

**Forest Resilience to Wildfire and Harvesting: A Comparison of Microclimate & Understory Plant Diversity in Island Remnants a Decade After Disturbance**

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Forest Biology and Management

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## **Abstract**

An important feature of ecosystem-based forest management in the boreal mixedwood of northern Alberta, Canada – and in other forests around the world - is the emulation of natural disturbances such as wildfire. Post-fire landscapes typically include unburned or partially burned patches of forest often referred to as remnants. Remnants are thought to support understory communities and microclimates similar to reference mature forest within a disturbed landscape. While forest managers leave remnant patches within harvest blocks to emulate the structural effects of fire, it is unknown if they are effective analogues. My objective was to examine if harvest and fire remnants are effective at maintaining microclimatic conditions and understory vascular plant communities, similar to those of reference forest, in a post-disturbance landscape, and to establish links between forest structure and understory plant assemblages. I also used a trait-based approach to uncover patterns of plant persistence or colonization within disturbed forest and remnants. I identified three harvested and three burned areas approximately a decade after disturbance, and within each area sampled 3-7 island remnants as well as the disturbed area adjacent to remnants. Each remnant was paired with a nearby “reference”, a mature continuous forest. At each island remnant, disturbed area, and reference, edge and interior plots were sampled to collect data on soil and surface air temperature, tree, and understory vegetation; these were then analyzed using a combination of taxonomic and trait-based approaches.

I found that fire and harvest remnants did not support similar understory plant communities; however, they did support communities similar to their respective reference forest. Remnants in both fires and harvests had similar richness, cover and diversity of understory

species compared to reference forest. Plant traits associated with plant persistence were more frequent in remnants of both disturbance types and references, while colonization plant traits were more common in the disturbed areas. There were no differences between the understory plant community or traits at edges versus the interiors of remnants of either disturbance type. There were limited positive associations between canopy cover and forest dependent understory plant species abundance and negative associations between canopy cover and early seral species. I did not find any evidence of tree mortality leading to increased abundance of early seral understory species or increases in temperature. While remnants of both disturbance types contained temperatures similar to reference forest, temperatures in fire remnant edges and fire disturbed plots were generally higher than reference forest, unlike the harvest remnant edges/disturbance.

These findings support the practice of patch retention within clearcuts, finding them to be similar to fire remnants, with some caveats. I confirm that both fire and harvest remnants are effective at providing a forest structure and microclimatic conditions similar to those of reference forest. I believe this research will help empower forest managers to make harvest decisions that enable the forests of the future to retain biodiversity and function effectively.

## **Acknowledgements**

I would first like to thank my supervisor, Dr Charles Nock, for the opportunity to conduct my research in his lab. I would further like to thank him for his guidance throughout the thesis process. I also want to thank my co-supervisor, Dr. Ellen Macdonald, for sharing your wealth of experience with me. I would also like to acknowledge our partners in the forestry industry, without their financial support and forest data this research would not have been possible. I would also like to thank the Alberta Conservation Association for their financial support.

I am grateful for everyone who supported my research in the field. To Lily Steinke, Shannon O'Brien, and Zach Olchowy thank you not only for the hard work you guys put into data collection all summer, but also for all the fun times we had over the summer. I'm truly grateful to have had your assistance and good humour throughout fieldwork.

To all my colleagues in the Nock lab, thank you for all the memories. Jessica, thank you for being a phone call away whenever I needed help coordinating fieldwork. I also appreciate all the feedback you were able to provide for practice presentations. Marcus, thank you for the in-depth discussions about our research, from experimental design to fire ecology, you helped me attain a deeper understanding of both my project, and ecology as a whole. Thank you for your quips and good humour, I don't think I've ever laughed so much doing fieldwork. Lance, thank you for all your hard work. I'm amazed at your work ethic and unwavering positivity despite all the scratches and crawling around fallen trees. Rosanise, I would like to thank you for all the help you provided to me while writing my thesis. I will also cherish the memories of long days wandering around the forest together, searching endlessly for suitable study sites.

Thank you to my parents and sister for everything, but especially supporting me in all my endeavours. A big thanks to all my friends for all the support and fun times throughout my thesis. Most of all, thank you to my wonderful partner for everything, I couldn't have done this without you!

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# 1 Introduction

Forests are the largest terrestrial biome on the earth, covering 31% of the global land area (Pan et al., 2013). From a basic anthropogenic point of view, they are indispensable, providing wood to build structures and burn as fuel. They are also a source of both plants and animals, resources that have been used as food, medicine, and clothing by humans since time immemorial (Kirch, 2005; Kwiatkowska, 2007; Williams, 2001). Forests, however, provide so much more. They regulate air and water quality; they regulate climate through carbon capture; they protect soil from erosion; they provide cultural, aesthetic, and recreation services (Mace et al., 2012; Weber & Van Cleve, 1981). Finally, forests are intrinsically important as a trove of biodiversity (Ghilarov, 2000), supporting hundreds of thousands of different species of plants, animals, and fungi (FAO & UNEP, 2020). Managing forests is a complex issue where both timber extraction and the value of ecosystem goods and services must be considered to preserve the integrity of the ecosystem long-term (Kuuluvainen et al. 2021).

## 1.1 The boreal forest

The boreal forest is a circumpolar biome of almost 1 billion hectares spanning the northern sections of Eurasia and North America (Burton et al. 2010). Boreal landscapes in Canada are dominated by forest and peatlands regularly interspersed with rivers and lakes, making it a uniquely important ecosystem. Within its forests and peatlands lies massive stores of carbon, critical to preserve in the fight against climate change. Within the rivers, wetlands, and lakes, lie massive reserves of fresh water, crucial for humans, plants, and wildlife alike (Badiou et al. 2013). Despite relatively poor soils and a short growing season, approximately 111 million m<sup>3</sup> of wood

is harvested from the Canadian boreal forest every year, primarily in Alberta, Quebec, and Ontario (Burton et al. 2013). While there is generally less human disturbance in the boreal compared to more southern biomes, human activity is increasing, further encroaching northward into more intact forest (Badiou et al. 2013). My thesis research focuses on the boreal forest, where there is increasing pressure to manage forests to protect the health and function of this critical biome (Bergeron et al. 1999; Cyr et al. 2009; Burton et al. 2010; Badiou et al. 2013; Kuuluvainen et al. 2021; Gauthier et al. 2023).

## **1.2 Forest management paradigms**

In the boreal forest of North America, the dominant forest management paradigm for timber extraction in the 20<sup>th</sup> century was sustained yield forest management (Gustafsson et al. 2012; Gauthier et al. 2023). This system is characterized by even-aged stand management, where a stand is clearcut when it achieves its maximum volume of wood (Gauthier et al. 2023). An apt comparison to this management system is agriculture, where trees were the crop, and the forest are the farmland (Namkoong 2008; Kuuluvainen et al. 2021). The application of these forestry practices in boreal forests in Europe and North America have been found to have simplified forest structure, leading to forest stands that are more homogenous than those found in nature (Burton et al., 2010; Cyr et al., 2009). The homogenous structure of a forest stand regenerating from a complete clearcut eliminates niches occupied by many types of biota, especially species dependant on deadwood for survival (Siitonen 2001; Lassauce et al. 2011). As a result, managed even-aged forest stands have been found to have lower biodiversity compared to natural forests (Cyr et al., 2009, Kuuluvainen et al., 2012). Biodiversity is intricately linked to ecosystem services: diverse forests often result in higher levels of ecosystem services compared to less diverse forests

(Mace et al., 2012; Gamfeldt et al., 2016; van der Plas et al., 2016; Champagne et al., 2017), although this is not always the case (e.g. Brokerhoff et al., 2017).

An alternative form of forest management, known as Ecosystem-Based Management (EBM), emerged in the late 1980's that aims to manage forests for multiple values, balancing timber harvest, while still maintaining key ecosystem processes that provide goods and services (Franklin 1989; Lindenmayer & Franklin 2002). A popular approach to EBM implementation in the boreal forest is the Emulation of Natural Disturbance (END), that uses naturally occurring disturbances in forest ecosystems to guide forest management (Franklin 1989; Stockdale et al. 2016). It is thought that if a harvest is done in a way that emulates the natural disturbance regime found in the ecosystem, the biota of that ecosystem (and thus the ecosystem processes) would be more resilient to the emulated disturbance versus a novel disturbance (i.e. a clearcut) (Franklin 1989; Lindenmayer et al. 2012). END is implemented at the landscape scale, to preserve a forest age class distribution similar to those under natural conditions (Bergeron et al. 1999), and at the stand scale to mimic the post-disturbance forest structure of natural stands (Gauthier et al. 2023). A popular management tool in the boreal forest to meet the stand-level objectives of END is green tree retention, in which living trees are left on the post-harvest landscape to provide a source of structural heterogeneity and material legacies (Gustafsson et al. 2012; Gauthier et al. 2023). Retained trees can be either dispersed throughout the cutblock, aggregated into patches, or a combination of the two. The number of trees retained can also vary but is typically at least 5-10% (Gustafsson et al. 2012). These more structurally complex forests contain more niches, thus more biotic diversity, and leaving living materials in situ will help forest



regeneration through the preservation of propagule sources (Baker et al. 2013; Franklin 1989; Lindenmayer et al. 2012; Fedrowitz et al. 2014).

### **1.3 Understory plants**

Conservation of understory plant diversity is an important component to managing for a multi functional forest as most of the overall plant diversity and animal food sources in the boreal forest are found in the understory (Gilliam 2007; Roberts 2004). The understory represents a small but significant proportion of the total forest net primary production and nutrient distribution and is thus a crucial element in nutrient cycling and annual turnover throughout the life history of a stand (Chapin 1983; Gilliam 2007; Gower et al. 1997; Muukkonen & Mäkipää 2006). The understory helps maintain the structure and health of the soil and exerts influence over forest floor microclimates (Gilliam 2007; Hogg & Lieffers 1991; Ziemer 1981). While tree canopies are often a driver of understory vegetation dynamics, the inverse is also true: the understory can often influence the species composition of future canopies through tree regeneration, and often delay or prevent the formation of a closed canopy (Gilliam 2007; Chen & Popadiouk 2002). For example, tall shrubs such as alder, ericaceous shrubs, and dense grass mats have been linked to delayed stand development due to their ability to invade optimal seedling microsites and out-compete established seedlings (Landhäusser & Lieffers 1998; Lieffers et al. 1993; Nilsson & Wardle 2005; Royo & Carson 2006).

Understory community composition is primarily driven by edaphic and geographical controls such as moisture, aspect, and nutrient availability (Hart & Chen, 2006). However, following canopy closure, light becomes a limiting factor for the understory layer and variations in tree density and canopy cover become an important source of heterogeneity in the

understory (Chen & Popadiouk 2002). Dense, closed tree canopies lead to lower understory cover, while open canopies and gaps allow light to reach the understory, leading to higher understory plant cover (Hart & Chen, 2006). Competition for light is another important driver of understory composition, with tall shrubs and forbs able to better monopolize light underneath the canopy (Hart & Chen, 2006).

Many studies have examined understory communities taxonomically, using measures of diversity and dissimilarity matrices that capture the presence and abundance of species. In recent years, plant functional traits have been increasingly used to explain understory communities in response to different environmental gradients (Diaz & Cabido 1997; Lavorel & Garnier 2002; Violle et al. 2007), and in response to disturbance (Mouillot et al. 2013). Disturbances have a filtering effect on plant functional communities. A change in environmental conditions, mediated by disturbance, can lead to a shift in plant community, as those traits that are poorly adapted to new conditions are replaced by species with more suitable traits (Mouillot et al. 2013). Increasing intensity of forest management has been found to filter understory community traits towards plant communities with colonization traits syndromes, or a group of traits that facilitate plant colonization of new environments (Patry et al. 2017). Less intensive forest management was linked to plant communities with persistent trait syndromes, or traits that enable plants to continue to remain in place (Patry et al. 2017).

#### **1.4 Edge influence**

When a forest borders a disturbed matrix following the death or removal of trees, it undergoes structural changes, known as edge influence (Harper et al. 2005). Within the boreal, the magnitude and distance of edge influence varies by the type of response variable, the type of

disturbance, and the time since disturbance (Harper et al 2015). According to Harper et al. (2005), responses to edge influence can be categorized as either primary or secondary responses. The loss of adjacent trees increases the light availability within a patch, increasing productivity, nutrient cycling, evapotranspiration, and warming the soil and forest floor (Chen et al. 1993; Harper et al. 2005). The disturbance process that created the edge can directly damage trees, but the increased exposure to wind and higher evapotranspiration at edges can also lead to increased tree mortality at the forest edge (Chen et al. 1993; Harper et al. 2005). These processes are classified as primary responses to edge influence (Harper et al. 2005). Secondary responses include the recruitment of saplings, increases in understory cover and changes in composition, further mediated by the primary responses (Harper et al. 2005; Harper et al. 2010). While increases in understory cover, diversity, and richness are often reported in forest edges, edge influence on understory in the boreal has been reported as “weak” (Harper & Macdonald 2002; Harper et al. 2015). While much of the focus of edge influence is on the forest, the forested matrix also exerts edge influence on the disturbed/unforested matrix, usually referred to as “forest influence” (Keenan & Kimmins 1993; Baker et al 2013). For vascular plants, forest influence allows the regeneration of plants within the disturbed matrix by providing propagules from within the forest (Baker et al 2013), and the amelioration of microclimate, described further below. The depth and magnitude of both edge and forest influence on the understory is thought to decrease over time, as forest regeneration reduces the contrast between the disturbed and undisturbed forest (Harper & Macdonald 2002; Harper et al 2015).

## **1.5 The importance of microclimate**

Another important factor in managing forested ecosystems are microclimatic temperatures. Continuous forests are thought to have a more stable microclimate than clearings; forests moderate wind speeds and reduce both incoming solar radiation and direct precipitation, while also preventing heat and moisture loss by trapping outgoing heat and evapotranspiration (Chen et al. 1999; Powell & Bork, 2006; Saunders et al. 1991). Exposed areas such as clearcuts tend to experience more extremes; wind speeds are higher, and the lack of shading leads to higher temperatures and evapotranspiration during clear summer days and rapid cooling at night (Chen et al. 1999; Saunders et al. 1991; Keenan & Kimmins 1993). Warmer temperatures and high rates of evapotranspiration can lead to plant mortality through desiccation, while cooler evening temperatures can lead to earlier frosts and plant damage (Saunders et al. 1991). Lower wind speeds at forest edges allow masses of warm air to stagnate, raising maximum daytime temperatures at the edge (Chen et al. 1993). Canopy cover has a direct influence on forest microclimatic temperatures (Heithecker & Halpern 2006), and tree mortality brought on by edge effects could be conducive to higher daytime temperatures. Changes in microclimatic conditions at forest edges have been linked to changes in nutrient cycling processes, increased plant desiccation, decreased plant growth, reductions in invertebrate abundance, and changes in animal interactions (Chen et al. 1993; Chen et al. 1999; Saunders et al. 1991). As above, the disturbed side of the edge also experiences forest influence from the adjacent mature forest, modifying the microclimate. Shading contributes to an amelioration of microclimate, with disturbed areas adjacent to the forest containing lower daytime maximum temperatures than the interiors of disturbed areas (Dovčiak and Brown 2014; Baker et al 2014). The distance and

magnitude of the forest influence is thought to vary by aspect, canopy height, time of day, and time since disturbance (Baker et al 2013; Dovčiak and Brown 2014; Baker et al 2014). As with understory vegetation, the magnitude of edge and forest influence is thought to decline with increasing time from edge creation, as the disturbed matrix regenerates (Baker et al 2013; Dovčiak and Brown 2014; Baker et al 2014).

## **1.6 Aggregate retention harvesting**

In the western boreal forest of North America, large stand-replacing fires occurring every 50-150 years are the dominant form of natural disturbance (Heinselman, 1981). Even within the most intense fires, burn severity varies across all spatial scales. Stands disturbed by fire often result in a matrix of mixed burn severity, resulting in patches of forest that remain untouched or only lightly burned while the surrounding forest experiences severe burns. Patches of lightly burned or unburned forest within a burn area are called island remnants, and these remnants are important as they maintain a portion of the pre-disturbance forest structure in a post-disturbance landscape (Andison, 2003). These remnants of pre-disturbance forest are thought to provide a refugia for plants, provide structural heterogeneity, provide habitat for animals, and maintain forest microclimatic conditions, features which are otherwise absent from a burn matrix. They are also thought to act as a source of forest influence, shading the adjacent disturbed area and providing material legacies such as seeds and other propagules that will aid in regenerating the forest (Andison, 2003; Baker et al., 2016; Moussaoui et al., 2016b). Beginning in the past ~15 years, forestry practices in Alberta included the use of aggregate retention to emulate a post-fire forest structure (Gauthier et al 2023). These retention patches aim to serve the same purpose as the island remnants after a fire.

### **1.6.1 Are harvest remnants analogous to fire remnants?**

While the concept of retention is generally well studied in the boreal, much of the research has focused on dispersed retention (e.g., Macdonald & Fenniak 2007; Craig & Macdonald 2009; Caners et al. 2013; Bartels et al. 2017; Echiverri & Macdonald 2020) as opposed to patch retention (see Bradbury 2004; Franklin et al. 2018). Additionally, despite the idea that aggregate retention patches are emulating post-fire remnants, few studies have directly compared the two (see Gandhi et al., 2004; Moussaoui et al. 2016a; Moussaoui et al. 2016b), and those that have did not investigate understory composition. A major threat to the function of residual patches is edge influence. Excessive tree mortality in a patch, mediated by edge influence, could result in different microclimates and understory plant communities than those of mature forest. Changes in understory community and the loss of canopy trees could reduce the ability of a patch to project both shade and propagules into the disturbance matrix.

The differences in stand structure and vegetation composition between harvest and burns arise directly from the different mechanisms of disturbance. Residual patches by contrast are not directly subjected to disturbance but undergo changes due to their proximity to disturbance. The type of disturbance is thought to give rise to different patterns of edge influence. Fire edges are thought to be “feathered”, characterized by a more gradual gradient as the fire burns out around the patch (Harper et al. 2004; Harper et al. 2015). These feathered edges, in addition to the burned snags within the disturbance are thought to moderate wind speeds, and better brace the living trees within the patch (McRae et al. 2001; Harper 2004; Braithwaite & Mallik 2012; Moussaoui 2016a). Harvest edges are more abrupt (Harper et al. 2004), and there are few to no standing snags to moderate the wind, that leads to increased tree mortality from windthrow

(Mascarúa-López et al. 2006). The increased tree mortality at the edge due to edge influence, as well as a lack of snags in the disturbed area, leads to increased light penetration and higher temperatures on the forest floor of harvested edges compared to post-fire edges (Braithwaite & Mallik 2012).

## **1.7 Objectives**

Overall, this thesis aims to assess if current END aggregate retention harvesting methods successfully emulate the remnants of wildfires a decade after disturbance. I focus on the diversity and composition of understory vascular plant species, but also investigate forest structure and microclimate, as important drivers of understory responses. I aim to test and answer the following research questions: 1) Are fire and/or harvest remnants supporting understory communities and microclimates similar to each other and to those of reference forest? 2) How does forest structure, understory composition, and microclimate vary from the edge to interior of patches (and as compared to reference forest) of fire and harvest remnants? 3) Does tree mortality and/or a reduction in overstory cover in forest plots (remnants and references) lead to changes in understory plant composition and/or microclimate? 4) Are there patterns of colonization and/or persistence trait syndromes within disturbances/remnants?

I hypothesize that remnants of both disturbance types will be able to support understory communities similar to each other and references. Based on the theory of edge influence, I expect to find that edges of patches contain more deadwood than the interior of patches, and the deadwood area/volume will be higher in harvest patch edges than fires. Furthermore, I hypothesize the edges of remnants will have different understory composition than the interiors of patches and reference forest. I also predict understory richness, cover, diversity, and

microclimatic temperatures will be higher at the edges compared to the interior of patches and reference forest. Because of hypothesized differences in edge structure, I predict the magnitude of difference in understory composition and microclimate will be higher in harvest remnant edges compared to fire. I expect plots with higher amounts of deadwood/lower overstory cover will have warmer microclimatic temperatures and increased abundance of shade intolerant understory plants. By contrast, I predict plots with lower amounts of deadwood/higher overstory cover will have lower microclimatic temperatures, and increased abundance of shade tolerant species. Finally, I hypothesize that disturbed plots will contain higher occurrences of plants with traits enabling colonization further from the patch, and higher occurrence of plants with traits enabling persistence closer to the patch. Within patches I expect to find higher occurrences of plants with traits enabling colonization at the patch edge, and higher occurrences of plants with traits enabling persistence in the interior. Overall, I expect to find more plants with traits enabling colonization in disturbed plots versus more plants with traits enabling persistence within patches and references. The results of this thesis will be a valuable addition to an interdisciplinary collection of research on EBM used to inform forest managers of the best practices to managing forests in Alberta and across Canada.

## **2 Methods**

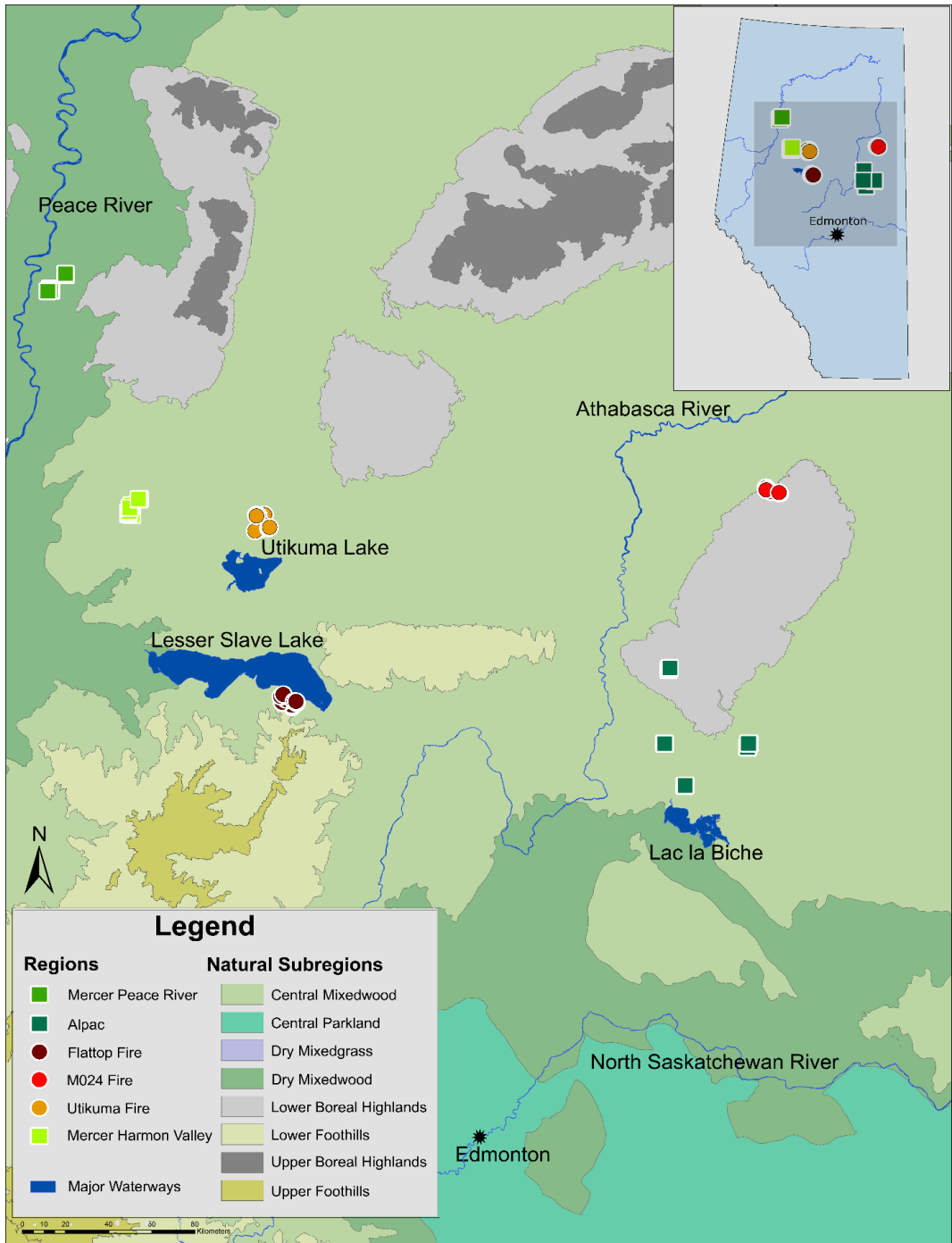
### **2.1 Study site**

The study was conducted within the boreal forest of northern Alberta (Figure 2.1). The climate is classified as subarctic boreal and the region is characterized by long, cold winters and short summers (Beck et al., 2018; Köppen, 2011). Using annual climatic averages from the past 25 years



interpolated by weather stations located near the study sites, a set of annual climatic normals were estimated for each site (Table 2.1).

