BORN TO BURN: CHARACTERIZING FUEL LOADS, FLAMMABILITY AND PLANT TRAITS ACROSS SPATIO-TEMPORAL GRADIENTS OF BLACK SPRUCE DOMINATED COMMUNITIES

By

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Abstract

The flammability of black spruce forests is influenced by the fuel loadings and quality of fuels within a site, whereas the ability of a site to self-replace after fire, and thus forest resiliency, depends on the fire-ecological trait attributes of the plant community. Black spruce plant communities have been undergoing self-replacement succession from low to moderate severity fires for thousands of years, however, recent intensification of interior Alaska's fire regime is leading to shifts in post-fire successional trajectories, resulting in many ecological implications. This study focuses on understanding the variation in black spruce forest flammability, based on fuel load quantity and quality, and fire-ecological plant traits in 28 black spruce dominated sites ranging across age and moisture gradients in interior Alaska. I quantified tree canopy, understory and below-ground fuel loads, developed models to predict fuel loads and then utilized my measurements of above-ground fuel load quantity and quality to calculate a site-level flammability index. Based on my analyses, significantly greater flammability indices, and thus burning potential, occur in sites greater than 34 years in age, at elevations greater than 302 m and with dry site moisture, which are representative of dry, nonacidic upland black spruce and dry, acidic upland black spruce-lichen forest ecosystems. Furthermore, although fire-ecological plant trait attributes of *Hylocomium splendens* and *Vaccinium uliginosum* vary with age and moisture gradients, the amount of intra-specific trait variation within a site could not be explained by stand age or moisture and thus forest resiliency is also likely independent of age and moisture gradients. Further research is necessary to explore both abiotic and biotic explanatory variables related to intra-specific plant trait variation to better understand variation in black spruce forest resiliency on the landscape. The results from this study can assist fire managers in the prediction of black spruce forest burning potential and its vulnerability to ecosystem shift post-fire.

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General Introduction

In the boreal forest biome, wildfires are a natural and important ecological process contributing to the spatiotemporal development of a vegetation mosaic that varies in age, size and species composition (Payette 1992). Within these ecosystems, fire promotes the cycling of nutrients through burning of plant fuels, maintains diversity through regeneration of the forest and prevents the decline of productivity associated with retrogression of old growth forests (Kurkowski et al. 2008; Nilsson and Wardle 2005; Payette 1992). In particular, landscapes in interior Alaska have been affected by regular intervals of low to moderate severity fire disturbances for the past 5500 years (Lynch et al. 2003). There is evidence to suggest that the approximate onset of the current fire regime in interior Alaska is concurrent with a vegetation shift to black spruce dominated plant communities (Lynch et al. 2003).

In recent decades, shifts in interior Alaska's fire regime are resulting in larger, more frequent and more severe fires (Kasischke and Turetsky 2006). The decade from 2000-2010 consisted of 50% more area burned in Alaska than any previous decade since the 1940s, as well as a decrease in the fire-return interval from 196 to 144 years in the interior Alaska region (Kasischke et al. 2010). Recent studies have indicated that there is correlation between large fire years and periods of drought resulting from warmer summer temperatures (Duffy et al. 2005; Gillett and Weaver 2004), which is particularly concerning because Alaska, and other northern regions globally, are warming at twice the global average rate (Wolken et al. 2011). Changes to the fire regime, particularly the occurrence of high severity fires, have the potential to shift black spruce forests to deciduous dominated forest types, which would have implications on nutrient cycling, permafrost stability, carbon storage and thus the global carbon cycle (Johnstone and Chapin 2006; Johnstone et al. 2010).

Notably, black spruce forests are also the most flammable forest type in interior Alaska (Cronan et al. 2012; Viereck et al. 1986) and thus have a greater potential to burn compared to other vegetation types across the landscape. As plant biomass or fuel loads build up during post-fire succession and become sufficient enough to ignite and sustain fire (Mack et al. 2008; Schimmel and Granström 1997), forest flammability also increases. Arguably, though, overall forest flammability will also depend on the quality of the fuels present or the species composition of the black spruce community as different plant types vary in their individual flammability and community flammability is highly influenced by the most flammable species present (van Altena et al. 2012). Thus, site-level flammability of black spruce communities will inevitably fluctuate along the landscape depending on the quality and quantity of fuel loads present within a pre-fire black spruce site.

Black spruce dominated forests, the dominant forest type in interior Alaska (van Cleve et al. 1983), have a strong relationship with fire, specifically, in terms of their plant community composition and fire-ecological plant traits (Nilsson and Wardle 2005; Roberts 2004). Following low to moderate severity fire disturbances, black spruce communities often undergo self-replacement during post-fire succession (van Cleve et al. 1991), wherein plant species from the pre-fire community return to the post-fire community over time. These communities contain assemblages of plant species that are particularly tolerant of low to moderate severity fire disturbances due to the occurrence of species that are capable of either fire resistance (i.e. species resist burning) or post-fire regeneration (Pyne 2010; Violle et al. 2007). Recent evidence on the benefits of intra-specific trait variation to ecosystem functioning suggests that greater amount of within-population intra-specific 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). Thus, black spruce communities that possess greater within-population intra-specific variation in fire-ecological plant traits will likely contain greater forest resiliency to changes in the fire regime.

Currently, there is a lack of knowledge on the spatiotemporal variation of black spruce forest flammability, based on fuel load quantity and quality, and fire-ecological plant traits in interior Alaska. These inherent qualities of black spruce forests provide insight into these ecosystems' potential to burn severely and the resilience of these ecosystems to a changing fire regime. Therefore, the aim of this study is to alleviate this knowledge gap by utilizing measurements of fuel loads to quantify site-level flammability indices and by exploring intra-specific variation in fire-ecological plant traits across age and moisture gradients in black spruce forests in interior Alaska. An understanding of the variability in black spruce forest flammability will assist fire managers in the proper prediction of fire potential and its behavior and will allow for the appropriate management of highly flammable ecosystem types that are most susceptible to ecosystem state shifts post-fire. Moreover, a greater understanding of how the attributes of fire-ecological plant traits vary cross spatiotemporal gradients and where intra-specific trait variation is the greatest will indicate which black spruce ecosystem types have the greatest resiliency to fluctuations in the fire regime based on the range of plant trait attributes within the community.

Chapter 1 Variation in black spruce forest fuel loads and flammability

Abstract

The flammability of black spruce forests is influenced by the quality and quantity of fuel loads which can vary across spatiotemporal gradients, such as stand age and site moisture. Current increases in climate change-related warming and drying are intensifying fire regimes in interior Alaska and making black spruce forests particularly vulnerable to ecosystem state shifts during post-fire succession. With the aim of increasing understanding of landscape variation in black spruce forest burning potential, I quantified organic matter pools of organic soils, understory plants and tree canopy as a proxy for fuel load, developed models to predict fuel loads and calculated a site-level flammability index based on aboveground fuel quantity and quality in 28 black spruce dominated sites in interior Alaska. Both stand age and site moisture were significant predictors of tree and organic soil fuel loads, but additional environmental variables, including active layer depth and elevation, were necessary to predict understory fuel loads. Flammability indices were significantly greater in sites greater than 34 years since fire, occurring at elevations greater than 302 m, with dry site moisture, indicating that these sites, which are representative of nonacidic, dry, upland black spruce and acidic, dry, upland black spruce-lichen forest ecosystems, have the greatest burning potential. Additionally, site flammability significantly increased with the proportion of evergreen tree and feather moss fuel loads (two highly flammable fuel types). The results from this study provide a detailed account of black spruce fuel loads and flammability, which can be utilized in fuel maps, assist in the prediction of black spruce forest burning potential and indicate the vulnerability of a site to experiencing adverse post-fire ecological changes.

1.1 Introduction

Natural disturbance regimes affect the organization and composition of plant communities, and consequentially, influence ecosystem functions and processes. The boreal forest region is regularly affected by wildfire, a disturbance that 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). Fuel load, or the amount of combustible organic matter per unit area, varies across the landscape and not only influences the burning potential of a stand, but also the behavior and intensity of fire (Kreye et al. 2013). In recent decades, climate change-related shifts in the wildfire regime of interior Alaska are causing higher frequencies of large, high severity fire events (Kasischke and Turetsky 2006). An intensified wildfire regime is likely to cause shifts from black spruce (*Picea mariana*) dominated forest stands to deciduous dominated stands, due to the competitive advantages deciduous tree seedlings have over black spruce seedlings in early succession (Johnstone et al. 2010). A shift to deciduous forest would change ecosystem services and decrease permafrost stability, consequentially impacting carbon and nutrient cycling, with implications for the global C cycle (Johnstone et al. 2010). Thus, a proper understanding of how fuel load, and thus forest flammability, varies across the landscape is necessary to better predict fire potential and to anticipate post-fire ecological effects.

Black spruce forests are the dominant forest type in interior Alaska, covering 39 % - 44 % of the landscape (Calef et al. 2008), and are more flammable compared to other vegetation types in Alaska (Cronan et al. 2012; van Cleve et al. 1983; Viereck et al. 1986). Flammability of black spruce forests is influenced by the fuel load and types or quality of fuel within a site, among other parameters like fuel moisture content, climatic conditions, and ignition sources

(Rothermel 1972; Kasischke et al. 2010; van Altena et al. 2012). 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 and Granström 1997). Additionally, individual plant species within black spruce forest communities vary in their flammability (based on their physical structure, chemistry, and moisture retention capacity) causing overall site flammability to also vary with the species composition (Schwilk and Caprio 2011; Plucinski and Anderson 2008; Bond and van Wilgen 1996). Sylvester and Wein (1981) estimated the relative flammability of 12 common understory species in black spruce forests and found that graminoids, evergreen shrubs and *Cladonia*-type lichens were the most flammable, whereas deciduous shrubs, *Sphagnum* mosses and forbs had relatively low flammability ratings. Furthermore, van Altena et al. (2012) found that the flammability of mixtures of common boreal plant species was strongly influenced by the most flammable species (*Hylacomium splendens* (splendid feather moss) and *Empetrum nigrum* (crowberry) present within the mixture. This suggests that even relatively small abundances of highly flammable species within a site may exert strong effects over fire dynamics.

Black spruce forest flammability varies over the landscape as the fuel load and plant community composition of these forests change along spatiotemporal gradients (Johnston et al. 2015). Young, recently burned stands are ineffective at spreading fire due to their lack of biomass and high proportion of low flammability fuels, and may even act as fuel breaks across the landscape (Héon et al. 2014; Schimmel and Granström, 1997). As time since fire increases and a site proceeds through postfire succession, increasing fuel loads and plant community flammability greatens the probability of burning. Schimmel and Granström (1997) found that three decades after fire, ground fuels in Swedish boreal forests shifted from dense leaf litter to thick mats of highly flammable pleurocarpus mosses and fruticose lichens, causing a progressive increase in forest flammability. Thus, stand age or time since fire is a major factor controlling black spruce forest flammability through its influence on fuel load quantities and plant community composition.

Additionally, site moisture has been shown to be a primary factor affecting overall forest flammability. As fuel loads in black spruce forests increase with site moisture due to greater primary production (Mack et al. 2008; van Cleve et al. 1991), higher site moisture further increases fuel loads by decreasing decomposition rates on the forest floor, resulting in greater belowground organic layer accumulation (Viereck et al. 1986; Cronan et al. 2012). Thompson et al. (2017) found that site moisture, as well as stand age, were important predictors of fuel load where mature, wet, upland conifer sites had significantly more fuel loads than dry conifer and tree-less wetland sites in boreal northwestern Canada. Despite lower fire occurrence in wetter, lowland black spruce sites (Larsen 1992), recent increases of climate change-related drought events are causing intensified drying of fuels and increased flammability of black spruce forests (Turetsky et al. 2011). Wetter black spruce sites, which developed large fuel loads during previously moist periods when they were not experiencing drought, are now becoming more vulnerable to burning during drought years (Turetsky et al. 2011). Lastly, environmental variables related to site moisture were some of the most important predictors of species composition in mature black spruce stands in interior Alaska (Hollingsworth et al. 2006), suggesting that site moisture also indirectly influences forest flammability through its effects on black spruce plant community composition and on the abundance of highly flammable plant species.

Organic soil biomass is important because of large boreal soil carbon stocks compared to other global soils and because approximately 70-80% of emissions from boreal fires comes from the combustion of organic soil layers (Amiro et al. 2001; de Groot et al. 2007). Woody tree biomass constitutes the majority of aboveground biomass in mature black spruce stands (Mack et al. 2008), and numerous studies have reported measurements of tree biomass and parameters related to canopy fuel loads in Alaska's black spruce forests (Barney and van Cleve 1973; Johnstone and Kasischke 2005; Yarie and Billings 2002). Therefore, much of the research investigating fuel loads in interior Alaska has been conducted on belowground organic soils and aboveground tree canopy (Johnson et al. 2011; Turetsky et al. 2011; Kasischke and Johnstone 2005; Harden et al. 2004; Miyanishi and Johnson 2002) and few studies, lacking landscape replication, have investigated understory plant fuel loads in interior Alaskan black spruce forests (Barney and van Cleve 1973; Mack et al. 2008). Understory plant species provide a near continuous layer of flammable surface fuels and are known to play an important role in fire behavior and post-fire plant community composition (Cronan et al. 2012; Bernhardt et al. 2011). However, few studies have comparatively assessed tree canopy, understory and organic soil fuel loads and no prior studies have assessed how variability in these fuel loads contributes to the heterogeneity of forest flammability across the black spruce landscape.

Because of the wide environmental range occupied by black spruce forests on the landscape (Cronan et al. 2012; Hollingsworth et al. 2006) and concurrent variation in species composition and organic soil developments (Hollingsworth et al. 2008), a more extensive understanding of overall black spruce forest fuel load quantity and quality is necessary to better predict the flammability and potential effects of fire in black spruce forests. Greater knowledge on this topic will assist in the proper prediction of fire behavior through the development of more detailed fuel maps and in the implementation of appropriate land management practices in highly flammable areas that are sensitive to severe burning. In this study I ask: How can fuel load quantity and quality be used to indicate the burning potential of black spruce communities? To answer this question, I first i) measured tree canopy, understory and organic soil fuel load in 28 sites, varying in age and moisture, ii) developed models to predict black spruce forest fuel loads from known environmental variables and iii) calculated site-level flammability indices based on aboveground vegetation biomass and specific leaf area (SLA) measurements (a trait highly related to plant flammability). Additionally, I ask: What factors are associated with high black spruce forest flammability? I answer this question by i) quantifying relationships between flammability index and environmental variables and ii) identifying black spruce forest ecosystem types with the highest flammability. The aim of this study is to contribute to the development of a comprehensive framework for a better prediction of black spruce forest flammability and for identification of locations along the landscape that may be susceptible to ecosystem state shift post-fire, based on fuel load quantity and quality.

1.2 Methods

1.2.1 Study area

The study area spans 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), within interior Alaska, USA (Fig. 1.1) and is characterized by swampy lowlands, gently sloping uplands, braided rivers and floodplains. The study area is underlain by discontinuous permafrost, which typically occurs on north-facing slopes and in low-lying areas, with a continental climate and extreme temperatures. The 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).

1.2.2 Field Sampling

During the summer of 2019, I sampled 28 black spruce dominated sites that were previously established by the Bonanza Creek Long Term Ecological Research (BNZ-LTER) group (Fig. 1.1). 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). The sites included young (0-15 years since fire), intermediate (40-60 years), and mature (>80 years) stands and ranged in site moisture (Table 1.1). Site moisture classes from driest to wettest include: xeric, subxeric, subxeric/mesic, mesic, mesic/subhygric and subhygric. Study sites were easily accessible along five highways in interior Alaska: the Dalton Highway, the Elliot Highway, the Steese Highway, the Richardson Highway and the Parks Highway. Study sites ranged in active layer depth (depth to permafrost) from 25-92 cm and in elevation from 128-770 m above sea level (Table 1.1). Previous burn severity of young sites ranged from low to high, but burn severity was unknown for intermediate and mature sites. Mature and intermediate sites were representative of black spruce community subtypes common to the interior Alaskan region (see Hollingsworth et al. 2006 for community descriptions). Young sites typically had minimal or no tree canopy and were dominated by black spruce or a mix of black spruce and hardwood tree saplings in their understory. Prior to the last fire, all sites were forests dominated by black spruce.

Each site covered 50 x 60 m in area, which included a 10 m wide border around each side, and twelve 10 x 10 m tree plots. Upon establishment of these sites in 2011, the BNZ-LTER measured environmental characteristics (age or time since fire, moisture, elevation, slope, aspect, active layer depth, topographic position, and surficial geology) and annually measures 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 datasets can be found at http://www.lter.uaf.edu/ .

1.2.3 Quantifying Fuel Loads

I quantified fuel loads in the following order: 1) understory plant fuels (vascular and non-vascular vegetation below 1 m in height), 2) organic soil biomass and dead downed wood, 3) 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 4) trees (greater than or equal to 2 inches diameter at breast height).

I 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. Each transect was initiated from the northeastern corner of each site, which was marked with a distinguishable metal stake. I ran the two transects away from the site boundaries in order to sample outside of the site as my methods were destructive. The two transects ran approximately perpendicular to each other in order to sample along two directional orientations and to reduce directional bias, although directional heterogeneity in plant fuels was not evident at any of the sites.

Understory plants and organic soils were measured and collected by destructively sampling three 20 x 20 cm plots at 10 m intervals along each transect on alternating sides, yielding 6 plots per site. Fuels were sampled by each plant functional type separately and systematically from "top to bottom", starting with vascular understory plant types (evergreen shrubs, deciduous shrubs, graminoids, forbs), then non-vascular understory plant types (*Sphagnum* mosses, feather mosses, colonizer mosses, lichens) and lastly organic soils (fibric and mesic). The maximum height of each vascular plant type was measured, followed by clipping and bagging of all vascular plant biomass within the plot area. To estimate non-vascular understory plant and organic soil biomass, I used a soil knife to cut along the edges of the plot, 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. On this cube of biomass, I 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 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 non-vascular, were sorted into their respective plant functional types. Once sorted, all understory plant and organic soil samples were dried at 60 °C until a constant mass was reached and then weighed immediately. 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 their 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.

Dead downed woody debris was inventoried along each transect using the line intersect method (Van Wagner 1968). The diameter of each piece of dead downed wood that intersected with the transect line was recorded using digital calipers. Methods for calculating dead downed woody fuel load followed the approach found in Johnston et al. (2015). The diameters of dead downed wood <7.0 cm were sorted into appropriate dead downed wood size classes (size classes I-V correspond to diameters <0.5 cm, 0.5-0.99 cm, 1.0-2.99 cm, 3.0-4.99 cm and 5.0-6.99 cm, respectively; Van Wagner 1982). Dead downed wood fuel loads for classes I-V were quantified by using the counts of intersecting pieces in each class and the equation and multiplier values found in Nalder et al. (1997) for dead downed woody surface fuels from black spruce forests in Northwest Territories, Canada. Fuel load for dead downed wood ≥7.0 cm in diameter was quantified using the equation found in Alexander (2004) along with the value for specific gravity, 0.427 g/cm^3 (Ter-mikaelian et al. 2008), for dead downed black spruce wood with little to no sign of decay (Maser et al. 1979). There were little to no signs of decay on the dead downed wood at the study sites and since all sites were typically dominated by black spruce or a recently burned black spruce stand (for young sites), all dead downed wood was assumed to be black spruce.

To quantify tall deciduous shrub (>1 m tall) and tree seedling biomass, I used inventory data collected as part of the BNZ-LTER (https://www.lter.uaf.edu/data/data-detail/id/530). I 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 quantify above-ground biomass (g). Biomass for tall shrubs was calculated for *Alnus viridis* (Siberian alder), *Betula glandulosa* (shrub birch), *B. nana* (dwarf birch), and *Salix* spp. (shrub willow) using the equations from Berner et al. (2015). Biomass for tree seedlings was calculated for *Picea mariana* (black spruce), *P. glauca* (white spruce), *Larix larcinia* (tamarack; using the equation for black spruce seedlings), *Populus balsamifera* (balsam poplar), *Betula neoalaskana* (Alaskan birch), and *Populus tremuloides* (quaking aspen) using the equations found in Alexander et al. (2012). Biomass values for each tall deciduous shrub, tree seedling and tree sapling were multiplied by the count number of individuals/ramets of that species in each basal diameter size class. Then, biomass for tall deciduous shrubs, tree seedlings and tree saplings in each site was summed and fuel load was determined by dividing the summed biomass by sampling area (2m x 50 m transect + 2 m x 60 m transect = 220 m^2 sampling area; refer to section 1.2.2 for details).

To quantify tree biomass, I again made use of the inventory data collected as part of the BNZ-LTER (https://www.lter.uaf.edu/data/data-detail/id/320). I used diameter at breast height (DBH; diameter (cm) at 1.37 m) to quantify aboveground biomass for the six tree species found throughout the study sites. Biomass was calculated for black spruce, white spruce, balsam poplar and Alaskan birch using the equations from Yarie et al. (2007), for quaking aspen using the equation from Alexander et al. (2012), and for tamarack using the equation from Carpenter (1983). Biomass was summed for trees in each plot and fuel load was determined by dividing the summed tree biomass by plot area (10 m x 10 m plot = 100 m^2 plot area; refer to section 1.2.2 for details).

1.2.4 Data Analysis

All statistical analyses were performed in R, version 3.5.2 (R Core Team 2014). To best depict trends in fuel load data, analyses were conducted on three fuel load classes separately, which I characterized as organic soil, understory (including dead downed wood, tall deciduous shrubs and tree seedlings and saplings) and tree canopy.

1.2.4.1 Describing fuel load quantity and quality

In the following analyses, all fuel load data were log + 1 transformed to achieve normality of residuals. To investigate the differences in fuel load quantity among fuel load classes and among fuel types within a fuel load class, I performed analysis of variance on plot-level fuel load measurements. Evidence from boreal black spruce forests in Northwest Territories, Canada, suggests that differences in soil organic matter is more distinguishable among three broader moisture classes rather than by the initial six classes of site moisture I used (Walker et al. 2018), thus I chose to condense site moisture into three classes for the following summary analysis. The three site moisture classes included dry (xeric and subxeric), moderate (subxeric/mesic and mesic) and wet (mesic/subhygric and subhygric) classes. To investigate the relationship of fuel load quantity as a function of stand age (time since fire), site moisture, and their interaction (age x moisture) for each fuel load class, I performed multiple regression analyses on plot-level fuel load measurements. Due to the lack of relationship between understory fuel load quantity and time since fire and moisture, Iinvestigated the relationship of fuel load quantity of individual understory plant types as a function of stand age, site moisture and their interaction.

I performed a principal component analysis (PCA) using the *prcomp* function in the *vegan* package to characterize the patterns in understory fuel load distribution, grouped by fuel type, relative to six known environmental variables across all sites. I conducted the PCA on one derived data matrix (AE'), which was the product of two primary data matrices. The main matrix (A) was composed of plot-level fuel load data for all understory fuel types for each sampling plot or transect (6 plots for each of evergreen shrub, deciduous shrub, graminoid, forb, lichen, feather moss, *Sphagnum* moss, colonizer moss; 2 transects for dead downed wood; 1 transect each for tall deciduous shrub and tree seedling and saplings; refer to sections 1.2.2 and 1.2.3 for details) within each site (28 sites by 52 plot-level fuel load measurements). The second matrix (E) contained data on six environmental variables, including: slope, aspect, time since fire, site moisture, elevation, average active layer depth (28 sites by 6 variables). The third, derived data matrix (AE') was created by multiplying the A and E matrices together to achieve a distribution of plot-level understory fuel load measurements across environmental variables (6 variables by 52 plot-level fuel load measurements). Environmental variables associated with ordination axes that explained >1 standard deviation of variance in the data were then plotted in a biplot.

1.2.4.2 Developing models to predict fuel loads based on environmental variables

To determine important environmental predictors of tree, understory and organic soil fuel loads, I developed linear mixed-effects models using the *lme4* package (Bates et al. 2015) on plot-level fuel load measurements. I tested between two random effects structures of site and plot nested within site using Aikaki's Information Criterion (AIC). For each model, site alone was used as the random effects structure because it resulted in the best AIC. With separate models for each fuel load class, I tested whether six fixed environmental factors (time since fire, moisture, average active layer depth, elevation, topographic position and surficial geology) were important in predicting black spruce forest fuel loads. Prior to creating the models, I conducted a correlation matrix using Pearson's r between the seven variables and found that none of the variables were significantly correlated. Active layer depth, elevation, slope and aspect were scaled to account for differences in units and magnitude of values. For each fuel load class, I 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, I determined biologically relevant fixed variable interactions to be time since fire*active layer depth and elevation*moisture. Final models for each fuel load class were then selected based on AIC and most parsimonious parameter number (K value).

1.2.4.3 Creating a flammability index

To determine the overall flammability of study sites, I calculated a site-level flammability index (FI) for all 28 sites based aboveground fuel load measurements (understory vegetation, including tall deciduous shrubs, and trees) and boreal plant SLA measurements reported in the literature. SLA is a trait known to be highly associated with plant flammability across many plant functional types and ecosystems (van Altena et al. 2012; Murray et al. 2013; Schwilk and Caprio 2011). Studies have shown that increases in SLA are associated less time to ignition or faster ignition, and thus SLA is positively associated with flammability (van Altena et al. 2012; Murray et al. 2013). However, SLA is likely only meaningful to plant flammability when plant fuels are dry because fuel moisture is also incredibly important for flammability of plant fuels (Norum and Miller 1984; Rothermel 1972). When plant fuels are highly saturated, they are significantly less likely to ignite during fire, regardless of their SLA. Currently, there are no reports in the literature of moisture retention rates or drying rates of boreal plants or organic soils, and it was out of the scope of this study to measure moisture retention in plant fuels. Thus, the following flammability index is a proxy for burning potential of black spruce forests under dry conditions but may not accurately indicate burning potential under wetter fuel moisture conditions.

