A Comparison of Residual Tree Mortality in Forest Island Remnants Following Wildfire and Harvest

by

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Abstract

As forested ecosystems are put under compounding stresses due to the effects of climate change and demand for resources, forest managers must develop innovative ways to utilize natural resources in less-impactful ways. In the boreal forests of Alberta, Ecosystem Based Forest Management (EBFM) is implemented is through emulation of natural disturbances such as wildfire using retention forestry to leave behind patches of intact forest during a harvest, called island remnants. Previous studies have compared residual tree mortality in dispersed retention or partial harvest to reference forests and clearcuts, but not against island remnants created by wildfires. The objectives of this study were the following: 1) examine the effects of disturbance type (fire and harvest) on post-disturbance tree mortality amounts in island remnants compared to reference forest; 2) determine if plots on forest edges experience higher post-disturbance mortality than plots located in the interior of these forests; 3) examine if certain tree species experience higher post-disturbance mortality rates and if this has any relation to disturbance type, island/reference plot or edge effects; 4) determine if tree size predicts mortality rates, and 5) assess if there are any temporal patterns of post-disturbance tree mortality following wildfire and harvest. Post-disturbance tree mortality was calculated by conducting stem surveys of each plot and tree cores were collected from standing snags for dendrochronological analysis. We determined the year of death for snags to determine if EBFM-created island remnants are functioning similarly to wildfire-created island remnants with respect to tree survival. Harvest created island remnants did not exhibit higher residual tree mortality than reference forest or similar sized fire island remnants, however edges of fire islands had higher mortality than fire reference edges. Aspen had overall higher mortality throughout the study area than spruce, and smaller sized trees also had a higher probability of mortality. These results support the continued implementation of retention forestry

using island remnants within the scope of EBFM in Alberta and may aid in promoting forest recovery and resilience following disturbances.

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The University of Alberta is located in Amiskwaciwâskahikan (Edmonton), the traditional lands of the Cree, Blackfoot, Métis, Nakota Sioux, Iriquois, Dene and Ojibway/Saulteaux/Anishinaabe nations; lands that are now part of Treaty 6 and 7 as well as the homeland of the Métis. I am grateful to have conducted field work for this research on the traditional lands of the Cree and Metis, situated in Treaties 6 and 7. These areas are traditional and contemporary lands of a variety of First Nations groups and the Métis people.

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CHAPTER 1: INTRODUCTION

Boreal forest

Spreading over 14 million km² in extent, the boreal forest accounts for one third of global forested area, making it one of the largest forest ecosystems on the planet (Burton et al., 2006; Perera and Buse, 2014). Thirty percent of the boreal forest is in Canada, which covers around 58% of the country's total land area (Burton et al., 2006). A substantial portion of the boreal forest in Canada is of mixedwood composition, a combination of broadleaf and coniferous trees with the structure and proportions of species varying across climatic and disturbance gradients (Bergeron et al., 2014). Broadleaf tree species include trembling aspen (*Populus tremuloides* Michx.) or balsam poplar (*Populus balsamifera* L.) in the West and paper birch (*Betula papifera* Marsh.) in the East; coniferous species are white spruce (*Picea glauca* (Moench.) Voss) or black spruce (*Picea mariana* (Mill.) Britton) in the West and often balsam fir (*Abies balsamea* [L.] Mill.) in the East (Bergeron et al., 2014).

Due to its size, the boreal forest contains one of the largest pools of carbon on Earth, making it a key biome in regulating the global carbon budget (Perera and Buse, 2014), as well as providing important economic, ecological and cultural goods and services (Brandt et al., 2013; Hassan et al., 2005). Boreal forests play a significant role in carbon storage and sequestration; additionally they help regulate regional climate through energy and water exchange, (Gauthier et al., 2015) are economically important for pulp and paper production, ecologically important as habitat and culturally significant to Indigenous groups (Perera and Buse, 2014). With increasing demand for natural resources, climate change ushering in warmer temperatures and drier conditions to the Northern Hemisphere (Hansen et al., 1996; Kasischke and Stocks, 2000), and an increase in frequency and severity of disturbances, specifically wildfires (Kasischke, 2000; Smith

et al., 1992), boreal forests are faced with increasing pressures and challenges to tree survival. An increase in fire frequency and severity will result in elevated tree mortality (Aakala et al., 2009) straining the resilience of this forest ecosystem.

Wildfire

Wildfires are a significant stand-replacing disturbance in both frequency and amount of area disturbed in Canadian forests (Weber and Flannigan, 1997). Boreal forests are susceptible to stand-replacing wildfire as a primary disturbance type due to long sunlight hours in the summer, low relative humidity levels, frequency of lightning storms, wax coated needles of coniferous trees and the duff layer of needles on the forest floor (Goldammer and Furyaev, 1996; Groeschl et al., 1992). Wildfires are often ignited in early spring by lightning or anthropogenic causes (Rowe and Scotter, 1973). Wildfire regimes in the Western boreal forests of Canada vary spatially due to natural regions and subregions, and prior to fire suppression a mosaic of varying-aged forest patches covered the landscape due to mixed-severity fire regimes (Rogeau et al., 2016). Spruce-dominated forests generally experience high-intensity crown fires that occur roughly every 100 years, whereas mixedwood forests experience an even lower frequency of fires (Perera and Buse, 2014). The majority of total area burned by wildfires occurs from a few high-severity and large-scale wildfires, rather than a high number of smaller fires (Kasischke, 2000; Perera and Buse, 2014). Wildfires are important as they influence forest age structure, species composition, landscape-scale diversity, and additional ecological processes (Goldammer and Furyaev, 1996; Perera and Buse, 2014). However, high severity wildfires cause significant tree mortality in boreal forests across the globe which contributes to over 180 Mt of carbon emissions each year (van der Werf et al., 2010).

Although wildfires cause substantial tree mortality events, they burn unevenly across landscapes and leave behind intact structural features including standing and fallen dead wood, multiple canopy layers, living trees, varied stem sizes and canopy gaps that contribute to forest regeneration (Kohm and Franklin, 1997a). Due to this spatial heterogeneity in fire behavior, wildfire residuals or island remnants are formed of intact forest, preserving pre-disturbance structures (Perera and Buse, 2014). The formation of island remnants is influenced by fire severity, topography, soil moisture, weather, vegetation and fuel loads and connectivity (Perera and Buse, 2014; Rowe and Scotter, 1973). In the boreal forest, island remnants of live trees and intact forest structure can comprise anywhere from three to 37 percent of total burned area (Eberhart and Woodard, 1987; Smyth et al., 2005). These island remnants are considered crucial to help forests recover from wildfires (Moussaoui et al., 2016). Live trees in disturbed landscapes provide seeds, help reduce soil erosion and preserve genetic diversity to aid in regeneration following disturbances (Dragotescu and Kneeshaw, 2012; Kohm and Franklin, 1997a; Perera and Buse, 2014). Remnants preserve old growth structures which provide habitat and refuge for wildlife and act as a lifeboat to connect landscapes across a disturbed area, foster biodiversity and promote forest recovery (Franklin et al., 1987; Moussaoui et al., 2016).

Harvest

Forests provide economic benefits to humans, including wood and related products from harvesting trees (Perera and Buse, 2014). In Canada, the forest sector accounts for over three-hundred thousand jobs and over seventy-two billion dollars in annual revenue (Statistics Canada 2021; NRCAN 2022). However, harvesting trees using traditional commercial techniques (i.e., clearcutting) results in a simplified and homogenous forest structure which reduces closed-canopy and internal forest structure habitats and alters site characteristics that influence forest regrowth

and regeneration, all of which can affect forest recovery following harvest (Gustafsson et al., 2012; Moussaoui et al., 2016).

In an effort to preserve heterogeneous forest structure, a variety of habitats, and promote successful forest regeneration following harvest, forestry practices have shifted to incorporate more ecologically sound forest management through retention forestry (Burton et al., 2006). During a harvest, forest managers intentionally leave uncut sections of forest within a cutblock (i.e., in-block retention) to maintain the supply of ecosystem services provided, promote biodiversity, increase public perception of harvesting, and enrich the structure and composition of postharvest forest (Gustafsson et al., 2012). Methods of retention include dispersed retention of single trees or clumps of trees, peninsular retention of a patch attached to an outer boundary edge or island retention of an undisturbed patch of forest within the harvest boundary (Timber Harvest Planning and Operating Ground Rules | Agriculture, Forestry and Rural Economic Development 2022 Government of Alberta). In Alberta, maintaining pre-disturbance retention patches or island remnants with structural complexity and old-growth characteristics in a variety of shapes and sizes aims to preserve biological legacies for wildlife and forest recovery following harvests (Timber Harvest Planning and Operating Ground Rules | Agriculture, Forestry and Rural Economic Development 2022 Government of Alberta).

In boreal forests, retention forestry aims to mimic large-scale natural disturbances that forests are adapted to and recover from to ensure forest survival for continued resource use and preservation of biodiversity (Grumbine, 1994; Gustafsson et al., 2012). Wildfires have a dominant influence on forest structure and dynamics in boreal ecosystems, therefore they are the disturbance type most often emulated in forest management practices in boreal forests (Dragotescu and Kneeshaw, 2012). With an aim to imitate the mosaic of forested landscape left behind following a

wildfire, retention forestry within the scope of Ecosystem Based Forest Management leaves behind live trees in uncut forest via the creation of island remnants (Franklin et al., 2018; Gustafsson et al., 2012). Mimicking wildfire residual patches using retention forestry may be a key component to help preserve the structural complexity of forest stands and promote biodiversity (Moussaoui et al., 2016).

Nevertheless, the functioning of harvest-created island remnants as analogues for wildfire residuals in terms of forest structure, a source of living trees and vegetation for wildlife habitat has yet to be fully explored. A 2012 study in the boreal mixedwood of Quebec compared wildfire and harvest residuals and found harvest residuals were larger and more abundant compared to similar sites affected by fire, although characteristics such as proximity to water, spatial distribution, and topography of forests influenced both types of residuals (Dragotescu and Kneeshaw, 2012). That study also found that harvest residuals were overall more elongated in their shapes, and they therefore had a higher edge-to-forest ratio (Dragotescu and Kneeshaw, 2012). If there are differences in edge characteristics of island remnants depending on what type of disturbance they were created by, this may ultimately influence post-disturbance forest structure, resilience, and tree mortality.

Edges

Disturbances and subsequent tree mortality create forest edges throughout the landscape, which are characterized by the contrast of ecological characteristics between a forested landscape and surrounding non-forested areas (Harper et al., 2015). Edge influence is defined as the differences in structure, composition and/or function between forest edge and forest interior (Dodonov et al., 2013; Harper et al., 2005).

Forest edges are a natural part of the landscape in boreal forests due to the presence of lakes and wetlands as well as frequent natural disturbances such as wildfires and insect outbreaks (Harper et al., 2015). These edges can have positive effects on forest landscapes. Lack of vegetation at edges opens up the canopy which increases sunlight availability and exposed mineral soil to facilitate seedling recruitment (Harper et al., 2015). Forest edges are preferred habitat for edge-dwelling species (Schlossberg and King, 2008) as well as shade-intolerant species (Chen et al., 1992). Edges are more exposed to stronger winds and receive more visits from seed-dispersing animals, making edges important for seed dispersal and forest development between fragmented sites (Ranney, 1977).

However, changes at forest edges can deteriorate intact forest over time (Gascon et al., 2000; Laurance et al., 2002) through tree mortality, loss of interior forest habitat and homogenization of forest structure (Ecke et al., 2002). Edge characteristics such as loss of canopy cover, sudden exposure to light (Laurance et al., 1998) and increased wind exposure (Chen et al., 1992; Murcia, 1995) can raise the environmental and physiological stresses that remaining trees experience and increase risk of tree mortality (Murcia, 1995). Tree mortality within the first 10 m of forest edges may be higher than in interior forest and persist up to 16 years after edge creation (Harper and Macdonald, 2002). Tree mortality at forest edges has important implications for succession, as dead trees may not be replaced by individuals of the same species (Franklin et al., 1987), and edge effects are ultimately linked to forest species' declines (Murcia, 1995; Harper et al., 2005).

The majority of research on edge effects is focused on tropical and temperate forests; however, there is less work exploring edge effects in boreal forests (Harper et al., 2015). In contrast to tropical and temperate forests, boreal forest species may be less susceptible to edge effects due

to frequent natural disturbances and the presence of natural edges from bodies of water (Gauthier et al., 2015; Harper et al., 2015). A common factor influencing forest edges is sunlight penetration because interior forest canopies normally block out significant amounts of solar radiation. Due to the high latitudes of the boreal forest region, lower solar angles may result in light penetration farther into interior forest, lessening the contrast of sunlight influence between edge and interior forests (Harper and Macdonald, 2002). Additionally, shorter canopy heights in boreal forests may result in reduced edge effects compared to temperate and tropical forests (Harper and Macdonald, 2002). A 2015 study found that edge influence on vegetation in boreal forests is generally weak, not very extensive and decreases over time (Harper et al., 2015). If boreal forests are less impacted by forest edges, there could be evidence to support continued resource use and harvesting in this ecosystem without concern for edge creation.

However, edges created by harvest may be different from naturally occurring edges, especially in the boreal forest. Complex fire boundaries create highly variable edges resulting in gradual transitions, whereas harvesting creates abrupt edges with harsher boundaries (Harper et al., 2015). Additionally, logging equipment can inadvertently injure living trees, causing crown damage, root compaction, and increasing stress that leads to high mortality at edges after a harvest (Thorpe et al., 2008). In fact, proximity to skid-trails and harvest edges is a direct predictor of post-harvest tree mortality (Thorpe et al., 2008). Trees at forest edges and close to clearcuts are more susceptible to death due to insect infestations and disease outbreaks which may develop following an increase in environmental stress (Ranney, 1977). Tree mortality at forest edges reduces canopy cover, increases abundance of snags and logs, exposes soil and results in lower shrub cover as compared to interior forest (Harper et al., 2005). It is unknown whether cut edges have a substantial

impact on forest response and tree mortality in boreal forests when compared directly to mortality responses in wildfire-created edges.

Tree mortality

From both an environmental and economic standpoint, tree mortality is an important forest response to disturbance. Tree mortality alters forest structure and facilitates regeneration (Aakala et al., 2009), can indicate ecosystem health, and affects forest stand yield projections (Franklin et al., 1987). Tree mortality is caused by a combination of factors, these can be biotic (disease or insect infestation) or abiotic (natural disturbances such as wildfire or drought, or anthropogenic causes such as harvesting, road construction or pollution) (Franklin et al., 1987). Light, water, and nutrient availability, as well as the complicated interactions between individual trees, environmental conditions, other species, and various agents of mortality can all affect the survival of trees (Franklin et al., 1987). Physiological stress from increased light or wind exposure due to the opening of a stand from harvest or other disturbances can increase the occurrence of standing dead mortality (Thorpe et al., 2008).