The formation of today's boreal forest began following a deglaciation period approximately 12,000 years ago (Beudoin & Oetelaar 2003). As a result, mineral soils, which are primarily found in upland areas, are Luvisols or Brunisols derived from glaciolacustrine, glaciofluvial, and till parent material. Poorly drained soils, found primarily in low-lying wetlands, are dominated by organic deposits (Alberta Environment and Parks, 2019). Upland forests in the boreal are usually dominated by trembling aspen (*Populus tremuloides* Michx.), jack or lodgepole pine (*Pinus banksiana* Lamb., and *Pinus contorta* Douglas), or black or white spruce (*Picea mariana* (Mill.) B.S.P. and *Picea glauca* (Moench) Voss), but balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marshall), and balsam fir (*Abies balsamea* (L.) Mill.) may be locally dominant or co-dominant. Treed lowland sites are dominated by black spruce and/or tamarack larch ((Du Roi) K. Koch). Common shrubs in the boreal mixedwood region include prickly rose (*Rosa acicularis* Lindl.), willows (*Salix* sp.), lowbush cranberry (*Viburnum edule* (Michx.) Raf.), saskatoon (*Amelanchier alnifolia* (Nutt.) Nutt.), raspberry (*Rubus idaeus* L.), and currants/gooseberries (*Ribes* sp.). Common herbaceous plants include bunchberry (*Cornus canadensis* L.), twinflower (*Linnaea borealis* L.), bishops cap (*Mitella nuda* L.), fireweed (*Epilobium angustifolium* L.), northern reed grass (*Calamagrostis canadensis* (Michx.) P.Beauv.), and horsetails (*Equisetum* sp.; Alberta Environment and Parks 2019).



**Figure 2.1.** Map of the study sites within northern Alberta. Squares represent harvest regions and circles fire regions. Also shown are the natural subregions of Alberta.

**Table 2.1.** Climate variables near our study sites based on interpolated averages from 1995-2020. Weather station data from the Alberta Climate Information Service (Government of Alberta, 2022).

Study Region	Frost Free Days	Winter Air Temp. Avg. (°C)	Growing Season Air Temp. Avg. (°C)	Yearly Precipitation (mm)	Proportion of precipitation as rain (%)
Alpac	117	-5.3	11.2	473	88.0
Flattop	122	-4.3	10.8	466	85.2
Harmon Valley	114	-4.8	11.1	436	86.1
M024	114	-6.0	11.0	494	88.4
Mercer East	120	-5.4	11.3	394	85.5
Utikuma	109	-5.1	11.0	433	87.6
Overall Average	116	-5.1	11.1	449	86.8

Study sites were spread out among three separate fires and three separate harvest regions to broaden the scope of inference of the results. Details of these individual fire and harvest disturbed regions are described below. All study sites were part of a plot network used in other studies examining different aspects of forest remnants. Our plot network consisted of 30 island remnants, 15 of which were post-fire and 15 were post-harvest (Appendix A). The remnants were between 0.76-2.7 hectares in size and were required to be composed of >70% deciduous (i.e., broadleaf) trees (*Populus tremuloides*, *P. balsamifera*, and *Betula papyrifera*) determined from the Alberta Vegetation Index (AVI) and subsequent ground truthing. Each remnant was paired with a nearby continuous forest stand with canopy composition similar to the remnant, that bordered the same disturbance on one side, hereafter referred to as a “reference” (Figure 2.2). Reference sizes were variable, but at the interior plot (Section 2.2) was always at least 100 m from the studied edge. An island remnant, the disturbed area adjacent to the remnant, and the paired reference are hereafter referred to as a “site” (Figure 2.2).

### **2.1.1 Flat top complex fire**

Seven study sites were located within the Flat Top (“FT”) complex fire, which is a grouping of three individual fires that were ignited near the Slave Lake, Alberta area in mid-May 2011. All of our sites were located within one fire of the complex, SWF-056, hereafter referred to as “Flattop” to distinguish it from the fire complex as a whole. The Flattop fire was ignited on May 14, 2011, in a recently harvested cutblock approximately 25 kilometers southeast of the Slave Lake area community of Canyon Creek (Alberta Agriculture and Forestry 2021a; Flat Top Complex Wildfire Review Committee 2012). The fire was a crown fire, burning 16011 hectares prior to being declared under control on May 28, 2011. The burn area straddles the Lower Foothills and Central Mixedwood natural subregions of Alberta (Government of Alberta, 2019) and encompasses a slightly hilly area typically dominated by upland forest of trembling aspen. The area is also noted to contain significant amounts of fir (*Abies lasiocarpa* (Hooker) Nuttall., or *A. balsamea*), a factor which is thought to have contributed to the size and severity of the fire (Flat Top Complex Wildfire Review Committee, 2012). Remnants within this fire ranged between 1.15-2.29 hectares in size.

### **2.1.2 M024 Fire**

Three sites were located within a small, unnamed fire located approximately 50 km south of Fort McMurray Alberta (“M024”); fire code MWF-024 assigned by the Government of Alberta. The M024 fire was a crown fire that ignited June 13, 2009, and was declared under control on June 23, 2009, burning 11506 hectares. The burned area straddles the Lower Boreal Highlands and Central Mixedwood natural subregions of Alberta (Government of Alberta, 2019). Remnants in the M024 fire ranged between 1.02 and 1.86 hectares in size.

### **2.1.3 Utikuma fire**

Five sites were located within the Utikuma complex fire (“UT”), a grouping of five fires with severity ranging from surface fire to crown fire ignited near each other approximately 25 km north of Utikuma Lake in mid-May 2011. All of our sites were specifically located within the largest fire, SWF-057, hereafter referred to as “Utikuma”. The Utikuma fire ignited on May 14, 2011, and was declared under control on June 18, 2011, burning through an area of 87659 hectares within the Central Mixedwood region of Alberta (Government of Alberta, 2019). Utikuma remnants ranged between 1.18 and 1.75 hectares in size.

### **2.1.4 Alpac Harvest Region**

Five study sites were in the Alpac harvest region (“ALP”), located within various Forest Management Agreement Units (FMUs) managed by Alberta-Pacific Forest Industries Inc. The sites are widely spread across the region (Figure 2.1). This region is almost entirely within the Central Mixedwood natural subregion, save one site located in the Lower Boreal Highlands (Government of Alberta, 2019). The cutblocks were all harvested by clearcutting with patch retention, in the years 2009, 2010, or 2012. Retention patches ranged between 0.76 and 2.7 hectares in size.

### **2.1.5 Harmon Valley Harvest Region**

Five sites were located along the Harmon Valley Road (“HV”) in North Central Alberta, within the southern portion of the P21 FMU, managed by Mercer Peace River Pulp Ltd. The sites are located relatively close to each other (Figure 2.1). The region lies entirely within the boreal Central Mixedwood natural subregion of Alberta (Government of Alberta, 2019). All of the remnants

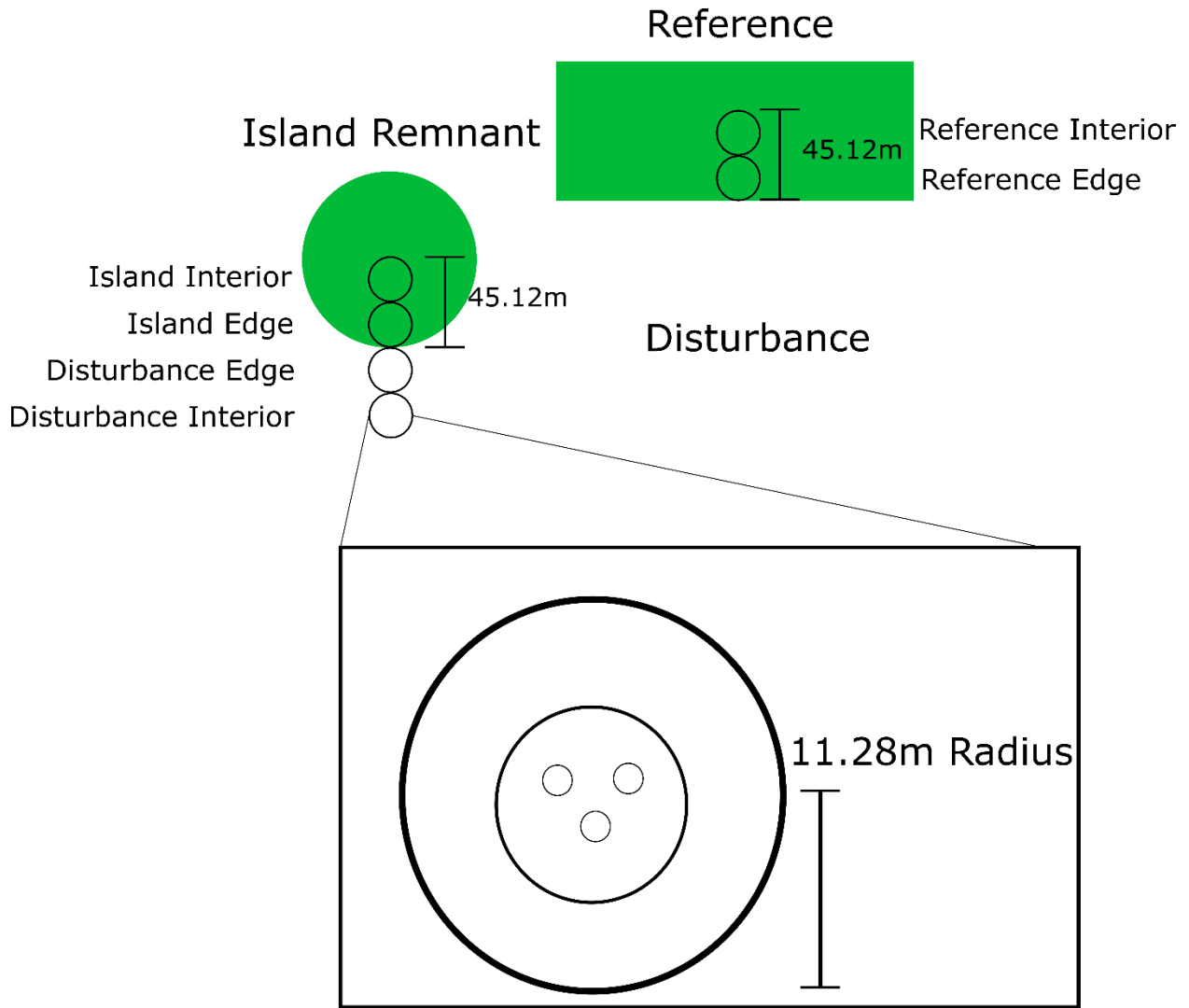
were located within cutblocks harvested in 2010, and remnants ranged from 0.65 to 1.62 hectares in size.

### **2.1.6 Mercer East Harvest Region**

Mercer East harvest region (“MEE”) is composed of five sites located along the East Haul Road, located approximately 75 kilometers north of the Peace River pulp mill. Located within the P21 FMU, managed by Mercer Peace River Pulp Ltd, all the remnants were within cutblocks harvested in 2009 and 2010. The region is located entirely within the Dry Mixedwood natural subregion of Alberta (Government of Alberta, 2019), and the remnants range in size from 1.40 to 1.63 hectares in size.

## **2.2 Plot layout**

Within each site we placed a total of six circular plots, with a radius of 11.28 meters (400 m<sup>2</sup>). Two plots were placed in each of the following: the island remnant, the disturbed area adjacent to the remnant and the reference (Figure 2.2). In each of those, one plot was placed at the edge and one in the interior. The aspect of the sampled edge was not consistent and resulted in edge plots distributed across all cardinal directions (Appendix A). This resulted in six plot locations: Disturbed Edge (DE), Disturbed Interior (DI), Island Edge (IE), Island Interior (II), Reference Edge (RE), and Reference Interior (RI). While they are named “interior”, interior plots begin 22.56 meters from the edge, and extend to 45.12 meters from the edge, and are thus not capturing true interior conditions from the perspective of edge effects (Harper et al. 2010). Within each plot, one smaller circular “sapling” plot (radius 5.56 m; 200 m<sup>2</sup>), and three circular subplots (0.5 m radius; 0.785 m<sup>2</sup>) were placed (Figure 2.1). Because time constraints precluded sampling all the plots within the network, not all plots were able to be sampled (Table 2.2) .



**Figure 2.2.** Conceptual plot layout within a site. Each plot has a radius of 11.28 metres, and within each plot there was one sapling subplot with a radius of 5.56m and three understory subplots with a radius of 0.5 meters.

**Table 2.2.** Number of sampled plots of each plot location\* by disturbance type. Plots with microclimate refers to the number of sampled plots of each treatment type with microclimate data that was uninterrupted between June 20- July 8.

	Fire							Harvest						
	DE	DI	IE	II	RE	RI	Fire Total	DE	DI	IE	II	RE	RI	Harvest Total
Sampled plots	13	13	12	12	13	13	76	12	12	12	12	10	10	68
Plots with microclimate	12	13	9	10	10	11	65	12	11	11	9	7	6	56

\*Disturbed Edge (DE); Disturbed Interior (DI); Island Edge (IE); Island Interior (II); Reference Edge (RE); Reference interior (RI)

## 2.3 Data collection

Within each of the 144 plots data at the plot and subplot level were collected to characterize forest structure, microclimate, and understory vascular plant communities. Plant trait data were acquired from the TOPIC (Aubin et al., 2020) and TRY (Kattage et al., 2020) databases.

### 2.3.1 Plot level data

Within remnant and reference location plots all trees with a diameter at 1.3 m (breast) height (DBH)  $\geq$  9.1 cm were tagged and the species, DBH, and condition (living/dead) were recorded. Dead trees were assigned a decay classification from 1-5 based on the observed level of decay (Appendix B-2; Odell, 2023). Tree basal area (m<sup>2</sup>) was calculated based on the DBH (cm) for each tree using the following formula:

$$BA = \pi \left( \frac{DBH}{200} \right)^2$$

Once calculated, plot-level basal area was summed for dead trees, living trees, and living trees grouped by coniferous/deciduous. Plot level basal area was then multiplied by 25 to get the basal



area per hectare. Data on Coarse Woody Debris (CWD) was collected for a specific CWD-focused project within the same plot network (Moore 2022). CWD was classified by decay class (Appendix B-2, Moore 2022), and the volume of decay class 1 & 2 CWD was estimated using the line intercept method with six radial transects separated by 60 degrees. Additionally, the volume of dead standing trees of decay classes 1 and 2 was estimated by multiplying their DBH by a species-specific constant developed by Lambert et al. (2005). In the smaller sapling plot, nested within the larger plot, we counted all smaller trees (height >1.3 m but DBH < 9.1 cm) by species (“Saplings”). Sapling counts were then multiplied by 100 to get a sapling density per hectare. At the centre of each plot, we placed a TMS-4 datalogger (Wild et al. 2019; TOMST, Prague CZ) to measure soil temperature and surface air temperature at the forest floor every 15 minutes. Microclimate dataloggers were installed between mid-May and early June 2021 and were removed in late August 2021.

### **2.3.2 Subplot level data**

Within each plot three circular subplots (0.5 m radius) were placed 2 m from plot centre in a triangular orientation. Within each subplot the thickness of the soil organic layer was measured at subplot centre and cover of leaf litter and the bryophytes on the ground were estimated. Canopy cover was recorded from the centre of each subplot by convex spherical densiometer measurements taken facing four orthogonal directions and then averaged. Species composition of the understory plant community was characterized in each subplot by visually estimating cover for each plant identified to the species level. For willows (*Salix* spp.), individuals were only identified to the genus level as morphological differences between species are difficult to discern. Plant cover was estimated using the following criteria: plants with less than 1% cover were

assessed at 0.1%, 0.5%, or 1%, rounding up. Covers between 1-10% were rounded up to the nearest integer. Plants with a cover greater than 10% were rounded to the nearest 5%. Shrubs of any height were included in the understory, while tree species are only considered part of the understory if they are less than 1.3 meters in height (“Seedlings”). Sampling took place between mid-June and mid-August 2021.

### 2.3.3 Plant trait data

Functional traits were selected based on a search of the literature of traits relating to either the colonizing ability or persistence ability of plants (Weiher et al. 1999; Aubin et al. 2007; Patry et al. 2017). I sought information for the following plant traits for all of our species: Raunkiaer Life Form, primary mode of reproduction, lateral extensions, resprouting ability, seed weight per 1000 seeds, maximum plant height, life cycle, specific leaf area, and foliage structure (Table 2.3). Trait values were primarily extracted from the TOPIC (Aubin et al., 2020) database, with some data extracted from the TRY (Kattage et al., 2020) database. Species without complete trait values were excluded from trait analyses (18% of species found), but those species with missing traits were often uncommon, occurring in only one or two plots, and generally had covers less than 5%.

**Table 2.3.** Description of plant traits used in analysis. Definitions were taken from the TOPIC database (Aubin et al. 2020).

Trait	Code	Data type	Trait Description	Assigned values
Raunkiaer Life Form	RA	Categorical	Raunkiaer life form. Categorized as: <b>ch</b> , chamaephyte; <b>g</b> , geophyte; <b>h</b> , hemicryptophyte; <b>mc</b> , micro-phanerophyte; <b>mg</b> , mega-phanerophyte; <b>t</b> , therophytes	N/A

Lateral Extension	LE	Semi-quantitative	Categorized by distance of lateral spread: <b>a</b> , absent; <b>l</b> , limited; <b>e</b> , extensive (non-phanerophyte); <b>pi</b> , phanerophyte intermediate; <b>ep</b> , phanerophyte extensive	a = 0; l = 1; e = 2; pi = 3; pe = 4
Resprouting Capability	VP	Binary	Resprouting capability <b>present/absent</b>	0 = no ability to resprout; 1 = able to resprout
Life Cycle	LC	Binary	Plant life cycle, grouped into two categories: <b>annual and biannual; perennial</b>	1, annual and biannual; 2, perennial
Seed Production	SPRO	Semi-quantitative	<b>f</b> , few; <b>s</b> , some; <b>a</b> , abundant	f = 1; s = 2; a = 3
Typical Maximum Height	HT	Quantitative	Measured in centimeters	Log transformed
Seed Weight	SDWT	Quantitative	Weight of 1000 seeds in grams	Log transformed
Specific Leaf Area	SLA	Quantitative	Specific leaf area with petioles, measured in cm <sup>2</sup> g <sup>-1</sup>	N/A
Primary Mode of Reproduction	REP	Categorical	<b>s</b> , reproduces only by seed; <b>svp</b> , reproduces primarily by seed, some vegetative reproduction; <b>vp</b> , reproduces primarily vegetatively	N/A
Foliage Structure	SFO	Categorical	<b>de</b> , decumbent or prostrate stem; <b>e</b> , erect leaves; <b>el</b> , erect leafy stem; <b>fa</b> , arched stem; <b>g</b> , graminoid leaves; <b>me</b> , mono stem erect phanerophyte;	N/A

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**ms**, mono stem spread out; **mu**, multi-stem; **r**, rosette;

**sr**, semi-rosette; **um**, umbel-shaped stem; **vi**, vine

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## 2.4 Statistical analyses

Data on understory cover, canopy cover, and organic layer thickness collected in the 432 subplots within each plot (144 total) were averaged to the plot level for all subsequent analyses. Vascular plant species richness was calculated from the number of unique species observed in a plot (sum of the three subplots). Understory cover and Hill diversity, derived from Shannon's entropy ("diversity"), were calculated using the R package "vegan", in R version 4.2.1 (Oksanen et al., 2022; R Core Team, 2022). Thirty-one of 144 of our microclimate sensors (22%) were found to be disturbed at some point during the field season, presumed to be pulled out of the ground by wildlife, resulting in a reduced number of plots with microclimatic data (Table 3). Temperature data were initially screened to verify data completeness and for disturbed sensors to determine when the sensor was pulled out of the ground. Since many of the sensors were only disturbed for part of the field season, I searched for a period of time that would allow for use of data that were collected before the sensors were disturbed. It was determined that the period of June 20-July 8, 2021, represented the greatest number of undisturbed microclimates (84%). For each 24-hour period the hottest air and soil temperature and the coolest air and soil temperature were recorded, as well as the temperature difference between the hottest and coldest daily temperature.

### **2.4.1 Analysis of understory variables, forest structure, and microclimate**

To test for differences in measures of understory community (Table 2.4A), forest structure (Table 2.4B), and microclimate (Table 2.4C) among treatments I fit linear mixed-effect models with disturbance type (fire, harvest) and plot location (DE, DI, IE, II, RE, RI) as the fixed effects, and region and site (nested within region) as the random effects. Microclimatic variables also included an additional random effect, a plot identifier unique to each plot, to address pseudoreplication caused by daily measurements. For some measures of forest structure only island remnant and reference plots were included in the model as there were no live trees left in the disturbed areas. Diagnostic Q-Q plots of the residuals and residual versus fitted scatterplots were visually assessed to see if linear models met their assumptions of homoscedasticity and normally distributed residuals. For models that did not meet assumptions the data were square-root transformed or log transformed to improve model fitting. For all the ANOVAs and pairwise testing, significance was assessed at  $\alpha = 0.05$ . For models with a significant effect of plot location and/or a significant interaction between disturbance type and plot location I completed post-hoc pairwise testing to compare among plot locations within each disturbance type. Statistical significance between plot locations of different disturbance types was not assessed, as the experimental layout made the comparison difficult. Statistical comparisons between plot locations of different disturbance types were not made under the assumption that it would be difficult to disentangle disturbance effects from regional effects. All linear modelling was done in R using the “nlme” (Pinheiro et al. 2022) package, and post-hoc pairwise comparisons were done using Tukey’s multiple comparison test with the “emmeans” (Lenth et al. 2022) and “multcomp” (Hothorn et al. 2022) packages.

**Table 2.4.** List of codes and descriptions for (A) measures of understory community, (B) measures of forest structure, (C) microclimatic variables.