To determine an average SLA value for each understory and canopy fuel type (excluding dead downed wood and tree seedlings/saplings), I obtained SLA measurements for different plant species from the literature (Sylvester and Wein 1981; Aerts et al. 1992; Bond-Lamberty and Gower 2007; van Altena et al. 2012; Michel et al. 2012). I found studies that were performed in boreal black spruce forest or sub-arctic tundra ecosystems, as well as one study performed in a temperate fen, that measured SLA for different plant species that were also found in my study sites. 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' functional growth form. I then determined mean SLA values for each of these fuel types. To determine plot-level FI for each fuel type, mean SLA values for each fuel type were multiplied by plot-level fuel load measurements for the respective fuel type in each site (SLA x Fuel Load = FI). To determine the overall site-level FI, I averaged the plot-level FIs for each fuel type (Table S1.3) and then summed the FI for each fuel type in each site (Table S1.4).

To examine how the flammability index of individual fuel types may change with the incorporation of drying rates, I rated each aboveground fuel type from 1 to 3, where 1 indicates slow drying rates and 3 indicates fast drying rate, based on qualitative reports on drying rates in the literature and on personal observations in the field. Then I multiplied the average flammability index for each fuel type by its drying rate index to infer on how actual drying rates may influence the flammability index. To confirm that the site-level FI is consistent with the proportion of highly flammable fuel loads, I performed linear regression analyses on site-level FI with the proportion of fuel load of the two most flammable fuel types at sites (evergreen tree and feather moss fuel loads). Furthermore, to examine how well site-level FI indicates the potential for a site to burn severely, I assessed FI with severity of the previous burn of young sites (for which burn severity is known) using analysis of variance.

Next, I investigated the relationship of site-level FI with time since fire and site moisture variables using multiple regression analysis. Additionally, I modeled site flammability index using regression tree analysis as a function of five environmental variables, including: time since fire, ecoregion, elevation, topographic position (categories 1-7 correspond to summit, shoulder, side slope, toe slope, valley bottom, drainage channel and depression, respectively) and surficial geology (categories 1-6 correspond to basin colluvium and organic deposits, glacial tills, glaciofluvial deposits, loess, residuum and stabilized alluvium, respectively). I chose these variables because they visually or spatially describe black spruce sites and are relatively easily attainable by fire managers. Prior to performing the analysis, I conducted a correlation matrix using Pearson's r on the five variables and did not find any significant correlations between the variables (all $r < 0.39$). 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 variables, and then ultimately considers the split that maximizes the deviance between a parent node and daughter node (Poor and 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. A regression tree model that includes all of the predictor variables can lead to overfitting the data. To prevent this, I selected the number of splits in the model that minimized the cross-validation error and I further pruned my model using a complexity parameter (the amount by which each split must improve model fit) of 0.05 and a minimum node size of 3. Although there is no established theoretical basis for determining a minimum node size, many studies with relatively small sample size have used minimum node sizes between 2 and 4 (Rejwan et al. 1999; Rothwell et al. 2008; Sass et al. 2008) or approximately 5 -10 % of their total sample size (Buja et al. 2001; Poor and Ullman 2010). Thus, I chose the minimum node size to be approximately 10% of the total sample size due to my relatively small sample size (28 compared to other studies with often hundreds of observations).

One outlier site, MDI4, was removed when conducting these analyses because its FI value was 6 times greater in magnitude than other FI values on average.

1.3 Results

1.3.1 Variation in fuel load quantity and quality across sites

Analysis of variance indicated that organic soil fuel loads (8.07 ± 0.81 $kg \cdot m^{-2}$) were significantly greater than both understory (1.19 ± 0.07 $kg \cdot m^{-2}$) and tree canopy (1.95 ± 0.51 $kg \cdot m^{-2}$) fuel loads (ANOVA $F_{2, 81} = 67.07$, $p < 0.001$). Tree fuel loads comprised 0 % to 60 % of the total fuel load across sites and ranged from 0 to 11.83 ± 2.51 $kg \cdot m^{-2}$. Tree fuels constituted the greatest portion to the above-ground fuel load in intermediate and mature sites, but contributed minimally or not at all to the above-ground fuel load in young sites, which was expected because young stands would not have had enough time for substantial tree growth. Understory plant fuel loads constituted the lowest portion of total fuel loads at sites, making up 3 % to 26 % of the total fuel load across sites. On average, non-vascular understory fuel loads occupied 4 ± 0.007 % of the total and vascular understory fuel loads occupied 8 ± 0.01 % of the total. Total understory fuel loads ranged from 0.42 ± 0.28 to 1.90 ± 0.26 $kg \cdot m^{-2}$ across all sites and were significantly lower than organic soil fuel loads ($p < 0.001$); however they were not significantly different from tree canopy fuel loads ($p = 0.95$). Organic soil fuel loads ranged from 2.93 ± 1.87 to 20.22 ± 7.31 $kg \cdot m^{-2}$ across all sites and constituted 36 % to 97% of the total fuel load at sites.

Analysis of variance of fuel loads between fuel types indicated evergreen tree fuel loads (1.59 ± 0.11 $kg \cdot m^{-2}$) were significantly greater than deciduous tree fuel loads (0.37 ± 0.08 $kg \cdot m^{-2}$) across sites (ANOVA $F_{1, 622} = 144.1$, $p < 0.001$). Understory fuel load quantities varied significantly between understory fuel types (ANOVA $F_{10, 1445} = 23.95$, $p < 0.001$). Additionally, mesic fuel loads (5.74 ± 0.35 kg·m^{-2}) were significantly greater than fibric fuel loads (2.33 ± 0.27 kg·m^{-2}) in the organic soil fuel load class (ANOVA $F_{1, 334} = 105.5$, $p < 0.001$), and overall, mesic fuel loads contributed the most to total site fuel loads compared to other fuel types across all of my sites (Table 1.2).

I used multiple regression to investigate variation in fuel load across time since fire and moisture variables. These results indicated that tree fuel loads and organic soil fuel loads were significantly affected by time since fire, site moisture, and the interaction effect of time since fire and moisture ($p < 0.001$, $r^2 = 0.23$, d.f. = 620 and $p < 0.001$, $r^2 = 0.08$, d.f. = 332, respectively; Fig. 1.2 & 1.3). When I regressed total fuel loads with time since fire and moisture, my results indicated that tree canopy fuel loads were significantly affected by time since fire and moisture ($p = 0.001$, $r^2 = 0.47$, d.f. = 26), whereas organic soil fuel loads were significantly affected by time since fire only ($p = 0.02$, $r^2 = 0.16$, d.f. = 26). The higher mean canopy fuel loads present in intermediate sites, compared to mature sites, are due to significantly greater deciduous tree fuel loads in intermediate sites ($F_{2, 309} = 45.69$, $p < 0.001$; Fig. 1.3B). Furthermore, regression analyses indicated that understory fuel loads were not affected by time since fire or site moisture (Fig. 1.2 & 1.3). When non-vascular understory fuel loads were regressed separately with time since fire and moisture, non-vascular fuel loads were significantly, but weakly, correlated with time since fire ($p = 0.008$, $r^2 = 0.009$, d.f. = 310); however, no relationships of vascular understory fuel loads with time since fire nor moisture were found. Lastly, when total fuel load was regressed with time since fire and moisture, it was only significantly affected by time since fire ($p = 0.004$, $r^2 = 0.24$, d.f. = 26; Fig. 1.2).

When fuel loads of individual understory fuel types were regressed against time since fire and site moisture separately, significant relationships with the variables did occur, although not every understory fuel type was significantly affected by both variables. Feather moss and colonizer moss fuel loads were both significantly affected by time since fire, moisture and their interaction ($p = 0.03$, $r^2 = 0.04$, d.f. = 164 and $p < 0.001$, $r^2 = 0.14$, d.f. = 164, respectively), where feather moss fuel loads increased with time since fire and moisture and were greatest in moderate moisture sites, whereas colonizer moss fuel loads decreased with time since fire and moisture (Table 1.2). *Sphagnum* moss fuel loads significantly increased with time since fire and moisture ($p < 0.001$, $r^2 = 0.18$, d.f. = 165) and lichen fuel loads significantly decreased with moisture ($p < 0.001$, $r^2 = 0.07$, d.f. = 166). Three of the four non-vascular fuel types (lichens, feather mosses, and *Sphagnum* mosses) encompassed different levels of the moisture gradient (Table 1.2; Fig. 1.3). Most notably, lichen fuel loads, known to be a highly flammable fuel type, were greatest in the mature, xeric site, whereas *Sphagnum* moss fuel loads, known for their inflammability due to their moisture-holding traits, were greatest in mature, subhygric sites (Table 1.2). Additionally, dead downed wood fuel loads significantly decreased with time since fire ($p = 0.002$, $r^2 = 0.15$, d.f. = 53), which was expected as there are typically many fallen trees on the ground surface in the first decade following fire. Graminoid fuel loads, which are known as a flashy, highly flammable fuel type, significantly decreased with stand age and increased with site moisture ($p = 0.001$, $r^2 = 0.07$, d.f. = 165); however, graminoids, along with forbs, tended to occupy the smallest proportion of the overall understory fuel load across all levels of moisture and age (Table 1.2; Fig. 1.3C & D). Lastly, fuel loads of evergreen and deciduous shrubs were both significantly affected by the main effect of moisture ($p = 0.029$, $r^2 = 0.01$, d.f. = 166), but they did not significantly differ with time since fire.

To further explore relationships between understory fuel loads and environmental variables, I conducted a PCA in understory fuel load-environmental space (Matrix AE’).

Cumulatively, the first two axes of the ordination explained 93 % of the variation in the understory fuel load data (Fig. 1.4). The first principal axis was highly correlated with slope (eigenvalue = -0.41), time since fire (eigenvalue = -0.40), site moisture (eigenvalue = -0.43) and elevation (eigenvalue = -0.44) (Fig. 1.4; Table S1.1). This suggests that understory fuel loads that occur in the right portion of the ordination space are negatively affected by slope, time since fire, moisture and elevation, whereas the fuel loads of understory fuel types that occur in the left portion of the ordination space are positively affected by axis 1-associated variables (Fig. 1.4). The second principle axis was highly correlated with aspect (eigenvalue = 0.46) and active layer depth (-0.75) (Fig. 1.4; Table S1.1). The opposite loading directions of aspect and active layer depth onto axis 2 suggest that the fuel loads of understory fuel types upper portion of the ordination space are positively affected by aspect and negatively affected by active layer depth, whereas the fuel loads of understory fuel types that occur in the lower portion of the ordination space are negatively affected by aspect and positively affected by active layer depth (Fig. 1.4). The PCA also indicated that some plant types, such as feather moss, *Sphagnum* moss, lichen and evergreen shrubs, occupied a greater range of the environmental space than other understory plant types, indicated by their relatively larger ellipses (Fig. 1.4). Specifically, *Sphagnum* moss and evergreen shrubs occupied a greater range of space along axis 1, whereas lichen and feather moss fuel loads occupied the greatest range of space along axis 2.

1.3.2 Environmental predictors of fuel loads

Linear mixed effects models were conducted on tree canopy, vascular understory, non-vascular understory and organic soil fuel loads separately to determine important environmental predictors of black spruce forest fuel loads (Table S1.2). For all LMER models, marginal R^2 was less than conditional R^2, indicating that the inclusion of site as a random effect of site 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 $R^2_c = 0.17$). Tree canopy fuel loads were best explained by the model that included time since fire, moisture, elevation, time since fire*average active layer, and moisture*elevation. The model indicated that time since fire, moisture, time since fire*active layer depth and moisture*elevation increased tree fuel loads ($t = 5.62, 0.56, 4.65$, and 0.67, respectively), whereas elevation reduced tree fuel loads ($t = -0.82$). The interaction effect of time since fire*active layer depth had the weakest effect on tree fuel loads.

Non-vascular understory fuel loads were best explained by the model that contained the predictors time since fire, moisture and average active layer (Table S1.2). The model indicated that non-vascular understory fuel loads increased with time since fire and moisture and decreased at site with greater active layer depth ($t = 2.89, 4.08$, and -0.14, respectively), where time since fire had the weakest effect of the three variables. Vascular understory fuel loads were best explained by the model that included the effects of time since fire and time since fire*average active layer (Table S1.2). The model indicated that both variables had a positive effect on vascular understory fuel loads ($t = 3.25$ and 1.24 for time since fire and time since fire*active layer depth, respectively).

Organic soil fuel loads were best explained by the model that contained time since fire and moisture as fixed predictors (Table S1.2). The model indicated that organic soil fuel loads increased with both time since fire and moisture across all sites, however the effect of time since fire was lower than the effect of moisture ($t = 3.48$ and 9.51, respectively). The results from the mixed effects model were in agreement with the multiple regression model results on organic soil fuel load.

1.3.3 Flammability Index

Calculation of the flammability index as the product of SLA and fuel load indicated that evergreen trees and feather mosses have the first and second highest flammability, respectively, and forbs have the lowest flammability (Table 1.3). However, incorporation of drying rate index with flammability index resulted in feather mosses having the greater and evergreen trees having the second greatest flammability index, respectively (Table 1.3). Unexpectedly, lichen had a relatively low flammability index, despite many reports in the literature of it being a highly flammable fuel type (Cronan et al. 2012; Lutz 1956; van Altena et al. 2012). The incorporation of drying rate increased lichen flammability index and it became greater than that of evergreen shrubs, which had a greater flammability index than lichens when drying rate was not incorporated. Regression analyses revealed that FI significantly increased with the proportion of evergreen tree ($p < 0.001$, $r^2 = 0.66$, d.f. = 25; Fig. 1.6) and feather moss ($p = 0.04$, $r^2 = 0.12$, d.f. = 25; Fig. 1.6) fuel loads stored within sites, which confirms the validity of my flammability index as it increases with greater proportion of highly flammable fuel loads in a site. Furthermore, assessing flammability indices of young sites with burn severity revealed that sites that burned at a high severity have lower mean flammability index (8.9 ± 0.7) than sites that burned at a low severity (14.7 ± 4.4), but this difference was not significant (Fig. 1.7).

One site, MDI4 (an intermediate, subxeric site), contained a dramatically higher FI relative to the rest of the sites which was likely due to high evergreen tree fuel loads (Table S1.4). In contrast, DCY14 (a young, subhygric site) contained the lowest FI relative to all other sites likely because it did not contain any tree canopy fuel load and very little understory fuel load quantity.

When the relationship of site-level FI was regressed with time since fire and site moisture, the analysis revealed that FI was significantly increased with time since fire and significantly decreased with site moisture ($p < 0.001$, $r^2 = 0.41$, d.f = 24; Fig. 1.5). Thus, older (intermediate and mature aged), drier (xeric and subxeric) black spruce forests are the most flammable black spruce sites, based on aboveground fuel load quantity and SLA, whereas younger, wetter (mesic-subhygric and subhygric) black spruce forests are the least flammable black spruce site types.

The regression tree model for site flammability index revealed that time since fire was the most important variable in explaining site flammability, followed by elevation and ecoregion, surficial geology, and topographic position (Fig. 1.8). The variables used in the final pruned regression tree included times since fire, elevation and topographic position. The primary split in flammability index was based on time since fire, with the lowest flammability index (FI = 14) occurring in sites less than 34 years in age, whereas sites greater than or equal to 34 years in age were further split based on elevation and topographic position (Fig. 1.8). Ecoregion, although not displayed in the tree, resulted in similar splits as time since fire, with the lowest flammability index occurring in sites within the Ray Mountains ecoregion, where sites tended to be younger, and higher flammability indices occurring in sites within the Tanana-Kuskokwim Lowlands and Yukon-Tanana Uplands ecoregions, where site tended to be older. The most flammable sites (FI = 38) occurred at elevations greater than or equal to 302 m (Fig. 1.8). The remaining terminal nodes contain moderate site flammability indices as a result of lower elevations (<302 m) and can be further subdivided by topographic position, where shoulders, side slopes and toe slopes result in lower site flammability (FI = 19) than valley bottoms, drainage channels and depressions (FI = 32).

From the multiple regression and regression tree analysis results, I can deduce that three of my study sites (i.e. DDM2, GSM5, UP4D) are representative of high flammability indices. Based on the black spruce community descriptions reported by Hollingsworth et al. (2006), these sites can be classified as non-acidic, dry, upland black spruce and acidic, dry, upland black spruce-lichen forest ecosystems.

1.4 Discussion

The burning potential of a site is in part determined by its inherent flammability, which is influenced by the quantity and quality of fuel present at a site (van Altena et al. 2012). With recent increases in frequency of larger, more severe wildfires throughout interior Alaska (Kasischke and Turetsky 2006), boreal ecosystems are at risk of post-fire shifts in plant community composition, C and N cycling patterns and permafrost stability and thus net C storage (Johnstone et al. 2010). In this study, I quantify landscape-level fuel loads, provide evidence of five important environmental predictors of black spruce forest fuel loads and identify areas of the landscape that have the highest flammability and thus, the greatest potential of experiencing severe wildfire events.

1.4.1 Landscape variation in black spruce forest fuel loads

Tree canopy fuel loads are best predicted by age of stand, and secondarily by site moisture. I found that tree canopy fuel loads constituted the greatest portion of the above-ground fuel load in intermediate and mature sites, which is consistent with previous work (Mack et al. 2008; Barney and van Cleve 1973). The highest canopy fuel loads occurred in dry, intermediate-aged sites, due to the abundance of deciduous tree fuel loads these mid-successional stands. Deciduous trees commonly establish along with black spruce trees in early succession, particularly in drier sites however, they are often outcompeted by longer lived black spruce trees later in succession (Johnstone and Chapin 2006). Processes like self-thinning and paludification, a common process in late successional black spruce stands by which forests are converted to peatlands (Simard et al. 2009), likely caused the reduction of canopy fuel loads in mature sites compared to intermediate stands. However, in contrast to the findings of Mack et al. (2008), tree canopy fuel loads in my intermediate and mature sites did not increase between dry and moderate (or mesic) moisture levels but declined with increasing site moisture (Fig. 1.3A). Reduced tree growth in wetter black spruce forests is common, due to waterlogging of roots and/or cooler soil temperatures from the proximity of permafrost to the soil surface (Roy et al. 1999), particularly in lowland areas, which likewise explains the relationships of active layer depth and elevation with tree fuel loads in the mixed-model.

Understory plant fuel loads have previously been shown to contribute the least to total fuel load (Mack et al. 2008), which is in line with my estimates of the understory contributing an average of 12 % to the total fuel load across all sites. This is greater than the proportion found for a previous studies in similar sites by Barney and van Cleve (1973), likely because they included biomass estimates of the live moss layer with organic soil biomass. Despite the low contribution of understory plants to the total fuel load, the understory is an important driver of fire behavior and spread, because it provides a continuous fuel source across the forest floor, allowing for the combustion of organic soils and fostering fire spread between highly flammable black spruce trees (Cronan et al. 2012; Todd and Jewkes 2006). My ordination analysis revealed that four understory fuel load types, specifically lichens, feather mosses, *Sphagnum* mosses and evergreen shrubs, encompassed a wider distribution across the environmental landscape compared to other understory fuel types. Highly flammable plant types, such as feather mosses, lichens, and evergreen shrubs (Cronan et al. 2012; Lutz 1956), have been shown to exert strong influences over overall forest fire dynamics even when in small abundances relative to other plant types (van Alten et al. 2012). Locations across the landscape where these three fuel types occur in high abundance may indicate highly flammable sites, in terms of their understory fuel load quality. This idea is supported by the flammability index results, where sites with a higher proportion of feather moss fuel load had significantly greater flammability index values. In contrast, *Sphagnum* mosses are relatively inflammable due to their high-moisture holding abilities (Turetsky et al. 2012). However, in recent years, drought events in interior Alaska are becoming more frequent, leading to the intensified drying of moss and organic soil layers in normally moist, relatively inflammable sites (Turetsky et al. 2011). Perhaps in the presence of feather moss, lichen and/or evergreen shrub fuel loads, *Sphagnum* moss' inflammability may be muted, particularly during abnormally dry fire seasons.

Organic soils constituted by far the largest fuel load in sites, and consistent with my results, recent studies quantifying soil depth showed evidence of deeper organic soil layers in older, wetter black spruce stands (Harden et al. 2004; Kasischke and Johnstone 2005; Miyanishi and Johnson 2002; Turetsky et al. 2011). In addition, I reported comparable soil depth, mean duff (organic soil) depth and bulk density values for mature black spruce dominated forests reported in the literature (Miyanishi and Johnson 2002). The greater organic soil fuel loads present in older, wetter sites can be attributed to the gradual accumulation of surface litter on the ground over time and the slower decomposition of organic matter in higher moisture conditions. Although active layer depth was not included as a predictor in the mixed model on organic soil fuel load, cooler soil temperatures in poorly drained sites where shallow active layer depths are common likely retarded decomposition rates of organic soils in these sites as well (Williams and Gray 1974).

1.4.2 Relevance of flammability index to burning potential

Fuel load quantity and quality are two inherent properties of a site that can translate to site-level flammability and allow us to make inferences about a site's burning potential or even its vulnerability to burning severely. Although sufficient amounts of fuel are needed to initiate and sustain wildfire, a large quantity of fuel does not necessarily equate to high site flammability, but rather this can largely be dependent on the quality of fuels present within a site. In a study by van Altena et al. (2012), it was found that even low quantities of highly flammable species can have large influences on fire dynamics that are out of proportion to their biomass. Because I was able to obtain measurements of SLA (a trait highly correlated with flammability) for above-ground fuel types, I was able to account for fuel load quality and quantity when quantifying the flammability indices of above-ground fuel loads. However, SLA is not representative of the flammability of and is of course not relevant for organic soils. In contrast, fuel moisture, and therefore drying rates, are major factors dictating the ignition and combustion of organic soils and all plant fuels in general (Rothermel 1972), in addition to weather conditions and the rainfall required to saturate them (Miyanishi and Johnson 2002; Van Wagner 1987). Drying or desiccation rates are influenced by the packing ratio, physical structure of plants, and surface area to volume ratios of different fuel types (Miyanishi 2001; Moussa et al. 1976; Turetsky et al. 2012). Relatively high bulk densities of organic soil biomass typically result in slow desiccation rates, allowing organic soils to remain saturated or moist for long periods despite changing weather conditions (Miyanishi and Johnson 2002), making it less flammable than other fuel types. However, I was unable to find quantitative reports of desiccation rates of organic soil or aboveground plants in the literature. Thus, I base the following inferences of site-level flammability solely on the flammability indices of aboveground fuels as a proxy of burning potential under dry conditions.

Similar to other studies on the flammability of boreal forest species (Cronan et al. 2012; Foote 1983; Lutz 1956; Todd and Jewkes 2006; van Altena et al. 2012; Viereck 1973, 1983), my results suggest that evergreen tree (specifically black spruce) and feather moss fuel loads had the highest flammability indices of all fuel types, even with the incorporation of a drying rate index. Notably, high site flammability indices are concurrent with significantly greater proportions of both evergreen tree and feather moss fuel loads. Additionally, the lower flammability index of young sites that burned at high severity relative to young sites that burned at low severity likely occurred because aboveground biomass takes more time to recover after severe fire and thus high severity sites have less fuel load to contribute to site flammability (Fig. 1.7). Young, high severity sites may also contain lower proportions of more flammable fuel types in their understory, such as feather moss, contributing to the decrease in their site flammability. To truly understand how well the flammability index performs, assessment of pre-fire site flammability index with burn severity of the site post-fire is necessary. I would expect that sites with high flammability index pre-fire would burn at a higher severity compared to pre-fire sites with lower flammability index; however, I do not have flammability index data for young sites prior to burning and thus I am unable to confirm this relationship. Future studies investigating burning potential of black spruce forests should consider investigating this relationship by quantifying flammability index of unburned sites as a proxy for the flammability index of nearby (within the same fire scar) burned sites of similar site characteristics where burn severity can be measured.

I found evidence that both time since fire and site moisture are significant predictors of flammability index, where older, drier black spruce sites have the highest flammability index and thus, have a greater potential of burning severely, whereas, young, wet sites contain the lowest flammability index of all sites and are least likely to experience severe burning. Specifically, the regression tree model indicated that the highest flammability indices occur in sites greater than 34 years old, within Tanana-Kuskokwim Lowland and Yukon-Tanana Upland ecoregions and at elevations greater than or equal to 302 m. Although not quantitatively supported by the flammability index, lower organic soil fuel loads in drier, higher elevation sites may also have lower bulk densities, and thus are likely more flammable due to faster desiccation rates.

From my results, I can deduce that non-acidic, dry, upland black spruce and acidic, dry, upland black spruce-lichen forest ecosystems are the most flammable and most likely black spruce ecosystems to burn in interior Alaska. Upland black spruce ecosystem types are prevalent within black spruce dominated landscapes, which occupy approximately 39-68 % of interior Alaska landscape (Calef et al. 2005; van Cleve et al. 1983). Black spruce-lichen woodland ecosystems, although occupying only ~5 % of interior Alaska, are much 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). The higher flammability of these ecosystems make them particularly vulnerable to burning severely during extreme wildfire years, which are becoming more common in interior Alaska, as well as other northern regions, due to climate change-related effects (Kasischke and Turetsky 2006). Severe fire events can completely combust organic soil layers and expose underlying mineral soil layers (Johnstone and Chapin 2006). Following low to moderate severity fire, sites contains patches of unburned, organic soil, which allows for newly establishing black spruce trees to outcompete other deciduous tree competitors. When the majority of the organic soil layer is combusted during severe fire, deciduous tree species have an advantage over black spruce trees establishing on mineral soils due to their faster growth rates, leading to black spruce seedlings being outcompeted by deciduous seedlings and a shift in the post-fire plant community (Johnstone and Chapin 2006). A shift to deciduous dominated forest types following severe fires would cause drastic changes to ecosystem services, C and N cycling, permafrost stability, C storage (Johnstone et al. 2010). Boreal soils, particularly permafrost-rich soils, store approximately one third of the Earth's terrestrial C stocks (IPCC 2007; Pan et al. 2011), thus a shift from black spruce forests to deciduous forest types results in significant losses of C during severe fire events (Genet et al. 2013).