Tree mortality is a natural process in forests when tree death is occurring at stable or background rates (Franklin et al., 1987). In the boreal forests of Alberta, background tree mortality ranges between 1-3% per year depending on species (Bladon et al., 2008). Tree deaths provide habitat through the influx of snags and downed woody debris for cavity nesters and invertebrates (Gandhi et al., 2001; Jönsson et al., 2007), as well as for certain species that specialize in edge occupation (Schlossberg and King, 2008). Dead trees create an opening in the forest canopy which can facilitate regeneration through the increase in sunlight and exposed mineral soil (Harper et al., 2015), they also contribute downed wood for decomposition and nutrient cycling processes.

However, tree mortality has negative consequences as well, and these become concerning when tree mortality rates become elevated above background rates. In Canada, boreal forests often experience large scale/episodic tree mortality events due to wildfires (Aakala et al., 2009; Dragotescu and Kneeshaw, 2012). When trees die, they switch from being a carbon sink to a carbon source (Hogg and Michaelian, 2015), so elevated or episodic tree mortality becomes an important factor to consider with respect to climate change and global carbon emissions. Tree death may remove habitat for species that depend on full living canopies and products from living trees such as seeds, fruit and vegetation (Ecke et al., 2002). In the event of widespread tree mortality, forest species may be at risk of takeover by invasive species or an ecosystem shift. Understanding patterns and causes of tree mortality aids in protecting existing forests, calculating forest yields, and quantifying the effects of climate change on such a significant pool of organic carbon (Franklin et al., 1987; Perera and Buse, 2014). As the climate warms and dries and large-scale natural disturbances become more frequent and severe in the boreal forest (Gauthier et al., 2015), an increase in tree mortality above background rates will influence carbon emissions, climate feedbacks and overall forest recovery and resilience.

The timing of tree mortality varies following large-scale disturbances. If a disturbance does not cause direct tree mortality, it may cause indirect mortality by weakening trees and making them more susceptible to insect attack or disease resulting in delayed mortality (Heikkala et al., 2014). Following light to moderate severity wildfire, burned stands initially leave a large number of trees left alive, but delayed tree mortality leads to an overall lower rate of tree survival than initially witnessed, postponing carbon emission release (Angers et al., 2011). If post-harvest island remnants exhibit a similar delay in residual tree mortality, retention forestry practices may not prove to be as successful in mitigating long-term tree mortality. However, there are indications

that residual post-fire tree survival may stabilize within a decade and trees alive ten years post-disturbance are strong enough for continued survival (Angers et al., 2011), yet it is unknown if this pattern of tree survival is replicated in post-harvest island remnants. Studying the timing of tree death following disturbance can elucidate the success of residual tree survival on a larger time scale.

Previous work in Western Canada has studied tree mortality responses to variable retention harvesting strategies (Solarik et al., 2012; Spence et al., 1999), including mortality due to interactions with tree-level characteristics and retention levels (Xing et al., 2018). One study directly compared dispersed retention tree survival to a "background mortality" in reference or "undisturbed forest stands" of similar species composition and stand age (Bladon et al., 2008), but the comparison of post-disturbance mortality rates in wildfire and harvest island remnants has yet to be explored. Due to the influence of wildfires, boreal forest landscapes contain a mosaic of forested areas, island remnants of live trees, and intact forest structure. Assessing differences or similarities in tree mortality responses in wildfire and harvest-created island remnants is a key component to widescale implementation of retention forestry and ecosystem-based management. This comparison allows isolation of disturbance effects on post-disturbance residual mortality, rather than comparing to tree mortality in undisturbed or reference forests.

Here, we examine tree mortality in island remnants created in wildfire and harvest disturbances, specifically with respect to temporal patterns of mortality, as well as the influence of individual tree characteristics on mortality such as species and size. Within these areas, we will also determine if there are significant edge effects on tree mortality compared to interior forest conditions. We expect to see temporal patterns of tree mortality with an increase in the first few years following disturbances, that different species and tree sizes will result in differing

probabilities of mortality and that edges will experience higher tree mortality than interior forest. With the goal to assess the current practice of retention forestry in efforts to mimic wildfire across the boreal landscape, the results of this research will inform forest managers how to best preserve remnant forests for future resiliency and use. This study uses in-situ observations of island remnants created during harvest from 2009-2012 and compares them with similar-sized wildfire residuals from fires that burned 2010-2011 to quantify and explore post-disturbance tree mortality across North-Central Alberta.

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CHAPTER 2: A COMPARISON OF RESIDUAL TREE MORTALITY IN FOREST ISLAND REMNANTS FOLLOWING WILDFIRE AND HARVEST

Introduction

Forests are adapted to natural disturbance regimes, which drive ecosystem dynamics and cause tree mortality (Franklin et al., 2002; Kuuluvainen and Aakala, 2011; Thorpe et al., 2008). These disturbances are important in maintaining forest heterogeneity, (Franklin et al., 1987), providing a variety of habitat types for wildlife (Franklin et al., 2002), and preserving pre-disturbance continuous forest structure, including old growth structure (Moussaoui et al., 2016). In the boreal forest, stand-replacing wildfire is the main natural disturbance that affects the landscape (Johnson and Johnson, 1996; Payette, 1992).

A cause of widespread tree mortality (Johnson and Johnson, 1996), wildfires burn unevenly across the landscape, resulting in intact, unburned forest patches that are surrounded by a burned area (Perera and Buse, 2014). These patches of forest are called wildfire residuals or island remnants, and they offer habitat and refuge for biodiversity (Moussaoui et al., 2016). Additionally, these remnants aid in natural regeneration processes by providing seeds from live trees (Perera and Buse, 2014), preserving genetic diversity, and helping forests retain heterogeneous structure (Dragotescu and Kneeshaw, 2012). Due to these attributes, island remnants are thought to be crucial for forest recovery following wildfire (Moussaoui et al., 2016).

Wildfire is the most influential disturbance in the boreal forest (Bergeron et al., 1998), but anthropogenic disturbances–specifically harvest–also affect the overall structure of forested landscapes. Traditional forest management practices (i.e. clearcutting) result in the simplification of forest structure and even-aged stands, and decrease availability of various habitats for species that utilize old growth forest structure (Moussaoui et al., 2016). Whereas wildfires leave behind diverse structural features including standing and fallen dead wood, multiple canopy layers, varied

stem sizes and canopy gaps that aid in forest regeneration (Kohm and Franklin, 1997), the homogenous forest structure left following clearcut harvest can be much more detrimental to forest recovery (Gustafsson et al., 2012).

With a goal of managing forests for multiple values, forest management has moved towards preserving complex forest structure. In addition to harvesting trees for wood and related products, modern goals of forest management include maintaining heterogeneous forest structure, preserving habitat for wildlife, minimizing incidental tree mortality, and promoting biodiversity (Kohm and Franklin, 1997; Moussaoui et al., 2016). As an alternative to resource-intensive extractive practices, the concept of Ecosystem Based Management was developed to protect ecological integrity for the future while also providing goods and services for humans (Grumbine, 1994). Within the scope of modern forest management, this involves moving away from clearcutting towards a form of structural retention.

In the boreal forest, retention forestry aims to mimic the mosaic of forested landscape left following a wildfire by leaving live trees or patches of uncut forest via the creation of island remnants (Gustafsson et al., 2012). These island remnants are thought to maintain the supply of ecosystem services, foster biodiversity, increase public perception of harvesting, and enrich the structure and composition of post-harvest forest (Kohm and Franklin, 1997; Gustafsson et al., 2012). Although retention aims to create island remnants that resemble those created by wildfires, there are noted differences between these disturbances and their effects on the landscape. Wildfires cause specific impacts on soils and habitats, and serotinous species rely on fire and heat to regenerate–characteristics that are missing in a harvest setting (Heikkala et al., 2014). As a disturbance, harvest leaves less coarse woody debris, more homogenous vertical vegetation structure and reduced soil microsite exposure for germination compared to wildfires (Mulverhill

et al., 2019). In addition, forest edges created by anthropogenic disturbances such as harvest have been shown to be functionally different from naturally created edges, resulting in variation in forest structure, understory plant composition and tree mortality (Harper et al., 2015).

Research in Eastern Canada (Quebec) on post-disturbance residual tree mortality revealed temporal patterns of tree death in plots monitored ten years after wildfire. Following wildfire, most tree mortality occurs within the first few years following disturbance but can range between 40-55% in cumulative mortality up to ten years after fire–this potential for delayed residual tree mortality following wildfire may lead to a considerably lower rate of tree survival over time (Angers et al., 2011). A study in Western Canada (Alberta) found that after harvesting, tree mortality at the edge of intact forest spiked within the first year after harvest at a 10% mortality rate compared to 5% the second year, likely due to wind exposure and windthrow mortality (Harper and Macdonald, 2002). These studies reveal that considering post-disturbance mortality throughout time is important to account for delayed tree mortality, because if island remnants experience heightened or continuous mortality, retention forestry practices may not be functioning as intended by providing live trees for habitat and preserving heterogenous forest structure.

Previous research has compared harvest island remnant tree mortality to reference forest or clearcuts (Bladon et al., 2008; Spence et al., 1999), but the direct comparison to tree mortality in island remnants created by wildfires has yet to be explored (Gandhi et al., 2004; Moussaoui et al., 2016). Overall, understanding the dynamics of tree mortality in island remnants created by both wildfire and harvest can reveal residual tree response to disturbances and determine the success of forest recovery. Monitoring residual tree mortality in created island remnants will help evaluate the effectiveness of this form of retention forestry and identify areas to prioritize for retention to ensure tree survival.

Objectives

This study compared post-disturbance tree mortality between wildfire and harvest island remnants. We quantified overall amounts of tree mortality with a focus on standing dead trees, as well as temporal patterns of tree mortality up to twelve years following the disturbances. Additionally, we measured tree mortality in edge and interior forest of both island remnants and reference forests to determine if tree mortality was higher at forest edges, if disturbance type influenced edge effects on tree mortality, and further if island remnant edges experienced higher mortality than reference forest edges.

These results can be used to inform future forest management practices and determine if retention forestry in the form of island retention results in high or similar amounts of post-disturbance residual tree mortality compared to similar sized wildfire island remnants. Specifically, our objectives were to 1) determine if there was a difference in post-disturbance mortality between wildfire and harvest created island remnants, 2) assess if there are any temporal patterns of post-disturbance tree mortality following wildfire and harvest, and 3) quantify if edge effects influenced mortality in island remnants and if there were differences in edge effects based on disturbance type. We integrated additional variables such as tree species, individual tree diameter and total plot basal area into our analysis to determine if those factors affected individual tree mortality. If there is a difference in tree mortality between fire and harvest created island remnants, the suitability of those remnants will be questioned as analogues for fire residuals. This will help determine the efficacy of implementing Ecosystem Based Management in harvesting protocols compared with natural disturbance caused tree mortality.

Methods

Site Selection

Research sites were located in North-Central Alberta in mixedwood boreal forest stands, in the Boreal Plains Ecozone (Canadian Council on Ecological Areas 2014). The climate in this area is characterized by long, cold winters and short, warm summers (National Ecological Framework of Canada, 1999). Climate variables for each region can be found in Table 1.

Table 1: Mean annual precipitation, mean annual temperature, and average number of frost-free days in each study region. All areas were boreal forest natural regions, with natural subregions listed. Government of Alberta Historical Climate Data from 1997-2021, https://acis.alberta.ca/weather-data-viewer.jsp and "Natural Regions and Subregions of Alberta" from the Government of Alberta, "Derived Ecosite Phase" November 2020.

Geographic Region	Natural Subregion	Climate Station	Mean annual precip (mm)	Mean annual temp (°C)	Number of Frost-Free Days
Mercer Peace River	Dry mixedwood	Three Creeks AGCM	394.24	1.66	119.5
Mercer Harmon Valley	Central mixedwood	Kimiwan Auto	436.22	1.94	114.3
Alpac	Central mixedwood & Lower boreal highlands	Round Hill Auto	473.15	1.74	116.9
Utikuma Fire	Central mixedwood	Whitefish Auto	433.29	1.76	109.4
Flattop Fire	Central mixedwood & Lower foothills	Slave Lake	465.64	2.08	122.4
M024 Fire	Central mixedwood & Lower boreal highlands	Algar Auto	493.97	1.18	113.7

Potential field sites were identified using geospatial data including Alberta Vegetation Inventory (AVI) provided by partners of the NSERC Industrial Research Chair in Ecosystem-based Forest Management, aerial imagery and baselayers from ArcGIS and Google Earth, as well as provincial and national datasets of dNBR (delta Normalized Burn Ratio) raster layers and historical fire perimeters from open-source databases (Alberta Agriculture and Forestry 2021; Natural Resources Canada 2021). The AVI data (2020) included information on dominant tree species composition, stand structure and stand age. In cases where AVI data were older than disturbance year or incomplete, patches of living trees or cutblocks were digitized at a 5 m resolution once species compositions were determined. Locations of salvage logging and remnant island polygons were provided by industry partners Alberta-Pacific Forest Industries (Alpac), Mercer International Inc., Tolko Industries Ltd. and West Fraser; selected sites in wildfire areas avoided salvage logging.

Mixedwood forest was defined as containing a mix of deciduous (mainly *Populus tremuloides* or *Populus balsamifera*, but sometimes *Betula spp.*) and coniferous (usually *Picea glauca* or *Picea mariana*) trees. We selected deciduous dominated stands with at least 70% composition of *P. tremuloides* or *P. balsamifera*, and *P. balsamifera* occurred intermittently compared to *P. tremuloides*. Additional canopy tree species present in study plots included *Abies balsamea, Pinus banksiana* and *Pinus contorta*, although these occurrences were minimal overall—less than 6% of total stems in sampling areas.

All sites were disturbed by fire or harvest within the past 9-12 years (between 2009-2012), because older disturbances would make tree mortality sampling and coring difficult due to decayed wood and because harvesting strategies have remained consistent for the past decade. The fires selected were SWF056 Flattop Complex, near Lesser Slave Lake, SWF057 Utikuma Complex

north of Utikuma Lake and MWF024 Complex, south of Fort McMurray, AB (Table 2). Harvest sites were selected from the Mercer FMA near Peace River, AB and Harmon Valley, AB, and Alpac FMA between Lac La Biche and Fort McMurray, AB (Table 3).

