



Wetland Successional State Affects Fire Severity in a Boreal Shield Landscape

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Abstract

Boreal peatland ecosystems are generally resilient to low severity wildfire. However, climate change may increase wildfire intensity and frequency, potentially shifting wetlands to less wildfire resistant states. Peatlands formed by infilling generally undergo a succession from open water to grounded peat, with spatially complex intermediate states which may impact wildfire resistance. We explored the relationship between wetland successional states and fire severity following a > 11,000 ha wildfire in Ontario's Boreal Shield landscape. We digitized 144 wetlands of varying successional states from aerial imagery and assessed fire severity using the Relative differenced Normalized Burn Ratio calculated from Sentinel-2A satellite imagery. Completely peat-filled wetlands were small in area (0.7 ± 2 ha) but were most frequent on the landscape ($n = 99/144$) compared to a smaller number ($n = 8$) of large (19 ± 2 ha) spatially complex wetlands that comprised > 30% of the total wetland area. In wetlands covered completely, or nearly completely, by peat, fire severity was significantly higher compared to wetlands with interspersed patches of shallow open water. Moreover, > 90% of fire resistant wetlands with open water were associated with beaver dams. Wetlands with more complex surface cover experienced lower mean fire severity but greater variability in fire severity suggesting that variable fuel configuration (i.e., spatially heterogeneous surface cover) in complex wetlands limit wildfire propagation across the wetland surface. Our findings are important for landscape conservation and wildfire management, as spatially complex wetlands host a diverse array of habitats for at-risk species and may offer protection from severe wildfires as fire refugia.

Keywords Wetland · Wildfire · Fire severity · Surface complexity · Beaver pond

Introduction

Northern peatlands are globally important ecosystems, storing approximately one-third of the soil carbon stock (~ 500 Gt C, Yu 2011). This carbon stock has accumulated over millennia as gross primary production has exceeded carbon losses from ecosystem respiration and combustion (Yu 2011). Peatlands also store approximately 10% of the world's surface fresh water (Holden 2005) and the ability of peatlands to retain high surface soil moisture and maintain high water tables during drought allow these ecosystems to act as climate change refugia (Stralberg et al. 2020). In addition, peatland ecosystems often provide habitat for species at risk to carry out necessary life activities (e.g., reptiles,

see Markle et al. 2020a). The persistence of many of these important ecosystem services is largely controlled by the response of peatland form and function to climate-mediated disturbances and land cover change (Harris et al. 2020) with wildfire accounting as the largest areal disturbance in boreal peatlands (Turetsky et al. 2002).

While some northern peatlands burn as frequently as every 100–120 years and can emit considerable amounts of carbon (e.g., Lukenbach et al. 2015), northern peatlands are generally resilient to low severity wildfire (Shetler et al. 2008; Lukenbach et al. 2015; Wilkinson et al. 2020) returning to net carbon sinks within approximately 20 years after wildfire (Wieder et al. 2009). The ability of northern peatlands to maintain their long-term ecosystem carbon sink function following wildfire is due to a combination of *Sphagnum* moss traits and a suite of negative feedbacks that work together to maintain a high peatland water table position and near-saturated conditions for much of the year (Waddington et al. 2015). As such, most fires that do burn in

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peatlands are of low burn severity combusting only a shallow surface layer of peat and typically leaving the majority of the peat profile intact (Hokanson et al. 2016). Nevertheless, there is concern that climate change will increase the frequency and severity of peat fires (Turetsky et al. 2015) as lower water table positions and drier near-surface peat become more common through enhanced evapotranspiration (Helbig et al. 2020) thereby increasing the risk of wildfire ignition and smouldering combustion (Wilkinson et al. 2020).

To address the growing peat fire risk, research has identified the primary drivers of variability in peat burn severity (Hokanson et al. 2016; Wilkinson et al. 2019). In general, peatlands with a higher tree cover, a higher proportion of peatland margin ecotone, and those periodically disconnected from regional groundwater systems are most vulnerable to high burn severity (Hokanson et al. 2016; Wilkinson et al. 2019). Complicating these cross-scale drivers of peatland burn severity and the prediction of future peatland wildfire regimes is the interaction of wetland surface composition (Wilkinson et al. 2020) and microtopography (Benscoter et al. 2015) which are controlled by wetland developmental state. Mapping landscape- and wetland-scale patterns in burn or fire severity can permit the identification of ‘hot spots’, or localized areas of high burn or fire severity, and elucidate landscape characteristics associated with wildfire severity potential (e.g., Shekede et al. 2021; Wilkinson et al. 2021). For instance, remotely sensed imagery has been used to map the potential for smouldering combustion in treed peatlands (Wilkinson et al. 2021), map the recovery of burned wetland vegetation (Potter 2018), and evaluate fire severity across wetlands (Li et al. 2020). Satellite imagery has been used in a similar manner for wildfire prediction in a variety of ecosystems (Leblon 2009; Spasojevic et al. 2016; Valdez et al. 2017) and to inform conservation decision-making (Rozario et al. 2018; Campos et al. 2020; Braun et al. 2021). As such, relating fire severity to spatial patterns at the landscape or wetland scale may be useful for wildfire management and for conservation practitioners as a strategy to support land management decisions (e.g., Aretano et al. 2015; Catarino et al. 2020).

At the wetland-scale, patterns in surface complexity and composition can be conceptualized into a five-state model as wetlands develop through a series of wetland developmental states (States A–E, see Markle et al. 2020a). For instance, basin wetlands are primarily formed by infilling, during which they undergo successional changes from shallow open water to a bog (Rydin et al. 2013). This occurs as organic matter accumulates at the wetland margins and floating vegetation mats develop horizontally and vertically until they become grounded. Along this successional pathway, there is a transition from an environment of primarily open water

(state A) to one dominated by peat (state E). In these initial (state A) and final states (state E), surface complexity is low. Yet in intermediate states, surface complexity is maximized, where the wetland is a mosaic of open water, floating vegetation and peat mats, and grounded peat. Because the spatial arrangement of vegetation assemblages causes variability in the accumulation of peat and moisture dynamics (Rydin et al. 2013), the role of surface complexity at the wetland scale is likely a key parameter in understanding patterns in burn severity (Kotze 2013).

Here, we investigate the relationship between wetland surface cover composition and complexity and wildfire severity in a spatially heterogeneous Boreal Shield landscape. Our first objective was to classify wetlands into successional states using pre-fire aerial imagery and assess the distribution of wetland states across the study area. Our second objective was to assess fire severity among wetlands of different successional states and surface complexities. We hypothesized that wetlands with a greater proportion of shallow open water and more variable fuel configuration (spatial complexity) would be more resistant to burning, while wetlands that were predominantly peat-filled with a more homogenous fuel configuration would be more vulnerable to burning (i.e., higher fire severity). We also examined the role of beaver dams on mitigating fire severity and hypothesized that wetlands with beaver dams would experience lower fire severity because beaver dams increase upstream water storage and open water extent. Our third objective was to examine the spatial variability of fire severity within wetlands. We predicted that wetlands with a higher proportion of peat cover would have larger patches with a higher fire severity compared to wetlands with more open water which would have larger fire-resistant patches.