1.5 Management Implications

This study provides detailed accounts of black spruce forest fuel loads across interior Alaska, from organic soil to vascular and non-vascular understory to tree canopy, which, along with the models I developed for predicting fuel load, can be applied to creating more detailed fuel maps to assist with the prediction of flammability and fire potential in black spruce forests. Site-level flammability indices based on above-ground plant fuel loads indicated that sites could be split into low, moderate and high flammability levels using time since fire, elevation, and topographic position as explanatory variables. Specifically, non-acidic, dry, upland black spruce and acidic, dry, upland black spruce-lichen forest ecosystem types with relatively large stores of evergreen tree and feather moss fuel load have the greatest potential of burning severely and thus, are most vulnerable to experiencing shifts in post-fire plant community types. Knowledge on site-level flammability can assist fire managers in prioritizing the management and protection of flammable sites that contain high ecosystem, economic and community values.

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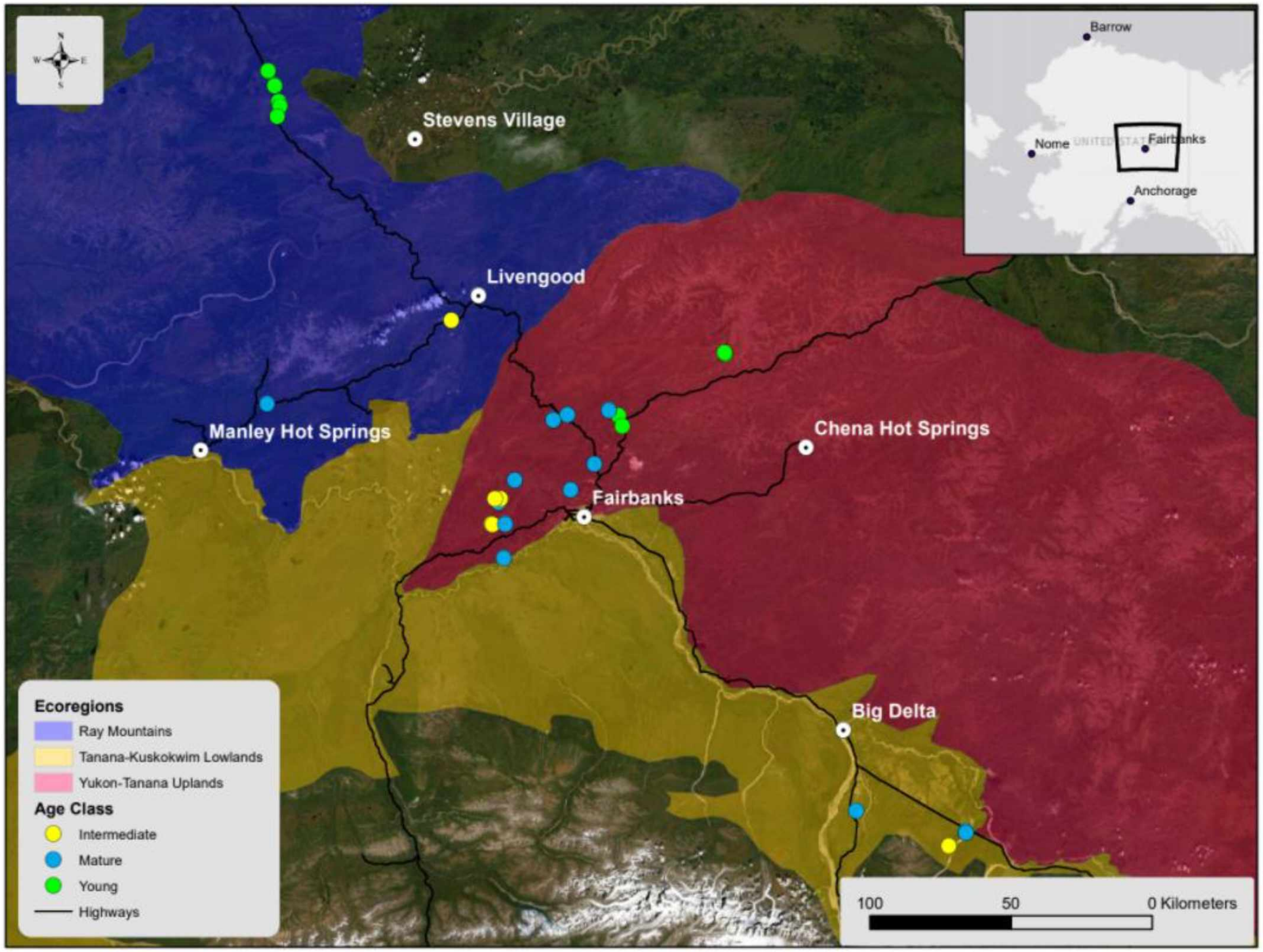

Figure 1.1 Map of the study region, within interior Alaska, USA, with ecoregions indicated in shaded areas (Ray Mountains = blue, Tanana-Kuskokwim Lowlands = yellow, Yukon-Tanaa Uplands = red). Circles indicate the locations of 28 young (0-15 years post-fire; green circles), intermediate (40-60 years post-fire; yellow) and mature (>80 years post-fire; blue) aged black spruce dominated study sites. Major highways are denoted by black lines. Map couresty of Jamie Hollingsworth, site manager of the Bonanza Creek Long-Term Ecological Research group.

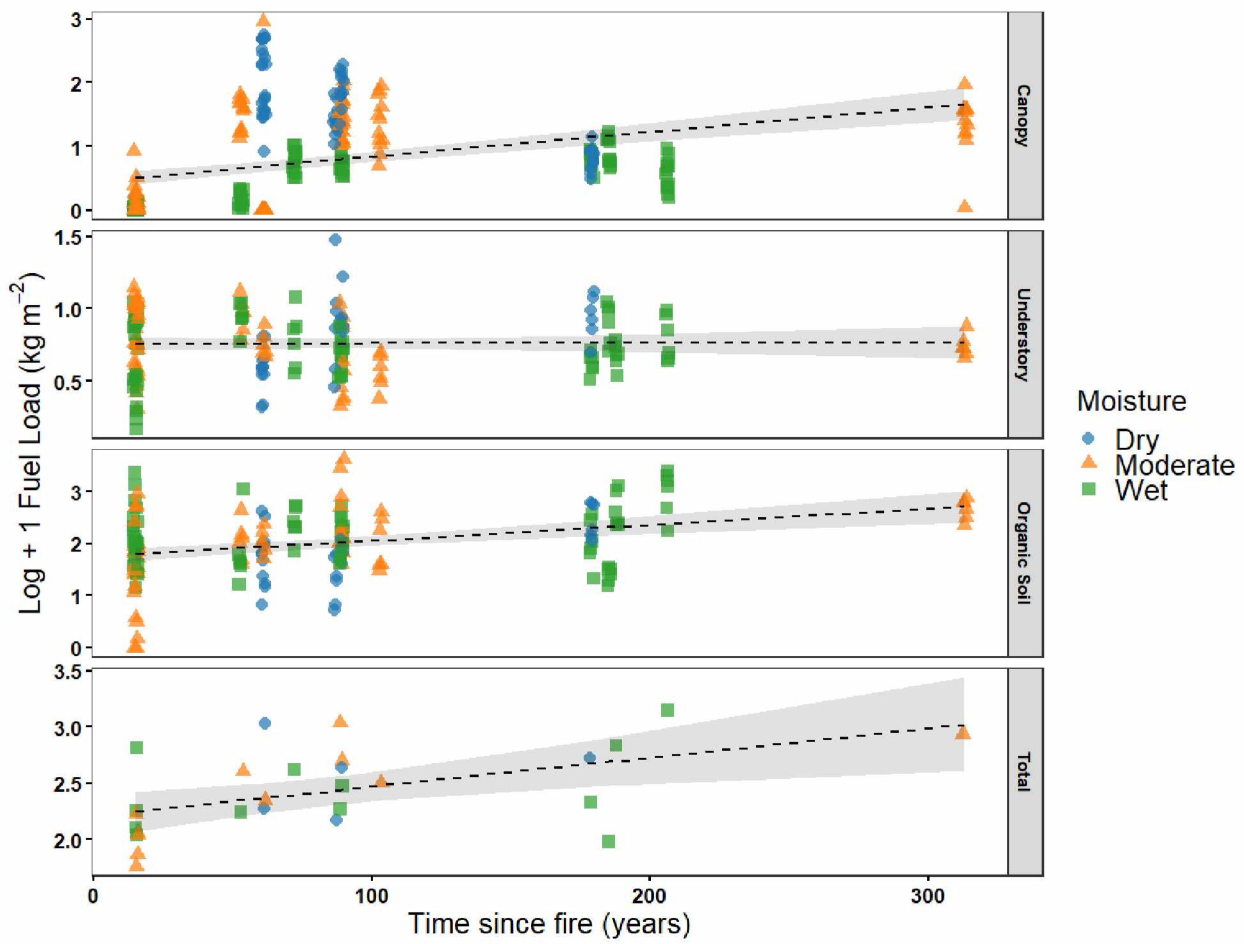

Figure 1.2 Plot-level fuel load quantities of tree, understory and organic soil fuels and site-level quantities of total fuel load as a function of time since fire. The fuel load axis is transformed by the addition of value of 1 and then by taking the natural log. The color of points within each panel indicate the site moisture of the plot/site (dry moisture = blue, moderate moisture = orange, wet moisture = green). Dotted lines in each panel represent linear regressions of tree, understory, organic soil and total fuel load quantity with time since fire. Gray areas surrounding each regression line represents 95 % confidence intervals.

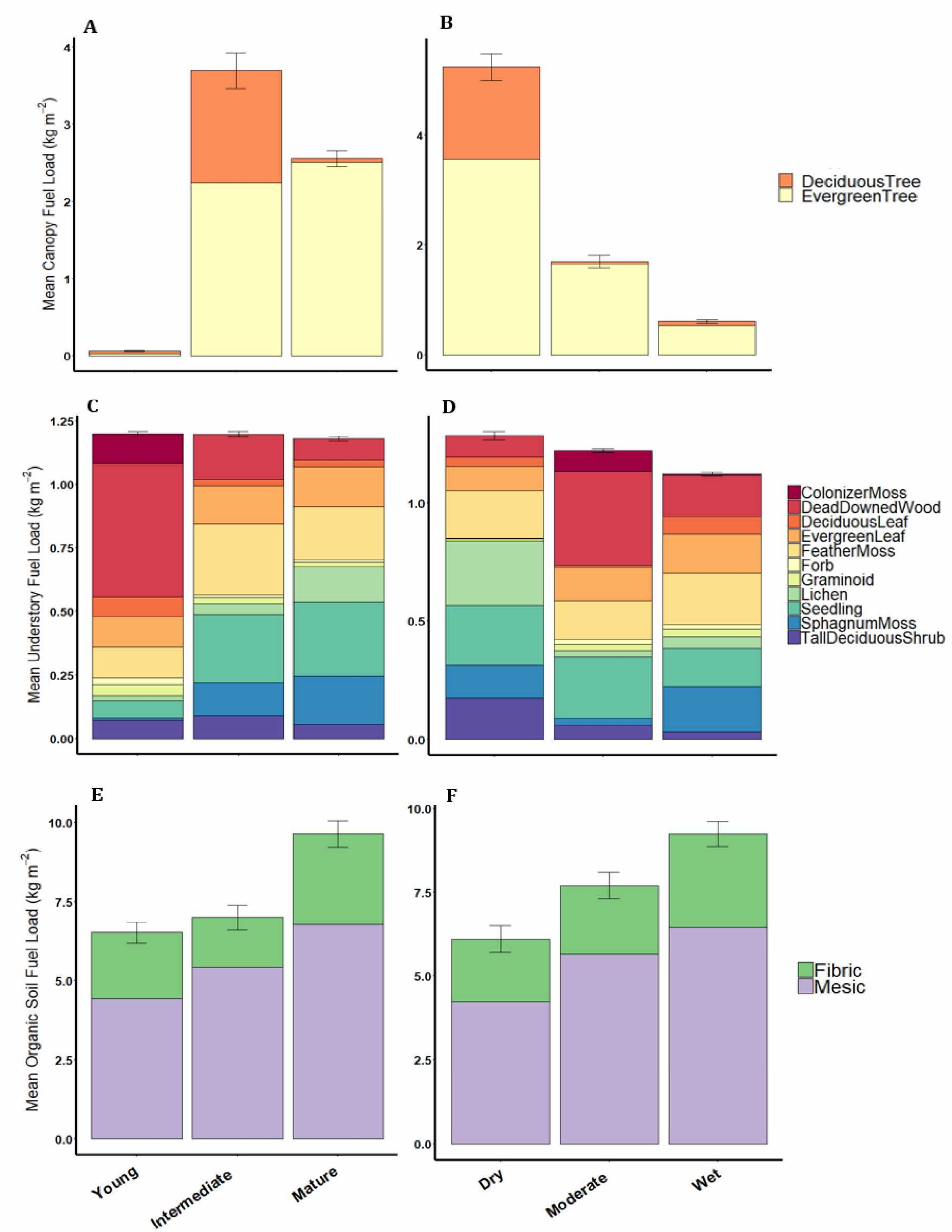

Figure 1.3 Mean (A, B) tree, (C, D) understory and (E, F) organic soil fuel loads (kg m^{-2}) plotted against stand age classes and site moisture levels. Error bars are ± the standard error for the total mean fuel load for each of tree canopy, understory and organic soil fuel load classes. Bar colors indicate a respective fuel type, presented in the plot legends.

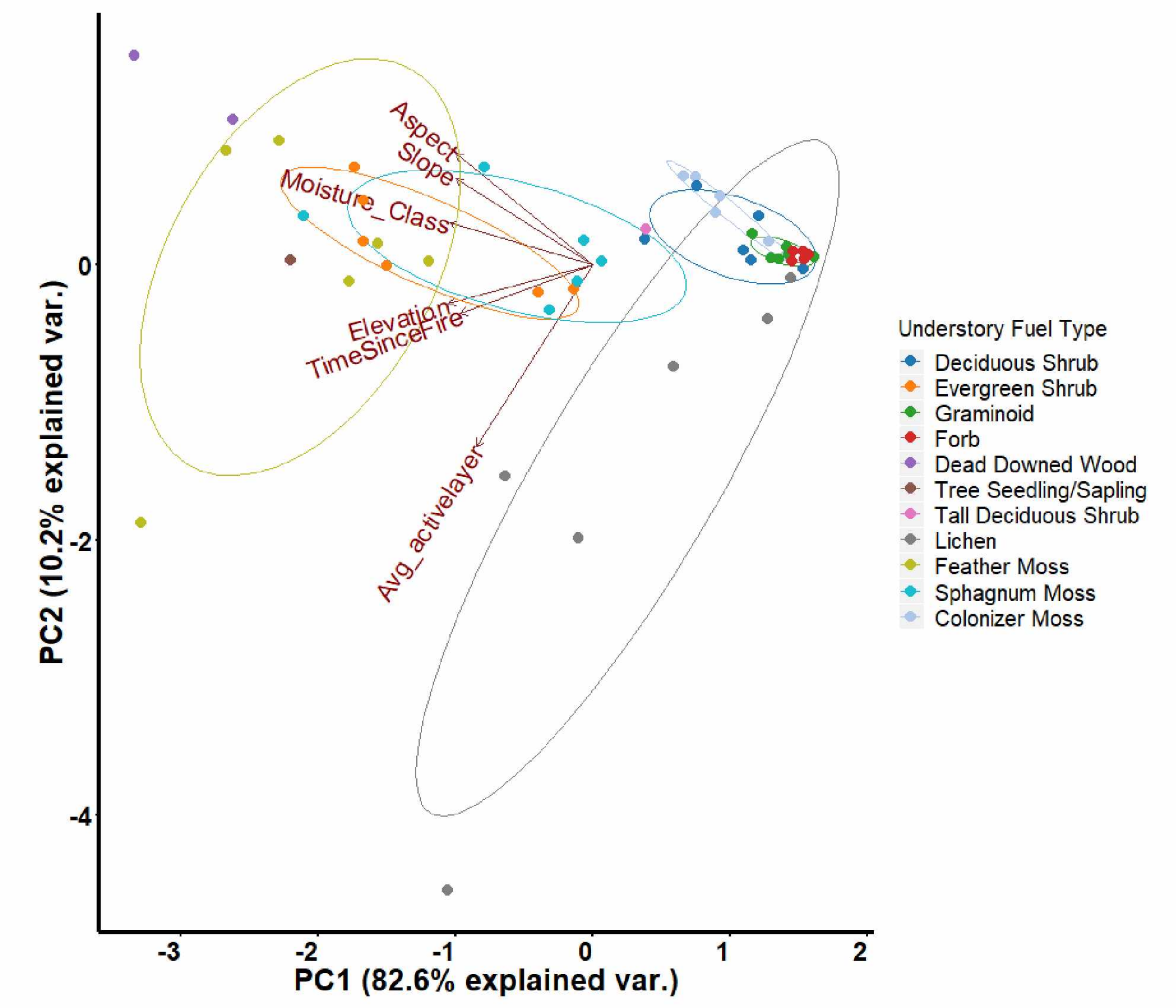

Figure 1.4 Principal component analysis (PCA) biplot showing the distribution of plot-level understory fuel load quantity, grouped by fuel type (plant functional type), in environmental space. The first and second principal components explained 82.6 % and 10.2 % of the variation in understory fuel loads, respectively. The positions of points within the ordination space correlate to their relationship with six environmental variables, indicated by the vectors in the plot (TimeSinceFire = stand age, Moisture_class = site moisture, Aspect, Slope, Elev = elevation, ActLay = average active layer). Arrows indicate the direction and weighting of each environmental variable.

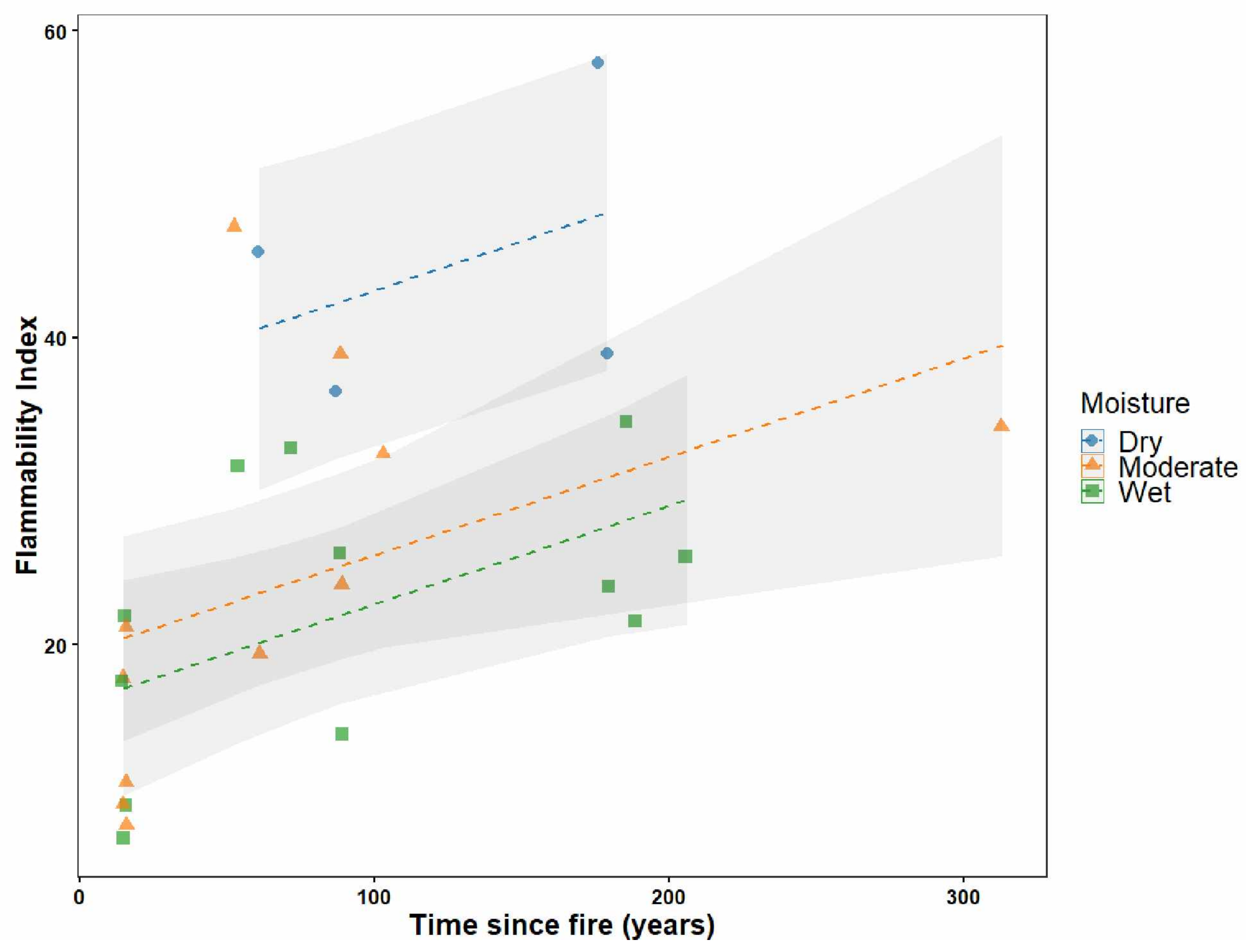

Figure 1.5 Site flammability index as a function of time since fire. Colors of points correspond to site moisture levels (dry moisture = blue, moderate moisture = orange, wet moisture = green). Dotted lines represent the regression of flammability index with time since fire and moisture levels. Gray areas surrounding regression lines are 95% confidence intervals.

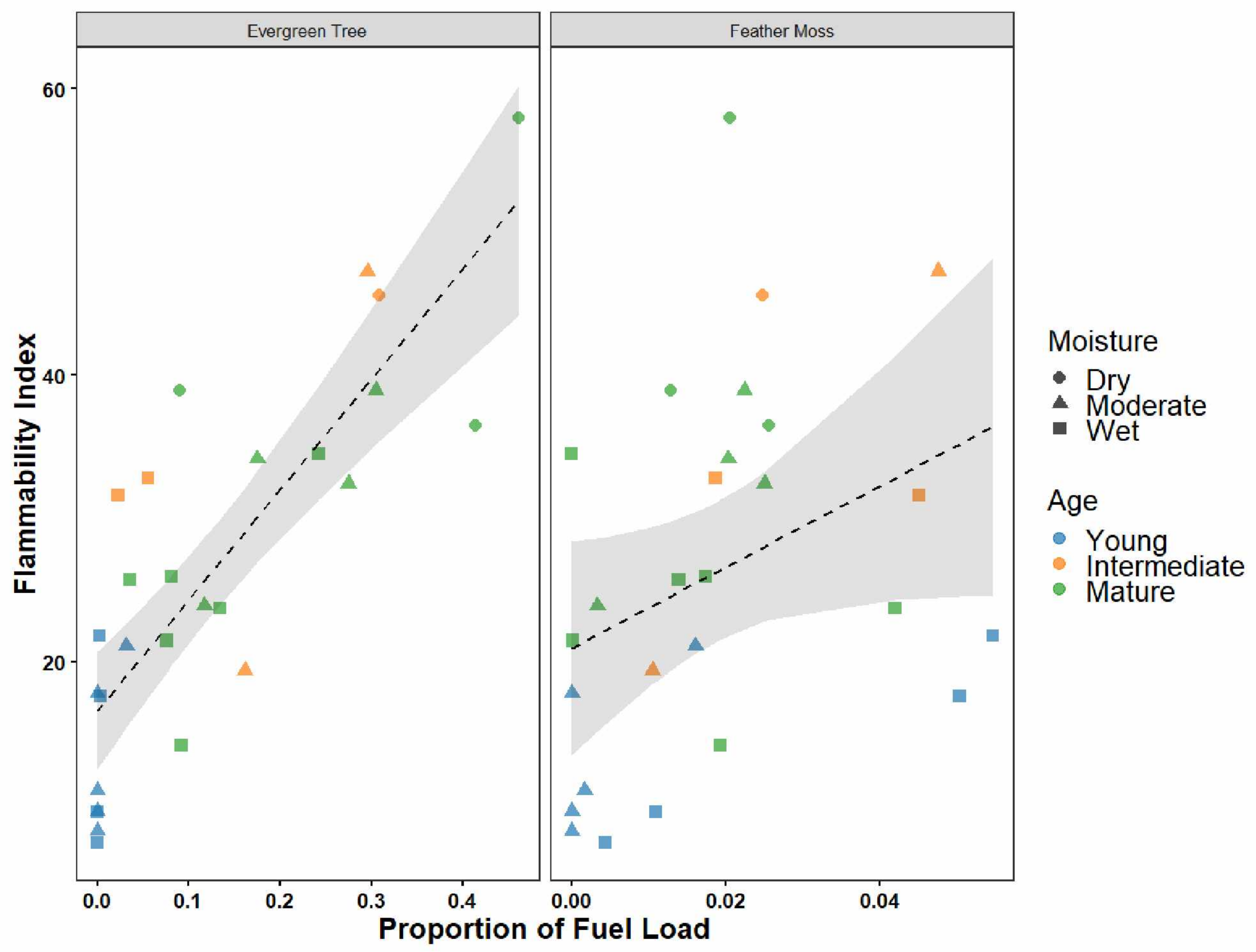

Figure 1.6 Site flammability index as a function of the proportion of evergreen tree and feather moss fuel load. Data points are grouped by age class (young = blue, intermediate = orange, mature = green) and moisture level (dry = circle, moderate = triangle, wet = square). Dotted lines represent the regression of flammability index with proportion of fuel load. Gray areas represent 95 % confidence intervals.

