Peatlands Reduce Fire Severity and Promote Fire Refugia in Boreal Forests

by

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

Master of Science

in

Forest Biology and Management

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Abstract

In the boreal biome of North America, large wildfires usually leave behind residual patches of unburned vegetation, termed refugia, which can strongly affect post-fire ecosystem processes. While topographic complexity is a major driver of fire refugia in mountainous terrain, refugia and fire severity (the ecological impacts of fire) in boreal landscapes are more likely driven by bottom-up controls affecting the extent and type of fuels. In this study, I investigate the role of hydrological (e.g., peatlands), ecological, and topographic heterogeneity on fire severity and the presence of fire refugia under different spatial and temporal climate moisture conditions in the Alberta boreal region over a 33-year (1985-2018) period. Fire severity was measured using the Relativized Burn Ratio (RBR). Generalized linear models were used to examine relationships of fire severity and probability of refugia as a function of bottom-up (vegetation, topography, site moisture, ecosystem) and top-down (normal and annual climatic moisture) controls. I then developed predictive maps of refugia probability and fire severity under normal and inter-annual climatic moisture conditions. I found that peatlands, stratified as bogs and fens, burned at lower severities and exhibited a higher probability of refugia than uplands, with vegetation (fuel) presenting a stronger control on fire than climate, topography, site moisture, or ecosystem type. In general, locations with wetter regional (normal) climatic moisture, a proxy for fuel amount, experienced increased fire severity and refugia probabilities when surrounded by more peatlands. While the amount of bogs affected both fire severity and refugia at intermediate scales (900-m area), fens affected fire severity most strongly when at a landscape scale (3000-m area) and refugia when at a local-scale (120-m area). Bogs decreased fire severity in adjacent uplands and peatlands under all regional and annual climatic moisture conditions but did not affect refugia probability in uplands. Fens reduced fire severity in adjacent uplands under all conditions and had varying effects on adjacent peatlands depending on moisture availability. Fens also increased refugia probability in adjacent uplands under all conditions, as well as in adjacent peatlands under all regional climatic moisture conditions. Areas of hydrologically-connected peatlands, particularly fens, may be capable of slowing future vegetation transitions, stemming from climate-driven increases to fire severity and post-disturbance moisture stress, in neighboring forests.

Acknowledgements

As a young child, my parents were disappointed when they realized I would never be an athlete as I hated running and preferred spending every t-ball game face down in the outfield playing with sticks and bugs. As an adult not much has changed, except now I play with sticks and bugs for a living.

The people in my early life may not have known they were raising a scientist but they certainly played a hand in contributing to my lifelong curiosity in the natural world. When we lived on Vancouver Island my parents, Michelle and Ralf, would take me to watch the salmon spawning behind the Safeway. I learned about how they moved from sea to river to breed and die, and saw how they fed the bears and eagles. It remains one of my most formative experiences. My daycare teacher at the time, Fran, also played a big role in this period of my life. Not only did she let me climb to the top of the tallest trees in the lot to inspect the unique bugs up there, she would also positively identify the old KFC bones I would dig up as bonafide fossils. I would not be who or where I am today without the experiences they all provided.

I would also like to thank the advisors who mentored me as a part of this research. My primary supervisor, Scott Nielsen, has pushed me to think more critically as a researcher, while always keeping the philosophy of science in mind. I have appreciated his ability to keep me on the right track when I have strayed off course and for providing a positive lab environment throughout all the challenges of 2020-2021. Ellen Whitman has taught me all I know about boreal fires and remote sensing, both of which were entirely new ground for me. She always lent me her total support and started and ended every conservation with kind words of praise and encouragement. This research, as well as my trajectory as an early career scientist, would not have been possible without the mentorship of Diana Stralberg. She has been the guiding force behind my study design, scripting, and analyses. She taught me how to be a scientist and has always made me feel like her main priority, despite her demanding schedule. My supervisors have been instrumental in my growth and I have appreciated how each has offered mentorship with the goal of training a future colleague.

Lastly, I would like to thank my friends Shachi, Kiran, Alyssa, and Cindy for keeping me sane throughout the last few years. Thank you for encouraging me to take breaks, believe in myself, and to keep at it. I promise to name a species after you someday.

Table of Contents

List of Tables

List of Figures

Glossary of Terms

ABMI: Alberta Biodiversity Monitoring Institute

ABoVE: Arctic Boreal Vulnerability Experiment

AIC: Akaike information criteria

ALPHA: Advanced landcover prediction and habitat assessment

ASA: Alberta severity atlas

AVHRR: Advanced very high resolution radiometer

CBI: Composite burn index

CMD: Climate moisture deficit

CNFDB: Canadian national fire database

CTI: Compound topographic index

DEM: Digital elevation model

Eref: Evapotranspiration

FTCP: Fine-textured clay plain

FTHM: Fine-textured hummocky moraine

GLM: Generalized linear model

HFI: Human footprint index

MAT: Mean annual temperature

MFST: Mean fire season temperature

NDVI: Normalized difference vegetation index

NOAA: National Oceanic and Atmospheric Administration

RBR: Relativized burn ratio

TPI: Topographic position index

Introduction

Wildfires do not burn homogeneously, often leaving behind residual patches of vegetation known as fire refugia (Krawchuk *et al.*, 2016). Given the importance of fire effects, such as burn severity, on post-fire vegetation recovery and forest resilience, areas within fire perimeters that do not burn, or remain largely unchanged by fire, can strongly affect post-fire ecosystem processes. Fire refugia are important for mitigating the combined effects of climate change and disturbance (Krawchuk *et* al., 2020) by acting as islands, mitigating changes to the plant communities within them and thereby increasing ecosystem resistance to the vegetation transitions resulting from increased fire severity and drought conditions (Tepley *et al.*, 2017). Previous research has identified topographic relief (complexity) as an important factor predicting fire refugia in areas with varying terrain. This terrain complexity has a bottom-up control on fire effects by influencing local variation in vegetation (fuels) and moisture (Krawchuk *et al*., 2016). In contrast, areas with little topographic relief facilitate fire spread (Harvey, Donato, and Turner, 2016; Falk *et al*., 2007) and decrease refugia predictability (Krawchuk *et al*., 2016). In these areas, fire refugia may relate more to hydrological and ecological aspects, driven by local patterns in terrain moisture and standing water (e.g., wetlands and lakes) (Krawchuk *et al.*, 2016; Nielsen *et al*., 2016; Ouarmim *et al.*, 2016).

The western boreal region of Canada is characterized by large-scale disturbances in the form of severe, stand-initiating wildfires with intervals of 50 to greater than 100 years between events (Kasischke and Turetsky, 2006; Boulanger *et al*., 2012). This region is particularly vulnerable to climate-mediated vegetation change following fire and is predicted to become increasingly vulnerable to drought events related to climate change (Stralberg *et al.*, 2018; Boucher *et al.*, 2018). Although some coniferous species in the boreal biome rely on fire to propagate (Buma *et al.*, 2013), an increase in fire intensity in conjunction with post-disturbance moisture stress (Stevens-Rumann *et al.*, 2017; Thompson *et al.*, 2013) has the potential to reduce conifer regeneration, resulting in widespread ecosystem transitions (Whitman *et al*., 2019; Johnstone *et al*., 2016; Boucher *et al.*, 2018).

Fire severity describes the ecological effects on vegetation and soils following a fire (Parks *et al.*, 2018). Severe fires have the ability to alter the regeneration of vegetation communities by damaging root systems during combustion of the soils, particularly in deciduous stands (Whittle *et al.*, 1997), and through overstory mortality of trees resulting in fewer mature trees needed for cone and seed production leading, ultimately, to the reduction of available seed sources needed to recolonize an area (Johnstone *et al*., 2016; Buma *et al*., 2013). This reduction of the pre-fire vegetation's ability to regenerate post-fire provides an opportunity for other early seral species to colonize and establish (Whitman *et al.*, 2018a; Johnstone *et al*., 2016).

In some areas, peatlands, in the form of open bogs and fens, have been demonstrated to burn at lower severities than uplands (Whitman *et al*., 2018b); however, their effects on fire refugia have yet to be explicitly examined. Through their ability to retain high water tables, peatlands are capable of resisting the drying effects of climate change (Schneider *et al.*, 2016; Thompson *et al.*, 2016; Thompson *et al.*, 2017). The presence of peatlands may therefore act as a driver of fire refugia in areas devoid of more complex terrain (Krawchuk *et al.*, 2016) by limiting the spread and severity of fires due to a high fuel moisture content and physical barriers presented by standing water when water tables are high (Thompson *et al*., 2019). These systems may also serve to reduce drought-induced effects on fire activity in upland ecosystems, depending on hydrologic connectivity (defined as connection to groundwater) (Thompson *et al.*, 2017; Hokanson *et al*., 2016). Peatland water retention and spatial patterning in the western boreal region is largely controlled by hydrologic connectivity stemming from the soil (pedology) on which peatlands are located (Hokanson *et al.*, 2016). Water tables are more stable in peatlands situated in lowland areas with coarse, well-drained soils and high connectivity to groundwater sources, while those located in regional topographic highs or on fine-textured silt and clay substrates are more likely to become disconnected from groundwater sources, leading to fluctuations in water tables and higher vulnerability to climate change (Hokanson *et al.*, 2016). Similarly, the severity and depth of burn in peatland fires has been shown to be higher in areas where peatlands are disconnected from one another and surrounded by a high amount of neighboring uplands (Hokanson *et al*., 2016).

Wildfires follow a seasonal cycle driven by a combination of changes in weather and vegetation (fuel), with short-term variation in precipitation, temperature, and phenology demonstrating a direct effect on the amount, flammability, and availability of fuel (Bajocco, Koutsias, and Ricotta, 2017). Fuel moisture content (a key component of flammability) is closely tied to vegetation phenology and has been shown to be an important factor in fire behavior worldwide (Bajocco, Koutsias, and Ricotta, 2017; Littell *et al.*, 2016; Kane *et al*., 2015).

Differences in flammability between uplands and peatlands during seasonal change or inter-annual drought yields distinctive fire potential between the two systems, with peatlands typically being less susceptible to fire relative to uplands under typical fire weather conditions but becoming a dense source of fuel during prolonged drought as water tables drop and vegetation dries (Thompson *et al*., 2017). The type (e.g., coniferous, deciduous) and configuration of vegetation (fuel) and disturbance (e.g., cutblocks) provide additional bottom-up controls on fire, which can promote or inhibit aspects of fire activity, including the size and shape of fire effects (Cansler and McKenzie, 2014; Harvey, Donato, and Turner, 2016). Areas with higher fuel homogeneity are more vulnerable to large, severe fires as increasingly extreme fire weather has the potential to overwhelm the bottom-up controls provided by vegetation (Cansler and McKenzie, 2014).

Although some models predict that widespread, climate- and disturbance-driven ecosystem transitions could occur throughout the western boreal region of Canada (Stralberg *et al*., 2018; Cadieux *et al*., 2020), current knowledge gaps limit their accuracy (Hart *et al.*, 2019). Included in these knowledge gaps are a lack of understanding regarding (a) the importance of bottom-up controls (e.g., vegetation composition, edaphic condition, ecosystem type) on fire activity in regions devoid of complex terrain, (b) the fire severity-reducing capabilities of peatlands on adjacent uplands, and (c) the extent to which these factors may lower fire severity during periods of drought. Using remotely-sensed fire severity data and a variety of geospatial inputs for the boreal region of Alberta, I developed a set of explanatory, thematically grouped (hereafter "component"), and parsimonious multivariate (hereafter "predictive") generalized linear models (GLM) to achieve the following objectives: (1) determine whether peatlands have a higher probability of fire refugia relative to uplands and, when burns do occur, whether peatlands burn at lower severities, (2) examine how the amount of surrounding peatland affects refugia probability in neighboring uplands and, when burns do occur, whether peatlands reduce fire severity, (3) determine whether fire refugia creation is affected by inter-annual changes in climatic moisture, and (4) determine the relative contribution of bottom-up (physical setting, vegetation, ecosystem) and top-down (climate) controls on fire severity and refugia probability. Finally, I built predictive maps of fire severity and refugia probability over a range of annual and seasonal conditions in northern Alberta's boreal biome.

Table 1. Research questions, hypotheses, and supporting literature used to predict the effects of peatlands on fire severity and refugia in boreal biomes.

Question	**Hypothesis**	**Supporting references**
Q_1: Do peatlands have a higher probability of refugia than uplands? If they do burn, do they burn at a lower severity?	**H_1:** Peatlands will have lower severities and higher refugia probabilities than upland forests as a function of differences in site moisture and fuel composition	Krawchuk et al (2016), Whitman et al (2018b), Whitman et al. (2019)
Q_2: If an upland burns, is its severity affected by the proportion of neighboring peatlands and is this effect influenced by drought?	**H_{2a}:** Fire severity in uplands will be negatively correlated with surrounding amount of peatland due to more hydrologic connectivity **H_{2b}:** During droughts, uplands with more surrounding peatland have lowered fire severity as function of hydrologic connectivity (*i*); however, this effect will decrease with drought intensity as fuel moisture decreases in the ecosystems (*ii*)	Collins et al (2019), Whitman et al (2018b), Thompson et al (2017), Madoui et al (2010)
Q_3: Does the proportion of surrounding peatlands promote refugia in uplands and how is this affected by drought?	**H_{3a}:** Refugia probability in uplands will be positively related with amount of surrounding peatland as a result of more hydrologic connectivity **H_{3b}:** Under droughts, uplands with more surrounding peatlands will have higher probability of refugia than those without,	Hokanson et al (2016), Turetsky et al (2004)

	as function of hydrologic connectivity (*i*), with probability decreasing as drought conditions intensify as a function of increases to fuel flammability and lowered water tables (*ii*)	
Q4: Of the bottom-up and top-down controls, which has the strongest influence on fire severity and refugia probability overall?	**H4:** Of the bottom-up controls, those pertaining to site moisture (e.g., pedology, terrain moisture, lake effects) will present the strongest control on fire severity and refugia probability due to the strong influence of site moisture on vegetation composition and physical barriers presented by water (e.g. lakes and rivers)	Krawchuk et al (2016), Thompson et al (2017), Nielsen et al (2016)

Methods

Study Area

The study area encompassed the majority of Alberta's boreal biome, covering an area of roughly 465,580 km^2. It includes four natural regions: the Canadian shield, foothills, the boreal forest natural region, and portions of parkland in the Peace region (Figure 1). The southern portion of the study area was truncated due to data limitations in the land cover dataset for this region. Latitude ranges from ~55°N to 60°N, with elevations ranging from 163 m to 1,777 m above sea level. The region has limited topographic complexity with the exception of the high plateaus, Rocky Mountain foothills, and major river valleys.