Code	Description
<b>(A)</b>	
Cover	Understory Cover (%). Total cover of vascular understory species from subplots, averaged to the plot level
Forb	Forb cover (%). Sum of forb cover from subplots, averaged to the plot level. Prostrate woody-stemmed species were considered forbs
Shrub	Shrub cover (%). Sum of shrub cover from subplots, averaged to the plot level
Graminoid	Graminoid cover (%). Sum of graminoid cover from subplots, averaged to the plot level
Richness	Number of unique vascular understory species within the three subplots composing a plot, a sampling area of 2.37 m <sup>2</sup>
Hill Diversity	Hill diversity. Effective number of species derived from Shannon's entropy of vascular understory species within the three subplots composing a plot, a sampling area of 2.37 m <sup>2</sup>
RSVR	Proportion of Recent Standing deadwood Volume. Proportion of decay class 1 & 2 snag (diameter >9.1 cm) volume per plot volume of living tree per plot
<b>(B)</b>	
Olayer	Organic layer thickness (cm). Thickness of the LFH layer measured in the centre of each subplot, averaged to the plot level
Litter	Litter cover (%). Cover of leaf litter within each subplot, averaged to the plot level
Saps	Saplings (number of stems ha <sup>-1</sup> ). Density of trees taller than 1.3 m, with a DBH <9.1 cm in the plot
Canopy	Canopy cover (%). Recorded at each subplot in four cardinal directions and averaged to the plot level
BAA	Basal Area Alive (m <sup>2</sup> ha <sup>-1</sup> ). Basal area of living trees per hectare
CONBAAR	Proportion of Coniferous Basal Area. Proportion of basal area of living coniferous trees to total living tree basal area at the plot level
RCV	Recent Coarse woody Volume (m <sup>3</sup> ha <sup>-1</sup> ). Volume per hectare of coarse woody debris (diameter >7 cm) of decay class 1 & 2.

RTV	Recent Total deadwood Volume ( $\text{m}^3 \text{ha}^{-1}$ ). Volume per hectare of snags (DBH >9.1) and coarse woody debris (diameter >7 cm) of decay class 1 & 2.
RSV	Recent Standing deadwood Volume ( $\text{m}^3 \text{ha}^{-1}$ ). Volume per hectare of snags (diameter >9.1 cm) of decay class 1 & 2.
RBADR	Proportion of Recent Dead Basal Area. Proportion of the basal area of decay class 1 & 2 snags per plot (diameter >9.1 cm) to the basal area of live trees per plot

(C)

$T_s$	Maximum Soil Temperature ( $^{\circ}\text{C}$ ). Daily maximum soil temperature recorded at plot centre, averaged from June 20-July 8, 2021
$\Delta T_s$	Daily Soil Temperature Difference ( $^{\circ}\text{C}$ ). Difference between the daily maximum and minimum soil temperatures recorded at plot centre, averaged from June 20-July 8, 2021
$T_A$	Maximum Surface Air Temperature ( $^{\circ}\text{C}$ ). Daily maximum surface air temperature recorded at plot centre, averaged from June 20-July 8, 2021
$\Delta T_A$	Daily Surface Air Temperature Difference ( $^{\circ}\text{C}$ ). Difference between the daily maximum and minimum surface air temperatures recorded at plot centre, averaged from June 20-July 8, 2021

#### 2.4.2 Analysis of understory composition

To test for differences in community composition among treatments I used Permutational Multivariate Analysis of Variance (PerMANOVA), with disturbance type and plot locations (DE, DI, IE, II, RE, RI) as explanatory variables. Significance was assessed by 999 permutations ( $\alpha = 0.05$ ). The PerMANOVA was performed using the function “adonis2” in the “vegan” package (Oksanen et al., 2022). While PerMANOVA represents a rigorous method to assess multivariate variance between groups, non-homogenous multivariate dispersion between treatment groups can lead to false rejection of the null hypothesis (Anderson & Walsh 2013). Therefore, subsequent analysis to verify conditions of homogeneity of multivariate dispersion was conducted using the “betadisper” function in the “vegan” package (Oksanen et al. 2022).

To visualize multivariate differences in understory community composition among treatments, the understory plant species cover matrix was first converted into a Bray-Curtis dissimilarity matrix (Borcard et al. 2011). Second, a Non-Metric Multidimensional Scaling (NMDS) analysis was conducted on the dissimilarity matrix using the “metaMDS” function in the “vegan” package (Oksanen et al., 2022). NMDS is a distance-based analysis suitable for analyzing high dimensional data with irregular distribution (Borcard et al. 2011). The function “metaMDS” also performs a principal coordinate analysis (PCoA) on the dissimilarity matrix and begins iterations from the first two axes of the PCoA to ensure the analysis doesn’t get stuck in local minima, a common issue in NMDS analysis (Borcard et al. 2011). Confidence ellipses indicating a standard deviation of 0.80 were added using the function “ordiellipse” in the “vegan” package (Oksanen et al. 2022).

To test for associations between understory species composition and treatments, a distance-based redundancy analysis (db-RDA) was performed on a Bray-Curtis dissimilarity matrix of the Hellinger transformed understory composition data. Disturbance type and plot location were using as explanatory variables, and the statistical significance of the explanatory variables and axes were assessed using 999 permutations. The db-RDA was made in R version 4.2.1 using the function “capscale” in the “vegan” package (Oksanen et al. 2022). Species displayed were selected using the circle of equilibrium method described by (Borcard et al. 2011), which determines species that make an above average contribution to the ordination.

### **2.4.3 Analysis of relationships between forest structure and microclimate**

To investigate relationships between forest structure and microclimate, a Principal Component Analysis (PCA) was performed on select forest structure and microclimatic variables. In this



analysis understory vegetation was considered as a forest structural variable as it could possibly influence microclimatic temperatures. The PCA was run in R version 4.2.1 using the default function “princomp” (R Core Team 2022).

#### **2.4.4 Analysis of relationships between forest structure and understory composition**

To test for associations between understory species and forest structural variables quantifying canopy closure and tree mortality, distance-based redundancy analyses (db-RDA) were performed on a Bray-Curtis dissimilarity matrix of the Hellinger-transformed understory composition data. A permutational backwards selection with the function “Ordistep” (Oksanen et al. 2022) was used to select a statistically significant and parsimonious model from the following explanatory variables: canopy cover (Canopy), living tree basal area (BAA), recent total deadwood volume (RTV), recent standing deadwood volume (RSV), proportion of recent dead basal area (RBADR), proportion of recent standing deadwood volume (RSVR; Codes explained in Table 2.4). Statistical significance of the optimal model was assessed at  $P < 0.05$  using 999 permutations. Db-RDAs were conducted in R version 4.2.1 using the function “capscale” in the “vegan” package (Oksanen et al. 2022). Species displayed were selected using the circle of equilibrium method described by (Borcard et al. 2011), which determines species that make an above average contribution to the ordination.

#### **2.4.5 Trait analysis**

To begin, trait data were first formatted for analysis (Table 2.3). A fourth corner analysis was used to analyze our trait data to reveal patterns in trait distribution mediated by various explanatory variables. The fourth corner analysis uses three matrices: a L matrix, consisting of plot by species cover, a Q matrix, consisting of species by trait measurements, and a R matrix, consisting of plots

by treatments (plot locations/disturbance type) and explanatory variables such as measures of forest structure. The result is a fourth matrix (the fourth corner), consisting of trait measurements by treatment or environmental variables (Dray and Legendre, 2008). Test statistics are generated for each pair of trait level and environmental variable level, and a global statistic is generated for each trait-environment category. The type of test statistic is dependent on the combination of trait and treatment investigated: Two numeric variables generate a correlation coefficient ( $r$ ). One numeric and one qualitative variable generate an F-statistic for the global test, and a correlation ratio coefficient for the relationship between each level of the nominal variable to the quantitative variable. A global test of two qualitative variables generates a G-statistic, while tests at each variable level combination are tested using a chi-squared test. Significance is determined by choosing one of the permutational models proposed by Dray & Legendre (2008). I chose permutational model 1 (Dray & Legendre 2008), that permutes values within each column of the species matrix ( $L$ ) and was run at 49,999 permutations. Significance for the global test statistics was assessed at two separate levels: an  $\alpha = 0.1$ , which were considered marginally significant, and  $\alpha = 0.05$ , considered significant. Individual trait-variable comparisons were made at  $\alpha = 0.05$  on  $P$ -values adjusted using the Holm's correction method (Holm 1979), and significance. The fourth corner analysis was completed in R version 4.2.1 (R Core Team 2022), using the package "ade4" (Dray et al. 2022). A total of eight fourth corner analyses were run on eight separate sets of matrices. One set of analyses examined all the plot locations split by disturbance type, a second just the forested (remnant and reference) plot locations split by disturbance type, and a third the disturbed plot locations split by disturbance type.

### 3 Results

Across the 144 plots sampled (432 subplots) 117 understory vascular species were found (Appendix B

**Appendix B-1).** Frequency of occurrence of the 20 most abundant species found in this study was summarized by disturbance type and plot location (Appendix B-5).

#### 3.1 Understory cover and diversity responses to disturbance and plot location

The results of the mixed-effect linear model indicate that plot location had a significant effect on all of our understory cover, richness, and diversity attributes (Table 3.1). There was a significant disturbance type treatment only for understory richness, and the only significant interaction between disturbance type and plot location was for shrub cover (Table 3.1).

**Table 3.1.** Results of linear mixed-effect models examining the influence of disturbance type (fire/harvest) and plot location (DE/DI/IE/II/RE/RI), and the interaction between disturbance ×

	Disturbance type			Plot location			Disturbance × Plot		
	F	df	P	F	df	P	F	df	P
Total Cover	3.958	1	0.118	7.743	5	<b>0.001</b>	1.694	5	0.142
Forb Cover*	1.044	1	0.365	2.896	5	<b>0.017</b>	1.103	5	0.363
Shrub Cover*	0.652	1	0.465	4.359	5	<b>0.001</b>	3.134	5	<b>0.011</b>
Graminoid Cover**	5.657	1	0.076	16.001	5	<b>0.001</b>	0.723	5	0.608
Richness	8.735	1	<b>0.042</b>	3.745	5	<b>0.004</b>	0.524	5	0.757
Hill Diversity	2.778	1	0.171	5.197	5	<b>0.003</b>	0.449	5	0.813

plot on vegetation covers and diversity. Disturbance region and site were used as random effects. P-values in bold and italics were considered significant at  $\alpha = 0.05$ .

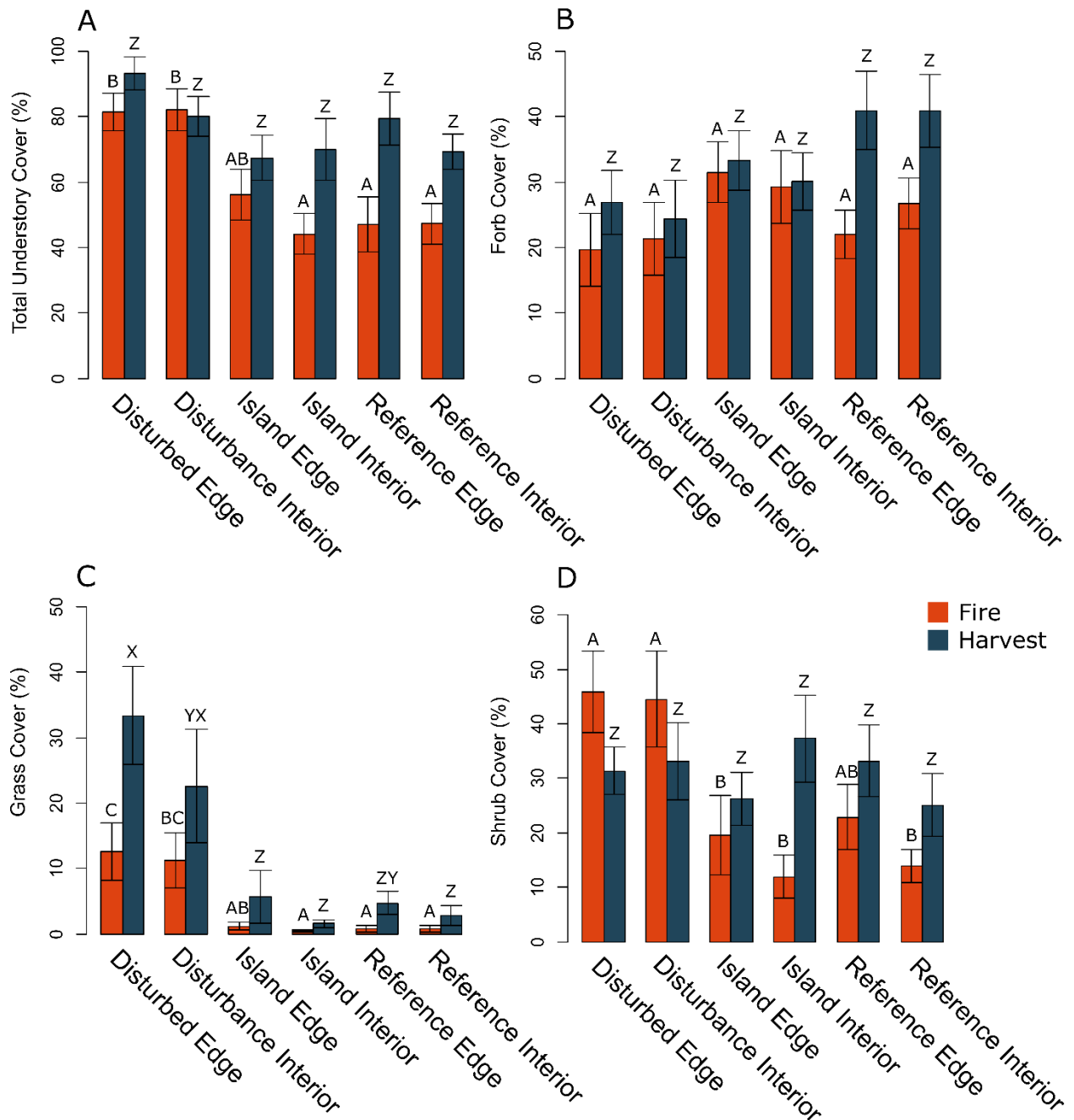
\*Data were square root transformed for analysis

\*\*Data were log-transformed for analysis

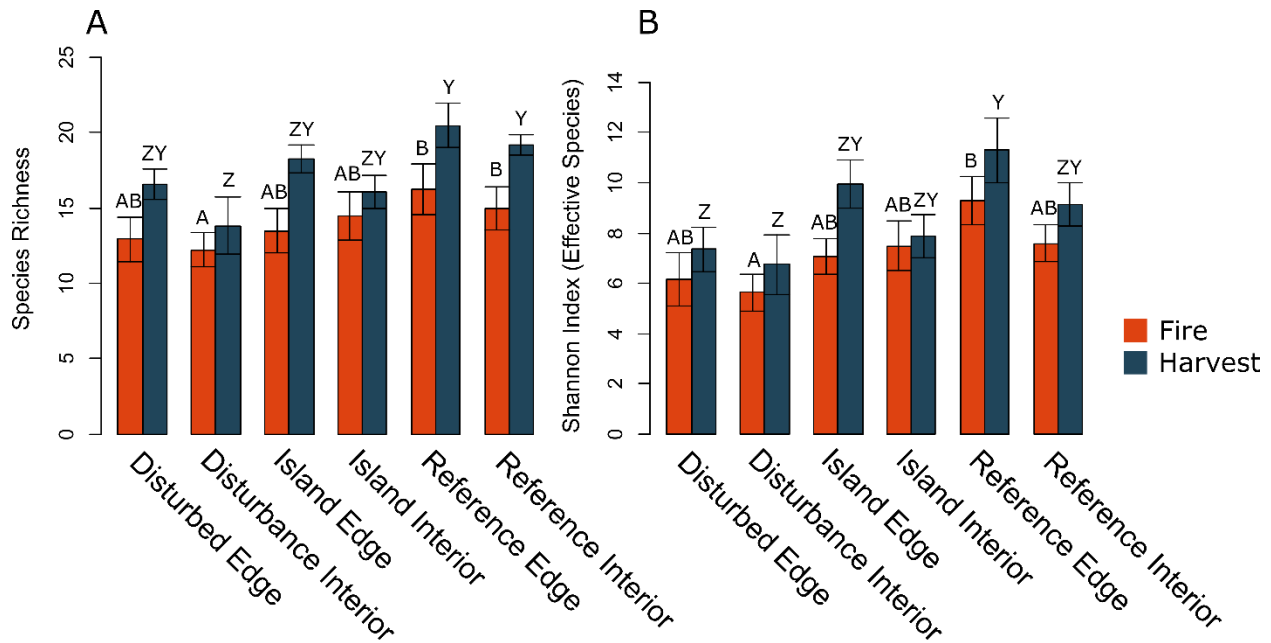
Post-hoc pairwise comparisons of total understory cover in fire plots showed understory cover was highest in disturbed areas (81.6-82.3%), which were significantly higher than the forested plots (island and reference; 44.2-47.3%); the exception was island edge which was intermediate (56.2%; Figure 3.1A). Forb cover did not vary significantly among plot locations, but was, on average, lowest in the disturbed edge (19.7%), and highest in the island edge (31.6%; Figure 3.1B). Average graminoid cover was highest in disturbed areas (11.2-12.6%), which were generally significantly higher than the forested plots (island and reference; 0.4-1.1% Figure 3.1C). Likewise, average shrub cover was highest in disturbed areas (44.6-45.9%), which were generally significantly higher than the reference plots (island and reference; 11.9-22.8% Figure 3.1D). Average richness in fire plots was lowest in the disturbed interior plots (12.2), which were significantly lower than the reference plots (15-16.2; Figure 4A). The disturbed edge (12.9) and island plots (13.5-14.5) had intermediate richness and did not differ from one another or the reference or disturbed interior (Figure 3.2A). Similarly, average diversity was lowest in the disturbed interior (5.6), and significantly lower than reference edges, which contained the highest average diversity (9.3). The remaining plots did not have significantly different diversity from any others, with averages between 6.1-7.6 (Figure 3.2B).

In harvest plots, there were no significant differences between plot locations for average total cover (67.4-93.4%; Figure 3.1A), forb cover (24.4-41.0%; Figure 3.1B), or shrub cover (25.1-37.0%; Figure 3.1D). Graminoid cover was highest in the disturbed plots (22.6-33.4%), which were generally significantly higher than the forested plots (1.6-5.6%; Figure 3.1C). Similar to the results

for fire plots, average harvest plot richness was lowest in the disturbed interior plots (13.8), which were not significantly lower than the island plots (16.1-18.3), and the disturbed edge (16.6), but were significantly lower than the reference plots (19.2-20.5; Figure 3.2A). Average diversity was lowest in the disturbed plots (6.8-7.3), which were significantly lower than reference edges (11.3), which contained the highest average diversity. The remaining plots were not significantly different from any others in diversity, with averages between 7.9-9.9 (Figure 3.2B).



**Figure 3.1.** Mean and standard error of (A) Total understory cover, (B) Forb cover, (C) Graminoid cover, and (D) Shrub cover by disturbance type and plot location. Within each disturbance type, means with different letters were significantly different in a pairwise comparison of the estimated marginal mean,  $P < 0.05$ .



**Figure 3.2.** Mean and standard error of (A) Species richness and (B) Shannon diversity by disturbance and plot location (plot area in all comparisons was 2.37 m<sup>2</sup>). Within each disturbance type, means with different letters were significantly different in a pairwise comparison of the estimated marginal mean,  $P < 0.05$ .

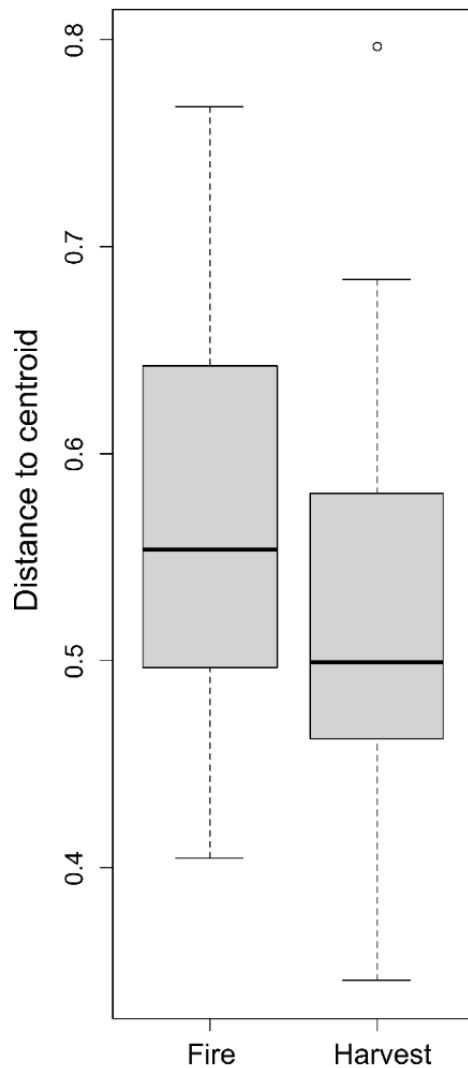
### 3.2 Understory species composition

According to the results of a PerMANOVA on the understory species composition of forested plots, there was a significant difference between the understory vegetation composition in fire

**Table 3.2.** Results of permutational multivariate analysis of variance examining the influence of disturbance type (fire/harvest), forested plot locations (IE/II/RE/RI), and the interaction between them on understory composition. P-values in bold and italics were considered significant at  $\alpha = 0.05$ .

Treatment	Df	SS	F	R <sup>2</sup>	P
Disturbance Type	1	1.10	3.55	0.04	<b><i>0.001</i></b>
Plot Location	3	0.83	0.89	0.03	0.715
Disturbance Type × Plot Location	3	0.77	0.83	0.03	0.831

plots versus harvest plots ( $P = 0.001$ ), but not between forested plot locations ( $P = 0.715$ ) or the interaction between reference plot locations and disturbance types ( $P = 0.831$ ; Table 3.2). According to an analysis of dispersion, the dispersion between forested fire plots was significantly higher than

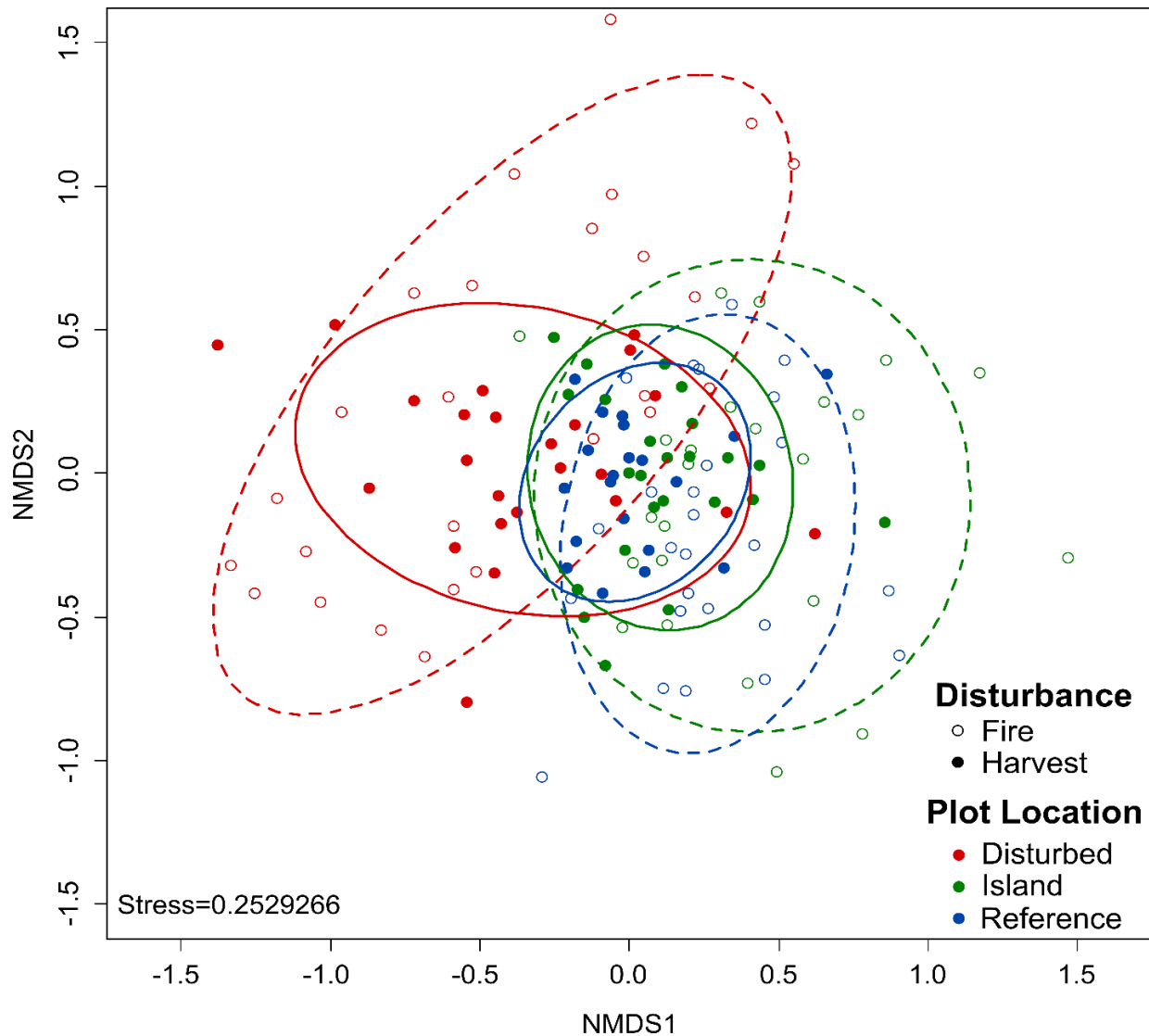


**Figure 3.3.** Results of a multivariate test of dispersion (betadisper) on the spatial medians of a Bray-Curtis dissimilarity matrix of forested understory composition by fire and harvest plots.

dispersion between forested harvest plots ( $P = 0.010$ ; Figure 3.3). A visualization of the understory community composition displays a gradient along the NMDS1 axis, with disturbed plots negatively associated, and forested plots positively associated with NMDS1 (Figure 3.4). In agreement with the PerMANOVA, visually, the forested plots do not seem to significantly differ from one another, although there is evidence of higher dispersion in forested fire plots compared to harvest plots, visualized by the confidence ellipses (Figure 3.4). Under a constrained ordination (db-RDA) of both disturbance type and plot location the first axis explained 7.7% of the variation in understory species composition with forested plots (island & reference) positively, and the disturbed plots negatively, associated with CAP1 (Figure 3.5). Separation along the CAP2 axis, which explained 3.1% of the variation, was driven by compositional differences between fire and

harvest plots, with harvest on the positive and fire on the negative side of the axis. Plot dispersion was greater along CAP1 than CAP2, and there was less dispersion along CAP2 for harvest plots compared to fire ones (Figure 3.5).

