



Spatial Heterogeneity of Surface Topography in Peatlands: Assessing Overwintering Habitat Availability for the Eastern Massasauga Rattlesnake

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Abstract

The eastern massasauga rattlesnake (*Sistrurus catenatus*) relies on small-scale differences in peatland surface elevation to survive harsh overwintering conditions at the northern limit of its range. We characterized the spatial heterogeneity of surface topography in peatlands within the eastern Georgian Bay rock barrens landscape of Ontario, Canada, to assess available snake overwintering habitat. At six peatlands, we used a differential global positioning system to collect surface-elevation data. We created spatially-explicit surface models to map peatland surface topography, quantify habitat that was likely to remain unflooded during the overwintering period, and identify key characteristics associated with greater habitat availability. While surface elevations were spatially heterogeneous within and among sites, larger peatlands were associated with greater surface spatial variability relative to the lowest elevation measured within each site. However, even peatlands with very little spatial heterogeneity (average of 0.24 m above lowest elevation), provided unflooded overwintering habitat. Inter-annual weather conditions and peatland and watershed characteristics likely control the availability and distribution of unflooded overwintering habitat. We found that trees, specifically white pine (*Pinus strobus*) and maple (*Acer spp.*), were spatially associated with higher surface elevations and could be used to identify areas of unflooded winter habitat. Our findings are useful for landscape-scale assessments of available overwintering habitat to prioritize conservation and management efforts.

Keywords Peatland · Surface topography · Snake habitat · Species at risk · *Sistrurus catenatus*

Introduction

Peatland ecosystems are considered key refugia capable of extended resistance to environmental change (Stralberg et al. 2020) and also play important roles in global atmospheric carbon sequestration (Yu 2012; Gorham 1991), global surface-water storage (Holden 2005), and maintaining local and regional biodiversity (Chapman et al. 2003). The long-

term stability of these ecosystem services is generally maintained by a suite of ecohydrological feedbacks (Belyea and Clymo 2001; Waddington et al. 2015), which are partially dependent on the presence and spatial distribution of hummock and hollow microtopography (Malhotra et al. 2016; Belyea and Baird 2006). Peatland microtopography provides spatial diversity in ecohydrological structure and biogeochemical function (Belyea and Clymo 2001; Belyea and Malmer 2004; Eppinga et al. 2008; Pedrotti et al. 2014; Malhotra et al. 2016) and can be randomly distributed across the peatland or patterned and organized, such as the linear ridge-pool patterning common in boreal peatlands (Foster et al. 1983; Harris et al. 2019). Hollows are depressions while hummocks are raised peat mounds (Belyea and Clymo 2001). Hummocks are usually drier than hollows and can be up to a metre above adjacent hollows (Rocheffort et al. 1990). Peatland microforms can remain stable despite climatic and environmental variation (Belyea and Clymo 2001; Kettridge et al. 2012), which is a critical characteristic required for climate-sensitive species such as the eastern massasauga rattlesnake (*Sistrurus*

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catenatus) that rely on hummocks for winter refugia to survive harsh winter conditions at northern latitudes (Johnson 2000; Rouse and Willson 2002; Markle et al. 2020a).

Microform type is influenced partially by the interplay between moss species composition (Andrus et al. 1983), vascular vegetation cover (Duberstein and Conner 2009; Pouliot et al. 2011b), and depth to water table (Rydin and McDonald 2013). Similarly, surface microtopography and average depth to water table partially control the growth, distribution and biomass of trees in peatlands (Liefvers and Rothwell 1987; Murphy et al. 2009). As such, mature trees tend to be associated with hummocks compared to hollows (Duberstein and Conner 2009), likely because hummocks provide a thicker aerobic zone for tree roots (Barry et al. 1996). However, increased tree survival and success on hummocks is only partially understood and can also be influenced by microclimate conditions and the stability of hummock microforms (Duberstein et al. 2013). Due to the structural support that tree roots provide, hummock forming *Sphagnum* species can proliferate under trees (Malmer et al. 1994) and, in turn, create or enhance peatland microtopography. Moreover, partial shading by trees provides a microclimate that enhances *Sphagnum* growth and reduces water loss via evaporation, both of which are important for hummock development (Pouliot et al. 2011b). Therefore, it is expected that trees and hummocks will be spatially linked.

Many studies relating water table depth to surface microtopography have focused on deep, expansive bogs and fens (e.g. Malhotra et al. 2016; Nungesser 2003), but many peatlands along the southern portion of the Canadian Shield accumulate peat in isolated bedrock depressions. In this geological setting, peatlands are constricted by their basin, and because of the low permeability of the underlying granitic bedrock, water table fluctuations are primarily controlled by evapotranspiration, precipitation, and surface flow. For example, flooding may occur in low-lying areas of the peatland particularly when there is no outflow or outflow is restricted from the basin, and during seasons (e.g. overwintering period) when evapotranspiration is low (Markle et al. 2020a, Markle et al. 2020b). These small-scale spatio-temporal differences in depth to water table have implications for surface microtopography and distribution of vascular vegetation, including trees such as the eastern redcedar (*Juniperus virginiana*), tamarack (*Larix laricina*), birch (*Betula* spp.), pine (*Pinus* spp.), and spruce (*Picea* spp., Zoltai and Vitt 1995).

The spatial variability in water table depth and distribution of peatland surface microtopography ultimately dictates the availability of diverse habitats used as refugia for species at risk. Such is the case for the eastern massasauga rattlesnake, considered a species at risk across the majority of its range in the Great Lakes region of Canada and the United States, which must retreat underground to survive freezing winter

air temperatures at northern latitudes. In the open rock barrens landscape east of Georgian Bay, Lake Huron, massasauga populations rely on small-scale variations in surface elevation within peatlands to survive the winter. In particular, snakes seek refuge inside hummocks or localized raised areas to avoid freezing (Gregory 1982) while remaining above the water table (Smolarz et al. 2018). In general, the taller the hummock, the more resilient the overwintering habitat is to changes in water table position and depth of the 0 °C isotherm (Smolarz et al. 2018). Although unflooded refugia are critical for snake survival, relatively little is known about the spatial complexity of peatland surface topography in this rock barrens landscape. A more thorough understanding of the spatial heterogeneity of available overwintering habitat within this landscape has important implications for the management and protection of peatlands supporting species at risk.