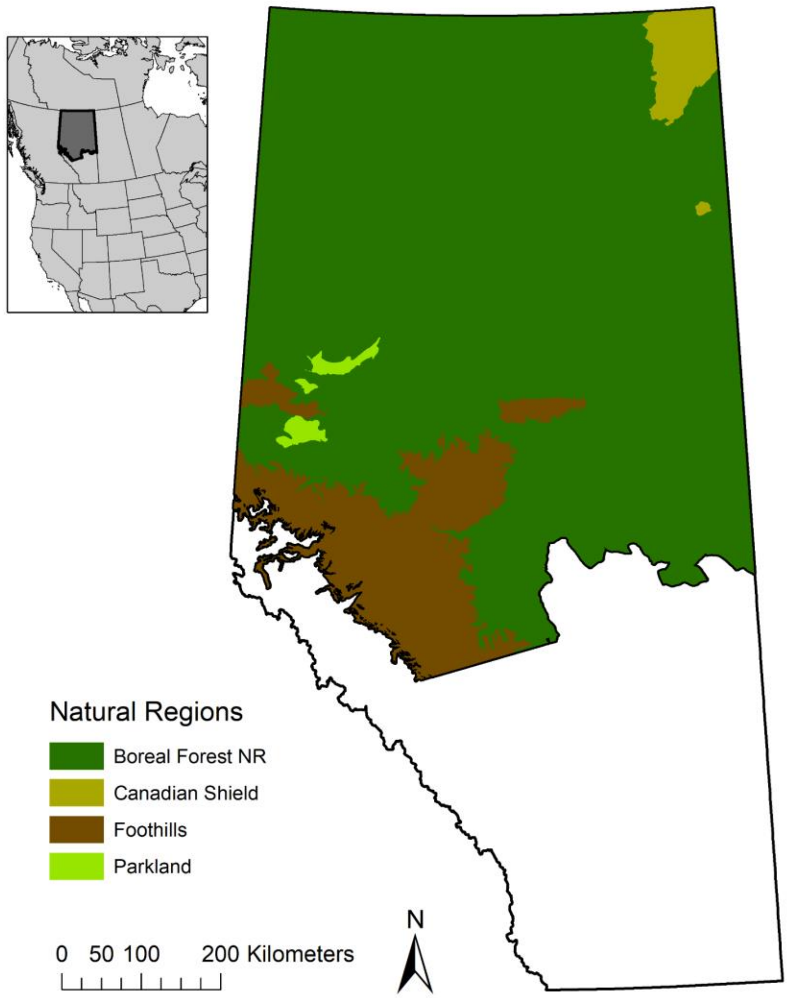


Fig. 1. The study region covers roughly half of the province of Alberta, and is primarily comprised of forested areas. The majority is made up of the boreal natural region, located within the boreal plain, with parts of the Canadian Shield included in the northeastern corner and the Rocky Mountain Foothills located towards the southwest. Portions of parkland habitat are found towards to west.

The climate is characterized by short summers averaging 15° C and long, cold winters averaging -10° C. Mean annual precipitation is 459 mm with 60-70% falling as rain between April and August (Downing and Pettapiece, 2006).

The area is made up of a patchwork of upland forests and extensive wetland systems. Upland forests are composed mainly of trembling aspen (*Populus tremuloides*) and white spruce

(*Picea glauca*) stands. Jack pine (*Pinus banksiana*) in the east and lodgepole pine (*Pinus contorta*) in the west are also common on well-drained soils. Peatlands, in the form of bogs and fens, cover nearly half the area and are either open, shrubby, or sparsely forested dominated by black spruce (*Picea mariana*) and larch (*Larix laricina*), respectively. The geologic setting consists of uplands corresponding with well-draining, coarse-textured soils, and wetland areas atop poorly-draining, fine-texture organic soils (Downing and Pettapiece, 2006). Fine-textured soils are common in lowlands, particularly those associated with glaciolacustrine, fine-textured moraines, and organics.

About 39% of the study area has experienced human disturbance, largely in the form of timber harvest and industrial development for the purpose of natural resource exploration and extraction (Schieck *et al.*, 2014). Fire is the most common form of natural disturbance in the boreal biome, with an average of 142,976 ha having burned annually in Alberta between 1961-2004; 73% of which occurred in the boreal forest natural region (Tymstra *et al*., 2007).

Study Design

I fit generalized linear models to explain the relationship between hydrological, topographic, and ecological bottom-up controls within the surrounding landscape (independent variables) and both fire severity and refugia probability (dependent variables). In particular, I was interested in exploring how these relationships were affected by interactions with normal and inter-annual climatic moisture conditions in uplands surrounded by a high proportion (amount) of peatlands. Variable sampling was conducted as either single point, in which values at the location of a sampled fire pixel were extracted, or as a set of 5 square-shaped moving windows (120 m, 300 m, 900 m, 1200 m, 3000 m), with a data resolution of 30 m, used to capture neighborhood effects and created through the 'focal statistics' tool in ArcMap. To determine which of the bottom-up and top-down controls present the strongest effect on fire severity and refugia, multiple predictor variables representing landscape and climate factors were grouped into thematic categories (i.e., component models) according to their role in forest fires (i.e., Climate, Physical Setting, Vegetation, Ecosystem) and compared to rank their importance. Finally, I developed two parsimonious multivariable models to create predictive maps of fire severity and refugia probability across the study area under a range of annual and seasonal scenarios. All analyses were performed in RStudio (RStudio Team, 2020; R Core Team, 2021) and mapped at a 30 m resolution and in a NAD 1983 Transverse Mercator projection.

Remote Sensing of Fires

Using the Alberta Severity Atlas (ASA) dataset I included all fires ≥ 200 ha in size which burned between 1985 and 2018 (Whitman *et al*., 2020). While only 3% reach this size, fires ≥ 200 ha are responsible for 97% of the total area burned annually in the Canadian boreal (Stocks *et al*., 2002). To represent the severity of each fire, I used the Relativized Burn Ratio (RBR) at a 30 m resolution. RBR is an index of fire severity that measures the difference in reflectance of healthy vegetation and changes to soils between pre- and post-fire satellite data (Parks *et al*., 2018). The RBR has been found to correspond meaningfully with field measures of fire severity, such as the Composite Burn Index (CBI). In the western Canadian boreal, RBR is mainly related to measures of overstory fire severity (Whitman *et al*., 2018b; 2020). In this study, pixels that were within fire polygons but contained an RBR value of ≤ 7.22 were considered as unburned fire refugia (Whitman *et al*., 2020). This threshold corresponds with measures of CBI considered to represent unburned areas within fires (CBI ≤ 0.1) (Whitman *et al*., 2020). As seasonality has been shown to influence fire activity in the boreal, each fire was assigned a date corresponding to the day, month, and year of first report as recorded in the Canadian National Fire Database (CNFDB; Canadian Forest Service, 2021). Corresponding with Alberta's typical fire season, only fires with a start date between March and October were included. Fire size (ha), created through raster calculations for each fire, was extracted for use in analysis as previous studies have shown that, while larger fires contain a higher proportion of severe burns compared to smaller fires (Cansler and McKenzie, 2014; Harvey, Donato, and Turner, 2016), they also result in higher proportions, and larger patches, of unburned residual stands (Whitman *et al*., 2018b). A total of 595 fires were sampled.

Terrain and Site Moisture

Topographic complexity was represented via a topographic position index (TPI) derived from a standard digital elevation model at a 50-m native resolution (DEM; Jenness, 2006) (Table 2). TPI is a comparative measure of the elevation of each pixel relative to the mean elevation of a specified neighborhood around that pixel. High values reflect locally high points in steep terrain, such as ridges, while negative values indicate low terrain, such as valleys. Those close to zero represent locations that are mid-elevation. TPI was extracted at the location of each fire pixel in the sample. Terrain moisture was measured through a compound topographic index (CTI) derived from the DEM (Table 2). CTI is a measure of water flow accumulation (i.e., potential wetness) based on fixed terrain features, such as slope, and is strongly correlated with soil qualities such as moisture and texture (Buttrick *et al*., 2015). Mean CTI values were calculated for the 5 moving-window sizes.

The Arctic Boreal Vulnerability Experiment's (ABoVE's) Landsat-derived Annual Dominant Landcover dataset (Wang *et al*., 2019) was used to delineate annual water boundaries, while the Alberta Biodiversity Monitoring Institute's (ABMI) ALPHA 3.0 Predictive Landcover dataset (DeLancey *et al*., 2019) was used as a static measure of water. To capture the effects on fire severity and refugia probability of the amount of both annual and static water availability, the mean proportions of water bodies from both datasets were calculated for the 5 spatial scales ranging from 120 m to 3000 m (Table 2). To create a distance to water variable, lake features from ALPHA were filtered such that only those ≥ 5000 ha were considered, as lakes above this size were most likely to influence fire spread according to Nielsen *et al*. (2016). A total of 28 lakes, ranging from 5072–785,000 ha, were retained. Distance to these lakes was measured using the Euclidean distance tool in ArcMap and further transformed to log10 scale (Nielsen *et al*., 2016) (Table 2).

Table 2: Variables and sampling methods used in analyses, as well as original data sources.

Association	**Variable**	**Temporal status**	**Sampling method**	**Data source**
Terrain, site moisture, pedology	Topographic position index (TPI)	Static	Single-point	DEM-derived
	Composite terrain index (CTI)	Static	Moving windows	DEM-derived
	Proportion of water	Static	Moving windows	ABMI ALPHA Predictive Landcover 3.0
	Proportion of annual water	Annual	Moving windows	ABoVE: Landsat-derived Annual Dominant Land Cover

	Distance to water (log10)	Static	Single-point	ABMI ALPHA Predictive Landcover 3.0
	Pedology: *bedrock* *coarse* *fine-textured clay plain* *fine-textured hummocky* *moraine*	Static	Moving windows	Soil Landscapes of Canada-Derived
Climate	Phenology: *max* *min* *mean*	Annual	Single-point	NOAA Climate Data Record of Normalized Difference Vegetation Index (NDVI), Version 4
	Climate normals: *Climate moisture deficit (CMD)* *Evapotranspiration (Eref)* *Mean fire season temperature (MFST)*	Static	Single-point	ClimateNA, Version 6.3
	Annual climate: *CMD* *Mean annual temperature (MAT)*	Annual	Single-point	ClimateNA, Version 6.3
Ecosystem	Bog Fen Upland Swamp Marsh	Static	Moving windows and single-point	ABMI ALPHA Predictive Landcover 3.0

Vegetation and disturbance	Dominant vegetation: *evergreen* *deciduous* *shrubland* *sparse vegetation* *barren* *herbaceous* *littoral* *annual bog* *annual fen*	Annual	Moving windows	ABoVE: Landsat-derived Annual Dominant Land Cover
	Proportion Cutblock	Annual	Moving windows	ABMI ALPHA Predictive Landcover 3.0

Pedology

To investigate the influence of pedology, variables were created from the Soil Landscapes of Canada version 3.2 dataset (Soil Landscapes of Canada Working Group, 2010), wherein soils were grouped into four classes based on grain (Table 3). The mean proportions of each pedology category were calculated for the 5 moving windows (120 m, 300 m, 900 m, 1200 m, 3000 m) to capture the heterogeneity of their textures (Table 2).

Table 3. Description of the soil classes, taken as proportions, comprising each category in the pedology variable.

Pedology category	**Surficial geology**
Bedrock	Bedrock
Fine-textured hummocky moraine (FTHM)	Moraine Stagnant ice moraine

Fine-textured clay plain (FTCP)	Glaciolacustrine
	Fine fluted moraine
	Fine ice-thrust moraine
	Organics
Coarse-textured	Fluvial
	Lacustrine
	Colluvial
	Pre-glacial fluvial
	Eolian
	Coarse fluted moraine
	Coarse ice-thrust moraine

Climate

Mean climate moisture deficit (CMD), mean evapotranspiration (Eref), and mean fire season (March – October) temperatures (MFST) from 1981-2010, captured at a 500 m resolution, were used to represent climate normals (Table 2). Annual climate variables consisted of mean annual CMD, a proxy for drought, and mean annual temperatures (MAT) (Table 2). Both normal and annual CMD were extracted for each sampled pixel. All measures of CMD were downscaled and calculated using ClimateNA, Version 6.3 (Wang *et al.*, 2016). Although local fire weather at the time of burning is an important factor in fire effects (FCFDG, 1992), particularly during extreme conditions (Dillon *et al.*, 2011; Krawchuk *et al.*, 2016), daily fire progression and associated weather conditions were not available within the study area for the entire period analyzed (1985-2018). For this reason, I was unable to examine the effect of fire weather and instead focused on the effects of broader (i.e., annual or 30-year period) climatic conditions.

Information on vegetation phenology was collected from the National Oceanic and Atmospheric Administration (NOAA) Climate Data Record of Normalized Difference Vegetation Index (NDVI) Version 4 dataset. This dataset uses Advanced Very High Resolution Radiometer (AVHRR) data to create daily records of NDVI values at a global scale (Vermote *et al.*, 2014). NDVI is a measure of plant productivity that is often used as a proxy for plant phenology, particularly when estimating the onset of 'greening' and 'browning' due to seasonality or drought. NDVI data was collected for each day between February 15 to October 31, corresponding to roughly two weeks before and after the start and end of a typical fire season in Alberta, for each year of the study period. I then calculated the minimum, maximum, and mean phenology values over 7- and 14-day periods prior to the date of first report for each sampled fire (Table 2).

Ecosystem

The ALPHA dataset provided the static location and classification of major ecosystem types (upland, bog, fen, swamp, marsh, water) at a 10-m native resolution (DeLancey *et al*., 2019). The ecosystem underlying each sampled pixel was extracted, while the amount of each type was also calculated for the 5 moving windows (120 m, 300 m, 900 m, 1200 m, 3000 m). Similarly, the ABoVE dataset was used to capture annual boundaries for bogs, fens, and water to better estimate changes in water tables resulting from inter-annual variation in climate. For each sampled point I calculated the amount of each class as proportions within the 5 moving windows.

Vegetation and Disturbance

The ABoVE landcover dataset (Wang *et al*., 2019) was used to determine dominant annual vegetation (Table 2). This dataset contains annual data for 10 vegetation and non-fuels classes updated annually from 1984-2014, capturing temporal changes as the result of human and natural disturbance. These disturbances are captured by classes pertaining to shorter vegetation classes, such as shrubland and barren ground, though these also occur naturally. The annual proportion of each vegetation class was calculated within the 5 moving windows and later extracted from the year prior to a fire to avoid an overestimation of low vegetation classes stemming from issues relating to the timing of imagery. As the ABoVE product does not contain data for 2015 onwards, the proportions of dominant vegetation and non-fuels for the year 2014 were held constant for 2016-2018 fires.

The ABMI's 2018 Human Footprint Inventory (HFI) contains the date and location of all timber harvest areas, termed cutblocks, throughout forested Alberta. As the flammability of a cutblock is partially dependent on age, these data were split into two groups – one for use as a variable and the other for use as a mask to reduce noise caused by potentially misclassifying locations of limited fuel as refugia (Guindon *et al*., 2021). The cutblock variable included the annual amount of all stands harvested 0-29 years pre-fire for the 5 spatial scales (those aged ≥ 30 years pre-fire were considered regenerated) (Thompson *et al*., 2017), while the mask included cutblocks aged 0-3 years pre- and post-fire (San-Miguel, Andison, and Coops, 2019, Guindon *et al*., 2021).

Spatial Analysis

A 3000 m buffer around the study area was used to ensure that the largest moving-window size could be computed for all fire pixels. To ensure that all pixels included in an analysis were the result of a burn and not a reflection of permanent non-fuels, areas within fire perimeters overlapping static water bodies (from ALPHA) or cutblocks aged ≤ 3 years pre- or post-fire (San-Miguel, Andison, and Coops, 2019; Guindon *et al*., 2021) were masked out, using the 'mask' function in R's raster package (Hijmans, 2019). A random 1% sample of the study area was then generated from each fire with NA values (e.g., masked pixels, data gaps) removed. Finally, a binary classification of refugia ("1") and burns ("0") was developed, wherein samples with a RBR value of ≤ 7.22 (Whitman *et al.,* 2020) were considered to be refugia. This resulted in a total of 1,526,087 sample points.

A random 30,000-point subset was selected for modelling and statistical analysis. This large sample size was chosen given the expansive study area and variability of the landscape (Nielsen *et al*., 2016). The subset was then partitioned into training and testing sets through a random 80:20 split. In non-forested areas, such as shrub or graminoid-dominated wetlands, low RBR values may be more indicative of the rapid speed at which resprouting vegetation recovers after fire than true locations of refugia (San-Miguel, Andison, and Coops, 2019). To more accurately capture true burn and refugia locations, the sample subset was further reduced such that only those overlapped by locations considered as forested in either the first year of the study (1985) or the last year of the ABoVE dataset (2014) were retained. Data used in models for fire severity were truncated to include only samples with an RBR value of ≥7.23 to focus on sites that burned.