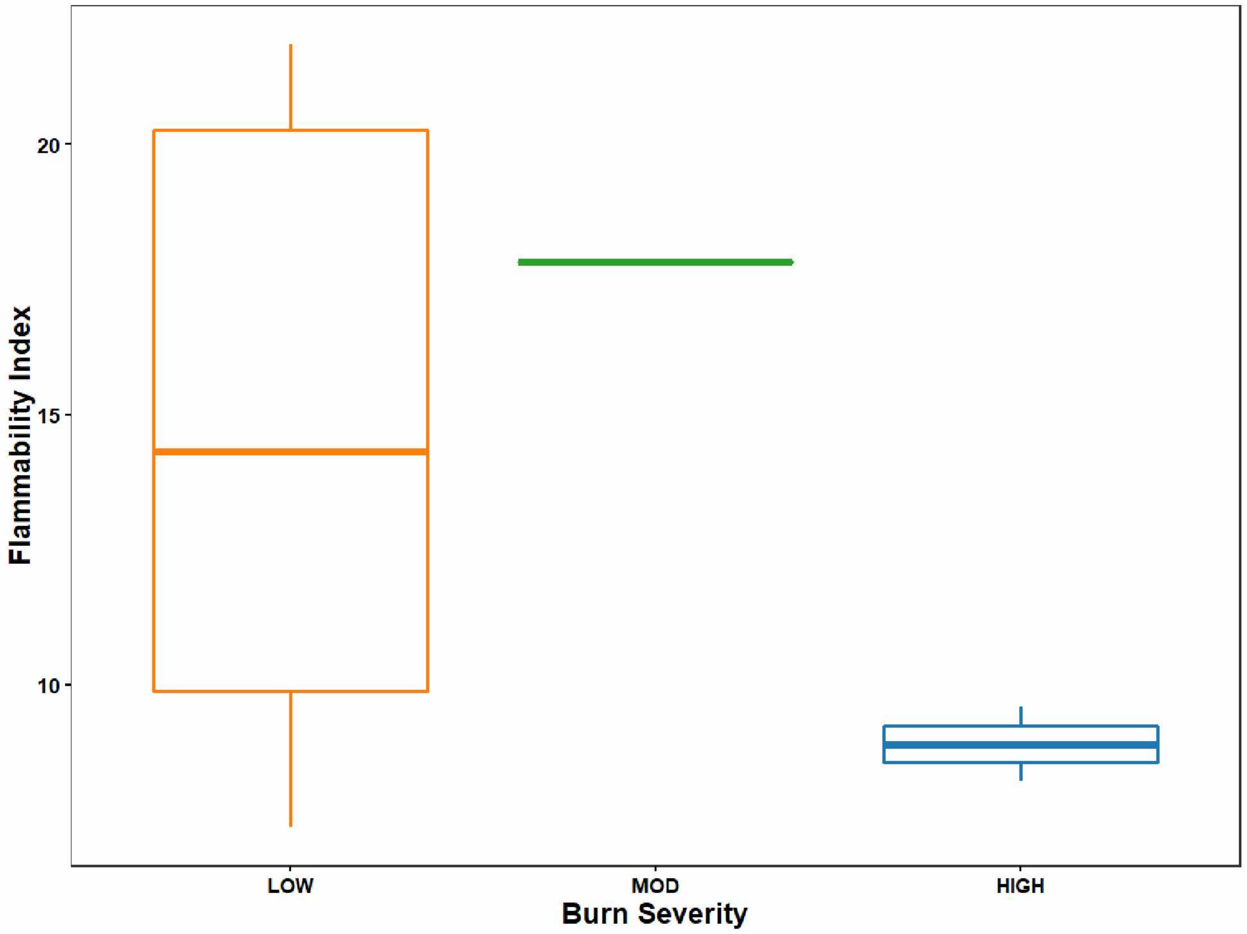

Figure 1.7 Boxplot of site flammability index with burn severity for young study sites only (n = 9). Site burn severity encompassed low (n = 6), moderate (n = 1) and high (n = 2) severities. Plot whiskers represent 95 % confidence intervals.

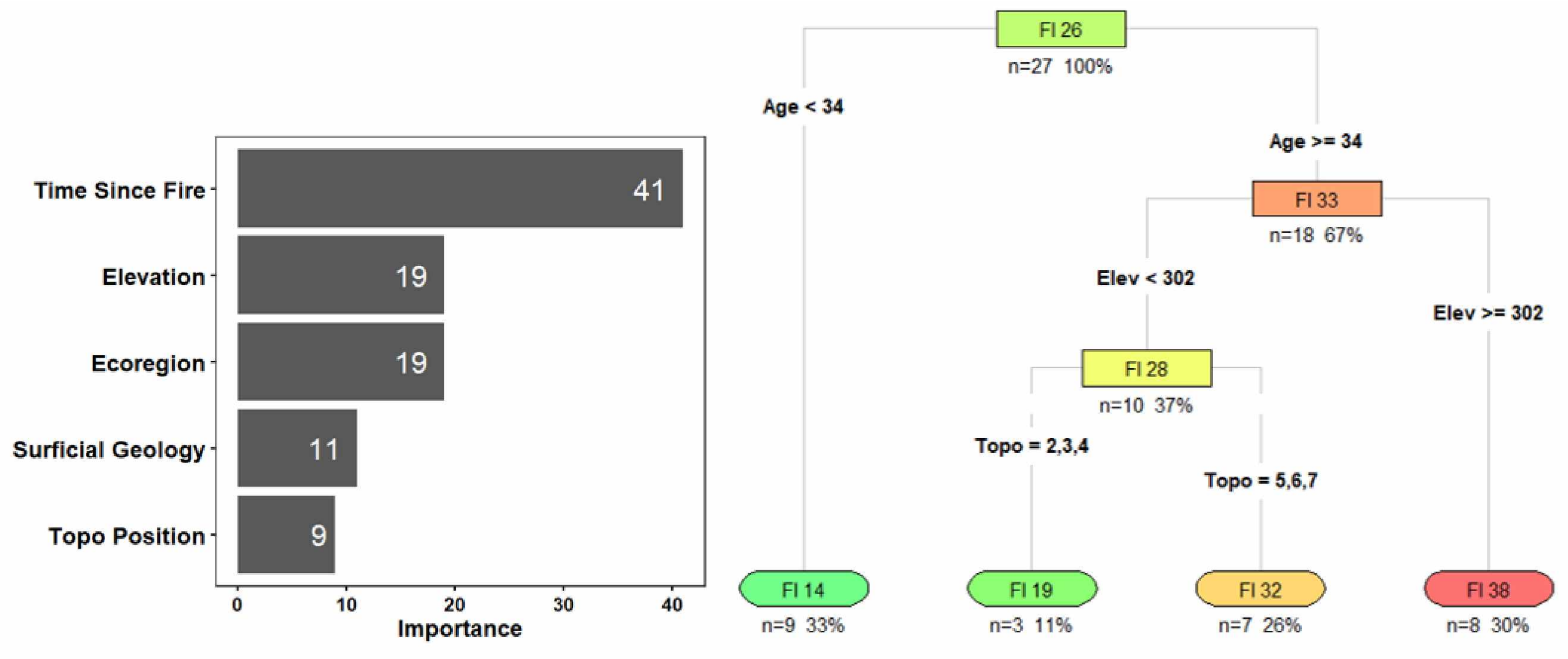

Figure 1.8 Relative importance of variables and regression tree model from a regression tree analysis predicting site flammability index with five environmental variables. Mean flammability index values are presented in the tree nodes. Sample size (n) and percentage of sites belonging to each node are presented below each node. Variables used in the construction of the final, pruned tree model include time since fire (Age), elevation (Elev) and topographic position (Topo). Topographic positions 1 through 7 correspond to summit, shoulder, side slope, toe slope, valley bottom, drainage channel and depression, respectively.

Table 1.1 Names of the 28 study sites and information on years since they last burned, age class (Young = 0-10 years, Intermediate = 40-60 years, and Mature = >80 years after fire), location (latitude and longitude are in decimal degrees; ecoregions YTU = Yukon-Tanana Uplands, RM = Ray Mountains, TKL = Tanana-Kuskokwim Lowlands), and site description (forest type BL SP = Black Spruce, MIX = Conifer-Deciduous Mixed; site moisture driest to wettest: xeric, subxeric, subxeric/mesic, mesic, mesic/subhygric, subhygric; average active layer depth -999 = nonexistent or too deep to measure, -888 = unable to measure due to mineral layer).

Site	**Time Since Fire**	**Age Class**	**Eco-region**	**Latitude (°)**	**Longitude (°)**	**Forest Type**	**Moisture**	**Burn Severity**	**Elevation (m)**	**Average active layer depth (cm)**
BFY10	15	Young	YTU	65.1187	-147.449	MIX	Subxeric/Mesic	MODERATE	445	-999
BFY7	15	Young	YTU	65.1537	-147.477	BL SP	Mesic/Subhygric	LOW	240	66.3
BFY8	15	Young	YTU	65.3493	-146.668	BL SP	Mesic	LOW	695	89.7
BFY9	15	Young	YTU	65.3531	-146.675	BL SP	Subxeric/Mesic	LOW	770	-999
DCY14	15	Young	RM	66.1203	-150.163	BL SP	Subhygric	LOW	170	-999
DCY2	15	Young	RM	66.2152	-150.258	MIX	Mesic/Subhygric	LOW	445	-999
DCY3	15	Young	RM	66.0723	-150.168	MIX	Subxeric/Mesic	HIGH	206	92.0
DCY4	15	Young	RM	66.1053	-150.151	MIX	Subhygric	LOW	220	81.3
DCY9	15	Young	RM	66.1686	-150.201	MIX	Mesic	HIGH	300	75.1
GRI1	72	Intermediate	TKL	63.7721	-145.079	BL SP	Subhygric	NA	552	41.5
GSI1	53	Intermediate	YTU	64.8000	-148.414	BL SP	Mesic	NA	244	80.7
GSI2	53	Intermediate	YTU	64.8026	-148.420	BL SP	Subhygric	NA	129	54.9
LGI2	61	Intermediate	RM	65.4465	-148.761	BL SP	Subxeric	NA	330	-888
MDI4	61	Intermediate	YTU	64.8827	-148.356	MIX	Subxeric	NA	205	155.1
MDI5	61	Intermediate	YTU	64.8829	-148.398	BL SP	Mesic	NA	226	47.3
BCEFM2	Pre 1930	Mature	YTU	64.6952	-148.323	BL SP	Subhygric	NA	128	29.8
BDM1	Pre 1930	Mature	RM	65.1579	-150.136	BL SP	Mesic	NA	241	-888
DDM2	87	Mature	TKL	63.8918	-145.741	BL SP	Xeric	NA	500	-888
GRM3	206	Mature	TKL	63.8137	-144.954	Bl SP	Mesic/Subhygric	NA	430	44.2
GRM4	313	Mature	TKL	63.8151	-144.956	BL SP	Subxeric/Mesic	NA	429	53.6
GSM1	179	Mature	YTU	64.8026	-148.317	BL SP	Subhygric	NA	180	25.2
GSM3	185	Mature	YTU	64.9162	-147.832	Bl SP	Subhygric	NA	187	70.7
GSM4	103	Mature	YTU	64.9422	-148.253	BL SP	Subxeric/Mesic	NA	497	-888
GSM5	179	Mature	YTU	64.9986	-147.657	BL SP	Subxeric	NA	431	42.2
MDM1	Pre 1930	Mature	YTU	64.8716	-148.371	BL SP	Mesic	NA	197	49.4
UP4D	Pre 1930	Mature	YTU	65.1691	-147.551	BL SP	Subxeric	NA	600	-999
WCM2	Pre 1930	Mature	YTU	65.1363	-147.971	BL SP	Mesic/Subhygric	NA	260	35.2
WCM3	188	Mature	YTU	65.1547	-147.863	BL SP	Subhygric	NA	274	53.5

Table 1.2 Mean fuel load and standard error (in brackets) for each plant fuel type (DDW = downed dead wood), each fuel category, and overall fuel total within stand age and site moisture classes. NA indicates data was not available.

			Fuel Load (kg·m^{-2})												
			Canopy		Understory										
Stand Age	Moisture	n	Deciduous tree	Evergreen tree	Tall deciduous shrub	Deciduous shrub	Evergreen shrub	Tree seedling	Graminoid	Forb	Sphagnum moss	Feather moss	Colonizer moss	Lichen	DDW
Young															
	Subxeric/Mesic	3	0.10 (0.05)	0.06 (0.02)	0.06 (0.05)	0.01 (0.01)	0.18 (0.07)	0.09 (0.09)	0.01 (0.00)	0.01 (0.01)	0.00 (0.00)	0.03 (0.03)	0.22 (0.05)	0.03 (0.02)	0.79 (0.23)
	Mesic	2	0.01 (0.01)	0.00 (0.00)	0.06 (0.01)	0.00 (0)	0.12 (0.04)	0.10 (0.09)	0.09 (0.03)	0.05 (0.01)	0.00 (0.00)	0.00 (0.00)	0.15 (0.04)	0.00 (0.00)	0.59 (0.25)
	Mesic/Subhygric	2	0.00 (0.00)	0.02 (0.01)	0.16 (0.15)	0.22 (0.09)	0.07 (0.03)	0.04 (0.02)	0.01 (0.01)	0.05 (0.01)	0.00 (0.00)	0.41 (0.07)	0.00 (0.00)	0.00 (0.00)	0.45 (0.14)
	Subhygric	2	0.00 (0.00)	0.00 (0.00)	0.02 (0.00)	0.11 (0.05)	0.09 (0.04)	0.02 (0.00)	0.06 (0.01)	0.01 (0.01)	0.04 (0.04)	0.07 (0.04)	0.04 (0.02)	0.04 (0.03)	0.15 (0.07)
Intermediate															
	Subxeric	2	4.12 (0.71)	3.67 (0.31)	0.08 (0.02)	0.00 (0)	0.05 (0.02)	0.31 (0.28)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.18 (0.05)	0.00 (0.00)	0.05 (0.04)	0.14 (0.09)
	Mesic	2	0.01 (0.01)	2.61 (0.8)	0.17 (0.08)	0.01 (0.01)	0.11 (0.04)	0.36 (0.01)	0.02 (0.01)	0.02 (0.01)	0.07 (0.04)	0.35 (0.1)	0.00 (0.00)	0.00 (0.00)	0.26 (0.08)
	Subhygric	2	0.23 (0.07)	0.45 (0.07)	0.02 (0.01)	0.07 (0.04)	0.29 (0.05)	0.13 (0.02)	0.05 (0.04)	0.01 (0.00)	0.33 (0.1)	0.31 (0.09)	0.00 (0.00)	0.07 (0.06)	0.13 (0.01)
Mature															
	Xeric	1	0.01 (0.01)	3.2 (0.28)	0.00 (NA)	0.00 (0)	0.13 (0.02)	0.12 (NA)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.20 (0.2)	0.00 (0.00)	1.06 (0.45)	0.09 (0.05)
	Subxeric	2	0.08 (0.06)	3.62 (0.55)	0.36 (0.36)	0.10 (0.07)	0.14 (0.03)	0.26 (0.08)	0.02 (0.01)	0.00 (0.00)	0.35 (0.11)	0.22 (0.06)	0.00 (0.00)	0.10 (0.05)	0.05 (0.02)
	Subxeric/Mesic	2	0.07 (0.03)	3.10 (0.31)	0.00 (0.00)	0.02 (0.01)	0.19 (0.05)	0.26 (0.15)	0.01 (0.00)	0.01 (0.01)	0.00 (0.00)	0.32 (0.03)	0.00 (0.00)	0.02 (0.01)	0.11 (0.04)
	Mesic	2	0.00 (0.00)	3.29 (0.28)	0.00 (0.00)	0.00 (0)	0.08 (0.02)	0.55 (0.37)	0.02 (0.01)	0.01 (0.00)	0.10 (0.06)	0.19 (0.05)	0.00 (0.00)	0.07 (0.05)	0.04 (0.02)
	Mesic/Subhygric	2	0.00 (0.00)	0.80 (0.09)	0.00 (0.00)	0.03 (0.02)	0.17 (0.05)	0.23 (0.04)	0.01 (0.01)	0.02 (0.00)	0.12 (0.06)	0.24 (0.09)	0.00 (0.00)	0.14 (0.04)	0.13 (0.05)
	Subhygric	4	0.07 (0.01)	1.21 (0.07)	0.00 (0.00)	0.01 (0.01)	0.18 (0.03)	0.27 (0.03)	0.02 (0.00)	0.01 (0.00)	0.34 (0.07)	0.14 (0.05)	0.00 (0.00)	0.02 (0.01)	0.09 (0.03)

			Organic Soil		Total Fuel Load				
Stand Age	Moisture	n	Fibric	Mesic	∑ Canopy	∑ Vascular understory	∑ Nonvascular understory	∑ Organic soil	∑ Fuel
Young									
	Subxeric/Mesic	3	1.06 (0.22)	4.20 (0.89)	0.16 (0.04)	1.16 (0.07)	0.29 (0.03)	5.25 (0.65)	6.85 (0.25)
	Mesic	2	0.78 (0.17)	3.78 (1.23)	0.01 (0.00)	1.02 (0.07)	0.16 (0.02)	4.55 (0.88)	5.73 (0.33)
	Mesic/Subhygric	2	3.14 (0.74)	3.26 (0.69)	0.03 (0.01)	1.00 (0.06)	0.41 (0.03)	6.40 (0.72)	7.84 (0.27)
	Subhygric	2	3.88 (1.09)	6.68 (1.31)	0.00 (0.00)	0.47 (0.04)	0.18 (0.03)	10.56 (1.2)	11.21 (0.45)
Intermediate									
	Subxeric	2	1.19 (0.18)	4.36 (0.97)	7.8 (0.55)	0.59 (0.06)	0.23 (0.03)	5.55 (0.7)	14.16 (0.39)
	Mesic	2	1.17 (0.24)	5.82 (0.58)	2.62 (0.56)	0.96 (0.03)	0.41 (0.05)	6.99 (0.45)	10.99 (0.34)
	Subhygric	2	2.37 (0.44)	6.09 (1.36)	0.68 (0.07)	0.70 (0.03)	0.71 (0.07)	8.46 (1.01)	10.54 (0.38)
Mature									
	Xeric	1	0.67 (0.22)	2.26 (0.73)	3.21 (0.2)	0.34 (0.02)	1.26 (0.25)	2.93 (0.54)	7.74 (0.26)
	Subxeric	2	3.18 (0.96)	5.09 (1.05)	3.69 (0.39)	0.92 (0.08)	0.67 (0.07)	8.26 (1.01)	13.55 (0.43)
	Subxeric/Mesic	2	1.96 (0.69)	8.46 (1.3)	3.16 (0.22)	0.60 (0.04)	0.34 (0.02)	10.42 (1.04)	14.52 (0.4)
	Mesic	2	5.8 (2.67)	6.73 (0.97)	3.29 (0.2)	0.70 (0.07)	0.37 (0.05)	12.53 (2.01)	16.87 (0.75)
	Mesic/Subhygric	2	1.43 (0.27)	12.15 (2.38)	0.80 (0.06)	0.60 (0.03)	0.50 (0.06)	13.57 (1.69)	15.46 (0.63)
	Subhygric	4	2.94 (0.64)	5.27 (0.55)	1.28 (0.05)	0.58 (0.02)	0.51 (0.04)	8.21 (0.6)	10.58 (0.22)

Table 1.3 Average flammability index (± SE), drying rate index (1 = slow drying rate, 3 = fast drying rate), and the product of flammability index and drying rate index (FI x DR) for each aboveground fuel type.

Fuel Type	Flammability index	Drying rate index	FI x DR
Evergreen tree	9.43 (1.93)	2	18.86
Feather moss	7.00 (1.09)	3	21.00
Deciduous tree	6.18 (4.59)	2	12.35
Sphagnum moss	3.81 (1.22)	1	3.81
Colonizer moss	1.73 (0.77)	2	3.47
Evergreen shrub	0.82 (0.11)	2	1.63
Lichen	0.68 (0.32)	3	2.05
Tall deciduous shrub	0.55 (0.22)	2	1.10
Deciduous shrub	0.46 (0.16)	2	0.92
Graminoid	0.31 (0.07)	2	0.61
Forb	0.18 (0.03)	2	0.36

Chapter 2 Utilizing intra-specific variation in fire-ecological plant traits to indicate black spruce forest resilience

Abstract

Boreal black spruce forests have a strong relationship with fire, particularly in terms of their plant community composition and fire-ecological plant traits. Recent evidence indicates benefits of within-population intra-specific plant trait variability to the functioning of ecosystems that are experiencing variable environmental conditions, suggesting that greater intra-specific trait variability may also be beneficial for forest resiliency to a changing fire regime. In this study, I investigate the variation in plant traits related to the fire ecology of two ubiquitous species in black spruce forests, *Hylacomium splendens* (splendid feather moss) and *Vaccinium uliginosum* (bog blueberry). I predict that intra-specific variation in fire-ecological plant traits will increase with time and vary with moisture gradients of the black spruce forest landscape. Plant traits of *H. splendens* and *V. uliginosum* varied significantly along age and moisture gradients. Additionally, certain sites did contain greater amounts of intra-specific variation (or CV) in *H. splendens* and in *V. uliginosum* traits, however, CV did not vary significantly with stand age or site moisture, which did not support my initial prediction and suggests that intra-specific trait variation and forest resilience may dependent on other environmental gradients. Future research investigating intra-specific trait variability should consider the effects of both abiotic and biotic variables, as well as their effects on traits of multiple plant functional types, to better understand what influences the amount of intra-specific trait variation, and thus forest resiliency, in boreal black spruce ecosystems.

2.1 Introduction

In the boreal forest biome, wildfires are a natural and important ecological process that promote the cycling of nutrients, maintenance of diversity and prevent the decline of productivity associated with retrogression of old growth forests (Kurkowski et al. 2008; Nilsson and Wardle 2005; Payette 1992). Landscapes in interior Alaska have been affected by regular intervals of low to moderate severity fire disturbances for the past 5500 years (Lynch et al. 2003), resulting in many interdependent relationships between boreal plant communities and fire. Black spruce (*Picea mariana*) plant communities, the dominant forest type in boreal interior Alaska (van Cleve et al. 1983), have a particularly strong relationship with fire. Black spruce forests are adapted to low to moderate severity fire and often undergo self-replacement during post-fire succession (van Cleve et al. 1991), although other post-fire successional pathways are known to occur (Johnstone et al. 2008). The interaction between fire and these plant communities has promoted the perpetuation of this forest type over thousands of years in interior Alaska (Lynch et al. 2003).

Boreal Alaska and other northern regions globally are experiencing climate warming twice as fast as the global average (Wolken et al. 2011). Climate is a strong predictor of the fire regime in Alaska and recent studies have indicated correlation between large fire years and periods of drought resulting from warmer summer temperatures (Duffy et al. 2005; Gillett and Weaver 2004). Recent shifts in interior Alaska's fire regime are resulting in larger, more frequent, and more severe fires (Kasischke and Turetsky 2006). Burn severity, defined as the proportion of organic matter combusted by fire (Rowe 1983), strongly influences post-fire successional trajectory (Johnstone & Chapin 2006). Under a normal, low to moderate severity fire regime, patches of highly organic soils are left-over after fire, providing a suitable seed bed for self-regenerating semi-serotinous black spruce trees. However, under an intensified fire regime, high severity fires that consume the thick, soil organic layers allow regenerating deciduous tree species to have a competitive advantage over black spruce seedlings, causing a break in the self-replacement cycle of black spruce forests (Johnstone & Chapin, 2006). Consequentially, a post-fire shift to deciduous dominated communities would impact the functioning and dynamics of boreal ecosystems, with implications for the global carbon cycle.

There is evidence of benefits of greater intra-specific trait variability within plant populations for ecosystem responses to environmental changes or disturbance (Cornelisson et al. 2003; Garnier et al. 2007; Helsen et al. 2017; Henn et al. 2018). The probability of a community persisting through fluctuations in environmental conditions or disturbance regimes increases when conspecific individuals together possess a greater range of functional trait values or “attributes” (Bolnick et al. 2011; Hooper et al. 2005). Under changing climatic conditions, the resilience of plant communities, and likely entire ecosystems, to fluctuations in the environment will likely be partially dependent on the amount of intra-specific variation possessed by populations (Violle et al. 2007). In the context of the boreal region, ecosystems that contain greater-within population variation in plant traits will have greater potential to remain resilient to changes in the fire regime and resist the shift to alternate ecological states during post-fire succession.

Black spruce plant communities, in particular, contain species that possess specific functional traits (referred to as fire-ecological traits for the remainder of this study) that allow individuals to cope and/or respond to low-moderate severity fire, either in the form of fire-resistance or post-fire reproductive success (Pyne 2010; Violle et al. 2007). For example, the abundance of *Sphagnum* mosses in the understory, a moss genus known for its high water retention abilities, resist burning during fire (Rochfort et al. 1990; Turetsky et al. 2010), whereas feather mosses and lichens, known for their rapid desiccation and high flammability (Cronan et al. 2012; Lutz 1956), assist in the spread of fire across a site. Incomplete burning of organic soil layers, typical of low-moderate severity fires, results in a highly organic post-fire seed bed, which promotes the establishment of black spruce seedlings (Johnstone & Chapin, 2006) after the heat from fire causes the aerial, semi-serotinous cones of black spruce to open and release seeds (Johnstone et al. 2008). Certain vascular understory species possess asexual reproduction strategies, such as resprouting from rhizomatous roots (Bernhardt et al. 2011; Lutz 1956; Viereck 1983), which allows them to successfully regenerate after fire even when fire destroys their seed source. The suite of fire-ecological traits of many species in black spruce communities helps promote a fire regime that fosters self-replacement successional pathways and resilience to fire (Chapin et al. 1993; Keeley et al. 2011; Nilsson and Wardle 2005; Roberts 2004). Additionally, many boreal plant species are known to have high phenotypic plasticity, likely because they live in relatively stressful environments (Chapin III et al. 1993; Roy and Mulder 2014), which suggests that plant species in black spruce communities will vary in their fire-ecological plant traits across the landscape.

