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Macrosystems Ecology

Peatlands promote fire refugia in boreal forests of northern Alberta, Canada

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Abstract

In the boreal forests of North America, large wildfires often leave residual patches of unburned vegetation, termed fire refugia, which can affect post-fire ecosystem processes. Although topographic complexity is a major driver of fire refugia in mountainous terrain, refugia in boreal plains are more likely driven by a combination of other bottom-up controls on fuel configuration as well as top-down climate controls. In this study, we investigated the role of hydrological, ecological, and topographic heterogeneity, as well as climate moisture patterns, on the presence of fire refugia in forested upland and peatland ecosystems within Alberta's subhumid boreal forests over a 33-year (1985–2018) period. Generalized linear models were used to model the probability of refugia in forested stands as a function of bottom-up (vegetation, topography, site moisture, and ecosystem) and top-down (normal and annual climate moisture deficit) controls. We then developed predictive maps of refugia probability for a range of normal and interannual climate moisture deficit values. We found that forested fens had a probability of refugia that was 64% higher than upland forests, while forested bogs did not differ from forested uplands in refugia likelihood. Climate and physical setting presented the strongest controls on fire refugia in uplands and peatlands, respectively. Increasing amounts of adjacent bogs, but not fens, produced a sixfold increase in refugia probability in uplands, while increasing amounts of adjacent bogs and fens produced roughly two times the refugia probability in forested peatlands. In these upland forest stands, fire refugia probability was negatively related to the interaction between regional climate moisture deficits and interannual deviations from these norms, thus increasing the probability of fire refugia during more severe drought conditions in areas with less arid climates, while decreasing refugia probabilities in drier climates. However, in peatlands themselves, neither regional climate moisture conditions nor the interannual deviations affected refugia. Fire size had a negative effect on fire refugia in all upland-based models and a positive effect in all peatland-based models. Our results suggest that large areas of intact peatlands may be capable of promoting fire refugia and thereby slowing climate-driven, fire-mediated vegetation transitions in surrounding forest ecosystems.

KEYWORDS
boreal forest, climate, fire refugia, peatlands, wildfire

INTRODUCTION

The boreal forest region is the largest biome in Canada and is important not only as a source of timber (Bogdanski, 2008) and habitat for many species (Hobson & Bayne, 2000) but also as a major carbon reservoir, especially in locations containing large areas of peatland ecosystems (Hugelius et al., 2020). Wildfire is the most common disturbance, and fires are particularly prevalent in the western part of the country, where large stand-initiating fires burn with intervals of 50 to >100 years between events (Boulanger et al., 2012; Kasischke & Turetsky, 2006). This region is particularly vulnerable to climate-mediated vegetation change following fire and is projected to be increasingly subjected to drought events related to climate change (Boucher et al., 2018; Stralberg et al., 2018). Although some coniferous tree species in the western boreal forest rely on fire to propagate (Buma et al., 2013), an increase in fire severity in conjunction with post-disturbance moisture stress (Stevens-Rumann et al., 2018; Thompson & Waddington, 2013) has the potential to reduce conifer regeneration, resulting in widespread ecosystem transitions (Boucher et al., 2018; Johnstone et al., 2016; Whitman et al., 2019).

Wildfires do not burn homogeneously, as they often leave behind residual patches of unburned vegetation, known as fire refugia (Krawchuk et al., 2016; Meddens et al., 2018), in which mature trees survive. Given the influence of burn severity on post-fire vegetation recovery and forest resilience (Johnstone & Chapin, 2006; Johnstone & Kasischke, 2005), areas within fire perimeters that do not burn can strongly affect post-fire ecosystem processes (Coop et al., 2019). Fire refugia are important for mitigating the combined effects of climate change and disturbance (Krawchuk et al., 2020) by acting as islands, limiting 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 (Rogeau et al., 2018). 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, landscapes with little topographic relief generally facilitate fire spread (Falk et al., 2007; Harvey et al., 2016). In these areas, fire refugia may relate more to hydrological and ecological characteristics, driven by local patterns in terrain moisture and standing water (e.g., wetlands and lakes) (Nielsen et al., 2016; Ouarmim et al., 2016).

In some settings, peat-forming wetlands (i.e., peatlands), in particular open bogs and fens, have been demonstrated to burn at lower severities than uplands (Whitman et al., 2018); however, their effects on fire refugia in both peatlands and surrounding uplands have yet to be explicitly examined. Through their ability to retain high water tables, peatlands resist long-term drying (Schneider et al., 2016; Thompson et al., 2016, 2017). The presence of peatlands may therefore promote the formation of fire refugia in areas with less complex terrain (Krawchuk et al., 2016) by limiting the spread and severity of fires due to a high fuel moisture content and the physical barriers presented by standing water when water tables are high (Thompson et al., 2019). These systems may also serve to impede the spread of fire to neighboring upland ecosystems, depending on hydrologic connectivity (defined as connection to groundwater; Hokanson et al., 2016; Thompson et al., 2017), by creating a heterogeneous fuel structure that presents a stronger control on patterns of fire spread and severity relative to more homogeneous landscapes (Hargrove et al., 2000). Given their influence on fire patterns (Turner et al., 1994, 1999), these heterogeneous fuel structures and standing water may also be capable of generating fire refugia in locations with limited topographic complexity.

Wildfires follow a seasonal cycle where short-term variations in precipitation, temperature, and phenology directly affect the amount, flammability, and availability of fuel (Bajocco et al., 2017). Live 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 activity worldwide (Kane et al., 2015; Littell et al., 2016). Differences in flammability between peatland types during seasonal change or interannual drought yield distinctive differences in fire potential. Because they are groundwater-fed, fens are less susceptible to fire than bogs under typical moisture conditions (Thompson et al., 2019). However, in the spring and especially during drought conditions, fens experience an increase in fire spread potential, owing to abundant senescent (cured and dried) sedge material that readily carries surface fire (Thompson et al., 2017). This is in contrast with the slower drying and slower burning *Sphagnum* mosses that dominate bogs (Waddington et al., 2015).

The spatial patterning of fuel is a major component of fire spread and severity. The type and configuration of vegetation (e.g., deciduous vs. coniferous composition) and forest disturbances (e.g., cutblocks) provide additional bottom-up controls on fire through differences in fuel moisture, structure, and amount, thereby creating a spatially heterogeneous landscape capable of affecting patterns of burn severity (Cansler & McKenzie, 2014; Harvey et al., 2016). Despite the well-documented effects of bottom-up controls on fire propagation and fire severity, increasingly extreme fire weather has the potential to overwhelm the bottom-up controls from fuels and the limiting effects from areas with less fuel or with fuel structures that reduce fire spread and flammability (Cansler & McKenzie, 2014).

Although some models project widespread climate- and disturbance-driven ecosystem transitions throughout the western boreal region of Canada (Cadieux et al., 2020; Stralberg et al., 2018), current knowledge gaps limit their accuracy (Hart et al., 2019). Among these knowledge gaps is a lack of understanding regarding how important bottom-up controls on fire activity may be in terms of their ability to limit future fire in regions lacking complex terrain. Using remotely sensed fire severity data and a variety of geospatial inputs for the boreal region of Alberta, we developed a set of thematically grouped (hereafter "component") models and parsimonious multivariate (hereafter "predictive") models. Our objectives were to: (1) determine whether peatlands have a higher probability of becoming fire refugia relative to uplands, (2) determine the relative contribution of bottom-up (physical setting, vegetation, ecosystem) and top-down (climate, phenology) controls on fire refugia probability, (3) examine how the amount of surrounding bogs and fens affects fire refugia probability in neighboring uplands and peatlands, and (4) determine how fire refugia in areas adjacent to bogs and fens respond to drought. Finally, we used the predictive models to produce maps of fire refugia probability (i.e., the probability of an area not burning within a single fire event) over a range of annual and seasonal conditions in northern Alberta's boreal biome.