Classification of hummock, hollow, and intermediate microforms is common when comparing their contributions to ecological, hydrological, and biogeochemical processes in peatlands (e.g. Moore et al. 2011; Malhotra et al. 2016; Harris et al. 2019; Asemaninejad et al. 2019). Classification methods range from visual assessments (Asemaninejad et al. 2019) to semi-automated quantitative approaches relying on high-resolution elevation data (Mercer and Westbrook 2016; Moore et al. 2019; Graham et al. 2020). Even in quantitative approaches, elevation data are often referenced to a common datum such as mean summer water table position or a surface-elevation threshold which results in different hummock-hollow classifications (Graham et al. 2020). Therefore, it is important that the classification method aligns with the research objectives. When quantifying the amount of winter refugia available to overwintering massasauga rattlesnakes, the position of the peatland surface relative to the winter water table is critical to assessing habitat (microforms) above the water table to reduce drowning risk (Smolarz et al. 2018; Markle et al. 2020a; Yagi et al. 2020). Classifying microtopography from a winter refugia perspective allows for spatio-temporal variability in habitat above the winter water table even though surface structure remains fairly stable.

Here, we examine the spatial heterogeneity of small-scale surface topography in six peatlands within the eastern Georgian Bay rock barrens landscape to assess availability of snake overwintering habitat. Our first objective was to characterize the variability in surface elevations and peat depths across our study peatlands. We predicted that higher relative peat surface heights would be associated with within-site characteristics such as presence of trees, and may vary among tree species. We then estimated available overwintering habitat by quantifying the peatland volume and height of surface topography that was likely to remain unflooded during three winters. We examined key peatland characteristics to determine if the amount of unflooded habitat was associated with landscape-scale factors such as peatland size (surface area,

volume), tree density, and watershed size. We also mapped the spatial distribution of unflooded overwintering habitat within each peatland. Understanding the spatial heterogeneity across a landscape represents an important step towards identifying peatlands that provide critical overwintering sites for species at risk.

Methods

Study Area

Situated on the Precambrian Shield, the eastern Georgian Bay region of Ontario, Canada, is characterized by a mosaic of mixed forest, granitic rock barrens, and permanent and ephemeral wetlands (Crins et al. 2009). The diversity of microhabitats and proximity to freshwater allows the eastern shore of Georgian Bay, Lake Huron, to support numerous species at risk and is considered a biodiversity hotspot designated as a UNESCO Biosphere Reserve (UNESCO 2015). This region has a humid and cool-temperate climate, with mean monthly temperatures ranging from -11.1°C in January to 18.9°C in July, and mean annual precipitation of 1118 mm per year (Environment and Climate Change Canada 2019). Additionally, a strong lake effect causes increased precipitation during the winter months. Average air temperature during the overwintering period (1 Oct–30 Apr) slightly decreased among the three seasons monitored during the study period, from 1.2°C in 2016–2017, to -0.5°C in 2017–2018, and -2.6°C in 2018–2019. Total precipitation in the winters of 2016–2017 and 2018–2019 were comparable, with 650.5 mm and 655.7 mm respectively. In comparison, the 2017–2018 season was relatively dry receiving 129.1 mm of precipitation (Environment and Climate Change Canada 2019).

Research was conducted at six peatlands within the Georgian Bay Biosphere Reserve, extending along the eastern coast of Georgian Bay, Lake Huron and located on Anishinabek territory. Our northernmost study peatland (B) was confirmed to provide overwintering habitat for the eastern massasauga rattlesnake by local biologists conducting field surveys. Approximately 45-km south are the remaining five peatlands (A, C–F). Although these peatlands are not confirmed to support overwintering massasaugas, the species has been confirmed in the surrounding 1-km^2 area. All of the peatlands are dominated by *Sphagnum* moss, and vascular vegetation including leatherleaf (*Chamaedaphne calyculata*), sedges (*Carex* spp.), tamarack (*Larix laricina*), and jack pine (*Pinus banksiana*). The six peatlands vary in size ($1000\text{--}10,645\text{ m}^2$; Table 1), shape, absolute elevation (190.7–232.4 m above sea level [masl]) and surface-water connectivity due to the underlying bedrock morphology. Hydrological connectivity is intermittent and best described by the fill-and-

spill model, where wetlands must reach a certain water level threshold before surface flows can occur (Spence and Woo 2003). In this system, hydrological inputs to the peatland are a result of precipitation and surface runoff rather than groundwater connectivity, due to the low permeability of the granitic bedrock which impedes subsurface flow.

Surface Topography

In August 2018, we used a differential global positioning system (D-GPS, Trimble R10 GNSS base-rover system with TSC3 controller) to collect absolute elevation data (masl) on a $3 \times 3\text{ m}$ grid pattern across the six peatlands. Low-quality data points collected with the D-GPS were removed when position dilution of precision >2.5 , vertical precision $>0.03\text{ m}$, or horizontal precision $>0.03\text{ m}$ to ensure accurate representation of the small-scale surface topography (Table S1). Peat depth (m) was also measured at each D-GPS location. We converted absolute elevation (masl) to relative elevation (surface height, m) within each peatland using the lowest recorded surface elevation to facilitate habitat comparisons among peatlands. Surface topography and peat depth models were interpolated to a 1-m^2 cell size in ArcMap 10.7.1 (Redlands, California, USA) using inverse distance weighting which is appropriate for high-resolution regularly-spaced data with no known directional bias and minimizes additional subjective user decisions (Li and Heap, 2014; Zarco-Perello and Simões, 2017). Moran's I spatial autocorrelation analysis was used to identify the presence and location of clusters of higher peat surface elevations.

Tree Surveys

We conducted tree surveys in the summers of 2016 and 2018 at three of the six peatlands. Within each peatland and along the margins, we recorded the location and species of every tree. For the remaining three peatlands, trees were digitized from high-resolution imagery (Central Ontario Orthophotography Project 2016). To determine if digitized tree data were suitable for our purposes, we compared a subset of digitized trees with trees confirmed in the field to assess accuracy. We calculated tree density (trees m^{-2}) for each peatland in ArcMap 10.7.1. We used generalized linear mixed-effects models to compare relative elevation and peat depth between locations with trees and all measured surface locations. Surface elevation and peat depth at each tree was estimated using the location of each tree to extract the corresponding value from the interpolated 1 m^2 surface. We fit the models in R 3.6.2 (R Core Team 2019) using relative surface elevation (m) or peat depth (m) as the response variable (gamma distribution, log link), including location type as a fixed effect (tree or surface) and peatland (since multiple points were collected per peatland) as a random effect. We also

Table 1 Site characteristics for the six peatlands surveyed in August 2018. Mean volume and percent of unflooded overwintering habitat was quantified based on the mean (95th and 5th percentiles) water table

position (using all available data) during the overwintering period (1 October – April 30) relative to the lowest measured surface elevation