In this study, I hypothesized that intra-specific variation in fire-ecological plant traits represents forest resilience to changes in the fire regime. I predicted that trait variation will increase with time and vary with moisture gradients. To investigate this, I examined variation fire-ecological plant trait attributes of the most ubiquitous non-vascular (*Hylocomium splendens*) and vascular (*Vaccinium uliginosum*) understory species in study sites across stand age and site moisture gradients. I calculated coefficient of variation (CV) or a measure of the amount of within site variation in fire-ecological traits and identified locations with the greatest CV, and thus likely the greatest forest resilience.

2.2 Methods

2.2.1 Study Area

The study area spans 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), within interior Alaska, USA (Fig. 2.1) and is characterized by swampy lowlands, gently sloping uplands, braided rivers and floodplains. The study area is underlain by discontinuous permafrost, which typically occurs on north-facing slopes and in low-lying areas, with a continental climate and extreme temperatures. The 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).

2.2.2 Field Sampling

During the summer of 2019, I sampled 26 black spruce dominated sites that were previously established by the Bonanza Creek Long Term Ecological Research (BNZ-LTER) program (Fig. 2.1). These sites span across a gradient of site moisture and across a gradient of stand age (time since fire). The sites ranged in moisture (moisture classes from driest to wettest include: xeric, subxeric, subxeric/mesic, mesic, mesic/subhygric and subhygric) and included young (0-15 years since fire), intermediate (40-60 years), and mature (>80 years) stands (Table

2.1). Study sites were easily accessible along five highways: the Dalton Highway, the Elliot Highway, the Steese Highway, the Richardson Highway and the Parks Highway. Study sites ranged in active layer depth (depth to permafrost) from 25-155 cm and in elevation from 128-770 m above sea level (Table 2.1). Previous burn severity of young sites ranged from low to moderate, but burn severity was unknown for intermediate and mature sites. Mature and intermediate sites were representative of black spruce community subtypes common to the interior Alaskan region (Hollingsworth et al. 2006). Young sites were dominated by black spruce or a mix of black spruce and hardwood tree saplings in their understory. Prior to the last fire, all sites were forests dominated by black spruce.

One permanent study plot (50 x 60 m) at each site included a 10 m wide border around each side. Upon establishment of these sites in 2011, the BNZ-LTER measured environmental characteristics (age or time since fire, moisture, elevation, slope, aspect, active layer depth, topographic position, and surficial geology) and annually measures active layer depth at each site.

2.2.3 Trait selection and sample collection

I selected different fire ecology-related plant traits for *H. splendens* (splendid feather moss) and *V. uliginosum* (bog blueberry), the most ubiquitous non-vascular and vascular understory plant species at study sites, based on the relevance of certain traits to each species' individual response to fire (Fig. 2.2). Feather mosses, such as *H. splendens*, are flammable when dry and are not very well adapted to post-fire regeneration, but are capable of absorbing and retaining 8-14 times their dry biomass in water, which allows them to resist burning (Busby et al. 1978). Thus, for *H. splendens* samples, I measured traits related to size, such as vertical length, horizontal width, and surface area, and moisture content at maximum capacity, which are known to be involved in the regulation of water retention in many non-vascular species (Bond-Lamberty and Gower 2007; Michel et al. 2012). In particular, high moisture content at maximum capacity, high aspect ratio or high width to length ratio and low specific leaf are (SLA, $cm^2 \cdot g^{-1}$) contribute to longer overall moisture retention in feather moss (Michel et al. 2012) and thus greater fire-resistance (Fig. 2.2).

During low-moderate severity fires, the aboveground tissues of *V. uliginosum* burn away and post-fire regeneration occurs from sprouting of unburned rhizomatous roots (Lutz 1956; Viereck 1983). These rhizomes root approximately 15 to 20 cm below the surface of the ground, in the organic layer (Maillette 1988), but they may root into deeper, more mineral soil layers (Jacquemart 1996), where they have been found to remain unburned even following more severe burning (Schimmel and Granstrom 1996). Greater depth of rhizomatous roots, as well as greater number of rhizomes of *V. uliginosum* result in greater post-fire regeneration success, thus I decided to measure these two traits because of their relevance to the fire-adaptivity of *V. uliginosum* (Fig. 2.2). Additionally, plant flammability is largely influenced by the moisture content of plant fuels (Norum and Miller 1984), where higher moisture contents increase the heat tolerance of plant tissues and decrease the chances of burning (Granstrom and Schimmel 1993). Studies from various fire-prone ecosystems have suggested that ratios of different plant parts that have varying moisture retentions can influence plant flammability (Papio and Trabaud 1991; Pausas et al. 2012; Paysen and Cohen 1990). Live wood, dead wood, new wood (the current year's growth) and leaf tissues have very different capacities of moisture retention and thus, the proportion of the individual that is comprised of each of these plant materials will influence aboveground flammability of *V. uliginosum*. Specifically, relatively high moisture content in plant tissues, high proportions of live wood and new wood to dead wood and leaves, low plant height and low dry leaf mass contribute to lower flammability in aboveground *V. uliginosum* tissues. Thus, I chose to measure plant height, dry leaf mass, moisture content % of plant tissues (live wood, new wood, 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* (Fig. 2.2).

I collected samples of *H. splendens* at 22 sites and *V. uliginosum* at 25 sites (26 sites total; Table 2.1). By destructively sampling along a transect at each site, I collected five cushions of *H. splendens* and five individuals of *V. uliginosum*. The transect began at the northeastern corner of the site, marked by a metal stake, and extended away from the site boundaries in order to sample outside of the actual site as my methods were destructive. Transects extended at least 20 m in length or more, which allowed for samples to be collected every 5 m or more, depending on if a cushion of *H. splendens* moss or *V. uliginosum* occurred every 5 m. I decided to sample every 5 m or more in order 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).

I collected samples of *H. splendens* by hand in order to minimize the compression and damage of moss individuals in the cushion, which is common when using a soil corer to extract samples. Moss samples were extracted down to the depth of the first organic soil layer, where there was evidence of organic matter decomposition, so that the sample encompassed the entire depth of the live and dead moss cushion. Moss samples were placed into Ziploc bags and care was taken to prevent their compression during transport to the lab.

Prior to collecting *V. uliginosum* samples, I measured maximum above-ground plant height, the number of belowground rhizomes and the depth to the deepest rhizome below the surface of the ground for each individual sample. Then, I collected the entire aboveground portion of the individual by cutting the plant off at the base of its stem.

All samples of *H. splendens* and *V. uliginosumi* were brought to the lab and stored at 4 °C.

2.2.4 Measuring fire ecology plant traits

For each *H. splendens* moss cushion samples, I selected up to six intact individuals from a single cushion sample; I considered all living and dead portions of the individual attached to the main stem as part of the intact individual. I did not use individuals that appeared damaged or to be missing portions of its stem/branches/etc. Moss individuals were washed thoroughly with de-ionized water to remove any foreign, non-moss particles such as soil, other plants and invertebrates. I allowed the moss individuals to fully hydrate by submerging them in de-ionized water over-night (at least 12 hours). Many morphological traits can dramatically change with water status (Elumeeva et al. 2011; Michel et al. 2012; Tuba et al. 1996), and thus rehydrating all moss individuals allowed us to achieve consistent water status for all samples.

Following rehydration, moss individuals were separated into live and dead tissue portions using the following criteria determined for *H. splendens*: i) Live tissue included at least the top 1.5 cm of the moss individual or approximately the upper two segments representing two years of growth and ii) dead tissue was distinguished by a change in the tissue color to brown/yellow and by evidence of some decomposition on the moss tissues (Bond-Lamberty and Gower 2007; Williams and Flanagan 1998). Live and dead parts of individuals were kept hydrated in between conducting each of the measurements. The wet weight of individuals was recorded by first 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 following the methods of Bond-Lamberty and Gower (2007) using an Epson Perfection V800 Photo flatbed scanner and the Easy Leaf Area computer software. In order to prevent the overlap of branches and the creation of shadows in the scanned image, I separated branches from the main stem of each individual and placed them flat on the scanner surface. 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. I calculated projected leaf area (PLA), which is 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 and Gower 2007). Lastly, live and dead moss parts were placed in a drying oven at 60 °C for 72 hours or until a constant mass was reached and weighed immediately upon removal from the oven to obtain dry mass (g). Finally, I calculated SLA by dividing HSLA (cm^2) by dry leaf mass (g) and calculated aspect ratio (W/L) for each live and dead moss sample.

For each *V. uliginosum* individual, I separated the aboveground biomass 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). I measured the wet weight of these 4 tissue types, then placed tissues into a drying oven at 60 °C for 72 hours or until a constant mass was reached, and then measured the dry weight of the materials. Using these measurements, I quantified the moisture content ((wet weight – dry weight) / dry weight) x 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. I was not able to obtain the moisture content of plant materials at maximum capacity because above-ground samples were cut off from their roots, preventing them from being rehydrated in a lab setting. However, moisture content of vascular plants does not change as rapidly over time compared to non-vascular plants, even under changing weather conditions, and thus I did not consider this to be a major source of error in calculating moisture contents of tissues.

2.2.5 Data Analysis

All statistical analyses were performed in R, version 3.5.2 (R Core Team 2014). Analyses were conducted on *H. splendens* and *V. uliginosum* data separately. I conducted analyses of variance to determine if *H. splendens* plant trait attributes differed between live and dead tissues. Thus, the following analyses were conducted on six traits for *H. splendens* (moisture content (MC), length, width, aspect ratio, live SLA and dead SLA) and on 12 traits for *V. uliginosum* (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)).

2.2.5.1 Investigating fire-ecological plant trait attributes across age and moisture gradients

To investigate the effects of time since fire and moisture on fire-ecological traits, together, I performed multivariate analyses of variance for *H. splendens* and *V. uliginosum* data. Multivariate analysis of variance can assess whether various group means, or the multivariate centroid, differs significantly between groups of data. To investigate the effects of time since fire and moisture on fire-ecological traits, individually, I performed analysis of variance.

To test the effect of time since fire and moisture on fire-ecological plant traits with the inclusion of random effects, I developed linear mixed-effects models using the *lme4* package (Bates et al. 2015). Prior to developing mixed-effects models, I reduced the dimensionality of *H. splendens* and *V. uliginosum* multivariate trait data using principal component analyses, which I will refer to as PCA^1 to prevent confusion with further PCAs performed in this study. The PCA^1 was performed using the *prcomp* function in the *vegan* package. I based my PCA^1 on a primary data matrix (A), which was composed of the fire-ecological traits for each individual sample within each site (551 samples (22 sites by 5 cushions per site by 3-6 samples per cushion) by 6 traits for *H. splendens* and 125 samples (25 sites by 5 samples per site) by 12 traits for *V. uliginosum*). I exported the first two PCA^1 axes and used them as my dependent variables in separate models. For *H. splendens* data, I developed models using the random effect structure of site and cushion nested within site, whereas for models on *V. uliginosum* data, I used the random effect structure of site. For each species, I tested whether time since fire, moisture and the interaction of time since fire and moisture were important in explaining the variability in the two primary PC axes. Final models for each species were then selected based on AIC and the most parsimonious parameter number (K value).

2.2.5.2 Investigating intra-specific trait variability within sites across age and moisture gradients

To further explore the differences in intra-specific trait variation among sites grouped by age and moisture, I conducted a second principal component analysis (PCA^2) on biomass-weighted mean traits values using the *vegan* package. Based on the ‘mass ratio’ theory, the effects of plant traits on ecosystem services or responses to the environment are in proportion to the plant's abundance or biomass. Mean biomass values for *H. splendens* and *V. uliginosum* for each site were derived from the mean fuel loads for feather moss fuel type and evergreen and deciduous shrub fuel types, respectively, quantified in chapter 1 of this thesis. *H. splendens* trait values were averaged for each cushion sample in each site. Trait values (or mean trait values for *H. splendens*) for each sample within a site were multiplied by mean biomass values for each site to determine biomass-weighted mean trait values. Then, PCA[2] was performed using a primary data matrix of biomass-weighted trait values by site (110 samples (22 sites by 5 cushions) by 6 biomass-weighted traits for *H. splendens* and 125 samples (25 sites by 5 samples) by 12 biomass-weighted traits for *V. uliginosum*). I plotted the ordination in a biplot and grouped the points by stand age and by site moisture for *H. splendens* and *V. uliginosum*. I then tested differences within and among groups (age and moisture classes), as well as between pairwise comparisons, using the multi-response permutation procedure (MRPP; Biondini et al. 1988). MRPP is a procedure often used in ecological studies to test for differences among pre-defined groups (e.g., age classes and moisture classes). The MRPP analysis provides an A statistic or effect size, which represents the amount of within-group homogeneity, and a p-value. When all observations within groups are identical, $A = 1$, whereas when within-group heterogeneity is equal to that expected by chance, $A = 0$ (McCune and Grace 2002). Typically in ecological community data, A values < 0.3 are common and indicate that within-group heterogeneity is greater than that expected by chance, however, an $A < 0$ may also result, indicating that within-group agreement is less than expected by chance (McCune and Grace 2002).

To determine the amount of intra-specific variation in fire-ecological traits of *H. splendens* and *V. uliginosum* within each site, I calculated a coefficient of variation (CV) on biomass-weighted mean trait values across sample plots. I conducted separate multiple regression models for each species to determine if there was an effect of time since fire and site moisture on the amount of intra-specific variation (CV) in each fire-ecological trait. To explore the dissimilarity between sites' trait CVs, I performed a third PCA (PCA^3) using the *vegan* package for each species. I used a primary data matrix of the CV of each plant trait by site (110 samples (22 sites by 5 cushions) by 6 trait CVs for *H. splendens* and 125 samples (25 sites by 5 samples) by 12 trait CVs for *V. uliginosum*) and grouped the sites by their respective age class when plotting the ordination in a biplot.

Lastly, to investigate intra-specific variation across all fire-ecological traits measured for each species, I calculated an overall trait CV ($\sum$ CV) for each site by summing the CVs of each trait for *H. splendens* and *V. uliginosum*. I conducted separate regression models for each species to determine if there was an effect of time since fire and moisture on $\sum$ CV.

2.3 Results

2.3.1 Variation in fire-ecological plant trait attributes across age and moisture

MANOVA indicated that the multi-variate centroid of *H. splendens*' fire-ecological plant traits increased significantly with the main and interaction effects of time since fire and moisture (for time since fire, $F_{6, 535} = 11.08$, $p < 0.001$; for moisture, $F_{30, 2695} = 10.47$, $p < 0.001$; for time since fire x moisture, $F_{24, 2152} = 6.53$, $p < 0.001$). In particular, ANOVA of individual traits with stand age indicated that both length and width were significantly greater in intermediate aged sites, both MC and live SLA significantly decreased with stand age, whereas neither aspect ratio nor dead SLA varied significantly with stand age (Fig. 2.3). ANOVA of *H. splendens* traits with site moisture revealed that length, width, MC and dead SLA significantly decreased with site moisture, whereas neither aspect ratio nor live SLA varied significantly with moisture (Fig. 2.4).

Despite the presence of significant relationships in some *H. splendens* traits with stand age and/or site moisture, trait attributes that would contribute to highest moisture-retention abilities in *H. splendens*, such as high MC, high aspect ratio and low live and dead SLA, did not occur in the same stand age or site moisture class (Table S2.1). For example, the highest mean MC occurred in mature, mesic sites, the greatest mean aspect ratio occurred in mature, mesic/subhygric sites and the lowest mean live and dead SLA values occurred in young subxeric/mesic sites (Table S2.1).

MANOVA on *V. uliginosum* data indicated that the multi-variate trait centroid significantly decreased with time since fire and moisture (for time since fire, $F_{12, 98} = 4.49$, $p < 0.001$; for moisture, $F_{60, 510} = 3.07$, $p < 0.001$; for time since fire x moisture, $F_{48, 404} = 1.95$, $p < 0.001$). ANOVA on individual *V. uliginosum* traits with stand age revealed that dry leaf mass, LLMC, LW MC, NW MC, LW:DW and plant height significantly decreased with stand age, NW:LL and rhizome depth significantly increased with stand age, the number of rhizomes was significantly greater in intermediate sites, whereas neither of DW MC, LW:LL, nor NW:DW varied significantly with stand age (Fig. 2.5). Lastly, ANOVA of *V. uliginosum*'s fire-ecological plant traits with site moisture indicated that only one trait, NW:LL, significantly decreased with site moisture, whereas all other *V. uliginosum* traits did not vary significantly with site moisture (Fig. 2.6). Similar to *H. splendens* data, *V. uliginosum* trait attributes that would contribute to the greatest post-fire reproduction success, such as high rhizome depth and rhizome number, and lowest above-ground flammability, such as low dry leaf mass, high tissue MC, and high live wood and new wood to dead wood and live leaf ratios, did not occur in the same age or moisture class (Table S2.2). For example, greater post-fire reproduction success likely occurs in older sites due to significantly greater rhizome depth and number of rhizomes in intermediate/mature and intermediate sites, respectively (Fig. 2.5; Table S2.2). However, it is difficult to ascertain which sites contain lower above-ground flammability because young sites contained significantly greater dry leaf mass and plant height (increasing flammability) and also contained significantly greater MC in LW, NW and LL tissues and greater LW:DW (decreasing flammability) (Fig. 2.5; Table S2.2).

In order to reduce the dimensionality of my data for mixed-effects models, I conducted a PCA^1 on fire-ecological traits across sites for *H. splendens* and *V. uliginosum*. The first two principal components of the PCA^1 on *H. splendens* fire-ecological traits cumulatively explained 64.2 % of the variation in the data. The first principal axis explained 39.4 % of the variation in *H. splendens* traits and was highly correlated with live SLA (eigenvalue = -0.43), dead SLA (eigenvalue = -0.46), moisture content (eigenvalue = -0.54) and width (eigenvalue = -0.31). The second principal axis explained 24.8 % of the variation in *H. splendens* traits and was highly correlated with length (eigenvalue = -0.62) and aspect ratio (eigenvalue = 0.51). Mixed-models conducted on the two PCs derived from *H. splendens*' fire-ecological trait data indicated that PC1 and PC2 were best explained by time since fire (t = 0.92) and moisture (t = 0.65), respectively (Table 2.2). Comparison of marginal and condition R^2 of mixed models on PC1 and PC2 revealed that the inclusion of site and cushion as random effects improved the model fit (for PC1, $R^2_m = 0.02$ and $R^2_c = 0.53$; for PC2, $R^2_m = 0.02$ and $R^2_c = 0.50$). Based on the association of *H.* splendens' traits with PC1 and PC2 and on the relationship of time since fire and moisture with these components, my mixed-models indicated that live SLA, dead SLA, MC and width decreased with increasing time since fire, whereas aspect ratio increased and length decreased with increasing site moisture (Table 2.2). The results from the mixed-models were generally in agreement with the ANOVA results, the models contrasted in the trends they indicated for width and aspect ratio, which was likely because the random effects of site and cushion explained additional variation in these two traits in the mixed effects models.

The first two principal components of the PCA[1] on *V. uliginosum* fire-ecological plant traits cumulatively explained 50.2 % of the variation in the data. The first principal axis explained 30.3 % of the variation in *V. uliginosum* traits and was highly correlated with rhizome depth (eigenvalue = -0.21), plant height (eigenvalue = 0.36), dry leaf mass (eigenvalue = 0.43), LW MC (eigenvalue = 0.46), NW MC (eigenvalue = 0.44) and LL MC (eigenvalue = 0.46). The second principal axis explained 20.0 % of the variation in *V. uliginosum* traits and was highly correlated with rhizome number (eigenvalue = 0.05), DW MC (-0.24), LW:DW (eigenvalue = -0.59), LW:LL (eigenvalue = -0.42), NW:DW (eigenvalue = -0.56) and NW:LL (eigenvalue = -0.26). Mixed-models conducted on the two PCs derived from *V. uliginosum* data indicated that PC1 and PC2 were both best explained by time since fire (t = -1.26 and t = 0.05, respectively; Table 2.2). Marginal and condition R^2 of mixed models on PC1 and PC2 revealed that the inclusion of site as random effects improved the model fit (for PC1, $R^2_m = 0.09$ and $R^2_c = 0.58$; for PC2, $R^2_m = 0.005$ and $R^2_c = 0.54$). Based on the association of the variables with PC1 and PC2 and on the relationship of these components with time since fire in the mixed-models, these results indicate rhizome depth and rhizome number increased with time since fire, whereas plant height, dry leaf mass, LW MC, DW MC, NW MC, LL MC, LW:DW, LW:LL, NW:DW and NW:LL decreased with time since fire. These results are generally in agreement with the trends of *V. uliginosum* traits with time since fire indicated by the ANOVA (Fig. 2.5) and support the lack of significant explanatory power of site moisture on *V. uliginosum* traits, which was also indicated by the ANOVA (Fig. 2.6). Overall, both the ANOVA and mixed-model results suggest that variation in *V. uliginosum* fire ecological traits should be estimated using time since fire and not site moisture.

2.3.2 Describing trends in the amount of intra-specific trait variability between sites

To examine whether biomass-weighted trait means of *H. splendens* and *V. uliginosum* varied between sites within age and moisture classes, I conducted a PCA^2 and MRPP analyses. The first two axes of the PCA^2 conducted on biomass-weighted mean trait values cumulatively explained 96.3 % of the variation in *H. splendens* trait data. The first principal component explained 91.1 % of the variation in the data and was associated with length (eigenvalue = 0.41), width (eigenvalue = 0.41) and live SLA (eigenvalue = 0.41). The second principal component explained 5.3 % of the variation in the data and was associated with moisture content (eigenvalue = 0.42), aspect ratio (eigenvalue = -0.54) and dead SLA (eigenvalue = 0.42). The PCA^2 biplot suggests that intra-specific variation in biomass-weighted trait means for *H. splendens* is the greatest among intermediate sites, compared to young and mature sites (Fig. 2.7). MRPP analysis indicated that there was significant intra-specific variation in biomass-weighted trait means within age classes (A = 0.11, p = 0.049; Table 2.3), but the difference in within-group variation was significant between young and intermediate age classes and between young and mature age classes, but not between intermediate and mature age classes (Table 2.3). When biomass-weighted trait means for *H. splendens* in the PCA^2 biplot were grouped by moisture, moderately moisture appeared to have the greatest intra-specific variation between sites (Fig. 2.7). However, MRPP analysis indicated that intra-specific variation in biomass-weighted trait means for *H. splendens* did not differ significantly in within-group heterogeneity among moisture classes (A = 0.018, p = 0.28).

The PCA^2 conducted on the biomass-weighted trait means of *V. uliginosum* indicated that the first two principal components cumulatively explained 80.0 % of the variation in the data. The first principal component explained 54.0 % of the variation and was associated rhizome number (eigenvalue = 0.24), plant height (eigenvalue = 0.38), dry leaf mass (eigenvalue = 0.33), LW MC (eignenvalue = 0.34), DW MC (eigenvalue = 0.12), NW MC (eigenvalue = 0.34), LW:LL (eigenvalue = 0.35) and NW:LL (eigenvalue = 0.34). The second principal component explained 22.0 % of the variation and was associated with rhizome depth (eigenvalue = 0.27), LL MC (eigenvalue = -0.33), LW:DW (eigenvalue = 0.47) and NW:DW (eigenvalue = 0.47). When biomass-weighted trait means for *V. uliginosum* were grouped by age class, neither the biplot nor the MRPP analysis (A = 0.004, p = 0.32) indicated significant differences in intra-specific variation among sites within age classes (Fig. 2.8; Table 2.3). When biomass-weighted trait means for *V. uliginosum* were grouped by moisture class, the PCA^2 biplot suggests that there may be greater intra-specific trait variation within the moderate moisture class (Fig. 2.8); however, MRPP analysis indicated that there was not significant difference in intra-specific variation within moisture classes (A = 0.001, p = 0.37; Table 2.3).

To examine the dissimilarity among sites with respect to the amount of intra-specific trait variation, I conducted a PCA^3 on the coefficient of variation on *H. splendens* and *V. uliginosum* trait data. The PCA^3 conducted on *H. splendens*' trait CVs indicated that the first two principal axes cumulatively explained 72.5 % of the variation in the data. The first principal axes explained 43.2 % of the variation and was associated with live SLA (eigenvalue = 0.53), dead SLA (eigenvalue = 0.54) and moisture content (eigenvalue = 0.56). This indicates that sites that possess high amounts of intra-specific variation in live SLA, dead SLA and moisture content load positively onto axis 1 (Fig. 2.9). The second principal component explained 29.4 % of the variation in the data and was associated with length (eigenvalue = 0.61), width (eigenvalue = 0.55) and aspect ratio (eigenvalue = 0.46). This indicates that study sites possessing high intraspecific variation in length, width and aspect ratio would load positively onto axis 2 (Fig. 2.9). Notably, the PCA^3 analysis indicates sites with *H. splendens* populations that contain high levels of intra-specific variation in all fire-ecological traits, load positively on both axis 1 and 2, such as GRM4 and GRI1 (Fig. 2.9). In contrast, sites that contain low overall intra-specific variation in all fire-ecological traits load negatively onto both axis 1 and 2, such as BCEFM2 and BDM1 (Fig. 2.9). Additionally, these results show that young sites occupy a wide range of space along axis 2, but a small space along axis 1, indicating that *H. splendens* populations in young sites typically have low live SLA, dead SLA and moisture content CV, but may vary in the CVs of their other traits, such as length, width and aspect ratio (Fig. 2.9). In contrast, intermediate and mature sites occupy wide ranges of space along both axis 1 and 2, suggesting that the amount of intra-specific variation in *H. splendens* traits varies among intermediate and mature sites (Fig. 2.9).