METHODS

Study area

The study area encompasses the majority of boreal forests within the province of Alberta, covering an area of roughly 465,580 km^2. It includes four of Alberta's natural regions (Downing & Pettapiece, 2006): Canadian shield, foothills, boreal forest, and portions of parkland. The southern portion of the study area was truncated due to data limitations in the land-cover dataset for this region. The latitude of the study area ranges from ~55° N to 60° N, and elevations range from 163 to 1777 m above sea level. The region has limited topographic complexity with the exception of the high plateaus to the north, the Rocky Mountain foothills, and some major river valleys. The climate is characterized by short summers (June–August) averaging 15°C and long, cold winters (November–February) averaging −10°C. Mean annual precipitation is 459 mm with 60%–70% falling as rain between April and August (Downing & Pettapiece, 2006). The geologic setting consists of uplands corresponding with well-draining, coarse-textured soils and wetland areas atop poorly draining, fine-textured organic soils (Downing & Pettapiece, 2006).

The area is composed of a patchwork of upland forests and extensive wetland systems (Figure 1). 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 in uplands on well-drained soils, whereas white spruce is more common on mesic sites in northern areas. Peat-forming wetlands (i.e., peatlands), in the form of bogs and fens, cover nearly half the area (with uplands dominating the other half), are either open, shrubby, or sparsely forested, and are dominated by black spruce (*Picea mariana*) and larch (*Larix laricina*), respectively. Peatlands differ from mineral wetlands (marshes and swamps) in that they have permanently saturated soils, anaerobic conditions, relatively stable water tables, and organic layers reaching depths of more than 40 cm (Halsey et al., 2003). Swamps in this area can be either treed or shrubby, while marshes are largely treeless and are dominated by either graminoid or aquatic vegetation (Branch & Floor, 2015).

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), with most of this disturbance occurring in upland ecosystems. Fire is the most common natural disturbance in the area, with an average of 142,976 ha having burned annually in Alberta between 1961 and 2004, 73% of which occurred in the boreal forest natural region (Tymstra et al., 2007). During this time period, an average of 0.7% of the study area burned each year.

Study design

We fit generalized linear models to explain the effects of hydrological, topographic, and ecological bottom-up

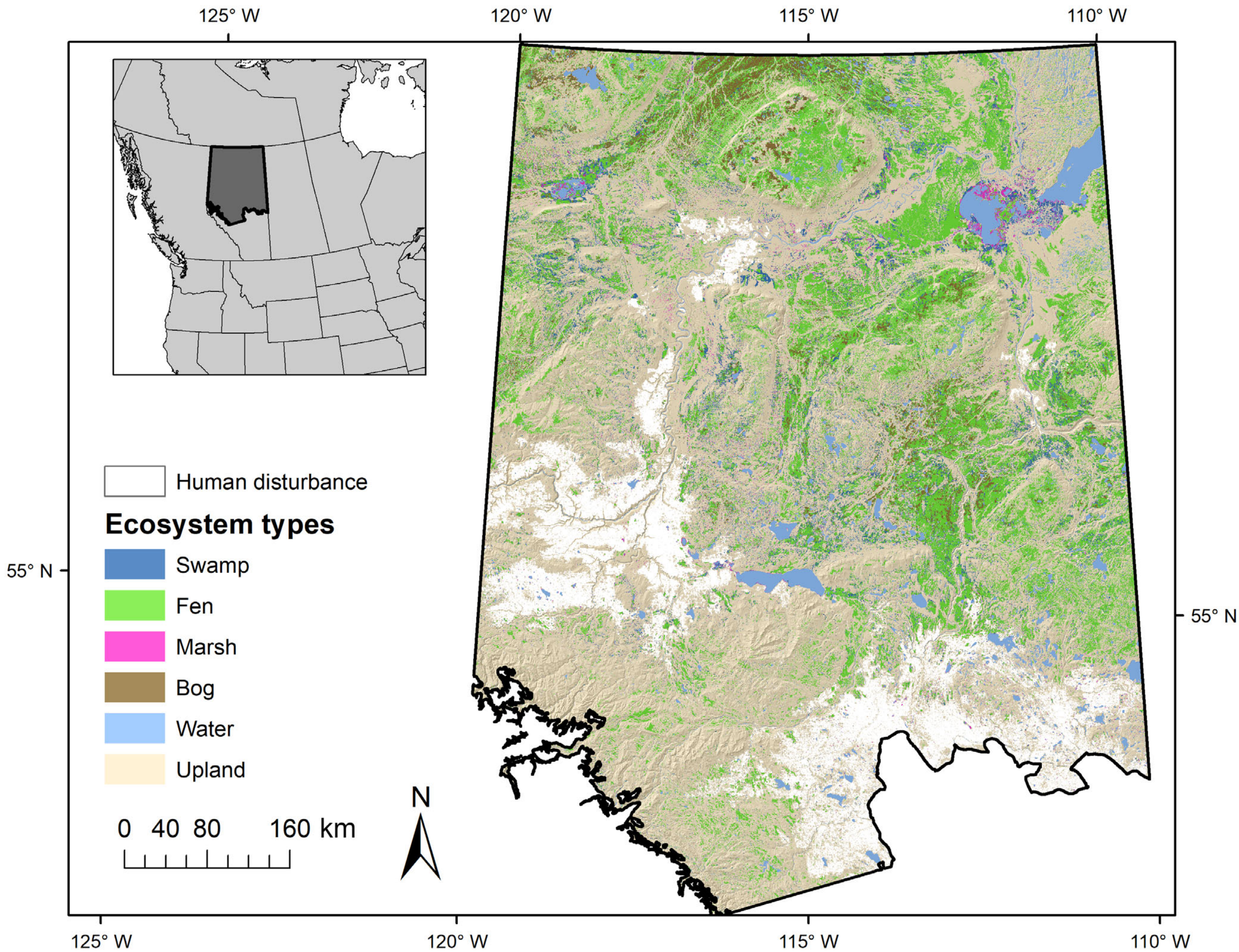

FIGURE 1 The study region covers roughly half of the province of Alberta and is largely forested. Uplands are the most numerous of the ecosystem types, followed by fens and bogs, while swamps and marshes are rare by comparison. Data come from Alberta Biodiversity Monitoring Institute's ALPHA 3.0 dataset (DeLancey et al., 2019).

controls within the surrounding landscape on fire refugia probability. We sampled the fire, climate, and environmental data using a random set of points representing 1% of all pixels within fire perimeters. Spatial covariates were calculated either as a point extraction or as a set of five square-shaped moving windows (120, 300, 900, 1200, and 3000 m on a side), 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 presented the strongest effects on fire refugia, we grouped multiple predictor variables representing landscape and climate factors into thematic categories (i.e., component models) according to their role in forest fires (i.e., climate, physical setting, fuels, surrounding wetlands, and vegetation phenology) and compared their importance. Finally, we developed two parsimonious, multi-variable models to create predictive maps of refugia probability in uplands and peatlands under a range of annual and seasonal scenarios, as measured by annual climate moisture conditions and vegetation phenology (antecedent normalized difference vegetation index [NDVI] values), respectively. All analyses were performed in RStudio (R Core Team, 2021; RStudio Team, 2020), and spatial predictions were mapped at a 30-m resolution with a NAD 1983 Transverse Mercator projection.