Site ID	Peatland surface area (m ²)	Ratio of watershed size (m ²) to peatland surface area (m ²)	Mean tree density (trees m ⁻²) ± SD (range)	Mean volume (m ³) of unflooded habitat (95-5th percentile)	Mean percent of peatland volume unflooded (95-5th percentile)	Winter seasons with water table data
A	999.9	4.5	0.10 ± 0.31 (0–2)	60.8 (15.1–118.4)	14.9 (3.7–29.1)	2016/17, 2017/18, 2018/19
B	1500.4	4.3	0.11 ± 0.32 (0–2)	91.3 (35.4–184.3)	11.7 (4.5–23.6)	2016/17, 2018/19
C	2337.3	16.6	0.07 ± 0.32 (0–6)	22.4 (2.8–177.0)	3.5 (0.4–27.7)	2016/17, 2017/18
D	3501.1	6.6	0.13 ± 0.48 (0–11)	433.0 (280.1–627.8)	32.1 (20.8–46.5)	2016/17, 2017/18, 2018/19
E	9158.8	7.8	0.09 ± 0.32 (0–3)	593.4 (85.2–2030.8)	6.3 (0.9–21.4)	2016/17, 2017/18, 2018/19
F	10,645.4	4.5	0.04 ± 0.19 (0–3)	916.2 (399.3–1835.4)	9.5 (4.1–19.0)	2018/19

compared estimated surface elevation among tree species using a Kruskal-Wallis followed by post hoc comparisons (Dunn test, bonferroni corrections for multiple comparisons).

Quantifying Unflooded Overwintering Habitat

We defined available snake overwintering habitat as the peat that remained unflooded during the overwintering period (1 October–30 April). To quantify unflooded overwintering habitat, we recorded depth to water table (m) every 10 min at all peatlands for one to three winter seasons (2016/17, 2017/18, 2018/19; Table 1). We used self-logging Levellogger Junior pressure transducers (Solinst, Georgetown, ON, Canada) in a 1–2 m deep groundwater well and corrected for changes in atmospheric pressure using a Barologger Edge barometric logger (Solinst, Georgetown, ON, Canada) or a Levellogger Junior pressure transducer (Solinst, Georgetown, ON, Canada).

We subtracted the winter water table (WT) position (mean WT, 95th percentile of WT, 5th percentile of WT) from the measured surface elevations to determine if a spatial location was unflooded (i.e. areas where the surface elevation is above the winter water table position) or flooded (i.e. areas where the surface elevation is below the winter water table position). To estimate the volume of unflooded habitat, we multiplied the depth to the water table (measured as the height of unflooded habitat from the peatland surface to the below-surface water table) by the area of the 3 × 3 m sampled grid cell (9 m²). Then, we calculated the percent of peatland habitat flooded during the winter by dividing the flooded volume by the sampled peatland volume and multiplied by 100. Sampled

peatland volume was calculated by multiplying the peat depth measurement by the area of the 3 × 3 m sampled grid cell (9 m²).

Pearson correlation analysis was used to determine if volume and percent of unflooded habitat were linearly related to peatland characteristics (i.e. volume, surface area, watershed size). Watershed size (catchment area, m²) was calculated for each peatland based on a LiDAR-derived digital elevation model (DEM, 1-m resolution) or from a DEM from the Central Ontario Orthophotography Project (2-m resolution). To model the spatial distribution of unflooded habitat and estimate the depth of unflooded habitat at each surveyed tree, we subtracted the mean winter water table position from the spatially-explicit surface models of peatland surface topography. Lastly, we compared the depth of unflooded habitat among tree species using a Kruskal-Wallis followed by post hoc comparisons (Dunn test, bonferroni corrections for multiple comparisons).

Results

Surface Topography

We measured surface elevation at over 2800 locations, ranging from 91 locations at the smaller peatlands to over 1000 at the larger peatlands with a high horizontal (0.012 ± 0.003 m; mean and standard deviation unless otherwise indicated) and vertical (0.018 ± 0.005 m) precision (Table S1). Peatlands with a greater surface area and total volume had more distinct surface topography compared to smaller peatlands (Table 1;

Fig. 1). Areas of higher surface elevation were spatially clustered in all peatlands, where in general, larger peatlands demonstrated a higher degree of clustering (e.g. peatland F, Moran's I (I) = 0.77, Z = 513.10, P < 0.001; peatland E, I = 0.65, Z = 395.95, P < 0.001) than smaller peatlands (e.g. peatland A, I = 0.61, Z = 123.65, P < 0.001; peatland B, I = 0.57, Z = 143.07, P < 0.001; peatland D, I = 0.56, Z = 205.83, P < 0.001; Fig. 2). However, peatland C was moderate in size and demonstrated a high degree of spatial clustering (I = 0.66, Z = 199.54, P < 0.001). In most peatlands, low surface elevation was indicative of large pools. Mean relative surface elevations (average deviation from the minimum surface elevation) ranged from 0.21 ± 0.07 m for smaller peatlands (e.g. peatland A) to over 0.32 ± 0.09 m for larger peatlands (e.g. peatland E and F), except for peatland C which was small and still had variable surface elevations (Fig. 3). Relative surface height rarely exceeded 0.5 m, although surface heights between 0.5 m and 1.0 m were recorded for the five largest peatlands (B–F; Fig. 3). Peat depth was highly variable among peatlands (Fig. 4) and weakly related to surface elevation (r = 0.13, P < 0.001). Mean peat depth was between 0.43 m and 0.52 m for peatlands A–D (maximum depths of 1.16–1.85 m)

and more than twice as deep for the two largest peatlands (E, 1.1 ± 0.7 m; F, 1.0 ± 0.5 m), with maximum peat depths of 2.74 m (peatland F) and 2.85 m (peatland E; Fig. 4).

When compared to ground-truthed field data, digitized tree data were 80% accurate, so both datasets were treated equally and merged. Although mean tree density was very low across all peatlands, averaging fewer than 1 tree m^{-2} , it was highly variable within a site where maximum tree density ranged between 2 to 11 trees m^{-2} (Table 1; Fig. 5). The majority of trees were located at higher surface elevations (t = 4.64, P < 0.001) and shallower peat depths (t = -8.45, P < 0.001) compared to surface locations without trees. Mean elevation at tree locations within peatlands was similar (i.e. peatlands A, B, E, F) or 0.03 m (e.g. peatland C) to 0.05 m (e.g. peatland D) higher than the mean surface elevation. Tree species occupied significantly different surface elevations (X^2 = 55.6, P < 0.001). Species such as birch (0.35 ± 0.07 m, Z = 4.9, P < 0.001, n = 74), tamarack (0.33 ± 0.05 m, Z = -4.6, P < 0.001, n = 141) and white pine (0.33 ± 0.06 m, Z = -5.9, P < 0.001, n = 482) occupied higher surface elevations compared to jack pine (0.30 ± 0.07 m, n = 525). Maple (0.31 ± 0.08 m, n = 88) was also found at lower surface elevations