This resulted in a training sample of 16,090 pixels for fire severity models and 20,092 for refugia. All variables measured through moving windows were then evaluated such that only the best fitting scales, measured via the Akaike Information Criterion (AIC) (Akaike, 1981), were retained. A correlation matrix was used to test for multicollinearity amongst the retained variables. Of pairs with correlation values of $r \geq |0.6|$, a single variable was retained based on its comparative R^2 value relative to either fire severity or refugia probability.

Once variable reductions were complete, a set of 13 linear (fire severity) and 13 logistic (refugia) GLMs were created. Each set of 13 models included 7 explanatory models in which hypotheses were tested, 5 component models analyzed for relative importance of the variables, and one predictive model for use in creating maps (Appendix A: Table 1). Included in the explanatory models are two ecological null models (ecosystem + fire size) created to test whether peatlands had a higher probability of refugia and lower severities, when burned, than uplands while holding fire size constant. Explanatory models, with the exception of the ecological nulls, were based on samples restricted to either upland or peatland locations, whereas the component models, predictive models, and ecological nulls were based on samples taken from the landscape as a whole. Following partition into the two ecosystems, sample sizes for upland fire severity and refugia were 10,907 and 13,335, respectively, while those for peatland fire severity and refugia were 4,634 and 6,051. Effect sizes for probability of refugia were calculated as $(\exp(\beta^{-1}))*100$, with beta (unstandardized) defined as the degree of change of individual variables per every 1-unit of change in fire severity or refugia probability. Component models were created through grouping variables by shared characteristics relative to fire behavior (Climate, Physical Setting, Vegetation, Ecosystem), whereas predictive models were created from the full suite of variables (Appendix A: Table 1). When a static and annual version of a variable was considered (i.e., proportions of bogs, fens, and water), static measures were used preferentially in the explanatory and component models, while annual measures were used in predictive models to capture temporal change resulting from inter-annual variation. To reduce overfitting, non-significant variables ($p > 0.05$) were removed from each model in a stepwise fashion. The exceptions to this rule were the two additive explanatory models, in which all variables were retained to examine differences in effect between fens and bogs. Component models were compared and ranked according to their relative AIC values.

Predictions were made using the 'predict' function in R's raster package (Hijmans, 2019). As peatlands and measures of CMD are the primary focus of this research, a number of terms were included in the predictive models to reflect the effect of interactions between variables (Appendix A: Table 1). To more accurately capture treed peatlands, models included interaction terms between the proportions of each annual peatland class and evergreen forest. Where needed, interactions reflected the best fitting scale for each peatland class (e.g., Annual Fen (120 m) $\times$ Evergreen (120 m)). In predictive models only, Annual CMD was replaced with the variable 'CMD anomalies' (annual CMD - normal CMD) to represent drought intensity. Predictive maps were created to reflect both early (May 1-14) and late (August 18-31) fire season phenological conditions, as well as examples of drought (2011) and non-drought (2009) years. Additional maps reflecting typical seasonal and annual conditions were created by averaging values for phenology and CMD anomalies across the study period. Maps for predicted severity depict fire probabilities ≥ 0.6. I did not produce predictions for regions that were excluded from mapping in the ASA to limit predictions to those regions from which the training data were gathered.

Results

Across the landscape, peatlands burned at significantly different severities than uplands. Standardized coefficients from the ecological null models ($\beta_{(std.)}$) showed that fens ($\beta_{(std.)} = -18.24$, SE = 2.23, $p < 0.001$) and bogs ($\beta_{(std.)} = -10.27$, SE = 5.05, $p < 0.001$) burned at lower severities than uplands ($\beta_{(std.)} = 209.79$) (Appendix A: Table 2a), with bogs having the lowest mean fire severity (Figure 2a). Fens had a higher probability of refugia than uplands ($\beta_{(std.)} = 0.16$, SE = 0.04, $p < 0.001$) (Figure 2b; Appendix A: Table 2b), while likelihood of refugia in bogs were similar to uplands ($p = 0.23$).

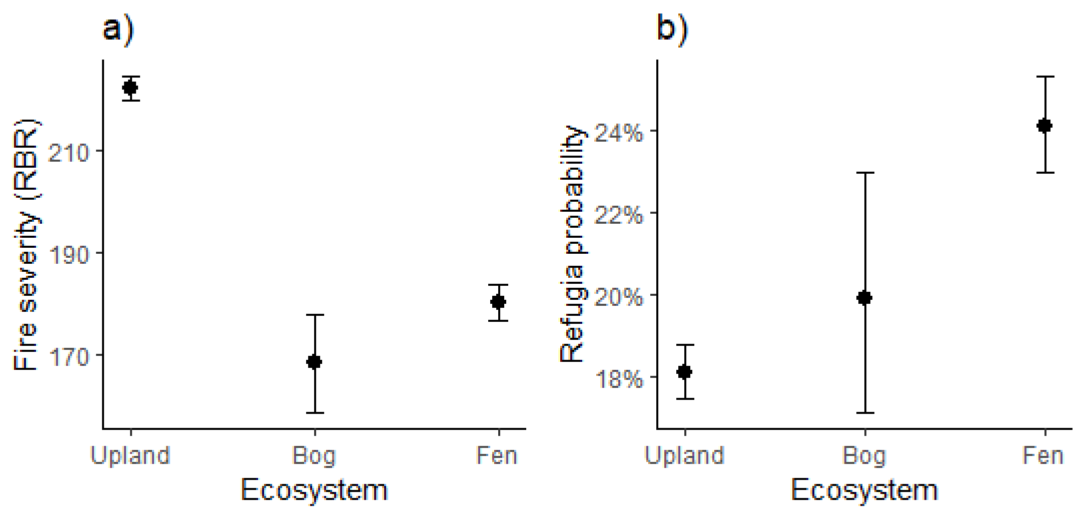


Fig. 2. Depiction of fire severity (a) and refugia probability (b) for the three ecosystems, taken from a sample of the full landscape and controlling for fire size. Error bars represent 95% confidence intervals.

The proportion (henceforth amount) of peatlands affected fire severity and refugia probability at different spatial scales. The amount of fens within a 3000-m area around a site (pixel), and bogs within a 900-m area, were negatively related to RBR (hereafter fire severity). While fire severity was affected by the amount of fens and bogs at larger scales, effects on refugia occurred at more intermediate scales. Specifically, the amount of fens within a 120-m area, and the amount of bogs within a 900-m area, best predicted the presence of refugia (Figure 3). These results suggest that, while the effects of bogs on fire severity and refugia probability occur at intermediate scales, fens affect fire severity most strongly at landscape scales and refugia at more local scales.

The amount of surrounding peatland, as well as fire size, influenced fire severity and refugia probability in adjacent ecosystems in models that did not include climate. Increasing fire sizes lowered fire severity in both uplands (β = -5.24e^{-05}, SE = 5.81e^{-06}, $p < 0.001$; Table 4a) and peatlands (β = -7.98e^{-05}, SE = 1.05e^{-05}, $p < 0.001$; Appendix A: Table 3a). However, fire size affected refugia differently depending on the ecosystem, decreasing probabilities in uplands (β = -4.88e^{-07}, SE = 1.16e^{-07}, $p < 0.001$; Table 4b) while increasing them in peatlands as fire size increased (β = 2.68e^{-06}, SE = 1.60e^{-07}, $p < 0.001$; Appendix A: Table 3b). In uplands, fire severity decreased by over 275 units (RBR) on average when the amount of surrounding fens was highest

(0.20; Figure 3a), while bogs decreased fire severity in uplands by only 25 units (Figure 3b). Refugia probabilities in uplands increased by 8% as fen amount increased, though bogs did not have a significant effect (Figure 3c; Table 4b). In peatlands, fire severity decreased by 35 units as the amount of bogs within a 900-m area increased (β = -80.96, SE = 12.99, $p < 0.001$; Appendix A: Figure 1a), while no significant effect was seen for the amount of fens within a 3000-m area (Appendix A: Table 3a). The probability of fire refugia in peatlands was significantly related to amount of fens and bogs in the surrounding area (β = 5.22, SE = 2.08, p = 0.012 and β = 0.994, SE = 0.26, $p < 0.001$, respectively) (Appendix A: Table 3a, Figure 1b,c), with probability of refugia increasing by 68.5% for every 10-fold increase in the amount of surrounding fens and a 10.5% for every 10-fold increase in the amount of surrounding bogs.

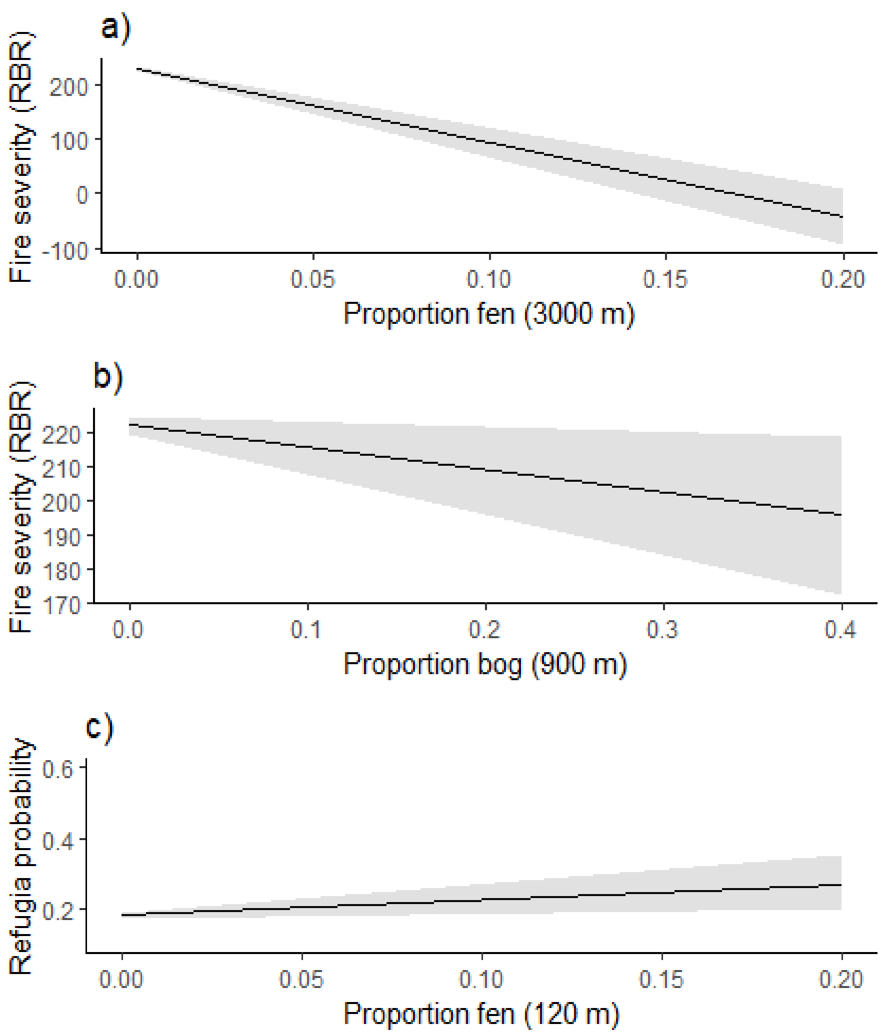


Fig. 3. The effects of the amount of surrounding peatland on fire severity (a, b) and refugia probability (c) in uplands, while controlling for fire size. Shaded areas represent 95% confidence intervals.

Table 4. Results for additive models for both fire severity (a) and refugia probability (b), using only samples located in uplands. Raw beta values are represented by β, while standardized beta values demonstrating strength of effect between factors are represented by $\beta_{(std.)}$.

a. Fire severity (upland additive model)

Variable	$\boldsymbol{\beta}$	**SE**	**p**	$\boldsymbol{\beta_{(std.)}}$
Fire size (ha)	$-5.24e^{-05}$	$5.81e^{-06}$	< 0.001	-10.87
Proportion bog (900 m)	-69.09	30.38	0.030	-2.62
Proportion fen (3000 m)	$-1.36e^{+03}$	130.40	< 0.001	-12.50
Intercept	237.20	1.68	< 0.001	221.77

b. Refugia probability (upland additive model)

Variable	$\boldsymbol{\beta}$	**SE**	**p**	**Odds ratio**	$\boldsymbol{\beta_{(std.)}}$
Fire size (ha)	$-4.88e^{-07}$	$1.16e^{-07}$	< 0.001	1.00	-0.10
Proportion bog (900 m)	-0.14	0.57	0.807	0.87	-0.01
Proportion fen (120 m)	2.58	1.03	0.012	13.23	0.05
Intercept	-1.44	0.03	< 0.001	0.24	-1.51

The amount of surrounding peatland, as well as fire size, influenced fire severity and refugia in uplands in models where normal CMD was considered, with wetter regions consistently showing higher fire severities and refugia probabilities relative to drier regions. Increasingly dry normal CMD conditions decreased fire severity (β = -0.15, SE = 0.03, p < 0.001), as did the amount of both fens within a 3000-m area (β = -1.12e^{+03}, SE = 139.20, p < 0.001) and bogs within a 900-m area (β = -59.89, SE = 30.37, p = 0.049) (Table 5a). Fire severity was also shown to decrease as fire size increased, when accounting for normal CMD (β = -4.51e^{-05}, SE = 6.00e^{-06}, p < 0.001). Uplands with higher amounts of fens in the surrounding landscape had lower fire severities than those without, with reductions of roughly 220 RBR in both wetter (CMD = 107) and drier regions (CMD = 192) (Figure 4a). There was a decrease in fire severity in uplands as the amount of bogs increased under all regional moisture conditions (reductions of 25 RBR and 23 RBR, respectively); however, wetter regions had consistently higher severities than drier regions (Figure 4b). Normal CMD also had a negative effect on refugia probability (β = -3.20e^{-03}, SE = 5.20e^{-04}, p < 0.001; Table 5b), decreasing it by 0.03% for every 10-fold increase in CMD. Increasing fire sizes also decreased refugia probability, in models that included normal CMD (β = -3.45e^{-07}, SE = 1.20e^{-07}, p = 0.004). The amount of fens within a 120-m area increased refugia probability in uplands (β = 3.11, SE = 1.03, p = 0.003) by 36.4% for every 10-fold increase in fen amount. Uplands with higher amounts of fens in the surrounding landscape had a higher probability of refugia than those without, regardless of normal CMD condition (Figure 4c). Refugia increased by roughly 10% in both wetter and drier regions, though refugia probability was consistently 5% lower in drier regions than in wetter regions.

In peatlands, the amount of both bogs and fens, as well as fire size, influenced fire severity and refugia probability in models where normal CMD conditions were included. Here, fire severity was affected differently depending on the type of surrounding peatland, as well as regional moisture conditions. In contrast, refugia probabilities in both bogs and fens were consistently higher in wetter regions. Fire severity in peatlands was positively related to climate normals of moisture deficit (normal CMD) (β = 0.14, SE = 0.04, p = 0.001), as well as to the amount of fens within a 3000-m area (β = 375.50, SE = 1.26e^{+03}, p = 0.003) (Appendix A: Table 4a). Fire size, however, was inversely related to fire severity (β = -8.17e^{-05}, SE = 1.06e^{-05}, p < 0.001), as was the amount of bogs within a 900-m area (β = -64.67, SE = 9.80, p < 0.001) and interactions between normal CMD and fen proportion (β = -22.14, SE = 6.75, p = 0.001). The amount of fens produced differing effects on fire severity depending on whether peatlands were located in wetter or drier regions. Specifically, peatlands in wetter regions experienced an increase of 230 units, while drier regions experienced decreases of 90 RBR, as the amount of fens rose (Appendix A: Figure 2a).

