THE OVERWINTERING HABITAT ECOHYDROLOGY OF AN AT-RISK SNAKE

ASSESSING THE OVERWINTERING HABITAT ECOHYDROLOGY OF AN AT-RISK SNAKE AFTER WILDFIRE

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Lay Abstract

The eastern massasauga rattlesnake is a species at risk native to Ontario and parts of the USA. In the eastern Georgian Bay region, massasaugas overwinter in wetlands for up to half the year. This is a sensitive period because flooding or freezing within the hibernacula can be fatal. Due in part to climate change, wetlands in this region are at increased wildfire risk which may threaten the quality of massasauga overwintering habitat. In 2018, a wildfire burned over 11,000 ha of land along eastern Georgian Bay, some of which was massasauga habitat. We monitored the water table position and soil temperature in potential massasauga overwintering habitat to assess its quality after wildfire. We found that wetlands provide unflooded and unfrozen habitat even when burned, and that wetland surface complexity is likely an important regulator of overwintering habitat quality. This research highlights the importance of identifying and protecting wetland ecosystems that provide resilient habitat in the face of a disturbance.

Abstract

Peatland ecosystems in the eastern Georgian Bay, Ontario, region often provide overwintering habitat for the eastern massasauga rattlesnake (Sistrurus c. catenatus), a species considered at-risk across its range. Suitable overwintering habitat requires a resilience zone with peat temperatures above 0°C and a water table position sufficient to provide moisture without risk of flooding and these ecohydrological conditions commonly occur in raised peatland microforms (hummocks). Due to a changing climate, these peatlands are at risk of increased wildfire frequency and burn severity which may threaten overwintering habitat availability and suitability. In 2018, a wildfire burned over 11,000 ha of the eastern Georgian Bay landscape which serves as critical habitat for the massasauga. We monitored water table position, snow depth, rainfall, and peat thermal dynamics in hummocks in three burned and three unburned peatlands to assess the potential impacts of wildfire on massasauga overwintering habitat. We found that hummocks were able to provide unfrozen and unflooded habitat regardless of peat burn severity and that surface complexity and peatland-scale characteristics provided the greatest control on microhabitat suitability. This research highlights the importance of conserving peatland ecosystems that provide resilient species at risk habitat.

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 peatland (macrohabitat)

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List of Abbreviations and Symbols

- ANOSIM Analysis of Similarities
- COOP Central Ontario Orthophotography Project
- GBB Georgian Bay Biosphere Mnidoo Gamii
- ha-Hectare
- LB Lightly Burned
- LiDAR Light Detection and Ranging
- MB Moderately Burned
- NMDS Non-Metric Multidimensional Scaling
- PS33 Parry Sound 33 Wildfire
- SB Severely Burned
- Spp. Species
- UB-Unburned
- UBR Unburned Reference
- UNESCO United Nations Educational, Scientific and Cultural Organization
- °C Degrees Celsius
- χ^2 Chi-Squared

Declaration of Academic Achievement

I, Taylor North, declare that I am the sole author of this document. I completed the data collection and conducted all analyses. My supervisor, Dr. Mike Waddington, and post-doctoral fellows Dr. Chantel Markle and Dr. Paul Moore provided guidance throughout, particularly for the analysis and final preparation of the document. Dr. Paul Moore, Ian Martin, Keegan Smith, Renée McDonald, and Greg Verkaik assisted with equipment installations, and Greg Verkaik and Hope Freeman assisted with data collection.

Chapter 1: General Introduction

Eastern Georgian Bay peatlands

The land along the eastern coast of Georgian Bay, Lake Huron, is characterized by granitic rock barrens, upland forests, and wetlands (Crins, 2009), and is renowned for its global ecological significance. It encompasses the world's largest freshwater archipelago, spanning over 200 km of shoreline from the Severn River to the French River, Ontario, Canada (Georgian Bay Biosphere, 2021) and was designated as a United Nations Educational, Scientific and Cultural Organization (UNESCO) Biosphere Reserve in 2004. The landscape provides a diversity of microhabitats that supports more than 50 species at risk, including birds, mammals, insects, amphibians, and reptiles (UNESCO, 2015).

Peat-filled wetlands are common on the eastern Georgian Bay landscape and form in poorly drained bedrock depressions of the Precambrian Shield. Once these depressions have accumulated over 40 cm of organic soil they are classified as peatlands (National Wetlands Working Group, 1997). Peatlands are diverse ecosystems that play a key role in atmospheric carbon accumulation (Gorham, 1991) and water storage (Holden, 2005), provide refugia from environmental change (Strahlberg et al., 2020), and can be biodiversity hotspots (Kingsford et al., 2016; Markle 2020a). Although some peatlands in this region are hydrologically connected to groundwater, due to the underlying impermeable bedrock many peatlands are relatively isolated and receive inputs from precipitation and surface runoff alone (Moore et al., 2021). This creates acidic conditions conducive to *Sphagnum* growth. Dominant vascular vegetation includes shrubs (e.g., *Chamaedaphne calyculata, Alnus incana*) and trees (e.g., *Pinus banksiana, Pinus strobus, Larix laricina*).