Methods

Study Area

This study was carried out in the Georgian Bay Biosphere Mnidoo Gamii, a UNESCO Biosphere situated on the Canadian Shield in the eastern Georgian Bay region of Ontario, Canada. The Georgian Bay Biosphere Mnidoo Gamii is situated within Anishinabek territory, including the Robinson-Huron Treaty and Williams Treaty, the Métis Nation of Ontario Region 7, and is home to many diverse Indigenous peoples. In this rock barrens Boreal Shield landscape, peat accumulates in impermeable bedrock depressions, creating a mosaic of wetlands, granite outcrops, and forested uplands with considerable topographic variation from 172–436 masl (Crins et al. 2009). From 18 July 2018 until 31 October 2018, 11,362 ha of the landscape burned in the Parry Sound 33 wildfire (Fig. 1). While there are records of fires in this area

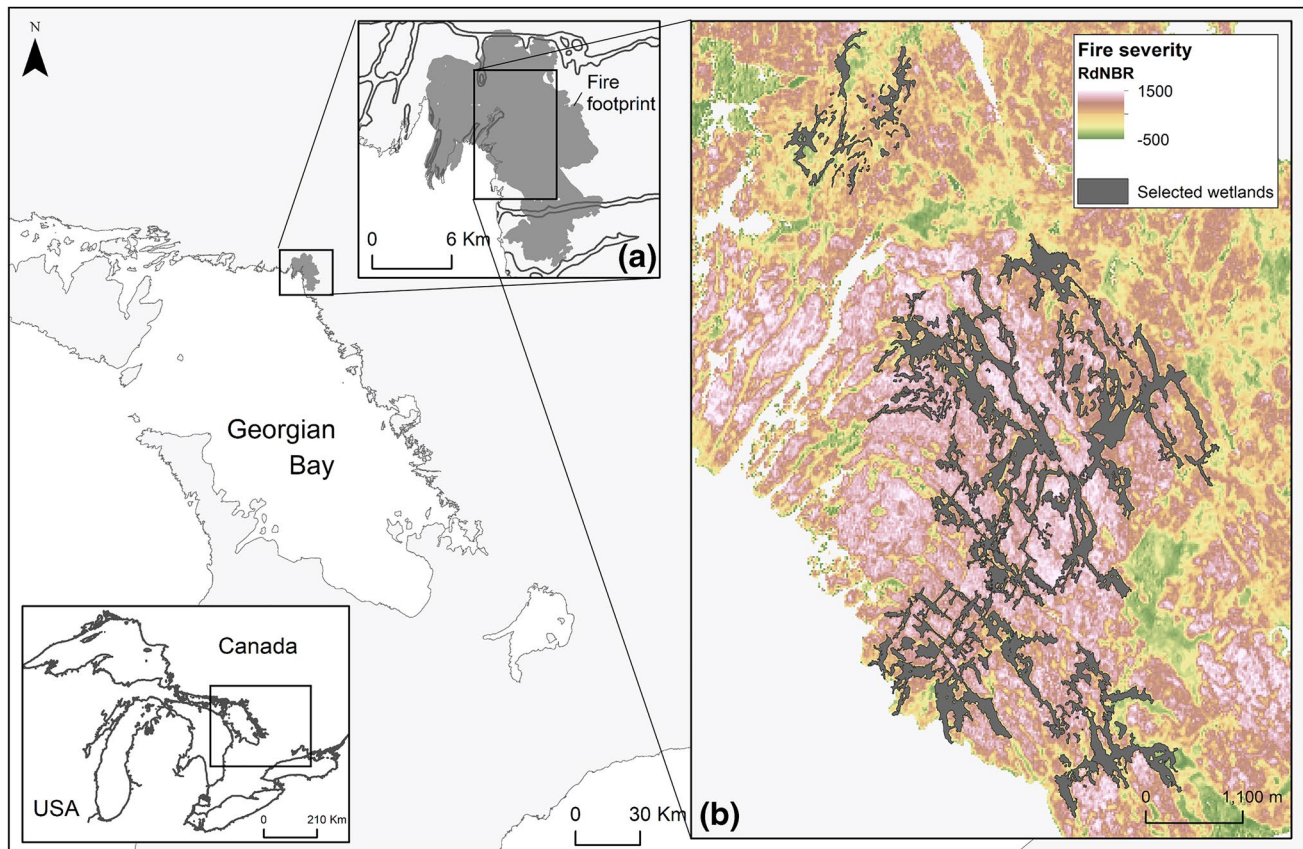


Fig. 1 The Georgian Bay ecoregion on the southern portion of the Canadian Boreal Shield in Ontario, Canada, highlighting the location of the Parry Sound #33 wildfire. **(a)** The fire footprint is shown in light grey with the study area delineated. **(b)** The 144 wetlands digitized as part of the study (dark grey) are overlaid on the fire severity map quantified using the Relative differenced Normalized Burn Ratio (RdNBR)

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(e.g., fires north of the French River in 1864 and 1871; 1877 Parry Sound fire) there have been no large fires recorded since 1950 in the Georgian Bay ecoregion (Markle et al. 2020b; Wilkinson et al. 2020; Natural Resources Canada 2022). The climate is humid continental with a mean annual precipitation of 1118 mm and monthly mean temperatures ranging from $-11.8\text{ }^{\circ}\text{C}$ in January to $19.8\text{ }^{\circ}\text{C}$ in July (Environment and Climate Change Canada 2018). However, on 18 July 2018 when the Parry Sound 33 wildfire started, the area had received 0.25% of typical precipitation for the month (Environment and Climate Change Canada 2018; Wilkinson et al. 2020).

Wetland Classification

To determine the study area within the 11,362 ha fire footprint (OMNRF 2022), we created a 1 km^2 hexagonal grid overlaid on the fire footprint in ArcGIS Pro 2.9.1. We randomly selected six 1 km^2 hexagons and the boundaries of all wetlands within the selected hexagons were digitized using the 2016 Central Ontario Orthophotography Project aerial imagery (COOP, 20 cm resolution) at a 1:800 scale

(Fig. 1). The study landscape has many expansive, connected wetland complexes where a single contiguous wetland contains many different wetland types (e.g., coniferous swamp ringing a fen). Therefore, to determine wetland boundaries, we followed the Ontario Wetland Evaluation System (Government of Ontario 2014) and treated an entire connected wetland complex as a single wetland. Features such as elevation changes and beaver dams were considered to demarcate wetland boundaries since they disconnect the hydrology of adjacent areas. Next, we examined the COOP imagery and visually classified wetland state using a decision key (Fig. S1) we created which aligned visual and textural characteristics with wetland states (A–E; Fig. 2) based on the conceptual model outlined in Markle et al. (2020a). Lastly, we conducted a visual assessment approximately 20 m around each wetland boundary to confirm the fire had reached the wetland edge to ensure we were examining wetlands which had an equal opportunity to burn.

