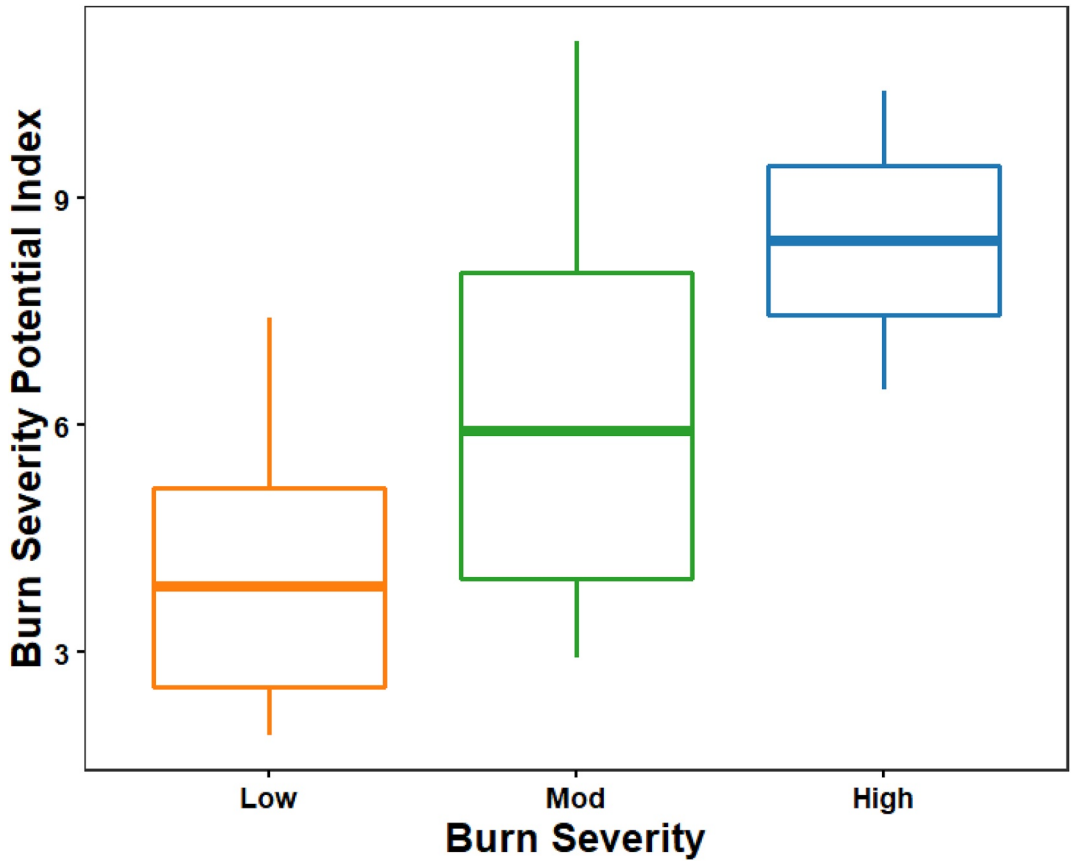

Figure 3. Boxplot of site burn severity potential index ($BSPI_m$) with burn severity for black spruce sites described by Bernhardt et al. (2011) and Butler et al. (2013) ($n = 15$). Site burn severity encompassed low ($n = 6$), moderate ($n = 7$), and high ($n = 2$) severities. Plot whiskers represent 95% confidence intervals. Regression of $BSPI_m$ with burn severity classes results in a significant relationship ($p < 0.001$; Table S5 in Supporting Information S1).

3.2. Verifying BSPI

For all LMER models conducted on tree canopy, vascular understory, nonvascular understory, and organic soil fuel loads, marginal R^2 was less than conditional R^2, indicating that the inclusion of site as a random effect provided some explanatory power in the variation of fuel loads (for tree canopy, $R^2_m = 0.29$ and $R^2_c = 0.49$; for nonvascular understory, $R^2_m = 0.02$ and $R^2_c = 0.03$; for vascular understory, $R^2_m = 0.006$ and $R^2_c = 0.009$; for organic soil, $R^2_m = 0.07$ and $R^2_c = 0.17$). Stand age was an important factor explaining each of tree canopy, vascular understory, nonvascular understory, and organic soil fuel loads, whereas elevation was only an important factor in explaining the latter (Table S3 in Supporting Information S1). Similarly, moisture and average active layer were important factors in explaining both nonvascular understory and organic soil fuel loads, whereas tree canopy was explained by moisture but not by average active layer and vascular fuel loads were explained by average active layer but not moisture (Table S3 in Supporting Information S1).