Based on criteria such as stand composition, island size, shape and accessibility, a reduced pool of sites was selected. These field sites were scouted prior to data collection for accessibility, to confirm canopy species composition, and install microclimate sensors. Sites were determined to be reasonably accessible if they were within an hour's hike from the truck one-way. Once sites were scouted in person and confirmed to match selection criteria, we took GPS points to confirm locations of sites and finalize site selection (Figs. 1 & 2).
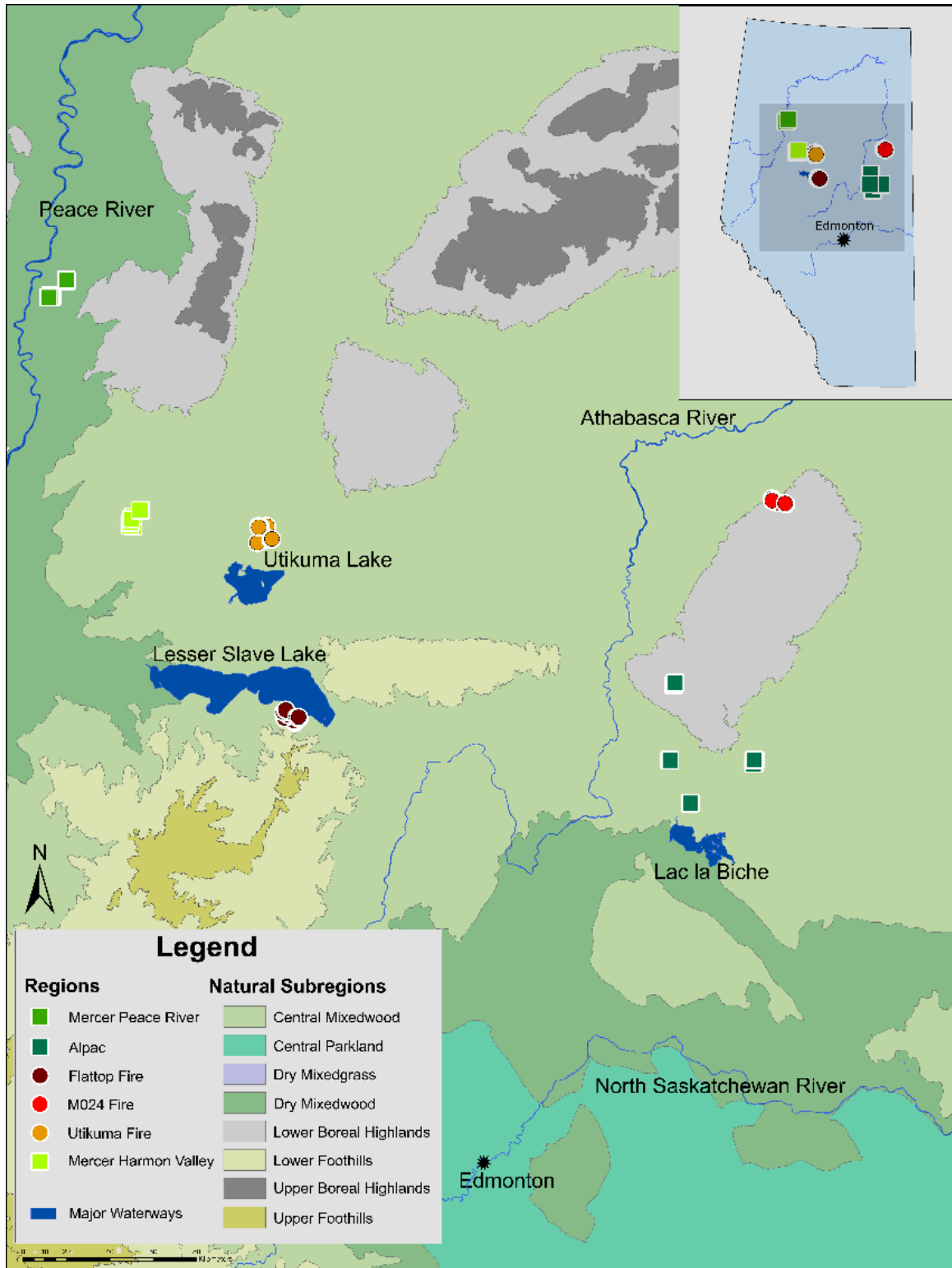
Figure 1: study areas in North-Central Alberta, north of Edmonton by roughly 200-450km. Region denotes the geographic area of each disturbance: Harvests in Mercer Peace River, Mercer Harmon Valley and Alpac, and fires in Flattop, Utikuma and M024. GPS coordinates for field sites are listed in Appendix Table A3.
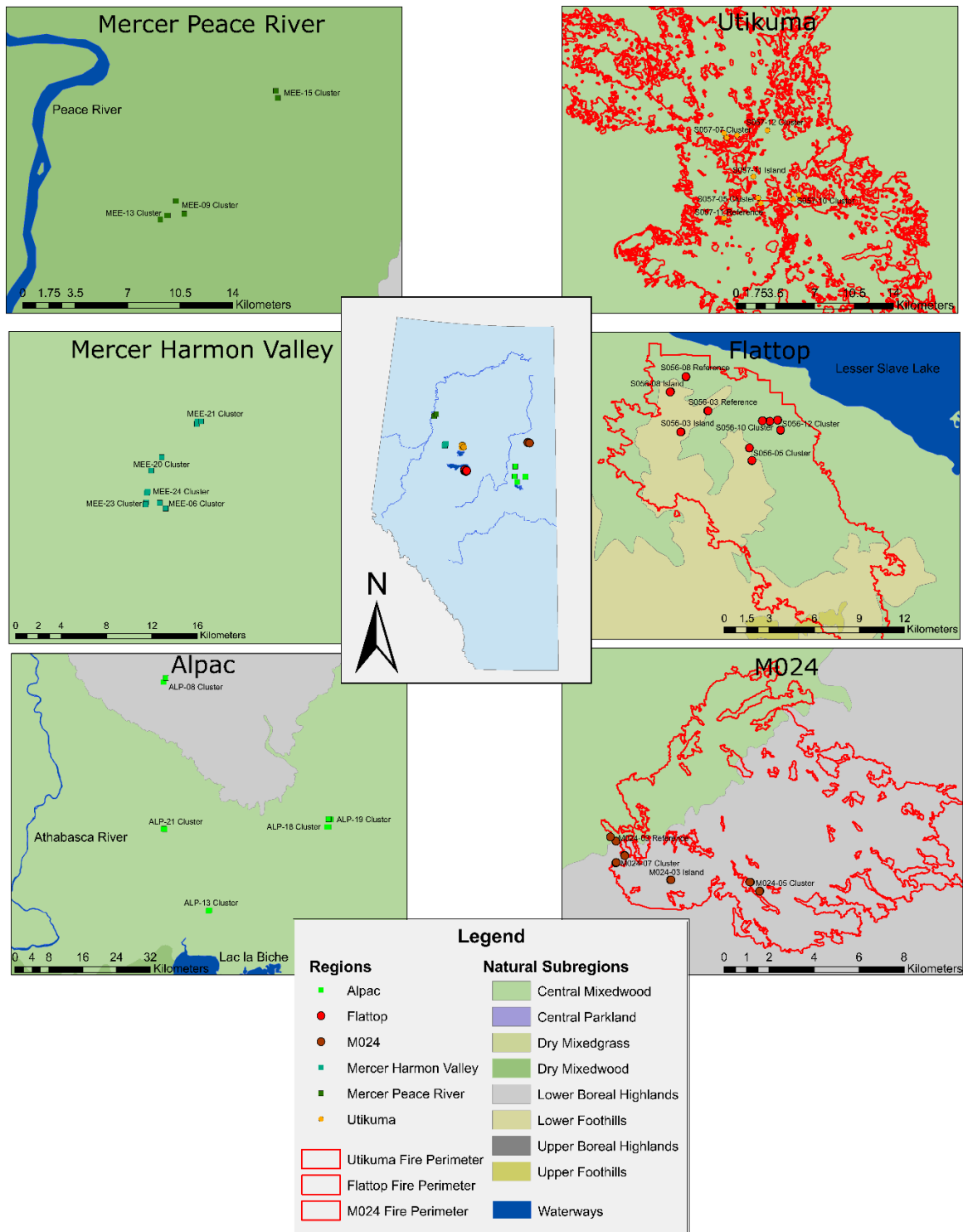
Figure 2: detailed view of study sites by Region: Alpac, Mercer Harmon Valley and Mercer Peace River are harvest regions, M024, Flattop and Utikuma are fire regions. Wildfire perimeters are outlined in red.

There were two types of locations sampled: island remnants and references. Island remnants were defined as an assemblage of trees mostly or completely unaffected by disturbance but surrounded by a disturbed area. Reference sites were intact forest not affected by the disturbance but bordered by disturbance along one edge, at least 200m in width and spatially located near selected island sites. In the event that island remnants were bordered by a seismic line, road, or other type of linear disturbance, plots were established, and sampling occurred on the far side of the island remnant away from the linear disturbance. Island remnants were selected to be at least 0.45 ha to ensure interior forest conditions for interior plots, and maximum island size selection was bound by the island size distributions of both fire and harvest islands; with a goal of comparing similar island sizes between disturbance types.

Each island remnant and reference stand had two plots: an edge and interior, placed directly adjacent to each other with edges of each circular plot touching (Fig. 3). The absence of cut stumps in post-harvest sites or scorch marks in post-fire sites indicated where each disturbance ended and the forested edge of either island remnant or reference forest began. Edge plots were established at the outer edge of island remnants and references. Interior plots were measured to be 20m into the interior of each forest stand from the inside border of edge plots. To maintain interior forest conditions, in misshapen islands or in cases of interfering linear disturbances, interior plots were offset and not directly adjacent to interior plots.

Table 2: Fires selected for field sites with corresponding year of fire, stand origin year for the unburned reference or island remnant (stand origin year accessed from AVI data), the number of island and references from within each fire and the total burn extent of the fire.

Fire Name	Year of Fire	Stand origin year	# Islands	# References	Burn extent
Flattop Complex (SWF056)	2011	1920, 1948, 1941, 1880	6	6	22,000 ha
Utikuma Complex (SWF057)	2011	1910, 1930, 1940	4	4	90,000 ha
M024 (MWF024)	2009	1930, 1950	3	2	11,500 ha

Table 3: Harvest areas selected for field sites with corresponding year of harvest, stand origin years for the unharvested reference or island remnant, (stand origin year accessed from AVI data) the number of island and references from within each harvest area and corresponding FMA holder.

Harvest Area	Year of disturbance	Stand origin year	# Islands	# References	FMA Holder
Mercer Peace River	2009, 2010	1900, 1930, 1960	3	2	Mercer Ltd.
Mercer Harmon Valley	2010	1920, 1930, 1940	5	5	Mercer Ltd.
Alpac	2009, 2010, 2012	1880, 1860, 1920, 1930, 1950, 1945	4	4	Alberta-Pacific Industries
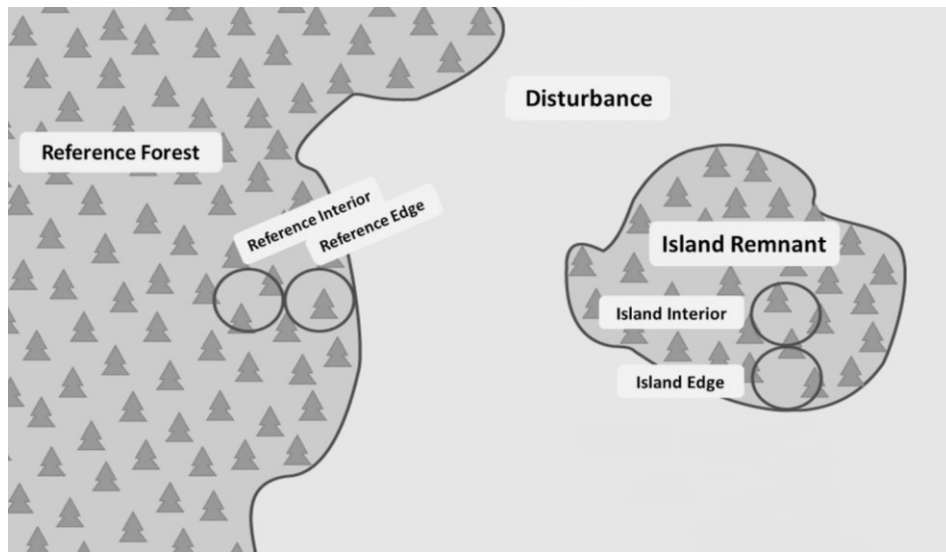
Figure 3: Field plot setup of edge and interior plots in island remnant and reference stands. The four plots in each pairing of island remnant and reference forest (Island Edge, Island Interior, Reference Edge, Reference Interior) are considered a "Location".

Plot Setup & Data Collection

Data were collected in the summer (June-September) of 2021 from circular plots with a radius of 11.28 m (400 m^2 in area). This design follows plot dimensions used for the Alberta Growth & Yield Initiative (2015). In each circular plot all standing live and dead trees measuring at least 9.1 cm diameter at breast height (1.3 m, dbh) were identified, tagged, and measured following the sampling protocol of Alberta Growth & Yield Initiative Permanent Sampling Plots (2015). Any damage to live or dead trees (bole scars, fruiting fungal bodies, dead top, broken top) was noted as a damage code.

Standing dead trees were assigned a decay class using Alberta Biodiversity Monitoring Institute (ABMI) Terrestrial Field Protocols (ABMI Terrestrial Field Protocols 2019), and additional literature sources. Decay classifications may point to an estimated range of time since tree death based on visual characteristics of dead trees, therefore we used decay class as an estimate of whether trees died in response to, or prior to, target disturbances of interest (the fire or harvest,

occurring from 2009-2012). ABMI defines decay class 1 snags as recently killed, with all twigs/branches present, wood hard, and bark (normally) intact, and decay class 2 snags retaining major branches but with twigs and small branches missing, with hard/solid wood (see Fig. 4 for example) (ABMI Terrestrial Field Protocols 2019). Recently dead aspen and spruce trees commonly retain their bark and fine branches, and these traits point to a tree death of ten years or less (Angers et al., 2012, 2011). Smithsonian ForestGEO (Forest Global Earth Observatory) deadwood protocols (Janík et al., n.d.) define Class 1 snags as freshly dead (0–5 years for many species) with the species still recognizable; branches of 3rd order present; and full height of stem is present unless there was prior damage, and with bark fully intact. Based on these traits, we made a conservative estimate that decay class 1 and 2 snags may have died in response to disturbances and snags of these decay classes were favored for further sampling—see below.