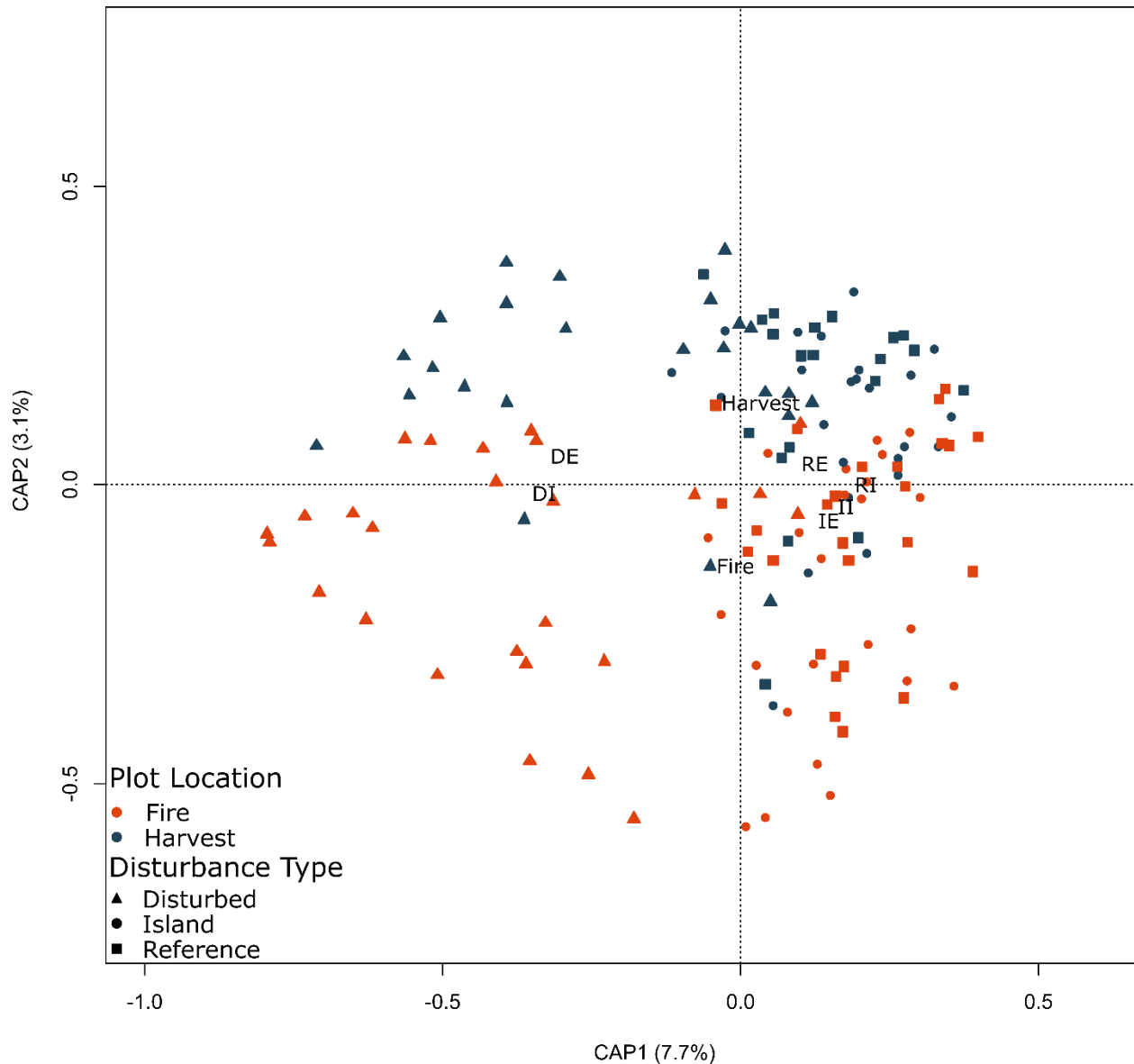




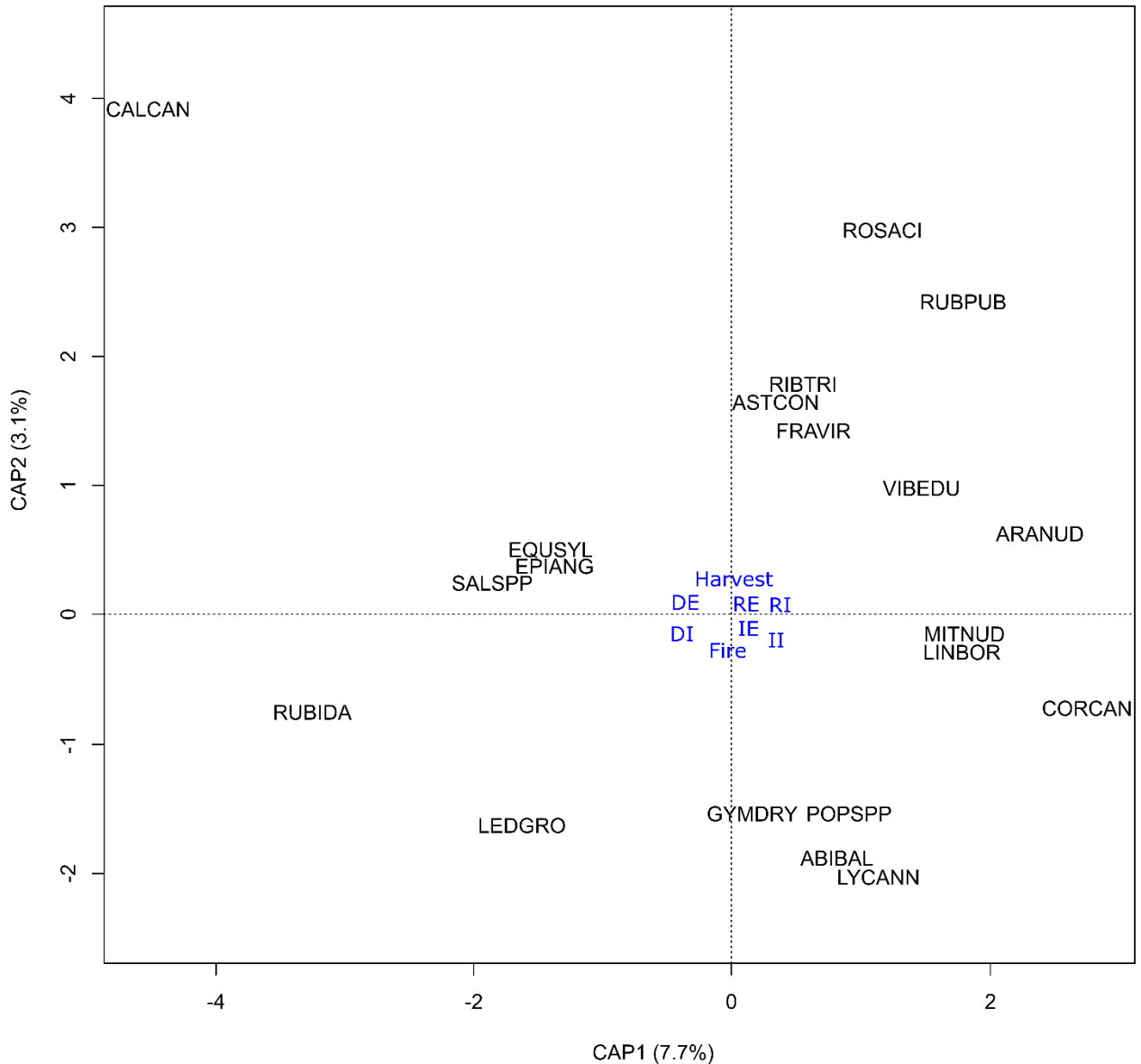
**Figure 3.4.** Non-metric multidimensional scaling plot of the Bray-Curtis dissimilarity of plot understory composition colored by plot location. Each point corresponds to the average plant cover found in the three sampling subplots within a plot. Confidence ellipses indicate a standard deviation of 0.80. Dashed ellipses represent the fire regions, while whole ellipses represent harvest regions.

Species associated with disturbed plots included *Epilobium angustifolium*, *Salix* spp., *Equisetum sylvaticum* L., and *Calamagrostis canadensis*, which were more associated with harvest plots, while *Ledum groenlandicum* Oeder. and *Rubus idaeus* were more abundant in disturbed fire plots (Figure 3.6). Conversely, species such as *Mitella nuda*, *Aralia nudicaulis*, *Linna borealis*, *Viburnum edule*, and *Cornus canadensis* were associated with forested plots with

no strong preference for disturbance type. *Gymnocarpium dryopteris* (L.) Newman, *Abies* spp. and *Populus* spp., seedlings as well as *Lycopodium annotinum* (L.), were more abundant in forested fire plots compared to harvest. Species more strongly associated with forested harvest plots include *Rosa acicularis*, *Rubus pubescens* Raf., and *Ribes triste* Pall. (Figure 3.6).



**Figure 3.5.** A distance-based redundancy analysis testing the influence of disturbance type and plot location on Hellinger-transformed understory vegetation cover data. Each symbol represents a plot and reflects the average understory composition within the three sampling subplots. The shape of the symbol depicts plot location where interior/edge are combined into one category. The color represents the plot disturbance type. The in-plot text represents the centroids of each constraining factor.



**Figure 3.6.** A distance-based redundancy analysis testing the influence of disturbance type and plot location on Hellinger-transformed understory vegetation cover data. The blue text represents the centroids of each constraining factor, that have been rescaled for visual clarity. Species that were determined to have made an above average contribution to the ordination using the circle of equilibrium method (Borcard et al., 2011) are displayed by their species code in black text. The six letters of each code are the first three letters of the genus followed by the first three letters of the specific epithet. For a list and an explanation of species codes, see Appendix B-1.

### 3.3 Microclimatic responses to disturbance and plot location

With all the microclimatic variables, the only significant effect was found in daily surface air temperature difference between plot locations (Table 3.3).

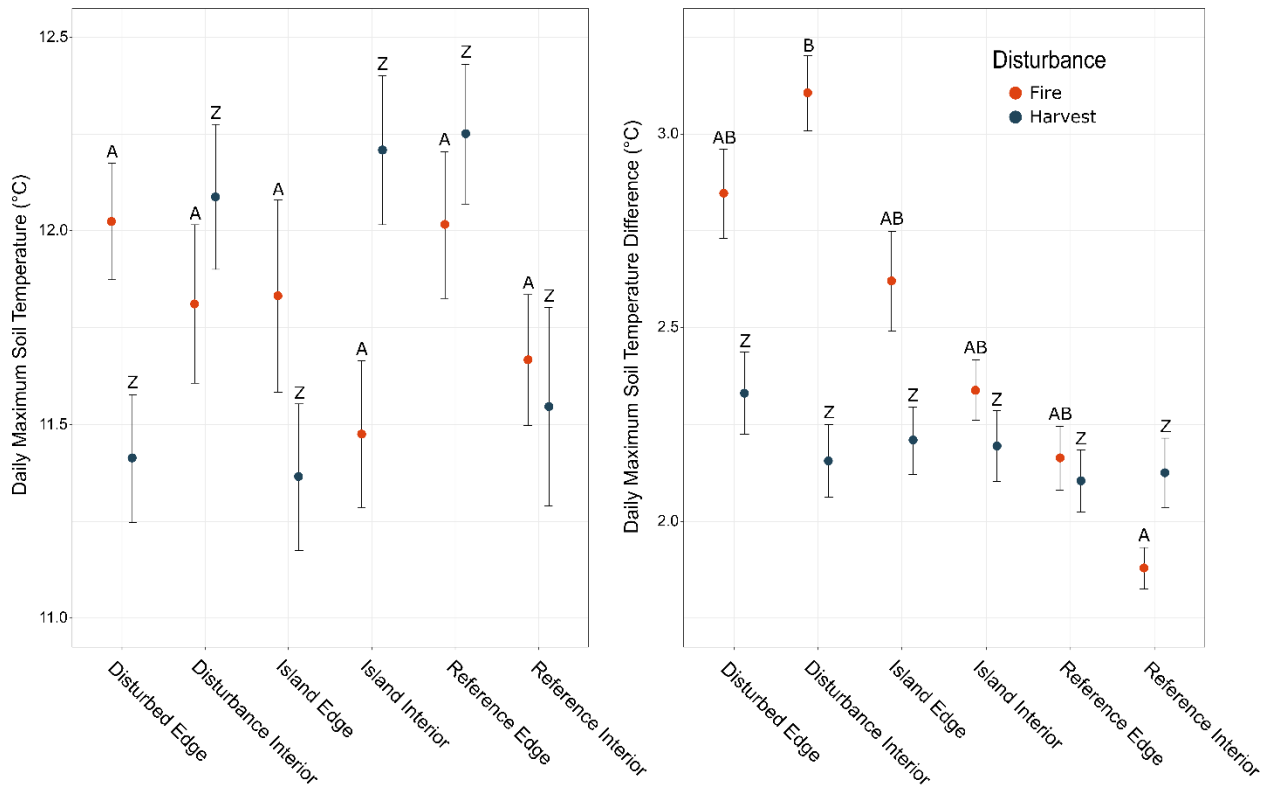
**Table 3.3.** Results of linear mixed-effect models examining the influence of disturbance type (fire/harvest) and plot location (DE/DI/IE/II/RE/RI), and the interaction between disturbance × plot on microclimatic variables. Disturbance region and site were used as random effects. P-values in bold and italics were considered significant at  $\alpha = 0.05$ .

	Disturbance			Plot Location			Disturbance × Plot Location		
	F	df	P	F	df	P	F	df	P
$T_s$	0.001	1	0.982	0.249	5	0.939	0.813	5	0.813
$\Delta T_s^{**}$	0.437	1	0.538	1.215	5	0.309	1.884	5	0.105
$T_A^*$	2.133	1	0.218	2.070	5	0.077	1.619	5	0.163
$\Delta T_A^*$	0.298	1	0.614	7.351	5	<b>0.001</b>	11.678	5	0.104

\*Data were square root transformed for analysis

\*\*Data were log-transformed for analysis

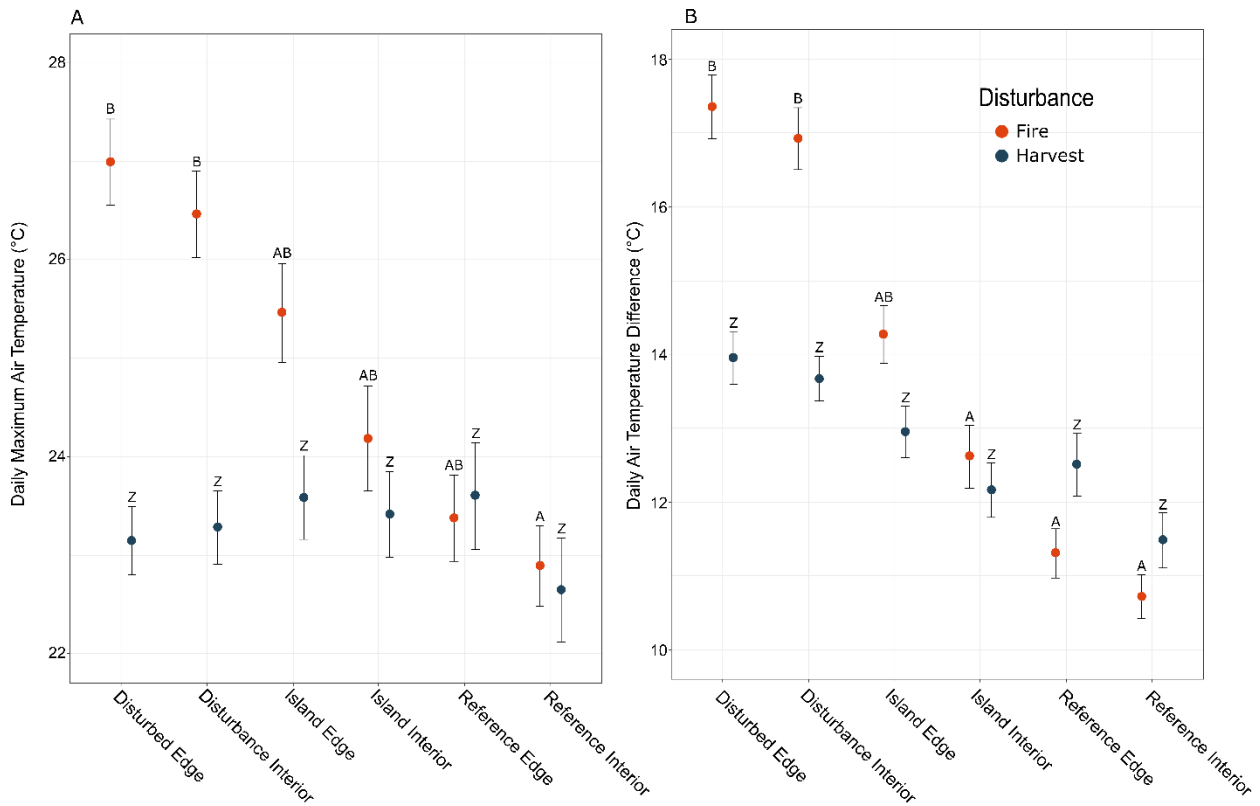
Daily maximum soil temperature ( $T_s$ ) in fire plots did not vary significantly between plot locations (11.5-12.0 °C); although it tended to be higher in edge plots compared to their associated interior locations, the differences were non-significant (Figure 3.7A). In harvest plots,  $T_s$  was lowest in the island edge (11.4 °C), and highest in the reference edge (12.3 °C), although differences were non-significant (Figure 3.7A). Soil temperature difference ( $\Delta T_s$ ) in fire plots was largest in the disturbed Interior (3.1 °C), significantly different from the smallest difference located in the reference interior (1.9 °C). Other values were not significantly different compared to either extreme, ranging between 2.2-2.8 °C (Figure 3.7B). In harvest plots, there were no significant differences in  $\Delta T_s$ , and values ranged between 2.3 °C in the disturbed edge and 2.1 °C in the reference interior (Figure 3.7B).



**Figure 3.7.** Mean and standard error of (A) Maximum daily soil temperature ( $T_s$ ), (B) Daily soil temperature differential ( $\Delta T_s$ ) by disturbance and plot location. Within each disturbance type, means with different letters were significantly different in a pairwise comparison of the estimated marginal mean,  $P < 0.05$ .

In fire plots, maximum surface air temperature ( $T_A$ ) followed a gradient of high temperatures in the disturbed (26.5-27.0 °C), intermediate in the island (24.2-25.5 °C), and lowest in references (22.9-23.4 °C), although the only significant differences occurred between the disturbed plots and the reference interiors.  $T_A$  in fire edge plots was higher than in their associated interior location, but not significantly so (Figure 3.8A). In harvest plots,  $T_A$  did not vary significantly between any of the plot locations (22.6-23.6 °C; Figure 3.8A). Surface air temperature difference ( $\Delta T_A$ ) in fire plots followed a similar pattern as fire plot  $T_A$ , with high temperature differences in the disturbed (16.9-17.4 °C), intermediate in the island (12.6-14.3 °C), and lowest in references (10.7-11.3 °C). As with  $T_A$ , edge plots had a larger, but non-significant,

difference compared to their associated interior locations (Figure 3.8B).  $\Delta T_A$  in the harvest plots was generally largest in the disturbed plots (13.7-14.0 °C), with island and reference plots generally lower (11.5-12.9 °C), except the harvest reference edge which had an intermediate value, which was not significantly lower than any other plot locations (Figure 3.8B).



**Figure 3.8.** Mean and standard error of (A) Maximum daily surface air temperature ( $T_A$ ), (B) Daily surface temperature differential ( $\Delta T_A$ ) by disturbance and plot location. Within each disturbance type, means with different letters were significantly different in a pairwise comparison of the estimated marginal mean,  $P < 0.05$ .

### 3.4 Forest structural responses to disturbance and plot location

In terms of forest structure, the main significant effects were of plot location and interactions between plot location and disturbance type (Table 3.4). Plot location had a significant effect on

sapling density, Recent Coarse woody material Volume (RCV), and Recent Total deadwood Volume (RTV). A significant interaction between disturbance and plot location was found for litter cover, sapling density, Recent Standing deadwood Volume (RSV), RCV, RTV, and total living tree basal area (BAA). Coniferous Basal Area Ratio (CONBAAR), canopy cover, Recent Dead Basal Area Ratio (RBADR), and Recent Standing deadwood Volume Ratio (RSVR) did not exhibit any significant treatment or interaction effects (Table 3.4).

**Table 3.4.** Results of linear mixed-effect models examining the influence of disturbance type (fire/harvest) and plot location (DE/DI/IE/II/RE/RI), and the interaction between disturbance × plot on forest structural variables. Disturbance region and site were used as random effects. P-values in bold and italics were considered significant at  $\alpha = 0.05$ .