The PCA^3 conducted on *V. uliginosum*'s trait CVs suggests that the first two principal axes cumulatively explained 45.5 % of the variation in the data. The first principal axes explained 25.0 % of the variation in the data and was associated with rhizome number (eigenvalue = -0.34), dry leaf mass (eigenvalue = 0.21), LW MC (eigenvalue = 0.42), DW MC (eigenvalue = -0.21), NW MC (eigenvalue = 0.49), LL MC (eigenvalue = 0.38), LW:LL (eigenvalue = 0.20), NW:LL (eigenvalue = 0.33). This indicates that sites that possess high intra-specific variation in dry leaf mass, LW MC, NW MC, LL MC, LW:LL, and NW:LL and low intra-specific variation in rhizome number and DW MC load positively onto axis 1 (Fig. 2.10). The second principal component explained 20.5 % of the variation in the data and was associated with rhizome depth (eigenvalue = -0.42), plant height (eigenvalue = -0.33), LW:DW (eigenvalue = -0.54), and NW:DW (eigenvalue = -0.53). This indicates that study sites that possess high intraspecific variation in rhizome depth, plant height, LW:DW, and NW:DW load negatively onto axis 2 (Fig. 2.10). There is no portion of the ordination space that shows high intra-specific variation in all *V. uliginosum* traits, which indicates that sites contain *V. uliginosum* populations with high intra-specific variation in some traits, but low intra-specific variation in other traits (Fig. 2.10). Specifically, young and mature sites tend to occupy the left portion of the ordination space, and a wide range of space along axis 2, indicating that *V. uliginosum* populations in these sites typically have high intra-specific variation in rhizome number and DW MC and low intra-specific variation in dry leaf mass, LW MC, NW MC, LL MC, LW:LL, NW:LL, but may vary in the amount of intra-specific variation in rhizome depth, plant height, LW:DW, and NWLDW. In contrast, these results show that intermediate sites occupy a wide range of space along both axis 1 and 2, indicating that the amount of intra-specific trait variation is high among intermediate sites (Fig. 2.10).

2.3.3 Identifying sites with high resilience based on intra-specific trait variation

ANOVA conducted on $\sum$ CV with age class and moisture class, indicated that $\sum$ CV did not vary significantly with time since fire or moisture for neither *H. splendens* nor *V. uliginosum* trait data. Although my results do not indicate that the amount of intra-specific trait variation differed between age and moisture classes, my results do show that GRM4, a mature, subxeric/mesic site, possessed the greatest overall intra-specific variation in *H. splendens* traits, and LGI2, an intermediate, subxeric (dry) site, contained the greatest overall intra-specific variation in *V. uliginosum* (Table 2.1). Due to the high amount of intra-specific variation in fire-ecological plant traits, GRM4 and LGI2 are likely to possess the greatest resilience to a changing fire regime. Based on the black spruce community descriptions by Hollingsworth et al. (2006), GRM4 is largely representative of a mesic, nonacidic black spruce/larch fen, while LGI2 is representative of a dry, upland, nonacidic black spruce forest.

2.4 Discussion

Studies have shown that greater range of plant trait attributes or greater intra-specific trait variation within a population increases the chances of populations persisting through changing environmental or disturbance conditions (Bolnick et al. 2011; Hoooper et al. 2005). Under a changing fire regime, black spruce plant communities will likely be able to better respond to variable fire conditions if they possess high intra-specific variation in their fire-ecological plant traits, allowing them to remain resilient to fluctuating fire perturbations. The results of this study suggest that the fire-ecological plant traits of *H. splendens* vary across gradients of stand age and site moisture, whereas the fire-ecological plant traits of *V. uliginosum* vary mainly across stand age in interior Alaska's black spruce forests. CVs of plant traits, a measure of the amount of intra-specific trait variation, differed among sites; however, this could not be explained by variation in stand age or site moisture for either species, and may likely be explained by other environmental gradients. In this study, I report black spruce site types that possess high levels of intra-specific variation in fire-ecological plant traits, which represent sites that contain greater potential for resilience to changes in the fire regime.

2.4.1 Spatiotemporal variation in fire-ecological plant trait attributes

Feather mosses, although known to be highly flammable when dry (Lutz 1956), are capable of retaining up to 14 times their dry biomass in water, allowing them to resist burning during fire events when hydrated (Busby et al. 1978). A suite of functional traits have been shown to affect moisture retention abilities in feather mosses, specifically, high moisture content at maximum capacity, high aspect ratio and low SLA contribute to greater overall moisture retention in feather moss individuals (Michel et al. 2012). In general, mean values for *H. splendens* traits (Table S2.1) were in agreement with values reported in the literature for these same traits (Bond-Lamberty and Gower 2007; Jandt et al. 2005; Michel et al. 2012). However, in contrast to Bond-Lamberty and Gower (2007), my results indicated that live SLA decreased with stand age (Fig. 2.4), instead of increasing over time. The difference in SLA trends along age gradients may be due to the fact that this study encompassed a wider range in stand age, whereas the study by Bond-Lamberty and Gower (2007) measured SLA in *H. splendens* at sites that ranged between 41 to 155 years of age. Although the attributes of *H. splendens* traits varied across spatiotemporal gradients, it is difficult to ascertain what sites across the landscape possess individuals with the greatest and lowest water retention capacities, based on trait measurements alone. My results indicate that the combination of trait attributes resulting in the greatest moisture retention in *H. splendens* (i.e. high moisture content at maximum capacity, high aspect ratio, low SLA) did not occur together along the landscape. I suspect that there are trade-offs occurring within *H. splendens* individuals that prevent them from containing the ideal combination of trait values that would result in the greatest moisture retention ability. For example, greater surface area in feather mosses maximizes light interception for photosynthesis (Whitehead and Gower 2001), and thus trade-offs between high SLA for better photosynthesis and low SLA for better moisture retention in *H. splendens* are likely to occur.

Bog blueberry, as well as some other boreal shrub species, possess rhizomatous roots which aid individuals in post-fire regeneration by re-sprouting from unburned, below-ground rhizomes (Lutz 1956; Viereck 1983). However, the flammability of above-ground tissues may hinder the post-fire regeneration success of the plant during high severity fires as high aboveground tissue flammability can aid in the heat-destruction of below-ground tissues. Thus, trait attributes that increase the post-fire reproduction success (deeper rhizomes and greater number of rhizomes) and decrease the flammability of above-ground tissues (low plant height, high tissue moisture content, low dry leaf mass, high ratios of live wood and new wood to dead wood and live leaves) will support *V. uliginosum* regeneration after fire events. Rhizome depths of *V. uliginosum* at my sites overlapped the range and occurred at even shallower depths than the range reported by Maillette (1988). My results suggest that greater post-fire reproduction success likely occurs in older sites as these sites contained *V. uliginosum* individuals with significantly deeper rhizomes and greater number of rhizomes, however, it is difficult to ascertain which sites contained individuals with the lowest above-ground flammability. Like *H. splendens* individuals, *V. uliginosum* individuals may be experiencing trade-offs in certain traits due to energetic demands that prevent individuals from possessing attributes in all traits that would result in lower above-ground flammability. *V. uliginosum* individuals are typically more productive in early succession as they are regenerating recently burned above-ground tissues (Wein 1974), and thus they require greater photosynthetically active leaf biomass to support their high energetic demands. Regardless, the occurrence of deeper and more numerous rhizomatous roots in *V. uliginosum* individuals in older sites suggests intermediate and mature sites will have more potential for successful post-fire regeneration under more severe fire disturbances.

2.4.2 Using intra-specific trait variation as a measure of forest resilience

Variation in biomass-weighted trait means have been previously linked to variation in particular ecological attributes that affect ecosystem services and dynamics (Bolnick et al. 2011). Thus, knowledge of how certain traits differ across the landscape may allow us to make predictions as to how an ecosystem may function under varying environmental conditions or disturbance regimes (Lavorel et al. 2011). I found significant within-group heterogeneity in *H. splendens* biomass-weighted trait means across stand age classes, where variation among sites was greatest within the intermediate age class. This suggests that black spruce sites within the same age class will vary in their response to different fire regimes with respect to the fire-ecological traits of feather mosses (represented by *H. splendens* in this study). Additionally, within-group heterogeneity in *V. uliginosum* biomass-weighted trait means was greatest among sites within the moderate site moisture class, suggesting that black spruce sites may vary in their response to different fire regimes with respect to the fire-ecological traits of short deciduous and evergreen shrubs (represented by *V. uliginosum*). Thus, estimating intra-specific trait variation within a site using age and moisture gradients may be difficult as my results reveal that sites within the same age or moisture class will vary in their response to different fire regimes.

Evidence of the benefits of greater within-population intra-specific trait variation to ecosystem functioning suggests that plant communities with greater intra-specific trait variation will be more likely to persist through fluctuating disturbance (Helsen et al. 2017; Henn et al. 2018; Hooper et al. 2005). Black spruce communities with a greater range of fire-ecological plant trait attributes within populations will have a greater probability of persisting through severe fires compared to communities with a small range of trait attributes and represent the most resilient part of the black spruce dominated landscape. Based on my results, I present a conceptual model of black spruce forest resilience and its relationships with various abiotic and biotic factors, such as climate, fire behavior and inter-specific trait variability (Fig. 2.11). Although I did find that certain sites did have greater intra-specific trait variation than others, the lack of significant correlation of trait CV with stand age or site moisture in either species suggested that intra-specific trait variability within a site may be dependent on additional environmental gradients, that may be indirectly related to stand age and site moisture gradients (Fig. 2.11). Helsen et al. (2017) found evidence that both abiotic and biotic stressors, such as soil nutrient stress, climatic stress and niche packing stress, induced both increases and decreases in intra-specific trait variation between individuals, thus highlighting the importance of assessing both biotic and abiotic factors on intra-specific trait variation. Additionally, the amount of intra-specific variation between individuals of different functional types may differ in their response to certain explanatory factors. Thus, future studies using the amount of intra-specific trait variation to indicate forest resilience should consider the effects of multiple abiotic and biotic variables and estimate community-level amounts of intra-specific variation within a site using representative species of all plant functional types.

As climate change-related effects are resulting in more severe fire events, determining distinct patterns in the amount of intra-specific variation in fire-ecological plant traits, and thus forest resilience to a changing fire regime, is becoming increasingly important. Specifically, the self-replacement of black spruce communities after fire is threatened as deciduous tree species obtain competitive advantages when regenerating on severely burning post-fire sites (Johnstone and Chapin 2006). A shift in the post-fire vegetation community would have many ecological implications, particularly for the cycling and storage of carbon in boreal forest soils (Genet et al. 2013; Johnstone et al. 2010). Thus, an understanding of how forest resilience varies across the landscape will indicate locations that will likely remain resistant to post-fire shifts in community composition, as well as locations that are vulnerable to post-fire community shift under an intensified fire regime.

2.5 Conclusion

I found clear evidence of the effects of stand age and site moisture on the fire-ecological plant traits in *H. splendens* and *V. uliginosum* at study sites, suggesting there is large landscape-level variation in fire-ecological plant trait attributes across interior Alaska's black spruce forests. In contrast to my expectations, my results suggest that the amount of intra-specific variation within a site (CV) is not affected by stand age or site moisture levels. Regardless, certain sites did contain higher levels of intra-specific variation than others, which supports the idea that some black spruce sites may have greater resilience to changes in the fire regime because of the greater range of fire-ecological plant trait attributes they possess. I propose that future studies investigating fire-ecological plant trait variation evaluate both abiotic and biotic effects simultaneously, as studies have shown the importance of different types of influences on intra-specific trait variation (Helsen et al. 2017). My study adds to the growing body of knowledge on within-population trait variation across landscapes and its relationship to ecosystem-level response to environmental change.

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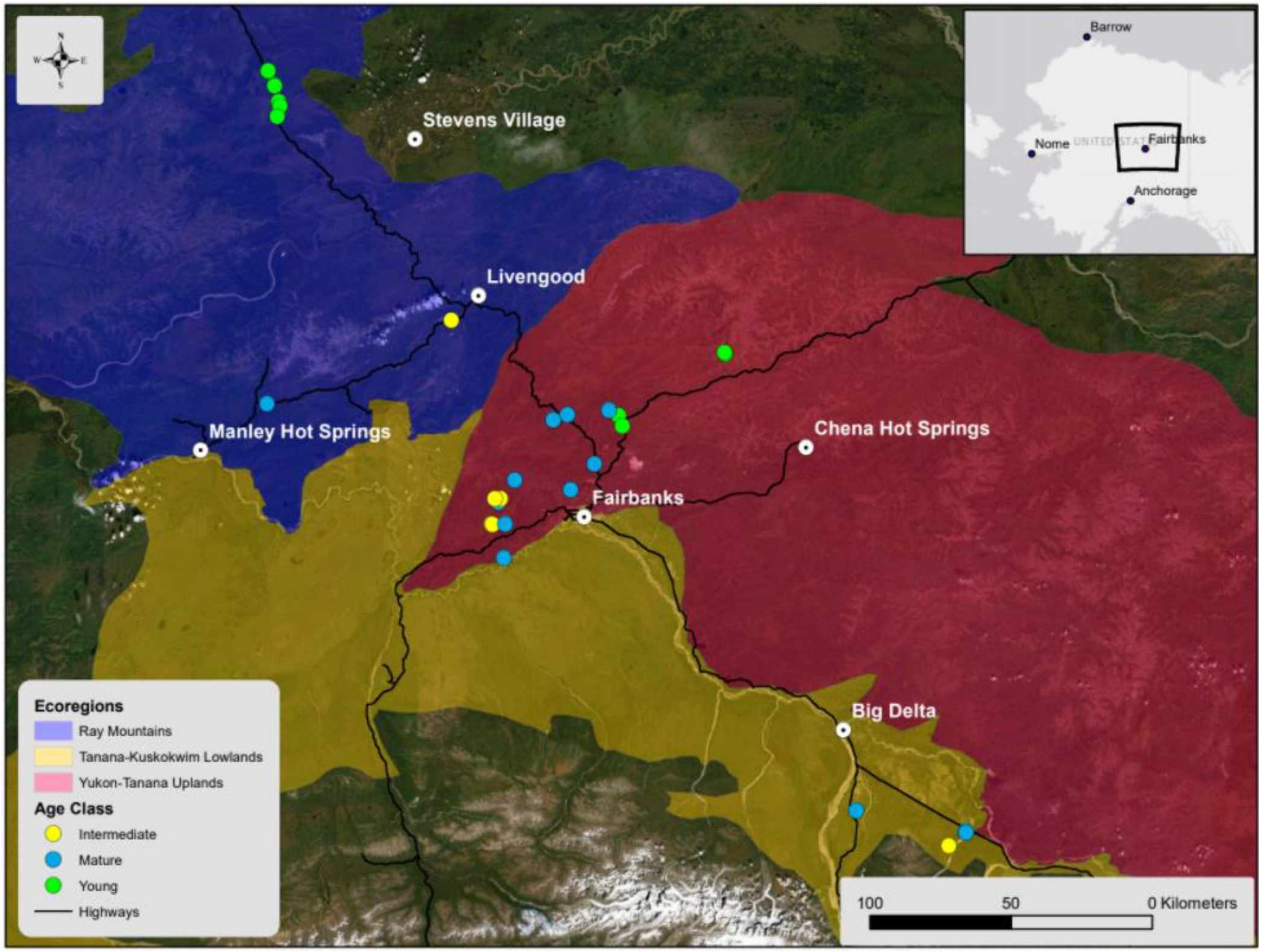

Figure 2.1 Map of study sites within interior Alaska, USA, with ecoregions indicated in shaded areas (Ray Mountains = blue, Tanana-Kuskokwim Lowlands = yellow, Yukon-Tanaa Uplands = red). Circles indicate the locations of 26 young (0-15 years post-fire; green circles), intermediate (40-60 years post-fire; yellow) and mature (>80 years post-fire; blue) aged black spruce dominated study sites. Major highways are indicated with black lines. Map couresty of Jamie Hollingsworth, site manager of the Bonanza Creek Long-Term Ecological Research group.

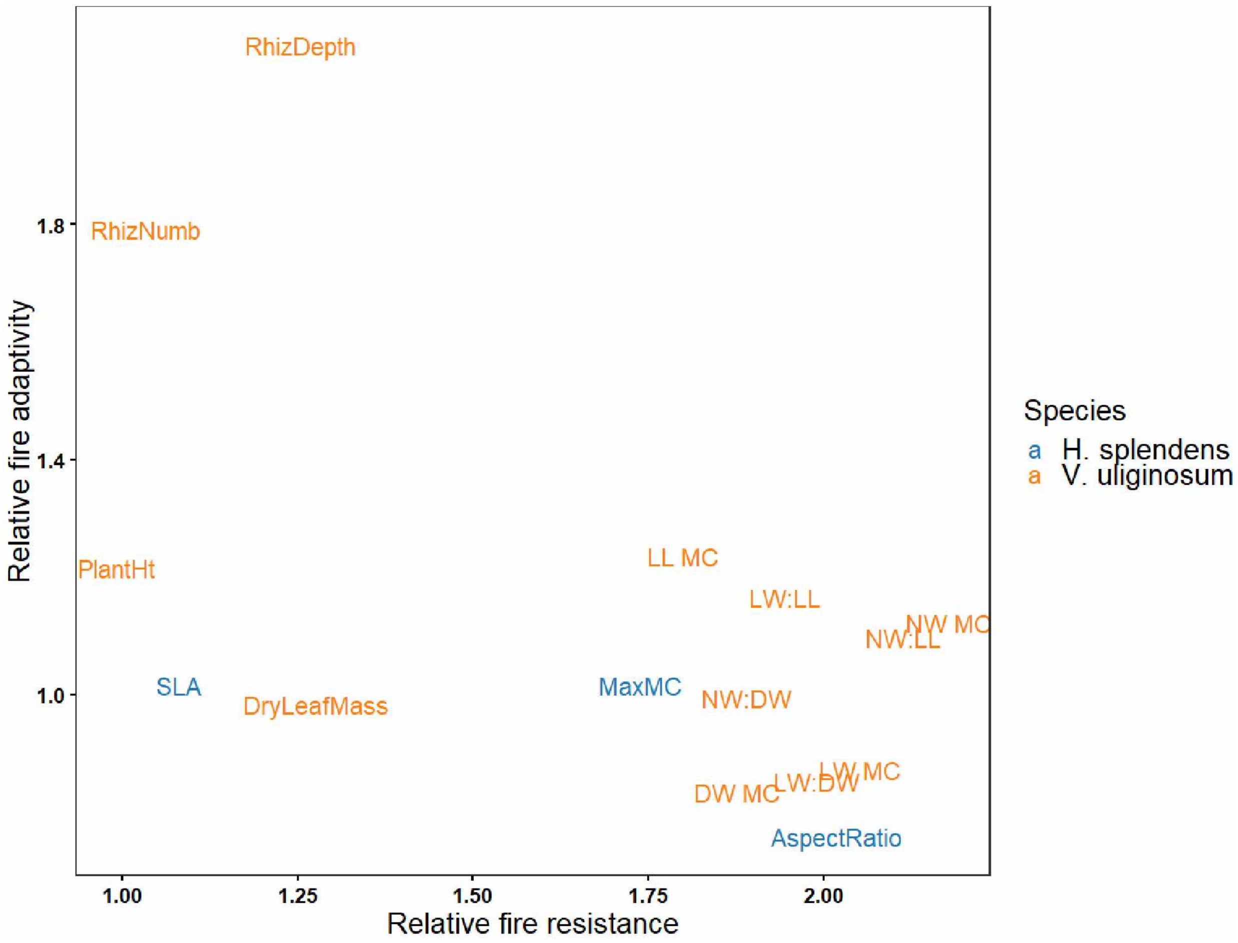

Figure 2.2 Fire-ecological plant traits of *H. splendens* (SLA = specific leaf area; MaxMC = moisture content % at maximum capacity; AspectRatio = aspect ratio or width to length ratio), in blue, and *V. uliginosum* (RhizDepth = rhizome depth; RhizNumb = number of rhizomes; PlantHt = plant height; DryLeafMass = 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 (post-fire regeneration ability). Based on reports of the responses to fire of these species' traits in the literature, traits were specified as either low (1.00) or high (2.00) fire resistance and fire adaptivity. When plotted, traits were positioned with a slight "jitter" so that observations did not overlap for visual clarity.

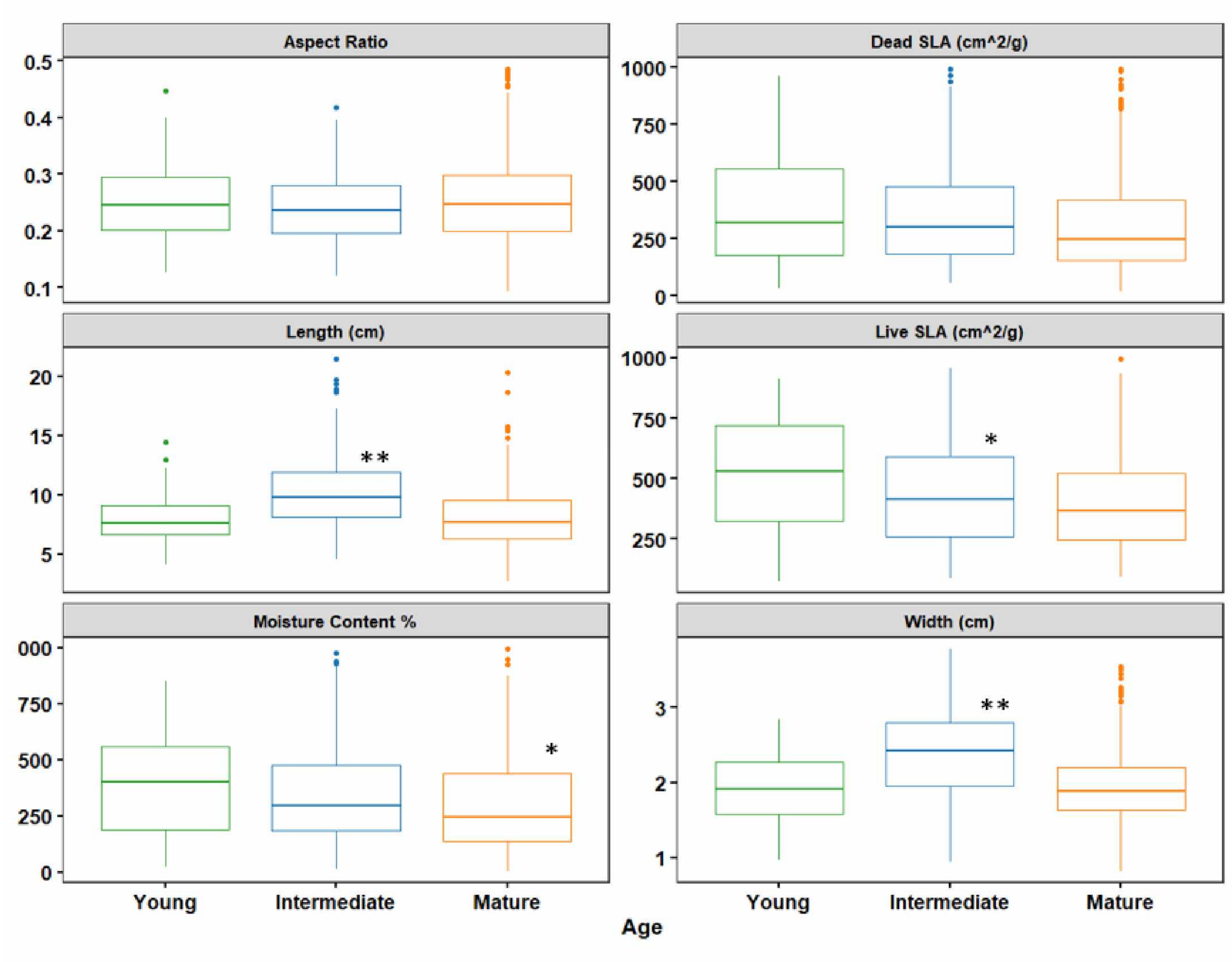

Figure 2.3 Boxplots of the distribution with 95% confidence intervals of attributes of six fire-ecological plant trait in *H. splendens* across age classes (Young = 0-10 years, Intermediate = 40-60 years, and Mature = >80 years after fire). * indicates significant difference of $p < 0.05$ and ** indicates significant differences of $p < 0.001$.