In each plot, standing snags (with a particular focus on snags classified as decay class 1 and 2) >9.1 cm dbh were cored with an increment borer (Haglof Increment Borer, 5.1 mm diameter, Sweden) twice, the two samples were taken at 90 degrees from each other or wherever the most solid wood was on the bole at roughly 1.3 m (dbh) from the ground. An effort was made to collect core samples from most if not all the decay class 1 and 2 snags, but tree cores were also collected from a smaller sample of decay class 3 and 4 snags to determine year of tree death in later decay classes. In cases where there were multiple snags of the same decay class, tree species and dbh class within 2-3 cm and generally located in similar areas of the plot, a subsample of snags (roughly three-quarters of dead aspen and spruce in decay class 1 and 2) were cored because coring all dead trees in each plot would limit replication across plots due to time constraints. In some cases, wood was too decayed to sample (e.g., wood consistency was powdery or slimy depending on moisture content). These cases of severely decayed wood were seen in snag decay class 3 and

4, indicating that they likely died many years prior to the disturbances of interest in this study. Dating downed trees to capture windthrow-caused mortality and related temporal patterns was outside the scope of this study. However, a companion study (Moore 2022, unpublished) provided decay classes for downed woody debris, here we assume similarly for standing dead that decay class 1 and 2 represent post-disturbance mortality, allowing us to speak to overall mortality including both standing and downed dead trees. Further, data collected on the species makeup of recent deadwood showed a higher proportion of aspen downed trees than spruce, although spruce trees are more likely to be blown down as a mechanism of tree death and aspen are more likely to die standing (Bladon et al., 2008). This allows us to address the question of differences in species amounts and corresponding mechanism of tree death, even though downed dead trees were not specifically measured in this study (Fig. A1 Appendix).

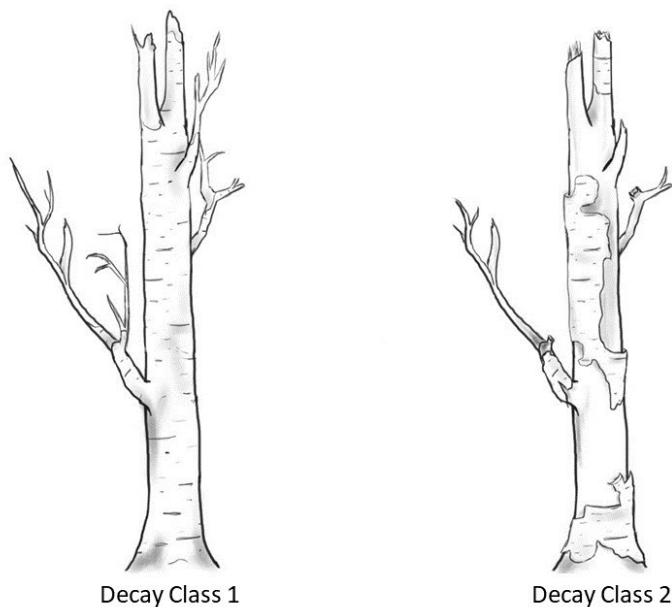Decay Class 1   Decay Class 2

Figure 4: sketch of decay class 1 and 2 deciduous trees, decay class 1 snags still have fine branches and bole surface is covered in bark, decay class 2 has fewer fine branches (2nd order branches still present) but may be missing some bark on bole surface. Drawing by Lana Mrochuk.

Dendrochronology

Dendrochronology was used to confirm post-disturbance tree deaths and reveal the accuracy of decay classification with respect to tree death, as well as provide information on the temporal occurrence of post-disturbance tree mortality. After collection, tree cores were placed in labeled straws, bark side inserted first and stapled shut with holes added for ventilation to prevent mold growth. After air drying, tree cores were glued to wooden mounts, sanded using progressively finer grit sandpaper (from 180-1000 grit depending on tree species), scanned at 2400 dpi resolution and analyzed. The dendrochronology lab at the University of Alberta was used to process samples according to standard dendrochronological techniques (Stokes and Smiley, 1968) and tree rings were cross dated using CDendro software (Cybis Elektronik & Data AB, www.cybis.se, Lars-Åke Larsson 2021). Tree rings were measured to the nearest 0.001 mm.

Reference chronologies of each tree species in each region were developed using cores sampled at the same study sites from living canopy trees. One mature live tree >9.1 cm dbh of each species per island/reference pair was cored using the same protocol to create a reference chronology to compare tree rings based on living growth patterns. Additionally, master chronologies for *P. tremuloides* (trembling aspen) and *P. glauca* (white spruce) were accessed from the Climate Impacts on Productivity and Health of Aspen/Spruce (CIPHA/CIPHS) plot network (CFS, Mike Michaelian & Trisha Hook) to aid with dating of aspen and spruce samples and compare reference chronologies against (Tables 4 & 5). Reference chronologies from CIPHA and CIPHS plots contained around 200 samples per site. Samples from dead trees were crossdated against reference chronologies using correlation values from the proportion of the last two years of growth limited, as this limits the influence of narrow rings in core samples based on the standard deviation of the reference chronology curve (Cybis Elektronik & Data AB, www.cybis.se, Lars-

Åke Larsson 2021). Year of tree death was determined to be the year the last growth ring was produced by the tree. When correlation values of individual samples compared to reference chronologies were higher than 0.3, they were considered robust enough for an accurate dating of year of death. In the event that the two core samples for one individual tree differed in their determined year of death, the sample with the highest correlation value, more complete core and better match with reference chronology marker years was selected as the correctly dated sample. Additional factors considered when finalizing year of tree death included assigned decay class and sampling region. Tree mortality for each plot was determined by comparing the number of trees that died following the disturbance to total stems in each plot.

Table 4: Aspen reference chronologies created from experimental field sampling compared with master chronologies provided by the Canadian Forest Service CIPHA plots. CFS master chronologies for aspen date from 1936-2020, depending on sampling area. Marker years indicated are for reference chronologies created from this experiment, bolded years indicate matching between experimental and CFS chronologies.

Sampling Site	CFS Site	Correlation	Marker Years
Mercer Peace River	NOT	0.58	**1961-1962, 1982, 1995,** 2013, 2016
Mercer Harmon Valley	RED	0.4	**1983 peak, 1999, 2002, 2013,** 2016, **2019**
Alpac	CAL	0.27	**1980, 1999**, 2007
Utikuma	RED	0.43	1990, 2005, **2014, 2015-2016 , 2019, 2020**
Flattop	CAL	0.25	1978, 1981-1982, 1983, **1989**, 1996, 2000, 2006, 2011
M024	NOT	0.29	**2000, 2001**, 2003, 2007, 2017, **1971** and 1981

Table 5: Spruce reference chronologies created from experimental field sampling compared with master chronologies provided by the CFS. CFS master chronologies for spruce date from 1860-2019 depending on sampling area. Marker years indicated are for reference chronologies created from this experiment, bolded years indicate matching between experimental and CFS chronologies.

Sampling Site	CFS Site	Correlation	Marker Years
Mercer Peace River	HAI	0.4	1999, **2000, 2002, 2003, 2004**
Mercer Harmon Valley	HAI	0.67	**1982, 2002, 2003, 2011, 2013**
Alpac	ANZ	0.23	**1962**, 1975, 1993, 1994, 2014, 2015, 2017
Utikuma	HAI	0.49	2000, **2001, 2003, 2004**
Flattop	MAR	0.26	**2002**, 2005, **2015**
M024	HAI/MAN/MAR	0.52/0.48/0.42	**2002, 2003, 2004**

Seventy-five percent of dead trees were aspen or spruce, and over 85% of all stems were aspen or spruce. Due to the large majority of trees being aspen and spruce, and because these species are economically important, statistical analysis focused on these species. Of dead trees decay class 1 and 2, a subsample of 72% of dead aspen and 72% of dead spruce trees were cored to determine year of tree death for survival analysis, selection of trees to core was determined by a random selection of similar sized trees in the same decay class and species. The mean year of death for dated decay class 1 aspen trees was 2010 and decay class 1 spruce trees was 2009 (Table 6). For undated dead trees, the visual decay classification was converted to a pre- or post-disturbance death based on trees that were crossdated. Dead trees that were not cored were assigned a pre- or post-disturbance death based on year of death from dated samples of the same species, with the same assigned decay class and considering the distribution of tree diameters of dated dead trees (Table 6). Of the uncored dead trees, selected trees of differing diameters were assigned a

post-disturbance death based on the proportion of dated dead trees across diameters, so that proportions of dead trees by tree diameter were maintained between cored and total dead trees.

Table 6: Cored and uncored aspen and spruce snags by decay class, with percent that died post-disturbance for each decay class of the dead trees that were cored. The percentages of trees that died post-disturbance based on cored dead trees were applied to uncored dead trees by their corresponding species, decay class, and dbh.

Species	Decay Class	Median Year of Death	Mean Year of Death	Range of Years of Death	% died post-disturbance	Total cored	Uncored dead
Aspen	1	2014	2010	1960-2021	68%	98	33
	2	2006	2001	1941-2021	40%	108	48
	3	1994	1988	1920-2013	1%	60	104
	4	1996	1992	1946-2011	0%	24	82
Spruce	1	2011	2009	1973-2019	54%	54	21
	2	2005	2000	1952-2020	54%	36	12
	3	1992	1989	1973-2002	0%	3	2
	4	1998	1998	1998-1998	0%	1	1

Statistical Analysis

To determine whether harvest island remnants had higher mortality than fire island remnants and if tree mortality was influenced by edge effects, we built logistic regression models using all live and post-disturbance dead trees as well as additional tree and plot-level covariates. Logistic regression allows for the testing of interaction effects of treatments in addition to the main effects of individual treatment groups. This was supplemented with a survival analysis using a subset of dated dead trees to identify if there were temporal patterns of post-disturbance mortality, however, survival analysis does not allow for incorporation of interactive effects of treatments. The response variable in both cases is binary with 0 indicating the tree is still living and observations are right-censored, and 1 indicating the tree died. Additional covariates of interest

including tree diameter, species and plot-level basal area were tested in both survival analysis and logistic regression models to determine if they had any effect on tree mortality. All statistical analyses were run in R version 4.2.1 (R Core Team 2022).

Logistic Regression

Using the dataset of all trees still living and those that died post-disturbance (including uncored dead trees with estimated post-disturbance deaths), we ran mixed effects logistic regressions to determine if there were differences in tree mortality based on differing combinations of treatment types/explanatory variables for the entire sampling area. We selected logistic regression because explanatory variables for logistic regression may be categorical and/or continuous (Quinn and Keough, 2002), and our response variable of dead/living trees is binary with 0 indicating the tree is still living and 1 indicating the tree died. Logistic regression calculates the probability of an event occurring, where the event in this study is tree death as coded by 1, therefore it calculates the probability of mortality. Logistic regression analysis was done using the lme4 package (Bates et al., 2015 in R version 4.2.1, R Core Team (2022)). The main explanatory variables selected to answer our research questions were disturbance type (fire/harvest) and location (island interior, island edge, reference edge, reference interior) to determine if fire islands and harvest islands differed with respect to plot-level mean tree mortality, as well as if edges contributed to differences in tree mortality. Additional predictor variables tested were as follows: size of tree (using dbh), plot-level basal area, and tree species. Each SiteID (the pairing of reference and island–4 total plots) within the corresponding Region (Mercer PR, Mercer HV, Alpac, Utikuma, Flattop, M024) was used for the random term in the models, this was a nested error term of SiteID nested within each Region. Candidate models were built, and model selection was based

on Akaike's Information Criterion (AIC) value, deviance, and the result of a Chi squared test to indicate a difference between models and if so, the more complex model was rejected in favor of the simpler model. Deviance measures model goodness-of-fit and unexplained variation within a model, a deviance of 0 indicates perfect model fit (Quinn and Keough, 2002). When DeltaAIC values were greater than 2, the model with lower AIC was selected as the preferred model (Burnham and Anderson, 2004). In the event that AIC values differed less than 2, if the addition of a covariate was not significant and didn't lower AIC significantly, that covariate would be left out in favor of the simpler model. Additionally, variance inflation was calculated to determine the quality of predictions based on the model. Finally, residual plots were examined to assess model goodness-of-fit using DHARMa package which scales residuals of logistic regression binary response variables, so interpretation of residuals is similar to that of linear models (Hartig F. in R version 4.2.1, R Core Team (2022)). Post-hoc testing compared estimated marginal means for treatment groups in the finalized logistic regression model to get expected values of mortality based on treatments and other covariates (Lenth R, emmeans package in R version 4.2.1, R Core Team (2022)).

Survival Analysis

Using all live trees and the subsample of cored and crossdated trees that died post-disturbance, survival analyses were run to analyze the influence of individual covariates on probability of survival over time following disturbance for individual trees in each plot location. Survival analysis incorporates time-dependent variables and although commonly used in medical settings, has only recently been used for tree mortality (Woodall et al., 2005). This method compares survival distributions of tree populations among different groups through time and deals with censored data when the timing of tree death is unknown (Allison, 2010). Although years of

tree death were determined in this study using dendrochronology, survival analysis accounts for censored datapoints that may have experienced the event (tree death) since their initial visit—trees that were recorded as alive may have died since data collection. The survival function,

$$S(t) = P(T \geq t)$$

defines S(t) as probability that death occurs at some time T which is at least as great as time t and larger than 0 (Oakes, 2000). As seventy-five percent of dead trees were aspen or spruce, and due to their economic importance, these two tree species were the focus of statistical analysis. Survival analysis was performed using the survival package (Therneau T (2022) in R version 4.2.1, R Core Team (2022)).

Kaplan-Meier and Cox Regression curves were calculated to determine the influence of covariates and treatment variables on individual tree survival or hazard of death. Covariates tested included disturbance type, plot location, tree species and tree diameter. Tree diameters were split into three even dbh classes: small (9.1 cm dbh - 15.5 cm dbh), medium (15.5 cm dbh - 22.5 cm dbh) and large (>22.5 cm dbh) based on the distribution of tree diameters in the dataset. The Kaplan-Meier is a non-parametric estimate of survival probability at a given time. A log-rank test statistic was calculated to compare the survival between treatment groups for each explanatory variable (Allison, 2010). Cox proportional hazards models were built to determine the effect size of covariates on tree survival, as well as incorporate all significant variables identified in Kaplan-Meier curves together. The cox proportional hazards model calculates hazard of death via:

$$h(t|Xi) = h0(t)\exp{(\beta 1 x1 + \cdots \beta k x k)}$$

where h(t) is the instantaneous rate at which the hazard of death occurs, h0(t) is the arbitrary baseline hazard, β is the regression coefficient of the set of explanatory variables, x1 to xk. Finally,

a hazard ratio forest plot shows the associated effect size of hazard of death for each covariate and indicates significance.

Results

A total of 5114 standing stems were visited in 94 individual plots. Of the 5114 stems, 921 were dead (18%). Seventy-five percent of dead trees were aspen or spruce, and over 85% of all standing stems were aspen or spruce. Of dead trees decay class 1 and 2, a subsample of 72% of dead aspen and 72% of dead spruce trees were cored for a total of 323 dead aspen and spruce trees sampled. Plot-level attributes such as total stem counts, tree diameters, total plot basal area and stand origin year (accessed from AVI data) varied across plot location, disturbance type, and between species. There were in general a higher number of aspen stems throughout plot types, which were slightly larger in tree diameter than spruce stems (Table 7). Mean plot level cumulative post-disturbance tree mortality varied from a high of 9.4% to a low of 3.6% within treatment and location categories throughout the study area, the highest observed mortality at the individual plot level was 27.3%, and some plots had no observed mortality (Table 8).