Remote sensing of fires

Using the Alberta Severity Atlas dataset (Whitman et al., 2020), we selected all fires ≥200 ha in size that burned between 1985 and 2018. While only 3% of fires reach this size, fires ≥200 ha are responsible for ~97% of the total area burned annually in the Canadian boreal forest (Stocks et al., 2002). We used the relativized burn ratio (RBR) to represent fire severity and identify fire refugia. RBR is an index of fire severity that measures the difference in reflectance of healthy vegetation and changes to soils between pre- and postfire satellite data (Parks et al., 2018). RBR has been found to correspond meaningfully with field measures of fire severity, such as the composite burn index (CBI) (Holsinger et al., 2022; Parks et al., 2014). In this study, pixels within fire polygons with an RBR value of ≤7.22 were considered unburned fire refugia that had survived at least one fire event (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). Each fire was assigned a date (day, month, and year) of first report as recorded in the Canadian National Fire Database (CNFDB; Canadian Forest Service, 2021). We limited the sample to fires with a start date between March and October, within the typical range of Alberta's fire season. Fires that burned outside of the normal fire season ($n = 8$) were removed from the sample to reduce the variability introduced by snow and vegetation conditions that would not appear in the rest of the study dataset. We also considered fire size in hectares (ha) as an explanatory variable extracted from the CNFDB, as previous studies have shown that in boreal forests, larger fires result in higher proportions and larger patches of unburned residual stands (Whitman et al., 2018). A total of 595 fires were sampled.

Terrain and site moisture

We represented topographic complexity via the topographic position index (TPI) (Jenness, 2006), derived from a standard digital elevation model (DEM), at a 30-m resolution (Table 1). We characterized terrain moisture through the compound topographic index (CTI), derived from the same DEM (Table 1). 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). We calculated mean CTI values per pixel at the five moving window sizes.

We used the Arctic Boreal Vulnerability Experiment (ABoVE) Landsat-derived Annual Dominant Landcover dataset (Wang et al., 2019) to delineate annual water boundaries. To capture the effects of the amount of annual water availability on refugia probability, we calculated the mean proportions of water bodies for the five spatial scales (Table 1). We filtered lake features from the Alberta Biodiversity Monitoring Institute's (ABMI) ALPHA 3.0 Predictive Landcover dataset (DeLancey et al., 2019) such that only those ≥5000 ha were retained (Nielsen et al., 2016), and then calculated the Euclidean distance to large water bodies for each pixel, in ArcMap. A total of 28 lakes, ranging from 5072 to 785,000 ha, were included. We then log-transformed the resulting distances (as per Nielsen et al., 2016; Table 1).

Pedology

We produced variables relating to pedology 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 texture (Appendix S1: Table S1). We calculated the mean proportions of each pedology category for the five moving windows to capture their heterogeneity across the landscape (Table 1). Variables for pedology and terrain and site moisture were grouped together in the component models to represent physical setting.

Climate

As weather station density in northern Canada is inadequate for analyses conducted over such large areas, variables representing climate were generated through downscaled gridded historical climate data using ClimateNA, Version 6.3 (Wang et al., 2016). Climate was represented as either normal, annual, or anomaly conditions. We used the mean climate moisture deficit (CMD; in millimeters), mean potential evapotranspiration (E_{ref}), and mean fire season (March–October) temperatures (MFST; in degrees Celsius) from 1981 to 2010, at a 500-m resolution, to represent climate normals and, more broadly, spatial climate patterns (Table 1). High CMD values represent more arid conditions, while lower values indicate wetter conditions. Temporal climate variables consisted of CMD anomalies (annual CMD − normal CMD), as a proxy for drought, and mean annual temperatures (MATs) (Table 1). We extracted normal and annual climate variables and calculated CMD anomalies for each sampled pixel. These variables were grouped together in the component models to represent climate.

Vegetation phenology

We used data from the National Oceanic and Atmospheric Administration (NOAA) Climate Data Record (CDR) of NDVI Version 4 dataset (Vermote et al., 2014) to represent phenology. 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, and is also used as an indication of fuel type. NDVI data were collected for each day between February 15 and 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. We then calculated the minimum, maximum, and mean NDVI values over 7- and 14-day periods prior to the date of the first report for each fire (Table 1). NDVI-based

TABLE 1 Variables and sampling methods used in analyses, as well as original data sources.

Association	Variable	Type	Temporal status	Sampling method	Data source
Terrain, site moisture, pedology	Topographic position index	Continuous	Static	Point	DEM-derived
	Compound topographic index	Continuous	Static	Moving windows	DEM-derived
	Proportion of water	Continuous	Annual	Moving windows	ABoVE Landsat-derived Annual Dominant Landcover dataset (Wang et al., 2019)
	Distance to lakes ($\log_{10}$)	Continuous	Static	Point	ALPHA 3.0 Predictive Landcover dataset (DeLancey et al., 2019)
	Pedology: bedrock; coarse-textured substrate; clay plain substrate; fine-textured hummocky moraine	Continuous	Static	Moving windows	Soil Landscapes of Canada-derived
Climate	Climate normals: CMD; potential evapotranspiration (E_{ref}); mean fire season temperature	Continuous	Static	Point	ClimateNA, Version 6.3
	Annual climate: CMD anomalies; mean annual temperature	Continuous	Annual	Point	ClimateNA, Version 6.3
Vegetation phenology	NDVI: max; min; mean	Continuous	Annual	Point	NOAA CDR AVHRR NDVI, Version 4
Ecosystem	Bog; fen; upland; swamp; marsh	Continuous (moving windows), discrete (point)	Static	Moving windows and point	ALPHA 3.0 Predictive Landcover dataset (DeLancey et al., 2019)
Vegetation and disturbance	Dominant vegetation: evergreen; deciduous; shrubland; sparse vegetation; barren; herbaceous; littoral; annual bog; annual fen	Continuous	Annual	Moving windows	ABoVE Landsat-derived Annual Dominant Landcover dataset (Wang et al., 2019)
	Proportion cutblock	Continuous	Annual	Moving windows	Human Footprint Index 2018 (ABMI, 2018)

Note: Moving windows represent focal statistics calculated with five square moving windows of sizes 120, 300, 900, 1200, and 3000 m.
Abbreviations: ABoVE, Arctic Boreal Vulnerability Experiment; AVHRR, Advanced Very High Resolution Radiometer; CMD, climate moisture deficit; DEM, digital elevation model; NDVI, normalized difference vegetation index; NOAA CDR, National Oceanic and Atmospheric Administration Climate Data Record.

variables were grouped together in the component models to represent vegetation phenology.

Ecosystem types

The ALPHA dataset provided the static location and classification of major ecosystem types (upland, bog, fen, swamp, marsh, and water) (DeLancey et al., 2019). The ecosystem type underlying each sampled pixel was extracted from this dataset, while the amount of each ecosystem type neighboring a pixel was also calculated. For each sampled point, we calculated the amount of each class as proportions within the five moving windows. These ecosystem types were used in the component models to represent the amount of surrounding wetlands.

Vegetation and disturbance

We used the ABoVE annual land-cover data (Wang et al., 2019) to represent dominant vegetation (Table 1). This dataset contains annual data for 10 vegetation and nonfuel classes from 1984 to 2014, capturing temporal changes as the result of human and natural disturbance. We calculated the annual proportion of each vegetation class within the five moving window sizes and extracted land-cover class from the year prior to a fire. As this dataset does not contain data for 2015 onwards, and given that there were relatively few disturbances (measured as percent area) during the 2014–2018 periods, the proportions of dominant vegetation and nonfuels 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 from 1956 to 2018. As the flammability of a cutblock is partially dependent on age, these data were used in two different ways—one as a variable and the other 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 prefire for the five spatial scales (those aged ≥30 years prefire were considered regenerated) (Thompson et al., 2017), while the mask included cutblocks aged 0–3 years pre- and postfire (Guindon et al., 2021; San-Miguel et al., 2019). Variables relating to fuels and cutblocks were grouped together in the component models to represent vegetation.