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An important aspect of peatlands is the surface microtopography, which can influence the ecological, hydrological, and biogeochemical properties of a peatland (Waddington et al., 2015). Hummocks are raised peat mounds that vary in height from centimetres to a metre tall (Rochefort et al., 1990) and remain relatively dry because they are raised from the water table. Conversely, hollows are low-lying depressions on the peatland surface that are closer to the water table and thus wetter (Belyea and Clymo, 2001). Both hummock and hollow microforms can remain stable despite climatic and environmental variation (Belyea and Clymo, 2001). Hummocks and hollows can be randomly distributed or patterned on a peatland surface (Nungesser, 2003). However, in these small basin peatlands, hummocks are often spatially clustered but not patterned (Markle et al., 2020b). Peatland microtopography is influenced by a multitude of factors, including water table depth (Rydin and Mcdonald, 2013), Sphagnum species composition (Andrus et al., 1983), and vascular vegetation cover (Duberstein and Conner, 2009; Pouliot et al., 2011). Hummock microforms are typically colonized by Sphagnum species with high water transport and water holding capacities, such as S. fuscum (Andrus et al., 1983). Hummocks also support the growth of woody vegetation and trees by maintaining their roots in the aerobic zone, preventing them from being inundated by water (Barry et al., 1996). Similarly, tree roots create a structural matrix that provides scaffolding to facilitate hummock formation (Malmer et al., 1994). In eastern Georgian Bay basin peatlands, there is a spatial correlation between the presence of trees and areas of higher peatland surface elevations (Markle et al., 2020b) however, hummocks are colonized by species that are not characterized by their high moisture retention properties and surface microtopography seems to be restricted by the ecohydrological setting (Harris et al., 2019). Peatland microtopography is important to provide a variety of microhabitats to support species that utilize peatlands, such as the eastern massasauga rattlesnake (Smolarz et al., 2018; Markle et al., 2020b).

The eastern massasauga rattlesnake

The eastern massasauga rattlesnake (*Sistrurus c. catenatus*) is a relatively small venomous snake belonging to the pit viper (*Crotalinae*) subfamily, characterized by the presence of facial pits that allow the snake to detect infrared radiation from predators and prey (Gracheva et al., 2010). Massasaugas are shy and elusive and can be identified by their light brown colouring with dark brown bow-tie-shaped blotch pattern, heart-shaped head, and vertical pupils (USFWS, 2019). Massasaugas reach maturity after 3–6 years (Middleton and Chu, 2004) and give birth to live young. They have low reproductive rates (Cross et al., 2015) and may have biennial reproduction (Reinert, 1981; Johnson 1995). Their diet is composed primarily of small mammals (Weatherhead et al., 2009).

The massasauga has a biphasic life history strategy, cycling annually between an active season and an overwintering season (Huey, 1982; Yagi, 2020). While the timing of the transition between active and overwintering seasons is dependent on the climate of the region and microhabitat conditions, the active season typically spans from April until November (Szymanski et al., 2016). During the active season, massasaugas use wetlands, adjacent uplands, and forests for basking, foraging, mating, and gestation (Siegel, 1986; Weatherhead and Prior, 1992; Szymanski, 1998) with most activity concentrated within a relatively small area (~1 ha; Weatherhead and Prior, 1992; Marshall et al., 2006). During the overwintering season, massasaugas will retreat into rodent or crayfish burrows, forested rock crevices, root systems, or peatland hummocks to overwinter (Harvey and Weatherhead, 2006). There, massasaugas will lower their metabolic rate and brumate until the active season begins once again. During brumation the massasauga is able to respond to environmental stimuli and can adjust its position within the

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hibernacula to respond to changes in temperature (Nordberg and Cobb, 2017). Furthermore, massasaugas have demonstrated fidelity for their overwintering sites and will often return to the same general area in subsequent years (Harvey and Weatherhead, 2006).

The massasauga rattlesnake is found discontinuously from south-central Ontario into the midwestern United States and is considered at-risk across the entire species range. The species is classified federally as Threatened in the USA (Fish and Wildlife Service, 2016) and in Canada (*Species at Risk Act*, SC 2002 c29; COSEWIC, 2012) though state and provincial classifications vary. Threats to the massasauga are numerous and the impacts are often synergistic (Bradke et al., 2018). Habitat loss, and in particular wetland destruction, is likely a main driver of range decline (Weller and Oldham, 1992). For example, in central and southern Ontario, over 60% of wetlands have been destroyed for agriculture, road construction, and commercial development (Snell, 1987). Historically, massasaugas were present in 23 districts in Ontario (Weller and Oldham, 1992), but by 1993 this number was reduced to 12 (Beltz, 1993). Road development may also reduce connectivity between wetland and upland habitats and can lead to road mortality and increased predation (Szymanski, 1998).

The isolation of massasauga populations throughout the species' range subjects them to demographic and genetic stochasticity which may threaten small local populations (Gibbs and Chiucchi, 2012). Small populations often have decreased genetic variability, are prone to genetic drift (Szymanski, 1998), and are more likely to become extirpated (Noss and Cooperrider, 1994). Genetic analysis of massasauga populations throughout the United States and Canada indicate that geographically separated populations are demographically and genetically distinct (Gibbs et al., 1997). Even populations that are relatively close (<50 km) displayed genetic distinctiveness,

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indicating restricted gene flow (Gibbs et al., 1997). However, migration between distinct genetic populations was likely low historically, suggesting that the formation of genetically distinct populations is not a result of highly fragmented habitat, but rather a biological feature of the species (Chiucchi and Gibbs, 2010).