Bogs, on the other hand, reduced severity under all regional moisture conditions, producing decreases of roughly 25 RBR in both wetter and drier regions, though drier regions had consistently higher fire severity relative to wetter regions (Appendix A: Figure 2b). Refugia probability in peatlands had a weak negative relationship with normal CMD (β = -7.45e^{-03}, SE = 2.19e^{-03}, p = 0.001) (Appendix A: Table 4b). Specifically, there was a 0.03% decrease in peatland refugia probability for every 10-fold increase in normal CMD. Increasing fire sizes (β = 2.62e^{-06}, SE = 1.62e^{-07}, p < 0.001), as well as the amount of both fens (β = 5.11, SE = 2.08, p = 0.014) and bogs (β = 0.86, SE = 0.26, p = 0.001) increased peatland refugia probability. Specifically, peatland refugia likelihood increased by 66.7% and 9.0% for every 10-fold increase in fen and bog amount, respectively. Refugia probability was consistently highest in wetter regions (Appendix A: Figure 2c,d).

Table 5. Results for final models describing fire severity (a) and refugia probability (b), as a function of the amount of surrounding peatland and CMD normals in uplands. Beta values on the left are raw, while those on the far right are standardized for comparing variable strength.

a. Fire severity (uplands)

Variable	β	**SE**	**p**	$\beta_{(std.)}$
Fire size (ha)	-4.51e^{-05}	6.00e^{-06}	< 0.001	-9.36
Normal CMD	-0.15	0.03	< 0.001	-6.38
Proportion bog (900 m)	-59.89	30.37	0.049	-2.38
Proportion fen (3000 m)	-1.12e^{+03}	139.20	< 0.001	-10.31
Intercept	257.40	4.50	< 0.001	221.76

b. Refugia probability (uplands)

				Odds

Variable	β	SE	p	ratio	$\beta_{(std.)}$
Fire size (ha)	-3.45e^{-07}	1.20e^{-07}	0.004	1.00	-0.07
Normal CMD	-3.20e^{-03}	5.20e^{-04}	< 0.001	1.00	-0.14
Proportion fen (120 m)	3.11	1.03	0.003	22.39	0.06
Intercept	-0.99	0.08	< 0.001	0.37	-1.51

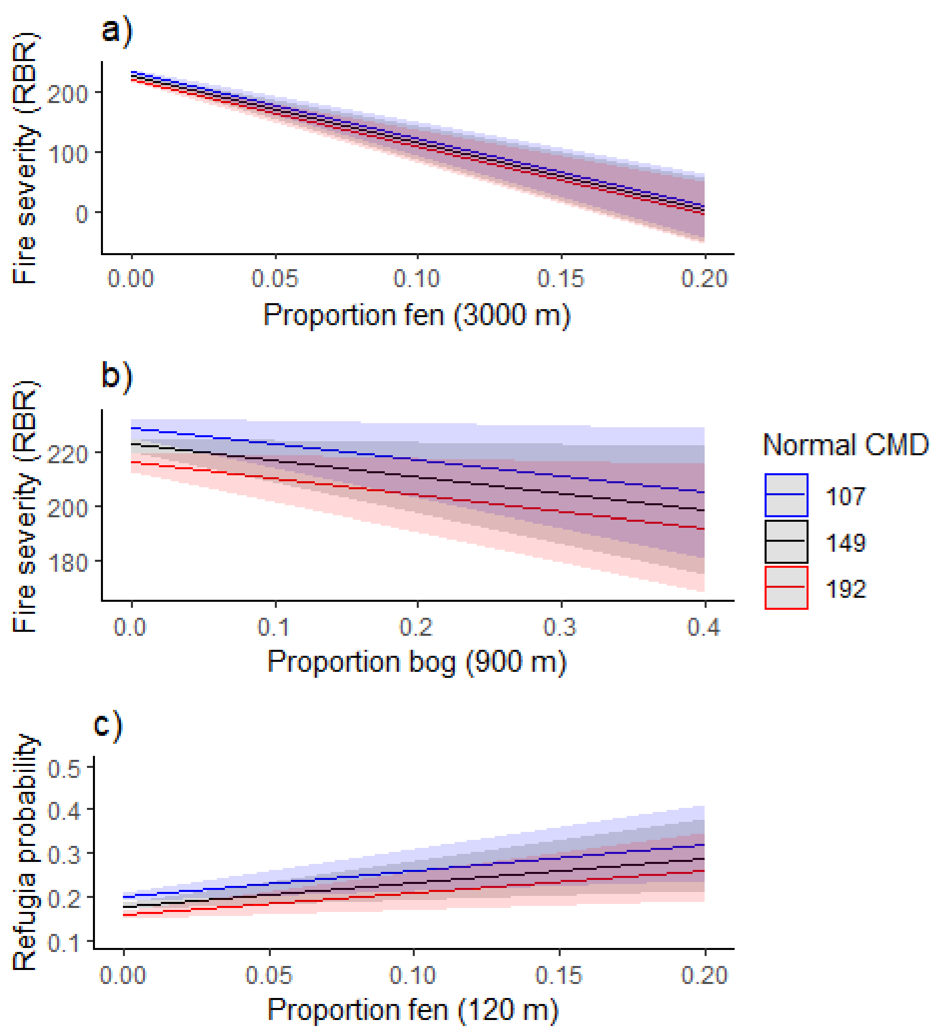


Fig. 4. Predicted effects of the amount of peatlands and normal CMD (1981 - 2010) on fire severity (a, b) and probability of refugia (c) in uplands. Error bars represent 95% confidence intervals. Blue denotes the wettest regions, while red represents the driest regions.

Both increasing fire size and peatland amounts decreased fire severity in uplands in models where annual CMD conditions were included, with fens producing the strongest negative effect. Increasing amounts of fens also increased refugia probability in uplands, while fire size and refugia had an inverse relationship. Annual CMD (drought) and fire size negatively affected fire severity in uplands (β = -0.12, SE = 0.03, p < 0.001 and β = -5.73e^{-05}, SE = 6.03e^{-06}, p < 0.001, respectively; Table 6a). The amount of both fens and bogs also had inverse relationships with fire severity in these models, with fens producing the larger effect (β = -3.44e^{+03}, SE = 634.50, p < 0.001 and β = -6.47, SE = 30.43, p = 0.034, respectively). The interaction between annual CMD and fen amount had a positive effect on fire severity (β = 9.25, SE = 2.70, p = 0.001). Uplands with no surrounding fens had similar severities and refugia probabilities regardless of annual CMD condition, though drier conditions (CMD = 275) produced higher fire severities than wetter conditions (CMD = 162) when fen amount exceeded roughly 0.03 (Figure 4a). As the amount of surrounding fens increased from 0 to 0.2 (the maximum amount in the study), fire severity in uplands decreased by 170 RBR under drier annual conditions and by 370 RBR under wetter annual conditions (Figure 5a). Similarly, fire severity under all annual conditions decreased by roughly 20 RBR units as bog amounts increased from 0 to their maximum (here, 0.40) (Figure 5b). Drier annual conditions produced lower fire severities relative to wetter conditions regardless of surrounding bog amount. Annual CMD had a positive effect on refugia probability (β = 2.20e^{-03}, SE = 4.23e^{-04}, p < 0.001) as did the amount of fens in a 120-m surrounding area (β = 2.41, SE = 1.03, p = 0.020; Table 6b), leading to increases in refugia of 0.02% and 27.3% for every 10-fold increase in annual CMD and fen amount, respectively. Fire size, however, had an inverse relationship with refugia in models that accounted for annual drought (β = -3.21e^{-07}, SE = 1.21e^{-07}, p = 0.008). Drier annual conditions produced a slightly higher probability of refugia than wetter annual conditions regardless of the amount of fens, increasing upland refugia likelihood by roughly 10% (Figure 5c).

Increasing surrounding peatland amounts lowered fire severity in peatland ecosystems under drought conditions in models where annual CMD was included as a variable. While the amount of both bogs and fens increased refugia probability in these ecosystems, their interactions with annual CMD did not produce a meaningful effect. Annual CMD was a significant positive predictor of fire severity in peatlands (β = 0.19, SE = 0.03, p < 0.001; Appendix A: Table 5a). Increasing amounts of fens within a 3000-m area increased fire severity (β = 1.50e^{+03}, SE = 763.20, p = 0.050) in models that included annual CMD, while the amount of bogs within a 900-m area had a negative effect (β = -89.09, SE = 12.99, p < 0.001). Increasing fire size also had an inverse relationship with fire severity in such models (β = -6.91e^{-05}, SE = 1.06e^{-05}, p < 0.001). The amount of surrounding fens produced differing effects depending on annual conditions. Specifically, fire severity increased by 30 units in wetter years and decreased by 275 RBR in drier years when surrounded by higher amounts of fens (Appendix A: Figure 3a). Bogs, on the other hand, lowered fire severity in peatlands regardless of annual conditions, with decreases of 35 RBR in wet years and 40 RBR in dry years (Appendix A: Figure 3b). Peatland fire severity was inversely related to interactions between annual CMD and the amount of fens within a 3000-m area (β = -7.97, SE = 3.23, p = 0.014). Fire size increased the probability of refugia in peatlands, in models that considered annual CMD (β = 2.68e^{-06}, SE = 1.60e^{-07}, p < 0.001; Appendix A: Table 5b). Increasing amounts of fens within a 120-m area also had a positive effect on refugia probability (β = 5.22, SE = 2.08, p = 0.012), producing a 68.5% increase for every 10-fold increase in fen amount. Similarly, high amounts of bogs within a 900-m area were positive predictors of refugia in peatlands (β = 0.99, SE = 0.26, p < 0.001), producing an increase of 10.5% for every 10-fold increase in bog amount.

Table 6. Results for models describing fire severity (a) and refugia probability (b), as a function of the amount of surrounding peatland and annual CMD in uplands. Beta values on the left are raw, while those on the far right are standardized for comparing variable strength.

a) Fire severity (uplands)

Variable	$\boldsymbol{\beta}$	**SE**	**p**	$\boldsymbol{\beta_{(std.)}}$
Fire size (ha)	-5.73e^{-05}	6.03e^{-06}	< 0.001	-11.90
Annual CMD	-0.12	0.03	< 0.001	-4.01
Proportion bog (900 m)	-6.47	30.43	0.034	-2.57
Proportion fen (3000 m)	-3.44e^{+03}	634.50	< 0.001	-13.37
Proportion fen (3000 m) × Annual CMD	9.25	2.70	0.001	4.59

Intercept	263.70	6.14	< 0.001	221.30

b) Refugia probability (uplands)

Variable	$\boldsymbol{\beta}$	**SE**	**p**	**Odds ratio**	$\boldsymbol{\beta_{(std.)}}$
Fire size (ha)	$-3.21e^{-07}$	$1.21e^{-07}$	0.008	1.00	-0.07
Annual CMD	$2.20e^{-03}$	$4.23e^{-04}$	< 0.001	1.00	0.12
Proportion fen (120 m)	2.41	1.03	0.020	11.14	0.05
Intercept	-1.94	0.10	< 0.001	0.14	-1.51

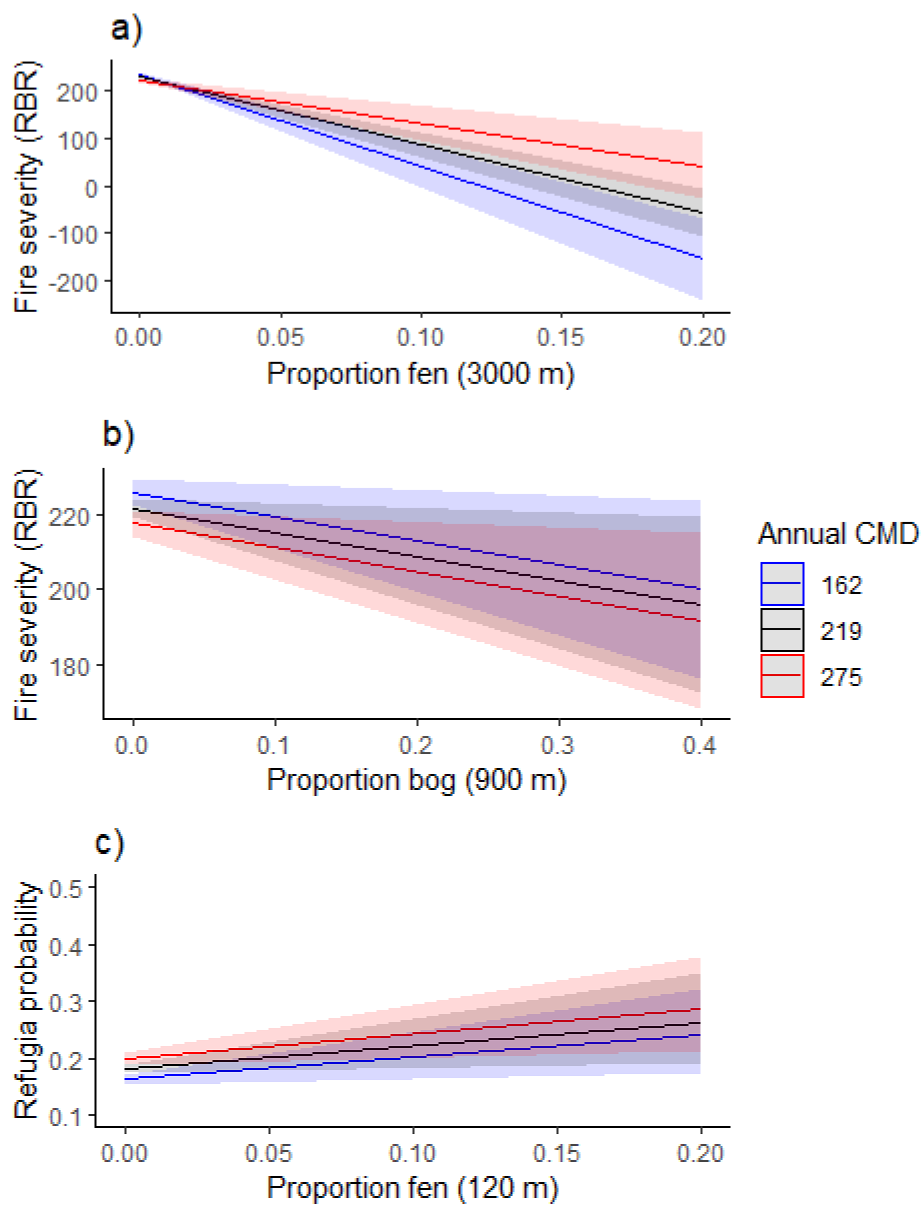


Fig. 5. Predicted effects of the amount of surrounding peatland and annual CMD on fire severity (a, b) and refugia probability (c) in uplands. Error bars are set at 95% confidence intervals. Wetter years are in blue, while drier years are in red.

While all component models (Climate, Physical Setting, Vegetation, Ecosystem) for fire severity outperformed the null and ecological null models, Vegetation (fuel) had the strongest single effect on fire severity (Table 7a). Climate was the next most supported model, followed by Physical Setting and Ecosystem. Similarly, all component models for refugia outperformed the two null models, with the most supported again being Vegetation, followed by Climate, Physical

Setting, and Ecosystem (Table 7b). Detailed results for each component model are found in Appendix A: Table 2.