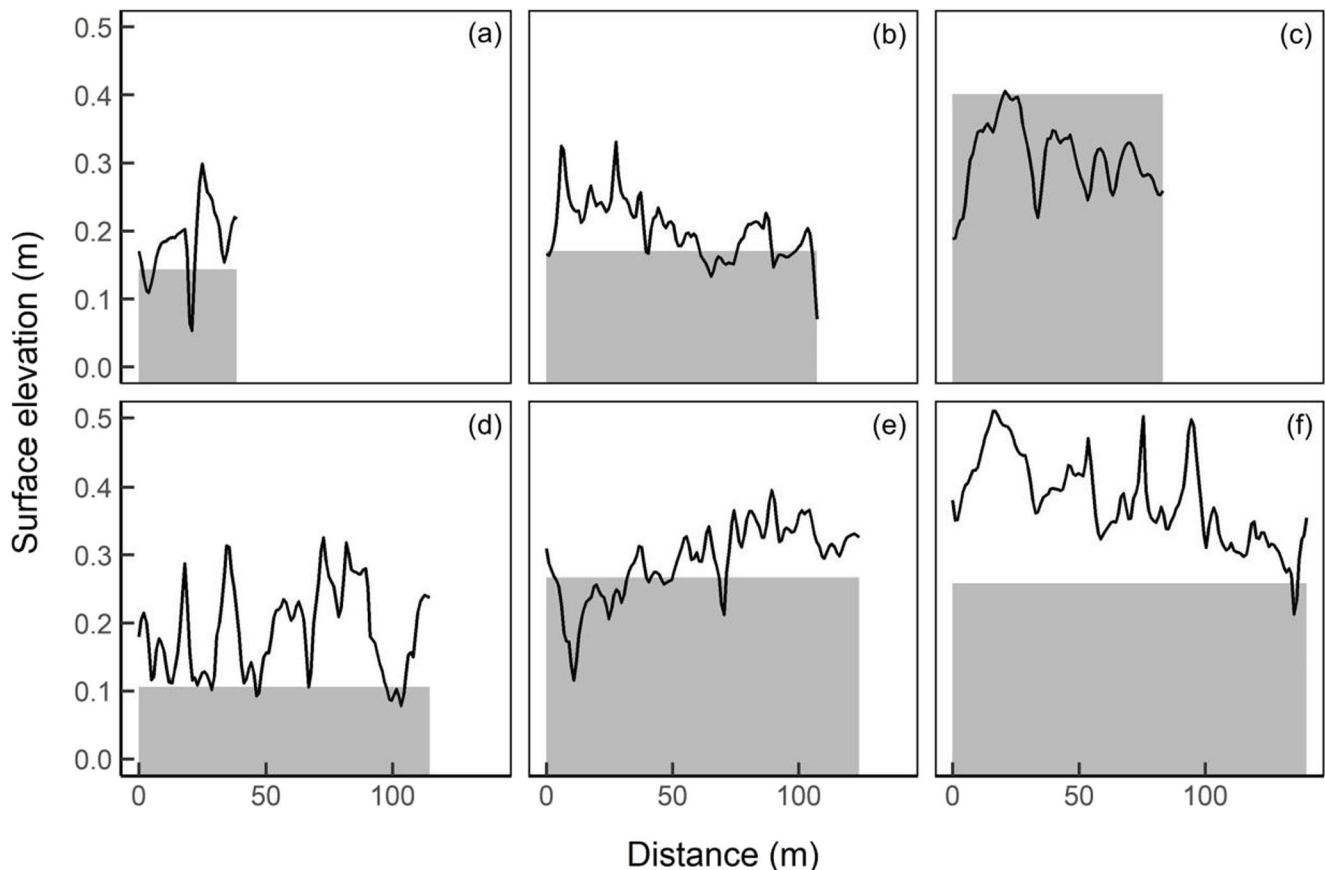
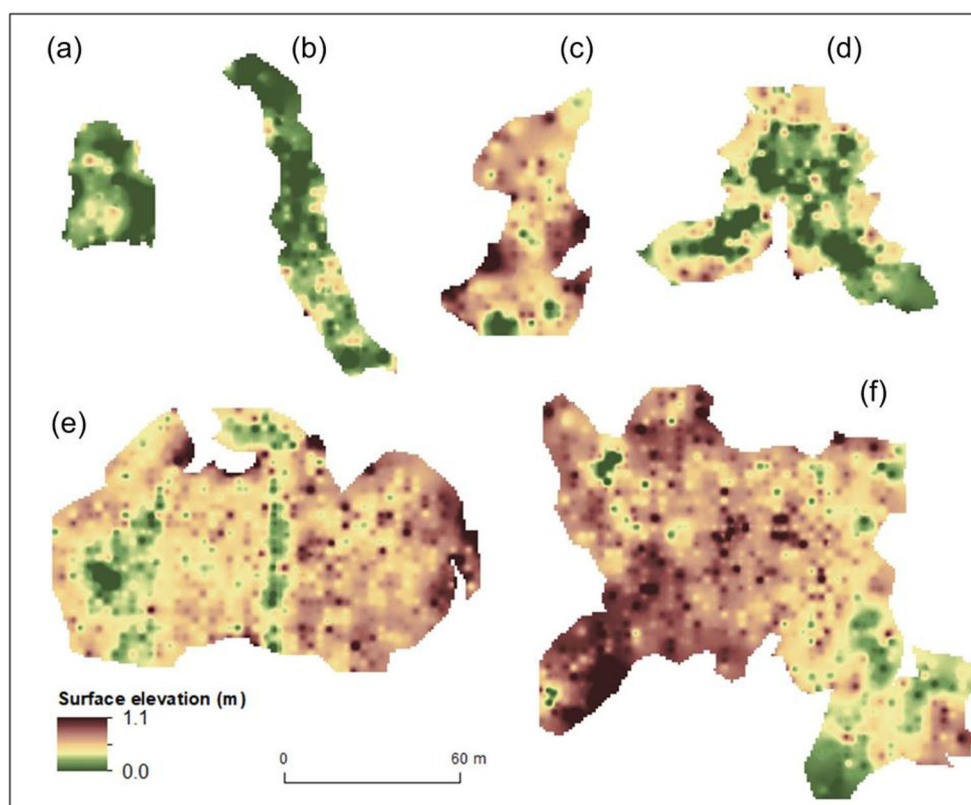


Fig. 1 Surface elevation (m, relative to the lowest measured surface elevation in each peatland) profiles of the modeled peatland surface (black solid line) along a transect through the middle of each of the six peatlands (a–f, Fig. S1). The shaded grey area represents the mean winter

water table (WT) position (for all available data, see Table 1) and the amount of flooded habitat. The modeled peatland surface (black solid line) above the mean winter WT position (grey area) represents the unflooded and available snake overwintering habitat

Fig. 2 Spatially-explicit surface elevation (m, relative to the lowest measured surface elevation in each peatland) model of surface topography for each of the six peatlands (a–f)



than birch ($Z = 3.3$, $P = 0.01$). Trees were located where mean peat depth (0.74 ± 0.52 m) was approximately 0.14 m shallower than mean peat depth across peatlands (0.88 ± 0.58 m).