Further threats to the massasauga include human persecution and snake fungal disease. Historically, regions with massasauga populations offered money in exchange for the removal and destruction of rattlesnakes (Szymanki, 1998) and even in modern times the intentional killing of snakes out of fear or dislike leaves the massasauga vulnerable to future population declines (Prior, 1991; Cross et al., 2015). Snake fungal disease is also becoming an emerging threat to the massasauga. Discovered in 2006, the disease causes lesions and swelling and has a 95% mortality rate (Parks Canada Agency, 2015). A proactive approach is necessary to prevent outbreaks and manage infected populations (Allender et al., 2015). Currently, threats to the massasauga and its habitat are ongoing and pervasive. However, strategic plans have been created to attempt to stabilize isolated populations and decrease the risk of extirpation. Actions include habitat protection and restoration, monitoring, education, and outreach (Parks Canada Agency, 2015).

The eastern Georgian Bay regional population

In Ontario there are four regional populations of the massasauga, one of which resides inland of eastern Georgian Bay, with an extent of occurrence of 7,632 km² spanning from Port Severn to Killarney (Parks Canada Agency, 2015). The eastern Georgian Bay regional population is the largest of the four regional populations and is thought to be relatively stable, though is still considered at-risk both provincially (COSSARO, 2013) and federally (*Species at Risk Act*, SC 2002 c29; COSEWIC, 2012). The landscape mosaic of wetlands, uplands, and forests that

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characterize the eastern Georgian Bay region (Crins et al., 2009) remain relatively undeveloped and provide massasaugas with the diversity of microhabitats required for resource acquisition, reproduction, and overwintering.

Located at the northern limit of the species' range, massasaugas in the eastern Georgian Bay regional population may overwinter for over six months of the year (approximately October to May). While in other parts of their range, massasaugas overwinter in tree roots, animal burrows, and rock crevices in forests (Harvey and Weatherhead, 2006), in the eastern Georgian Bay region massasaugas overwinter in peatland hummocks. Hummocks can provide conditions that optimize overwintering habitat suitability for the massasauga because they are often raised above the water table which decreases the risk of drowning and are colonized by Sphagnum mosses that have high moisture retention (Luken, 1985) which may prevent desiccation. Furthermore, hummocks can provide stable temperatures throughout the winter (Smolarz et al., 2018) to allow the snake to stay cool enough to reduce its metabolic state but warm enough so that it will not freeze (Macartney et al., 1989). The space inside the hummock that is above the water table and below the 0°C isotherm was termed the resilience zone by Smolarz et al. (2018) and quantifies overwintering habitat suitability for the massasauga. However, not all hummocks provide suitable habitat. Hummocks that provide suitable overwintering conditions are those cool enough to allow the snake to lower its metabolic rate to brumate (Macartney et al., 1989) but remain above freezing (Gregory, 1982), and are close to the water table to prevent desiccation without the risk of drowning (Ultsch, 1989). Peatlands that provide suitable overwintering habitat may be limited, and eastern massasauga rattlesnake distribution may be restricted by the availability of suitable overwintering habitat (Harvey and Weatherhead, 2006).

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Quantified as the linear distance between the water table and the 0°C isotherm, the resilience zone is in constant flux throughout the overwintering season in response to environmental conditions. For example, combinations of highly variable winter weather conditions (e.g., warm, rainy days preceding days remaining below 0°C) can lead to a significant reduction in habitat suitability in hummocks within eastern Georgian Bay peatlands during certain portions of the overwintering season (Markle et al., 2020c). Hummocks can lose the resilience zone for hours to days at a time, and in general, peatlands occupied by the massasauga for overwintering have less resilience zone losses than peatlands that are unconfirmed as overwintering habitat (Markle et al., 2020c). Though massasaugas can likely survive a short amount of time if the resilience zone is lost (Yagi et al., 2020), it is unknown how long massasaugas can endure frozen or flooded conditions. In addition to winter weather conditions, hummock height, structure, width, and spatial arrangement, tree density, canopy openness, duration of snowpack, snow depth, and timing of snowfall could all be factors that influence habitat suitability (Smolarz et al., 2018).

There may be hummock- and peatland-scale characteristics that indicate overwintering habitat suitability for the massasauga. At the microhabitat scale, taller hummocks have been associated with providing a larger resilience zone that is present for a longer duration than shorter hummocks (Smolarz et al., 2018). The presence of trees at the macrohabitat scale may also indicate unflooded overwintering habitat (Markle et al., 2020b). Additionally, peatland volume and surface area may be associated with higher surface spatial variability and taller hummock heights, which may increase overwintering habitat availability (Markle et al., 2020b).

Despite the importance of peatlands as habitat for the at-risk massasauga rattlesnake, peatlands in the eastern Georgian Bay region are vulnerable to threats including climate change,

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highway expansion, and urban development (Flower, 2015). Impacts to peatlands can be cumulative, where multiple threats are compounded (Turetsky and St. Louis, 2006). Therefore, protecting peatlands that provide suitable habitat for the massasauga is an important conservation strategy (Markle et al., 2020b). More recently, wildfire may also be an emerging threat to eastern Georgian Bay peatland habitats under predicted future climate regimes, as evidenced by a large, high severity fire occurring in the eastern Georgian Bay region in the summer of 2018.