Table 7. Evaluation of component models for fire severity (a) and refugia probability (b) based on samples from the full landscape. The null models contain only the intercept, while the ecological nulls represent fire severity and refugia when fire size and the single-point measures for ecosystem are accounted for. Models are ranked from the most to the least supported via Akaike's Information Criteria (AIC). Rank, model name, number of parameters (K), AIC, and change in AIC (ΔAIC) are listed.

a)

Rank	**Model**	***K***	**AIC**	**ΔAIC**
1	Vegetation	14	197,130.1	0
2	Climate	10	199,352.5	2,222.4
3	Physical setting	13	199,509.0	2,378.9
4	Ecosystem	10	199,581.4	2,451.3
5	Ecological null	7	199,732.2	2,602.1
6	Null	2	200,194.6	3,064.5

b)

Rank	**Model**	***K***	**AIC**	**ΔAIC**
1	Vegetation	9	18,317.5	0
2	Climate	9	19,713.1	1,395.7
3	Physical setting	8	19,888.7	1,571.2
4	Ecosystem	8	19,940.4	1,622.9

5	Ecological null	6	19,953.6	1,636.2
6	Null	1	20,064.6	1,747.2

The full predictive models, which contain the entire suite of variables (Figure 6, 7; Appendix A: Table 3), outperformed the top-component model (Vegetation) for both fire severity and refugia (Table 8). Predictive accuracy and goodness of fit are described in Appendix A: Table 8. Maps generated from these models illustrate that deciduous areas and regional topographic lows, particularly in Wood Buffalo National Park and surrounding areas, have the highest probability of refugia, while fire probability (≥ 0.60) was highest in coniferous areas and regional topographic highs. Fire severity, meanwhile, was highest in the coniferous foothill regions and areas surrounding Fort McMurray. All maps (2009, 2011, average) showed a higher probability of refugia in the early fire season (May) relative to the late fire season (August). Fire severity followed a similar trend, with the highest severities occurring in August. Refugia were less common in a dry year (2011) than a wet year (2009), with severe fires being more likely in wet years. Maps depicting refugia probability during average seasonal conditions were similar to those for 2011, while maps of fire severity under average seasonal conditions showed lower predicted severities than either 2009 or 2011. A limitation of the predictive fire severity maps is the exclusion of daily fire weather conditions, which is a major factor affecting fire spread and behavior.

Table 8. Comparison of the top-component models for fire severity (a) and probability of refugia (b) based on Akaike's Information Criteria (AIC) values. Model name, number of parameters (K), AIC, and change in AIC (ΔAIC) are included. The predictive models outperformed the top-component models in both cases.

a) Fire severity

Model	***K***	**AIC**	**ΔAIC**
Predictive fire severity	22	196611.4	0

Vegetation (component)	14	197130.1	518.7

b) Refugia probability

Model	***K***	**AIC**	**ΔAIC**
Predictive refugia	25	17,888.2	0
Vegetation (component)	9	18,317.5	429.27

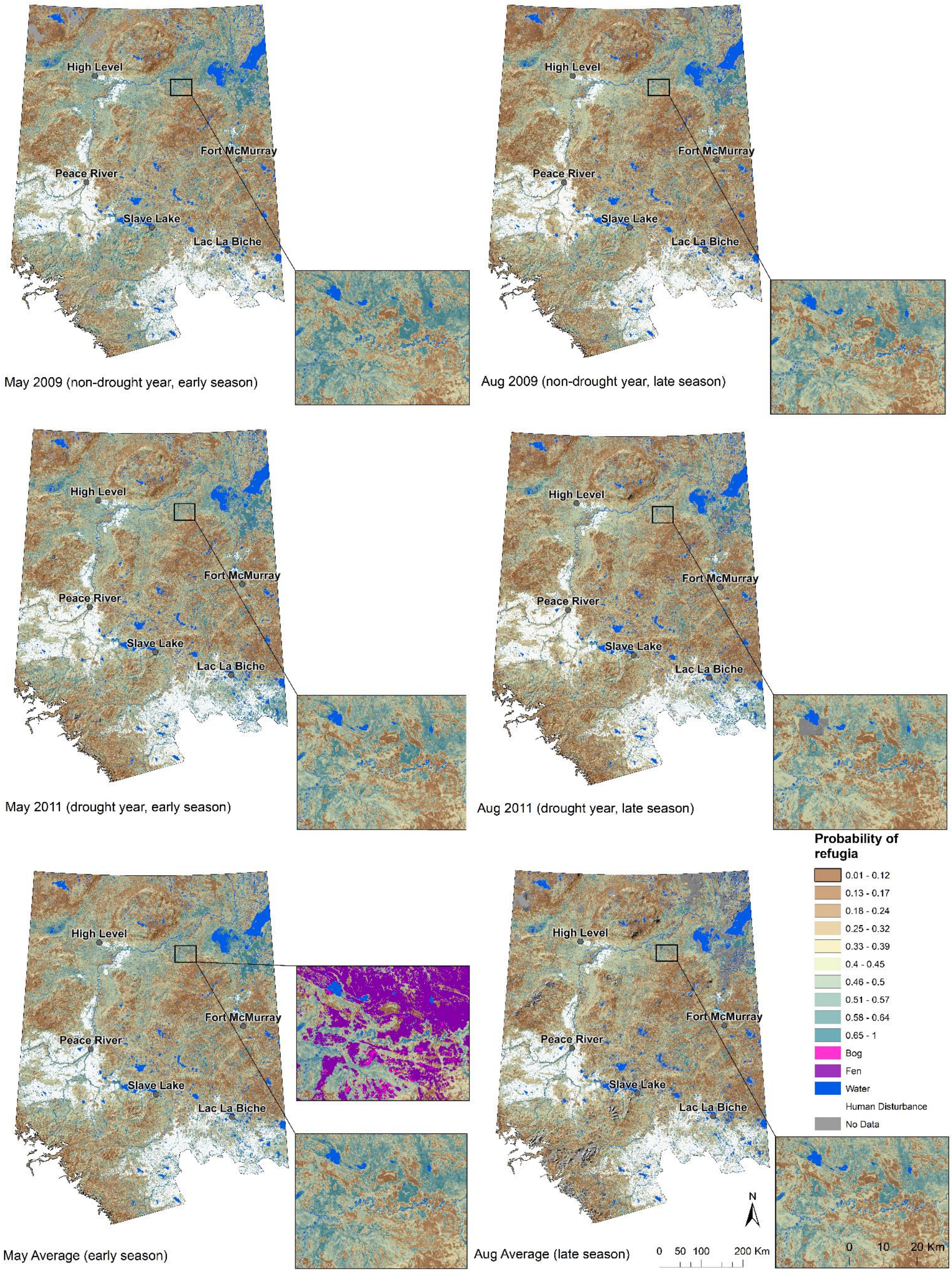
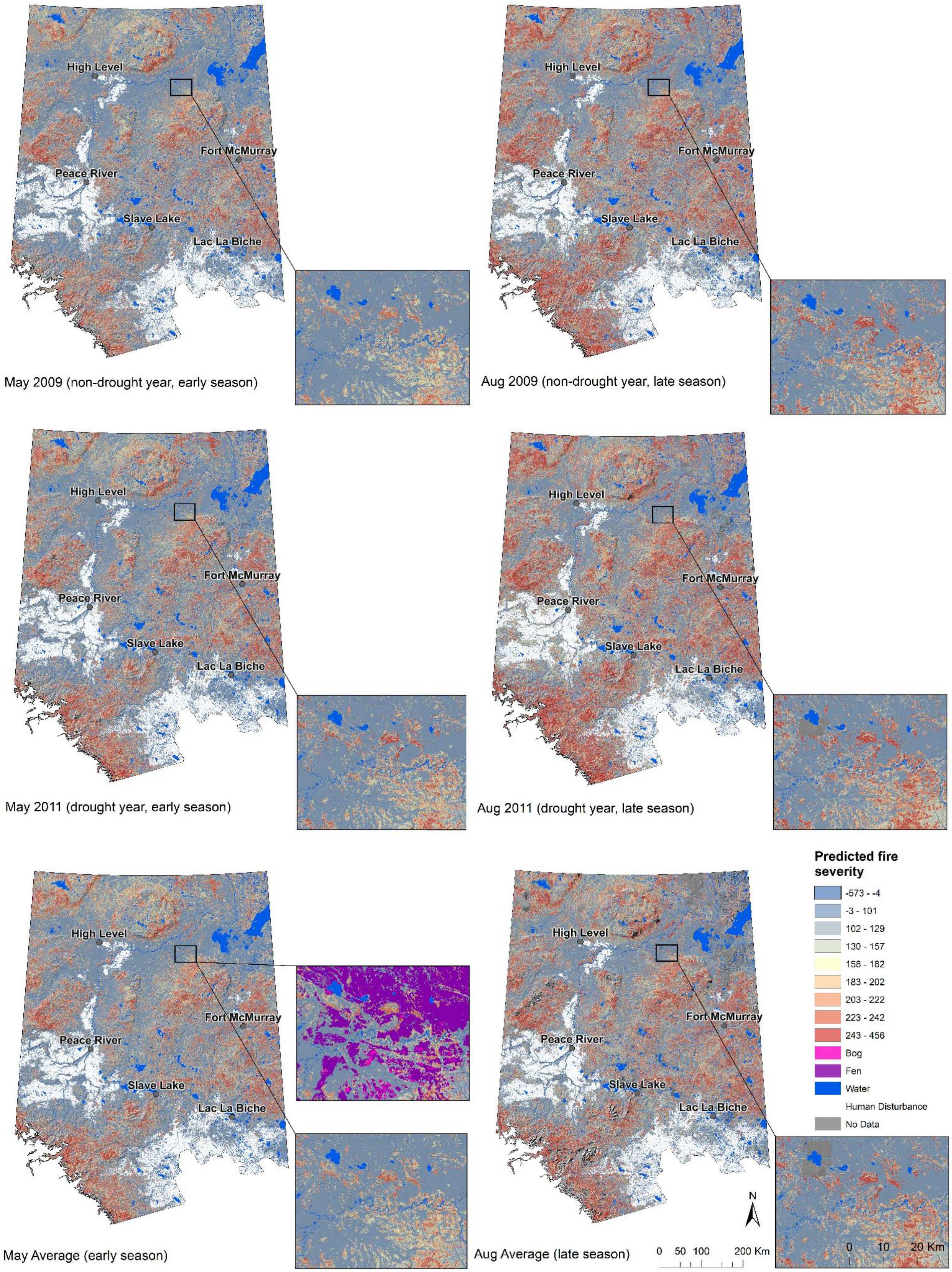

High Level
Fort McMurray
Peace River
Slave Lake
Lac La Biche
May 2009 (non-drought year, early season)
Aug 2009 (non-drought year, late season)
May 2011 (drought year, early season)
Aug 2011 (drought year, late season)
May Average (early season)
Aug Average (late season)
Probability of refugia
0.01 - 0.12
0.13 - 0.17
0.18 - 0.24
0.25 - 0.32
0.33 - 0.39
0.4 - 0.45
0.46 - 0.5
0.51 - 0.57
0.58 - 0.64
0.65 - 1
Bog
Fen
Water
Human Disturbance
No Data
N
0 50 100 200 Km
0 10 20 Km

Fig. 6. Predictive maps of fire refugia (probability) based on a full suite of bottom-up and top-down control variables. Maps depict conditions of drought (2011) and non-drought (2009) years, as well as average CMD conditions (calculated as average annual CMD anomalies over the study period). Changes relating to seasonal phenological conditions were included to compare spring (May 1-14) to late summer (Aug 18-31) time periods. Urban and agricultural areas were masked (white areas) using data from Latifovic et al (2017). Six inset maps are used to demonstrate differences in predicted refugia location at a 1:300,000 scale, while the seventh displays fen and bog distribution in the area.



High Level
Fort McMurray
Peace River
Slave Lake
Lac La Biche
May 2009 (non-drought year, early season)
Aug 2009 (non-drought year, late season)
May 2011 (drought year, early season)
Aug 2011 (drought year, late season)
May Average (early season)
Aug Average (late season)
Predicted fire severity
-573 - -4
-3 - 101
102 - 129
130 - 157
158 - 182
183 - 202
203 - 222
223 - 242
243 - 456
Bog
Fen
Water
Human Disturbance
No Data
N
0 50 100 200 Km
0 10 20 Km

Fig. 7. Predictive maps of fire severity based on the full suite of top-down and bottom-up variables. Maps depict conditions of drought (2011) and non-drought (2009) years, as well as average CMD conditions (calculated as average annual CMD anomalies over the study period). Changes relating to seasonal phenological conditions were included to compare spring (May 1-14) to late summer (Aug 18-31) time periods. Human disturbance was masked (white areas) using data from Latifovic et al (2017). These maps are dependent on those created for refugia and represent the predicted fire severity for locations with ≥ 0.6 fire probability. Six inset maps are used to demonstrate differences in predicted fire severity at a 1:300,000 scale, while the seventh displays peatland coverage. The accuracy of these maps is limited by the exclusion of variables corresponding to daily fire weather conditions, which are major factors influencing fire spread and behavior.

Discussion

My results, based on a comprehensive analysis of fires across the Alberta boreal region, found that peatlands burn at consistently lower severities than uplands, supporting hypothesis H_1 (Table 9). Fire severity in uplands decreased, and probability of refugia increased, as the amount of surrounding peatland increased, supporting hypotheses H_{2a} and H_{3a} respectively (Table 9). This negative effect on fire severity weakened for fens while under drier annual CMD conditions, leading me to accept hypothesis H_{2b}. Uplands surrounded by bogs had slightly higher fire severities under wetter annual conditions, however. Results partly supported hypothesis H_{3b} for fens, with bogs having no significant effect on refugia in uplands; however, drier annual conditions produced a higher probability of refugia regardless of fen amount, running counter to the initial hypothesis. The component model comparisons showed that annual vegetation (fuel or lack thereof) was the most important factor driving differences in both fire severity and refugia probability across the landscape. This was counter to my hypothesis that variables associated with physical setting would have the greatest effect, leading me to reject hypothesis H_4.

Table 9. Restatement of the hypotheses and their annotations, as well as whether support was found for each following analysis.

Hypothesis	**Supported**

H_1: Peatlands will have lower severities and higher refugia probabilities than uplands as a function of differences in site moisture and fuel composition	Yes
H_{2a}: Fire severity in uplands will be negatively correlated with surrounding amount of peatland due to hydrologic connectivity	Yes
H_{2b}: Under droughts, uplands with more surrounding peatland will reduce fire severity as function of hydrologic connectivity (*i*); however, this will decrease with drought intensity as fuel moisture decreases in the ecosystems (*ii*)	(*i*): Yes (*ii*): Yes (fens) No (bogs)
H_{3a}: Refugia probability in uplands will be positively correlated with amount of surrounding peatland as a result of hydrologic connectivity	Yes (fens)
H_{3b}: Under droughts, uplands with more surrounding peatlands will have higher refugia probabilities than those without, as function of hydrologic connectivity (*i*), with probability decreasing as drought conditions intensify and fuel flammability increases (*ii*)	(*i*): Yes (fens) (*ii*): No (fens and bogs)
H_4: Of the bottom-up controls, those pertaining to site moisture (e.g., pedology, terrain moisture, lake effects) will present the strongest influence on fire severity and refugia probability due to the strong influence of site moisture on vegetation composition and the physical barrier standing water presents to fire	No

My results showed that, on average, fire severities are lower and refugia probabilities are higher in peatlands relative to uplands. Uplands with higher amounts of surrounding peatland coverage experienced lower fire severities than those without. Uplands with high amounts of surrounding fens had an increased probability of refugia compared to those without; however, the amount of surrounding bog coverage did not have a significant effect on refugia in upland ecosystems. In the western boreal region, fens are more resistant to the effects of fire than bogs due to their more stable water tables (Schiks *et al*., 2016; Ferone and Devito, 2004); however, the vegetation in fens is more sensitive to drying when water tables drop below a critical threshold (Thompson *et al*., 2019; Waddington *et al*., 2015). From a fire perspective, the fuel structure of bogs more closely resembles that of coniferous uplands than fens (Johnson e*t al*, 2015; Thompson *et al*., 2019). This difference in fuel structure and moisture results in higher fire severities in bogs relative to fens when the fuel moisture content in fens is highest, suggesting that the differing results for the two peatland classes may be driven by a combination of water-table dynamics and fuel structure.