Availability of Unflooded Overwintering Habitat

The mean percent of unflooded habitat was fairly consistent among winter seasons for peatlands B and C, varying by less than 5% (Fig. 6). For two of the larger peatlands (D and E), the mean percent of unflooded habitat was 7.9–13.7% higher in the relatively colder, drier winter (2018/19) compared to the warmer, wetter winters (2016/17 and 2017/18; Fig. 3). This was very evident for peatland E since the distribution of water table depths in 2018/19 were below the mean surface elevation and only overlapped with a small portion of the distribution of surface elevations, meaning that a larger proportion of unflooded habitat was available (Fig. 3e). Even with the inter-annual fluctuations, the volume of unflooded habitat in peatland E was quite high because of the peatland's size, ranging from 85 m^3 (0.9%) to 2031 m^3 (21.4%) of the total peatland volume during 90% of the three overwintering seasons (Table 1). On the other hand, the smallest peatland (A) had a lower availability of unflooded habitat in the drier winter (9.8%, 2018/19) compared to the wetter winters (17.6%, 2016/17; 18.0%, 2017/18; Fig. 3a). However, the availability of unflooded habitat in peatland A dropped below 3.7% (or 15

m^3) for only 5% of the three overwintering seasons (Table 1). The mean percent of unflooded habitat was not significantly different among the 2016/17 ($13.4 \pm 11.9\%$), 2017/18 ($13.6 \pm 12.1\%$) and 2018/19 ($16.3 \pm 11.6\%$) winter seasons ($X^2 = 0.54$, $P = 0.91$) likely because the percent of unflooded habitat among peatlands was highly variable (Fig. 3a), so the water table data was pooled from all winter seasons for the majority of the analyses.

The location of unflooded overwintering habitat (Fig. 5) tended to occur in areas of higher surface elevations (Fig. 2) although there were a few exceptions. In peatland C, the mean winter water table position was above the majority of the peatland surface (Fig. 1; Fig. 3c) resulting in flooding of 84.2% of the surface (Fig. 5; Fig. S2) despite having a mean relative surface height of 0.34 ± 0.1 m and a maximum height of 0.62 m. The availability of unflooded habitat was also limited across the winter seasons because 90% of time, the volume of unflooded habitat ranged from only 0.4% (2.8 m^3) to 28% (177 m^3 ; Table 1). In comparison, peatland D had intermediate surface heights (Fig. 3d) but was resistant to winter flooding (Fig. 1d) with 43.9% of the surface area providing over 0.15 m of unflooded overwintering habitat (Fig. 5d; Fig. S2). Peatland D provided the greatest amount of unflooded habitat consistently throughout the winter seasons; volume of unflooded habitat ranged from 21% (280 m^3) to 46.5% (628 m^3) of the total peatland for 90% of the overwintering period (Table 1).

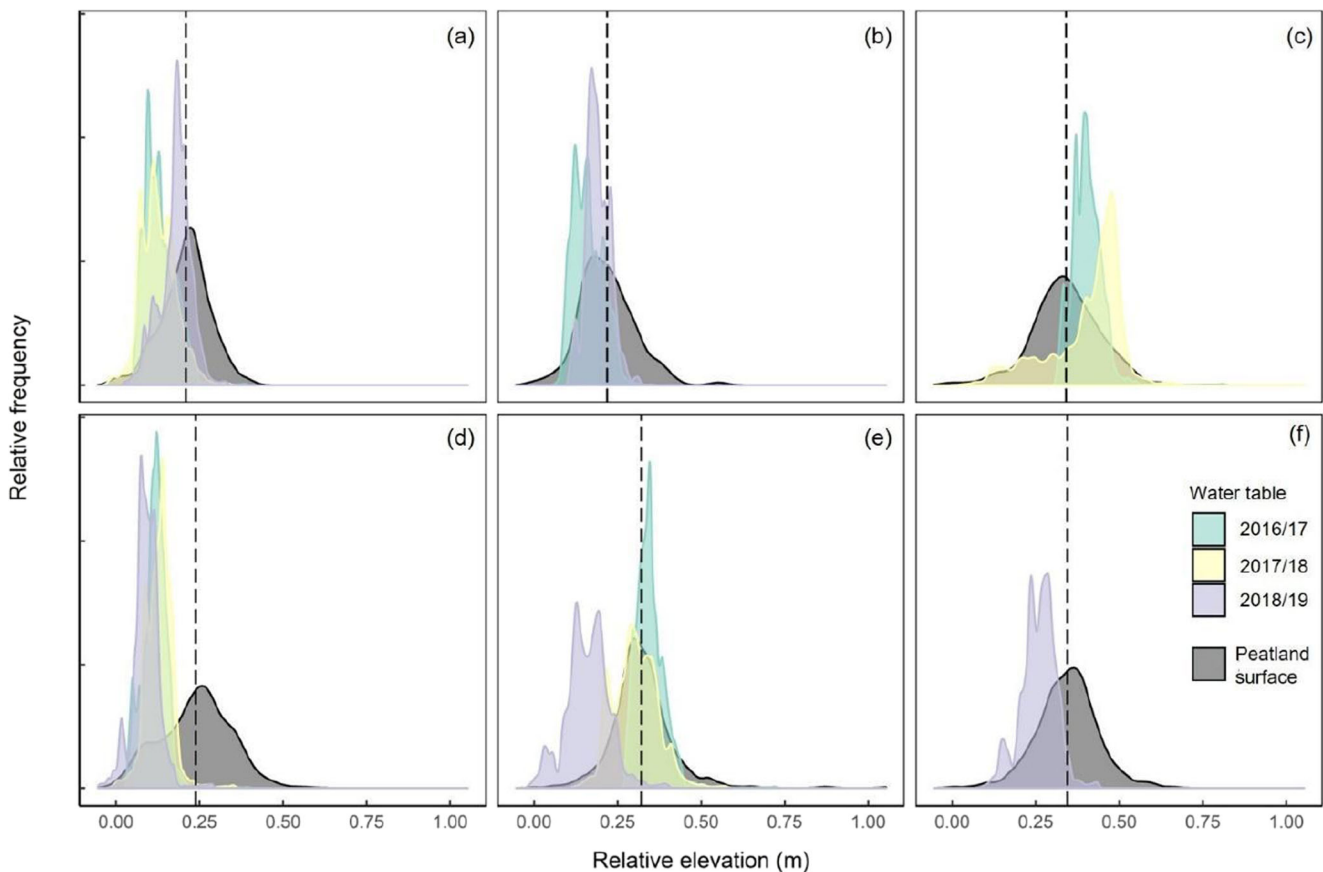


Fig. 3 Relative frequency distributions of measured peatland surface elevations (m, relative to the lowest measured surface elevation in each peatland) for each of the six peatlands (a–f, grey). The black dashed line is the peatland's mean relative surface elevation. Relative frequency

distributions of annual winter water table position relative to the peatland's minimum surface elevation where overlap between water table and peatland surface distributions represent flooded habitat (2016/17, blue; 2017/18, yellow; 2018/19, purple)