Wildfire in Ontario and the eastern Georgian Bay region

Wildfire is the greatest natural disturbance in the boreal forest (Johnson, 1992; Payette, 1992; Turetsky et al., 2002) and is the largest disturbance to boreal peatland ecosystems by spatial extent (Turetsky et al., 2004). Wildfire is a cyclical process that is integral for forest regeneration, surface fuel reduction, maintaining biodiversity, and increasing ecosystem health (Keane et al., 2008; Keane and Karau, 2010) but may also have detrimental impacts to humans and the environment including, but not limited to, loss of life and property (Alexander, 2010), reduced air and water quality (Matz et al., 2020; Emmerton et al., 2020), and encroachment of invasive species (McKenzie et al., 2004).

Assessing wildfire risk, which encompasses the potential impacts of a wildfire and the probability of its occurrence, is important to protect both natural ecosystems and the built environment. Climate projections estimate that the mean annual global temperature will increase 2–5°C by 2100 (Raftery et al., 2017), increasing wildfire frequency, fire occurrence (Wotton et al., 2010), and area burned (Flannigan et al., 2005) across Canada. Under similar assumptions, Wotton (2005) predicted that fire occurrence in Ontario would increase by 50% by the end of the century and be coupled with a 54% increase in fire management costs. Anthropogenic climate change is

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creating conditions that are more conducive to fire ignition and propagation across the landscape and models predict increases in area burned, occurrence, severity, and fire season length (Gralewicz et al., 2012). In addition to climate variables, the expansion of the wildland–urban interface (Johnston and Flannigan, 2016), insect outbreaks (James et al., 2017; Natural Resources Canada, 2020), and widespread fire suppression since the 20th century (Parisien et al., 2020) may increase wildfire risk in Canada.

Wildfire history in south-central Ontario has been profoundly influenced by human population distribution and land-use decisions (Dey and Gueyette, 2000). Since the last glaciation ~11,000 years ago, wildfire has played a cyclical role shaping the landscape east of Georgian Bay during the Holocene epoch (Anderson, 1995). The limited palaeoecological record, consisting of charred wood remnants, charcoal stratigraphy in lake sediments, and pollen records indicate that the fire return interval ranged from ~50–150 years during this time (Cwynar, 1977; Terasmae and Weeks, 1979). Fire activity, in conjunction with climatic changes, topography, and soil and hydrological changes likely contributed to the development and composition of the forests within the Great Lakes region (Anderson, 1995).

Prior to European settlement, Indigenous groups were using shkode (fire) as a land management tool to increase productivity, enhance ecological restoration (Davidson-Hunt, 2003), clear travel corridors, and hunt (Lewis, 1993), among other purposes, and were highly adept with shkode technology (Kimmerer and Lake, 2001). Indigenous peoples were living along Mnidoo Gamii (in the eastern Georgian Bay region) as early as 1200 C.E. (Lovisek, 1991), and by the 17th and 18th centuries, Anishinaabek villages of up to 500 individuals were present (Dey and Guyette, 1996). Throughout history, shkode may have been used in the eastern Georgian Bay region to deter

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insects, clear land (Lovisek, 1991), improve wildlife habitat (Dey and Guyette, 1996), and increase food production (Davidson-Hunt, 2003). In particular, the use of shkode by the Anishinaabek to increase blueberry yields was very successful (Davidson-Hunt, 2003). However, European settlers had a very different relationship with fire. After early legislation was passed in Ontario (e.g., the Act to Protect Forests from Fire in 1878 and the Forest Fires Prevention Act in 1917), wildfire suppression became the dominant fire management technique in the 1920s (Forest History Society of Ontario, 2013) to protect life and property and maximize timber production (Davidson-Hunt, 2003). Through colonialism and assimilation, the Anishinaabek became disconnected from their traditional shkode practices (Crafts, 2020). Today, wildfire management in Ontario is more nuanced and each fire is assessed before an appropriate response is undertaken (MNRF, 2019).

Due in part to the role of fire suppression in modern wildfire management, large wildfires in the eastern Georgian Bay region are relatively rare. However, notable fires occurred in 1877 in the Parry Sound area, and in 1864 and 1871 north of the French River (Hambly, 2013). Most recently, in 2018 a wildfire burned over 11,000 hectares of land between the Key and Pickerel Rivers, displacing people from their homes and restricting water and road access. This fire occurred within the current distribution of many at-risk reptiles including the massasauga (Markle et al., 2020d), and burned areas of critical habitat for the massasauga.

The eastern massasauga rattlesnake and wildfire

The massasauga has been considered a fire specialist (Cross et al., 2015) and in many cases prescribed burning has been used to manage massasauga habitat. Controlled, low severity burns reduce canopy and shrub cover post-fire and may increase habitat suitability by providing improved opportunity for thermal regulation (Davis and Doherty, 2015). However, decreased prey

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density and increased predation risk may offset these benefits (Cross et al., 2015). For example, small mammals are an important prey item for the massasauga (Keenlyne and Beer, 1973) and were identified at low abundance after a prescribed burn designed to create open habitat (Johnson, 1995). During a prescribed burn, Cross (2009) found that retreat sites, which were often peatland hummocks or burrows, provided sufficient thermal conditions (<40°C) to protect snakes from fire-related mortality. Mortality resulted from insufficient retreat locations or attempting to flee (Cross, 2009). Post-fire, snakes did not change their daily movements or home range. Although prescribed burning may result in individual mortality, it may have little impact on the population as a whole (Cross, 2009). However, the loss of a few individuals can lead to population crashes (Siegel and Shiel, 1999) and to understand the impacts of direct mortality from fire, a thorough understanding of the genetic viability and overall population size is necessary (Cross, 2009).