	Disturbance			Plot Location			Disturbance × Plot		
	F	df	P	F	df	P	F	df	P
O Layer*	0.009	1	0.928	0.285	5	0.285	0.644	5	0.667
Litter	1.246	1	0.327	0.739	5	0.595	3.103	5	<b>0.011</b>
Saplings**	0.016	1	0.907	9.384	5	<b>0.001</b>	4.262	5	<b>0.002</b>
RCV**	0.241	1	0.626	8.955	5	<b>0.001</b>	6.301	5	<b>0.004</b>
RSV**	1.171	1	0.340	0.876	3	0.459	3.026	3	<b>0.036</b>
RTV**	2.143	1	0.217	27.232	5	<b>0.001</b>	4.181	5	<b>0.002</b>
CONBAAR*	0.068	1	0.807	1.358	3	0.270	1.142	3	0.344
BAA	0.003	1	0.961	1.359	3	0.264	5.523	3	<b>0.002</b>
Canopy	0.730	1	0.441	1.361	3	0.268	2.049	3	0.121
RBADR*	3.931	1	0.118	1.313	3	0.284	1.824	3	0.159
RSVR*	0.796	1	0.423	1.313	3	0.284	1.824	3	0.159

\*Data were square root transformed for analysis

\*\*Data were log-transformed for analysis

### 3.4.1 Forest structural variables- fire plots

For fire plots, the only forest structural variables with significant differences between plot locations were total living tree Basal Area (BAA) and Recent Total deadwood Volume (RTV);Table



3.5). BAA was lowest in the island edge at 31.75 m<sup>2</sup> ha<sup>-1</sup>, which was significantly lower than the reference edge (42 m<sup>2</sup> ha<sup>-1</sup>) and reference interior (44.25 m<sup>2</sup> ha<sup>-1</sup>) while the island interior was intermediate to these. RTV was generally higher in the forested plots (35.68-95.39 m<sup>3</sup> ha<sup>-1</sup>), which did not differ from one another, compared to the disturbed plots (12.85-30.5 m<sup>3</sup> ha<sup>-1</sup>). The disturbed interior had the lowest RTC, which was significant different from all four forested plot locations. There was a large amount of variation within measurements of RTV of the plot locations as evidenced by the large standard errors (Table 3.5).

**Table 3.5.** Means (standard error presented below in italics) of forest structure variables in fire plots. Superscripts indicate significant differences in variable means in pairwise Tukey HSD tests at  $\alpha = 0.05$ .

	Disturbed Edge	Disturbed Interior	Island Edge	Island Interior	Reference Edge	Reference Interior
Olayer (cm)	7.56 <i>2.77</i>	8.97 <i>2.87</i>	7.11 <i>0.98</i>	7.86 <i>0.78</i>	7.61 <i>0.87</i>	7.08 <i>0.54</i>
Litter (%)	59.87 <i>8.48</i>	49.79 <i>6.96</i>	61.81 <i>4.10</i>	67.78 <i>7.11</i>	69.62 <i>5.77</i>	68.97 <i>4.28</i>
Saplings ha <sup>-1</sup>	3 300 <i>1 190</i>	7 223 <i>1 723</i>	4 667 <i>1 491</i>	1 840 <i>601</i>	2 810 <i>814</i>	1 509 <i>699</i>
BAA (m <sup>2</sup> ha <sup>-1</sup> )	-	-	31.75 <sup>a</sup> <i>2.75</i>	39 <sup>ab</sup> <i>2.52</i>	42 <sup>b</sup> <i>3.66</i>	44.25 <sup>b</sup> <i>2.95</i>
Canopy (%)	-	-	74.56 <i>5.25</i>	83.10 <i>1.31</i>	80.97 <i>2.09</i>	82.55 <i>1.16</i>
CONBAAR	-	-	0.31 <i>0.08</i>	0.30 <i>0.05</i>	0.30 <i>0.07</i>	0.34 <i>0.07</i>
RCV (m <sup>3</sup> ha <sup>-1</sup> )	30.5 <i>13.01</i>	12.85 <i>4.21</i>	46.99 <i>21.42</i>	22.91 <i>13.15</i>	29.92 <i>11.87</i>	16.86 <i>5.30</i>
RTV (m <sup>3</sup> ha <sup>-1</sup> )	30.5 <sup>ab</sup>	12.85 <sup>a</sup>	95.39 <sup>c</sup>	51.41 <sup>bc</sup>	54.45 <sup>bc</sup>	35.68 <sup>bc</sup>

		<i>13.01</i>	<i>4.21</i>	<i>26.00</i>	<i>15.89</i>	<i>16.08</i>	<i>6.44</i>
RSV (m <sup>3</sup> ha <sup>-1</sup> )	-	-	48.4	28.5	24.53	18.82	
	-	-	<i>11.82</i>	<i>5.15</i>	<i>7.10</i>	<i>2.30</i>	
RBADR	-	-	0.29	0.12	0.08	0.06	
	-	-	<i>0.12</i>	<i>0.04</i>	<i>0.03</i>	<i>0.01</i>	
RSVR	-	-	0.53	0.15	0.12	0.09	
	-	-	<i>0.30</i>	<i>0.06</i>	<i>0.03</i>	<i>0.02</i>	

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### 3.4.2 Forest structural variables- harvest plots

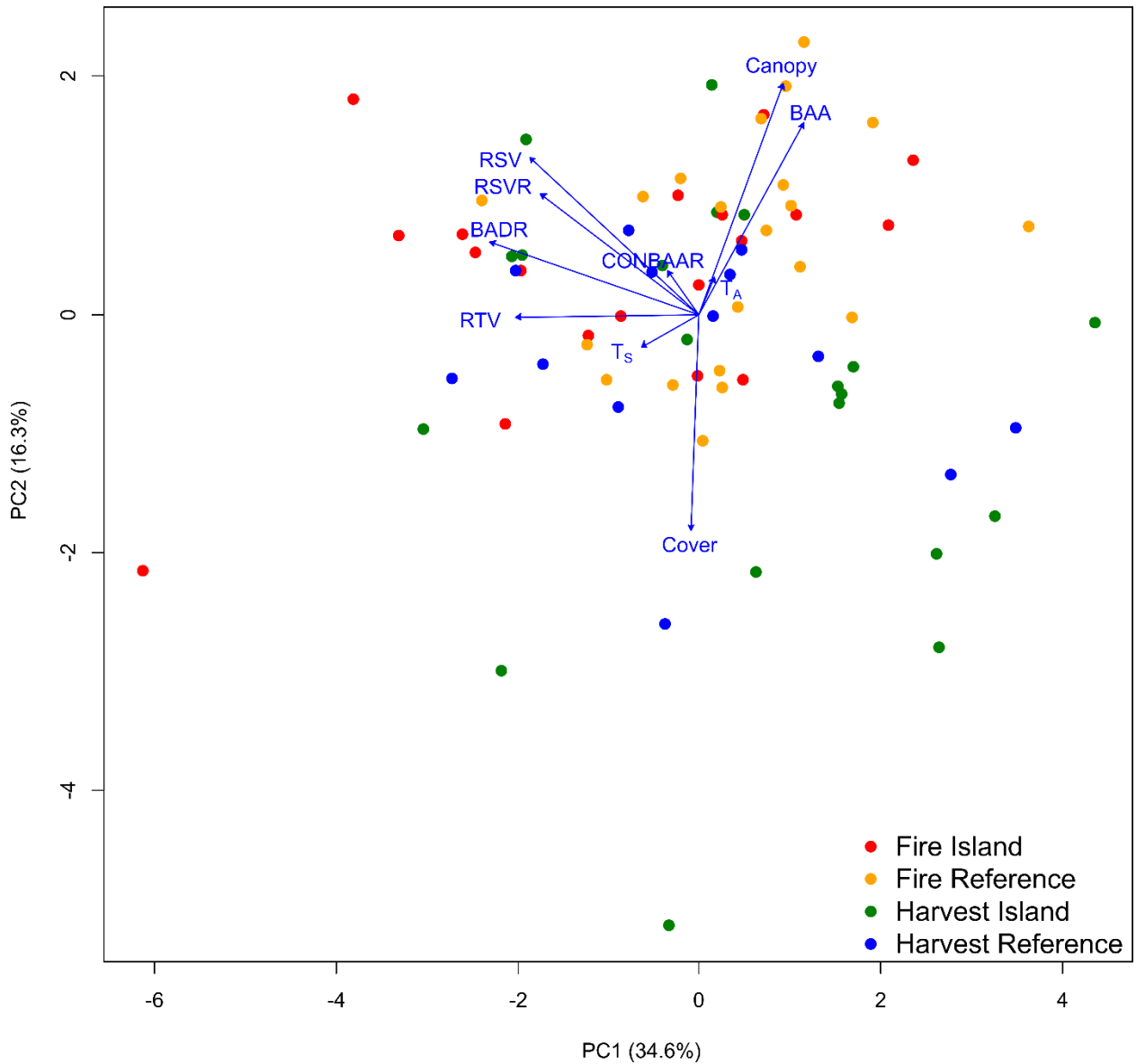
Three forest structural variables had significant differences between harvest plot locations: Sapling density, Recent Coarse woody material Volume (RCV), and RTV (Table 3.6). Sapling density was highest in the disturbed plots (10 400-13 040 stems ha<sup>-1</sup>), which was significantly higher than the forested plots (350-2618 stems ha<sup>-1</sup>). RCV was generally significantly higher in the forested plots (12.73-43.87 m<sup>3</sup> ha<sup>-1</sup>) than the disturbed plots (0.97-1.46 m<sup>3</sup> ha<sup>-1</sup>), although disturbed edge and reference interior were not significantly different (Table 3.6). RTV was significantly higher in harvest forested plots (41.53-71.37 m<sup>3</sup> ha<sup>-1</sup>) than the disturbed plots (0.97-1.46 m<sup>3</sup> ha<sup>-1</sup>).

**Table 3.6.** Means (standard error presented below in italics) of forest structure variables in harvest plots. Superscripts indicate significant differences in variable means in pairwise Tukey HSD tests at  $\alpha = 0.05$ .

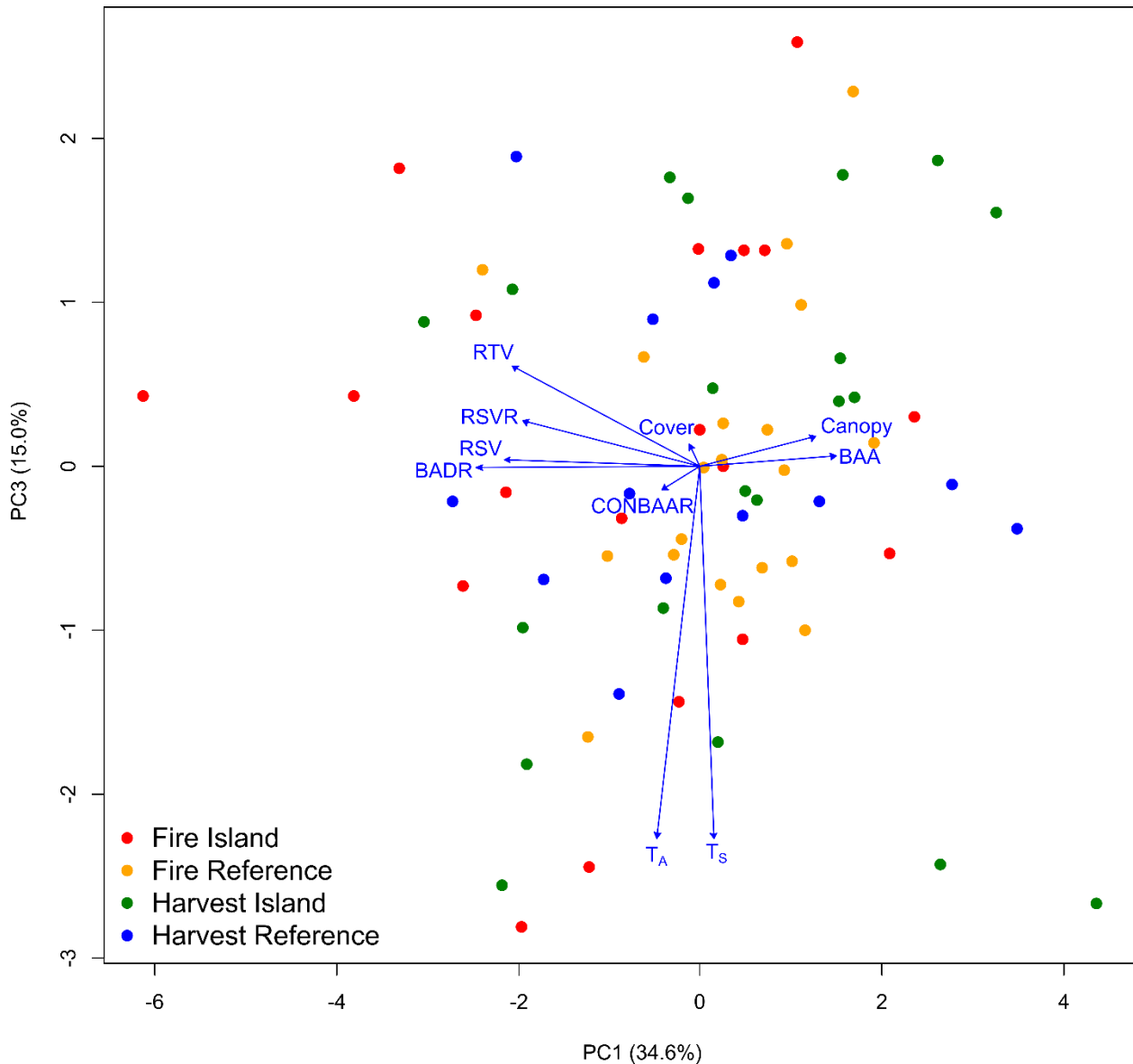
	Disturbed Edge	Disturbed Interior	Island Edge	Island Interior	Reference Edge	Reference Interior
Olayer (cm)	5.69 <i>0.69</i>	6.03 <i>0.87</i>	7.08 <i>0.74</i>	8.17 <i>0.94</i>	8.96 <i>1.03</i>	7.63 <i>1.21</i>
Litter (%)	77.58 <i>6.98</i>	82.88 <i>4.92</i>	62.36 <i>8.12</i>	76.81 <i>3.15</i>	68.44 <i>9.35</i>	70.00 <i>8.74</i>
Saplings ha <sup>-1</sup>	10 400 <sup>a</sup> <i>2 395</i>	13 040 <sup>a</sup> <i>3 010</i>	2618 <sup>b</sup> <i>795</i>	1178 <sup>b</sup> <i>598</i>	1400 <sup>b</sup> <i>1 201</i>	350 <sup>b</sup> <i>213</i>
BAA (m <sup>2</sup> ha <sup>-1</sup> )	- -	- -	42.25 <i>3.37</i>	43.25 <i>3.52</i>	32.75 <i>4.60</i>	36.5 <i>3.60</i>
Canopy (%)	- -	- -	77.33 <i>4.29</i>	76.78 <i>4.86</i>	72.43 <i>2.56</i>	80.28 <i>2.00</i>
CONBAAR	- -	- -	0.34 <i>0.07</i>	0.26 <i>0.11</i>	0.26 <i>0.10</i>	0.24 <i>0.09</i>
RCV (m <sup>3</sup> ha <sup>-1</sup> )	1.46 <sup>ab</sup> <i>0.92</i>	0.97 <sup>a</sup> <i>0.97</i>	43.87 <sup>c</sup> <i>18.04</i>	26.42 <sup>c</sup> <i>21.10</i>	24.99 <sup>c</sup> <i>8.44</i>	12.73 <sup>bc</sup> <i>10.21</i>
RTV (m <sup>3</sup> ha <sup>-1</sup> )	1.46 <sup>a</sup> <i>0.92</i>	0.97 <sup>a</sup> <i>0.97</i>	71.37 <sup>b</sup> <i>19.63</i>	41.53 <sup>b</sup> <i>26.14</i>	54.57 <sup>b</sup> <i>14.86</i>	54.43 <sup>b</sup> <i>23.36</i>
RSV (m <sup>3</sup> ha <sup>-1</sup> )	- -	- -	27.5 <i>7.90</i>	15.11 <i>4.44</i>	29.58 <i>7.72</i>	41.7 <i>11.60</i>
RBADR	- -	- -	0.11 <i>0.04</i>	0.08 <i>0.04</i>	0.12 <i>0.04</i>	0.10 <i>0.03</i>
RSVR	- -	- -	0.11 <i>0.03</i>	0.05 <i>0.01</i>	0.13 <i>0.04</i>	0.10 <i>0.03</i>

### **3.5 Forest structure and microclimate**

As seen in the Principal Component Analysis (PCA) on forest structure variables and microclimate, the first principal component (PC1) explained 34.6% of the variation (Figure 3.9). It primarily reflects a negative correlation with variables measuring deadwood proportions or volumes and, to a lesser degree, a positive correlation with measures of overstory structure (canopy cover and living tree basal area). Principal component 2 (PC2) explained 16.3% of the variation, and was negatively correlated with understory plant cover, and positively correlated with the aforementioned measures of overstory cover. While some measures of deadwood (total deadwood volume and the proportion of the basal area of recently deceased standing deadwood to living tree basal area) were orthogonal with PC2, while others (recently deceased standing deadwood volume and proportion of recently deceased standing deadwood volume to living tree volume) were slightly positively correlated. Both PC1 and PC2 explained little variance in proportion of conifer basal area and average maximum surface and soil temperatures (Figure 3.9). Maximum daily microclimate temperatures (air and soil) were strongly negatively correlated with PC3, which explained 15.0% of the variation (Figure 3.10). No other variables were strongly correlated with PC3. Overall, the first three axes represented 65.9% of the total variation in the dataset.



**Figure 3.9.** Principal components 1 & 2 of a principal component analysis on microclimatic and forest structural variables, represented by blue vectors. Each point represents the microclimate and forest structural measurements taken within each plot. Refer to Table 2.4 for descriptions of the variables.



**Figure 3.10.** Principal components 1 & 3 of a principal component analysis on microclimatic and forest structural variables, represented by blue vectors. Each point represents the microclimate and forest structural measurements taken within each plot. Refer to Table 2.4 for descriptions of the variables.

### 3.6 Forest structure and understory composition

Backwards selection of six explanatory variables on an ordination (db-RDA) of understory vegetation composition identified only one significant explanatory variable: canopy cover. Contrary to expectations, there were no significant associations between various measures of

tree mortality (i.e., RBADR, RSVR, RSV,RTV) and understory composition. Canopy cover explained 1.9% of the variation in understory community composition and was not positively correlated with any understory species (Table 3.7). Species negatively associated with canopy cover include *Epilobium angustifolium*, *Viburnum edule*, *Calamagrostis canadensis*, and *Aster conspicuus* Lindl.

### 3.7 Plant trait analysis

#### 3.7.1 Overall plot location analysis

Within fourth corner analyses of plot location examining fire and harvest separately, many trends were similar in both disturbance types (

Figure 3.11A;

**Table 3.7.** Results of a distance-based redundancy analysis testing the influence of canopy cover on understory vegetation composition (Adjusted  $R^2 = 0.019$ ). Species that were determined to have made an above average contribution to the ordination using the circle of equilibrium method (Borcard et al., 2011) are listed with their position along the constrained axis. The six letters of each code are the first three letters of the genus, followed by the first three letters of the specific epithet. For a list and an explanation of species codes, see Appendix 1.

	Axis 1
<i>Constraining Variable Score</i>	
Canopy	-1
<i>Species Scores</i>	
EPIANG	2.82
VIBEDU	2.18
CALCAN	1.63
ASTCON	1.40

Figure 3.11B). Species with high seed production were positively correlated with the disturbed plots, and negatively correlated with select forested plots. Species with higher seed weights were positively associated with forested plots, and negatively correlated with disturbed plots. Foliage structure traits varied significantly in harvest plots, but only marginally significant in fire plots. The only clear patterns of foliage structure

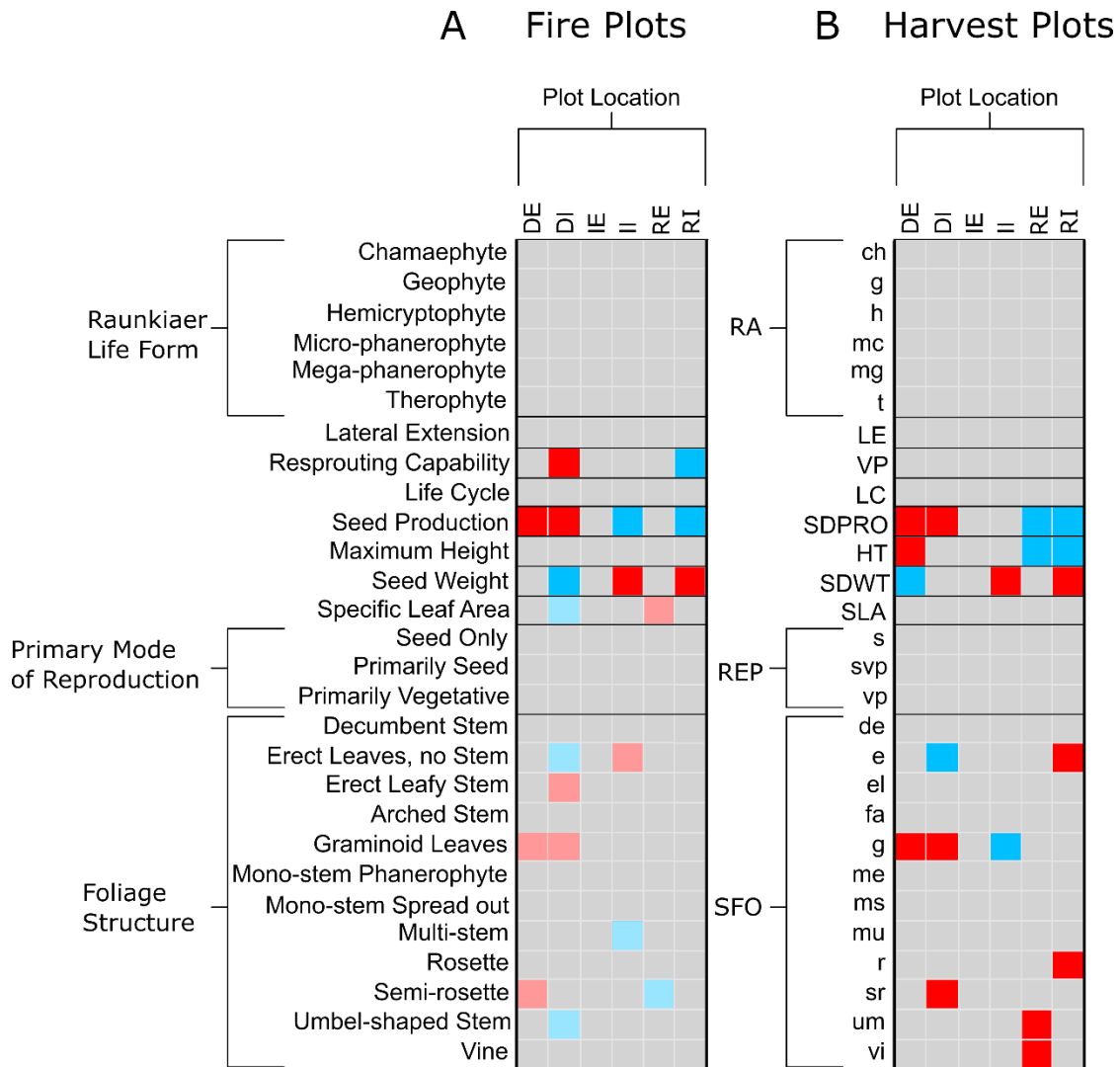
distribution were a positive correlation between graminoid leaf structures and disturbed plots, and a positive correlation between stemless plants with erect leaves with some forested plots and a negative correlation with disturbed interiors (

Figure **3.11A**;

Figure **3.11B**). Unlike fire plots, harvest plots had significant differences in maximum plant height traits, where disturbed edge plots were positively correlated with maximum plant height and reference plots were negatively correlated (

Figure **3.11B**).