For each delineated wetland, we classified wetland surface cover in ArcGIS Pro 2.9.1 using an unsupervised classification approach (ISO cluster algorithm) on the

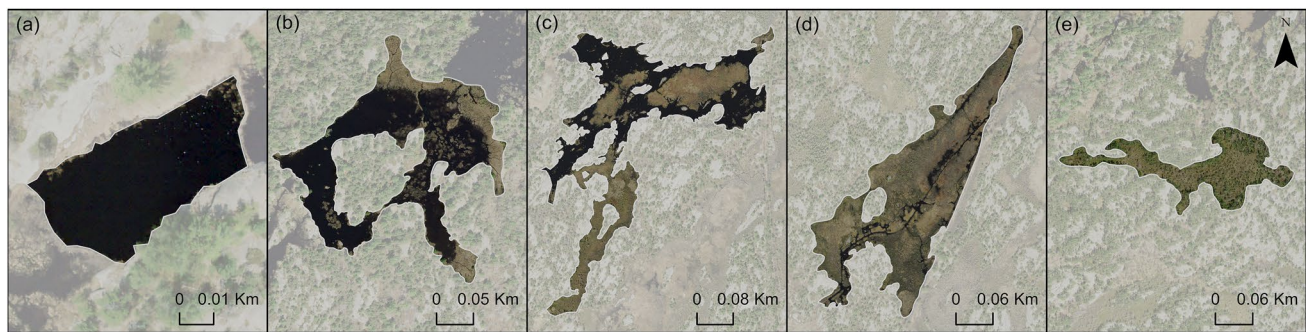


Fig. 2 Wetlands classified according to a five-state system (state A to E; a–e) which represents an infilling succession from shallow open water (a) to an infilled peatland (e). State C (c) has the highest surface

complexity and is a network of floating peat, grounded peat, open water, and bedrock

2016 high-resolution COOP imagery. We classified the wetland surface cover composition into two broad classes, shallow open water and other surface cover. We defined shallow open water (herein referred to as open water) as areas which appeared as pools of open water in the spring (i.e., in the COOP imagery) but supported floating aquatic vegetation (e.g., *Nymphaea odorata*, *Nuphar variegatum*, *Brasenia schreberi*) and some emergent vegetation (e.g., *Schoenoplectus* spp., *Scirpus* spp.) in the summer. In the study area, other wetland surface cover types included floating and grounded *Sphagnum* spp. peat and vegetation (e.g., *Chamaedaphne calyculata*, *Vaccinium* spp.) mats, more densely growing emergent vegetation (e.g., *Typha* spp., *Sagittaria* spp.), other shrubs (e.g., *Myrica gale*, *Rhododendron groenlandicum*, *Kalmia polifolia*), and trees (e.g., *Larix laricina*, *Pinus banksiana*). To reduce spurious pixel classifications from tree shadows, the resolution of the classified layer was set at 2 m and was subsequently filtered to remove single pixels completely surrounded by a different land cover class. Next, we conducted a visual accuracy assessment to compare the resulting classification with ground-truth data extracted from the COOP imagery. We randomly selected points for accuracy assessment until we had 150 points representing shallow open water and 150 points representing other surface cover. Finally, we calculated the percent shallow open water for each wetland.

We assessed all wetlands for evidence of beaver activity by visually inspecting high-resolution COOP aerial imagery which has been shown to be an accurate method for identifying beaver-impacted wetlands (Morrison et al. 2015). Similar to Morrison et al. 2015, we classified a wetland as beaver impacted if wetlands had clear identifying features such as dams which appeared as distinct linear structures.

Spectral Indices

We used Sentinel-2A L1C imagery taken on 12 September 2017 and 7 September 2018 for spectral analysis pre- and

post-fire, respectively. Although the fire was officially declared out on 31 October 2018, the fire was being held (did not increase in size) on 9 August 2018 with only smouldering combustion thereafter. Before use, the Sentinel-2 L1C images were atmospherically corrected to L2A products using the Sen2Cor v2.8.0 Atmospheric Correction Processor in the SNAP application package (version 8.0.1). We also used the unsupervised classification approach in SNAP to mask out pixels identified as deep open water in September in the Sentinel-2A imagery. This removed water bodies such as lakes and rivers, and areas of deep open water (i.e., no vegetation in summer) in some wetlands. To assess fire severity, we calculated the Relative differenced Normalized Burn Ratio (RdNBR; Eq. 1, Miller and Thode 2007) in ArcGIS Pro 2.9.4, a standard metric which discriminates the spectral properties of burned and unburned surfaces and accounts for pre-fire vegetation variability (Miller and Thode 2007).

$$RdNBR = dNBR / \sqrt{|NBR_{prefire}|} \quad (1)$$

where dNBR is the differenced Normalized Burn Ratio and NBR is the Normalized Burn Ratio. First, we calculated the Normalized Burn Ratio (Eq. 2, Delcourt et al. 2021) for pre- and post-fire imagery which assumes that near-infrared and short-wave infrared reflectance responds oppositely to fire.

$$NBR = NIR - ISWIR / NIR + ISWIR \quad (2)$$

where NIR represents near-infrared wavelengths (Band 8a with band center at 865 nm, 20 m resolution) and ISWIR represents the upper-end of the short-wave infrared spectrum (Band 12 with band center at 2190 nm, 20 m resolution; Delcourt et al. 2021). Changes between the pre- and post-fire imagery are determined by calculating the differenced Normalized Burn Ratio (dNBR; Eq. 3, Delcourt et al. 2021):

$$dNBR = NBR_{prefire} - NBR_{postfire} \quad (3)$$

The dNBR layer was calibrated using surrounding unburned cells 5 km outside of the fire footprint to account for any changes unrelated to the fire (e.g., phenology). An average unburned bias value was calculated for the land area 5 km outside of the fire footprint and subtracted from each pixel within the fire footprint as the calibration factor. Additionally, any extreme values ($1500 < \text{RdNBR} < -500$) were removed.

Statistical and Spatial Analyses

In order to determine which wetland successional states were most resistant or vulnerable to wildfire, we calculated fire severity as the mean and standard deviation of RdNBR values within the digitized wetland boundaries in ArcGIS Pro 2.9.1. To assess the effect of surface cover spatial complexity on fire severity, we calculated the landscape shape index (LSI) for each wetland. The LSI provides a standardized measure of the total length of edge in each wetland (including outer boundary and all interior patch boundaries) while controlling for total wetland size (McGarigal 2015). The LSI is the same as the habitat diversity index (Patton 1975) and can be interpreted as a measure of overall spatial complexity of the wetland surface cover or as a measure of wetland cover disaggregation. For each wetland, LSI was calculated as:

$$[0.25 \times E] \div \sqrt{A} \quad (4)$$

where E is the total length of edge (m) in a wetland and A is the total wetland area (m^2). For example, when LSI equals one, the wetland is characterized by a single habitat cover type and the LSI increases (without limit) as the length of each habitat cover type (patch) increases and different habitat types become more dispersed within the wetland. The LSI for each wetland was calculated using the ‘landscapemetrics’ package (Hesselbarth et al. 2019) in RStudio 4.2.0. We used non-parametric Kruskal–Wallis tests to test for differences in mean wetland area, fire severity (RdNBR values), percentage of open water, variability of fire severity (standard deviation in RdNBR), and landscape shape index among successional states. Where applicable, we used post-hoc Conover-Iman tests using rank sums and corrected for multiple comparisons with a Holm’s sequential correction (Holm 1979).