The mean volume of unflooded habitat was positively related to peatland surface area ($r=0.96$, $P<0.001$) and total peatland volume ($r=0.96$, $P=0.003$). Therefore, larger peatlands tended to have a higher availability of unflooded habitat (Fig. 4; Table 1). However, the proportion of unflooded habitat was not related to peatland size (surface area, $r=-0.30$, $P=0.56$; volume, $r=-0.38$, $P=0.46$). Only a relatively small proportion of the total peatland volume was unflooded during the winter, where mean availability ranged from 3.5 to 32.1% (Table 1). The absolute volume and proportion of unflooded habitat were not significantly correlated with watershed size ($r=0.68$, $P=0.14$; $r=-0.48$, $P=0.33$; respectively) nor the ratio of watershed size to peatland size ($r=-0.34$, $P=0.51$; $r=-0.41$, $P=0.41$; respectively).

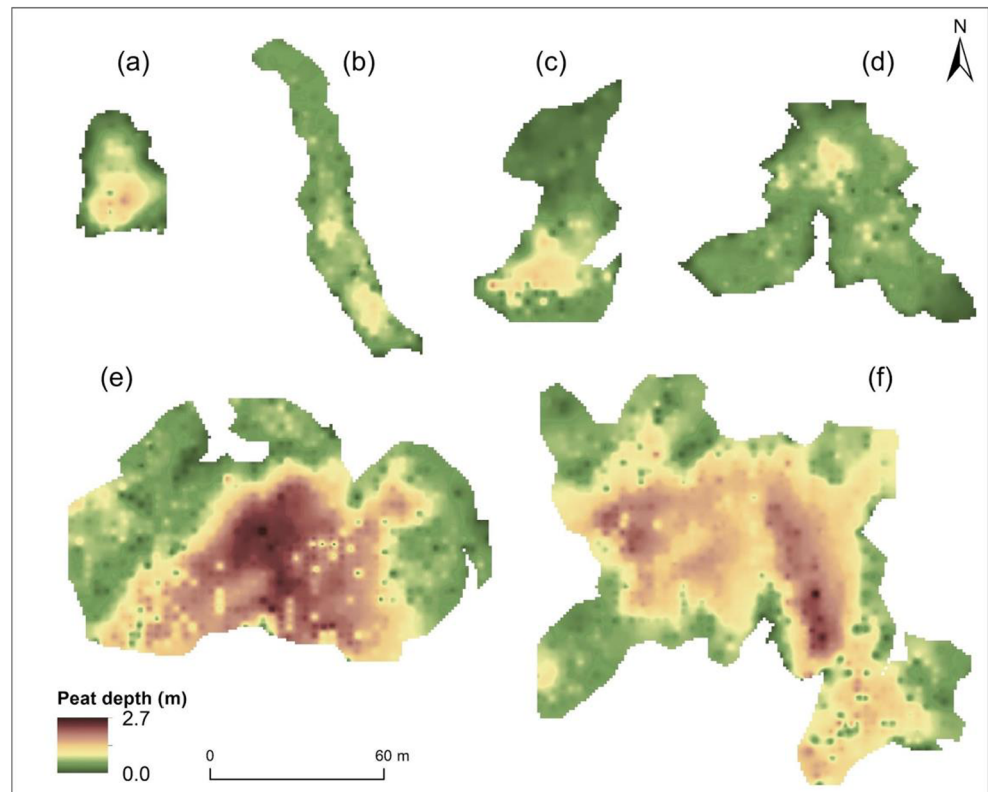
Although there was a lot of variability, a larger proportion of the vertical column tended to remain unflooded at higher surface elevations ($r=0.26$, $P<0.001$). Except for peatland C which experienced substantial winter flooding, trees were, on average, indicative of unflooded conditions (Fig. 5). Under mean winter water levels, trees in peatland C were located in areas with 0.03 m of water above the moss surface. In all other peatlands, mean winter water level position at tree locations

was less than 0.1 m (peatlands A, B, E, F) and greater than 0.15 m (peatland D) below the surface. The depth of unflooded habitat at trees varied by species ($X^2=47.5$, $P<0.001$) where maple (0.11 ± 0.10 m, $Z=4.6$, $P<0.001$), white pine (0.09 ± 0.07 m, $Z=-3.8$, $P<0.001$), and jack pine (0.11 ± 0.10 m, $Z=5.8$, $P<0.001$) were in locations with significantly deeper unflooded peat compared to tamarack (0.07 ± 0.06 m). Although the mean depth of unflooded peat was greater for jack pine than tamarack, jack pine was found at the largest range of conditions where the mean winter WT position was 0.29 m above the surface at some jack pine locations to 0.33 m below the surface.

Discussion

Peatland surface elevations were spatially heterogeneous within and among sites but larger peatlands had more distinct and variable surface topography compared to smaller peatlands. Peatlands smaller than 1500 m² had a mean surface height less than 0.22 m and were characterized predominantly by extensive pools and intermediate lawns. Larger peatlands

Fig. 4 Spatially-explicit peat depth (m) model for each of the six peatlands (a–f)



($\sim 10,000 \text{ m}^2$) had a mean surface elevation greater than 0.32 m with some heights between 0.5–1.0 m. Similarly, at a large peatland ($\sim 28 \text{ km}^2$) in eastern Ontario, surface topography had a range of 0.7 m, with a mean elevation of 0.3 m near

the peatland margin and 0.4 m further toward the peatland centre (Malhotra et al., 2016). Although the areas of higher elevation were spatially clustered within our peatlands, with higher features around the peatland margins (e.g. peatland D)

Fig. 5 Tree distribution (circles) and spatially-explicit model of flooded and unflooded overwintering habitat for the six peatlands (a–f). Available snake overwintering habitat is categorized based on depth of unflooded habitat (0–0.05 m, 0.05–0.10 m, 0.10–0.15 m, 0.15+ m). Depth of unflooded habitat was quantified using the winter mean water table position for each peatland