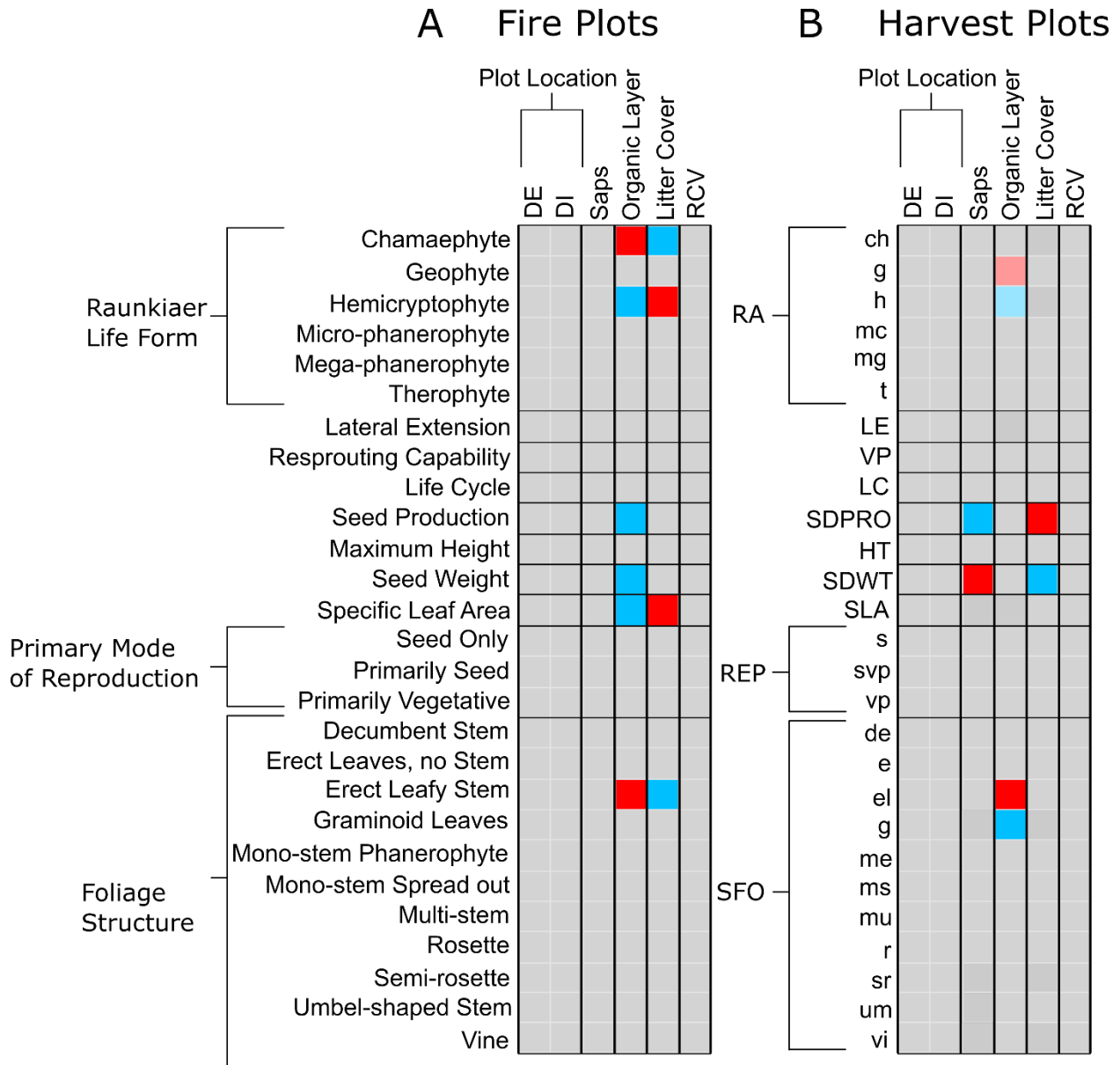
**Figure 3.11.** Results of a fourth-corner analysis showing the influence of disturbance type (A), plot location of fire plots (B), and plot location of harvest plots (C). Colored squares indicate that the test statistic of a trait level/environmental variable level was significantly higher (red) or lower (blue) than the expected value generated by permutation. Only globally significant ( $\alpha = 0.05$ ) and marginally significant ( $\alpha = 0.1$ , faded colors) trait-variable relationships following Holm's correction were plotted.

### 3.7.2 Analysis of trait patterns in disturbed areas

In the analysis of plots disturbed by fire, a dichotomy emerged between organic layer thickness and litter cover. Organic layer thickness was positively correlated with chamaephytes and plants with erect leafy stems, and negatively correlated with hemicryptophytes, seed

production, seed weight, and SLA. By contrast, litter cover was positively correlated with hemicryptophytes and SLA, and negatively correlated with chamaephytes and plants with erect leafy stems (Figure **3.12A**).

In the analysis of plots disturbed by harvest, organic layer thickness was positively correlated with plants with erect leafy stems, and negatively correlated with graminoid leaves. Organic layer thickness was also marginally correlated with geophytes and negatively correlated with hemicryptophytes. Litter cover was positively correlated with seed production and negatively correlated with seed weight. Sapling density was positively correlated with seed weight and negatively correlated with seed production (Figure **3.12B**).



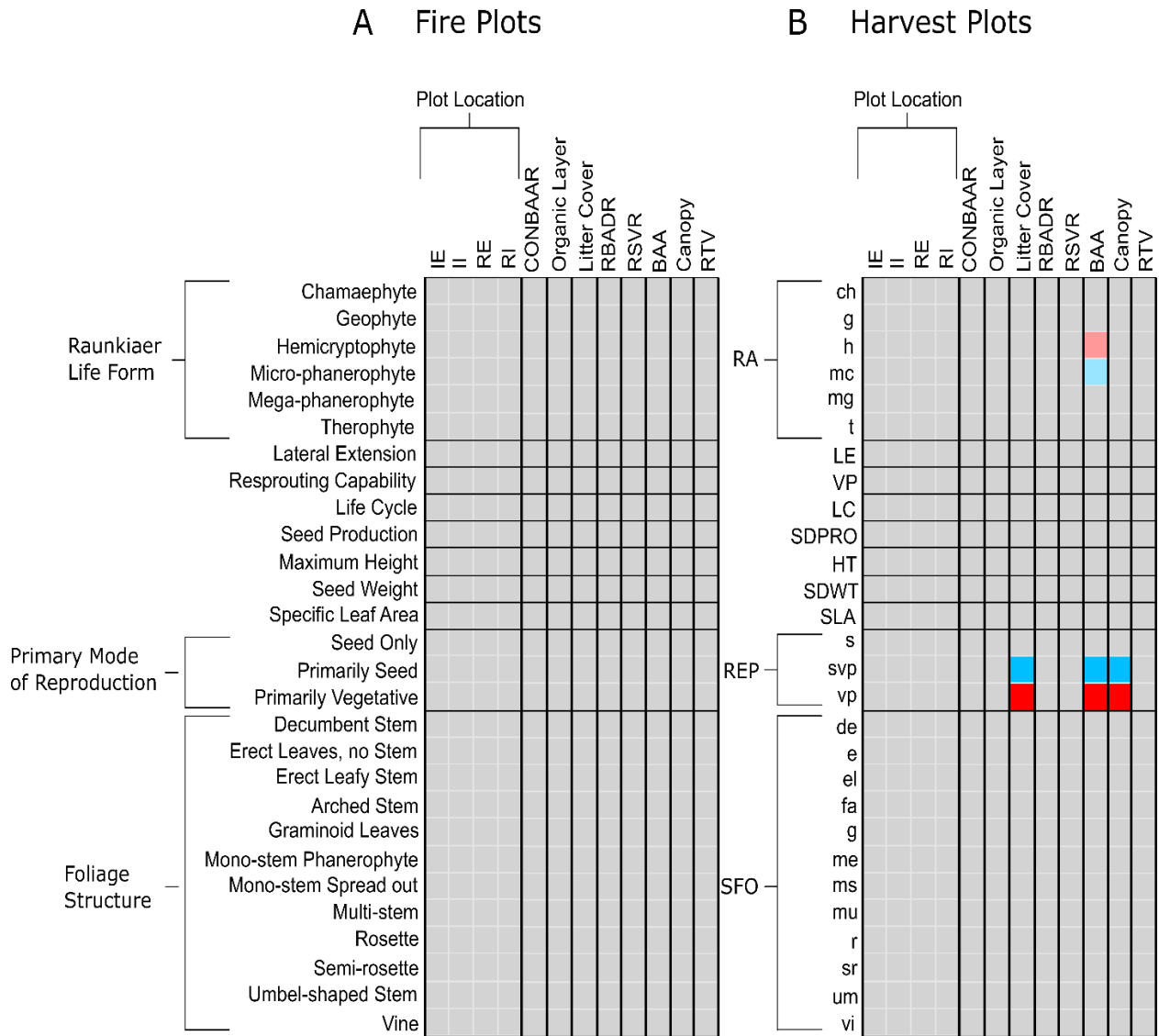
**Figure 3.12.** Results of a fourth-corner analysis showing the influence of disturbance type (A), plot location and environmental variables of fire plots (B), and plot location and environmental variables of harvest plots (C) on the disturbed plots. Colored squares indicate that the test statistic of a trait level/environmental variable level was significantly higher (red) or lower (blue) than the expected value generated by permutation. Only globally significant ( $\alpha = 0.05$ ) and marginally significant ( $\alpha = 0.1$ , faded colors) trait-variable relationships following Holm's correction were plotted.

### 3.7.3 Analysis of trait patterns in forested areas

Within an analysis of fire forested plots, no significant correlations between traits and treatments/environmental variables were found in forested fire plots (

Figure **3.13A**). Raunkiaer life form was marginally significant in harvest plots, with hemicryptophytes positively and micro-phanerophytes negatively correlated with living tree basal area (BAA). Plants with frequent vegetative reproduction were positively correlated with litter cover, BAA, and canopy cover, and plants that reproduce primarily by seed were negatively correlated with the aforementioned environmental variables (

Figure **3.13B**).



**Figure 3.13.** Results of a fourth-corner analysis showing the influence of disturbance type (A), plot location and environmental variables of fire plots (B), and plot location and environmental variables of harvest plots (C) on the forested plots. Colored squares indicate that the test statistic of a trait level/environmental variable level was significantly higher (red) or lower (blue) than the expected value generated by permutation. Only globally significant ( $\alpha = 0.05$ ) and marginally significant ( $\alpha = 0.1$ , faded colors) trait-variable relationships following Holm's correction were plotted.

## 4 Discussion

Under natural disturbance-based forest management in the boreal mixedwood of northern Alberta, aggregate retention patches of trees are left unharvested within a clearcut to emulate patches of trees that remain following a wildfire, the dominant natural disturbance in the ecosystem. These patches, also known as island remnants, are thought to provide a heterogenous forest structure and the stand and landscape scale, a refugia for pre-disturbance vegetation communities, and a source of microclimatic influence and propagules to aid in the regeneration of the disturbed forest. The purpose of this study was to fill some knowledge gaps in the study of aggregate retention. While harvest remnants are supposed to be emulating post-fire remnants, the two are rarely directly compared (but see Gandhi et al. 2004; Dragotescu and Kneeshaw 2012; Moussaoui et al. 2016a; Moussaoui et al. 2016b). Instead, comparisons are usually made between harvest and unharvested forest. It is also known that patches within clearcuts are susceptible to tree mortality due to edge influence, but it is unknown whether a patch's ability to sustain pre-disturbance plant species and microclimatic conditions may be compromised by changes to forest structure caused by this tree mortality. Primarily, I wanted to compare the vascular understory vegetation communities of fire and harvest island remnants to assess if they are supporting understory communities and microclimates similar to each other and/or to reference forest a decade after disturbance. Second, I wanted to determine if forest structure, understory community, and microclimates were altered due to edge influence at remnant edges. Third, I wanted to assess if forest structure, as a reflection of tree mortality since remnant creation leads to changes in understory composition or microclimate within forested

plots (remnants and reference). Finally, I wanted to assess patterns of plant traits associated with colonization and persistence within remnants, disturbances, and references.

Similar to other studies, I found harvest remnants were able to sustain similar understory communities as reference forest (Nelson & Halpern 2005; Franklin et al. 2018). I also found that remnants could sustain microclimates similar to reference forest, in accordance with other studies in different forest biomes (Heithecker & Halpern 2007; Baker et al. 2016). In general, I did not find clear evidence of that edge influence differed at the edge compared to the interior of patches. While I did find evidence of overstory structure, particularly canopy cover, influencing understory species composition, I did not find any evidence of links between overstory structure and microclimate. Additionally, recent tree mortality in forested plots was not found to have a significant effect on understory vegetation composition. Finally, using a functional trait approach, I was able to determine patterns of colonization and persistence trait syndromes within remnants and disturbed plots.

#### **4.1 Fire remnants compared to harvest remnants: understory composition**

Contrary to expectations, my findings indicate that harvest and fire remnants did not have understory compositions similar to one another, and forested plots from the fire disturbance had a significantly higher multivariate dispersion than reference plots from the harvest disturbance. The significant result found in the PerMANOVA can indicate either a significant difference in the location and/or dispersion of a given factor (Anderson et al. 2008), although PerMANOVA is not as sensitive to heterogeneous dispersions compared to other tests (Anderson & Walsh 2013). Both an analysis of dispersion and visualization of the composition suggest a heterogeneous dispersion, as fire plots had a statistically and visually larger dispersion than the harvest plots.

Disentangling the effects of two different disturbance types adjacent to remnants on the understory community from the effects of geographical separation both within and between disturbance types is a difficult task. Other studies in the boreal forests of Canada with large distances between sites have identified the issue of geographical variation overpowering treatment effects (Grewal 1995; MacIsaac and Crites 1999; Dragotescu and Kneeshaw 2012). Dragotescu and Kneeshaw (2012) accounted for regional variation by blocking by region and ensuring both disturbance treatments were located within each block. When measuring boreal aspen stand characteristics in Alberta, Grewal (1995) discovered that if site conditions such as “ecosystem association” (equivalent to ecosite phase as defined in Alberta Environment and Parks 2019), moisture, and soil drainage class were similar, regional differences were not meaningful. While they ultimately found significant differences in aspen regeneration in harvested vs fire sites, MacIsaac and Crites (1999) also noted significant differences in aspen regeneration between regions for the same disturbance type, attributing it to spatial variation in topography, moisture, and soil type. A potential solution to regional variability is the use of large-scale forest experiments such as EMEND in Northern Alberta (Spence et al. 1999). Such experiments allow for a far greater degree of experimental control over confounding variables, but difficulties in implementing experimental burns at a large scale prevented the use of such an experimental setup. Because this is an observational study, the pool of study sites (especially fire remnants) had to be drawn from a limited pool of candidates that we had little experimental control over. There was, however, greater experimental control over harvest remnants than fire remnants. Provincial forestry regulations mandate that remnants must be representative of the harvested forest, cannot be placed on steep slopes, and are to be distinct from waterbody buffers



(Government of Alberta 2022). This essentially guarantees that harvest remnants and the cutblock are in productive aspen-dominated stands and helps control hydrologic and topographical variation, which ensures plots are located within similar ecosites. Controlling for site characteristics in fire remnants was more challenging: Topography, hydrology, weather during the fire, seasonality, and fuel continuity are all factors that could lead to the formation of post-fire remnants (Rowe & Scotter 1973; Ferster et al. 2016; San-Miguel et al. 2020). Some of the fire remnants were located near bodies of water or within small concave depressions and ravines. Forests near bodies of water or within a small ravine have cooler air and higher soil and air moisture, decreasing their chances of burning (Rowe & Scotter 1973; Kafka et al. 2001; San-Miguel et al. 2020). Other remnants were located within a mosaic of fuel types. Less flammable fuels (e.g., *Populus* spp.) interspersed within more flammable fuels (e.g., *Picea* or *Pinus* spp.) increases the amount of vegetation retained following a fire (San-Miguel et al. 2020; Ferster et al. 2016). Furthermore, Araya et al. (2015) found deciduous trees were overrepresented in post-fire remnants relative to their abundance in unburned landscapes in the boreal forest of Quebec. While not always the case, it is thus likely that the diversity in topography, hydrology, and fuel matrix within and surrounding fire remnants leads to a wide variety of site conditions within remnants, which would also be reflected in the understory composition. Since this study did not control site characteristics, but rather focused on the overstory composition in remnants and references, I cannot reject the possibility of geographical differences overpowering variation caused by the disturbance type treatment. Naturally occurring variable site conditions within fire remnants versus the lower variability in harvest remnants could also explain the significant difference in dispersion between forested fire and harvest plots.

Within the db-RDA constrained by plot location there is further evidence of regional variation in understory communities. *Gymnocarpium dryopteris* and *Abies* spp. seedlings were highly associated with forested fire plots, neither were present in any harvest regions, and both were only present in one of the three fires: The flattop fire, which was noted to take place in an area with a significant presence of *Abies* spp. trees (Flat Top Complex Wildfire Review Committee, 2012). Since both *G. dryopteris* and *Abies* spp. were only present in one fire region but are identified as having significant associations with forested fire plots as a whole, is unlikely that this analysis is exclusively reflecting differences in the disturbance type treatment and is instead being confounded by a strong regional effect.

#### **4.2 Remnants compared to references: understory composition**

As expected, analyses of understory cover, richness, and diversity did not reveal any significant differences between island remnants and reference forest of either disturbance type. The PerMANOVA analysis did not find significant differences between compositions of island remnants and references. Plots associated with remnants and references of both disturbance types were characterized by higher covers of *Aralia nudicaulis*, *Cornus canadensis*, *Linnaea borealis*, *Mitella nuda*, and *Viburnum edule* compared to the adjacent disturbed area. These species are common boreal species, identified in many studies as occurring most abundantly in mature forest (Aubin et al. 2014; Bradbury 2004; Harper & Macdonald 2002; Macdonald & Feeniak 2007).

In a study of various sizes of harvest remnants after disturbance in an aspen-dominated boreal forest in Alberta, Bradbury (2004) found harvest remnants were supporting different species than the pre-disturbance forest a year after harvest. They found that patches were

instead an intermediate form of habitat, supporting different communities than both the pre-disturbance forest and cutblock matrix. They also found larger remnants (0.5-0.75 ha) supported more forest obligate/generalist species than smaller remnants (0.03-0.2 ha; Bradbury 2004). Franklin et al. (2018) found that 15-year-old retention patches in the boreal mixedwood of Alberta were effective as refugia for forest dependent species, especially when surrounded by higher levels of dispersed retention, but found that patches surrounded by clearcuts were supporting different vegetation communities than reference forest. While my results did not conform with their findings, both Bradbury (2004), and Franklin et al. (2018), noted patches were ecologically valuable, contained different species than the surrounding cutblock, and larger patches could sustain forest-dependent species more effectively than smaller ones. It is important to note that Bradbury (2004) studied patches in three size classes (0.03, 0.20, 0.78 ha respectively) and Franklin et al. (2018) studied two patch sizes (0.20 or 0.45 ha), both smaller patch sizes than my study (range 0.76-2.70 ha; average 1.47 ha). The larger patches in my study could explain why I found understory communities in remnants that were not significantly different than reference forest. To that effect, my results are in line with those of Nelson & Halpern (2005), who found that larger, 1-hectare, post-harvest aggregate retention patches in the Pacific Northwest showed minimal change in composition from pre-harvest composition two years after harvest. To my knowledge, this is the first study specifically investigating the understory vegetation of post-fire remnants. As such, there are no studies to directly compare my results to. However, remnants of both disturbance types did not show significant differences in cover, richness, and diversity of understory species when compared to their reference forest, indicating they perform similar ecological roles.

### **4.3 Remnant compared to reference: microclimate**

#### **4.3.1 Surface air temperatures**

With few exceptions, island remnants were found to support similar soil and surface air temperatures as reference forest.

Daily maximum air temperatures ( $T_A$ ) and diurnal temperature differences ( $\Delta T_A$ ) did not vary significantly between plot locations for the harvest disturbance. Within fire plot locations,  $T_A$  and  $\Delta T_A$  were significantly higher in the disturbed plots than the forested ones. Fire remnants contained higher  $T_A$ , and  $\Delta T_A$  than reference interiors, these values were significantly higher than reference interiors in the edges and remnant interior  $\Delta T_A$ .

As seen in my harvest plots, a study in the temperate eucalypt forests of Tasmania compared retention patches and intact forest and found early morning and midday microclimatic temperatures 50 meters into patches were not significantly different than temperatures 50 meters into intact forest (Baker et al. 2016). Remnant patches in that experiment were 3–4-years-old and generally large, ranging from 1-6.7 hectares (Baker et al. 2016). By contrast, in three regions of Douglas-fir forest in the Pacific Northwest, Heithecker & Halpern (2007) compared microclimates within 6–7-year-old retention patches 1 hectare in size with clearcuts and reference forest. In two of the three regions, they found mean and maximum temperatures in the centre of patches were warmer than reference forest, while patches in the third region sustained temperatures equivalent to reference forest. They hypothesized that the differences in temperature were possibly caused by increased light penetration into the remnants compared to intact forest (Heithecker & Halpern 2007). Another possible explanation for warmer microclimates in fire remnants compared to references is advective heating, a process by which air warmed in the exposed disturbance is moved by wind. Winds within a disturbed matrix are

generally stopped by continuous forest, resulting in warm pockets of air coalescing at the forest edge (Chen et al. 1995; Heithecker & Halpern 2007). Because of their relatively small size, remnant patches are thought to be unable to stop these winds, allowing the warm air to move through the entirety of a patch. Intact forest by contrast, is a more effective windbreak, preventing warm winds from penetrating into the forest (Heithecker & Halpern 2007). Advective heating could also explain different trends in microclimates observed in forested plot locations of the different disturbance types. Because of lower sapling densities, the more exposed disturbed matrix in fire plots is perhaps more conducive to air movement across the landscape and through remnants, but is unable to penetrate the reference, resulting in warmer air temperatures in fire remnants compared to reference forest. Harvest cutblock were less exposed, owing to higher sapling densities, lowering the incoming solar radiation, and impeding wind from moving through the remnants. Unfortunately, this is ultimately speculative, as wind speed was not measured, preventing me from explicitly testing this theory.

While many studies report greater maximum air temperature in disturbed landscapes versus mature forest (e.g., Chen et al. 1993; Heithecker & Halpern 2007), my study only found this to be the case in fire plots. With increasingly successful forest regeneration, the microclimate tends to converge with that of reference forest, as high densities of saplings absorb or reflect much of the incoming solar radiation and reduce the contrast between disturbance and mature forest (Constabel & Liefers 1996; Baker et al. 2013). Another less likely possibility is the mediation of microclimates in harvest plots by dense thatches of grass, a phenomenon found to significantly reduce ground temperatures in cutblocks in the boreal forest of Alberta (Hogg & Liefers 1991). Either of these explanations could explain differences seen in fire-disturbed and

harvest-disturbed plots relative to remnants, because the cover of graminoids and the density of saplings were both greater in cutblocks than burns.

#### **4.3.2 Soil temperatures**

The results for maximum soil temperatures ( $T_s$ ) were simpler. There were no significant differences in  $T_s$  between different plot locations in fire remnants, and in harvest  $T_s$  was not significantly different between remnants and reference interiors.