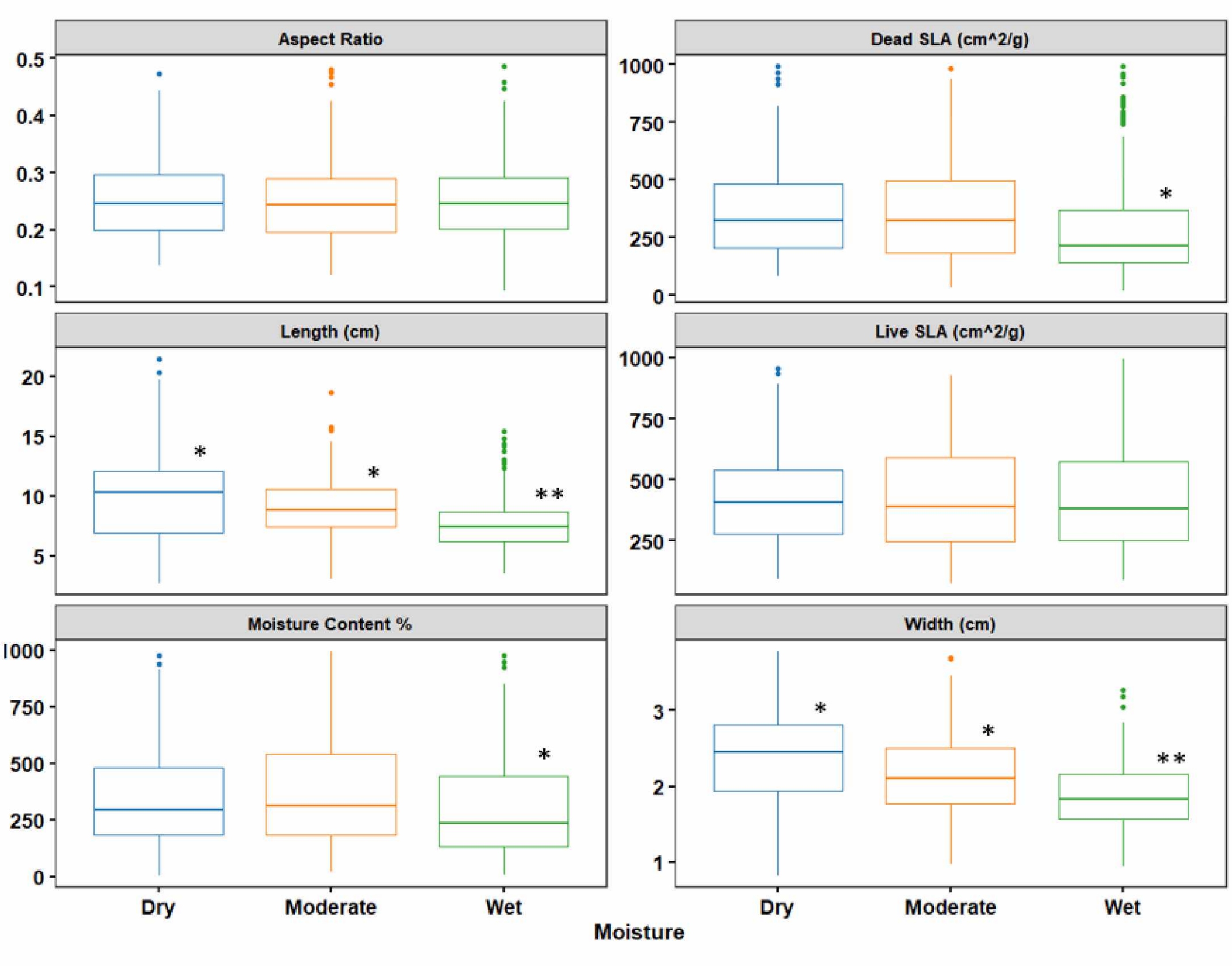

Figure 2.4 Boxplots of the distribution with 95% confidence intervals of attributes of six fire-ecological plant trait in *H. splendens* across moisture levels (Dry = xeric and subxeric, Moderate = subxeric/mesic and mesic, and Wet = mesic/subhygric and subhygric). * indicates significant difference of $p < 0.05$ and ** indicates significant differences of $p < 0.001$.

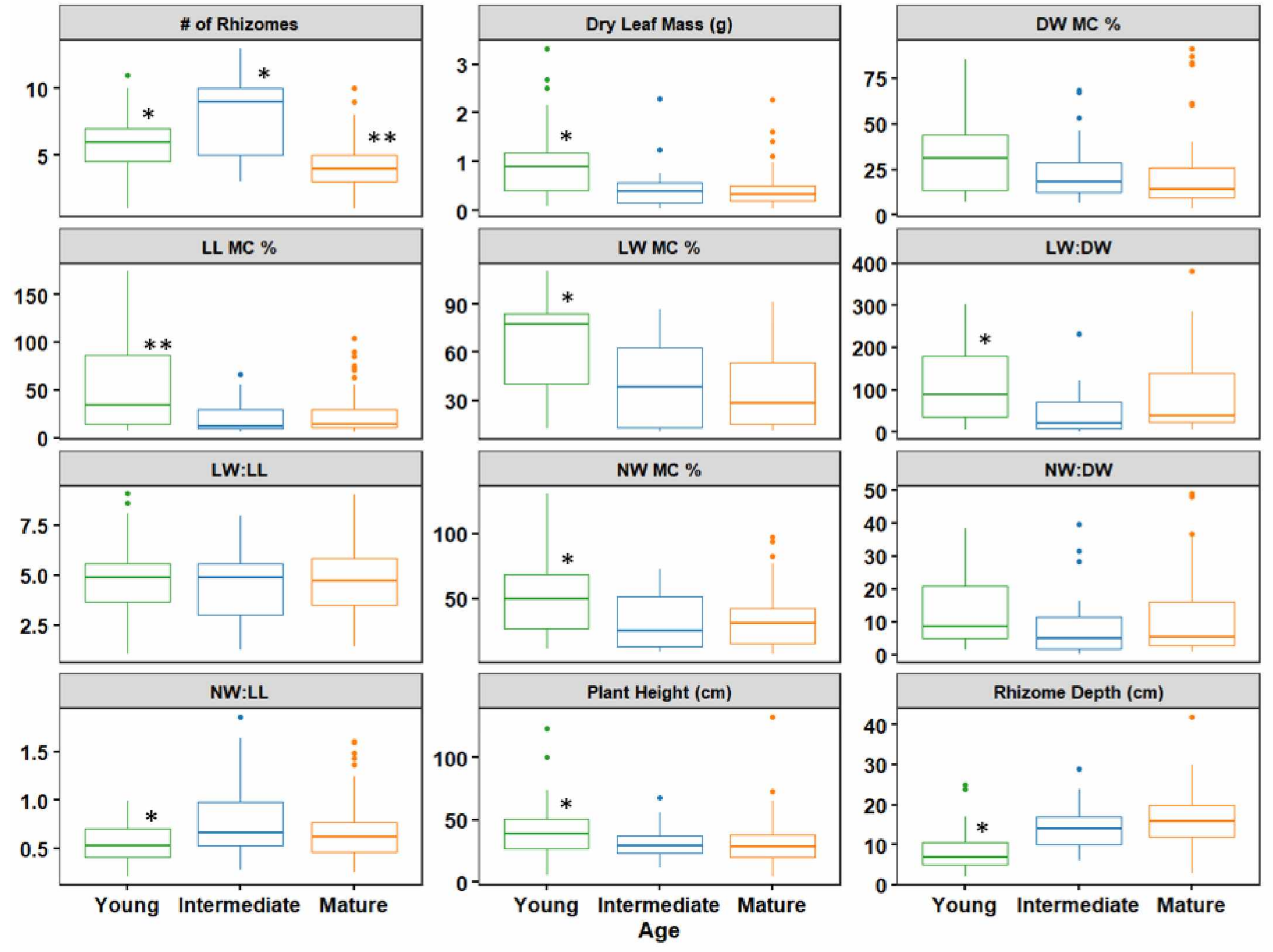

Figure 2.5 Boxplots of the distribution with 95% confidence intervals of attributes of twelve fire-ecological plant traits in V. *uliginosum* across age classes (Young = 0-10 years, Intermediate = 40-60 years, and Mature = >80 years after fire). * indicates significant difference of $p < 0.05$ and ** indicates significant differences of $p < 0.001$.

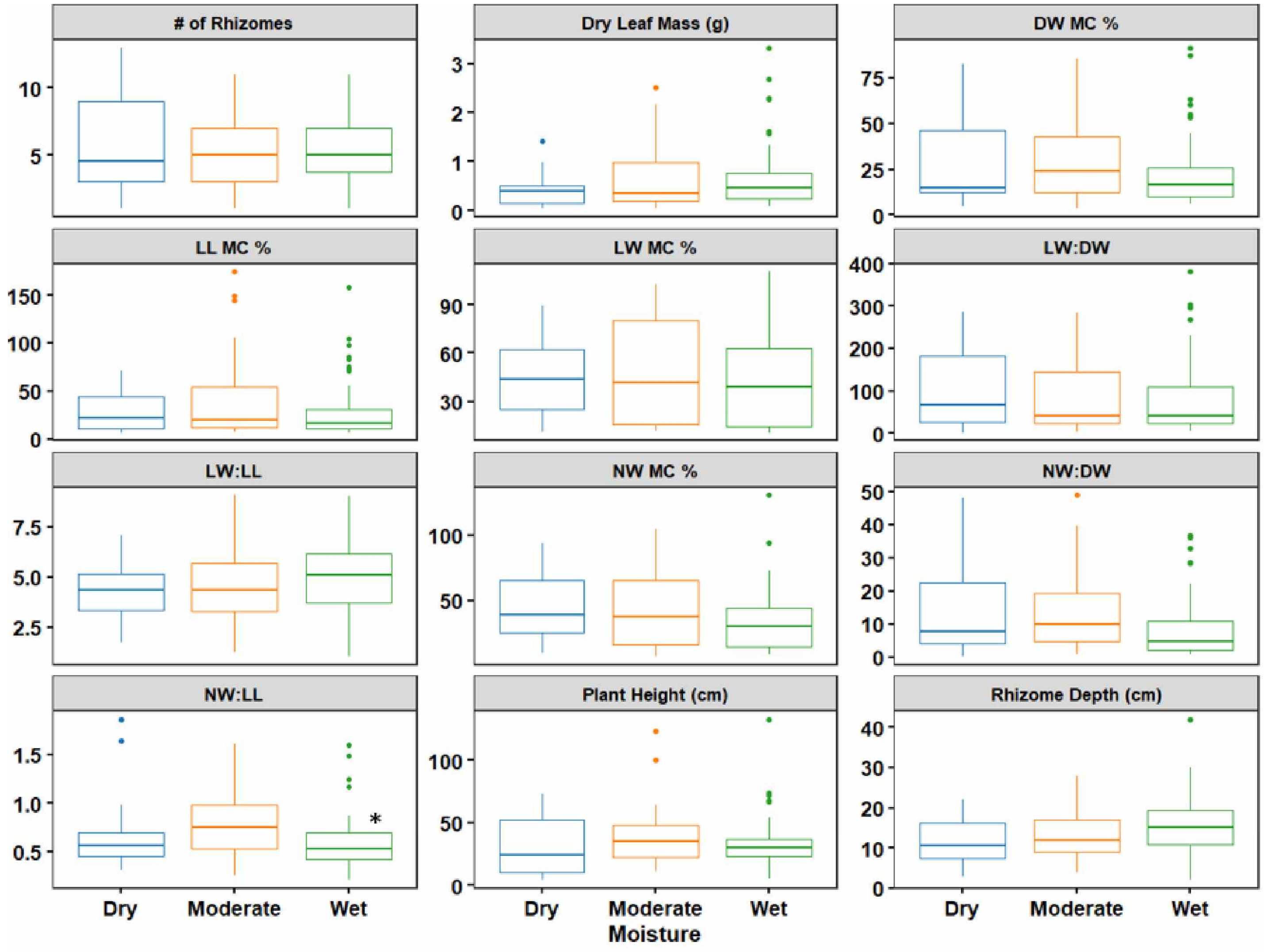

Figure 2.6 Boxplots of the distribution with 95% confidence intervals of attributes of twelve fire-ecological plant traits in V. *uliginosum* across moisture levels (Dry = xeric and subxeric, Moderate = subxeric/mesic and mesic, and Wet = mesic/subhygric and subhygric). * indicates significant difference of $p < 0.05$ and ** indicates significant differences of $p < 0.001$.

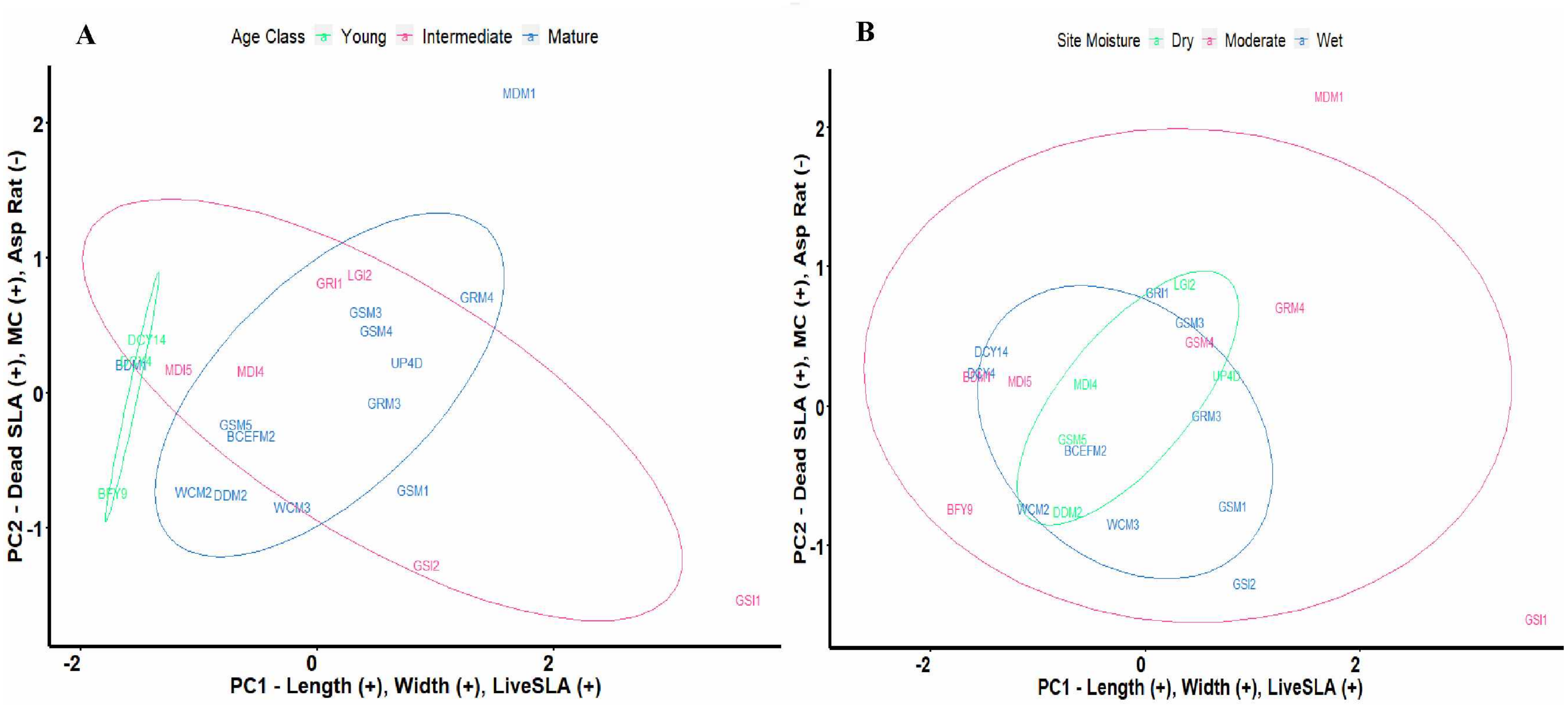

Figure 2.7 Biplot of the PCA of sites in biomass-weighted mean trait space for *H. splendens* data grouped by age class (A) and site moisture (B). Axes titles indicate which traits are associated with each axis (MC = Moisture Content, L = Length, W = Width, Asp Rat = Aspect Ratio, SLA = Surface Leaf Area), where '+' indicates positive association and '-' indicates negative association.

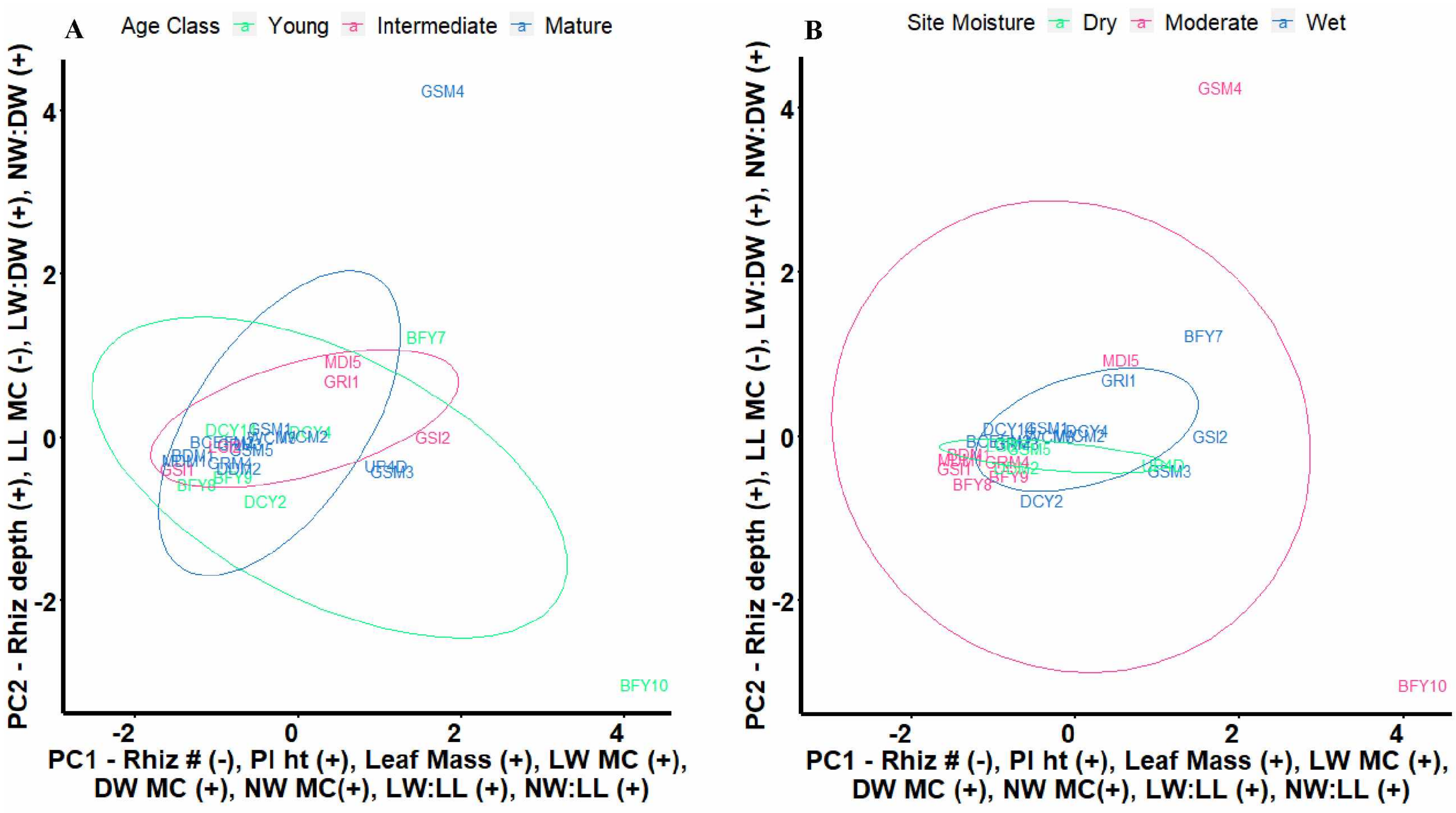

Figure 2.8 Biplots of the PCA of sites in biomass-weighted mean trait space for *V. uliginosum* data grouped by age class (A) and site moisture (B). Axes titles indicate which traits are associated with each axis (Rhiz depth = Rhizome depth, Rhiz # = Rhizome number, Pl ht = Plant height, Leaf Mass = Dry leaf mass, LW MC = live wood moisture content, DW MC = dead wood moisture content, NW MC = New wood moisture content, LL MC = live leaf moisture content, LW:DW = live wood to dead wood, LW:LL = live wood to live leaf, NW:DW = new wood to dead wood, NW:LL = new wood to live leaf), where '+' indicates positive association and '-' indicates negative association.

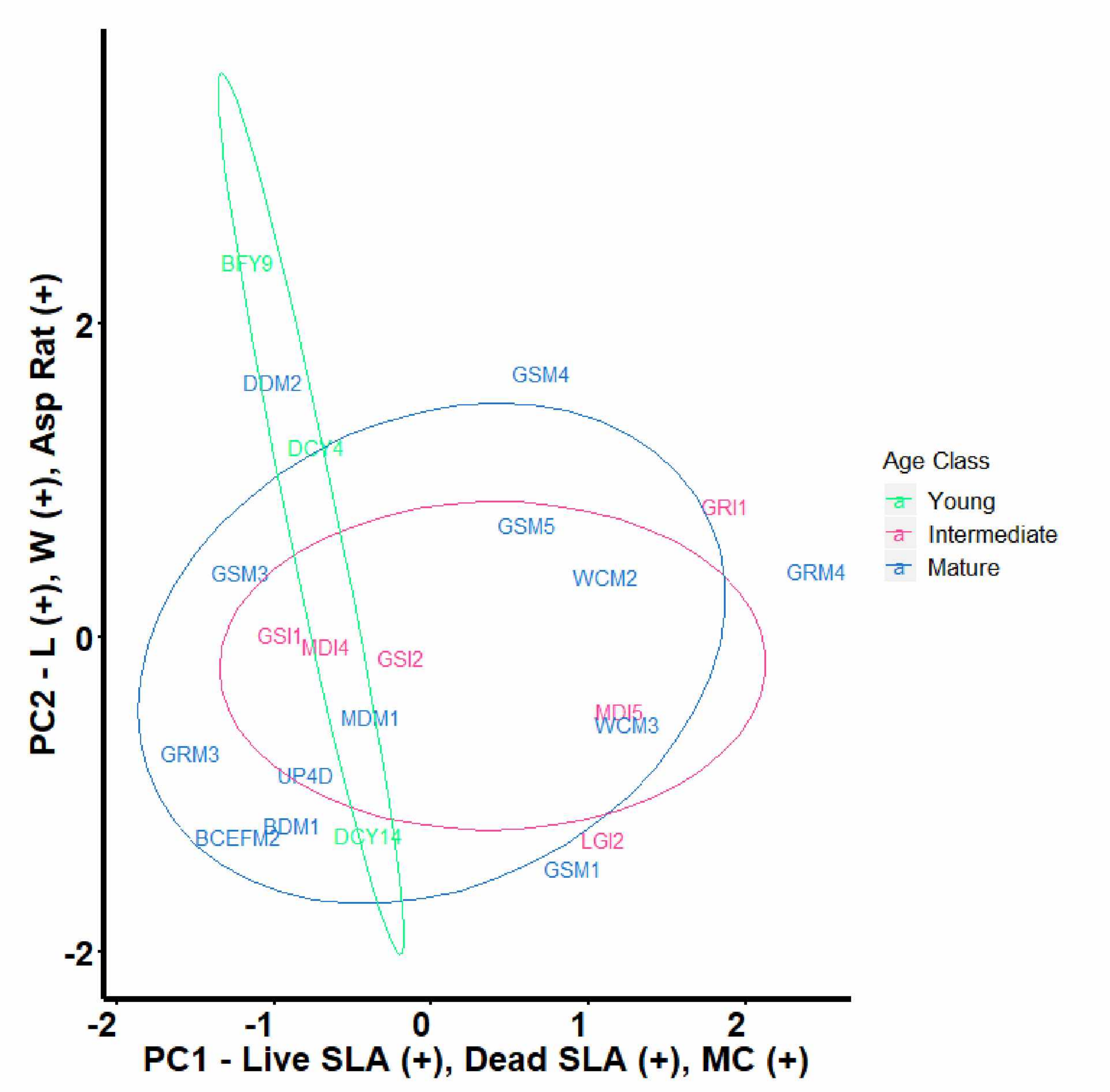

Figure 2.9 Biplot of the PCA depicting the similarities of sites with respect to their CVs for six fire-ecological plant trait of *H. splendens*. Axes titles indicate which traits are associated with each axis (MC = Moisture Content, L = Length, W = Width, Asp Rat = Aspect Ratio, SLA = Surface Leaf Area), where '+' indicates positive association and '-' indicates negative association.. Sites are grouped by their respective age class (Young = 0-10 years, Intermediate = 40-60 years, and Mature = >80 years after fire).