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. Pixels within fire perimeters overlapping static water bodies (ALPHA) or cutblocks aged ≤3 years pre- or postfire (Guindon et al., 2021; San-Miguel et al., 2019) were removed. We generated a random 1% sample of the 30-m resolution rasters from each fire with NA values removed (i.e., masked pixels, data gaps). This resulted in a total of 1,526,087 sample points. The sample was further reduced such that only pixels in locations considered forested in either the year prior to the first fire in the dataset (1984) or the last year of the ABoVE dataset (2014) were retained. Despite efforts to limit the sample to treed landscapes, a small number of marshes (typically considered to be treeless) were retained in the final sample, likely as a result of classification discrepancies between the ALPHA and ABoVE datasets.

A random 30,000-point subset of the sampled pixels was selected for modeling 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 datasets through a random 80:20 split, resulting in a training sample of 24,000 points. We evaluated all variables measured through moving windows such that, for each variable, we retained the single best-fitting scale measured via the Akaike information criterion (AIC; Akaike, 1981). We tested for multicollinearity (Pearson's R) among 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 fire refugia probability through univariate generalized regression modeling.

Using the sampled data, we fit 17 logistic regression models (GLMs with a binomial distribution and log link function) to assess the probability of fire refugia at a location. These consisted of ecosystem comparison model, 14 component models, and two predictive models (Appendix S1: Table S2). The sample was partitioned into pixels located in either forested uplands or forested peatlands. Following this partition, upland samples totaled 15,993 points, while peatlands totaled 7061 (6217 for fens, 844 for bogs). While the component and predictive models used data subsets for either uplands or peatlands, the ecosystem comparison model used data from the full landscape. All models included a measure of fire size (in hectares). To reduce overfitting, nonsignificant variables ($p > 0.05$) were removed in a backward-stepwise fashion. Component models were compared and ranked according to their relative AIC values.

We produced predictive maps using the "predict" function in the 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 such variables (Appendix S1: Table S2). To more accurately capture treed peatlands and effects of NDVI, these models included interaction terms between the proportions of each peatland class and evergreen forest, as well as between peatlands and measures of NDVI. Where included, these interactions reflected the best-fitting scale for each peatland class (e.g., proportion fen [120 m] × proportion evergreen [120 m]). To determine possible effects on fire refugia when influenced by both normal and anomalous climate moisture conditions, an interaction between the two CMD variables was included. We generated predictive maps reflecting both early (May) and late (August) fire-season phenological states, as well as anomalous CMD conditions during both wet and dry years. Early fire seasons included NDVI values from May 1–7 (7-day window) and May 1–14 (14-day window). Similarly, late fire seasons included

NDVI values from August 25–31 (7-day window) and August 18–31 (14-day window). Phenology for these fire season classifications was calculated as NDVI minimum (7-day) and maximum (14-day) across the last five years of the study period (2014–2018). For predicting, we produced rasters of artificial wet and dry years using histograms of CMD anomalies from the full training sample to determine appropriate cutoff values for each. We considered years with a CMD anomaly of −200 mm to be wet, whereas dry years had a CMD anomaly of +200 mm. For generating predictions, we took variables associated with annual dominant vegetation (e.g., amount of deciduous forest within a 300-m area) from the last year of the ABoVE dataset (2014).

RESULTS

Treed fens and swamps had a higher probability of fire refugia relative to uplands ($\beta = 0.49$, SE = 0.04, $p < 0.001$ and $\beta = 0.31$, SE = 0.08, $p < 0.001$, respectively), whereas treed bogs and uplands did not differ significantly ($p = 0.072$) (Table 2; Figure 2). Marshes (where mapped as treed) had the highest probability of being refugia of all the ecosystem types ($\beta = 1.84$, SE = 0.25, $p < 0.001$); however, their inclusion in this study was incidental, likely resulting from differences between the ABoVE and ALPHA datasets. In this model, fire size (in hectares) had a slight but positive effect on fire refugia likelihood ($\beta = 5.42e{-}07$, SE = 7.85e−08, $p < 0.001$).

Of the component models, climate had the strongest influence on fire refugia probability in upland stands, followed by vegetation phenology, while physical setting and amount of wetlands, respectively, were the top two performing peatland models (Table 3a,b). While all component models based on the sample of uplands outperformed the two null models, the vegetation phenology and ecological null models based on peatlands shared the same AIC value. In all upland component models, fire size (in hectares) had a negative relationship with fire refugia probability, whereas all peatland models showed a positive relationship between fire size and refugia (Appendix S1: Tables S3 and S4).

In uplands, the amount of bogs within a 1200 × 1200-m area ($\beta = 1.82$, SE = 0.56, $p = 0.001$) and the amount of marshes within a 300 × 300-m area ($\beta = 5.43$, SE = 0.94, $p < 0.001$) had positive relationships with fire refugia probability (Table 4; Figure 3a), wherein fire refugia were six times (odds ratio = 6.19) more likely in uplands completely surrounded by bogs (maximum observed value = 0.75) and 228 times (odds ratio = 228.48) more likely when completely surrounded by marshes (maximum observed value = 0.38). Fens, however, did not have a significant effect on the likelihood of fire refugia in uplands. Normal CMD also had no significant effect; however, CMD anomalies had a small positive effect on fire refugia probability ($\beta = 0.01$, SE = 9.32e−04, $p < 0.001$). There was a negative interaction between the two CMD measures ($\beta = -4.22e{-}05$, SE = 5.95e−06, $p < 0.001$), with less arid climates experiencing an increase

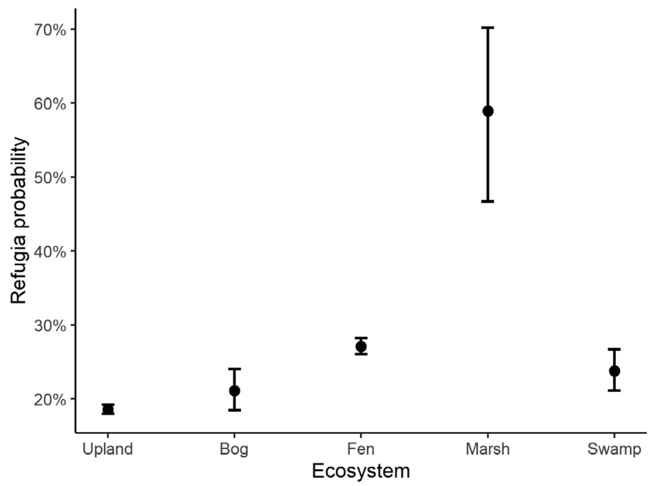

FIGURE 2 Fire refugia probability for the five ecosystems, taken from a sample of the full landscape and controlling for fire size. Error bars represent 95% confidence intervals.

TABLE 2 Results for the ecosystem comparison model used to determine fire refugia probability between the different ecosystem types.

Variable	β	SE	p	Odds ratio	β_{std}
Bog	0.16	0.09	0.072	1.17	0.03
Fen	0.49	0.04	<0.001***	1.63	0.21
Marsh	1.84	0.25	<0.001***	6.30	0.10
Swamp	0.31	0.08	<0.001***	1.37	0.06
Fire size (ha)	5.42e−07	7.85e−08	<0.001***	1.00	0.11
Intercept	−1.56	0.02	<0.001***	0.21	−1.32

Note: Upland is the reference category. Raw beta coefficients are represented by β, while standardized beta coefficients demonstrating strength of effect between factors are represented by β_{std}. Effect sizes are represented by the odds ratio.
***$p < 0.001$.

TABLE 3 Evaluation of component models for fire refugia probability based on samples from uplands (a) and peatlands (b).