Prefire site $BSPI_m$ was related to burn severity ($p < 0.001$; Table S5 in Supporting Information S1). Sites with greater prefire $BSPI_m$ burned at a higher severity during fire (Figure 3), thus supporting the reliability of BSPI as an indicator of a site's burn severity potential.

3.3. Integrating Fuel Load Quantity and Quality Into Burn Severity Potential Across the Landscape

We were interested in how BSPI, a variable that integrated both quantity and quality of fuel loads, correlated with easy-to-measure environmental variables. BSPI values for young, intermediate, and mature aged sites ranged from 0.5 to 4.9, 3.2 to 11.1, and 1.4 to 12.7, respectively (Figure 4). BSPI increased with active layer depth ($p < 0.05$, $r^2 = 0.20$, d.f. = 25), and decreased with site moisture ($p < 0.001$, $r^2 = 0.38$, d.f. = 25) and topographic

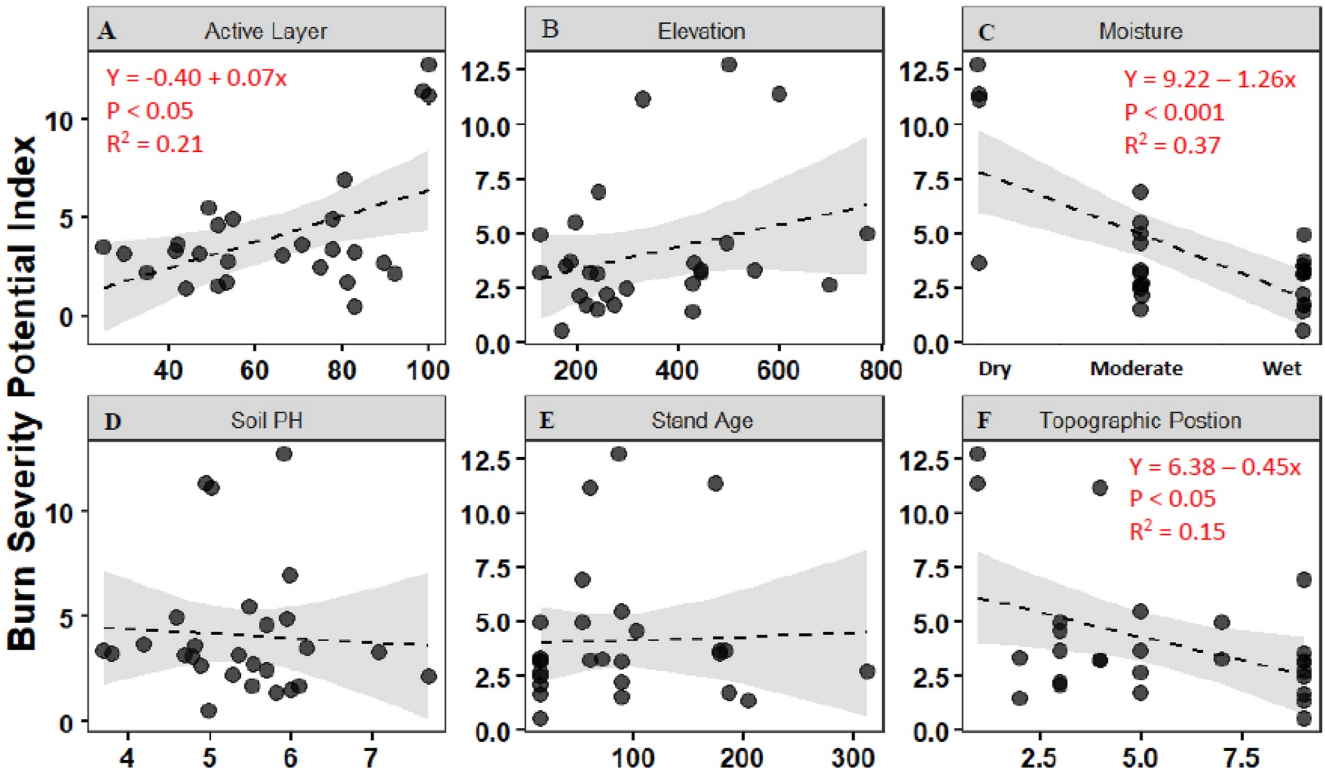

Figure 4. Plots of Burn severity potential index (BSPI) with six different environmental variables. Topographic positions 1 through 9 correspond to summit, shoulder, side slope, toe slope, valley bottom, drainage channel, depression, lake/pond, and lowland, respectively. Dotted lines represent the regression of BSPI with each environmental variable. Gray areas surrounding regression lines are 95% confidence intervals. Significant relationships are indicated with linear equation, *p*-value, and R^2 in red.

position ($p < 0.05$, $r^2 = 0.15$, d.f. = 25; Figure 4), suggesting that drier, topographically higher sites with thicker active layers have the greatest potential to burn severely. In contrast, BSPI was not correlated with elevation, soil pH, or stand age (Figure 4).