Although research on massasauga behaviour after prescribed burning has been relatively well documented, little research has been undertaken regarding the impact of wildfire on massasauga habitat, and even less so during the overwintering season. The massasauga has been known to use habitat that has been impacted by wildfire as evidenced by the presence of both overwintering and gestation sites in burned peatlands (Johnson, 1995). In fact, some gravid females spend the entire active and overwintering season in burned peatlands, while males and non-gravid females leave the peatland after overwintering (Johnson, 1995). However, the impacts of wildfire on massasauga habitat, particularly during the overwintering season, remains a critical knowledge gap.

As the climate in Canada becomes more variable and wildfire risk increases, it will be increasingly important to understand the impacts of wildfire on massasauga habitat. Hummocks

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are the preferred overwintering habitat for massasaugas in the eastern Georgian Bay region. Peat temperature and water table position are the two main parameters that determine overwintering habitat suitability for the massasauga (Smolarz et al., 2018). Wildfire can change the hydrological and thermal regime of peatlands, and the impact of these changes on massasauga overwintering habitat suitability is unknown. Although hummocks may be less vulnerable to combustion because of their low bulk density and water retention properties (Thompson and Waddington, 2013), hummocks are subject to high pore water pressures post-burn and therefore have a greater chance of disequilibrium between the water table and the peatland surface (Thompson and Waddington, 2013) which may impact the recolonization of Sphagnum mosses and recovery after fire (Kettridge et al., 2016). Fire can also alter peatland microtopography. Hummocks have an equal chance of being sustained or becoming a hollow via combustion during wildfire (Benscoter et al., 2005). Conversely, hollows are likely to persist post-wildfire leading to an overall reduction in hummock microforms (Benscoter et al., 2005). This may have implications for overwintering habitat availability on a burned landscape. Further alterations of hummock shape, structure, and microform proportion and distribution within the peatland after fire may impact both habitat suitability and availability for the massasauga.

Potential impacts of wildfire on massasauga overwintering habitat suitability

The resilience zone can be conceptualized as the space within a hummock that remains unflooded and unfrozen (Smolarz et al., 2018), and thus overwintering habitat suitability is tightly coupled with peatland hydrological and thermal dynamics. These dynamics are shaped by a series of complex feedbacks and interactions that drive the function of suitable overwintering habitat for the massasauga and the presence and size of the resilience zone (Markle et al., 2020a). These

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interactions incorporate the water storage and runoff, thermal, vegetation, and peat properties of a peatland. The nature of these interactions is outlined fully in Markle et al. (2020a). Here, the feedbacks and interactions that determine overwintering habitat suitability (Markle et al., 2020a) are adapted and conceptualized for a rock barrens landscape after wildfire.



Water storage and runoff-fire-resilience zone interactions

Figure 1.1. Water storage and runoff interactions that influence the resilience zone and predicted post-fire outcomes. Black and red lines indicate positive and negative relationships, respectively. Positive (+) and negative (-) symbols demonstrate whether the response after wildfire will increase, decrease, or be variable (+/-). Fire icons indicate direct impacts from wildfire. Adapted from Markle et al. (2020a).

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Peatland water table position is a critical parameter and the dynamic lower boundary of the resilience zone. The water table must remain below the 0°C isotherm to provide suitable environmental conditions for overwintering (Smolarz et al., 2018). The massasauga may be able to tolerate short periods of anoxia (Smith, 2009) however, this duration has never been quantified. A low, stable water table is ideal to reduce flooding risk and avoid anoxic conditions within the hibernacula.

During a wildfire, the surface layer of peat may be lost via combustion (e.g., Benscoter and Weider, 2003; Lukenbach et al., 2015), decreasing the water table depth relative to the peatland surface (Figure 1.1a) and exposing peat with increased bulk density and decreased specific yield at the surface (Figure 1.4b). These properties cause the peatland water table to become flashier and increasingly responsive to smaller rain events (Thompson and Waddington, 2013). Moreover, the combustion of moss and lichen mats on the upland rock barrens (Markle et al., 2020d) may reduce upland water storage capacity and increase runoff into the peatland, thus raising peatland water levels (Figure 1.1b). Taken together, the increase in water table responsiveness to inputs and the increased watershed run-off potential that is common after fire (e.g., Kinoshita and Hogue, 2011) may increase the flood risk of massasauga hummock hibernacula.

Since peatlands in eastern Georgian Bay are underlain by impermeable bedrock, hydrological connectivity is dominated by fill-and-spill dynamics, where the peatland water level must exceed a certain threshold before outflow can occur (Spence and Woo, 2003). Wildfire may burn away the surface layer of peat, which may enhance peatland drainage (Figure 1.1c). However, if the outflow is blocked, either by sediment, ice, or snow, the water table will continue to rise (Markle et al., 2020a, 2020d). For example, downed trees may trap sediment or snow (Sedell et al., 1988) restricting outflow from the peatland after wildfire (Figure 1.1d).