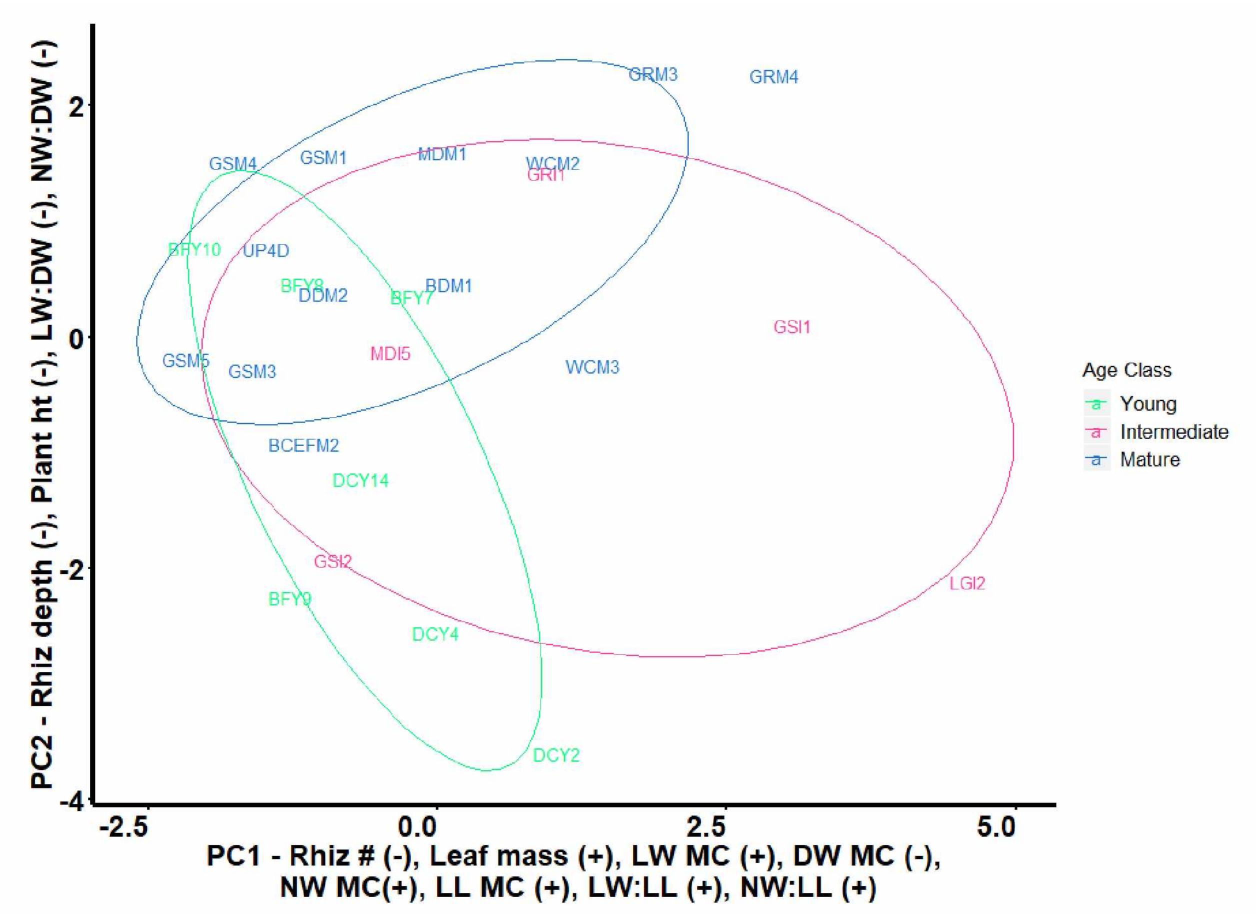

Figure 2.10 Biplot of the PCA depicting the similarities of sites with respect to their CVs for twelve fire-ecological plant trait of *V. uliginosum*. Axes titles indicate which traits are associated with each axis (Rhiz depth = Rhizome depth, Rhiz # = Rhizome #, Plant ht = Plant height, LW = Live Wood, DW = Dead Wood, NW = New Wood, LL = Live Lead, MC = Moisture Content), where '+' indicates positive association and '-' indicates negative association. Sites are grouped by their respective age class (Young = 0-10 years, Intermediate = 40-60 years, and Mature = >80 years after fire).

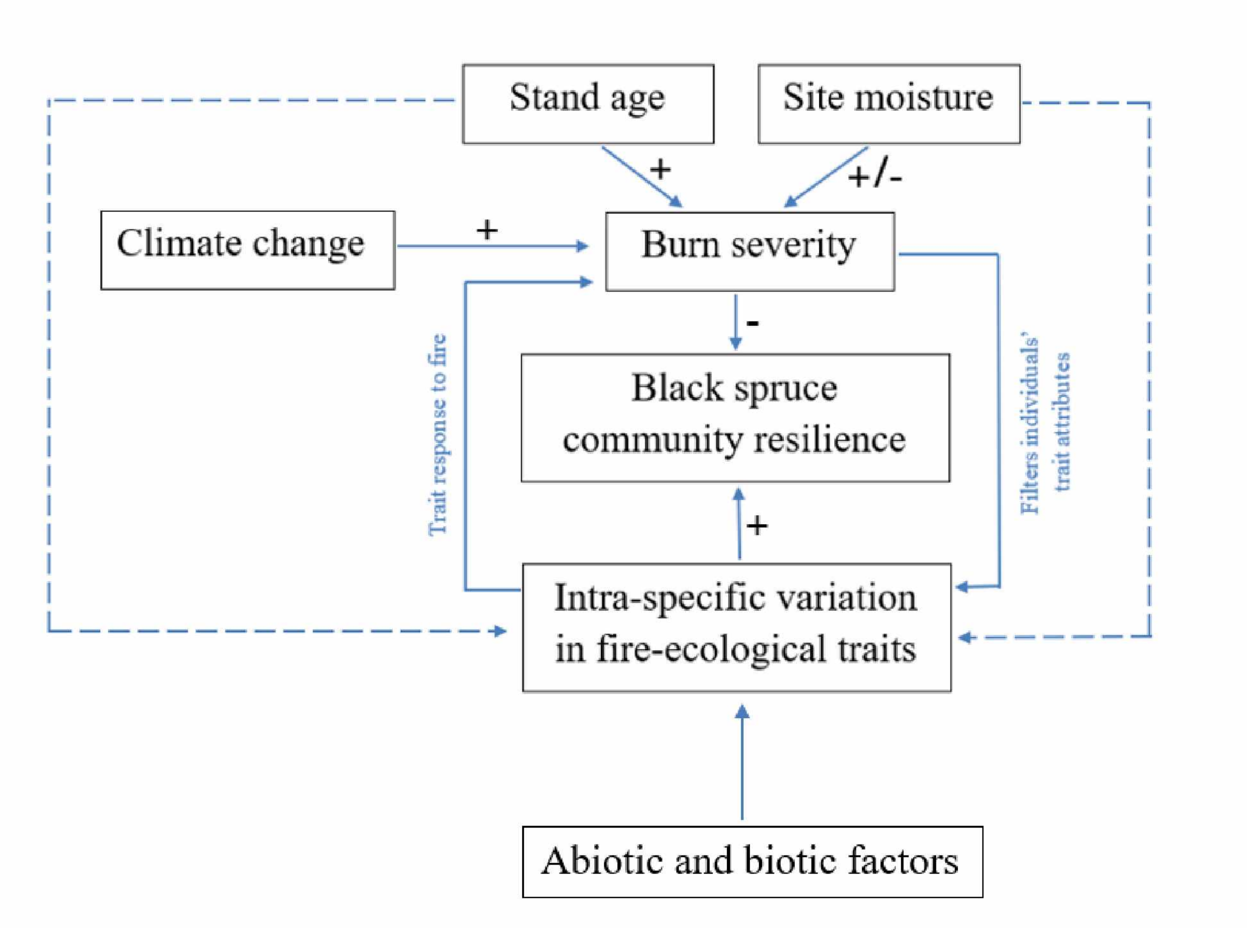

Figure 2.11 Conceptual framework depicting the direct and indirect effects of various explanatory factors, fire effects and intra-specific plant trait variation on black spruce community resilience to fire perturbations. Solid lines represent direct effects, whereas dashed lines represent indirect effects. '+' indicates positive effects, whereas '-'indicates negative effects.

Table 2.1 Names of the 26 study sites and information on years since their last burn, age class (Young = 0-10 years, Intermediate = 40-60 years, and Mature = >80 years after fire), location (latitude and longitude are in decimal degrees; ecoregions YTU = Yukon-Tanana Uplands, RM = Ray Mountains, TKL = Tanana-Kuskokwim Lowlands), environmental characteristics (forest type BL SP = Black Spruce, MIX = Conifer-Deciduous Mixed; site moisture driest to wettest: xeric, subxeric, subxeric/mesic, mesic, mesic/subhygric, subhygric; average active layer depth -999 = nonexistent or too deep to measure, -888 = unable to measure due to mineral layer), and whether fire-ecological traits were measured for *H. splendens* (HS) only, *V. uliginosum* (VS) only), or both species.

Site	Time Since Fire	Age Class	Eco-region	Latitude (°)	Longitude (°)	Forest Type	Moisture	Burn Severity	Elevation (m)	Average active layer depth (cm)	Traits measured for HS, VU, or both
BFY10	15	Young	YTU	65.1187	-147.449	MIX	Subxeric/Mesic	MODERATE	445	-999	VU
BFY7	15	Young	YTU	65.1537	-147.477	BL SP	Mesic/Subhygric	LOW	240	66.3	VU
BFY8	15	Young	YTU	65.3493	-146.668	BL SP	Mesic	LOW	695	89.7	VU
BFY9	15	Young	YTU	65.3531	-146.675	BL SP	Subxeric/Mesic	LOW	770	-999	Both
DCY14	15	Young	RM	66.1203	-150.163	BL SP	Subhygric	LOW	170	-999	Both
DCY2	15	Young	RM	66.2152	-150.258	MIX	Mesic/Subhygric	LOW	445	-999	VU
DCY4	15	Young	RM	66.1053	-150.151	MIX	Subhygric	LOW	220	81.3	Both
GRI1	72	Intermediate	TKL	63.7721	-145.079	BL SP	Subhygric	NA	552	41.5	Both
GSI1	53	Intermediate	YTU	64.8000	-148.414	BL SP	Mesic	NA	244	80.7	Both
GSI2	53	Intermediate	YTU	64.8026	-148.420	BL SP	Subhygric	NA	129	54.9	Both
LGI2	61	Intermediate	RM	65.4465	-148.761	BL SP	Subxeric	NA	330	-888	Both
MDI4	61	Intermediate	YTU	64.8827	-148.356	MIX	Subxeric	NA	205	155.1	HS
MDI5	61	Intermediate	YTU	64.8829	-148.398	BL SP	Mesic	NA	226	47.3	Both
BCEFM2	Pre 1930	Mature	YTU	64.6952	-148.323	BL SP	Subhygric	NA	128	29.8	Both
BDM1	Pre 1930	Mature	RM	65.1579	-150.136	BL SP	Mesic	NA	241	-888	Both
DDM2	87	Mature	TKL	63.8918	-145.741	BL SP	Xeric	NA	500	-888	Both
GRM3	206	Mature	TKL	63.8137	-144.954	Bl SP	Mesic/Subhygric	NA	430	44.2	Both
GRM4	313	Mature	TKL	63.8151	-144.956	BL SP	Subxeric/Mesic	NA	429	53.6	Both
GSM1	179	Mature	YTU	64.8026	-148.317	BL SP	Subhygric	NA	180	25.2	Both
GSM3	185	Mature	YTU	64.9162	-147.832	Bl SP	Subhygric	NA	187	70.7	Both
GSM4	103	Mature	YTU	64.9422	-148.253	BL SP	Subxeric/Mesic	NA	497	-888	Both
GSM5	179	Mature	YTU	64.9986	-147.657	BL SP	Subxeric	NA	431	42.2	Both
MDM1	Pre 1930	Mature	YTU	64.8716	-148.371	BL SP	Mesic	NA	197	49.4	Both
UP4D	Pre 1930	Mature	YTU	65.1691	-147.551	BL SP	Subxeric	NA	600	-999	Both
WCM2	Pre 1930	Mature	YTU	65.1363	-147.971	BL SP	Mesic/Subhygric	NA	260	35.2	Both
WCM3	188	Mature	YTU	65.1547	-147.863	BL SP	Subhygric	NA	274	53.5	Both

Table 2.2 Results from the best linear mixed-effect models in explaining variation in the first and second principal components derived from PCA[1] on *H. splendens* and *V. uliginosum* fire-ecological plant traits.

Response Variable	Random Effect	Fixed Effect	Parameter Estimate	Standard Error	t-value
PC1 (*H. splendens*)	(1 | Site/Cushion)	TSF	0.0013	0.0014	0.92
PC2 (*H. splendens*)	(1 | Site/Cushion)	M	0.019	0.029	0.65
PC1 (*V. uliginosum*)	(1 | Site)	TSF	-0.0033	0.0026	-1.26
PC2 (*V. uliginosum*)	(1 | Site)	TSF	0.00011	0.0022	0.051

Table 2.3 Results from MRPP analysis on heterogeneity in biomass-weighted traits means for *H. splendens* and *V. uliginosum* among within groups and between pairwise-comparisons of age and moisture classes.

		Hylocomium splendens		*Vaccinium uliginosum*	
		A	p-value	A	p-value
Age		0.11	0.049	0.004	0.32
	Young vs Intermediate	0.28	0.034	-0.018	0.55
	Young vs Mature	0.17	0.015	0.024	0.079
	Intermediate vs Mature	-0.042	0.94	-0.017	0.88
Moisture		0.018	0.28	0.0011	0.37
	Dry vs Moderate	0.025	0.27	0.0024	0.40
	Dry vs Wet	-0.027	0.51	-0.011	0.46
	Moderate vs Wet	0.027	0.20	0.0022	0.29

General Conclusion

Fuel load, site-level flammability and fire-ecological plant traits are inherent properties of black spruce forests that contribute to the burning potential and capacity of a site to undergo self-replacement after fire. Knowledge on the spatiotemporal variation of these properties provides a greater understanding of locations across the black spruce landscape in interior Alaska that are more likely to burn severely and/or have greater resiliency to a changing fire regime. Black spruce forest fuel loads varied incredibly with stand age and site moisture, and fuel load can additionally be explained by active layer depth and elevation. I found significantly higher flammability indices in sites greater than 34 years since fire, occurring at elevations greater than 302 m, with dry site moisture, indicating the greater vulnerability of these sites to experiencing severe fire disturbances. Specifically, these sites are representative of nonacidic, dry, upland black spruce and acidic, dry, upland black spruce-lichen forest ecosystems, which are prevalent across interior Alaska and the greater North American region. Additionally, I did not find significant relationships of the amount of intra-specific variation in fire-ecological plant traits of *H. splendens* and *V. uliginosum* with stand age and site moisture gradients, which suggests that patterns in black spruce forest resilience may likely be independent of these variables as well. Regardless, I did find that some sites did contain greater intra-specific trait variation, suggesting that these sites likely possess greater forest resiliency to a changing fire regime than other sites along the black spruce forest landscape. I recommend that future studies investigate fire-ecological plant traits across both abiotic and biotic variables in multiple plant species that are representative of the various plant functional groups present in black spruce sites.

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Appendix

Table S1.1 Environmental variable loadings on each principal component from the principle component analysis on understory fuel loads with six environmental variables.

	PC1	PC2	PC3	PC4	PC5	PC6
Slope	-0.41204	0.357667	-0.41381	-0.58174	0.263258	-0.35119
Aspect	-0.41245	0.463095	-0.11911	0.488371	0.307833	0.517665
Elevation	-0.43657	-0.15967	-0.23384	-0.1805	-0.75329	0.35944
Moisture	-0.4316	0.173875	0.346515	0.415111	-0.29669	-0.63488
Average active layer	-0.35156	-0.74936	-0.33554	0.262493	0.338901	-0.13611
Time since fire	-0.39956	-0.20088	0.72611	-0.38635	0.256128	0.24061

Table S1.2 Results from best linear mixed-effect model in explaining black spruce forest fuel loads with four environmental variables (TSF = Time since fire; M = Moisture; AAL = Average active layer; E = Elevation).

Response Variable	Random Effect	Fixed Effects	Estimate	Standard Error	t-value	Upper CI	Lower CI	K	AICc
Organic soil fuel load	(1|Site)	TSF	0.0033	0.00095	3.48	0.0052	0.0014	5	744.39
		M	0.23	0.0243	9.505	0.28	0.18		
Vascular understory fuel load	(1|Site)	TSF	0.00037	0.000116	3.248	0.00088	0.0003	5	-656.49
		TSF:AAL	0.00017	0.000139	1.239	0.00052	-0.0002		
Non-vascular understory fuel load	(1|Site)	TSF	0.00034	0.000118	2.889	0.00057	0.00011	6	-479.96
		M	0.01188	0.002912	4.081	0.018	0.00622		
		AAL	-0.00144	0.01018	-0.142	0.019	-0.021		
Canopy fuel load	(1|Site)	TSF	0.00566	0.001	5.624	0.0076	0.0037	8	899.78
		TSF:AAL	0.0043	0.00092	4.651	0.006	-0.0025		
		M	0.0127	0.0228	0.556	0.057	-0.032		
		E	-0.169	0.2065	-0.82	0.24	-0.57		
		M:E	0.0334	0.04987	0.670	0.13	-0.064		

Table S1.3 Flammability indices for each site, from highest to lowest FI, with corresponding age and moisture class.

Site	FI	Age	Moisture
MDI4	162.825	Intermediate	Subxeric
UP4D	57.9222	Mature	Subxeric
GSI1	47.2513	Intermediate	Mesic
LGI2	45.5607	Intermediate	Subxeric
GSM5	38.9605	Mature	Subxeric
MDM1	38.9453	Mature	Mesic
DDM2	36.5121	Mature	Xeric
GSM3	34.5205	Mature	Subhygric
GRM4	34.185	Mature	Subxeric/mesic
GRI1	32.7917	Intermediate	Subhygric
GSM4	32.4436	Mature	Subxeric/mesic
GSI2	31.6211	Intermediate	Subhygric
BCEFM2	25.93	Mature	Subhygric
GRM3	25.7259	Mature	Mesic/subhygric
BDM1	23.9203	Mature	Mesic
GSM1	23.757	Mature	Subhygric
BFY7	21.8319	Young	Mesic/subhygric
WCM3	21.494	Mature	Subhygric
BFY9	21.1367	Young	Subxeric/mesic
MDI5	19.3954	Intermediate	Mesic
BFY10	17.8214	Young	Subxeric/mesic
DCY2	17.6086	Young	Mesic/subhygric
WCM2	14.1579	Mature	Mesic/subhygric
BFY8	11.0223	Young	Mesic
DCY9	9.58719	Young	Mesic
DCY4	9.50677	Young	Subhygric
DCY3	8.21733	Young	Subxeric/mesic
DCY14	7.37426	Young	Subhygric

Table S2.1 Mean trait values and standard deviation (in parentheses) for each *H. splendens* fire-ecological plant trait within each age and moisture class. MC = Moisture Content, SLA = Surface Leaf Area.

			Fire-ecological plant traits					
Stand Age	Moisture	n	MC %	Length (cm)	Width (cm)	Aspect Ratio	Live SLA ($cm^2 \cdot g^{-1}$)	Dead SLA ($cm^2 \cdot g^{-1}$)
Young								
	Subxeric/Mesic	1	155.11 (128.27)	7.67 (2.22)	2.04 (0.5)	0.27 (0.06)	233.61 (79.88)	168.72 (83.83)
	Subhygric	2	463.53 (202.35)	8.10 (1.94)	1.88 (0.43)	0.24 (0.07)	603.02 (184.62)	450.92 (259.48)
Intermediate								
	Subxeric	2	392.48 (226.52)	12.53 (3.14)	2.69 (0.41)	0.23 (0.06)	515.92 (207.83)	435.99 (237.58)
	Mesic	2	363.48 (231.21)	10.66 (2.53)	2.53 (0.54)	0.24 (0.06)	386.99 (196.88)	333.01 (208.72)
	Subhygric	2	316.99 (238)	7.89 (2.04)	1.99 (0.46)	0.26 (0.06)	379.61 (200.61)	317.44 (239.05)
Mature								
	Xeric	1	247.58 (179.82)	5.32 (2.27)	1.62 (0.46)	0.33 (0.08)	279.45 (144.85)	239.97 (123.82)
	Subxeric	2	331.90 (192.57)	9.58 (3.26)	2.33 (0.62)	0.25 (0.06)	379.74 (161.5)	351.86 (177.95)
	Subxeric/Mesic	2	326.70 (259.84)	7.48 (2.05)	1.94 (0.4)	0.27 (0.08)	426.17 (242.91)	358.26 (226.75)
	Mesic	2	470.37 (209.08)	9.81 (2.34)	2.15 (0.47)	0.23 (0.06)	537.21 (183.96)	468.52 (211.01)
	Mesic/Subhygric	2	242.63 (175.59)	6.80 (1.58)	1.82 (0.38)	0.28 (0.08)	379.17 (195.79)	225.81 (139.5)
	Subhygric	4	256.42 (197.19)	7.96 (2.18)	1.85 (0.4)	0.24 (0.06)	368.00 (188.03)	266.38 (204.85)

Table S2.2 Mean trait values and standard deviation (in parentheses) for each *V. uliginosum* fire-ecological plant trait within each age and moisture class. LW = Live Wood, DW = Dead Wood, NW = New Wood, LL = Live Leaf, MC = Moisture Content.

			Fire-ecological plant traits						
Stand Age	Moisture	n	Rhizome Depth (cm)	# of Rhizomes	Dry Leaf Mass (g)	LW MC %	DW MC %	NW MC %	LL MC %
Young									
	Subxeric/Mesic	2	6.60 (3.63)	4.00 (1.94)	1.88 (1.83)	85.54 (7.5)	36.38 (24.17)	71.54 (18.78)	83.15 (41.59)
	Mesic	1	7.80 (1.79)	7.60 (1.95)	0.99 (0.39)	82.01 (11.44)	37.72 (28.5)	62.64 (18)	76.00 (62.75)
	Mesic/Subhygric	2	12.00 (8.21)	7.10 (2.73)	1.18 (1.08)	51.90 (39.96)	34.37 (20.89)	45.26 (40.95)	42.50 (52.16)
	Subhygric	2	9.10 (4.01)	6.30 (3.09)	0.43 (0.31)	40.23 (20.95)	44.81 (40.56)	31.45 (12.14)	24.32 (18.34)
Intermediate									
	Subxeric	1	9.20 (2.59)	8.80 (3.27)	0.23 (0.23)	33.35 (29.98)	35.48 (25.91)	25.53 (24)	15.32 (16.27)
	Mesic	2	14.60 (4.4)	8.20 (2.94)	0.41 (0.38)	38.30 (20.58)	246.37 (467.95)	35.51 (21.12)	23.58 (17.99)
	Subhygric	2	16.70 (5.5)	6.40 (2.8)	0.63 (0.6)	43.16 (31.15)	32.60 (42.82)	33.62 (24.52)	21.68 (15.46)
Mature									
	Xeric	1	6.40 (2.7)	6.40 (3.36)	0.18 (0.13)	39.85 (19.95)	95.99 (148.21)	91.49 (51.92)	51.60 (13.42)
	Subxeric	2	16.10 (5.36)	3.50 (2.42)	0.62 (0.37)	54.64 (21.85)	52.22 (62.06)	44.22 (19.12)	24.31 (16.62)
	Subxeric/Mesic	2	16.30 (5.58)	4.30 (2.54)	0.34 (0.12)	33.92 (26.54)	34.07 (50.5)	31.35 (26.51)	21.27 (24.22)
	Mesic	2	16.10 (5.45)	4.00 (1.89)	0.19 (0.09)	18.35 (7.84)	60.38 (43.21)	18.40 (11)	12.72 (6.9)
	Mesic/Subhygric	2	15.70 (4.14)	4.60 (1.26)	0.42 (0.26)	29.63 (19.11)	11.73 (10.14)	22.18 (13.5)	22.46 (24.45)
	Subhygric	4	19.55 (7.52)	3.80 (2.07)	0.59 (0.54)	39.18 (23.98)	45.57 (96.76)	33.96 (16.2)	28.93 (27.69)

Table S2.2 (continued) Mean trait values and standard deviation (in parentheses) for each *V. uliginosum* fire-ecological plant trait within each age and moisture class. LW = Live Wood, DW = Dead Wood, NW = New Wood, LL = Live Leaf, MC = Moisture Content.

			Fire-ecological plant traits			
Stand Age	Moisture	n	LW:DW	LW:LL	NW:DW	NW:LL
Young						
	Subxeric/Mesic	2	252.89 (416.55)	5.73 (1.94)	26.38 (48.65)	0.57 (0.21)
	Mesic	1	118.40 (85.08)	4.57 (1)	21.63 (16.57)	0.78 (0.17)
	Mesic/Subhygric	2	175.63 (216.08)	5.38 (2.69)	16.09 (21.65)	0.53 (0.17)
	Subhygric	2	338.73 (433.47)	3.88 (1.59)	42.42 (54.45)	0.48 (0.16)
Intermediate						
	Subxeric	1	51.47 (101.18)	6.00 (4.42)	7.10 (13.7)	1.08 (0.62)
	Mesic	2	243.65 (391.47)	4.63 (3.04)	33.76 (50.97)	0.92 (0.31)
	Subhygric	2	116.12 (183.04)	6.12 (2.98)	7.88 (8.23)	0.50 (0.14)
Mature						
	Xeric	1	327.47 (191.31)	4.09 (2.1)	39.43 (25.3)	0.42 (0.11)
	Subxeric	2	75.39 (54.49)	4.32 (1.1)	10.76 (7.76)	0.62 (0.18)
	Subxeric/Mesic	2	1172.61 (1375.61)	8.46 (5.5)	96.68 (118.83)	0.83 (0.41)
	Mesic	2	82.43 (72.55)	3.23 (1.76)	18.05 (13.75)	0.75 (0.35)
	Mesic/Subhygric	2	28.60 (11.98)	6.63 (3.09)	2.50 (1.35)	0.58 (0.29)
	Subhygric	4	92.07 (104.93)	6.58 (4.56)	10.06 (10.88)	0.73 (0.33)

Table S2.3 Results from all linear mixed effect models on principal components derived from PCA on *H. splendens* and *V. uliginosum* fire-ecological plant traits with the main, additive and interaction effects of time since fire (TSF) and moisture (M).

Response	Random	Fixed	K	AICc	Cumulative weight	Log-likelihood
PC1 (*H. splendens*)	(1|Site/Cushion)	TSF*M	7	1828.4	1.00	-907.1
		TSF + M	6	1826.4	0.93	-907.1
		TSF	5	1824.8	0.45	-907.3
		M	5	1825.7	0.73	-907.8
PC2 (*H. splendens*)	(1|Site/Cushion)	TSF*M	7	1583.1	1.00	-784.5
		TSF + M	6	1582.8	0.27	-785.3
		TSF	5	1583.0	0.23	-786.4
		M	5	1582.9	0.25	-786.5
PC1 (*V. uliginosum*)	(1|Site)	TSF*M	6	443.9	0.86	-215.6
		TSF + M	4	442.7	0.27	-216.1
		TSF	5	441.7	0.44	-216.7
		M	5	444.1	0.14	-217.9
PC2 (*V. uliginosum*)	(1|Site)	TSF*M	6	398.3	1.00	-192.8
		TSF + M	5	396.5	0.94	-193.0
		TSF	4	395.0	0.78	-193.4
		M	4	394.4	0.45	-193.1