Site moisture was the most important variable in explaining BSPI (relative importance = 59), followed by surficial geology, soil pH, stand age, and elevation (relative importance = 18, 13, 8, and 2, respectively; Figure 5).

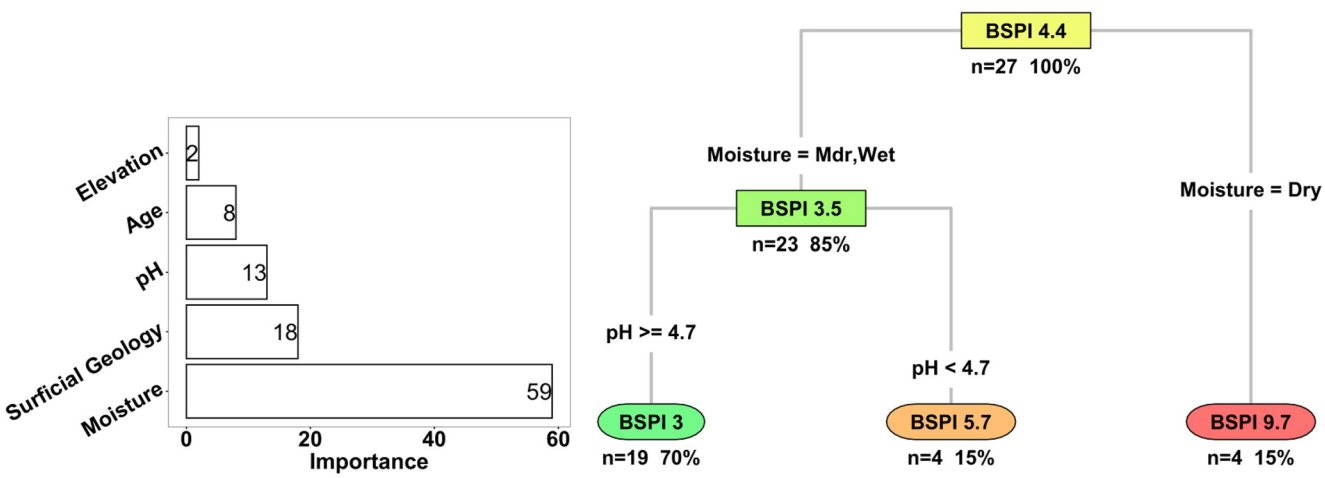

Figure 5. Relative importance of variables and regression tree model from a regression tree analysis predicting site burn severity potential index (BSPI) with five environmental variables. Mean BSPI values are presented in the tree nodes. Sample size (n) and percentage of sites belonging to each node are presented below each node. Variables used in the construction of the final, pruned tree model include soil pH and moisture.