Rank	Model	K	AIC	ΔAIC
(a) Upland models				
1	Climate	4	15,112	…
2	Vegetation phenology	4	15,277	164
3	Amount of wetlands	4	15,351	239
4	Physical setting	5	15,368	255
5	Fuels	3	15,387	274
6	Ecological null	2	15,389	276
7	Null	1	15,403	291
(b) Peatland models				
1	Physical setting	4	7582	…
2	Amount of wetlands	6	7669	87
3	Climate	4	7709	127
4	Fuels	4	7716	134
5	Vegetation phenology	2	7718	136
6	Ecological null	2	7718	136
7	Null	1	8117	535

Note: The null models contain only the intercept, while the ecological nulls represent refugia when fire size is accounted for. Models are ranked from the most to the least supported via Akaike information criterion (AIC). Rank, model name, number of parameters (K), AIC, and change in AIC (ΔAIC) are listed.

in fire refugia probability and drier climates experiencing a decrease as CMD anomalies increased (Figure 3b). Spatial distributions of the amount of bogs within a 1200×1200-m area and normal CMD conditions are shown in Figure 3c,d, respectively. Fire size (in hectares) had a small but significant negative effect ($\beta = -1.21e{-}06$, SE $= 1.32e{-}07$, $p < 0.001$) on fire refugia. Of the variables relating to physical setting, all but distance to lakes exhibited negative effects on fire refugia likelihood. Increasing amounts of deciduous forest within a 300-m area, normal MFST, and the 7-day prefire NDVI minimum value all had positive effects on fire refugia probability, while the relationship with the 14-day prefire NDVI maximum value was negative. Importance plots for all variables in the final upland predictive model are found in Appendix S1: Figure S1a.

In peatlands, surrounding bogs (1200×1200-m area) and fens (120×120-m area) both had positive effects on fire refugia probability ($\beta = 0.76$, SE $= 0.23$, $p = 0.001$ and $\beta = 0.66$, SE $= 0.15$, $p < 0.001$, respectively) (Table 5; Figure 4a,b), although refugia probability between the two classes did not differ significantly ($p = 0.756$). Fire refugia were twice as likely to occur (odds ratio $= 2.15$) when a peatland was completely surrounded by bogs, and 94% more likely when completely surrounded by fens, compared to those without. Spatial distributions of the amount of fens within a 120×120-m area and the amount of bogs within a 1200×1200-m area are shown in Figure 4c,d, respectively. Neither normal CMD, CMD anomalies, nor their interactions had a significant effect on fire refugia likelihood in peatlands, although normal MFST was negatively associated with fire refugia probability ($\beta = -0.09$, SE $= 0.03$, $p = 0.002$). Fire size (in hectares) had a small but positive effect ($\beta = 2.93e{-}06$, SE $= 1.86e{-}07$, $p < 0.001$) on fire refugia. Site moisture (CTI) within a 120-m area and amount of bedrock within a 300-m area both had positive relationships with fire refugia, whereas the relationship with TPI was negative. The largest effect was produced by the interaction between the 7-day minimum and 14-day maximum NDVI values ($\beta = 9.14$, SE $= 4.38$, $p = 0.037$). Importance plots for all variables in the final peatland predictive model are found in Appendix S1: Figure S1b.

The full predictive models for both uplands and peatlands outperformed the top component models (climate and physical setting, respectively), as well as null models. Predictive accuracy and goodness of fit are described in Appendix S1: Table S5. The predictive maps generated from these models (Figure 5) illustrate that fire refugia probability is highest in valleys, with the exception of late-season fires under dry annual conditions. In uplands, wet annual conditions consistently produced higher fire refugia probabilities relative to dry conditions, while early-season fires produced higher refugia probabilities relative to the late fire season. The early fire season also produced more fire refugia in peatlands relative to the late season; however, as measures of CMD anomalies did not survive variable selection in the predictive peatland model, fire refugia probability in peatlands did not vary under differing annual moisture conditions.

DISCUSSION

This comprehensive analysis of fires across the Alberta boreal region demonstrated that treed peatlands had higher probabilities of fire refugia than upland stands and that climate and physical setting had the strongest influence on fire refugia likelihood in uplands and peatlands, respectively. Results from the predictive models indicated that larger amounts of surrounding peatlands were capable of increasing refugia probability in both uplands and peatlands, while drought influenced fire refugia occurrence in uplands only. A limitation of the predictive models was the exclusion of daily fire weather conditions, which is a major factor affecting fire spread.

TABLE 4 Results of the full predictive generalized linear model (binomial distribution, logit link) for upland fire refugia probability.

Variable	β	SE	*p*	Odds ratio	β_{std}
Fire size (ha)	−1.21e−06	1.32e−07	<0.001***	1.00	−0.24
Distance to lakes ($\log_{10}$)	0.14	0.06	0.015**	1.15	0.05
Topographic position index	−0.04	0.01	<0.001***	0.96	−0.08
Proportion marsh (300 × 300 m)	5.43	0.94	<0.001***	228.48	0.10
Proportion bog (1200 × 1200 m)	1.82	0.56	0.001***	6.19	0.06
Proportion fen (120 × 120 m)	0.06	0.19	0.744	1.06	−0.04
Proportion coarse-textured substrate (120 × 120 m)	−0.02	0.09	0.026*	0.82	−0.08
Proportion clay plain substrate (900 × 900 m)	−0.32	0.10	0.001***	0.72	−0.13
Proportion fine-textured hummocky moraine (900 × 900 m)	−0.32	0.10	0.001***	0.73	−0.15
Proportion deciduous (300 × 300 m)	0.19	0.09	0.036*	1.21	0.04
Normal mean fire season temperature	0.31	0.09	<0.001***	1.36	0.37
Anomalous CMD	0.01	9.32e−04	<0.001***	1.01	0.02
NDVI 7-day minimum	1.00	0.31	0.001***	2.71	0.04
NDVI 14-day maximum	−1.74	0.24	<0.001***	0.18	−0.17
Normal CMD	−6.76e−04	9.29e−04	0.467	1.00	−0.17
Anomalous CMD × normal CMD	−4.22e−05	5.95e−06	<0.001***	1.00	−0.13
NDVI 7-day minimum × proportion fen (120 × 120 m)	−8.44	2.36	<0.001***	2.16e−04	−0.08
Intercept	−3.06	0.35	<0.001***	0.05	−1.61

Note: Variables containing "NDVI" denote normalized difference vegetation index values used as measures of vegetation phenology. Beta coefficients on the left are raw, while those on the far right are standardized for comparing variable strength. Effect size is indicated by the odds ratio.
Abbreviation: CMD, climate moisture deficit.
*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.

All treed wetland types other than bogs (i.e., fens, marshes, and swamps) had higher probabilities of fire refugia relative to upland stands. Of these, marshes had the highest overall fire refugia probability; however, marshes occur rarely throughout the study area in comparison to the other wetland types, and generally lack trees, so their inclusion in this study was incidental (Appendix S1: Figure S2). In the western boreal region, fens are more resistant to the effects of fire than bogs due to their more stable water tables (Ferone & Devito, 2004; Schiks et al., 2016), although 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 the perspective of fuel structure, bogs more closely resemble coniferous uplands than do fens (Johnston et al., 2015; Thompson et al., 2019). Additionally, the water table in bogs is usually held below the soil surface, while fens contain pockets of standing water above the surface (Branch & Floor, 2015), providing a physical barrier to fire and promoting "skips" (i.e., fire refugia) on the side opposite to wind direction during fires (Mansuy et al., 2014). These differences in fuel structure and moisture result in a higher probability of fire refugia in fens relative to bogs, suggesting that the differences observed in this study for the two peatland types may be driven by a combination of water-table dynamics and fuel structure.