To examine the potential influence of beaver dams on fire severity, we used a Mann–Whitney U test to examine differences in fire severity (mean RdNBR), variability of fire severity (standard deviation of RdNBR), percentage of open water, number of open water patches, and landscape shape index between wetlands with and without beaver dams. We calculated the number of open water patches using the ‘landscapemetrics’ package (Hesselbarth et al. 2019) in RStudio 4.2.0.

We conducted a spatial autocorrelation and hot spot analysis within each wetland containing > 30 Sentinel-2A pixels to assess fire severity patterns at the wetland-scale, similar to studies examining wildfire patterns in broadleaf forests (Coluzzi et al. 2010) and landscapes dominated by wetlands and peatlands (Arisanty et al. 2021). First, we used the Global Moran’s Index (Moran’s I) to determine spatial autocorrelation, testing whether fire severity within a wetland was either clustered, randomly distributed or dispersed with 95% confidence threshold (Prasannakumar et al. 2011). Moran’s I coefficient varies between 1 (complete spatial correlation) and -1 (total spatial dispersion), where zero indicates a random distribution. The observed Moran’s I coefficient is then compared with the expected coefficient in a completely random environment. If Moran’s I is significant and fire severity is not randomly distributed within a wetland, hot spot analyses were used to identify clusters within each wetland based on the RdNBR values (fire severity). To do this, we used the Getis-Ord G_i^* statistic to identify areas of strong spatial autocorrelation within the wetland and applied a false discovery rate correction (Ord and Getis 2001). Spatial relationships were conceptualized using a spatial weights matrix with a fixed distance of 46 m and a minimum of 8 neighbours. The fixed distance of 46 m was determined by calculating the average distance to 8 neighbours for each individual wetland and taking the group mean. We defined areas where there was significant positive local autocorrelation (large and positive G_i^*) as ‘hot spots’ or areas within the wetland with higher fire severity. Conversely, we defined areas where there was significant negative local autocorrelation (large and negative G_i^*) as ‘cold spots’ or areas within the wetland that had lower fire severity or were more fire resistant. Using the point output from the Getis-Ord G_i^* statistic, we calculated the number, size, and distribution of hot and cold spots in each wetland. Hot and cold spot distribution was determined by calculating the distance of each significant hot or cold point from the wetland edge.

Results

Pre-fire Wetland Characteristics

Of the 144 wetlands digitized within the study area, only a few state A ($n=7$) and C ($n=8$) wetlands were observed. The relative frequency of wetlands in successional states B and D was approximately equal at 10% ($n=14$) and 11% ($n=16$), respectively (Fig. 3a). Peat-filled wetlands (state E, $n=99$) were nearly seven times more frequent and represented almost 69% of the wetlands in the study area (Fig. 3a). While state E wetlands were most abundant, they only occupied 15% of the wetland area digitized whereas

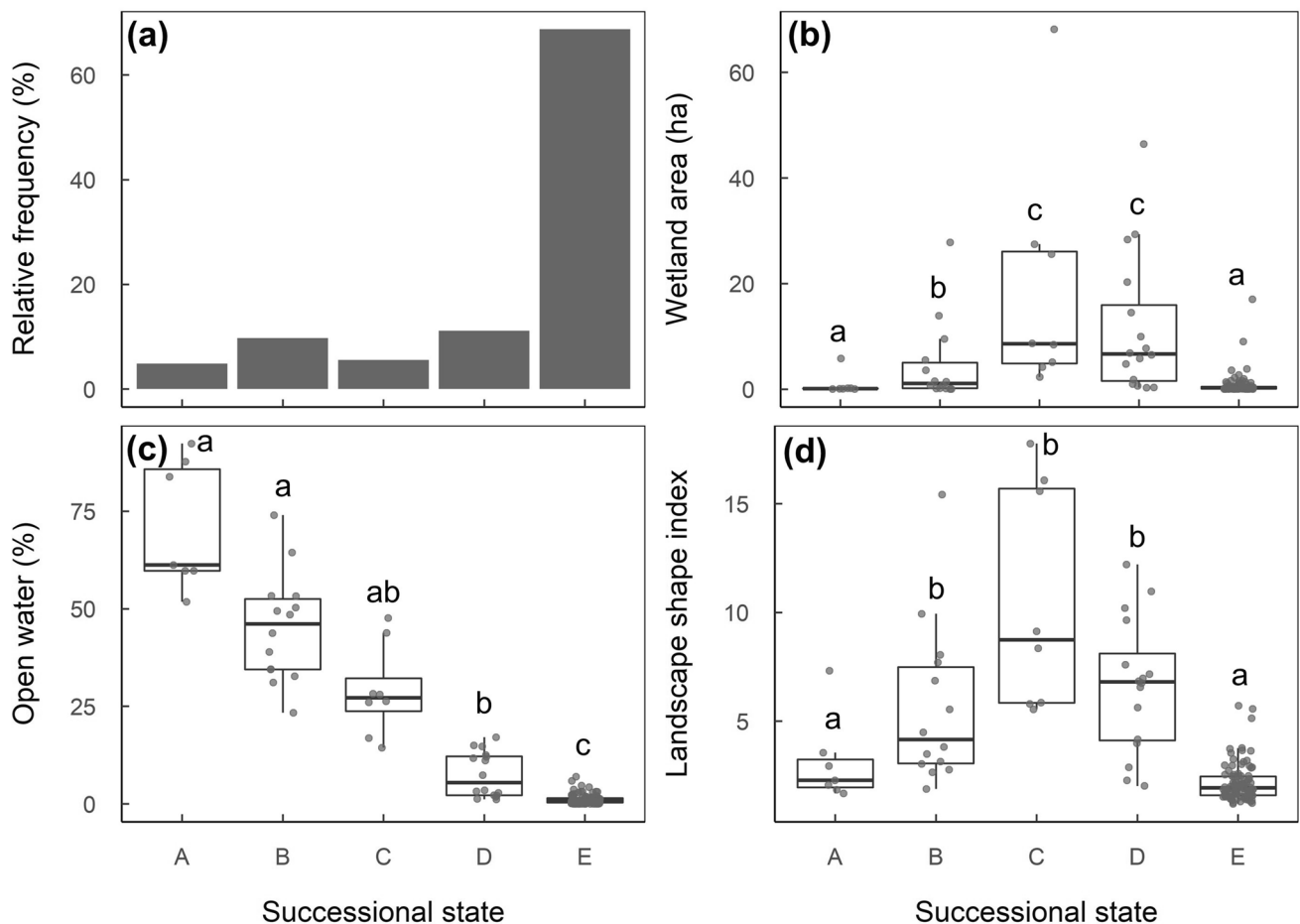


Fig. 3 Relative frequency (a), surface area (b), percent open water (c), and landscape shape index (d) for 144 wetlands digitized within the study area on the Canadian Boreal Shield in Ontario, Canada.