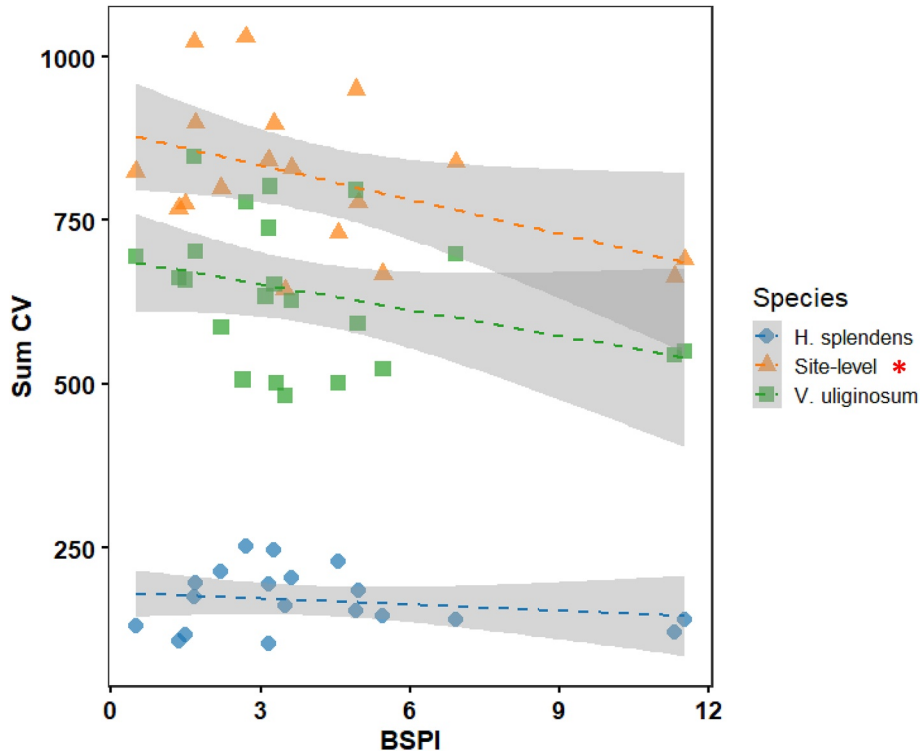

Figure 6. Plot of ∑ CV (amount of plant trait variation) for *H. splendens* (blue) and *V. uliginosum* (green) and site-level CV (orange) with burn severity potential index (BSPI). Dotted lines represent linear regressions of ∑ CVs and site-level CV with BSPI. Gray areas surrounding each regression line represent 95% confidence intervals. Significant relationships are indicated with a red asterisk.

The variables used in the final pruned regression tree included site moisture and soil pH (cross-validation error = 0.86). The primary split in the model was based on moisture with the greatest BSPI (BSPI = 9.7) occurring in dry sites, whereas sites with moderate or wet site moisture were further split based on soil pH (Figure 5). The lowest BSPI (BSPI = 3.0) occurred in sites with soil pH greater than or equal to 4.7 (Figure 5). The remaining terminal node with moderate BSPI (BSPI = 5.7) occurred in sites with soil pH less than 4.7 (Figure 5).

Our multiple regression and regression tree analyses indicated that three of our sites in particular (i.e., DDM2, LGI2, and UP4D) are representative of sites with high burn severity potential indices. Based on the black spruce community descriptions reported by Hollingsworth et al. (2006), these sites are classified as dry nonacidic upland black spruce and dry acidic upland black spruce-lichen forest plant communities.

3.4. Identifying Sites With High Resilience to Severe Burning Based on Intraspecific Trait Variation

For *H. splendens*, MC was correlated with live SLA ($r = 0.85$) and dead SLA (0.75), indicating that MC can be used to represent all three traits. Length was mildly correlated with width (0.57) and aspect ratio (0.42). In contrast, few *V. uliginosum* plant traits were correlated with each other; LW moisture content was correlated with NG moisture content (0.52) and LW:DW was correlated with NG:DW (0.87), and thus live wood and new growth can likely be measured together as one trait in future studies investigating these plant traits.

There were no relationships between ∑ CV for *H. splendens* and *V. uliginosum* and BSPI; however, site-level CV was negatively related to BSPI ($p < 0.05$, $r^2 = 0.18$, d.f. = 16; Figure 6). Similarly, there were no relationships between ∑ CV for each species or site-level CV and environmental variables. One exception is that site-level CV varied with ecoregion ($F_{2,18} = 4.025$, $p < 0.05$; Figure 7); significantly lower site-level CV occurred in Yukon-Tanana Uplands, where upland black spruce forest types are prevalent, compared to the Ray Mountains and Tanana-Kuskokwim Lowlands, where a higher proportion of flat, lowland black spruce forests are present.