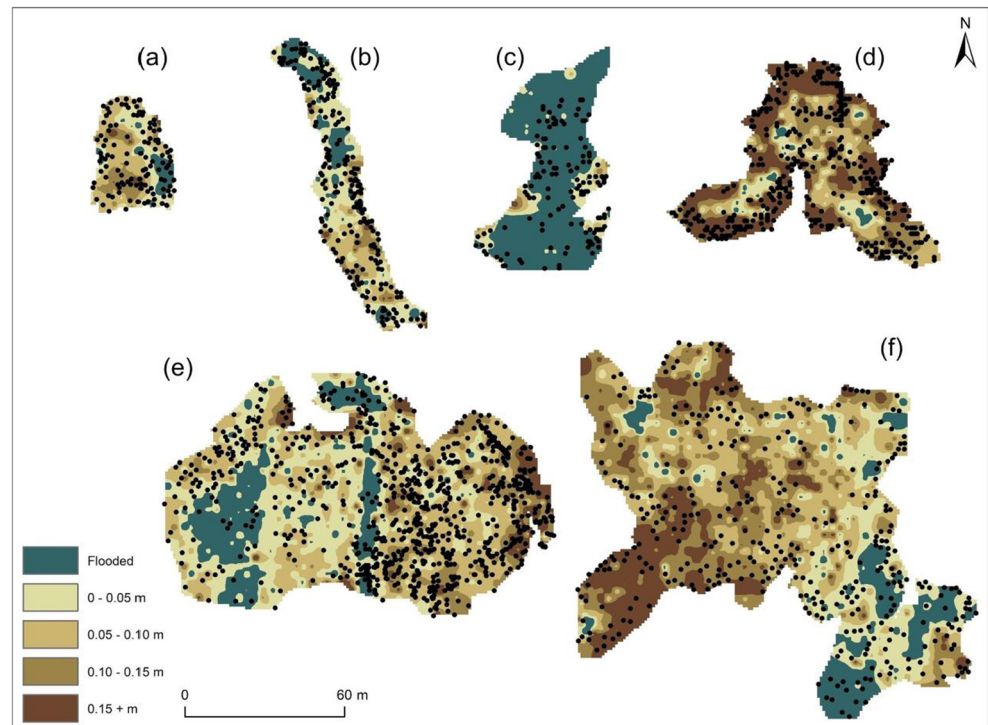
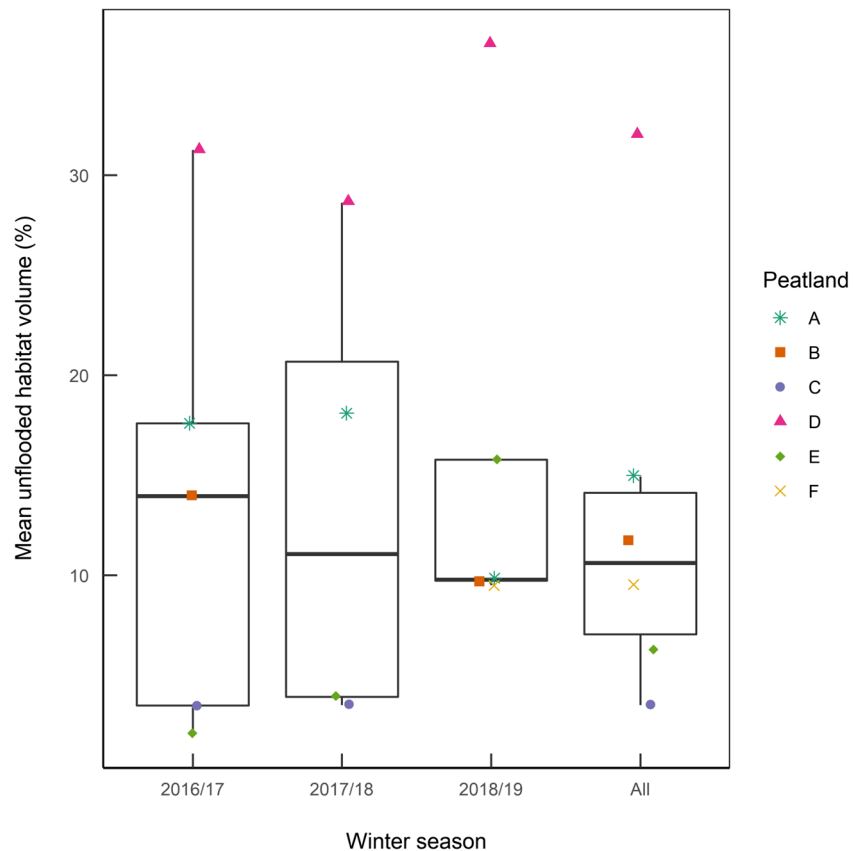


Fig. 6 Mean percent of unflooded habitat volume during the overwintering period (1 Oct – 30 April) for each of the six peatlands (A–F) for the 2016/17, 2017/18, and 2018/19 winter seasons, and the average percent of unflooded habitat across all years (All) where data are available (see Table 1)



or in the middle (e.g. peatland A), our sites do not display the same level of topographic spatial patterning seen in much more extensive, interconnected peatlands (e.g. Hudson Bay Lowlands; Glaser et al. 2004; Harris et al. 2019).

The position of the winter water table provides the dynamic lower limit of the resilience zone and is a critical component to determine the suitability of snake overwintering habitat (Smolarz et al. 2018; Markle et al. 2020b; Yagi et al. 2020). While the massasauga rattlesnake's tolerance to flooded conditions remains uncertain, prolonged exposure to flooded conditions is likely detrimental (Smith 2009; Markle et al. 2020a; Markle et al. 2020b; Yagi et al. 2020). Although our study peatlands had relatively little small-scale topographic complexity compared to other northern peatlands (Moore et al. 2019), they all provided unflooded areas, or snake overwintering habitat, throughout the winter. In fact, peatland B, which was actively used by the eastern massasauga rattlesnake for overwintering, had intermediate surface heights (Fig. 3b) but almost 12% of the peatland volume was unflooded (Table 1) and had a range of unflooded surface topography heights (Fig. 5). Subsequently, even peatlands with moderate surface topographic variability provide unflooded overwintering habitat. On the other hand, peatland C had higher surface elevations (Fig. 3c) but was flooded extensively throughout the winter (Fig. 5, Fig. 3c) while

peatland D had intermediate surface heights (Fig. 3d) but remained almost entirely unflooded (Fig. 5, Fig. 3d). Therefore, even peatlands with high surface heights may be flooded under mean winter water levels suggesting that although surface elevation is an important element of overwintering habitat, it is not the primary determinant of habitat availability.