Results of the post-hoc tests for each variable are denoted by lower case letters where wetland successional states (A–E) are not significantly different ($p > 0.05$) if they share the same letter

states C and D occupied over half of the area combined (~31% and 39%, respectively). One notable state C wetland occupied greater than 14% of the total digitized wetland area, and one state D occupied almost 10% of the total area. The proportion of digitized wetland area occupied by states A (1.3%) and B (14%) was relatively small.

We found a significant difference in mean wetland area among successional states ($\chi^2 = 48.6$, $P < 0.001$; Fig. 3b). State C wetlands had the largest mean area (mean \pm SD; 19 ± 22 ha) and were comparable to state D wetlands because of the large range in wetland sizes (12 ± 13 ha; $t = 0.7$, $P = 0.5$; Fig. 3b). In comparison, state E and state A wetlands were significantly smaller with mean areas of only 0.7 ± 2 ha (E vs. C, $t = -5.5$, $P < 0.001$; E vs. D, $t = -6.4$, $P < 0.001$) and 0.9 ± 2 ha, (A vs. C, $t = -4.8$, $P < 0.001$; A vs. D, $t = -4.8$, $P < 0.001$) respectively (Fig. 3b). State B wetlands were an intermediate size of 5 ± 8 ha (Fig. 3b).

Shallow open water was classified with a 94% accuracy ($n = 141/150$) and all other surface cover with 99% accuracy

($n = 149/150$) for an overall accuracy of 97%. Instances of incorrect classification of surface cover as open water were mainly from tree shadows. Mean percent open water decreased from state A to state E wetlands ($\chi^2 = 88.1$, $P < 0.001$; Fig. 3c). State A had an average of $71 \pm 16\%$ open water followed by $45 \pm 14\%$ open water in state B and $29 \pm 12\%$ in state C; however, they did not differ significantly (Fig. 3c). In comparison, state D ($7 \pm 6\%$) and E ($1 \pm 1\%$) wetlands had almost no open water (Fig. 3c).

Surface spatial complexity varied significantly among the wetland states ($\chi^2 = 66.9$, $P < 0.001$; Fig. 3d). State C wetlands had the highest surface complexity with a landscape shape index of 10.5 ± 5.1 . Although not significantly different from state C wetlands, state B and state D wetlands were less spatially complex with mean landscape shape index values of 5.6 ± 3.7 and 6.6 ± 3.1 , respectively. State A and state E wetlands had significantly lower spatial complexity than all other wetland states with a mean landscape shape index of 3.1 ± 2.0 and 2.1 ± 1.0 , respectively (Fig. 3d).

We identified 41 of the 144 digitized wetlands as being beaver impacted. All state A and C wetlands ($n = 7/7$ and $n = 8/8$ wetlands, respectively), and nearly all state B ($n = 13/14$) wetlands, were impacted by beaver dams. Many state D ($n = 13/16$) wetlands had beaver dams, yet none of the E wetlands were associated with dams ($n = 0/99$). Wetlands with beaver dams had significantly higher open water cover ($35 \pm 25\%$) than those without beaver dams ($2 \pm 5\%$; $W = 129$, $P < 0.001$; Fig. 4a). Wetlands with beaver dams were more spatially complex (6.7 ± 4.2) than wetlands without dams (2.2 ± 1.0 ; $W = 382$, $P < 0.001$; Fig. 4b) and also had an average of 53 ± 81 patches of open water compared to only 6 ± 13 patches in wetlands without beaver dams ($W = 914$, $P < 0.001$).

Fire Severity

Of the 144 wetlands, 19 wetlands had a single RdNBR value because of their small area and the comparatively coarse resolution (20 m) of the fire severity data. Therefore, for

all fire severity analyses, we excluded the 19 wetlands with only 1 RdNBR pixel value (2 state A, 2 state B, 15 state E) to avoid quantifying the fire severity of the uplands surrounding the small wetland (Figs. 4c, d and 5).

We observed a significant difference in mean RdNBR between wetland successional states ($\chi^2 = 43.8$, $P < 0.001$). Mean RdNBR values suggest that state E (777 ± 293 , $n = 84$) and D (491 ± 174 , $n = 16$) wetlands experienced the highest fire severity, while there was little difference in fire severity among states A (428 ± 215 , $n = 5$), B (303 ± 181 , $n = 12$), and C (313 ± 155 , $n = 8$; Fig. 5a). Pairwise comparisons indicate that the mean RdNBR of state E wetlands was different from all other successional states; A ($t = 2.9$, $P = 0.03$), B ($t = 5.9$, $P < 0.001$) and C ($t = 4.9$, $P < 0.001$), and D ($t = 4.1$, $P < 0.001$; Fig. 5a). Comparisons among all states containing some amount of interspersed open water (A–D) were not significantly different (Fig. 5a). Additionally, wetlands with beaver dams had a significantly lower mean RdNBR (401 ± 194) than those without beaver dams (759 ± 302 ; $W = 2742$, $P < 0.001$; Fig. 4c). The distribution