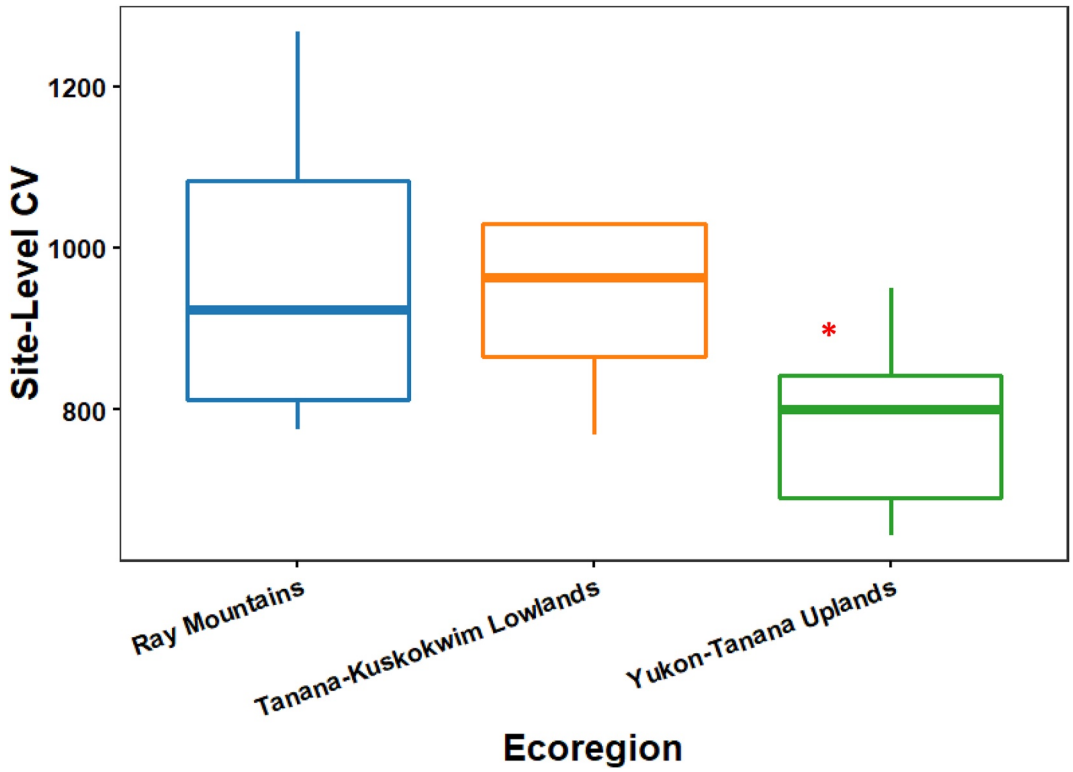

Figure 7. Boxplot of site-level coefficient of variation (CV) with ecoregion for black spruce sites where both *H. splendens* and *V. uliginosum* traits were measured ($n = 21$). Plot whiskers represent 95% confidence intervals. Analysis of variance of site-level CV with ecoregion resulted in a significant relationship ($F_{2,18} = 4.025$, $p < 0.05$), which is indicated with a red asterisk.

Stand age (relative importance = 54) was the most important variable explaining site-level CV, followed by site moisture, soil pH, surficial geology, and elevation (relative importance = 17, 14, 8, and 7, respectively; Figure 8). Once pruned to prevent overfitting of data, the final model only included stand age as a variable (cross-validation error = 1.03). The primary split in the model indicated that plant populations in sites less than 88 years old contained the greatest site-level CV (CV = 943; Figure 8) and thus, the greatest amount of intraspecific trait