Climate, followed by vegetation phenology and the amount of surrounding wetlands, had the strongest influence on fire refugia probability in uplands. Uplands are more vulnerable to drying during periods of drought than peatlands, and, as a function of seasonal changes to fuel moisture, deciduous trees are particularly vulnerable to fire prior to leaf-out, becoming more resistant to burning when green (Alexander, 2010). In this study, early-fire season pixels (March 1–June 21) (Bourgeau-Chavez et al., 2020) constituted 57% of the sample. Drier years (CMD anomalies >0) made up 84% of the sample. The strong relationship between climate, vegetation phenology, and fire refugia probability in uplands is likely related to fuel moisture content at the time of burning.

Conversely, physical setting had the strongest effect on peatlands. Soil texture and potential wetness, in part, control the location and type of peatlands present in an area (Hokanson et al., 2016), the vegetation that grows in them (Girardin et al., 2001), and the moisture content of fuels under severe fire weather conditions, such as

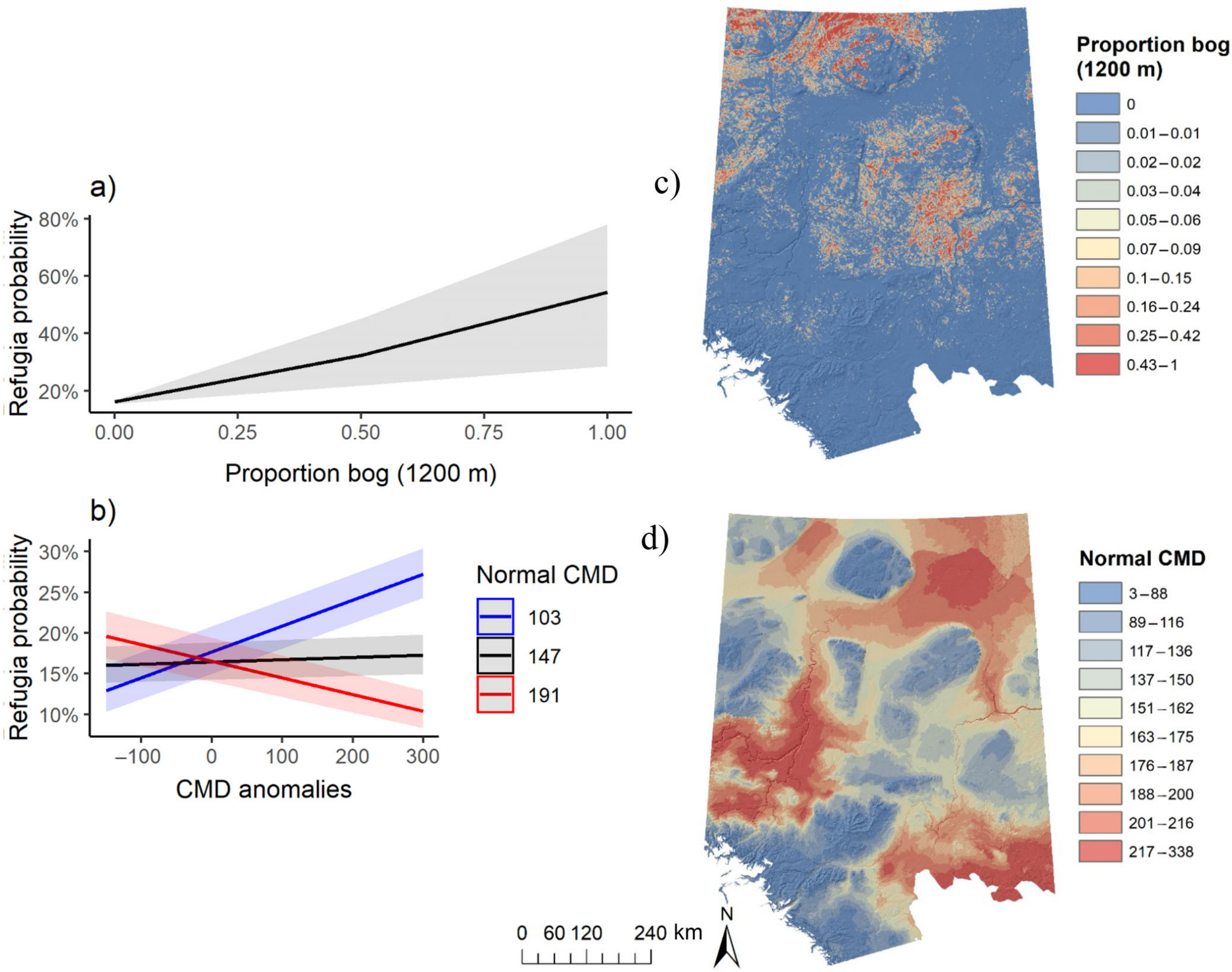

FIGURE 3 The effect of the amount of bogs within a 1200 × 1200-m area (a) and interactions between normal and anomalous climate moisture deficit (CMD) measures on fire refugia probability in forested uplands (b), wherein red and blue lines represent lower (wetter) and higher (drier) climates (normal CMD), respectively. Maps represent the distribution of bog proportions calculated within a 1200 × 1200-m area (c) and normal CMD conditions for the 1981–2010 period (d) across the study area.

drought (Turetsky et al., 2004). Previous research suggests that wetlands (including peatlands) that are hydrologically connected to groundwater supplies are more resistant to drought than those with more limited connectivity (Hokanson et al., 2016).

In uplands, increasing amounts of surrounding bogs had a positive effect on fire refugia, while fens did not have an effect. This may be due to the fact that uplands (with widespread broadleaf forests) and fens are affected by seasonal changes to vegetation, while bogs maintain consistent fuel moisture contents throughout the year due to their more coniferous vegetation. This difference in vegetation moisture in early fire-season months leads to bogs, relative to fens, providing more effective fuel breaks at this time of year, thereby increasing fire refugia probability in uplands with more surrounding bogs. Variables related to climate moisture also had an effect on fire refugia likelihood. The interaction between normal and anomalous CMD conditions saw fire refugia probability increase in uplands with wetter climates during drought, whereas refugia decreased in uplands with drier climates during drought. Uplands with wetter climates experiencing wetter than normal conditions comprised <1% of the burned pixels taken from the upland sample, while 46% were under drought conditions. The vegetation in uplands with wetter climates is normally more resistant to fire due to higher levels of precipitation but becomes vulnerable to burning as drought conditions intensify and fuel moisture levels decrease (Wotton et al., 2005). Under these intense conditions, fires are better able to spread through normally moist areas, thereby increasing the probability of fire refugia occurrence as a

TABLE 5 Results of the full fire refugia predictive model for peatlands.

Variable	β	SE	*p*	Odds ratio	$β_{std}$
Fen	0.05	0.17	0.756	1.05	0.02
Fire size (ha)	2.93e−06	1.86e−07	<0.001***	1.00	0.52
Topographic position index	−0.09	0.04	0.052*	0.92	−0.06
Proportion bog (1200 × 1200 m)	0.76	0.23	0.001***	2.15	0.14
Proportion fen (120 × 120 m)	0.66	0.15	<0.001***	1.94	0.21
Proportion bedrock (300 × 300 m)	0.82	0.18	<0.001***	2.28	0.13
Site moisture (CTI 120 × 120 m)	0.17	0.02	<0.001***	1.18	0.28
Normal mean fire season temperature	−0.09	0.03	0.002**	0.91	−0.11
NDVI 7-day minimum	−4.70	2.60	0.071	0.01	0.02
NDVI 14-day maximum	−0.49	0.36	0.172	9.14e−03	−0.01
NDVI 7-day minimum × NDVI 14-day maximum	9.14	4.38	0.037**	9336.30	0.07
Intercept	−3.15	0.34	<0.001***	0.04	−1.14

Note: Titles of NDVI denote normalized difference vegetation index values used as measures of vegetation phenology. Beta coefficients (left) are raw, while those on the far right are standardized for comparing variable strength. Effect size is given by the odds ratio.
Abbreviation: CTI, compound topographic index.
*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.