In uplands, increasing amounts of bogs and fens decreased fire severity under all regional climate moisture conditions, although wetter regions had consistently higher fire severities than those in drier regions. In Alberta, regions of higher climatic moisture can support more live vegetation (Knapp and Smith, 2001; Downing and Pettapiece, 2006), thereby providing more live fuel than is found in drier regions (Thompson *et al*., 2017). These wetter locations also support highly flammable spruce species, while drier locations support comparatively less flammable vegetation in the form of deciduous and pine species (Walker *et al*., 2020). These higher fuel loads and increased flammability result in fires with higher average severities than those occurring in areas that are more fuel limited (Parks *et al*., 2014). Additionally, graminoid vegetation in fens is more deciduous in nature than that of largely-coniferous bogs, and is subject to stronger seasonal phenological changes in comparison. This deciduous vegetation contains higher fuel moisture contents, when green, than that found in bogs, thereby providing a stronger control on fire severity (Schiks *et al.,* 2016) and causing the amount of surrounding fens to have a stronger effect on severity in uplands than surrounding bogs. The amount of fens also increased the probability of refugia in uplands, particularly in wetter regions, though the amount of bogs had no effect. While both peatland types retain high water tables relative to upland sites, bogs hold the majority of their water beneath the soil surface while much of the moisture in fens occurs as pockets of standing water aboveground (Branch and Floor, 2015). This standing water, at a local scale (120-m area), may increase refugia probability by providing a physical barrier to fire and creating unburned skips (i.e., refugia) on sides opposite wind direction at the time of burning (Mansuy *et al.,* 2014). In peatlands, increasing amounts of bogs lowered severity under all regional climatic moisture conditions; however, fens decreased fire severity in drier regions only. Both bogs and fens increased the probability of refugia in peatlands under all regional climatic moisture conditions, with this effect being strongest in wetter regions. While both bogs and fens reduced severity and increased refugia probability in nearby upland and peatlands, fens produced the strongest effect in all cases. These results suggest that hydrologically connected peatlands, particularly fens, confer significant reductions in fire severity to neighboring upland stands under all regional climatic moisture conditions (Hokanson *et al*., 2016).

Increased peatland coverage decreased fire severity in uplands under all annual climatic moisture conditions, including during drought. The effect of fens on fire severity, while strong overall, decreased under drier annual conditions, likely owing to the lowered water tables and drying of fuels in fens during periods of drought (Thompson *et al*., 2019). Bogs, in contrast, negatively affected fire severity in uplands most strongly while under drought conditions. This result may owe less to the effect of bogs on fire severity and more to that of differences in fire size under various climatic moisture conditions. Years that are drier on average produce larger fires than those in wetter years (Thompson *et al*., 2019). These larger fires can burn over considerable spatial and temporal scales, thereby encountering greater variability in the landscape features (e.g., topography, site moisture, vegetation) and fire weather conditions (Whitman *et al*., 2018b) through which they burn relative to those encountered by smaller fires (Eberhart and Woodard, 1987; Madoui *et al*., 2010). This variability in landscape and weather conditions at the time of burning produces greater variability in fire severity (Krawchuk *et al*., 2016). The effects of large fires may also explain why increasing fen amounts had the strongest effect on refugia probability in uplands under drought conditions, although fens did increase refugia in uplands under all annual climatic moisture conditions. Bogs, in comparison, did not have an effect on refugia in uplands. This difference in effect under various annual conditions supports the notion that differences in the fuel moisture content (Schiks *et al.,* 2016; Thompson *et al*., 2019), standing water (Mansuy *et al.*, 2014), and hydrologic connectivity (Hokanson *et al.*, 2016) between bogs and fens produces different effects on refugia probability in neighboring uplands. In peatlands, increasing amounts of surrounding bogs also decreased fire severity under all annual climatic moisture conditions. Surrounding fens, however, only lowered fire severity in peatlands during drought conditions, with wetter annual conditions producing increased severity.

Peatlands are important ecosystems due, in part, to their ability to cool the global climate over long time periods by sequestering carbon through photosynthesis (Hugelius *et al.,* 2020). However, this carbon sequestration ability has been threatened by the synergistic effects of climate change and increased disturbance from fire (Harris *et al*., 2021). While peatlands in the western boreal region of Canada are considered particularly vulnerable to these changes, climate-induced effects here can potentially be mitigated in areas where peatlands retain stable (i.e., hydrologically well connected) water tables (Harris *et al*., 2021). The results of my research suggest that the ecological benefit of these well-connected peatland complexes extends beyond the peatlands themselves and grants a measure of protection from severe fire to neighboring upland stands, further adding to peatland importance in promoting ecosystem resistance to climate- and disturbance-induced change.

Although counter to my initial hypothesis, the results from the component models support the idea that differences in fuel type and composition are the driving force behind the effects on fire severity and refugia probability seen as the amount of fen and bog increased. These results are similar to the findings of Parks et al (2018) and Walker et al (2020) that fuel was the most important factor driving both high severity fires and combustion, respectively, when models included annual vegetation, as well as variables pertaining to climate, topography, and fire weather. Although past studies (Krawchuk *et al*., 2016; Kane *et al*., 2015) have found that both climate and topography are major drivers of fire severity and refugia, these studies often did not include variables for annual live vegetation. As both climate and topography can be considered as indirect measures of plant biomass over large spatial and temporal extents (Parks *et al*., 2018), the importance of these variables in models where live annual fuel is not considered may be overstated. The significance of annual vegetation in models pertaining to fire effects is important to understand as fire and land managers can control the level and nature of fuel sources (e.g., fuel thinning) in areas of concern, whereas there is considerably less control over aspects of local climate and topography influencing fire.

The difference in the scale at which bogs and fens affected fire severity and refugia models is notable. While the amount of surrounding bogs affected both fire severity and refugia formation at the intermediate-scale (900-m area), scales for fens changed from landscape (3000-m area) in fire severity models to local (120-m area) in refugia models. The differences in scale between bogs and fens in relation to fire severity may relate to the amount of each peatland type present in the study area. While fens occur in high numbers across the landscape, particularly in northern and eastern portions of the study area, bogs are considerably less common. The relative scarcity of bogs may have led to smaller proportions, and therefore the strength of effects, present at larger scales (i.e., 1200 m and 3000 m). Changes in scale for fens from local (refugia) to landscape (fire severity) are likely due to the effects of standing water and fuel moisture in these ecosystems, respectively. While smaller areas of standing water are capable of creating refugia on the side opposite wind direction, larger areas are required to reduce fire severity through barriers of fuel moisture. This is particularly true during periods of increased seasonal or annual drying when the vegetation in fens begins to cure and becomes increasingly available to burn. Though the vegetation in fens may still contain higher fuel moisture levels than uplands, depending on the intensity of drying conditions, larger areas of this vegetation are required to reduce fire severity.

Limitations, Future Research, and Management Implications

Despite demonstrating that peatlands lower fire severity under various normal and annual climate moisture conditions, there are some limitations to the conclusions drawn from this research. Fire weather at the time of burning is an important factor in predicting fire behavior; however, due to limited data relating to daily fire progression and associated weather conditions for the 1985-2018 study period, I was unable to account for fire weather beyond the inclusion of relative annual drought. Open peatland vegetation (e.g., sedges and shrubs) is capable of re-growing quickly following fire and, despite efforts to limit analyses to forested pixels, it is possible that some low-severity burns were misclassified as refugia, leading to an overstatement of the fire severity reduction potential of peatlands.

Field verification to assess true fire severity and vegetation regeneration speed following fire would help to validate the strength of effects seen in uplands, especially those surrounded by fens. Further remote sensing studies to differentiate between locations of ephemeral and long-term, as well as local and landscape-level, fire refugia would help to prioritize locations to conserve as potential seed sources in the face of widespread vegetation transition. Future research into the effects of hydrologic connectivity between uplands and peatlands on fire could focus on the extent of this effect in different hydrologic and climatic settings, and how this connectivity influences fire spread or return interval.

Fire severity and refugia probability was explained by a combination of ecosystem and vegetation composition, showing that landscape heterogeneity is an important factor in controlling fire severity. Variables pertaining to physical setting (e.g., CTI, lake effects) were less important than expected, likely stemming from the inclusion of annual dominant vegetation classes for which topography, site moisture, and amount of standing water can be considered as indirect measures (Parks *et al*., 2018; Nielsen *et al.,* 2016). Results showed that high amounts of peatlands can mitigate fire severity and increase refugia probability in hydrologically connected uplands, as well as in forested peatlands. While forested and open peatlands likely produce different effects on fire severity and refugia in neighboring forests, differentiating between the two over an expansive spatial and temporal scale is challenging and beyond the scope of this research. Given that nearly half of the study area is comprised of peatland ecosystems (Downing and Pettapiece, 2006), the majority of which are forested (Thompson *et al*., 2015), differences in effect on fire severity between open and treed peatlands warrants further study. As current fire prediction systems can regard peatlands as static barriers to fire, or conversely, as flammable regardless of high water tables (Thompson *et al*., 2019), fire managers can use the results of my research to better predict the probability of a wildfire burning through their jurisdictions, as well as the severity at which burns may occur.

These findings, as well as the predictive maps (Figure 6, 7), will help managers to better allocate resources for suppression efforts and prescribed burns to areas where these tactics would be most effective. For example, fuel mitigation efforts, such as thinning of flammable vegetation, could target areas located near valuable human assets (e.g., townsites and oil and gas infrastructure) predicted to burn severely. Similarly, prescription burns or burnout operations might be avoided in areas of ecological concern (e.g., old growth forests, hydrologically connected peatlands) predicted to either lower fire severity or promote refugia, instead retaining these areas for their fire severity-lowering properties or potential as seed sources.

Conclusion

Major climate- and disturbance-driven ecosystem transitions have been predicted to occur in the western boreal region of Canada under a warming climate (Stralberg *et al*., 2018; Cadieux *et al*., 2020); however, there is a lack of understanding regarding bottom-up ecological and hydrological controls on fire severity in flat, wet boreal landscapes, particularly during periods of drought (Hart *et al.*, 2019). The results of my study demonstrate that peatlands in the boreal biome of Alberta are capable of decreasing fire severity and promoting refugia under drought conditions. This effect also extends to neighboring upland stands, particularly those in areas surrounded by a high amount of hydrologically connected fens. While the true strength and extent of these fire severity-lowering effects warrant further study, areas of well-connected peatland systems may provide resistance to vegetation transitions resulting from increased fire severity and post-disturbance moisture stress, including in neighboring ecosystems, as the climate warms and dries. In addition to our current knowledge of peatlands as major sources of potential carbon sequestration, the results of my study provide further evidence of the importance of intact peatland systems in the face of climate change and stresses the need for further protection of these ecosystems into the future.

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Appendix A

Table 1. Following selection of spatial scales and tests for multicollinearity, analyses were split into three modelling approaches for each response variable: component, explanatory, and predictive. Variables in component and predictive models were tested for significance and removed in a stepwise fashion. In the case of duplicate variables between the static and annual datasets, component and explanatory models used the static (ALPHA) measures while predictive models used the dynamic (ABoVE) versions to more accurately capture annual variation.

Models	Response variable	Variables (full suite)	Variables (final models)
Component			
Null	Severity / Refugia	NA	NA
Physical setting	Severity	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	Fire size (ha)
		Distance to water (log10)	Distance to water (log10)
		TPI	TPI
		Proportion bedrock (900 m)	Proportion coarse (900 m)
		Proportion coarse (900 m)	Proportion FTCP (3000 m)
		Proportion FTCP (3000 m)	CTI (120 m)
		Proportion FTHM (900 m)	Proportion water (3000 m)

		CTI (120 m)	
		Proportion water (3000 m)	
	Refugia	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	Fire size (ha)
		TPI	TPI
		Proportion bedrock (120 m)	CTI (120 m)
		Proportion coarse (300 m)	
		Proportion FTCP (300 m)	
		Proportion FTHM (300 m)	
		Distance to water (log10)	
		Proportion water (300 m)	
		CTI (120 m)	
Vegetation	Severity	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	Fire size (ha)
		Proportion cutblock (300 m)	Proportion cutblock (300 m)
		Proportion evergreen (120 m)	Proportion evergreen (120 m)

		Proportion shrubland (300 m)	Proportion shrubland (300 m)
		Proportion herbaceous (900 m)	Proportion herbaceous (900 m)
		Proportion sparse (120 m)	Proportion sparse (120 m)
		Proportion barren (3000 m)	Proportion barren (3000 m)
		Proportion littoral (300 m)	Proportion littoral (300 m)
	Refugia	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	Proportion cutblock (900 m)
		Proportion cutblock (900 m)	Proportion evergreen (120 m)
		Proportion evergreen (120 m)	Proportion barren (1200 m)
		Proportion shrubland (300 m)	Proportion herbaceous (300 m)
		Proportion herbaceous (300 m)	
		Proportion sparse (300 m)	
		Proportion barren (1200 m)	
		Proportion littoral (300 m)	
Climate	Severity	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	Annual CMD

		Annual CMD	Mean fire season temperature
		Normal CMD	14-day phenology (min)
		Mean fire season temperature	14-day phenology (min)
		14-day phenology (min)	
		14-day phenology (max)	
	Refugia	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	Annual CMD
		Annual CMD	Normal CMD
		Normal CMD	Mean annual temperature
		Mean annual temp	14-day phenology (max)
		7-day phenology (min)	
		14-day phenology (max)	
Ecosystem	Severity	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	Fire size (ha)
		Proportion upland (120 m)	Proportion swamp (3000 m)
		Proportion swamp (3000 m)	Proportion bog (900 m)

		Proportion bog (900 m)	Proportion fen (3000 m)
		Proportion fen (3000 m)	
	Refugia	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	Fire size (ha)
		Proportion upland (120 m)	Proportion bog (900 m)
		Proportion swamp (1200 m)	Proportion fen (120 m)
		Proportion bog (900 m)	
		Proportion fen (120 m)	
Explanatory			
Ecological null	Severity	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	Fire size (ha)
	Refugia	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	Fire size (ha)

Peatland additive	Severity	Bog	Bog
		Fen	Fen
		Fire size (ha)	Fire size (ha)
		Proportion bog (900 m)	Proportion bog (900 m)
		Proportion Fen (3000 m)	Proportion fen (3000 m)
	Refugia	Bog	Bog
		Fen	Fen
		Fire size (ha)	Fire size (ha)
		Proportion bog (900 m)	Proportion bog (900 m)
		Proportion fen (120 m)	Proportion fen (120 m)
Upland additive	Severity	Fire size (ha)	Fire size (ha)
		Proportion bog (900 m)	Proportion bog (900 m)
		Proportion fen (3000 m)	Proportion fen (3000 m)
	Refugia	Fire size (ha)	Fire size (ha)
		Proportion bog (900 m)	Proportion bog (900 m)
		Proportion fen (120 m)	Proportion fen (120 m)
Normal CMD (uplands)	Severity	Fire size (ha)	Fire size (ha)
		Proportion bog (900 m)	Proportion bog (900 m)
		Proportion fen (3000 m)	Proportion fen (3000 m)
		Normal CMD	Normal CMD
		Proportion bog (900 m) × Normal CMD	

		Proportion fen (3000 m) × Normal CMD	
	Refugia	Fire size (ha) Proportion bog (900 m) Proportion fen (120 m) Normal CMD Proportion bog (900 m) × Normal CMD Proportion fen (120 m) × Normal CMD	Fire size (ha) Proportion fen (120 m) Normal CMD
Normal CMD (peatlands)	Severity	Bog Fen Fire size (ha) Proportion bog (900 m) Proportion fen (3000 m) Normal CMD Proportion bog (900 m) × Normal CMD Proportion fen (3000 m) × Normal CMD Bog × Normal CMD Fen × Normal CMD	Fire size (ha) Proportion bog (900 m) Proportion fen (3000 m) Normal CMD Proportion fen (3000 m) × Normal CMD
		Bog	