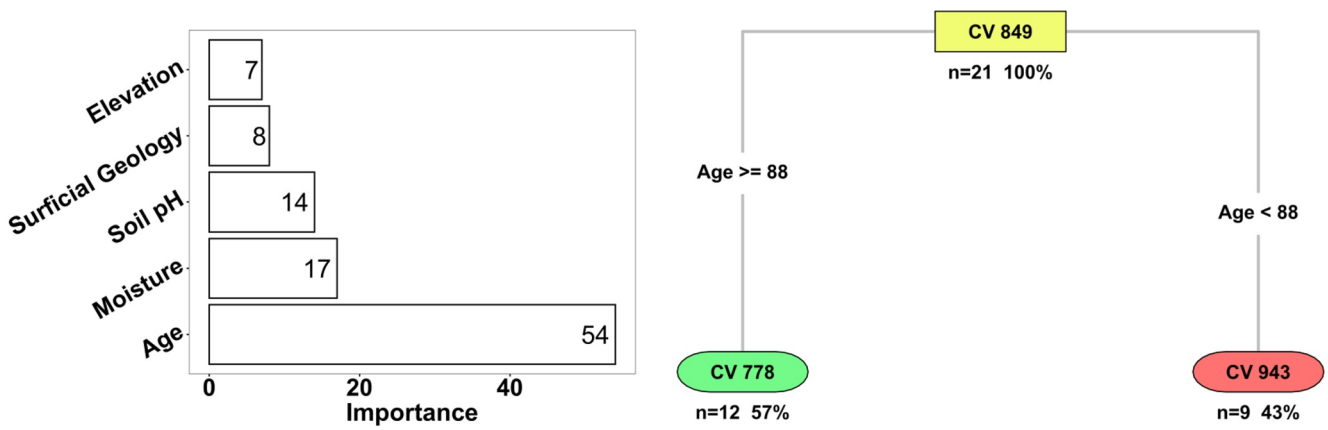

Figure 8. Relative importance of variables and regression tree model from a regression tree analysis predicting site-level coefficient of variation (CV) with five environmental variables. Mean site-level CV values are presented in the tree nodes. Sample size (n) and percentage of sites belonging to each node are presented below each node. Variables used in the construction of the final, pruned tree model include stand age. Surficial geology categories 1–6 correspond to basin colluvium and organic deposits, glacial tills, glaciofluvial deposits, loess, residuum, and stabilized alluvium, respectively.

variation, whereas sites more than or equal to 88 years old contained lower site-level CV (CV = 778; Figure 8) and thus the lowest amount of intraspecific trait variation.

4. Discussion

We used site-level measurements of fuel load and plant traits to characterize community-level properties of vulnerability and resilience of black spruce forests to severe burning and fire-induced vegetation shifts under a changing fire regime. Based on the relationship of $BSPI_m$ with burn severity, we demonstrated that BSPI is expected to be a reasonable indicator of black spruce forests' inherent potential to burn, although future testing of this relationship using actual pre- and postfire data is warranted. Our results show that two types of black spruce forests (dry, nonacidic upland black spruce and dry acidic upland black spruce-lichen) are the most vulnerable to deep, severe burning based on the quantity and quality of fuel load. We also found a negative correlation between BSPI and site-level plant trait CV, an indicator of resilience to severe burning.

4.1. Variability in Fuel Load Quantity and Quality Confers Heterogeneity in Site Burning Potential

Tree canopy, understory, and organic soil fuel loads, among other climatic and weather-related variables, play a role in influencing fire behavior and ultimately postfire ecosystem effects. While increases in aboveground fuel load quantity and flammable quality increase a site's capacity to support fire (Mack et al., 2008; Schimmel & Granström, 1997), increases in organic soil fuel loads in contrast can reduce a site's burning potential and the likelihood it will burn down to mineral soil (Johnstone et al., 2010). We found evidence of greater organic soil fuel loads in older, wetter black spruce stands in accordance with previous research (Harden et al., 2004; Kasischke & Johnstone, 2005; Miyanishi & Johnson, 2002; Turetsky et al., 2011). Due to the strong dependence of burn severity on the extent of organic soil fuel loads (Johnstone et al., 2020), the likelihood of severe burning in cool, wet sites, regardless of aboveground fuel load quantity and quality, will likely be low; whereas the burning potential of warm, dry sites where organic soil fuel loads are low will evidently be greater. Additionally, consistent with previous work (Barney & van Cleve, 1973; Mack et al., 2008), our results indicated that tree fuel loads constituted the greatest portion of the aboveground fuel load in intermediate and mature sites and decreased with high site moisture, suggesting greater burning potential in drier, mid-to late-successional stands. Moreover, similar to Mack et al. (2008), we found that understory plant fuel loads contributed the least to total fuel loads and did not vary significantly in quantity across our sites. Variability in the quality of understory fuel loads across sites, based on understory species composition, has been previously correlated with stand age and site moisture-related variables (Hollingsworth et al., 2006; Schimmel & Granström, 1997). Despite consistently small quantities of understory fuel load among sites, variability in understory fuel load quality and in particular the presence of highly flammable understory plant types contribute to large differences in site burning potential and overall fire dynamics among sites (van Altena et al., 2012). Essentially, total fuel load quantity may be similar among black spruce forest sites; however, burning potential will vary substantially based on the quality of fuel load, and especially, the relative proportion of organic soil fuel loads.

4.2. Vulnerability of Black Spruce Forests to Severe Burning From a Changing Fire Regime

Our results demonstrate that severe burning of black spruce forests and their vulnerability of shifting to deciduous-dominated forest stands are largely influenced by site moisture and other associated variables, such as topographic position and active layer depth. Numerous studies that have investigated factors of postfire successional trajectory and site vulnerability in Alaska's boreal forests have similarly demonstrated that prefire drought stress or site moisture and hillside position exert strong effects over burn severity and thus over postfire forest stand composition (Johnstone et al., 2020; Mack et al., 2021; Walker et al., 2017). In contrast to previous studies, which only utilized a single measure to depict site vulnerability to severe burning, such as organic soil depth or change in black spruce tree density (Johnstone et al., 2020), our indicator, BSPI, was based on both above and belowground fuel load quantity and quality. Moreover, no prior studies have utilized measures of understory plant quantity or quality to indicate site vulnerability and few studies have investigated understory fuel quantity and quality together (Barney & van Cleve, 1973; Mack et al., 2008). Despite the relatively low fuel load quantity of understory plants, the understory is an important driver of fire behavior as it provides a continuous fuel source across the forest floor, fostering the combustion and spread of fire into organic soils and between highly flammable