Figure 1.2. Thermal interactions that influence the resilience zone and predicted post-fire outcomes. Black and red lines indicate positive and negative relationships, respectively. Positive (+) and negative (-) symbols demonstrate whether the response after wildfire will increase, decrease, or be variable (+/-). Fire icons indicate direct impacts from wildfire. Adapted from Markle et al. (2020a).

The position of the 0°C isotherm, and thus peat temperature, is the second key parameter and the dynamic upper boundary that regulates the resilience zone in peatland hummocks. Peat temperature in the winter is regulated primarily by the interaction between the snow–insulation and peat–water–groundwater feedbacks (Markle et al., 2020a).

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Snow has insulative properties due to its high albedo, emissivity, and low thermal conductivity (Zhang, 2004) and provides thermally stable and moist conditions (Zhu et al., 2019). These conditions are driven at least partially by the depth and density of the snow and the duration of the snowpack (Pauli et al., 2013). However, snow cover is extremely variable both spatially and temporally (Zhang, 2004). In general, snow improves the stability of the resilience zone by buffering cold winter temperatures, but snow depth has been declining in Canada since the 1950s (Brown et al., 2007) and freeze-thaw cycles are increasing (Pauli et al., 2013). These rapid fluctuations in winter weather conditions can increase flooding risk if there is an established snowpack on top of the hummock (Markle et al., 2020c).

Post-fire changes in snow cover and depth may impact the resilience zone of hummock hibernacula. Snow depth can be reduced in burned forests compared to unburned forests under certain conditions (e.g., Maxwell et al., 2019) and may decrease with burn severity (e.g., Stevens, 2017), however the impacts of wildfire on snow depth in peatlands has yet to be elucidated (Figure 1.2a). Winkler (2011) found that in forests, snow water equivalent increased due to the lack of interception (Figure 1.3b) while ablation increased because of higher energy inputs at the surface after wildfire. However, the impacts of wildfire on snow water equivalent are inconsistent (e.g., Maxwell et al., 2019). Additionally, a decrease in blowing snow interception may occur after the loss of vegetation due to fire (Figure 1.3f). Moreover, groundwater inputs to a peatland during the winter may buffer peat temperatures and provide thermal refugia (Kaandorp et al., 2019). However, this feedback may have minimal function in isolated rock barrens peatlands.





Figure 1.3. Vegetation interactions that influence the resilience zone and predicted post-fire outcomes. Black and red lines indicate positive and negative relationships, respectively. Positive (+) and negative (-) symbols demonstrate whether the response after wildfire will increase, decrease, or be variable (+/-). Fire icons indicate direct impacts from wildfire. Adapted from Markle et al. (2020a).

Peatland vegetation comprises both vascular and non-vascular plants including shrubs, trees, and bryophytes and participates in multiple feedbacks that influence peatland water table position and peat temperature. For example, hummocks are often colonized by species that have high moisture retention such as *S. fuscum* (Andrus et al., 1983) which may keep the hummock moist throughout the winter. Additionally, through transpiration, trees can lower the water table which may lead to a positive drying feedback (Waddington et al., 2015). Finally, through the

processes of interception, ablation, and shading, trees and other vegetation can impact both peat thermal characteristics and hydrological dynamics.

Wildfire may lead to the complete or partial loss of Sphagnum moss from a peatland, however, hummocks are generally resistant to combustion because of the high moisture retention properties of Sphagnum fuscum (Thompson and Waddington, 2013). During a moderate-to-high severity wildfire, vascular vegetation is burned which may lead to a partial or complete opening of the canopy (Figure 1.3a). This can reduce snowfall interception (Figure 1.3b) and transpiration (Figure 1.3c) so water is conserved by the peatland. However, this is counteracted by more incident solar radiation at the peatland surface because of reduced shading (Figure 1.3d) which can increase evaporation (Waddington et al., 2015). In addition, the reduction of vegetation may alter snow accumulation and ablation patterns in the peatland (Winkler, 2011). Reduction in the canopy will decrease interception which may increase snow depth (Figure 1.3a, e). However, trees can accumulate blowing snow underneath them and this effect may be lost when trees have burned and fallen over (Figure 1.3f). For example, in the prairies, blowing snow can remove almost 70% of annual snowfall (Pomeroy et al., 1993). As an added complexity, vascular vegetation can recover quickly after wildfire (Thompson et al., 2014), so the impacts could be muted. Therefore, the impact on massasauga habitat suitability will depend on the magnitude of these counteracting feedbacks (Figure 1.3e).





Figure 1.4. Peat interactions that influence the resilience zone and predicted post-fire outcomes. Black and red lines indicate positive and negative relationships, respectively. Dashed lines indicate that the strength of the interaction can increase or decrease. Positive (+) and negative (-) symbols demonstrate whether the response after wildfire will increase, decrease, or be variable (+/-). Fire icons indicate direct impacts from wildfire. Adapted from Markle et al. (2020a).