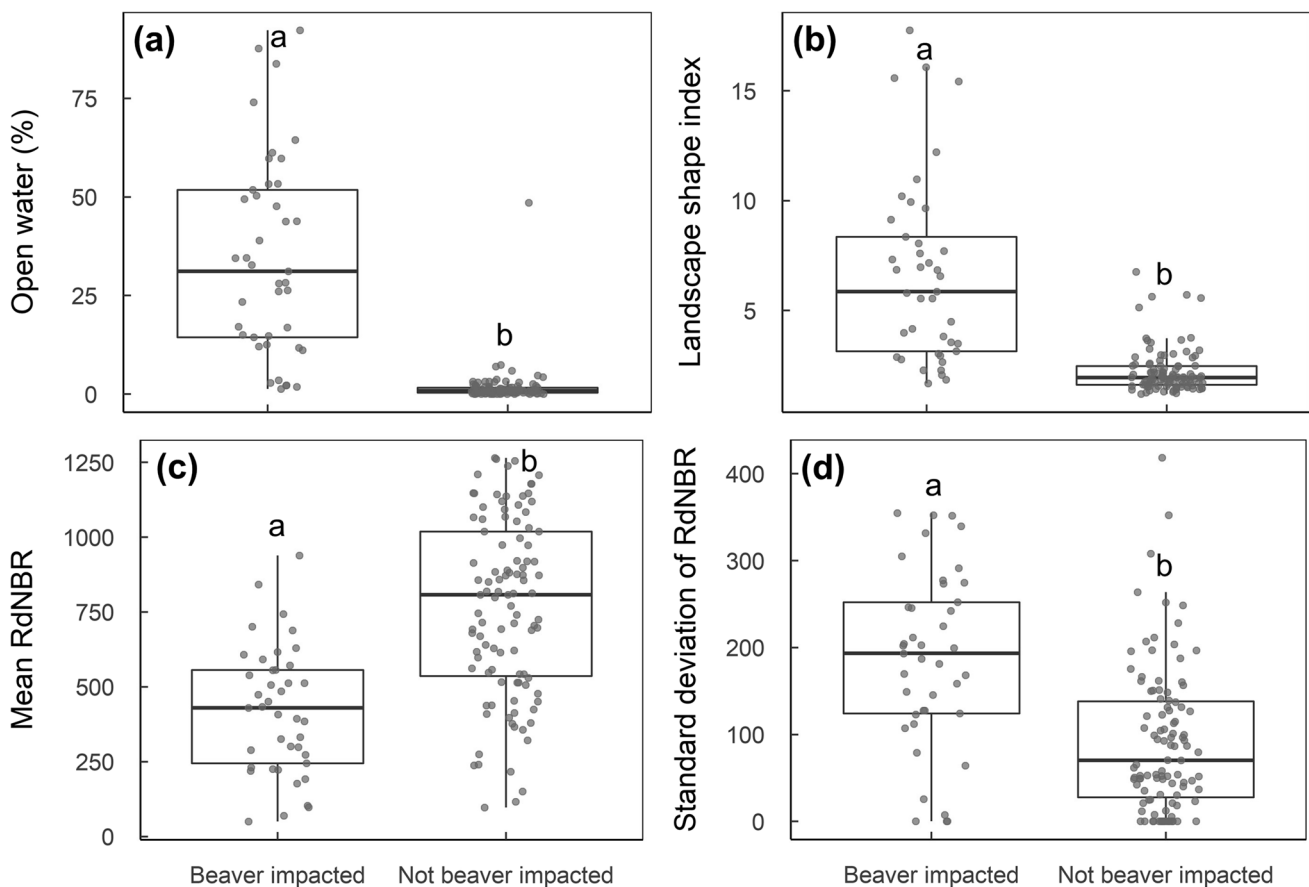


Fig. 4 Percent open water (a), landscape shape index (b), mean RdNBR (c), and standard deviation of RdNBR (d) for 144 wetlands digitized within the study area on the Canadian Boreal Shield in Ontario, Canada. Results of the post-hoc tests for each variable are

denoted by lower case letters where wetlands not impacted ($n = 103$) or impacted by beavers ($n = 41$) are not significantly different ($p > 0.05$) if they share the same letter

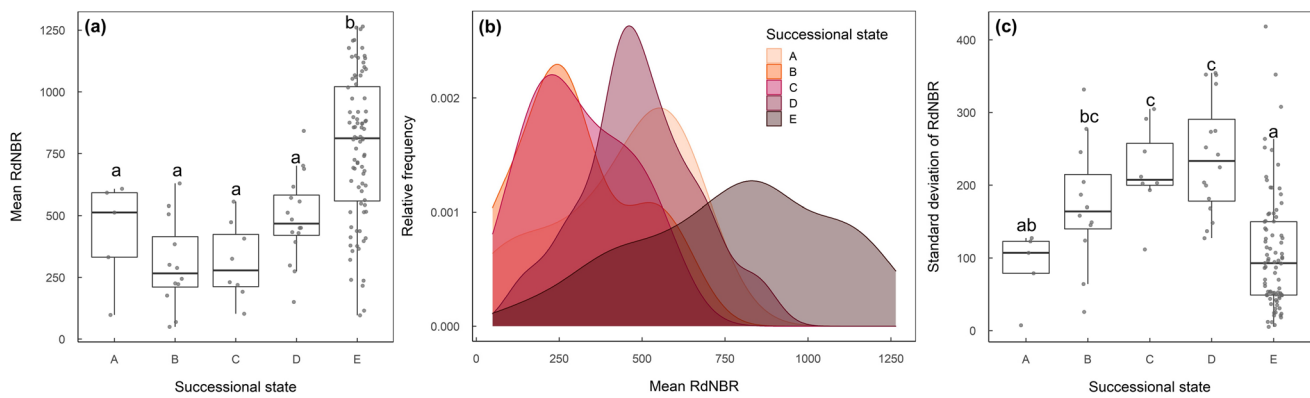


Fig. 5 Mean Relative differenced Normalized Burn Ratio (RdNBR; a), relative frequency distribution of mean RdNBR values (b), and standard deviation of RdNBR values (c) for 144 wetlands digitized within the study area on the Canadian Boreal Shield in Ontario,

Canada. Results of the post-hoc tests for each variable are denoted by lower case letters where wetland successional states (A–E) are not significantly different ($p > 0.05$) if they share the same letter

of mean RdNBR among wetlands was widest for state E and skewed toward higher RdNBR values (Fig. 5b). The variance of the distribution (width) decreased and was centered near lower RdNBR values moving from successional states with less open water (state D) to more open water (states A and B; Fig. 5b) and higher surface spatial complexity (state C; Fig. 5b).

Within-wetland standard deviation in RdNBR was significantly different among successional states ($\chi^2 = 38.5$, $P < 0.001$; Fig. 5c). On average, states B, (174 ± 85), C (220 ± 61) and D (239 ± 79) showed the highest mean standard deviation, while we observed considerably lower standard deviation in RdNBR among wetlands of states A (89 ± 49) and E (106 ± 80 ; Fig. 5c). Similarly, standard deviation in RdNBR for wetlands with beaver dams was double (201 ± 90) that for wetlands without beaver dams (108 ± 80 , $W = 695$, $P < 0.001$; Fig. 4d).

A total of 41 wetlands met the size threshold (> 30 pixels) for spatial hot spot analyses with 1 state A, 7 state B, 8 state C, 12 state D, and 13 state E wetlands (Table 1). We found RdNBR to be spatially autocorrelated within each wetland. Getis-Ord G_i^* detected 154 high fire severity hot spots and 94 fire resistant cold spots. On average, state C and D wetlands had the greatest number (5 ± 6 and 6 ± 4 hot spots, respectively) and largest sized hot spots (0.61 ± 0.91 ha and 0.67 ± 1.0 ha; Table 1). However, these hot spots represented a small percentage of the state C and D wetlands ($2.5 \pm 3.8\%$ and $3.4 \pm 4.3\%$, respectively; Table 1) In comparison, state B wetlands had 3 ± 4 and E had only 1 ± 1 hot spots which were intermediate in size (0.50 ± 0.56 ha and 0.42 ± 0.34 ha; Table 1), but hot spots in state E wetlands comprised $11.2 \pm 9.9\%$ of the total wetland surface area. Following a similar trend, state C and D wetlands had the greatest number of cold spots (3 ± 3 and 3 ± 3 , respectively) which

Table 1 Wetland state characteristics from the spatial analysis performed on 41 wetlands with > 30 pixels