black spruce trees (Cronan et al., 2012; Todd & Jewkes, 2006). Our measurements of understory fuel load can be used in future models of fuel spread through black spruce forest understory, an area of study that is becoming increasingly important as climate change-related effects continue to intensify interior Alaska's fire regime.

Because BSPI, our indicator of vulnerability to severe burning, is based on both quality and quantity of all understory fuels, we were able to link BSPI to community composition of black spruce forests and show that nonacidic dry upland black spruce and acidic dry upland black spruce-lichen forest plant communities are the most vulnerable black spruce ecosystems to severe burning and therefore shifts to deciduous-dominated successional trajectories postfire. Black spruce-dominated landscapes occupy approximately 39%–68% of interior Alaska's landscape (Calef et al., 2005; Van Cleve et al., 1983), and these upland black spruce community types are a prevalent component of the black spruce landscape. We estimated land coverage by these two black spruce forest types using existing digital elevation models and vegetation cover maps (https://composite.accs.axiomdatascience.com/#map) and found that 27% of the landscape within our three ecoregions is occupied by black spruce forests with a high potential of burning severely and vulnerability to experiencing postfire ecosystem state shifts. Black spruce-lichen woodland ecosystems, in particular, are even more common in glaciated areas of boreal Canada, particularly in northeastern Canada where their prevalence has been found to be increasing within the closed-crown forest zone of their distribution range of 47°N to 52°N (Girard et al., 2008, 2011). This suggests that even higher percentages of the landscape across boreal North America will be vulnerable to state shifts, imparting large changes to ecosystem services, functioning, and diversity.

4.3. Within-Population Trait Variation as an Indicator of Black Spruce Forest Resilience to Fire

Black spruce plant communities contain species with specific functional and life history traits that are well adapted to surviving through or recolonizing following fire, thus promoting the self-replacement and resilience of black spruce forests to fire (Hollingsworth et al., 2013; Van Cleve et al., 1991). Under a normal low to moderate severity fire regime, species common to black spruce forest communities, such as black spruce trees with semi-serotinous cones (Johnstone & Chapin, 2006; Johnstone et al., 2008) and various vascular shrubs with rhizomatous roots (Lutz, 1956; Viereck, 1983), are effective at regenerating from surviving on-site seeds or roots, whereas other early-colonizing species, such as fireweed, can effectively re-establish via off-site seeds from reproductively mature parent plants. The nature of interior Alaska's fire regime dictates the plant species that succeed on the postfire sites, and then those species in turn foster a disturbance regime that promotes self-replacement of black spruce, allowing them to prevail over time (Hollingsworth et al., 2013).

Due to recent evidence supporting the benefits of plant functional trait variation to community persistence through changing environmental or disturbance conditions, many studies are using trait variation of dominant plant species to investigate community resilience to climate change (Anderegg et al., 2018; Bolnick et al., 2011; Hooper et al., 2005). Because our study timeline did not allow for measurement of traits from all dominant plant species, we measured trait variation in the most ubiquitous vascular and nonvascular plant species across our sites. However, we recognize that a more accurate representation of resilience would result from measuring trait variation in numerous dominant plant species of each different plant functional type at each site. As we combined CV from both species to create site-level CV, correlations with site-level CV and BSPI as well as other environmental variables were found, suggesting that inclusion of trait variation from more species in a site-level CV would likely result in stronger correlations with important variables. Additionally, we found that certain traits were correlated with each other, such as moisture content and SLA in *H. splendens* and live wood and new growth wood in *V. uliginosum*, indicating that measuring one of two or more correlated traits would have been sufficient for the purpose of this study. Future studies investigating site-level trait variation as an indicator of resilience should consider measurement of fewer, well-represented traits in a more diverse and numerous set of plant species.