	Refugia	Fen Fire size (ha) Proportion bog (900 m) Proportion fen (120 m) Normal CMD Proportion bog (900 m) × Normal CMD Proportion fen (120 m) × Normal CMD Bog × Normal CMD Fen × Normal CMD	Bog Fen Fire size (ha) Proportion bog (900 m) Proportion fen (120 m) Normal CMD Bog × Normal CMD Fen × Normal CMD
Annual CMD (uplands)	Severity	Fire size (ha) Proportion bog (900 m) Proportion fen (3000 m) Annual CMD Proportion bog (900 m) × Annual CMD Proportion fen (3000 m) × Annual CMD	Fire size (ha) Proportion bog (900 m) Proportion fen (3000 m) Proportion fen (3000 m) × Annual CMD
	Refugia	Fire size (ha) Proportion bog (900 m) Proportion fen (120 m)	Fire size (ha) Proportion fen (120 m) Annual CMD

		Annual CMD Proportion bog (900 m) × Annual CMD Proportion fen (120 m) × Annual CMD	
Annual CMD (peatlands)	Severity	Bog Fen Fire size (ha) Proportion bog (900 m) Proportion fen (3000 m) Annual CMD Proportion bog (900 m) × Annual CMD Proportion fen (3000 m) × Annual CMD Bog × Annual CMD Fen × Annual CMD	Bog Fen Fire size (ha) Proportion bog (900 m) Proportion fen (3000 m) Annual CMD Proportion fen (3000 m) × Annual CMD
Annual CMD (peatlands)	Refugia	Bog Fen Fire size (ha) Proportion bog (900 m) Proportion fen (120 m)	Bog Fen Fire size (ha) Proportion bog (900 m) Proportion fen (120 m)

			Annual CMD	
			Proportion bog (900 m) × Annual CMD	
			Proportion fen (120 m) × Annual CMD	
			Bog × Annual CMD	
			Fen × Annual CMD	
Predictive				
	Full	Severity	Bog	Bog
			Fen	Fen
			Marsh	Marsh
			Swamp	Swamp
			Fire size (ha)	Normal CMD
			Normal CMD	Mean fire season temperature
			CMD anomalies	14-day phenology (max)
			14-day phenology (min)	TPI
			14-day phenology (max)	Proportion FTHM (900 m)
			Mean fire season temperature	CTI (120 m)
			Distance to water (log10)	Proportion cutblock (300 m)
			TPI	Proportion evergreen (120 m)
			Proportion bedrock (900 m)	Proportion sparse (120 m)
			Proportion coarse (900 m)	

Proportion FTCP (3000 m)

Proportion FTHM (900 m)

CTI (120 m)

Proportion annual water (120 m)

Proportion cutblock (300 m)
Proportion evergreen (120 m)

Proportion shrubland (300 m)
Proportion herbaceous (900 m)

Proportion sparse (120 m)

Proportion barren (3000 m)

Proportion littoral (300 m)

Proportion upland (120 m)

Proportion swamp (3000 m)

Proportion annual bog (300 m)

Proportion annual fen (120 m)

Proportion evergreen (120 m) ×
Proportion annual fen (120 m)

Proportion evergreen (300 m) ×
Proportion annual bog (300 m)

Proportion annual bog (300 m) ×
Proportion annual fen (300 m)

Proportion annual bog (120 m) ×
Proportion annual fen (120 m)

Proportion annual bog (300 m)
Proportion annual fen (120 m)

Proportion evergreen (120 m) ×
Proportion annual fen (120 m)

Proportion evergreen (300 m) ×
Proportion annual bog (300 m)

CMD anomalies × Normal CMD

		Proportion annual bog (300 m) × CMD anomalies	
		Proportion annual fen (120 m) × CMD anomalies	
		CMD anomalies × Normal CMD	
Full	Refugia	Bog	Bog
		Fen	Fen
		Marsh	Marsh
		Swamp	Swamp
		Fire size (ha)	CMD anomalies
		CMD anomalies	Normal CMD
		Normal CMD	14-day phenology (max)
		Mean annual temperature	TPI
		14-day phenology (max)	Proportion FTCP (300 m)
		7-day phenology (min)	Proportion FTHM (300 m)
		TPI	Proportion coarse (300 m)
		Proportion bedrock (120 m)	CTI (120 m)
		Proportion coarse (300 m)	Proportion upland (120 m)
		Proportion FTCP (300 m)	Proportion cutblock (900 m)
		Proportion FTHM (300 m)	Proportion evergreen (120 m)
		Distance to water (log10)	Proportion shrubland (300 m)
		CTI (120 m)	Proportion herbaceous (300 m)
		Proportion annual water (1200 m)	Proportion barren (1200 m)

Proportion upland (120 m)	Proportion annual fen (300 m)
Proportion swamp (1200 m)	Proportion annual bog (1200 m)
Proportion annual bog (1200 m)	Proportion evergreen (300 m) × Proportion annual fen (300 m)
Proportion annual fen (300 m)	CMD anomalies × Proportion annual bog (1200 m)
Proportion cutblock (900 m)	CMD anomalies × Normal CMD
Proportion evergreen (120 m)	
Proportion shrubland (300 m)	
Proportion herbaceous (300 m)	
Proportion sparse (300 m)	
Proportion barren (1200 m)	
Proportion littoral (300 m)	
Proportion evergreen (1200 m) × Proportion annual bog (1200 m)	
Proportion evergreen (300 m) × Proportion annual fen (300 m)	
CMD anomalies × Proportion annual bog (1200 m)	
CMD anomalies × proportion annual fen (300 m)	
CMD anomalies × Normal CMD	
Proportion annual bog (1200 m) × Proportion annual fen (1200 m)	

Proportion annual bog (300 m) × Proportion annual fen (300 m)				

Table 2. Results for ecological null models for both fire severity (a) and refugia probability (b), using the full sample of the landscape. The upland ecosystem is used as a reference category. Raw beta values are represented by β, while standardized beta values demonstrating strength between factors are represented by $\beta_{(std.)}$.

a. Fire severity (ecological null model)

Variable	$\boldsymbol{\beta}$	**SE**	**p**	$\boldsymbol{\beta}$ ***(std.)***
Bog	-54.18	5.05	<0.001	-10.27
Fen	-42.08	2.23	<0.001	-18.24
Marsh	-77.14	26.21	0.003	-2.79
Swamp	3.78	5.38	0.482	0.67
Fire size (ha)	$-4.47e^{-05}$	$4.87e^{-06}$	<0.001	-3.30
Intercept	228.7	1.38	<0.001	209.79

b. Refugia probability (ecological null model)

Variable	$\boldsymbol{\beta}$	**SE**	**p**	**Odds Ratio**	$\boldsymbol{\beta}$ ***(std.)***
Bog	0.12	0.10	0.230	1.12	0.02
Fen	0.36	0.04	<0.001	1.43	0.16
Marsh	1.59	0.30	<0.001	4.91	0.07
Swamp	0.09	0.10	0.377	1.09	0.02
Fire size (ha)	$4.04e^{-07}$	$8.75e^{-08}$	<0.001	1.00	0.08
Intercept	-1.57	0.03	<0.001	0.21	-1.54

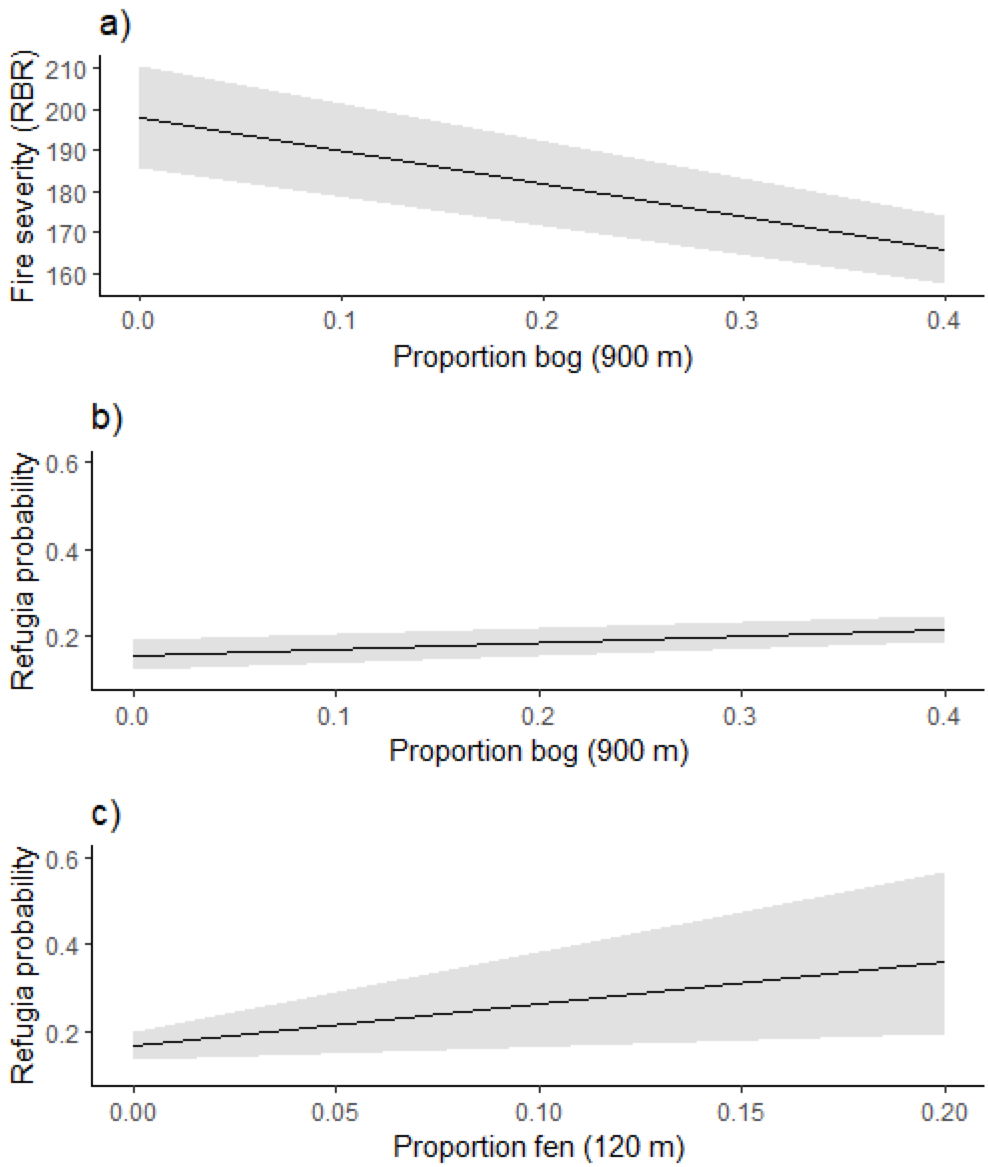

Fig. 1. Figure (a) represents fire severity (RBR) in peatlands as a function of the amount of bogs present within a 900-m area. Figures (b, c) represent refugia probability in peatlands as the amount of bogs (900-m area) and fens (120-m area) increase. Error bars represent 95% confidence intervals.

Table 3. Results for additive models for both fire severity (a) and refugia probability (b) in peatlands. The bog ecosystem is used as a reference category. Raw beta values are represented by β, while standardized beta values demonstrating strength between factors are represented by $\beta_{(std.)}$.

a. Fire severity (peatland additive model)

Variable	β	SE	p	$\beta_{(std.)}$
Fen	-12.20	6.14	0.047	-4.10
Fire size (ha)	$-7.98e^{-05}$	$1.05e^{-05}$	< 0.001	-11.76
Proportion bog (900 m)	-80.96	12.99	< 0.001	-12.99
Proportion fen (3000 m)	-177.20	183.40	0.334	-1.48
Intercept	206.60	6.51	< 0.001	180.70

b. Refugia probability (peatland additive model)

Variable	β	SE	p	Odds Ratio	$\beta_{(std.)}$
Fen	0.43	0.13	0.001	1.53	0.14
Fire size (ha)	$2.68e^{-06}$	$1.60e^{-07}$	< 0.001	1.00	0.47
Proportion bog (900 m)	0.99	0.26	< 0.001	2.70	0.16
Proportion fen (120 m)	5.22	2.08	0.012	185.26	0.07
Intercept	-2.02	0.14	< 0.001	0.13	-1.24

Table 4. Results for final models describing fire severity (a) and refugia probability (b), as a function of the amount of surrounding peatland and CMD normals, for samples located in peatlands. The bog ecosystem used as a reference category. Beta values on the left are raw, while those on the far right are standardized for comparing variable strength.

a. Fire severity (peatlands)

Variables	β	SE	p	$\beta_{(std.)}$

Fire size (ha)	-8.17e^{-05}	1.06e^{-05}	< 0.001	-12.05
CMD normals	0.14	0.04	0.001	1.62
Proportion bog (900 m)	-64.67	9.80	< 0.001	-10.37
Proportion fen (3000 m)	375.50	1.26e^{+03}	0.003	3.45
Proportion fen (3000 m) X CMD normals	-22.14	6.75	0.001	-7.50
Intercept	173.10	6.27	< 0.001	183.03

b. Refugia probability (peatlands)

Variable	***β***	**SE**	**p**	**Odds Ratio**	***β*** ***(std.)***
Fire size (ha)	2.62e^{-06}	1.62e^{-07}	< 0.001	1.00	0.46
CMD normals	-7.45e^{-03}	2.19e^{-03}	0.001	0.99	0.01
Proportion bog (900 m)	0.86	0.26	0.001	2.36	0.14
Proportion fen (120 m)	5.11	2.08	0.014	165.04	0.07
Fen	-0.95	0.39	0.015	0.39	0.12
Normal CMD X Fen	8.76e^{-03}	2.36e^{-03}	< 0.001	1.01	0.12
Intercept	-0.82	0.37	0.026	0.44	-1.23

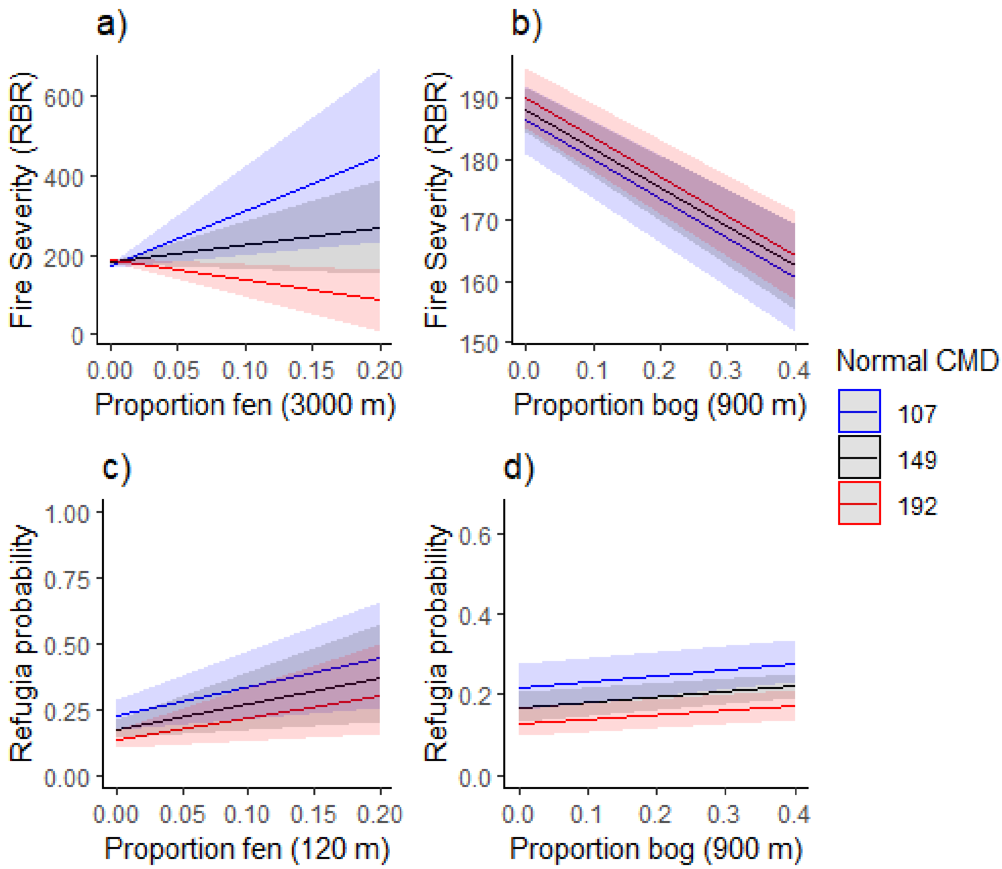

Fig. 2. Predicted effects of the amount of peatlands and normal CMD (1981 - 2010) on fire severity (a, b) and probability of refugia (c, d) in peatlands. Error bars represent 95% confidence intervals. Blue denotes the wettest climates, while red represents the driest climates.