During a wildfire, the combustion of near surface peat exposes denser peat at the surface, which increases bulk density (Thompson and Waddington, 2013). Increased bulk density may lead to a decrease in water table stability, amplifying water table fluctuations (Figure 1.4a; Markle et al., 2020a). In addition, and as mentioned earlier, specific yield tends to decrease after wildfire (Figure 1.4b), resulting in a flashier water table which is more responsive to rain events (Thompson and Waddington, 2013). Since most water inputs to peatlands in the eastern Georgian Bay region

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are by atmospheric inputs rather than groundwater inputs, sensitivity to rain events may be detrimental to overwintering snakes by increasing hibernacula flooding risk. Thus, due to the increased bulk density (lower porosity) and lower specific yield of peat post-fire (Figure 1.4b, c), the stability of the water table and the sensitivity to precipitation events may reduce habitat suitability after fire.

Thesis objectives

Understanding the complex ecohydrological interactions that regulate overwintering habitat suitability is critical to identify resilient hibernacula and guide in the conservation and restoration of habitat for species at risk (Markle et al., 2020a). In particular, applying these feedbacks in the context of wildfire (and other climate-mediated disturbances) is critical to prepare for massasauga habitat management and protection under the projected future climate regime. With these feedbacks in mind, the overarching goal of this thesis is to assess massasauga overwintering habitat suitability across a range of hummock burn severities. To do this, we instrumented hummocks in burned and unburned peatlands in the eastern Georgian Bay region. We measured the resilience zone dynamics including peat temperature and water table position and characterized peatland- and hummock-scale characteristics that might influence the resilience zone, taking into consideration the complex ecohydrological interactions that regulate habitat suitability. We collected data over two winters to capture the interannual variability of massasauga overwintering habitat suitability. This research is critical to inform the conservation and protection of the overwintering habitat for a species-at-risk snake at the northern limit of its range.

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Chapter 2: Assessing the overwintering habitat ecohydrology of an at-risk snake after wildfire

<u>Abstract</u>

Peatlands in the eastern Georgian Bay, Ontario, region often provide overwintering habitat for the eastern massasauga rattlesnake (Sistrurus c. catenatus), a species considered at-risk across its North American range. Overwintering habitat is considered suitable when peat temperatures are above 0°C and the water table position provides moisture without risk of flooding. This combination of suitable ecohydrological conditions, also known as the resilience zone, commonly occurs in hummocks which are raised microforms on the peatland surface. Due to a changing climate, peatlands are at risk of increased wildfire frequency and burn severity which may threaten overwintering habitat availability and suitability through changes in peat thermal and hydrological properties. In 2018, a wildfire burned over 11,000 ha of the eastern Georgian Bay landscape which supports critical habitat for the massasauga. To assess the potential impact of wildfire on massasauga overwintering habitat, we monitored water table, snow depth, rainfall, and peat thermal dynamics in hummocks across a gradient in burn severity (unburned-severely burned) in three burned and three unburned peatlands from 2019–2021. We found that hummocks were able to provide unfrozen and unflooded habitat regardless of peat burn severity and that interactions between peatland surface topography and watershed-scale characteristics likely provide the greatest control on microhabitat suitability. We argue there is an urgent need to examine how upland ecohydrology influences overwintering habitat suitability and availability after wildfire in a rock barrens landscape to identify peatland ecosystems that provide resilient species at risk habitat.

Introduction

The eastern massasauga rattlesnake (Sistrurus c. catenatus) is a thick-bodied venomous snake native to Canada and the United States of America (Beltz, 1993). Considered at-risk across its entire range, the species exists in small, isolated areas that are genetically and demographically distinct from one another (Chiucchi and Gibbs, 2010). Habitat loss (Weller and Oldham, 1992), disease (Parks Canada Agency, 2015), persecution by humans (Cross et al., 2015), and genetic and life history traits (Gibbs et al., 1997) have resulted in the population decline of a species that was once found continuously from southern Ontario to eastern Missouri (Conant and Collins, 1991; Parks Canada Agency, 2015). In Canada, the massasauga rattlesnake exists in two distinct subpopulations. The Carolinian subpopulation is located in southwestern Ontario, at the Ojibway Prairie Complex in Windsor and the Wainfleet Bog near Port Colborne. This subpopulation is especially vulnerable to extirpation due to urban development and industrialization and is listed as Endangered (COSEWIC, 2012; COSSARO, 2013). Population estimates suggest there are approximately 70 adult individuals in the subpopulation, occupying 16 km² (Parks Canada Agency, 2015). The Great Lakes/St. Lawrence subpopulation is located on the Bruce Peninsula and along eastern Georgian Bay and is classified as Threatened both federally (Species at Risk Act, SC 2002 c29; COSEWIC, 2012) and provincially (COSSARO, 2013). It is estimated that the subpopulation occupies approximately 1,620 km² (Parks Canada Agency, 2015) and consists of approximately 22,000 individuals (Rouse and Willson, 2002). The isolation of the Carolinian and Great Lakes/St. Lawrence subpopulations subjects massasaugas to demographic and genetic stochasticity which may threaten already small local populations (Gibbs et al., 2012).

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Within the Great Lakes/St. Lawrence subpopulation, a large and relatively stable regional population resides inland of eastern Georgian Bay, Ontario (Parks Canada Agency, 2015). This regional population is one of the few suspected strongholds in Canada, and therefore habitat preservation and conservation is important to maintain population stability (Parks Canada Agency, 2015). However, this regional population resides at the northern limit of the species' range and is therefore faced with unique challenges. For example, a short active season (June–September) restricts time for resource acquisition and reproduction while a lengthy overwintering season allows massasaugas to overwinter for up to six months of the year (October–May; Gregory, 1982; Harvey and Weatherhead, 2006). In the eastern Georgian Bay region, massasaugas overwinter within peatland hummocks (Parks Canada Agency, 2015) which are raised peat mounds on the peatland surface that range in height from a few centimetres to approximately 35 cm (Smolarz et al., 2018).