The relationships we found between site-level plant trait CV, our indicator of overall site resilience, and BSPI and ecoregion agree with the results from previous studies, as they suggest that high site resilience occurs in regions characterized by high site moisture, low topographic position, and shallow, near-surface active layer or thick permafrost (Johnstone et al., 2020; Kane et al., 2007; Turetsky et al., 2011; Walker et al., 2017). It is well known that high site moisture corresponds to deeper SOL in black spruce stands (Cronan et al., 2012) and as a result diminishes the chances of stand shifts to deciduous dominated forest. Due to the gradual development of thick SOL and the establishment of reproductively mature black spruce trees over time (Hayes & Buma, 2021;

Johnstone et al., 2004; Kasischke & Johnstone, 2005), mature black spruce sites are known to be more resilient to fire than young and intermediate aged sites (Hoy et al., 2016). In fact, with increasing frequency of reburns in the boreal forest due to climate change (Kasischke & Turetsky, 2006), evidence shows that a large proportion of regenerating black spruce forests that reburn shift to deciduous forest trajectories, in both upland and lowland landscapes, due to the lack of reproductively mature black spruce at the time of burning (Hayes & Buma, 2021; Hoy et al., 2016). Although our site-level CV does not include measures of black spruce's postfire reproductive traits, previous research illustrates the low resilience of younger black spruce stands to fire, which contradicts our regression tree results. It is likely that the *H. splendens* and *V. uliginosum* individuals measured in younger sites for this study were surviving individuals from prefire populations, and our site-level CV in young and intermediate sites is a reflection of trait variation in the prefire site and likely not broadly representative of the resilience of young sites. A more representative site-level CV from the measurement of numerous dominant plant species specific to a site (rather than species ubiquitous to all sites), particularly black spruce trees and "early-colonizer" species common in young sites, would likely provide a better understanding of resilience of black spruce sites to a changing fire regime.

4.4. Emergent Properties Provide Insight Into the Future State of the Boreal Forest

Emergent properties, known to arise from individual system components collectively, provide insight into the greater functioning of a whole community or even ecosystem. In this study, we attempted to investigate emergent properties of vulnerability and resilience in black spruce forests using site-level measurements of BSPI and plant trait variation, respectively. Because we were able to demonstrate the effectiveness of $BSPI_m$ as an indicator of burn severity potential, we are confident that our site-level measurement of BSPI reasonably represents the emergent property of vulnerability, although further verification of BSPI using actual pre- and postfire data is recommended. As land managers and others begin to understand the magnitude of black spruce forest shift to deciduous-dominated postfire stands, BSPI can be conscientiously used at the site-level to anticipate the postfire socioecological effects of severe burning on a particular site.

Although we were not able to verify site-level CV as a reliable indicator of site resilience, this was the first study in boreal Alaska to quantify plant trait variation as a surrogate for resilience and correlate it with environmental predictors. Moreover, our results suggest that the reliability of CV as an indicator will likely increase with the measurement of trait variation in more species. Nevertheless, previous studies have verified trait variation as a reliable indicator of ecosystem resilience in temperate and boreal landscapes (Anderegg et al., 2018; Bolnick et al., 2011; Hooper et al., 2005), supporting the value of future measurement and use of trait variation as an indicator of resilience in the boreal forest.

5. Conclusion

As the occurrence of extreme wildfire years continues to increase in interior Alaska as well as in other northern regions (Kasischke & Turetsky, 2006), a significant portion of the North American boreal landscape may be converted from black spruce forest to deciduous-dominated forest stands. We demonstrate that burn severity potential index or BSPI is likely a reliable predictor of black spruce forest vulnerability to deep burning and fire-induced forest cover change. Relationships between black spruce forest resilience to severe burning and factors, such as BSPI and ecoregion, add to the growing body of knowledge on plant trait variation and its relationship to community-level resilience properties. This demonstrates how community-level measures can provide insights into emergent properties of ecosystems, such as vulnerability and resilience of black spruce forests to severe burning. These measures are likely to be important tools for predicting future ecological and landscape shifts in response to changing climate and disturbance regimes in the boreal forest region.

Data Availability Statement

The fuel load and plant trait data used in this paper, and the tree and shrub measurements used to calculate tree and shrub fuel load, are publicly available through the Bonanza Creek LTER's data catalog https://www.lter.uaf.edu/data/data-catalog (Grzesik et al., 2020a, 2020b, 2020c; Hollingsworth & Bonanza Creek LTER, 2021; Van Cleve et al., 2016). Figures were made with R Software version 3.5.2 (R Core Team, 2014). The software

(version 1.1.0) associated with this manuscript is licensed under MIT and published on GitHub https://github.com/ejgrzesik/fuel-loads-and-plant-traits/tree/v1.1.0 (Grzesik, 2021).

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