Wetland state	Total number of hot spots	Mean (\pm SD) number of hot spots per wetland	Mean (\pm SD) hot spot area (ha)	Mean (\pm SD) hot spot area relative to wetland area (%)	Total number of cold spots	Mean (\pm SD) number of cold spots per wetland	Mean (\pm SD) cold spot area (ha)	Mean (\pm SD) cold spot area relative to wetland area (%)
State A $n = 1$	3	3	0.37 ± 0.17	6.4 ± 2.9	1	1	1.52	26
State B $n = 7$	24	3 ± 4	0.50 ± 0.56	4.4 ± 6.0	13	2 ± 2	1.42 ± 1.74	11.2 ± 11.1
State C $n = 8$	41	5 ± 6	0.61 ± 0.91	2.5 ± 3.8	24	3 ± 3	1.87 ± 2.31	7.8 ± 8.3
State D $n = 12$	66	6 ± 4	0.67 ± 1.0	3.4 ± 4.3	40	3 ± 3	1.36 ± 1.73	7.6 ± 9.0
State E $n = 13$	20	1 ± 1	0.42 ± 0.34	11.2 ± 9.9	16	1 ± 1	0.82 ± 1.21	22 ± 16.1

were over double the size of the hot spots (1.87 ± 2.31 ha and 1.36 ± 1.73 ha; Table 1). State B wetlands had 2 ± 2 cold spots which were also quite large with an average size of 1.42 ± 1.74 ha (Table 1). The smallest wetlands, state E, had only 1 ± 1 cold spots that were only 0.82 ± 1.21 ha, but represented a relatively high percent of the total wetland area ($22 \pm 16.1\%$, Table 1). The single state A wetland included in the spatial analysis had 3 hot spots that were very small in size (0.37 ± 0.17 ha) and 1 large cold spot that was 1.52 ha (Table 1). Furthermore, hot spots occurred along the edge of wetlands (16 ± 21 m from wetland edge), whereas cold spots were twice as far from the wetland edge (30 ± 28 m from wetland edge; $Z = -24$, $P < 0.001$).

Discussion

Pre-fire Wetland Characteristics

Our findings support the existence of wetland successional states on the landscape and emphasize that they possess unique surface cover characteristics which influence fire severity. Surface cover mapping was consistent with the conceptual model discussed in Markle et al. (2020a). State A wetlands had the highest percent of shallow open water cover and state E wetlands were almost completely peat-filled, both which resulted in the lowest surface complexities as defined by the LSI. Wetlands with an intermediate surface complexity (state B and D) had some peat-water surface cover interspersion, with state B wetlands having more shallow open water than state D wetlands. State C wetlands had the highest surface complexity and were characterized by highly interspersed water-peat surface cover and intermediate percent cover of shallow open water. The association between beaver dams and certain wetland states suggests that beaver activity is important for wetland successional development (Morrison et al. 2015). All of state C and the majority of state B (93%) and D (81%) wetlands, yet no state E wetlands, were beaver impacted. Beavers are ecosystem engineers which expand areas of open water by creating dams and digging water-filled canals (Fairfax and Whittle 2020), impacting ecosystems directly and indirectly (Larsen et al. 2021). We found that wetlands with beaver dams had almost nine times as many open water patches, suggesting beavers may also influence within-peatland spatial complexity. By creating new open water features in areas where they did not previously exist, beavers can significantly modify wetland structure (Morrison et al., 2015). However, although all state A wetlands were beaver impacted, these were almost all relatively small beaver ponds ($n = 6/7$) and had low spatial complexity because they were primarily open water wetlands. These small beaver ponds were typically located

adjacent to larger, more spatially complex wetlands. The association and potential importance of small beaver ponds for wetland resilience to dam breaches is an important question for habitats within and species occupying the large, connected network of wetlands.

Although only a few spatially complex state C wetlands were identified on the landscape, they were the largest wetlands (19 ± 22 ha) and comprised $> 30\%$ of total wetland area mapped. State D wetlands were similarly large in area (12 ± 13 ha). On the other hand, state E wetlands had the smallest mean area (0.7 ± 2 ha) and occupied only 15% of the mapped area despite comprising 69% of the digitized wetlands. In addition to the association between beaver activity and proportion of open water, and thus spatial complexity, these results support findings that beaver-impacted wetlands also tend to be larger (Cunningham et al. 2006; Hood and Bayley, 2008; Morrison et al. 2015). However, many factors influence wetland area and structure, including landscape position, groundwater connectivity, sedimentation, and basin depth (e.g., Winter and Woo 1990; Hayashi and van der Kamp 2000; Larsen and Harvey 2010). In particular, in the rock barrens landscape of the Canadian Boreal Shield, depression depth and morphology are important for wetland (and therefore landscape) hydrology and connectivity (Devito et al. 1996; Markle et al. 2020c; Moore et al. 2021). We suggest that a modelling approach similar to the wetland evolution modelling implemented by Larsen and Harvey (2010), would provide a more thorough understanding of the complex feedbacks influencing the development of infilled wetlands and may be beneficial to understanding the future of wetlands in this region.

Factors Influencing Wetland Fire Severity

Wetland states E and D experienced the highest fire severity, while states with the greatest amount of shallow open water (A, B, C) had a comparatively lower fire severity. This suggests that late-successional wetlands, with a lower proportion of open water and a higher proportion of peat cover, are less resistant to fire than those in the earlier successional states. Intuitively, more energy is required for areas of wetter peat to burn compared to vegetated areas with drier peat (Frandsen 1987; Benscoter et al. 2011). By definition, wetlands in the early successional states have less extensive peat and shrub cover and therefore a lower fuel load (Klinger 1996; Markle et al. 2020a). In beaver-impacted wetlands in western USA, higher water table positions and open water cover increased moisture levels in vegetation at the margins (Fairfax and Whittle 2020), which reduced fire severity along the wetland perimeter and decreased the probability for fire to propagate to areas of peat within the middle of the wetland. However, we found increased fire severity along the margins or edges of wetlands (particularly in states

B, C, and D), likely due to disconnection of these wetland areas from the water table as the water table depth increased (Wilkinson et al. 2020). The higher fire severity (this study) and depth of burn (Wilkinson et al. 2020) along the wetland edges in a rock barrens landscape may result in pools of water developing in the burned margins. This increase in patches of shallow open water along the wetland edge may be a mechanism for wetlands in later successional states to transition to wetlands with more complex surface cover composition. While there are certainly trade-offs between burn severity and impact on carbon storage and peatland form and function, the role of wildfire in wetland succession is likely an important dynamic for understanding and managing wetland-dominated landscapes.

As wetlands in the intermediate successional states transition from a fen to a bog, there is a reduction in moisture and an increase in fuel load which increases susceptibility to fire (Bourgeau-Chavez et al. 2020). Similarly, Zoltai et al. (1998) observed moisture and fuel characteristics across a variety of boreal wetland types, finding that bogs are more likely to have a moisture content low enough for ignition compared to fens. This transition from fen to bog, similar to the transition from a state C to E wetland, can also be associated with an increase in tree and shrub cover due to more grounded peat (Rydin et al. 2013). Further, a positive drying feedback whereby water is lost via transpiration and the water table is lowered, facilitating further afforestation, may occur (Markle et al. 2020a). Although we did not distinguish between fen and bog peatland types in this study, the greater mean wetland fire severity in the later succession wetlands (state D and E) could be a result of differences in peatland types and the associated increases of tree and shrub cover. The range in mean and standard deviation of wetland fire severity and fire hot spots across the small state E wetlands may also reflect the difference in tree and shrub cover whereby wetlands with increased above-ground biomass correlates with higher peat burn severity in other boreal wetlands (Wilkinson et al. 2018).