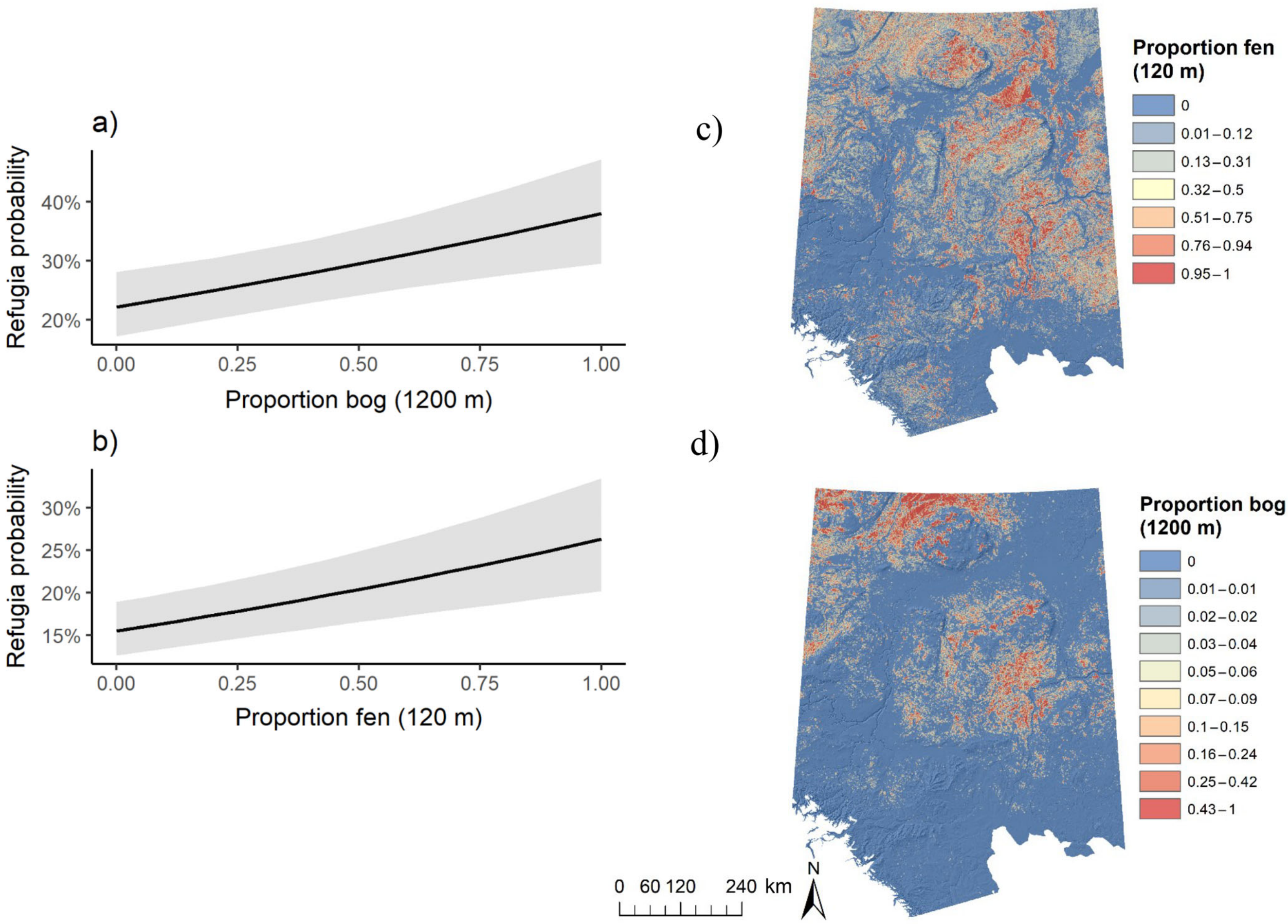

FIGURE 4 Depictions of the effects of increasing amounts of bogs within a 1200 × 1200-m area (a) and fens within a 120 × 120-m area (b) on fire refugia probability in forested peatlands. Maps represent the distribution of fen proportions calculated within a 120 × 120-m area (c) and bog proportions within a 1200 × 1200-m area (d) across the study area.

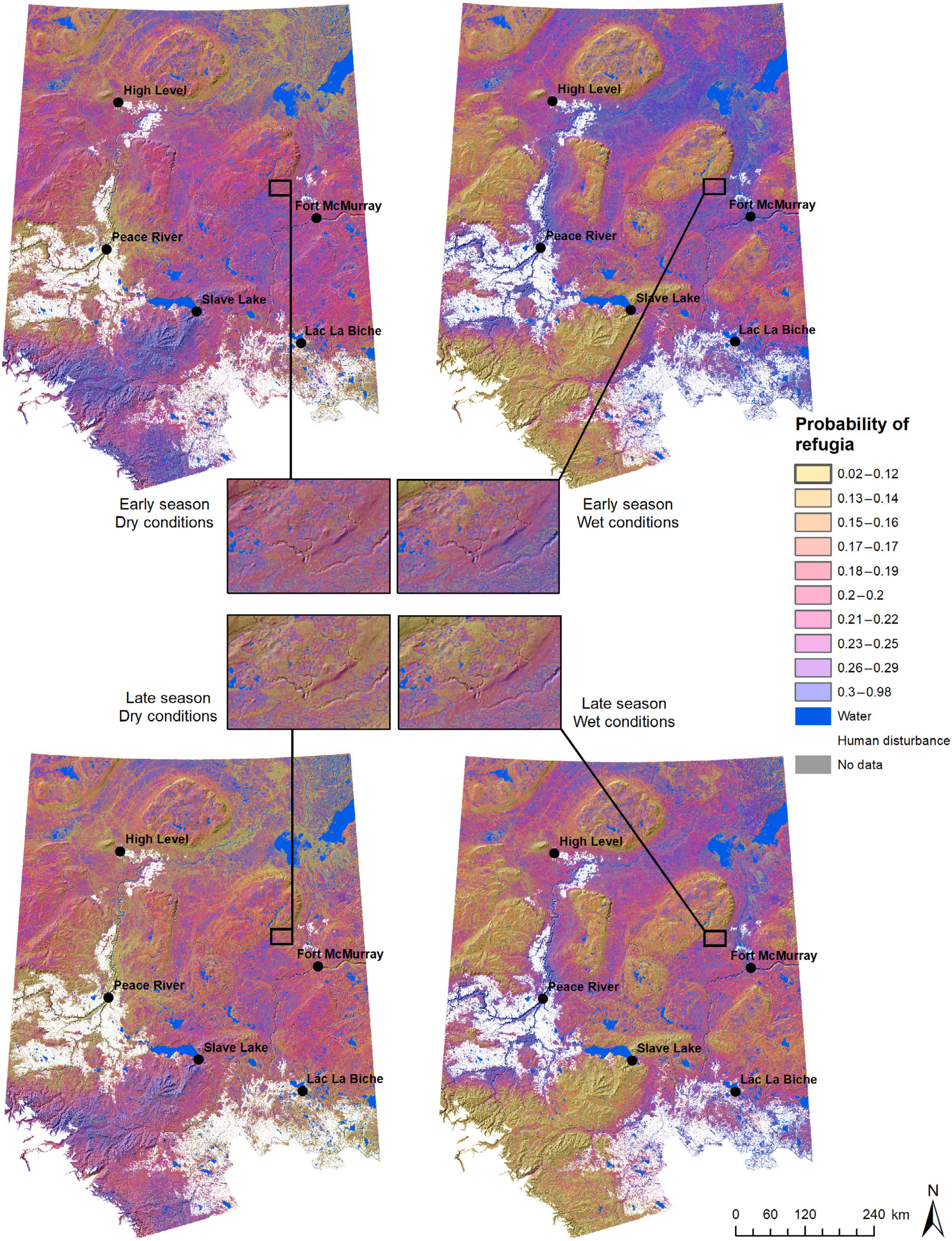

FIGURE 5 Legend on next page.

function of increased fire activity. In contrast, uplands with drier climates saw a decrease in fire refugia probability as drought conditions intensified. In these drier climates, fire refugia may be less prevalent as a function of increasingly dry vegetation creating a more homogenous fuel structure with fewer fuel breaks, limiting the chances of fire refugia forming while under drought. However, areas with drier climates also tended to be less affected by year-to-year CMD variability than wetter climates.