Table 5. Results for final models describing fire severity (a) and refugia probability (b) as a function of peatland amount and annual CMD in peatlands. The reference ecosystem category is bog. Raw beta values (*β)* are represented in the leftmost column while standardized beta values ($\beta_{(std.)}$) representing strength between variables are on the right.

a. Fire severity (peatlands)

Variables	***β***	**SE**	**p**	$\boldsymbol{\beta}_{(std.)}$
Fire size (ha)	-6.91e^{-05}	1.06e^{-05}	< 0.001	-10.18

Annual CMD	0.19	0.03	< 0.001	9.41
Proportion bog (900 m)	-89.09	12.99	< 0.001	-14.29
Proportion fen (3000 m)	$1.50e^{+03}$	763.20	0.050	-2.55
Proportion fen (3000 m) X Annual CMD	-7.97	3.23	0.014	-4.08
Fen	-12.90	6.12	0.035	-4.33
Intercept	165.90	9.02	< 0.001	181.26

b. Refugia probability (peatlands)

Variable	$\boldsymbol{\beta}$	**SE**	**p**	**Odds Ratio**	$\boldsymbol{\beta}_{(std.)}$
Fire size (ha)	$2.68e^{-06}$	$1.60e^{-07}$	< 0.001	1.00	0.47
Proportion bog (900 m)	0.99	0.26	< 0.001	2.70	0.16
Proportion fen (120 m)	5.22	2.08	0.012	185.26	0.07
Fen	0.43	0.13	0.001	1.53	0.14
Intercept	-2.02	0.14	< 0.001	0.13	-1.24

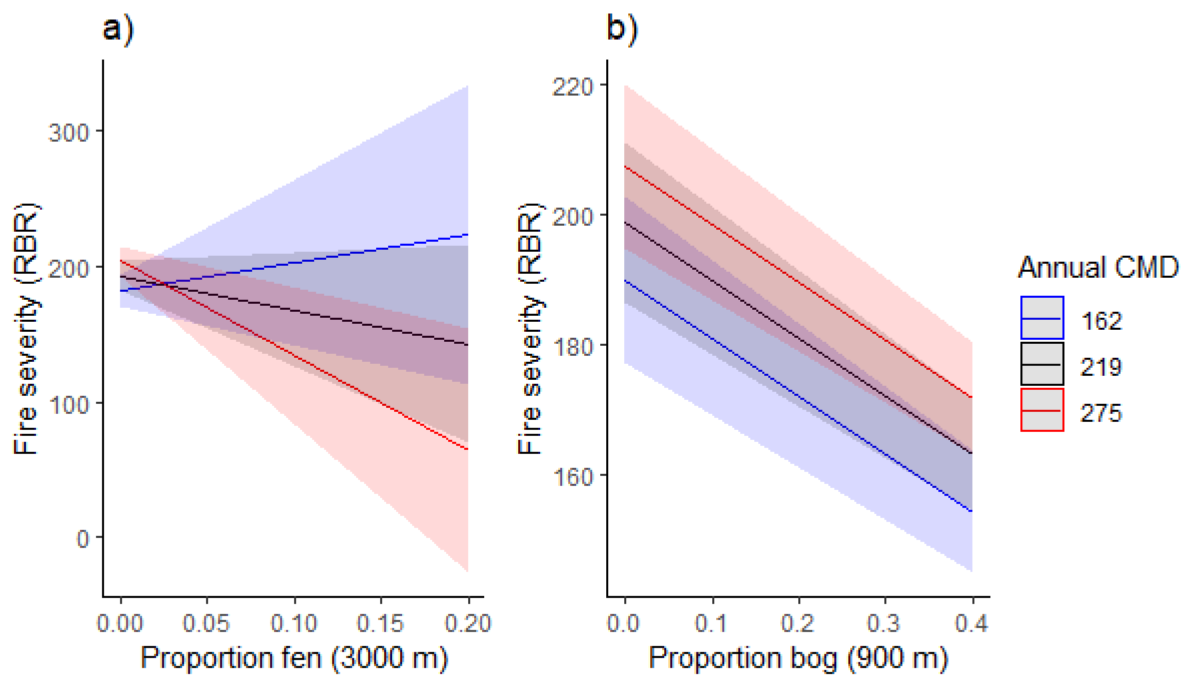

Fig. 3. Results for annual models of fire severity in peatlands relative to the amount of fens (a) and bogs (b). Error bars represent 95% confidence intervals. Blue denotes the wettest years, while red represents the driest years.

Table 6. Component model results for fire severity (a) and refugia probability (b) as a function of variables relating to vegetation, climate, ecosystem, and physical setting. β represents raw values, while $\beta_{(std.)}$ are standardized

a)

Model	**Variable**	$\boldsymbol{\beta}$	**SE**	**p**	$\boldsymbol{\beta_{(std.)}}$
Vegetation	Bog	-73.50	4.68	< 0.001	-13.94
	Fen	-54.83	2.09	< 0.001	-23.76
	Marsh	-15.71	24.33	0.519	-0.57
	Swamp	-3.27	5.00	0.513	-0.58
	Proportion cutblock (300 m)	-42.17	8.72	< 0.001	-4.82
	Fire size (ha)	$-1.84e^{-05}$	$4.57e^{-06}$	< 0.001	-3.63
	Proportion evergreen (120 m)	148.20	3.70	< 0.001	44.09

	Proportion shrubland (300 m)	-53.00	14.05	< 0.001	-3.86
	Proportion herbaceous (900 m)	-76.00	27.22	0.005	-2.95
	Proportion sparse vegetation (120 m)	44.35	7.79	< 0.001	5.43
	Proportion barren (3000 m)	-185.30	85.93	0.031	-1.91
	Proportion littoral (300 m)	-284.1	99.40	0.004	-2.51
	Intercept	111.1	3.61	< 0.001	209.79
Climate	Bog	-59.77	5.02	< 0.001	-11.33
	Fen	-41.57	2.19	< 0.001	-18.02
	Marsh	-61.33	25.92	0.018	-2.21
	Swamp	8.93	5.33	0.094	1.59
	Annual CMD	-0.07	0.02	< 0.001	-4.13
	Mean fire season temperature	-5.54	0.84	< 0.001	-6.65
	14-day phenology (min)	45.14	22.69	0.047	1.98
	14-day phenology (max)	191.74	191.74	< 0.001	18.03
	Intercept	173.40	9.39	< 0.001	209.79
Ecosystem	Bog	-28.62	6.77	< 0.001	-5.43
	Fen	-34.36	2.26	< 0.001	-17.29
	Marsh	-34.36	26.35	0.192	-1.24
	Swamp	16.55	5.75	0.004	2.95
	Fire size (ha)	$-4.77e^{-05}$	$5.05e^{-06}$	< 0.001	-9.41
	Proportion swamp (3000 m)	-42.89	20.30	0.035	-2.25
	Proportion bog (900 m)	-73.03	12.96	< 0.001	-7.20
	Proportion fen (3000 m)	$-1.01e^{-03}$	94.85	< 0.001	-10.35
	Intercept	236.00	1.50	< 0.001	209.79
Physical setting	Bog	-44.95	5.20	< 0.001	-8.52
	Fen	-36.77	2.35	< 0.001	-15.94
	Marsh	-53.31	26.10	0.041	-1.92
	Swamp	14.01	5.47	0.011	2.50

Fire size (ha)	$-3.45e^{-05}$	$5.09e^{-06}$	< 0.001	-6.81
Distance to water (log10)	18.47	2.52	< 0.001	7.38
TPI	3.45	0.68	< 0.001	5.05
CTI (120 m)	-3.45	0.71	< 0.001	-5.26
Proportion water (3000 m)	-35.26	12.19	0.004	-2.91
Proportion coarse (900 m)	-17.89	2.92	< 0.001	-6.31
Proportion FTCP (3000 m)	-21.54	2.91	< 0.001	-7.74
Intercept	186.50	13.26	< 0.001	209.79

b)

Model	**Variable**	***β***	**SE**	**p**	**Odds Ratio**	***β*** ***(std.)***
Vegetation	Bog	0.62	0.10	<0.001	1.85	0.12
	Fen	0.73	0.04	<0.001	2.07	0.32
	Marsh	1.17	0.32	<0.001	3.23	0.05
	Swamp	0.32	0.10	0.002	1.38	0.06
	Proportion cutblock (900 m)	1.22	0.16	<0.001	3.37	0.14
	Proportion evergreen (120 m)	-1.84	0.05	<0.001	0.16	-0.61
	Proportion barren (1200 m)	4.80	1.57	0.002	121.76	0.05
	Proportion herbaceous (300 m)	4.80	0.29	0.009	2.14	0.05
	Intercept	-0.40	0.04	<0.001	0.67	-1.53
Climate	Bog	0.27	0.10	0.005	1.31	0.05
	Fen	0.39	0.04	<0.001	1.48	0.17

	Marsh	1.65	0.31	<0.001	5.21	0.08
	Swamp	0.07	0.10	0.482	1.07	0.01
	14-day phenology (max)	-2.03	0.22	<0.001	0.13	-0.19
	Annual CMD	$2.15e^{-03}$	$3.58e^{-04}$	<0.001	1.00	0.12
	Normal CMD	$-3.11e^{-03}$	$4.46e^{-04}$	<0.001	1.00	-0.13
	Mean annual temperature	0.08	0.01	<0.001	1.08	0.16
	Intercept	-0.46	0.13	<0.001	0.63	-1.42
Ecosystem	Bog	-0.10	0.13	0.416	0.90	-0.02
	Fen	0.34	0.04	<0.001	1.41	0.15
	Marsh	0.76	0.40	0.056	2.15	0.04
	Swamp	0.06	0.10	0.576	1.06	0.01
	Fire size (ha)	$4.28e^{-07}$	$8.78e^{-08}$	<0.001	1.00	0.09
	Proportion bog (900 m)	0.62	0.23	0.006	1.85	0.06
	Proportion fen (120 m)	2.34	0.73	0.001	10.36	0.06
	Intercept	-1.58	0.03	<0.001	0.21	-1.40
Physical setting	Bog	0.05	0.10	0.613	1.05	0.01
	Fen	0.29	0.04	<0.001	1.34	0.13
	Marsh	1.39	0.03	<0.001	4.03	0.07
	Swamp	$-7.24e^{-04}$	0.10	0.994	1.00	-0.0001
	Fire size (ha)	$3.91e^{-07}$	$8.76e^{-08}$	<0.001	1.00	0.08
	CTI (120 m)	0.05	0.01	<0.001	1.05	0.08

TPI	-0.08	0.01	<0.001	0.93	-0.12
Intercept	-2.05	0.13	<0.001	0.13	-1.41

Table 7. Results for the most parsimonious predictive models describing fire severity (a) and refugia probability (b) as a function of the full suite of variables. β represents raw beta values, while $\beta_{(std.)}$ are standardized versions.

a)

Variables	$\boldsymbol{\beta}$	**SE**	**p**	$\boldsymbol{\beta}_{(std.)}$
Bog	-64.48	4.88	< 0.001	-12.23
Fen	-48.86	2.19	< 0.001	-21.18
Marsh	-8.21	23.86	0.731	-0.30
Swamp	-0.41	4.97	0.935	-0.07
14-day phenology (max)	121.30	10.73	< 0.001	11.40
Normal CMD	-0.029	0.04	0.458	6.06
CMD anomalies	-0.35	0.05	< 0.001	1.77
Mean fire season temperature	3.35	0.82	< 0.001	4.02
TPI	4.53	0.63	< 0.001	6.63
Proportion FTHM (900 m)	16.47	2.16	< 0.001	7.41
CTI (120 m)	-2.48	0.69	< 0.001	-3.78
Proportion cutblock (300 m)	-48.28	8.11	< 0.001	-5.52
Proportion evergreen (120 m)	107.50	7.28	< 0.001	30.32
Proportion sparse vegetation (120 m)	58.75	7.82	< 0.001	7.20
Proportion annual bog (300 m)	305.2	56.47	< 0.001	-8.60
Proportion annual fen (120 m)	43.62	20.90	0.037	-10.66
Proportion evergreen (300 m)	63.40	7.88	< 0.001	15.61
Proportion evergreen (120 m) $\times$ Proportion annual fen (120 m)	-214.60	40.25	< 0.001	-5.19

Proportion evergreen (300 m) × Proportion annual bog (300 m)	-649.10	92.50	< 0.001	-7.50
Normal CMD × CMD anomalies	$2.55e^{-03}$	$3.47e^{-04}$	< 0.001	6.51
Intercept	25.05	12.13	0.039	210.77

b)

Variable	***β***	**SE**	**p**	**Odds Ratio**	***β*** ***(std.)***
Bog	0.39	0.13	0.003	1.48	0.07
Fen	0.41	0.08	< 0.001	1.52	0.19
Marsh	0.81	0.33	0.015	2.24	0.04
Swamp	0.05	0.13	0.716	1.05	0.01
CMD anomalies	$9.68e^{-03}$	$1.03e^{-03}$	< 0.001	1.01	0.05
Normal CMD	$-7.47e^{-04}$	$8.23e^{-04}$	0.403	1.00	-0.20
14-day phenology (max)	-0.71	0.23	0.002	0.49	-0.07
TPI	-0.07	0.01	< 0.001	0.93	-0.11
Proportion course (300 m)	-0.33	0.09	< 0.001	0.72	-0.13
Proportion FTCP (300 m)	-0.55	0.09	< 0.001	0.58	-0.25
Proportion FTHM (300 m)	-0.51	0.09	< 0.001	0.60	-0.24
CTI (120 m)	0.06	0.02	< 0.001	1.06	0.09
Proportion upland (120 m)	-0.35	0.11	0.001	0.70	-0.13
Proportion cutblock (900 m)	0.78	0.17	< 0.001	2.18	0.09
Proportion evergreen (120 m)	-1.58	0.14	< 0.001	0.21	-0.53
Proportion shrub (300 m)	-0.54	0.23	0.021	0.58	-0.04
Proportion herb (300 m)	0.96	0.30	0.002	2.62	0.06
Proportion barren (1200 m)	3.54	1.61	0.028	34.59	0.04
Proportion annual fen (300 m)	0.50	0.37	0.169	1.66	0.21
Proportion annual bog (1200 m)	3.77	0.77	< 0.001	43.26	0.09

Proportion evergreen (300 m)	-0.54	0.16	0.001	0.58	-0.13
CMD anomalies × Normal CMD	$-5.85e^{-05}$	$7.05e^{-06}$	< 0.001	1.00	-0.16
Proportion evergreen (300 m) × Proportion annual fen (300 m)	2.54	0.74	< 0.001	12.69	0.07
CMD anomalies × Proportion annual bog (1200 m)	-0.07	$5.99e^{-03}$	< 0.001	0.98	-0.04
Intercept	0.20	0.27	0.458	1.22	-1.63

Table 8. Accuracy and estimates of fit for predictive models of fire severity and refugia probability.

Measures	**Fire severity**	**Refugia probability**
R^2	0.20	-
R^2 adj.	0.20	-
RMSE	109.35	-
Deviance	11958.00	0.90
pR^2	-	0.11
pR^2 adj.	-	0.11
AUC	-	0.73