Peat-filled wetlands had the highest mean fire severity but spatially complex wetlands had the highest variability in wetland fire severity suggesting that wetland surface complexity plays a role in fire resistance. This is likely a result of the spatial arrangement of bottom-up fire controls such as fuel type, fuel moisture, and topography across a wetland surface which impact fire patterns (Benscoter and Wieder 2003). Rodriguez Gonzalez et al. (2008) emphasize that the presence of 'slow' fire-resistant fuels can inhibit the spread of fire because heterogeneity is more important than the nature of the fuels themselves. Moreover, fuel contrast at the edges of patches play a significant role in attenuating fire propagation by reducing the contiguity of fuels at large and small scales (González et al. 2005; Rodriguez Gonzalez et al. 2008) which further highlights the role of water-peat interspersed patterns and spatial complexity in reducing fire

severity. Therefore, a fire is more likely to propagate if fuels on the landscape are connected than if they are separated by fire-resistant patches (e.g., Thompson et al. 2019), which aligns with our findings that completely peat-filled state E wetlands experienced a significantly higher fire severity than all other wetlands and fire hot spots that are proportionally larger. This is important for species habitat and ecosystem recovery whereby different severity patches recover at different rates (Benscoter and Wieder 2003; Lukenbach et al. 2015). However, bottom-up fire controls are not the only determinant of fire severity and additional work should consider the role of top-down controls, particularly weather, in fire severity patterns, especially given the abnormally low precipitation in the weeks prior to the Parry Sound 33 wildfire and the importance of climate and weather on fire activity in boreal ecosystems (Podur and Martell 2009).

Although we found differences in the spatial variability of fire severity at the wetland-scale, the distribution of different wetland states across the landscape also contributes to larger scale patterns in fire severity. The small area of state E wetlands may further exacerbate landscape fire severity by reducing the distance between patches of forested uplands. Several studies have documented higher burn or fire severity in uplands compared to wetlands (Thompson et al. 2017; Whitman et al. 2018; Wilkinson et al. 2020). At the landscape scale, open water wetlands and spatially complex wetlands may act as fire breaks by creating patches of 'slow' fuel that disrupt continuously forested uplands (Araya et al. 2015). If this is the case, the size of the wetland will influence the degree to which fire propagation and severity is disrupted; smaller wetlands, or narrow swaths of peat in larger wetlands, would burn more severely as fire can propagate more easily through patches to nearby uplands. In line with this, our hot spot analysis demonstrated that wetland edges, forested rock islands, and narrow swaths of peat acted as high fire severity hot spots emphasizing the role of these areas in propagating wildfire. This suggests that fire resistance can be overcome by proximity to uplands and small patch size which has important implications for management and conservation strategies, especially in areas with species-at-risk habitat such as the eastern Georgian Bay region.

As expected, cold spots that were more fire resistant were located further from the wetland edge where peat moisture and water table position are generally higher (Wilkinson et al. 2020). Accordingly, we observed a significantly lower mean fire severity in wetlands with beaver dams than those without. Because beaver-impacted wetlands were associated with increased open water cover these wetlands were more resistant to burning and were able to act as fire breaks on the landscape. Few studies have empirically examined the relationship between beaver activity and wildfire resistance in wetlands, although Fairfax and Whittle (2020) found that the mean Normalized Difference Vegetation Index in

beaver-impacted areas was over three times higher following a wildfire than those without beaver activity. This suggests that beaver dams protect riparian vegetation from burning by increasing moisture and open water and these areas act as refugia during periods of fire. Morrison et al. (2015) emphasized that beaver alter the hydrology of the system they inhabit by increasing water storage and shifting runoff dynamics, which may ultimately provide resistance to pre-fire drought and reduce fire severity by maintaining a high water table position (Wilkinson et al. 2020). Moreover, similar to our study, beaver-impacted wetlands had more open water patches and higher spatial complexity supporting that beaver activity creates spatial complexity within individual wetlands as surface cover changes (Law et al. 2017). This may play a role in the resistance to high severity fire because the spatially complex wetlands (state B and C) had a lower fire severity. At the landscape scale, and over longer temporal scales, beaver increase spatiotemporal heterogeneity due to the colonization and abandonment of sites following disturbance (Cunningham et al. 2006). This creates a shifting network of wetlands, whose size, surface complexity, water table, and ultimately resistance to fire depends, in part, on beaver activity.

Management Implications

Our study has important conservation implications because we found that spatially complex wetlands in intermediate successional states and those impacted by beavers are more resistant to wildfire. These spatially complex wetlands facilitate the co-occurrence of both aquatic and semi-aquatic species-at-risk reptile assemblages in the region, providing critical habitat for many reptile species (Markle et al. 2020a). For example, wetlands in intermediate successional states (particularly state C) provide suitable overwintering for at-risk turtle species, which require cool above-zero water temperatures, sufficient dissolved oxygen, and substrate for burying, as well as raised hummocks which provide overwintering sites that are insulated and moist, but unflooded, for the threatened eastern massasauga rattlesnake (*Sistrurus catenatus*; Markle et al. 2020a; Yagi et al. 2020). Furthermore, spatially complex wetlands possess long-term resilience to drivers of succession such as drought and flooding, and are therefore resistant to regression or succession toward new states (Markle et al. 2020a). This means that spatially complex wetlands less impacted by wildfire are likely to persist as sites of overwintering habitat and have a greater potential to act as, or harbour, fire refugia over long timescales.

Understanding which wetland successional states are resistant to fire is important to create effective management strategies which prioritize sites that are both able to facilitate the co-occurrence of at-risk species and act as

fire refugia. Conserving and restoring spatially complex wetlands will help protect critical habitat during wildfire. Our findings also suggest that beaver may play a central role in creating and maintaining fire-resistant and spatially complex wetlands on the landscape. This is supported by the long history of Indigenous knowledge which recognizes beavers as important for wetland and riparian restoration (e.g., Albert and Trimble 2000, Blackfeet Nation 2018; Blackfeet Nation and Levitus 2019), and supports the concept that beavers are an effective tool for climate mitigation (Dittbrenner et al. 2018; Jordan and Fairfax 2022) and may act as low-cost, natural wildfire managers on the landscape (Fairfax and Whittle 2020; Weirich 2021). At the wetland scale, individual beaver-impacted wetlands may act as refugia by maintaining a high water table and preserving riparian vegetation (Fairfax and Whittle 2020). Beaver enhance heterogeneity and reduce fuel contiguity by creating open water fire breaks at the landscape scale. Ultimately, the persistence of beaver ponds is influenced by dam intactness (Woo and Waddington 1990; Ronnquist and Westbrook 2021) and modifications to wetland structure by beavers may be temporally variable (Morrison et al. 2015; Cunningham et al. 2006) and, as such, the role of dam blow outs on the fire landscape should be investigated further.

Finally, we suggest that wetland surface cover and complexity can be used as an indicator of wetland vulnerability to wildfire. The methods used in this study illustrate that wetland successional states can be observed and classified using aerial imagery, which can contribute to fire hazard mapping. However, it should be noted that dynamics of succession are controlled by a variety of drivers which may impact the spatiotemporal distribution of wetland states (and hence, fire resistance) on the landscape. This prompts further work into the evolution of wetlands via infilling and how successional trajectories can be enhanced or reversed by perturbations such as wildfire and climate change which may alter the vulnerability of wetlands to future fires.

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Data Availability The datasets generated during and/or analyzed during the current study are available by request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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