Table 7: Plot-level attributes and summary statistics for aspen and spruce stem counts, tree diameters (dbh), average number of stems per hectare (measure of plot density including trees of all species), plot basal area, stand origin year for all plots grouped by locations and disturbance type.

Disturbance	Location	n aspen stems	Aspen DBH (cm) Median | Range		n spruce stems	Spruce DBH (cm) Median | Range		Avg. n Stems/ha	Plot Basal Area (m²) Mean | Range		Stand Origin Year Median | Range	
Fire	Island Edge	286	17.50	9.1-46.6	228	12.75	9.1-32.5	1633	1.756	1.046-2.462	1935	1910-1950
Fire	Island Interior	325	19.1	9.2-48	222	14.45	9.1-40.1	1558	1.820	1.406-2.114	1940	1910-1950
Fire	Reference Edge	372	21.2	9.3-44.7	215	15.2	9.1-33.5	1529	2.020	1.294-2.915	1935	1920-1950
Fire	Reference Interior	402	21.3	9.1-42	226	14.3	9.2-34.8	1637	2.032	1.334-2.663	1941	1910-1950
Harvest	Island Edge	252	23.0	9.4-45.7	179	17.6	9.1-41.5	931	1.983	0.929-2.607	1920	1860-1940
Harvest	Island Interior	270	22.9	10.5-47.4	127	18.8	9.2-40.4	893	1.844	0.910-2.583	1930	1860-1960
Harvest	Reference Edge	248	19.7	9.2-43.8	129	15.0	9.1-46.5	1010	1.743	1.035-2.254	1920	1900-1945
Harvest	Reference Interior	227	20.3	9.3-49.6	161	16.2	9.1-48.3	1032	2.030	1.802-2.411	1930	1860-1945

Table 8: Median, mean and range of post-disturbance plot-level mortality in each disturbance type by Disturbance and Location.

Disturbance	Location	Median Mortality	Mean Mortality	Range of Mortality
Fire	Island Edge	7.7%	9.4%	0-27.3%
Fire	Island Interior	5.2%	5.5%	0-17.8%
Fire	Reference Edge	3.6%	3.6%	0-8.3%
Fire	Reference Interior	3.9%	4.9%	0-16.9%
Harvest	Island Edge	3.3%	5.0%	0-20.0%
Harvest	Island Interior	5.0%	4.1%	0-13.3%
Harvest	Reference Edge	4.0%	4.7%	0-14.3%
Harvest	Reference Interior	4.9%	7.0%	0-20.0%

Logistic regression model building & evaluation

From field sampling, all 3869 living and post-disturbance dead aspen and spruce trees (including uncored dead trees that were assigned a post-disturbance death) were used to fit logistic regression models. Logistic regression models were built to test the both the interactions and main effects of variables of interest: disturbance type and location (island or reference, edge, and interior plots). This allowed for comparing post-disturbance mortality between disturbance types, location types, and locations within each disturbance (i.e., fire island edge/interior, fire reference edge/interior, harvest island edge/interior and harvest reference edge/interior). Multiple logistic regression models were built to determine which covariates improved model fit, which included the interactive and main effects of disturbance and plot location, and the additive effects of tree

species, tree diameter, and plot basal area. Models were built starting with all covariates and interactions included and then compared to simpler models omitting individual covariates (Table 9). Tree species and tree diameter were identified to significantly improve the model and were included in the selected model, mod1. Lower AIC and deviance values confirmed the selection of mod1 over other models fit (Table 9). Models mod1.3 and mod1.6 have ΔAIC of 2 or less; however, mod1.3 includes a covariate (total plot basal area) that does not show significance in further testing, and mod1.6 omits the interaction term of location and disturbance type which are central to the study design and research question (Table 9).Variance Inflation Factors (VIFs) were calculated to check for multicollinearity and the instability of mod1, all VIFs were less than 1.5 for variables included–indicating that mod1 with included covariates is stable and there is no concern for multicollinearity (Table A2 Appendix). Model parameters used in mod1 were significant based on the likelihood ratio test, and an ANOVA of simpler models vs. the model with included terms. The selected model—mod1—was evaluated with the DHARMa package (Hartig F (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level /Mixed) Regression Models), with results indicating no concern for over/under dispersion, no heteroscedasticity and well-fitting residual plots (Fig. A2 Appendix).

Table 9: Logistic regression models built with nested random term and covariates, modeling the response variable of probability of mortality where 1=tree death and 0=tree is alive. Region refers to the geographic fire or harvest region: Alpac, Mercer Harmon Valley, Mercer Peace River, Flattop, Utikuma and M024. SiteID is the pairing of each reference and island for 4 total plots: Island Edge, Island Interior, Reference Edge and Reference Interior. Lower AIC and Deviance values indicate better-fitting models, therefore the mod1 is the best candidate for this dataset (as indicated by bolded text).

Model name	Model	AIC	Δ AIC	Deviance	Test to Include:
Nullmod	~1 + (1 | SiteID/ Region)	1592	31	1586	Null model, all variation due to randomness
mod0	~ Disturbance * Location + (1 | SiteID/Region)	1594	33	1574	Study design interaction with no additive effects
mod1	**~Disturbance * Location + Species + DBH + (1 | SiteID/Region)**	**1561**	**0**	**1537**	
mod1.2	~ Disturbance * Location + DBH + total_ba +(1 | SiteID/Region)	1588	27	1564	Tree species
mod1.3	~ Disturbance * Location +Species + total_ba + DBH + (1 | SiteID/Region)	1562	1	1536	Total plot basal area
mod1.4	~ Disturbance * Location +Species + total_ba + (1 | SiteID/Region)	1582	21	1558	Tree diameter (dbh)
mod1.6	~ Species * DBH +Location +Disturbance + total_ba + (1 | SiteID/Region)	1563	2	1541	Species and dbh interaction

Logistic regression model indicates plot location, species, and size affect tree mortality

With significant p-values ($p < 0.05$), plot location, tree species, and diameter were determined to influence the response variable of tree mortality (Table 11, Figs. 5 & 6). Following

an estimated marginal means post-hoc test, there was one significant contrast: fire island edge plots had 2.4% higher mean post-disturbance mortality than fire reference edge plots (p<0.05, Fig. 7).

Figure 5: Predicted post-disturbance tree mortality from the selected logistic regression model (mod1) by plot location and disturbance type. Error bars indicate 95% confidence intervals. Mod1 indicated that Fire Island Edge plots had higher mortality than other plot locations or any harvest plots.

Additionally, the logistic regression model showed aspen trees had a higher mortality than spruce trees (p<0.05, Table 10). Estimated marginal means post-hoc tests supported this finding, with aspen expected to have around 10% mean mortality compared to spruce with 4% mean mortality (Fig. 6). Further, smaller sized trees had higher mortality than larger ones (p<0.05), with the smallest measured trees of 9.1cm dbh mortality at just under 8% and largest sized trees of 45-50 cm dbh with mortality of around 1% (Fig. 6).

Table 10: output of selected model, mod1, with nested error term (SiteID/Region), covariates of Species, DBH, disturbance, location and interaction term of Disturbance*Location. Significant p-values <0.05 indicate variables that influence post-disturbance tree mortality, including Location, Species and DBH, which are bolded below. Model fit: AIC= 1561.01, BIC= 1636.14, Pseudo-R² (fixed effects) = 0.08 Pseudo-R² (total) = 0.19.

| Fixed Effects	Est.	S.E.	Z value	p
Intercept	**-2.07**	**0.33**	**-6.37**	**<0.001**
DisturbanceHarvest	-0.36	0.41	-0.89	0.37
LocationIslandInterior	-0.33	0.25	-1.30	0.19
LocationReferenceEdge	**-0.88**	**0.29**	**-3.06**	**<0.001**
LocationReferenceInterior	**-0.63**	**0.27**	**-2.35**	**0.02**
SpeciesPOTR	**0.93**	**0.18**	**5.12**	**<0.001**
DBH	**-0.05**	**0.01**	**-4.45**	**<0.001**
DisturbanceHarvest:LocationIslandInterior	-0.16	0.41	-0.39	0.69
DisturbanceHarvest:LocationReferenceEdge	0.69	0.44	1.56	0.12
DisturbanceHarvest:LocationReferenceInterior	0.55	0.44	1.25	0.21
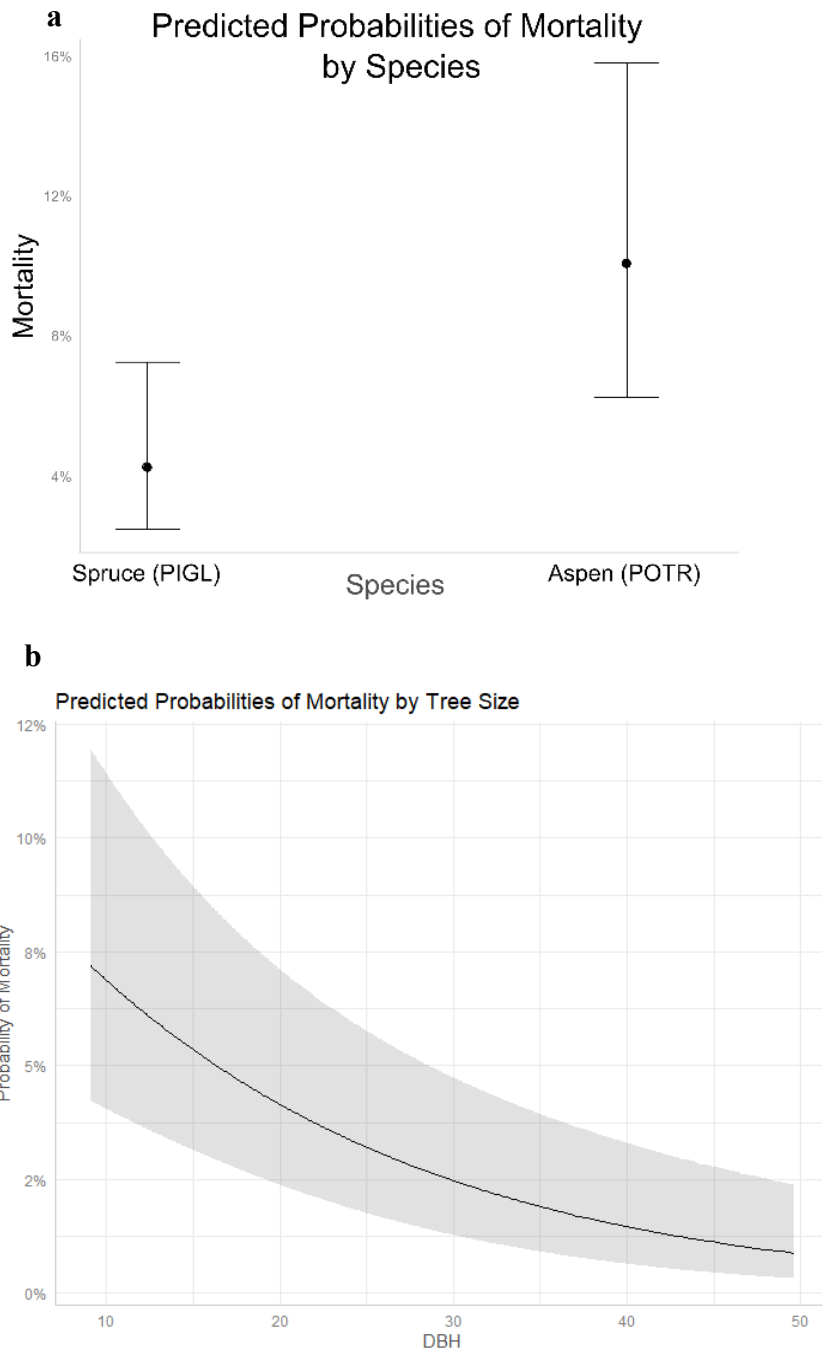
Figure 6: Mod1 predicted post-disturbance mortality of trees based on tree species (either Aspen or Spruce) **(a)**, aspen have higher mortality under these research conditions than spruce, error bars are 95% confidence intervals—and tree diameter **(b)**, where smaller sized trees have higher probability of mortality than larger sized trees, error bars are 95% confidence intervals.
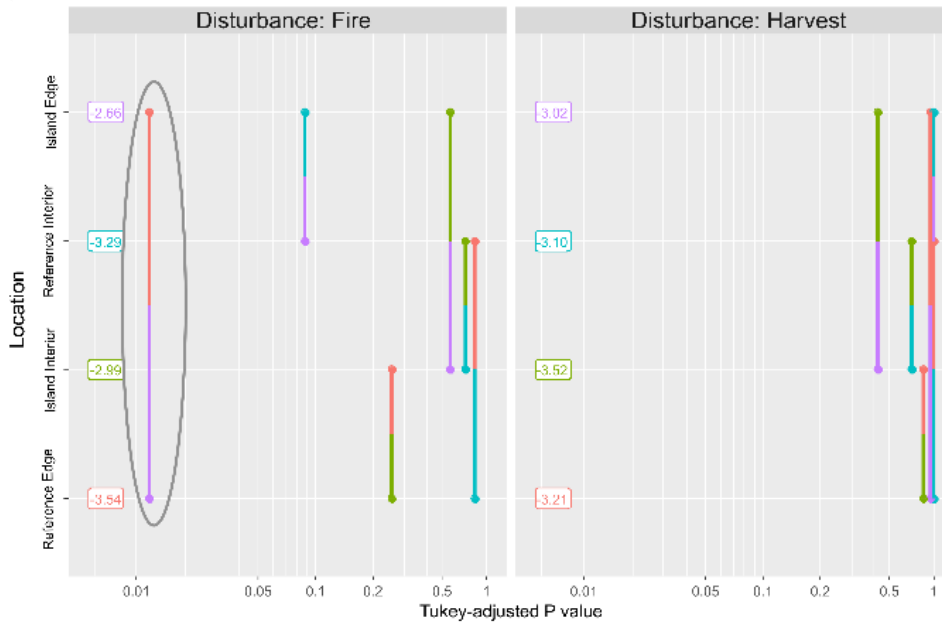
Figure 7: Pairwise p-value plots of estimated marginal means of post-hoc tests for interaction of Disturbance and Location of mod1. Vertical lines connect two treatments being compared. In an estimated marginal means between locations in each disturbance type, the only significant difference was between Fire Island Edge and Fire Reference Edge plots, which is circled above.