In peatlands, the amount of peatlands surrounding a site (pixel) increased the fire refugia probability, with bogs having a slightly stronger effect than fens. Fires burning through peatland complexes encounter a heterogeneous, often wet, landscape produced as a function of fuel structure (low vegetation) and water table dynamics (standing water, high fuel moisture, hydrological connectivity). Bogs in particular are often located within topographic depressions of higher elevation regional plateaus (Appendix S1: Figure S2), which retain more moisture than other portions of the study area (Waddington et al., 2015). However, no variables relating to climate moisture affected fire refugia in peatlands. This is, perhaps, unsurprising given that fens, which are fed by a combination of groundwater and precipitation (Weltzin et al., 2003), constitute 88% of the peatland sample, while bogs, which are fed solely by precipitation, make up only 12% of the sample. Thus, our sample primarily reflected fen-dominated peatland landscapes that are less affected by dry climates and periods of drought. The CTI, which is highest in low-lying areas and reflects site moisture, had a positive effect on fire refugia in peatlands, while the TPI, which increases with elevation, had a negative effect. Peatland water retention and spatial patterns in the western boreal region are largely controlled by hydrologic connectivity stemming from abiotic site characteristics (Hokanson et al., 2016). Water tables are more stable in peatlands situated in regional low-lying areas with high connectivity to groundwater sources, whereas those located in regional topographic highs 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). Given that it can take several years of drought to reduce water levels in peatlands (Elmes et al., 2018), particularly in fens, these results suggest that hydrologic connectivity is an important factor influencing fire refugia probability in peatland ecosystems.

While past research has shown that larger fires result in more fire refugia (Eberhart & Woodard, 1987; Madoui et al., 2010), our study found that fire size had variable effects on fire refugia probability depending on whether a burn occurred in an upland or a peatland. Fire size had a positive effect on fire refugia in all peatland models, while the relationship was negative in all upland models. This difference in the effect of fire size on fire refugia is likely due to the spatially isolated nature of peatland complexes compared to uplands. Large fires capable of overwhelming the bottom-up controls provided by fuel structures and site moisture would be required to burn through expansive peatland complexes. Thus, large fires would likely encompass a higher proportion of peatlands than smaller fires, thereby increasing the probability of fire refugia in peatlands but not uplands.

IMPLICATIONS UNDER CLIMATE CHANGE

The results of our research have shown that treed peatlands are more likely to serve as fire refugia than are upland stands and, in some cases, are also capable of promoting the formation of fire refugia in neighboring uplands. Given that interactions between fire and climate are likely to facilitate forest vegetation transitions, fire refugia are important factors in sustaining patches of intact boreal forest to act as habitat refugia and seed sources. While the persistence of peatland-mediated fire refugia may be limited due to drying, the ability of peatlands to maintain stable water tables indicates that they may prove important in mediating vegetation transitions under climate change. Peatlands are also important ecosystems due, in part, to their ability to cool the global climate over long time periods by storing large quantities of carbon (Hugelius et al., 2020). However, these carbon stores are threatened by the compound but related 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 there

FIGURE 5 Predictive maps of fire refugia probability based on a full suite of bottom-up and top-down control variables. Maps depict conditions of drought (climate moisture deficit [CMD] anomalies = 200) and nondrought (CMD anomalies = −200) years. Changes relating to seasonal phenological conditions were included to compare the early fire season (May 1–14) to the late fire season (August 18–31) time periods. Urban and agricultural areas were masked (white areas) using data from Latifovic et al. (2017). Swamps, marshes (DeLancey et al., 2019), and nonforested areas (Wang et al., 2019) were also removed as these were not targeted locations in this study. Four inset maps are used to demonstrate differences in predicted refugia location at a local scale.

can potentially be mitigated by preventing additional disturbance (Harris et al., 2021).

LIMITATIONS, FUTURE RESEARCH, AND MANAGEMENT IMPLICATIONS

Despite the strength of these findings, there are some limitations to the conclusions that may be drawn. Fire weather at the time of burning is an important factor in predicting fire activity; however, due to limited data relating to daily fire progression and associated weather conditions for the 1985–2018 study period, we were unable to account for fire weather beyond the inclusion of relative annual drought. Open peatland vegetation (e.g., sedges and shrubs) can regrow quickly following fire, and, despite efforts to limit the sample to forested pixels, it is possible that some low-severity burns were misclassified as unburned (fire refugia), leading to an overstatement of the refugia-promoting potential of peatlands.

Fire refugia probability was explained by a combination of ecosystem type and vegetation composition, suggesting that landscape heterogeneity is an important factor in controlling fire patterns. Our results showed that large amounts of bogs and fens can increase fire refugia probability in forested peatlands. While forested and open peatlands likely produce different effects on fire 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 & Pettapiece, 2006), the majority of which are forested (Thompson et al., 2016), differences in effect on fire refugia between open and treed peatlands warrants further study. Fire growth models often consider peatlands as static barriers to fire or, conversely, as flammable regardless of high water tables (Thompson et al., 2019).

CONCLUSION

The results of our study demonstrate that large amounts of peatlands in the boreal region of Alberta promote fire refugia not only in treed peatland complexes but also in neighboring upland stands, depending on whether they are located adjacent to bogs or fens, as well as the phenological state of vegetation. We found that the generation of fire refugia is driven largely by the heterogeneity of fuel structure and moisture at the time of burning, depending on the ecosystem in question. Given their role in producing fire refugia, large areas of well-connected peatlands could promote resistance to climate-induced vegetation transitions resulting from increased fire severity and post-disturbance moisture stress as the climate warms and dries. Live residual trees that survive fire within peatlands may offer places on the landscape of higher inertia in the face of mismatches between altered climate and extant vegetation, whereas burned areas with extensive mature tree mortality may be subject to more rapid changes. In addition to our current knowledge of peatlands as major sources of potential carbon sequestration, the results of our study provide further evidence of the importance of intact peatland systems in the face of climate change and stress the need for further protection of these ecosystems in the future. Our findings, as well as the predictive maps, can help managers determine where prescribed burns or timber harvest locations may be detrimental to persistent fire refugia. Using these maps, prescribed burns, burnout operations, and harvest locations might be avoided in areas of ecological concern (e.g., old growth forests and hydrologically connected peatlands) predicted to promote fire refugia, instead retaining these areas for their fire-mitigating effects or potential as seed sources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kuntzemann et al., 2023) are available from Zenodo: https://doi.org/10.5281/zenodo.7490027. Data pertaining to the fire severity rasters used in analysis, produced by Whitman et al. (2020), are available from Zenodo: https://doi.org/10.5281/zenodo.7723387.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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