The lack of differences in  $T_s$  indicate possible mediation of soil temperature by an interaction of local factors like understory cover, saplings, tree canopies, litter, and slash (Heithecker & Halpern 2006). These findings contrast much of the literature, where disturbed plots have consistently higher soil temperatures than aggregate remnants or reference forest (e.g., Chen et al. 1993; Heithecker & Halpern 2007). While some studies have noted soil temperatures in cutblocks to be lower underneath understory cover than fully exposed soil, these were not compared to soil temperatures at mature forest sites (Hogg & Lieffers 1991; Balisky & Burton 1995).

#### **4.4 Remnant edge compared to interior: forest structure**

Contrary to expectations, I only found weak evidence that fire or harvest remnant edges had different forest structure than the remnant interiors. Fire island edges had lower living tree basal area, higher recent tree mortality, more deadwood, and more saplings, but ultimately none were significantly higher. Harvest remnants edges had higher sapling densities and deadwood volumes than the interiors, but again not significantly so. Similarly, there were no significant differences between the forest structure in either harvest or fire remnants and their reference forest, except for living tree basal area in fire edges, which was significantly lower than the reference.

#### **4.5 Remnant edge compared to interior: understory composition**

In concordance with forest structure, I did not find any evidence that fire or harvest remnant edges were supporting different understory plant communities than the remnant interiors. In a study of edge influence in harvest remnants, Nelson & Halpern (2005) found increased richness of early seral species and compositional differences between the center and edge of the remnant, although these were confined to <10 meters into the remnant. Franklin et al. (2018) reported similar results to my study, in which the composition of patches did not differ significantly between the edge and interior of remnants. They did however find graminoid cover was significantly higher in the edges of remnants compared to interiors (Franklin et al. 2018), and while I found the edges had higher graminoid covers than the interiors, the difference was non-significant.

The lack of variation between the interior of the remnants and the edge can be attributed to edge effects encompassing the entirety of the remnant (Franklin et al. 2018; Harper et al. 2005). It is important to note however, the boreal forest generally does not experience high magnitudes of edge influence (Harper & Macdonald 2002; Harper et al. 2015). Harper and Macdonald (2002) identified heterogenous forest structure and the disturbance prone nature of the boreal as factors that reduce edge influence on the understory community. Because of the relatively high disturbance frequency in the boreal, most understory plants have adapted to be able to tolerate a wide variety of conditions, allowing them to persist in both interior and edge conditions (Harper & Macdonald 2002; Aubin et al. 2014).

#### **4.6 Remnant edge compared to interior: microclimate**

In island remnants of both disturbance types, surface air temperature was higher in the edge compared to the interiors but not significantly so. Oddly, soil temperature did not hold to the same pattern, where harvest remnants edges were significantly colder than the interiors, while fire remnants showed no significant differences. In their study in the Pacific Northwest, Heithecker & Halpern (2007), found significantly higher temperatures at the edge of patches, but the depth of edge influence varied by aspect, penetrating no more than 10 meters in North/East facing edges, and 30-40 meters in South/West facing edges. I was unable to make such distinctions because first, I did not control the edge aspect in this experiment, and second, I did not have a true transect of microclimates where estimates of depth of edge influence could be precisely measured. Ultimately, considering neither forest structure nor understory community showed significant differences between the edges and interiors of remnants, it is unsurprising that there was little difference in microclimate.

#### **4.7 Influence of overstory structure on understory composition**

Analyses of forest structure did not reveal a significant relationship between measures of recent deadwood and understory composition but did find significant relationships between canopy cover and understory composition. The influence of canopy cover on composition was low and explained little variance in understory community composition, although in an observational study this is common, and the residual variation would be explained by the many unmeasured variables that influence the understory community. *C. canadensis* and *E. angustifolium*, two of the species with a negative relationship to canopy cover are well-known early successional species in the boreal and occur most abundantly with increasing removal of the overstory (Craig



& Macdonald 2009; Chávez & Macdonald 2010). While most abundant in full light conditions, both species can maintain themselves underneath canopies through vegetative means, allowing them to expand quickly should the canopy be removed (Lieffers & Stadt 1994). Lieffers & Stadt (1994) found that *C. canadensis* could persist under canopies with a light transmittance of 10% of full light. Additionally, the frequency of *C. canadensis* occurrence was near 100% at 15% light transmittance or greater, and since the lowest light transmittance they recorded in aspen stands was 14%, it's unlikely that *C. canadensis* would be eliminated from such stands. In the same study, both *C. canadensis* and *E. angustifolium* cover were found to have increased linearly relative to light transmittance (Lieffers & Stadt 1994). Another species negatively correlated with canopy cover, *Aster conspicuus*, is more of a generalist, and has been found in other studies to occur more commonly at edges (Harper & Macdonald 2002), with increasing canopy removal (Craig & Macdonald 2009), or as an indicator of pre-disturbance forest (Bradbury 2004). The final species that showed increasing abundance with decreasing canopy cover (*Viburnum edule*) is a shrub characteristic of the boreal forest. *V. edule* has been described as a forest generalist, characteristic of mature broadleaf and mixedwood boreal forest (Macdonald & Feeniak 2007; Bradbury 2004; Harper & Macdonald 2002), while also being able to persist in high abundance in canopy gaps (Chávez & Macdonald 2010) and in lower abundance in dispersed retention harvest (Macdonald & Feeniak 2007). In general, increased cover of shrubs is expected in higher light conditions, as they are better able to compete for light using their height advantage (Chávez & Macdonald 2010; Constabel & Lieffers 1996).

While lower canopy covers were found to cause changes in the understory composition, it wasn't entirely as hypothesized. Against expectations, I did not find any associations between

high canopy covers and forest-dependent species but did find associations between low canopy covers and shade intolerant species, although this was not linked to measures of tree mortality as predicted. Canopy cover explained very little of the compositional variance, indicating that overstory cover was relatively unimportant in determining community assemblages, probably because the canopies in deciduous boreal forest are not particularly oppressive (Constabel & Lieffers 1996), and understory species in the boreal are resilient to disturbance, and are generally able to persist in slightly unfavorable conditions (Harper & Macdonald 2002; Aubin et al. 2014).

#### **4.8 Influence of overstory structure on microclimate**

Overall, I found little correlation between the average maximum daily soil and air temperatures with forest structure. Both microclimatic measurements had orthogonal relationships to measures of canopy mortality such as recent deadwood and deadwood ratios, as well as measures of canopy intactness such as canopy cover and tree basal area. I did not detect any relationship between the proportion of coniferous to deciduous basal area, a factor which had been identified as a potential influence on microclimate (Macdonald and Fenniak 2007). Our results are somewhat surprising at first glance, given the well-studied associations between overstory structure and microclimate (Chen et al. 1999; Heithecker & Halpern 2006). At second glance, there are a number of possible reasons for the lack of associations between overstory structure and microclimatic temperatures. First, mature boreal broadleaf deciduous forests in Alberta do not form particularly continuous or oppressive canopies. Constabel & Lieffers (1996) found an average light transmittance of 32% below the canopy at 1.3 meters, compared to 13% in mixed aspen/spruce stands. Similarly, Lieffers & Stadt (1993) found light transmittance levels of up to 40% at 1.3 meters in pure aspen stands compared to a maximum of 10% in spruce

dominated stands. For perspective, light transmittance in American eastern hardwood forests was measured to be between 1-4% (Brown & Parker 1994). Second, the tree mortality recorded in this study was low, as on average less than 10% of the total stand basal area and volume was recently dead trees. Because of the porous, structurally heterogenous canopy (Chen et al. 1999) and the low solar angle at the latitude of the study area (Harper et al. 2002; Lieffers et al. 1999) it is unlikely that the small amounts of tree mortality recorded in our plots significantly increased the amount of incoming solar radiation, the main driver of microclimatic temperatures in forests (Chen et al. 1999). Further, because my study recorded surface air temperature underneath the understory layer, even if tree mortality leads to increased light penetration, compensatory growth in the understory layer will reduce light penetration despite overstory mortality. Heithecker & Halpern (2006) found canopy cover could explain much of the variation in air temperature measured above the understory, while it could explain little of the variation in soil temperature. They attributed this discrepancy to understory and slash cover, which mediate soil temperatures alongside canopy cover (Heithecker & Halpern 2006).

## **4.9 Trait analysis**

### **4.9.1 Plot locations by disturbance type**

Trait analyses of all plot locations separated by disturbance type revealed trait syndromes favoring colonization in disturbed plots of both disturbance types. Abundant production of light seeds is indicative of fast-growing shade intolerant plants with high dispersal ability, allowing them to colonize disturbed areas (Aubin et al. 2014; Halpern 1989; Weiher et al. 1999; Westoby 1998). The presence of graminoid leaf structure indicates an abundance of graminoids, mostly *Calamagrostis canadensis*, a grass which produces many light seeds and is particularly suited to

post-disturbance conditions in the boreal forest (Lieffers et al. 1993). Conversely, there were traits associated to plant persistence in the forested plots of both disturbance types: Low production of large seeds (Weiher et al. 1999; Westoby 1998). These traits are correlated most consistently with the reference interiors, and significant correlations with seed weight was found in island interiors. In general, Specific Leaf Area (SLA) is seen as a measure of resource use (Aubin et al. 2009; Aubin et al. 2014; Weiher et al. 1999; Westoby 1998). Plants in resource rich environments are expected to allocate large proportions of energy to their leaves to stay competitive, generally resulting in larger, short-lived leaves with high SLA. Conversely, plants under stress (such as under a canopy) generally allocate less energy to their leaves, resulting in longer lasting smaller leaves (Weiher et al. 1999; Westoby 1998). While the increase of nutrient and light availability following a disturbance is expected to increase abundances of plants with high SLA in disturbed plots, this was not the case. Instead, fire disturbed plots were negatively correlated to SLA, reflecting the dominance of ericaceous shrubs in the disturbed plots, which have thick, slow-growing leaves with higher SLA. The high SLA values in the forest are likely a reflection of the light and nutrient conditions within the forest stands, as deciduous dominated stands are not particularly limited by either light (Constabel & Lieffers 1996) nor nutrients (Hart & Chen 2006; Johnstone et al. 2010), allowing higher SLA plants to thrive.

#### **4.9.2 Forested plot locations by disturbance type**

A trait analysis of the forested plots conforms to the results of the taxonomic analysis which did not find any significant differences between forested plot locations of each disturbance type. I found significant associations between plants that rely primarily on vegetative means of reproduction with living tree basal area and canopy cover within forested harvest plots. As

canopy cover increases, decreasing light availability to the understory, plants that prefer vegetative reproduction have a competitive advantage over those that prefer seeds, as they don't need to invest energy into reproductive structures such as flowers/fruit to maintain themselves (Lieffers et al. 1993; Hart & Chen 2006).

#### **4.9.3 Disturbed plot locations by disturbance type**

Significant fire-disturbed plot trait correlations were found with organic layer thickness and ground litter cover, though there were no spatial patterns in trait distributions in the edge versus interior of fire-disturbed plots. There was evidence of persistence trait syndromes correlated with organic layer thickness, with which chamaephytes (mostly *Ledum groenlandicum*), were positively correlated with thick organic layers, while hemicryptophytes (various graminoids and forbs) were correlated with the high litter sites. Chamaephytes are slow growing and sensitive to disturbance and were previously found to be most abundant in mature forest and decrease in response to disturbance (Aubin et al. 2007; Patry et al. 2017). The thick evergreen leaves of *L. groenlandicum* have low SLA and contribute to lower litter cover, explaining the negative correlation of chamaephytes to litter cover. The relatively fast-growing, short-lived leaves of grasses and forbs have relatively high SLA by comparison. Other traits correlated with thick organic layers, low seed weight and erect leafy stem foliage structures are all indicative of *L. groenlandicum*.

Fire plots with thick organic layers were located in the M024 fire and to a lesser extent the Utikuma fire, which occurred within wetter, nutrient-poor, conifer-dominated ecosystems with interspersed aspen stands. Plots with thick organic layers of these plots facilitated persistence of pre-disturbance functional communities characterized by chamaephytes with low SLA and seed

production. The organic layer provides refuges to shoots and roots of the chamaephytes, allowing them to resprout in-situ, and denied colonizing plants favorable microsites on which to germinate (Johnstone et al. 2010).

Much like fire, significant trait correlations in harvest-disturbed plots were found with organic layer thickness and ground litter cover, but also with sapling density. Litter cover was correlated with colonizer traits, indicators of *Calamagrostis canadensis*, by far the most dominant grass in harvest plots. Similar to fire plots, there was a correlation between organic layer thickness and geophytes, another Raunkiaer growth form that decreases with increasing intensity of disturbance (Aubin et al. 2007; Patry et al. 2017). Traits correlated with sapling densities were reminiscent of those found in forested plots: Lower seed production and higher seed weights, marginally significant positive and negative correlations with SLA and graminoid leaf structure respectively. Within harvests, the presence of thicker organic layers could be an indicator of lower soil disturbance (Harvey & Brais 2002), and the correlation with geophytes, who are especially sensitive to soil disturbance (Patry et al. 2017), is a further sign of undisturbed soil.

Harvested plots with high litter covers exhibited colonizer trait syndromes, and were likely dominated by *C. canadensis*, a fast-growing grass which produces a thick thatch over time, reducing the growth and establishment of tree seedlings (Hogg & Lieffers 1991; Landhäusser & Lieffers 1998; Lieffers et al. 1993; Royo & Carson 2006). The rapid dominance of grass likely occurred shortly after canopy removal (within ~3 years) occupying most of the available microsites (Lieffers et al. 1993). Eventually, grasses are outcompeted by shrubs or saplings (Lieffers et al. 1993), but the dominance of saplings was possibly delayed at these plots by either

a suppression of suckering by retained trees (David et al. 2001; Prévost & Pothier 2003), or higher site moisture which is favorable for *C. canadensis* (Lieffers et al. 1993), but not aspen (Echiverri & Macdonald 2020; Nijland et al. 2015).

Within harvested plots I also found evidence of functional communities with trait syndromes more focused on persistence than colonization. These functional communities arose in plots with thicker organic layers and/or with high densities of saplings. Plots with this functional group likely did not experience severe soil disturbance, allowing much of the pre-disturbance community to persist. The forest-like microclimate mediated by sapling densities would lower light availability to the forest floor, preventing a takeover by shade intolerant grass. Light transmittance levels in young aspen stands (10-20 years old) measured by Constabel & Lieffers (1996) found only 12% of light was transmitted to 0.5 meters, below the 15% of light Lieffers & Stadt (1994) determined was required for the survival of *C. canadensis*. Furthermore, Echiverri & Macdonald (2020) found increased understory community resilience to disturbance in harvested plots with high densities of aspen regeneration 15 years after harvest.

The taxonomic analysis of understory composition was similar to the trait analysis: *L. groenlandicum*, a chamaephyte prevalent in peatlands and *Rubus ideaus*, a hemicryptophyte associated with mineral soil were abundant in post-fire plots. *C. canadensis* was strongly associated with harvest plots, while *Equisetum sylvaticum*, and *Epilobium angustifolium*, both geophytes, were also found abundantly in harvests. Within ordinations, there appears to be a convergence of the understory community in certain harvested plots with the composition of unharvested plots, which didn't materialize as strongly in fire-disturbed plots. This matches the correlation of persistence trait syndromes with sapling density found in disturbed harvest plots.

It is unclear why fire plots did not display as strong of a convergence, but lower sapling densities in fire plots may explain the discrepancy. Alternatively, I would posit that differences in site characteristics and thus pre-disturbance plant community between remnants and disturbed fire plots could also explain the lack of convergence in understory composition.

#### **4.10 Temporal scales of change**

Throughout this study, all the response variables (understory composition, forest structure, and microclimate) are studied at only one point in time, approximately a decade following disturbance. It is important to note that all of these variables are not static, but rather change throughout time and at different temporal scales. Understory composition at the edge, for example, has been found to exhibit a “lag effect”, where changes do not occur immediately, but rather after primary processes such as tree mortality occur (Harper et al. 2005). While the time scale of a decade after disturbance was partially chosen to account for the lag effect, the lack of significant differences in understory composition at the edge vs interior could be due to sampling before edge effects had the time to develop. The same factor could explain some of the non-significant differences in microclimatic temperatures- the contrast between disturbed and forested plots would likely be greater immediately following disturbance and be ameliorated with increasing revegetation.

## **5 Conclusions**

Overall, while fire and harvest remnants did not contain similar understory compositions, remnants of both disturbance types had understory richness, diversity, cover, and composition similar to that of nearby reference forest. Microclimatic temperatures in remnants were similar



to reference forest and appeared to be ameliorated by increased regeneration of saplings within the disturbance. I did not detect differences in understory composition or microclimate at the edges versus the interiors of remnants. I did find increases in abundance of certain species with decreasing canopy cover, but it explained little variation. Likewise, tree mortality in remnants was not a significant cause of microclimatic warming or vegetation community change. Trait analyses were able to uncover evidence of persistent vegetation within remnants and found colonization traits within the disturbance. Occurrence of traits associated with plant persistence within the disturbed matrix increased with increasing sapling density and depth of the soil organic layer.

## **5.1 Limitations**

It must be acknowledged that there are limitations to this study in addition to those mentioned throughout the discussion. The selection of remnants is inherently biased towards remnants that have persisted over the years and may not accurately reflect all remnants which were present on the landscape immediately following disturbance.

Despite being able to sample 3 regions of each disturbance type, I was only able to get between 3-6 replicates at each location. Increasing the number of replicates in each region would increase the statistical power of my analyses, perhaps reducing the high variability in some of my response variables.

Furthermore, Dissimilarity-based analyses can overlook small and rare species such as orchids and myco-heterotrophs that may be especially sensitive to edge influence. The specific associations with fungi and/or plant roots make these species especially sensitive to disturbance,

and assessing if island remnants are effective at maintaining such species is of particular ecological concern (Haeussler et al. 2002)

Due to the placement of vegetation edge subplots ~10 meters away from the actual edge, I was unable to characterize edge influence at the actual edge itself. Second, because the subplots at the centre of reference interior plots are positioned ~30 meters from the edge, they were likely still experiencing edge influence and are thus not representing true interior forest (Harper et al. 2005), although edge influence is generally lower within the boreal mixedwood forest (Harper et al. 2015).

Within analyses of microclimate, this study does not control for edge aspect, analyze daily temporal patterns, or measure remnant tree heights all of which were previously identified as factors for determining edge and/or forest influence on microclimate (Baker et al. 2016; Chen et al. 1995; Chen et al. 1999; Heithecker & Halpern 2007). Placing plots 10 and 20 meters from edges was likely too coarse of a scale to measure microclimatic gradients, potentially missing finer scale variation in edge influence. Increasing the number of sites in each region would have been helpful to be able to analyze microclimates separately by region as done by Heithecker & Halpern (2007) who researched remnant microclimates in the DEMO project (Aubry & Halpern 2020). This reduces confounding variables including topographical and regional climatic differences in the analysis.

## **5.2 Management implications**

As it stands, current aggregate retention patches in deciduous-dominated boreal mixedwood forest are effective at conserving the understory plant community of mature forest a decade after disturbance, with the caveat that low statistical power in the experiment increases the

possibility of committing a type II error. While it was difficult to make direct comparisons between remnants of different disturbance types due to the natural variability in the boreal forest that is difficult to control for in an observational study, fire remnants preserved similar understory communities to reference forest as well.

Overall, successful microclimate amelioration in remnants appeared to be aided by successful regeneration of saplings in the cutblock matrix, and understory plant persistence is enhanced with increasing sapling densities and decreasing soil disturbance. Most boreal plants have traits that allow for persistence following disturbance, allowing them to persist in reduced abundance until conditions return to favorable (Aubin et al. 2014). A dense sapling layer will also sharply decrease light availability, preventing the development of a recalcitrant layer of *Calamagrostis canadensis* (Lieffers et al. 1993; Royo & Carson 2006). To promote plant persistence and microclimate amelioration, silvicultural practices in deciduous-dominated boreal forest should focus on ensuring dense sapling regeneration in the cutblock.

It is important to note that these findings are applicable to deciduous dominated and mixedwood boreal forest and may not reflect conditions in stands dominated by different tree species in the boreal or within other biomes. Because of the disturbance prone nature of this forest type, most understory species are less sensitive to the effects of canopy removal and edge influence compared to species from other stand types and biomes with plants less adapted to severe disturbance.

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## **Appendix A**

### **A1 Site selection**

The goal of our site selection was to identify a network of 15 post-fire remnants, 15 post-harvest remnants and associate each with a mature reference forest. In this study a remnant is defined as a group of any size composed of mature, living trees that is completely surrounded by a clearcut or high severity fire, and no closer than 50 meters to other living trees. A reference is a forest that borders a similar disturbance type as the associated remnant and is at least 100 meters by 100 meters in size. To broaden our scope of inference, we decided to sample at least three fires and pair each fire with a nearby harvest for blocking. We set the following baseline parameters for our remnants and references:

- > 60% deciduous canopy cover
- Stands had similar age of origin
- Disturbances occurred between (2009-2012), based on the time period aggregate retention started becoming common enough to provide ample study locations

We started with identifying candidate fires within the target range of calendar years, assuming that they would be more challenging to identify than harvested areas.

#### **A1.1 Fire site selection**

We first accessed provincial historical wildfire perimeter data (Alberta Agriculture and Forestry, 2021b) to identify wildfires that matched the following criteria:

- Burned between 2009-2012
- Were class “E” fires (i.e., burned area >200 ha)

- Were located in the Boreal Forest natural region of Alberta (Natural regions Committee 2006)
- Significant portion of the burned area was located in mixedwood forest
- Significant portion of the burned area was not salvage logged

This search returned 94 candidate fires, which were then further filtered by a second set of criteria:

- Large enough burn area to support a large number of remnants (burned area ~ >5000 ha)
- No more than one kilometer from a road

This filter returned 6 candidate fires, within which we identified remnants. Post-fire remnants were identified using a combination of existing wildfire perimeter data (Alberta Agriculture and Forestry, 2021b), a differentiated Normalized Burn Ratio layer (dNBR) (Hermosilla et al., 2016), and the ESRI basemap, with imagery from 2019 sourced from Maxar Technologies Inc., which provides a resolution of 5m within our study areas (ESRI, 2009). Once found, the boundaries of a remnant were easily discernable, and digitized using satellite imagery, given a unique identifier and its area was measured. A polygon centroid was used to extract coordinates for each remnant and the forest composition of the remnant was determined using Alberta Vegetation Inventory (AVI) data from our partners.

## **A1.2 Harvest site selection**

To locate post-harvest retention patches we used polygons provided by forest industry partners supporting the NSERC IRC in Ecosystem-based Forest Management and selected cutblocks

harvested between 2009-2012 that had in-block patch retention. Because forest operations over a couple years often consist of multiple cutblocks in relatively close proximity to one another, our potential harvest sites were clustered into regions harvested within the same year much like our potential fire plots were clustered within a fire.