No temporal patterns of post-disturbance tree survival

The Kaplan-Meier curve of all living and dated dead aspen and spruce trees shows no specific temporal patterns or single years with a sharp decrease in survival; overall tree survival remained high (>95%) for the entire study area twelve years following disturbance (Fig. 8). Tree survival did not differ significantly between disturbance types (log-rank test, p=0.25) or location type (log-rank test, p=0.30) (Fig. 9). Within island plots, both disturbance type and plot placement (edge/interior) did not have any significant effect on tree survival (p>0.05). Between the two tree species of interest, aspen had a lower probability of survival than spruce (log-rank test, p=0.0021). Further, smaller sized trees (dbh 9.1-15.5 cm) showed a lower probability of survival than medium (dbh 15.5-22.5 cm) and large-sized (dbh 22.5+ cm) trees (log-rank test, p=0.017) (Fig. 10).
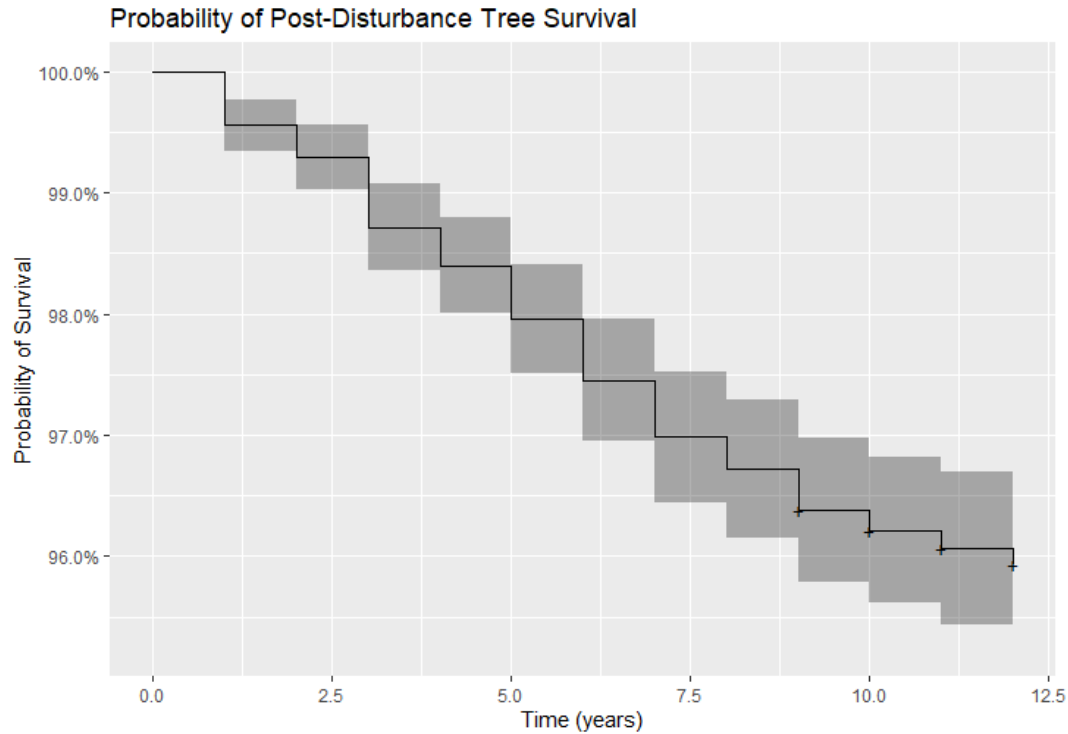
Figure 8: Aspen and spruce tree survival up to 12.5 years after disturbances–all disturbance types, plot types included. No one year has a sharp decrease in survival, and throughout time the probability of survival stays above 95%. The grey area around the line represents 95% confidence intervals. The + signs indicate data that are censored.

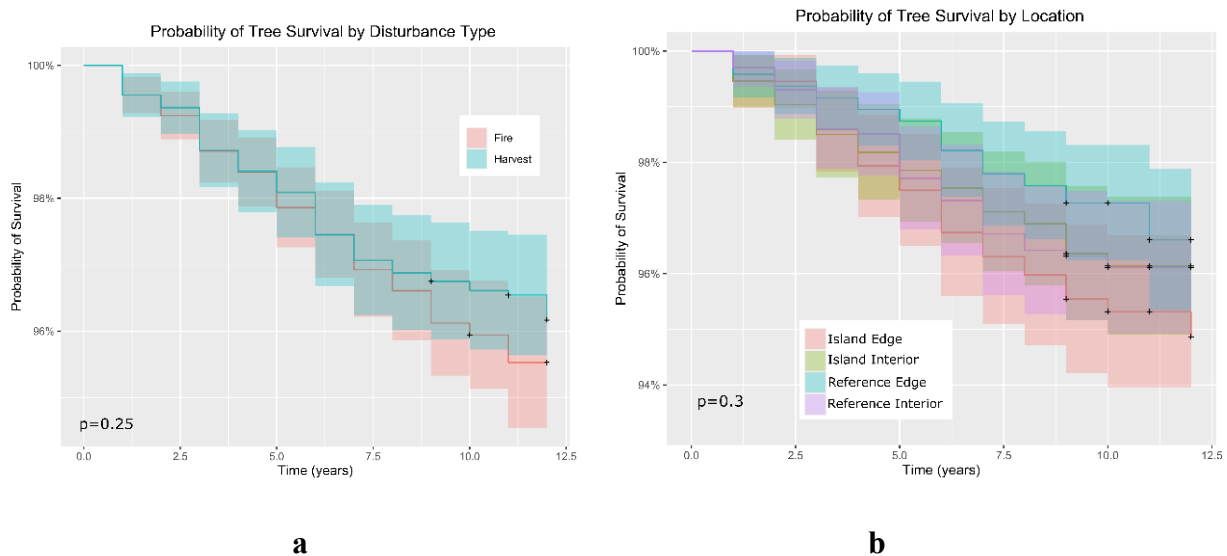a   b

Figure 9: probability of survival based on disturbance (a) and location (b), neither treatment results in a significant difference in probability of survival between treatment groups (p>0.05). The + signs indicate data that are censored, colors around each line represent 95% confidence intervals.
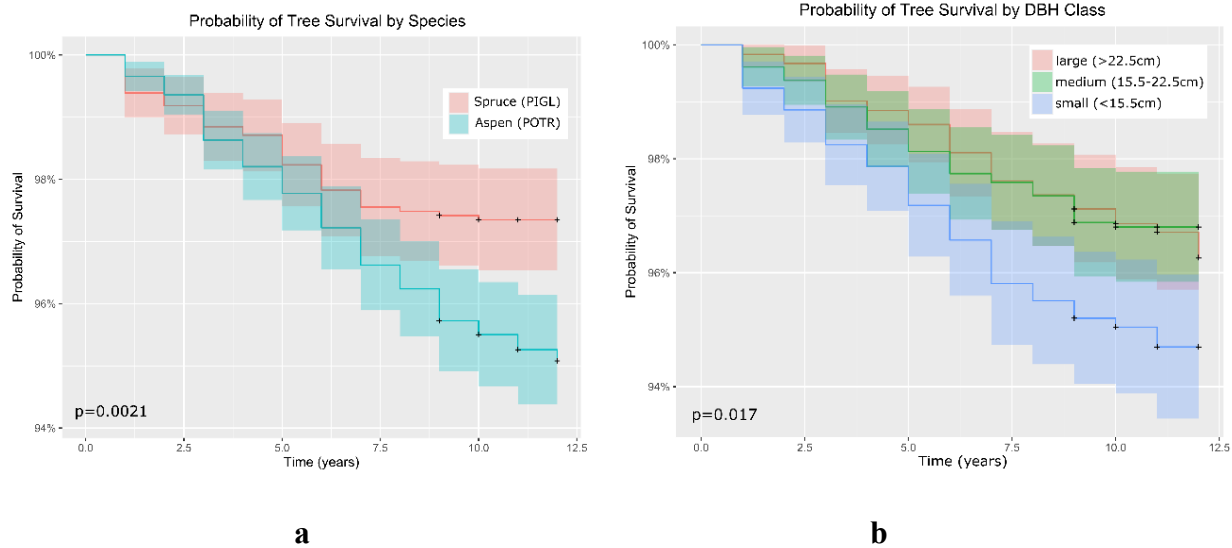
a   b

Figure 10: (a) tree survival curves comparing aspen and spruce and **(b)** by diameter class of trees (both aspen and spruce combined). Aspen trees show a significant difference of lower probability of survival compared to spruce, and smaller sized trees (9.1-15.5 cm dbh) show a lower probability of survival than larger sized trees (>15.5 cm dbh). The + signs indicate data that are censored, colors around each line represent 95% confidence intervals.

Smaller aspen trees (dbh 9.1-15.5 cm) show a significantly lower survival probability than larger sized aspen trees (log-rank test, p<0.0001), whereas the diameter of spruce trees did not affect tree survival (Fig. 11). The survival curve of spruce trees leveled off and became less steep after approximately seven years following disturbance, possibly indicating stabilizing survival, although survival is still quite high at over 96%. The survival curve of aspen trees did not appear to level off and tree survival continued to decrease through the twelve years following disturbance. Finally, among spruce trees, there was a marginally significant difference between fire and harvest disturbances, with spruce in harvest plots having slightly higher probability of survival at 98.4% compared to spruce in fire plots with survival at 96.6% (log-rank test, p=0.058) (Fig. 12).

a   **b**
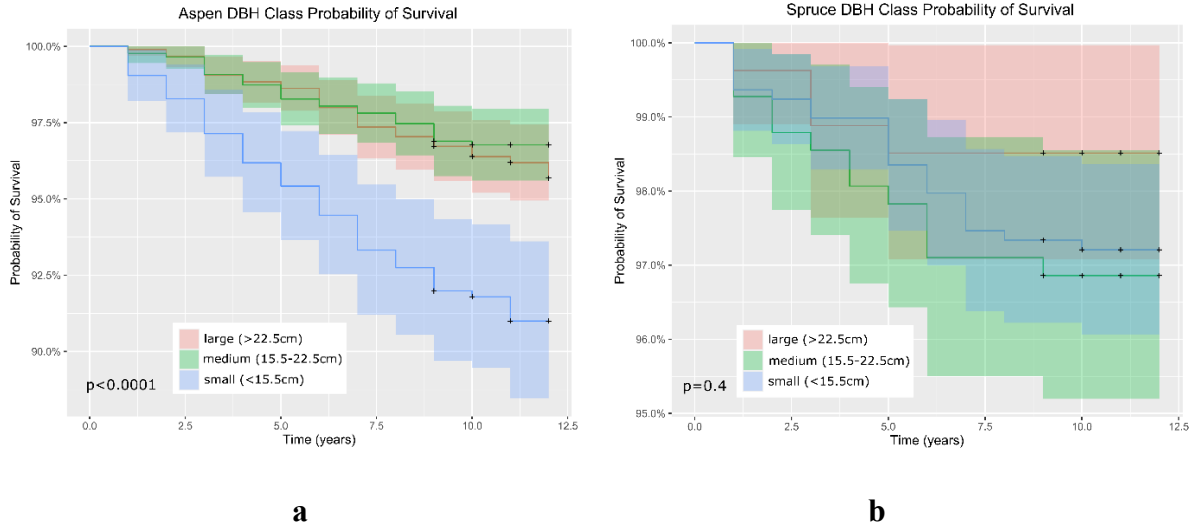
Figure 11: Probability of survival separated by tree species: small aspen trees have a lower probability of survival than larger sized aspen trees (a), spruce tree size does not affect the probability of tree survival (b). The + signs indicate data that are censored, colors around each line represent 95% confidence intervals.

Figure 12: Spruce survival curves following disturbance, with a marginal difference between fire and harvest disturbances (log-rank test, p=0.058), with spruce in fire sites showing lower probability of survival than those in harvest sites. The + signs indicate data that are censored, colors around each line represent 95% confidence intervals.

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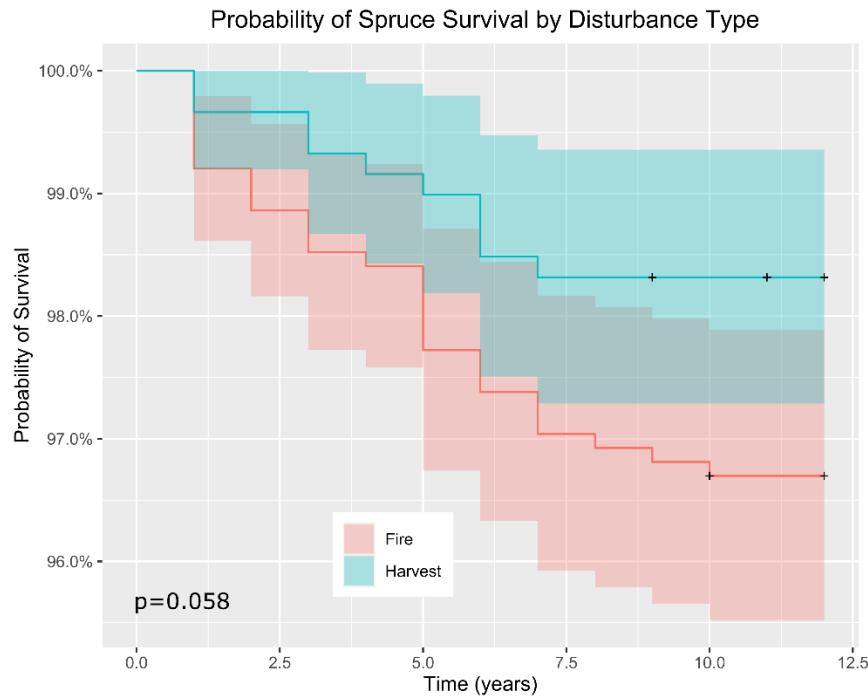Smaller sized trees, as well as aspen trees exhibited higher hazard of death via hazard ratios (Fig. 13), with significant differences ($p<0.05$). Aspen trees were 2.25 times more likely to die than spruce trees, and smaller sized trees (dbh 9.1-15.5cm) were 2.02 times more likely to die than larger sized trees (dbh>22.5cm). Finally, small aspen trees were 2.36 times more likely to die than larger sized aspen trees.
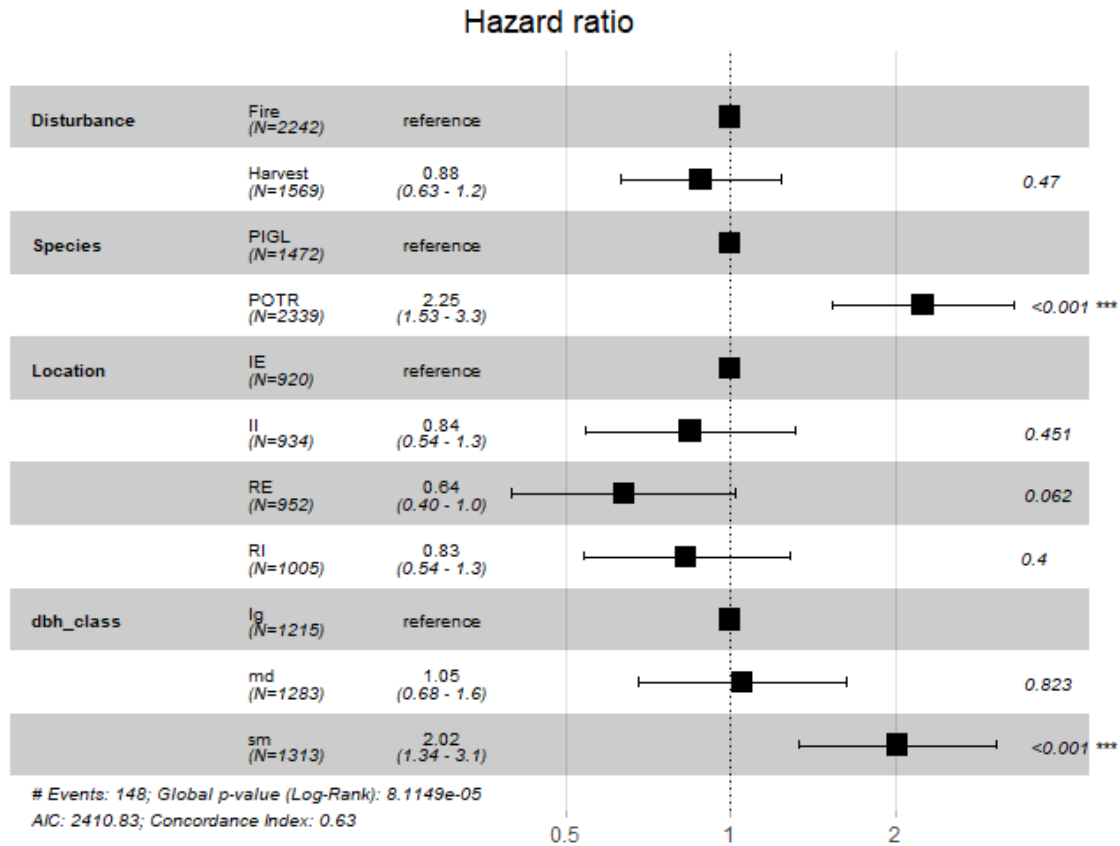
Figure 13: Hazard ratios for each treatment in cox regression curve, right column with asterisk indicates significant p-values for differences in treatment groups. Values above 1 indicate higher hazard of death, values below 1 indicate lower hazard of death. Aspen (POTR) is 2.25 times more likely to experience the hazard of tree death than spruce (PIGL), and smaller sized trees have roughly twice as high hazard of death than larger sized trees.