In addition to surface topography, variability of the winter water table position suggests that the availability and distribution of unflooded habitat is also controlled by inter-annual winter weather conditions such as air temperature and precipitation (Markle et al. 2020a). For peatlands B and C, the mean percent of unflooded habitat was consistent between the relatively cold, dry winter (2018/2019) and the warm, wet winters (2016/2017, 2017/2018). In the colder, drier winter, two of the larger peatlands (D and E) had an increase in available unflooded habitat whereas the smallest peatland (A) had a decrease. A decrease in unflooded habitat due to a higher water table position was unexpected during the drier winter because the winter water table in basin peatlands fluctuates inter- and intra-annually by responding to water inputs via precipitation, snowmelt, and surface runoff. Flooded conditions in a drier winter could be a result of an ice jam blocking the outflow resulting in an elevated water table position compared to the wetter winter (see Markle et al. 2020b). While

some peatlands appear to have a low risk of flooding under variable winter weather conditions, others may be at a higher risk of winter flooding within or across seasons which, in turn, poses a risk to overwintering snakes. A long-term study comparing winter water table dynamics during relatively wetter and drier years could help elucidate factors contributing to peatland flooding risk.

A variety of tree species, each with unique tolerances for soil quality and root submersion (Whitlow and Harris 1979), are found within peatlands along the southern portion of the Canadian Shield. Trees encourage hummock formation by providing shading (Pouliot et al. 2011b) and a structural matrix to support *Sphagnum* biomass (Malmer et al. 1994). This internal structural matrix may also be an important characteristic of overwintering habitat for snakes (Johnson 1995). Conversely, as hummocks form, trees begin encroaching on areas of higher surface elevation, because their roots can remain in the aerobic zone. As expected, trees and unflooded habitat were often located at higher surface elevations suggesting that trees could be used as a visual indicator of unflooded habitat and thus available snake overwintering habitat. Except for peatland C, which experienced significant flooding during the study period, mean winter water level was <0.1 m (peatland A, B, E, F) or >0.15 m (peatland D) below the surface at tree locations. In our study peatlands, species such as white pine were located at both higher surface elevations and areas of deeper unflooded peat, and maple were located in areas with deeper unflooded peat. Jack pine seemed to be most tolerant of a range of conditions, growing at lower surface elevations than other species and found in the widest range of conditions where the water table was 0.33 m below the surface or up to 0.29 m above the surface. Our results are consistent with known species tolerances for root inundation (USDA 2019), except for jack pine which grows readily in acidic but well-drained soil (USDA 2019). That said, trees in northern peatlands often experience stunted growth or high mortality due to waterlogged soils (Boggie 1972; Jeglum 1974) and low nutrient availability (Jeglum 1974).

While the presence of white pine and maple within a peatland may be indicative of increased unflooded winter habitat, extensive tree cover is not necessarily preferable for snakes during emergence in the springtime. Increased tree density results in fewer opportunities for basking because of increased canopy cover and could reduce thermal variability of microhabitats (Shoemaker and Gibbs 2010). Although snakes do overwinter in peatlands with high tree density (peatland B, this study; Smolarz et al. 2018), the distribution of trees was spatially variable across the peatland surface in our study (Fig. 5). For example, areas of the peatland may have no trees while other areas can have up to 11 trees m⁻² (Table 1). The spatial complexity of tree distributions may be important for basking where access to open canopy areas is in

close proximity to overwintering habitat. This could be especially important during periods of winter melt or in early spring, where snakes emerge from their overwintering site for short periods of time to bask (Marshall et al. 2006) before moving to upland rock barrens in early summer (Seigel 1986).

We assessed additional landscape-scale factors as potential indicators of unflooded overwintering habitat, including peatland surface area and peat volume, peat depth, and watershed size. Peatland size and volume were indicative of surface topographic complexity and surface height variability, where larger peatlands were associated with taller relative heights. This was consistent across the study peatlands except for peatland C which was small and had relatively high surface heights and spatial variability. The total volume of unflooded habitat also increased with peatland size, although this relationship did not scale proportionally. Nonetheless, large peatlands may indicate increased habitat availability; however, although unflooded habitat may increase with peatland size, even small peatlands (e.g. peatland B) can support overwintering snakes. As such, although habitat availability may increase with peatland surface area and volume, smaller peatlands provide suitable overwintering habitat which are critical to sustaining local snake populations and must also be protected.

We found a weak association between surface elevation and peat depth at the study peatlands, suggesting that peat depth is a poor indicator of unflooded overwintering habitat. Peat depths were highly variable (Fig. 4), likely due to the shape of the underlying bedrock, which influences both water table position and peat depth. Similarly, watershed size was not statistically related to availability of unflooded habitat likely because most of our peatlands had smaller watershed to surface area ratios (Table 1). The watershed size in the study peatlands was relatively proportional to their surface area, except for peatland C, where the watershed was disproportionately large (Table 1). This may be why peatland C remained flooded throughout the overwintering season, and could indicate that watershed size is an important control on winter flooding potential which is the case for basin watersheds where the size of the contributing area strongly impacts discharge (Spence and Woo 2006). Moreover, the lack of relationship between watershed size and unflooded habitat also suggests that peatland runoff efficiency (the ratio of peatland runoff to precipitation and surface water inputs) is a primary driver of winter flooding potential.

Conservation and Management Implications

The spatial heterogeneity of surface topography is important to at-risk snakes who require insulated, unflooded habitats to survive overwinter (Smolarz et al. 2018; Markle et al. 2020a; Markle et al. 2020b; Yagi et al. 2020). As such, we characterized the surface complexity of peatlands in the eastern

Georgian Bay region to investigate the association between unflooded peat volume, surface topography, and other landscape-scale features. As road expansion and development threaten ecosystems in the region (Flower 2015), identifying peatlands that provide overwintering habitat will be important for conservation and management efforts. Tools to aid in the assessment of available snake overwintering habitat across large spatial scales can be useful to prioritize peatland protection and avoid overwintering habitat degradation and destruction. We identified surface elevation and the presence of trees, specifically maple and white pine, to indicate unflooded winter habitat. In restored peatlands, incorporating trees and vascular vegetation could increase peat accumulation (Berube and Rochefort 2018) and facilitate hummock development (Pouliot et al. 2011a) to potentially provide winter refugia from flooded conditions. Since massasauga rattlesnakes often return to the same overwintering area each year (Harvey and Weatherhead 2006; Smith 2009), and suitable overwintering habitat may be limited at the northern limit of their range (Harvey and Weatherhead 2006), protecting peatlands that are confirmed or provide suitable habitat is an important conservation strategy.

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