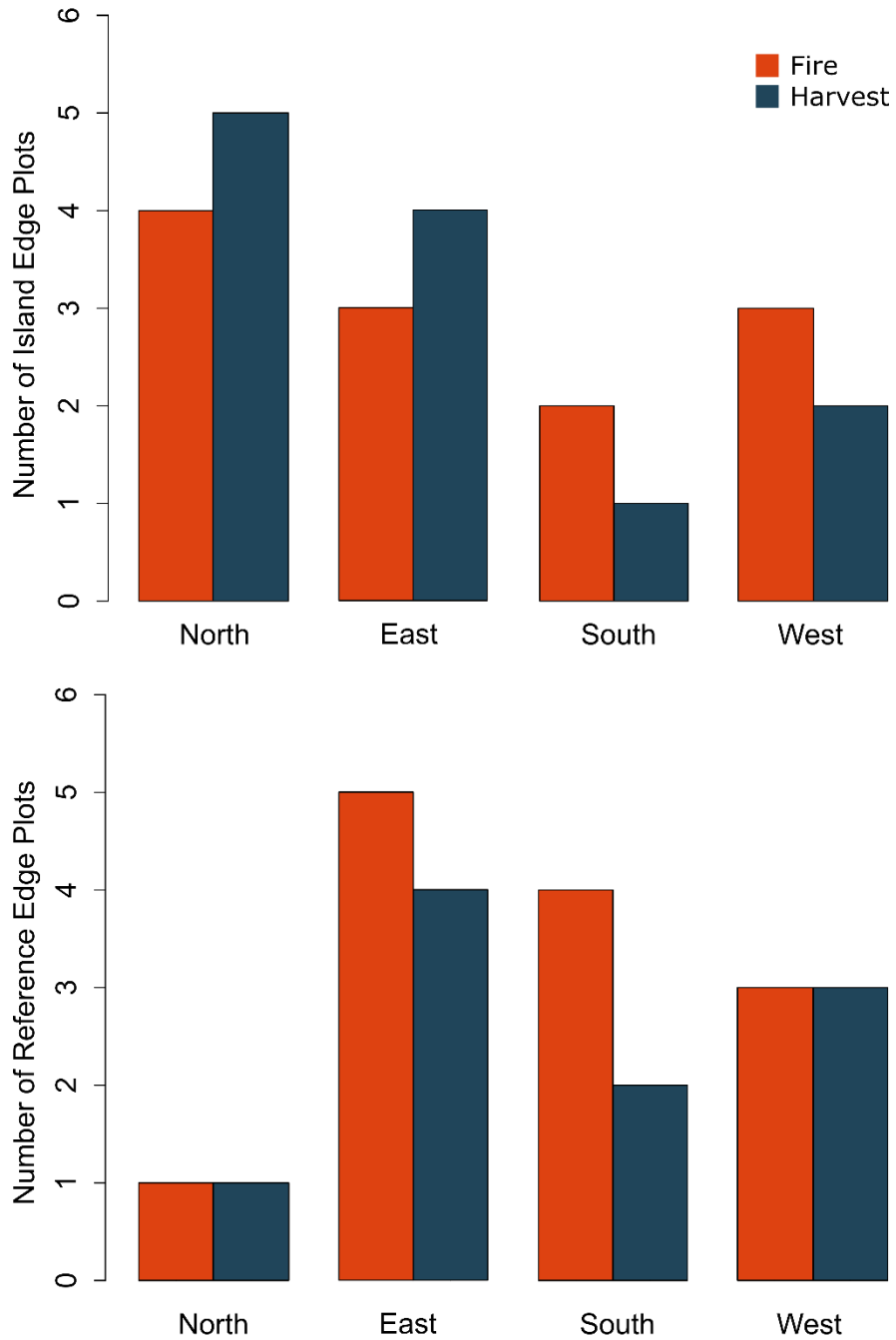
### **A1.3 Remnant selection**

After identifying a pool of possible fire and harvest remnants, we filtered the candidates by the following criteria:

- 60% or more deciduous dominated (trembling aspen, balsam poplar, birch)
- 0.5-2.5 hectares in size (determined by looking at the overall size distribution of remnants, and selecting a size range abundant in both fire and harvest remnants)

From this pool we visited potential study areas in May 2021, prioritizing fire and harvest regions with road access and larger numbers of suitable remnants. During scouting we ensured the forest composition was >60% deciduous, rejecting those that were too conifer dominated. During scouting, we paired each remnant with a nearby continuous forest bordering the same disturbance with a similar composition as the paired remnant; these areas served as a reference. These references had to be continuous forest where an interior plot could be placed over 100 meters from the nearest edge (not including the edge being studied) and were identified with the use of vegetation inventory data, satellite imagery, and ground scouting.





**Appendix A-1.** Edge aspect of A) sampled island plots and B) sampled reference plots by disturbance type. The azimuth was calculated in degrees and categorized using the following criteria: East (45-135°); North (45-315°); South (135-225°); West (225-315°)

## Appendix B

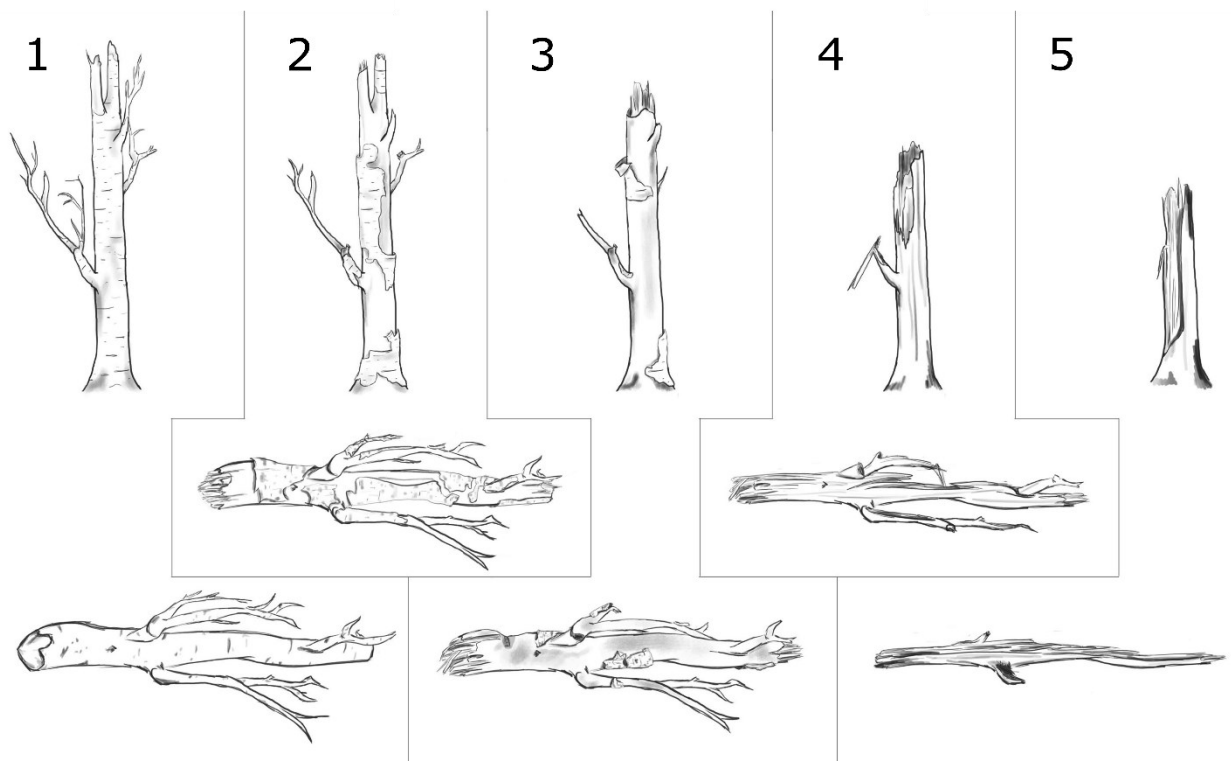
**Appendix B-1.** Species found in sampling subplots and the corresponding species code. Nomenclature follows Moss (1983).

Abbreviation	Latin Binomial	Abbreviation	Latin Binomial
ABISPP	<i>Abies spp.</i>	GALTRI	<i>Galium triflorum</i>
ACHMIL	<i>Achillea millefolium</i>	GALTRIFIDUM	<i>Galium trifidum</i>
ACHSIB	<i>Achillea sibirica</i>	GEOLIV	<i>Geocaulon lividum</i>
ACTRUB	<i>Actaea rubra</i>	GEUALE	<i>Geum aleppicum</i>
ADOMOS	<i>Adoxa moschatellina</i>	GYMDRY	<i>Gymnocarpium dryopteris</i>
AGRREP	<i>Agropyron repens</i>	HABOBT	<i>Habenaria obtusata</i>
AGRSCA	<i>Agrostis scabra</i>	HERLAN	<i>Heracleum lanatum</i>
ALNCRI	<i>Alnus crispa</i>	HIEUMB	<i>Hieracium umbellatum</i>
AMEALN	<i>Amelachier alnifolia</i>	LABISPP	<i>Labiata spp.</i>
ARANUD	<i>Aralia nudicaulis</i>	LATOCH	<i>Lathyrus ochroleucus</i>
ARNCHA	<i>Arnica chamissonis</i>	LATSPP	<i>Lathyrus spp.</i>
ASTAME	<i>Astragalus americanus</i>	LEDGRO	<i>Ledum groenlandicum</i>
ASTCIL	<i>Aster ciliolatus</i>	LILISPP	<i>Lilium spp.</i>
ASTCON	<i>Aster conspicuus</i>	LINBOR	<i>Linnaea borealis</i>
ASTPUN	<i>Aster puniceus</i>	LISBOR	<i>Listera borealis</i>
ASTSPP	<i>Aster spp</i>	LONCAE	<i>Lonicera caerulea</i>
ATHFIL	<i>Athyrium filix-femina</i>	LONDIO	<i>Lonicera dioica</i>
BETPUM	<i>Betula pumilla</i>	LONINV	<i>Lonicera involucrata</i>
BETSPP	<i>Betula spp.</i>	LYCANN	<i>Lycopodium annotinum</i>
BROMCIL	<i>Bromus ciliatus</i>	LYCCOM	<i>Lycopodium complanatum</i>
CALCAN	<i>Calamagrostis canadensis</i>	LYCOBS	<i>Lycopodium obscurum</i>
CERNUT	<i>Cerastium nutans</i>	MAICAN	<i>Maianthemum canadense</i>
CIRALP	<i>Circaea alpina</i>	MALMON	<i>Malaxis monophylla</i>
CIRARV	<i>Cirsium arvense</i>	MATSTR	<i>Matteuccia struthiopteris</i>
COPTRI	<i>Coptis trifolia</i>	MERPAN	<i>Mertensia paniculata</i>
CORCAN	<i>Cornus canadensis</i>	MITNUD	<i>Mitella nuda</i>
CORCOR	<i>Corylus cornuta</i>	MOELAT	<i>Moehringia lateriflora</i>
CORSTO	<i>Cornus stolonifera</i>	ORCHSPP	<i>Orchid spp.</i>
CORTRI	<i>Corallorhiza trifida</i>	ORTSEC	<i>Orthilia secunda</i>
ELYINN	<i>Elymus innovatus</i>	ORYASP	<i>Oryzopsis asperifolia</i>
EMPNIG	<i>Empetrum nigrum</i>	OSMDEP	<i>Osmorhiza depauperata</i>
EPIANG	<i>Epilobium angustifolium</i>	OXYMIC	<i>Oxycoccus microcarpus</i>
EPIGLA	<i>Epilobium ciliatum</i>	PEDSPP	<i>Pedicularis spp.</i>
EQUARV	<i>Equisetum arvense</i>	PETPAL	<i>Petasites palmatus</i>
EQUPra	<i>Equisetum pratense</i>	PETSAG	<i>Petaites sagittatus</i>
EQUSCI	<i>Equisetum scirpoides</i>	PICSPP	<i>Picea spp.</i>
EQU SYL	<i>Equisetum sylvaticum</i>	PINSPP	<i>Pinus spp.</i>

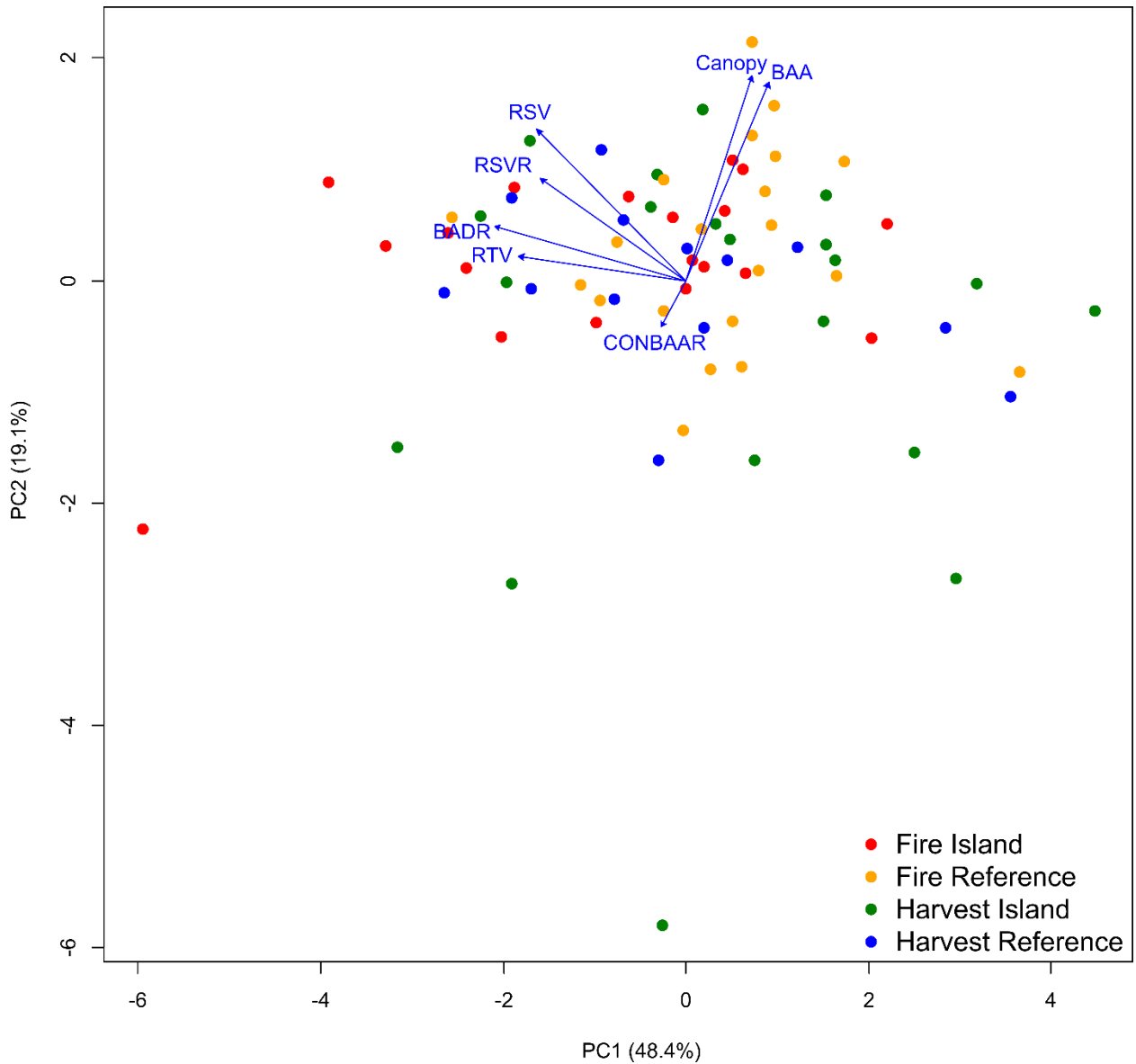
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FRAVES	<i>Fragaria vesca</i>	POAPAL	<i>Poa palustris</i>
FRAVIR	<i>Fragaria virginiana</i>	POAPRA	<i>Poa pratensis</i>
GALBOR	<i>Galium boreale</i>	POPSPP	<i>Populus spp.</i>
GALTET	<i>Galeopsis tetrahit</i>	PYRASA	<i>Pyrola asarifolia</i>
RIBAME	<i>Ribes americanum</i>	SORSCO	<i>Sorbus scopulina</i>
RIBGLA	<i>Ribes glandulosum</i>	STECRA	<i>Stellaria crassifolia</i>
RIBHUD	<i>Ribes hudsonianum</i>	STRAMB	<i>Streptopus amplexifolius</i>
RIBLAC	<i>Ribes lacustre</i>	SYMALB	<i>Symphoricarpos albus</i>
RIBOXY	<i>Ribes oxycanthoides</i>	TAROFF	<i>Taraxacum officianale</i>
RIBTRI	<i>Ribes triste</i>	THAVEN	<i>Thalictrum venulosum</i>
ROSACI	<i>Rosa acicularis</i>	TRIBOR	<i>Trientalis borealis</i>
RUBART	<i>Rubus articus</i>	TRIHYP	<i>Trifolium hybridum</i>
RUBCHA	<i>Rubus chamaemorus</i>	UNK GRASS	<i>Unknown grass</i>
RUBIDA	<i>Rubus ideaus</i>	UNK HERB	<i>Unknown herb</i>
RUBPUB	<i>Rubus pubescens</i>	URTDIO	<i>Urtica dioica</i>
SALSPP	<i>Salix spp.</i>	VACMYR	<i>Vaccinium myrtilloides</i>
SCHPUR	<i>Schizachne purpurascens</i>	VACVIT	<i>Vaccinium vitis-idea</i>
SHECAN	<i>Shepherdia canadensis</i>	VIBEDU	<i>Viburnum edule</i>
SMISTE	<i>Smilicina stellata</i>	VICAME	<i>Vicia americana</i>
SMITRI	<i>Smilacina trifolia</i>	VIOCAN	<i>Viola canadensis</i>
SOLCAN	<i>Solidago canadensis</i>	VIOREN	<i>Viola renifolia</i>
SOLSPP	<i>Solidago spp.</i>		

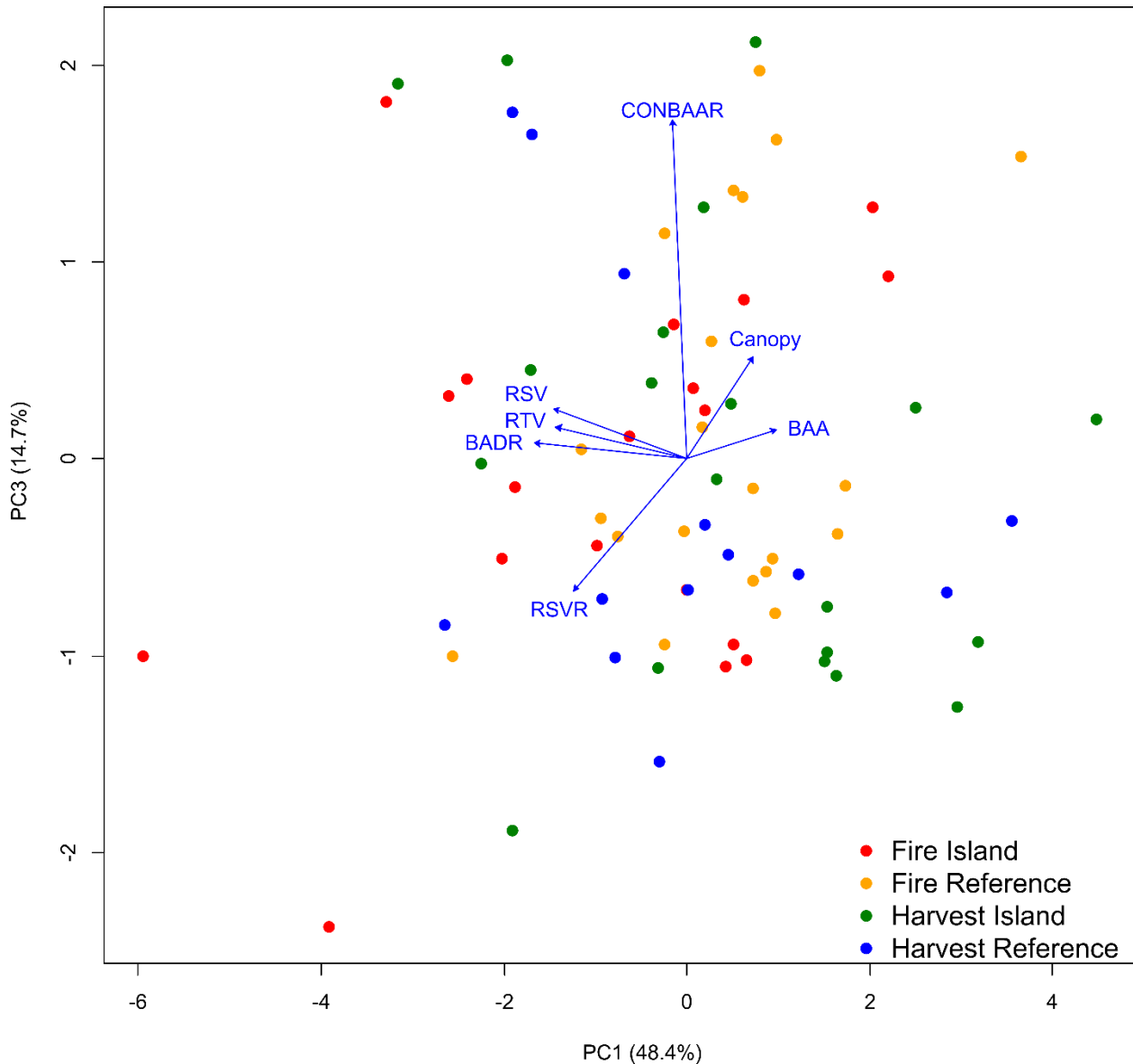
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**Appendix B-2.** Illustration of decay classification for snags and coarse woody debris. See Moore (2022) for details on coarse woody debris decay classification, and Odell (2022) for details on snag decay classification. Decay classes 1 & 2 are considered recent tree mortality (estimated to have died ~ 10 years before sampling). Illustration by Lana Mrochuk.



**Appendix B-3.** Principal components 1 & 2 of a principal component analysis on forest structural variables, represented by blue vectors. Each point represents a plot – with the location in ordination space reflecting the forest structural measurements. refer to Table 2.4 for descriptions of structural variables.



**Appendix B-4.** Principal components 1 & 3 of a principal component analysis on forest structural variables, represented by blue vectors. Each point represents a plot – with the location in ordination space reflecting the forest structural measurements. refer to Table 2.4 for descriptions of structural variables.

**Appendix B-5.** Frequency of occurrence (%) of the 20 most abundant species found in the experiment, separated by disturbance type and plot location. Species codes are explained in Appendix B-1.

	Fire						Harvest					
	DE	DI	IE	II	RE	RI	DE	DI	IE	II	RE	RI
<i>ALNCRI</i>	8	8	8	17	23	0	17	17	25	17	20	10
<i>ARANUD</i>	23	0	50	42	54	54	50	25	50	58	50	70
<i>CALCAN</i>	62	54	25	33	38	23	83	58	50	42	90	40
<i>CHAANG</i>	54	62	33	33	23	38	58	50	33	33	50	30
<i>CORCAN</i>	62	62	92	83	85	85	58	58	100	92	100	100
<i>EQUSYL</i>	85	77	42	8	31	31	42	50	42	25	50	40
<i>LEDGRO</i>	31	38	17	17	0	15	8	8	8	8	20	10
<i>LINBOR</i>	31	8	58	58	46	62	42	33	92	92	70	70
<i>LONINV</i>	15	8	8	17	23	8	17	8	17	17	20	30
<i>LYCANN</i>	0	0	33	50	23	23	25	8	17	17	10	10
<i>MITNUD</i>	31	8	75	50	77	92	42	58	83	58	90	90
<i>PETPAL</i>	38	38	42	58	31	46	58	50	67	33	60	80
<i>RIBTRI</i>	8	15	0	50	62	31	75	50	33	67	70	70
<i>ROSACI</i>	62	54	58	58	69	69	75	67	92	83	80	90
<i>RUBPUB</i>	38	15	58	58	54	77	83	75	83	83	80	100
<i>RUBIDA</i>	69	77	8	0	15	0	42	50	0	25	20	20
<i>SALSPP</i>	23	46	17	17	15	0	50	25	0	8	20	0
<i>SHECAN</i>	8	0	17	17	23	15	25	25	33	33	30	20
<i>VACMYR</i>	31	15	33	33	23	15	8	8	17	17	10	20
<i>VIBEDU</i>	38	8	42	58	69	54	50	58	75	67	70	80