Discussion

This study provides an in-situ comparison of post-disturbance tree mortality in wildfire and harvest island remnants in the Western boreal forest of Canada, with a focus on standing dead mortality. While windthrown-caused mortality was not specifically measured in this study, considering the results of a companion study on recent downed deadwood that found no significant difference between either disturbance-created island remnant type and no edge effects observed, (Moore 2022 unpublished), we believe that overall post-disturbance tree mortality would not differ significantly based on treatments and covariates. However, these results on downed trees do not offer any insight into temporal patterns of windthrown caused mortality as the downed wood was not dated. Further, Moore (2022) found that the species makeup of downed deadwood had higher amounts of *Populus spp.* than *Picea spp.* in island remnant and reference forest sampling plots, so there is not an unaccounted-for influx of dead spruce that would otherwise influence overall post-disturbance mortality amounts when comparing tree species.

To our knowledge, the direct comparison of tree mortality in island remnants of wildfires and harvests within the paradigm of ecosystem-based management, or more specifically retention forestry, has not been made until now. Results from a large-scale retention experiment which implemented varying amounts of tree retention (EMEND experiment with 10, 20, 50, 75 and 100% retention) only compared residual tree mortality to reference forest or clearcuts, without the comparison to naturally created wildfire residuals (Solarik et al., 2012; Spence et al., 1999). Research in Finland examined post-disturbance mortality of both wildfire and harvest, but applied prescribed burns following harvest to the same study sites and harvest retention was not applied as island retention (Hämäläinen et al., 2016). Island remnant residual tree mortality following wildfire was analyzed in the Eastern boreal forest of Quebec (Angers et al., 2011), but with no

direct comparison to post-harvest mortality. Although the above studies examined tree mortality responses to individual disturbances (harvest and wildfire), there has been no explicit comparison made between wildfire and harvest island remnant tree mortality. Our results include tree mortality responses in both wildfire and harvest island remnants, integrating edge effects and individual tree characteristics to explain post-disturbance tree mortality in a comprehensive real-world study located in the Western boreal forests of Alberta.

Disturbances and edge effects on tree mortality

The results of the selected logistic regression model revealed that fire island edge plots had almost 6% higher mean mortality than fire reference edge plots based on post-hoc estimated marginal means comparisons. There was no overall difference detected in tree mortality by disturbance type or plot location in either the survival analysis or logistic regression analysis, as both forms of analyses measured the main effects of treatments, and datasets were relatively similar. Because survival analysis does not measure interactive effects and is focused on temporal patterns of singular effects, the pairing of these two analyses paints a comprehensive picture of post-disturbance standing dead mortality considering all covariates, treatments, interactions, and temporal patterns. Reference edge plots did not have higher mortality than reference interior plots, suggesting that the combination of island and edge location affects tree mortality more than simply edge effects alone. Harvest sites had no significant difference in tree mortality based on any plot location or interior/edge conditions. These findings support results from a study that found edge influence was more extensive at fire edges than cut edges (Harper et al., 2015). Trees along forest edges that were not initially killed due to wildfires may be damaged and more susceptible to mortality-causing agents, which could lead to the increased post-wildfire mortality seen in our study. However, residual trees left following harvest may also be damaged by logging equipment

resulting in higher post-harvest mortality compared to intact reference forest (Thorpe et al., 2008), although higher post-harvest tree mortality in island remnants compared to reference forest was not detected in this study.

The results of the survival analysis showed no apparent temporal patterns or peaks of tree mortality following either type of disturbance in this study. These results differ from findings in similar post-disturbance studies that found a strong pulse in tree mortality in the first two years following wildfire (Angers et al., 2011) and a peak in standing dead tree mortality following harvest (Thorpe et al., 2008). However, a caveat is that we did not account for windthrow-caused mortality in this study because dating downed wood was not feasible for the timeframe of this project, therefore it's possible not all post-disturbance mortality was captured, and unmeasured blowdown could contribute to temporal patterns seen in previous studies.

Individual tree covariates affect mortality

At the individual tree level, smaller tree diameter negatively affected the survival of trees in both the survival analysis and logistic regression models. Smaller sized trees had higher mortality throughout the decade after disturbances, although this pattern was more apparent in wildfire sites than harvest sites. These results support previous studies that documented a relationship between stem size and susceptibility to mortality, with smaller sized trees having higher mortality rates (Bladon et al., 2008; Caspersen, 2006; Yao et al., 2001). Smaller sized trees in younger and more dense stands are likely to self-thin, whereas smaller trees in mature stands are likely to be suppressed (Yao et al., 2001), which could explain the higher mortality seen in smaller diameter trees in the present study.

Our results suggested aspen trees were more likely to die than spruce, and further that smaller sized aspen trees have a lower probability of survival. There are several factors that could

support this finding. Tree death is influenced by the successional stage of forest stands, and aspen are early successional trees. We made an effort to sample areas with similar stand origin years, however the stand origin years in our plots ranged from 1860-1960 depending on the sampling region (Table 9), though we note that island remnant/reference pairs had similar or the same stand origin years. Stand origin years were provided from AVI data, and aerial imagery used to estimate stand ages may not be as accurate as on-the-ground measurements, although median stand origin years between fires and harvests were generally similar within twenty years. It is possible that some of the mortality captured is due to aging aspen stands, although the highest mortality overall was in fire island edge plots and based on the distribution of stand origin years, we would expect to see higher mortality across all sites with the same or similar stand origin years if this was due to aging aspen stands. In fact, the oldest stands were in harvest plots in all locations, which did not contain the highest standing dead mortality. A potential explanation for why aspen trees, and specifically smaller aspen trees had higher mortality than spruce or larger aspen trees is that when canopy cover decreases and wind exposure increases, smaller aspen stems experience more physical bending and this may damage their xylem, leading to water stress and possible mortality (Bladon et al., 2008). Finally, deciduous trees have been found to be less fire resistant than conifers and thin-barked aspen are the least fire resistant and have the highest mortality following wildfire, which could contribute to the higher mortality rates in our study in fire island edge plots and higher mortality rates of aspen trees (Hély et al., 2003).

Additional factors may influence tree mortality

Size or area of wildfire residuals and island remnants may be a factor that influences residual tree mortality. A study in Sweden found tree mortality decreased with increasing fragment/island remnant size when island remnants varied from 1/16–1 ha in size (Jönsson et al.,

2007). The size of island remnants measured in this study only varied from 1-2.5 ha, which is not entirely representative of the variety of island sizes created by wildfire or harvests. We selected study sites to compare similarly sized island remnants between both disturbance types, rather than including sites throughout the distribution of potential island sizes. This could indicate that at the size of 1 ha or larger, tree mortality may not differ significantly, although additional research on patch size is necessary to accurately estimate tree mortality between disturbance types with island size as a factor. Finally, we did not find total plot basal area—a measure of stand density—to be a significant covariate in predicting post-disturbance tree mortality. In contrast, a study in mixed conifer forests of the Lake Tahoe Basin found increased stand density to increase probability of tree mortality due to increased competition between trees, especially during a drought period (Van Gunst et al., 2016).

The present study captures post-disturbance standing mortality over a ten-year response period to determine if harvesting leaves a long-term impact on forest island remnants compared with fire island remnants. Establishing permanent sampling plots with consecutive site visits to capture immediate mortality following disturbances (as in Angers et al., 2011) in addition to long-term responses to treatments could improve sampling methods. Fire residual patches may decrease in size or even disappear throughout the years following fire because edges at residuals are highly dynamic, experience high rates of windthrow and exhibit delayed mortality in the transitional zones between burned and unburned areas (Perera and Buse 2014). Because our study sites were sampled only once a decade after disturbances, there may exist unmeasured island remnants that experienced higher mortality than we captured, incorporating these instances could better describe post-disturbance mortality in future studies.

Mortality from windthrow was not possible to include due to sampling methods and one season of data collection. Future work could explore collecting tree core samples from downed trees, although because downed wood decays faster it may be harder to collect solid cores for dendrochronological processing and accurately determining year of tree death. However, one study found that windthrow and standing death contributed equally to overall post-harvest mortality (Thorpe et al., 2008), suggesting that although we did not capture windthrow mortality in our study, patterns of mortality due to treatments and covariates could remain similar with or without incorporating windthrow. Although the data for this research was restricted to standing dead trees, downed deadwood was studied in a companion project using the same sampling plots. Total amounts of recent downed deadwood (defined as decay class 1-2 using similar morphological characteristics as methods listed above) were calculated and models built to detect differences. The results of this study found no differences in recent downed deadwood amounts in island remnants created by wildfire and harvest, as well as no edge effects on downed woody debris in reference or island remnant stands (Moore 2022, unpublished). These results from the same study sites allow us to speak to downed woody debris amounts; because there was no significant difference in recent deadwood between fire and island remnants or any measured edge effects, we can estimate that windthrow-caused mortality would not likely influence the results of this study even though this was not specifically measured.

Estimating year of tree death

Morphological attributes of dead wood such as presence of fine branches, bark coverage and intact top on trees have been used to classify decay stage and estimate time since tree death (Lombardi et al., 2008). Decay classifications are not species-specific and various tree species follow similar decay patterns. However, deadwood often contains characteristics associated with

multiple decay classes such as a snag having fine branches but no bark coverage, this can cause confusion when determining decay class (Angers et al., 2012). The accuracy of decay classification as a measure of time since tree death is questionable due to the variability in visual characteristics, assessments and additional factors that influence wood decay (Lombardi et al., 2008). Additionally, snags burned by wildfires may lack fine branches used to indicate decay stage. However, our study sites were specifically selected in unburned stands of forest with no visual evidence of burning, therefore this concern does not apply.

Research in coniferous subalpine forests in the Colorado Rocky Mountains provided an estimate that, although trees in older decay classes were dead longer than trees in younger decay classes (8-31 years difference in mean year of death between decay classes), the range of years of death for each decay class overlapped between decay classes and was too broad to accurately approximate year of tree death based on a given decay class (Mast and Veblen, 1994). The results of our study show similar results to existing research that decay class can provide an estimate but not define an accurate year of tree death based on dead wood characteristics.

Using tree rings and dendrochronological methods are useful to describe tree mortality patterns (Mast and Veblen, 1994) but in this study the years of death are meant only as an estimation of tree death timing as a response to disturbances. The last ring used in dendrochronological analysis may not correspond to the actual year of tree death because trees can stop producing rings 1-3 years before they die (Mast and Veblen, 1994). However, contemporary studies use tree rings and dendrochronology to estimate year of tree death, with the last ring produced as the year of tree death with an accuracy of one calendar year (Angers et al., 2011; Helama et al., 2012; Lombardi et al., 2008; Fritts 2012), and we feel confident that the crossdating methods and reference chronologies used here are robust enough for the objectives of this study.

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CONCLUSIONS

Implications for ecosystem-based management

Following wide scale disturbances, forest remnants of live trees and intact forest structure can aid in forest regeneration and provide important habitat to wildlife (Kohm and Franklin, 1997; Moussaoui et al., 2016). However, if there is high tree mortality in these island remnants, they may not function as effectively to provide these ecosystem services. This study found that tree mortality was not higher in harvest island remnant plots compared to fire island plots, providing evidence to support the continued implementation of island retention forestry within the scope of ecosystem-based management.

Certain tree-level attributes may better predict susceptibility to mortality; therefore, forest managers may choose to implement island retention in specific ways to decrease post-disturbance residual mortality. Minimizing edge creation by creating more round patches, especially in island remnants, may support residual tree survival. As small-diameter aspen trees are more susceptible to mortality, leaving behind larger sized aspen trees and higher amounts of spruce trees, when possible, could aid in island retention survival and persistence. Trees in forest island remnants that survive over ten years past disturbances are unlikely to die due to the effect of island creation and as they continue living, they provide canopy cover and habitat for wildlife, resources for forest regeneration, and contribute to structural diversity aiding in forest recovery (Angers et al., 2011).

Finally, our observational study provides real-world results based on what forest managers and operators are doing in the field, rather than experimental conditions set up by researchers that may not be followed closely in practice. By utilizing forest island remnants created in normal forest harvest operations, we can evaluate their resilience by quantifying post-harvest tree mortality. In harvest sites, residual tree mortality was similar regardless of edge or interior plot placement. In

the past, green tree retention has been criticized due to residual tree mortality, however our results show that in the decade following harvest, the loss of residual trees is not elevated in island remnants compared to reference forest or to post-fire residual tree mortality in the Western boreal forest.

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Appendix

Table A1: GPS coordinates of each sampling plot.

Plot	Island/Reference	Edge/Interior	Plot Centre Coordinates
ALP-08-IE	Island	Edge	55.521073,-112.288586
ALP-08-II	Island	Interior	55.520886,-112.288448
ALP-08-RE	Reference	Edge	55.529237,-112.280288
ALP-08-RI	Reference	Interior	55.52949,-112.280192
ALP-13-IE	Island	Edge	55.030638,-112.155542
ALP-13-II	Island	Interior	55.030475,-112.15565
ALP-13-RE	Reference	Edge	55.031569,-112.151908
ALP-13-RI	Reference	Interior	55.031843,-112.15187
ALP-18-IE	Island	Edge	55.197339,-111.698039
ALP-18-II	Island	Interior	55.197317,-111.698438
ALP-18-RE	Reference	Edge	55.197663,-111.701233
ALP-18-RI	Reference	Interior	55.197703,-111.701592
ALP-19-IE	Island	Edge	55.213238,-111.689193
ALP-19-II	Island	Interior	55.21342,-111.689022
ALP-19-RE	Reference	Edge	55.213967,-111.696339
ALP-19-RI	Reference	Interior	55.2138,-111.696434
M024-03-IE	Island	Edge	56.281412,-111.54275
M024-03-II	Island	Interior	56.281383,-111.542395
M024-05-IE	Island	Edge	56.275209,-111.479292
M024-05-II	Island	Interior	56.27508,-111.479459
M024-05-RE	Reference	Edge	56.27887,-111.485658
M024-05-RI	Reference	Interior	56.278843,-111.485897
M024-07-IE	Island	Edge	56.29209,-111.574658
M024-07-II	Island	Interior	56.291938,-111.574742
M024-07-RE	Reference	Edge	56.289346,-111.58131
M024-07-RI	Reference	Interior	56.289494,-111.581054
MEE-06-IE	Island	Edge	56.075134,-116.316069
MEE-06-II	Island	Interior	56.074986,-116.316293
MEE-06-RE	Reference	Edge	56.070544,-116.3082
MEE-06-RI	Reference	Interior	56.070497,-116.308
MEE-09-IE	Island	Edge	56.989972,-117.056543
MEE-09-II	Island	Interior	56.98982,-117.056633
MEE-09-RE	Reference	Edge	56.997292,-117.066089
MEE-09-RI	Reference	Interior	56.997442,-117.065747
MEE-13-IE	Island	Edge	56.988695,-117.074661
MEE-13-II	Island	Interior	56.988545,-117.075001
MEE-15-IE	Island	Edge	57.061119,-116.957634
MEE-15-II	Island	Interior	57.061109,-116.957846
MEE-20-IE	Island	Edge	56.11139,-116.314657
MEE-20-II	Island	Interior	56.111218,-116.314733
MEE-20-RE	Reference	Edge	56.100313,-116.328908
MEE-20-RI	Reference	Interior	56.100284,-116.329303
MEE-21-IE	Island	Edge	56.13818,-116.266201
MEE-21-II	Island	Interior	56.13812,-116.265915
MEE-21-RE	Reference	Edge	56.140141,-116.260025
MEE-21-RI	Reference	Interior	56.140247,-116.25981

Plot	Island/Reference	Edge/Interior	Plot Centre Coordinates
MEE-23-IE	Island	Edge	56.075103,-116.335233
MEE-23-II	Island	Interior	56.075039,-116.335501
MEE-23-RE	Reference	Edge	56.073484,-116.336217
MEE-23-RI	Reference	Interior	56.073525,-116.33666
MEE-24-IE	Island	Edge	56.082619,-116.335177
MEE-24-II	Island	Interior	56.082485,-116.334865
MEE-24-RE	Reference	Edge	56.083734,-116.333743
MEE-24-RI	Reference	Interior	56.083742,-116.333283
S056-03-IE	Island	Edge	55.321126,-115.108782
S056-03-II	Island	Interior	55.321097,-115.109153
S056-03-RE	Reference	Edge	55.333873,-115.080626
S056-03-RI	Reference	Interior	55.333891,-115.080121
S056-05-IE	Island	Edge	55.303963,-115.034154
S056-05-II	Island	Interior	55.30416,-115.033954
S056-05-RE	Reference	Edge	55.311594,-115.036921
S056-05-RI	Reference	Interior	55.311768,-115.036708
S056-07-IE	Island	Edge	55.278147,-115.072658
S056-07-II	Island	Interior	55.2783, -115.072
S056-07-RE	Reference	Edge	55.297631,-115.061836
S056-07-RI	Reference	Interior	55.297715,-115.06144
S056-08-RE	Reference	Edge	55.354256,-115.103644
S056-08-RI	Reference	Interior	55.354444,-115.103644
S056-10-IE	Island	Edge	55.327633,-115.01525
S056-10-II	Island	Interior	55.32771,-115.015112
S056-10-RE	Reference	Edge	55.328058,-115.022955
S056-10-RI	Reference	Interior	55.327952,-115.023257
S056-12-IE	Island	Edge	55.322263,-115.003944
S056-12-II	Island	Interior	55.322456,-115.004083
S056-12-RE	Reference	Edge	55.328375,-115.006833
S056-12-RI	Reference	Interior	55.32836,-115.007106
S057-05-IE	Island	Edge	56.05535,-115.337124
S057-05-II	Island	Interior	56.055298,-115.337378
S057-05-RE	Reference	Edge	56.050939,-115.333904
S057-05-RI	Reference	Interior	56.051011,-115.333537
S057-07-IE	Island	Edge	56.106898,-115.386439
S057-07-II	Island	Interior	56.106766,-115.386713
S057-07-RE	Reference	Edge	56.103632,-115.383104
S057-07-RI	Reference	Interior	56.103261,-115.382857
S057-10-RE	Reference	Edge	56.057713,-115.27985
S057-10-RI	Reference	Interior	56.057963,-115.279633
S057-11-IE	Island	Edge	56.072397,-115.344216
S057-11-II	Island	Interior	56.072162,-115.344525
S057-11-RE	Reference	Edge	56.038836,-115.385793
S057-11-RI	Reference	Interior	56.038878,-115.386073
S057-12-IE	Island	Edge	56.109796,-115.324851
S057-12-II	Island	Interior	56.109282,-115.324749
S057-12-RE	Reference	Edge	56.10543,-115.367932
S057-12-RI	Reference	Interior	56.105349,-115.368161

Table A2: Variance Inflation Factor (VIF) values for covariates included in logistic regression models to check for multicollinearity. Values less than 1.5 indicate stability in the model.

Covariate	GVIF	Df	GVIF^(1/(2*Df))
Disturbance	1.512869	1	1.229987
Location	4.464620	3	1.283209
Species	1.142249	1	1.068761
DBH	1.151938	1	1.073284
Disturbance*Location	5.820747	3	1.341209

Table A3: summary statistics of aspen and spruce trees included in logistic regression modeling: live and dead stems, with corresponding decay class, mean diameter and range of diameters. Dead trees were determined as having died after each target disturbance, therefore there are no aspen trees of decay class 4 and no spruce trees of decay class 3 and 4 included in the modeling dataset.

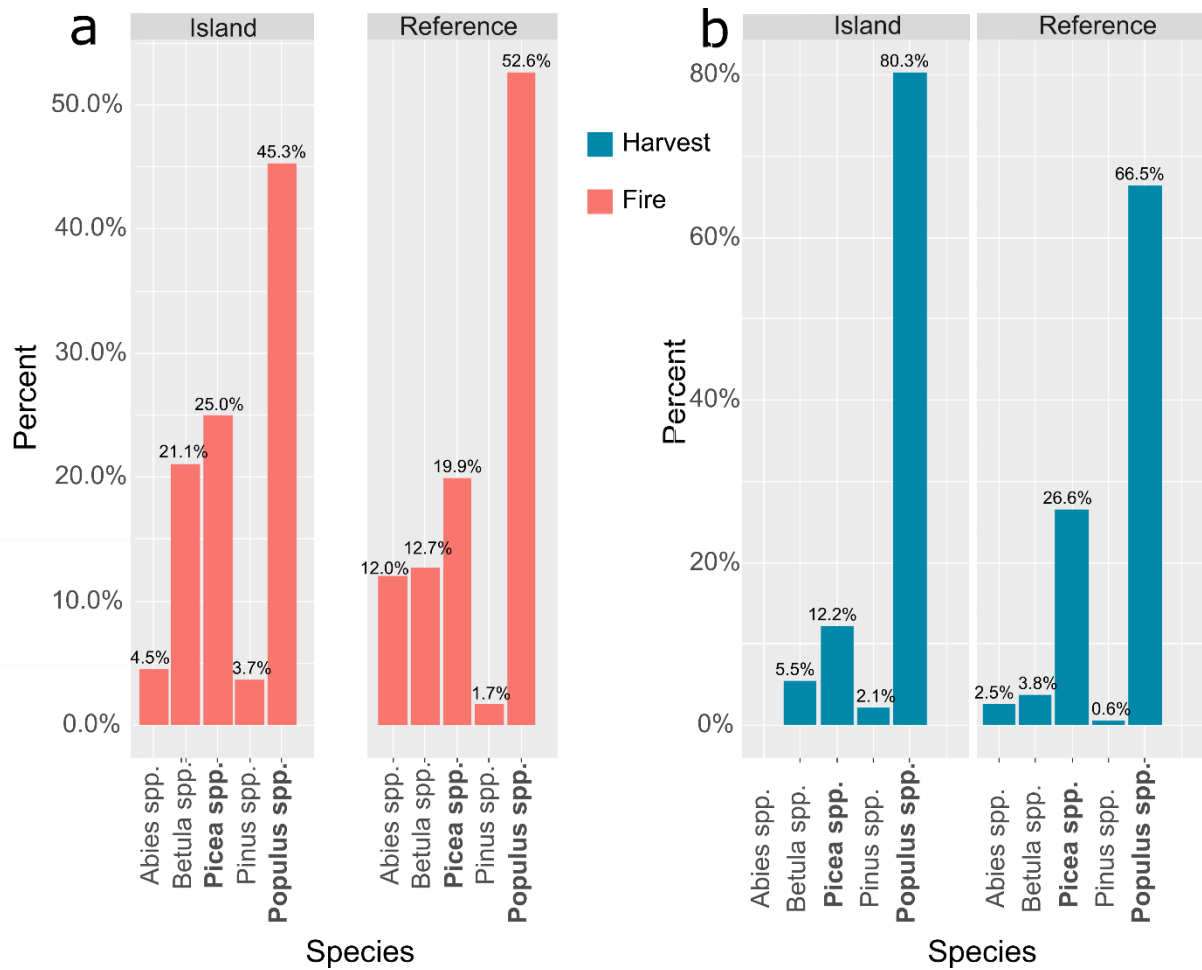| Species	Life Condition	Decay Class	n	Mean DBH (cm)	DBH Range (cm)
Aspen	Live	n/a	2230	21.8	9.1-49.6
	Dead	1	89	20.5	9.3-48.1
	Dead	2	61	17.1	9.1-39.7
	Dead	3	2	31.6	30.4-32.7
	Dead	4	0		
Spruce	Live	n/a	1433	16.8	9.1-48.3
	Dead	1	38	15.3	9.2-33.4
	Dead	2	16	15.8	9.2-33.7
	Dead	3	0		
	Dead	4	0		

Figure A1: Results of species compositions of recent downed deadwood in the same sampling plots (provided by Lance Moore) in fire disturbance (a) and harvest disturbance (b). In both reference and island remnant plots, *Populus spp.* are represented in higher amounts than *Picea spp.*, indicating that there was not an unaccounted-for flux of downed spruce that would otherwise influence results from this study.
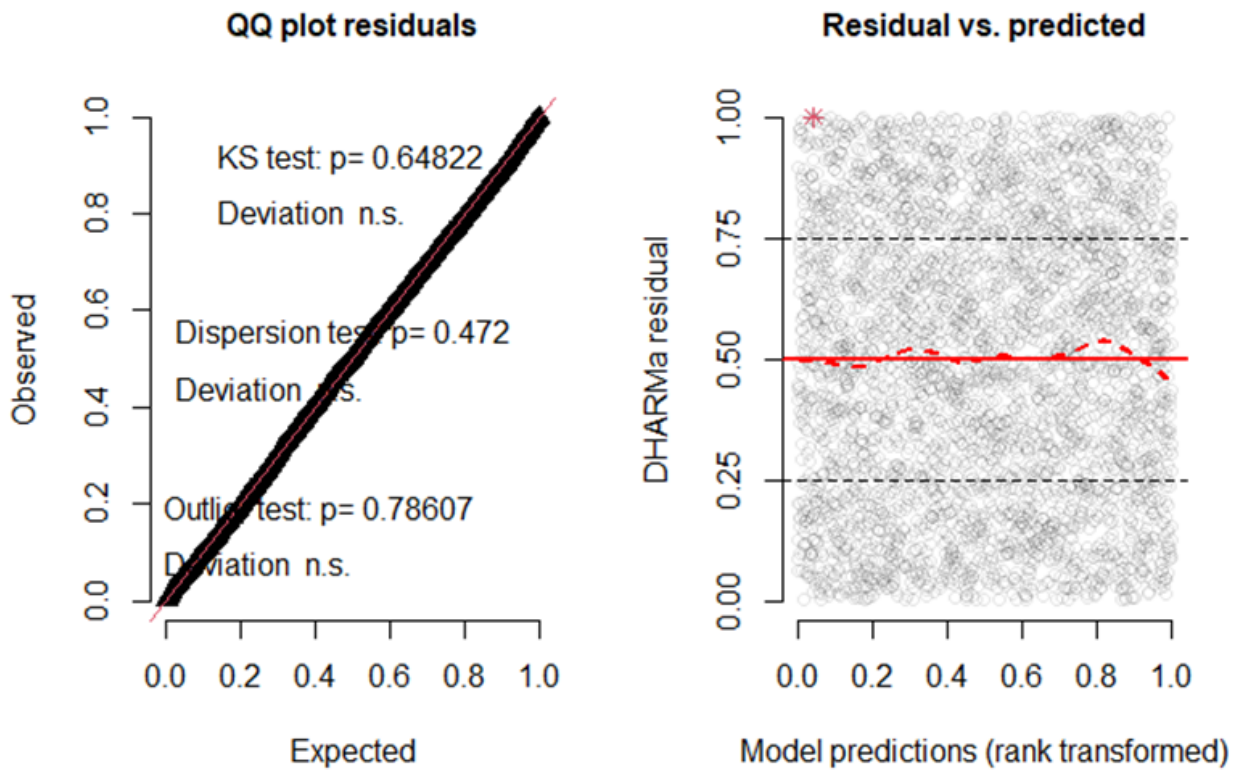
Figure A2: Residual plot outputs from DHARMa packages. A scaled residual value of 0.5 indicates that half of the simulated data are higher than the observed value, and half of them lower, therefore we see a uniform distribution in this output. Red stars indicate simulation outliers. With no significant p-values calculated in the QQ plot residuals and uniform distribution across the x and y axis in both plot outputs, expected model outputs and observed values are similar and model goodness-of-fit is sufficient.