The landscape east of Georgian Bay consists of a mosaic of forests, open rock barrens, and peatlands, which provides diverse microhabitats that allow massasaugas to meet various needs throughout their life (Parks Canada Agency, 2015). For example, open rock barrens provide snakes with gestation and foraging sites during the active season (Rouse, 2006), and peatland hummocks provide overwintering habitat (Szymansky, 1998). The benefits of overwintering in peatland hummocks are twofold: first, to allow the snake to be at a sufficient distance from the water table to stay moist but not drown (Ultsch, 1989), and second, to remain insulated from potentially lethal winter temperatures (Gregory, 1982). The distance between the water table and the 0°C isotherm was termed the resilience zone by Smolarz et al. (2018) and quantifies the vertical space that provides suitable subterranean conditions for snake overwintering. Hummocks can lose the resilience zone during the winter for hours to days at a time (Markle et al., 2020a), and while

massasaugas have been submerged for up to nine hours in controlled experiments (Yagi, 2020), it is unknown how long massasaugas can endure flooded or frozen conditions.

Although peatlands are common across the Georgian Bay regional landscape, peatlands that provide suitable overwintering habitat (unflooded and unfrozen conditions) may be limited, restricting massasauga distribution (Harvey and Weatherhead, 2006). Furthermore, massasaugas have demonstrated fidelity to their overwintering sites (Harvey and Weatherhead, 2006) and may have difficulty adapting after peatland destruction or disturbance (e.g., Rogers, 2015). In this region, peatlands are vulnerable to threats including infrastructure development (MacKinnon et al., 2005), climate change (Dove-Thompson et al., 2011), and wildfire (Wilkinson et al., 2020). Summers in central Ontario are projected to become hotter and drier while winter temperatures are expected to increase by $2-3^{\circ}$ C and be coupled with a 10–20% decrease in precipitation (Colombo et al., 2007). Wotton et al. (2005) predicted a province-wide increase in the number of forest fires due to drier forest floor conditions. While cyclical, low intensity wildfire has shaped the landscape east of Georgian Bay for millennia (Anderson, 1995) and is important for forest regeneration and maintaining biodiversity (Keane et al., 2008; Keane and Karau, 2010), under a warming climate, conditions will be more conducive to wildfire ignition and wildfire occurrence and severity will increase (Wotton et al., 2010; Flannigan et al., 2015).

While the impacts of wildfire on massasauga habitat remains a critical knowledge gap, research on eastern massasauga rattlesnake behaviour after prescribed burning has been relatively well documented, particularly in prairie wetland and old field habitats (e.g., Cross et al., 2015; Steen et al., 2015; Hileman et al., 2018). During a prescribed burn of prairie fen habitat, peatlands maintained sufficient thermal conditions to provide retreat sites, allowing massasaugas to avoid

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their critical thermal maximum (~40°C; Cross, 2009). Lack of retreat locations resulted in massasauga mortalities when individuals attempted to flee the prescribed burn (Cross, 2009). Furthermore, it has been suggested that the species may be fire specialists (Cross et al., 2015) because snakes do not appear to change their daily movements or home range after a prescribed burn. In fact, prescribed burns have been used as a method to manage massasauga habitat in old fields and wet prairies by promoting early successional habitats that provide improved opportunities for thermal regulation (Hileman et al., 2018; Steen et al., 2018). However, prescribed burns (and the associated benefits) may not be congruous with wildfire. Prescribed burns are controlled, relatively low in intensity, and often create a mosaic of unburned patches while wildfire can be high intensity and may result in homogenous burned areas (Pastro et al., 2011). Moreover, prescribed burns for massasauga habitat management tend to take place during times when massasaugas are inactive (October–May, Hileman et al., 2018), while wildfire activity occurs most often during the active season (June–September).

Although wildfires are generally more severe than prescribed burns, massasaugas will use habitat that has been impacted by wildfire as evidenced by the presence of both overwintering and gestation sites in burned peatlands (Johnson, 1995; Ravesi, 2016). However, most previous research has focussed on the impacts of wildfire to massasaugas during the active season (e.g., Johnson, 1995; Ravesi, 2016), with less emphasis on overwintering habitat quantity and quality. For a regional population that overwinters for up to half of the year, it is critical to examine the impact of wildfire on peatland overwintering habitat to guide conservation strategies for eastern massasauga rattlesnake habitat, particularly as wildfire frequency and severity is increasing under warming climate conditions (Coogan et al., 2019).

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Our research aims to assess the ecohydrology of eastern massasauga rattlesnake overwintering habitat at the microhabitat scale (i.e., hummock) after wildfire. Our first objective was to quantify the size of the resilience zone and the duration it was present throughout the 2019-2020 and 2020–2021 winters across a burn severity gradient in three burned peatlands (containing unburned, lightly burned, moderately burned, and severely burned hummocks) and three unburned peatlands (containing unburned reference hummocks). We predicted that resilience zone dynamics would differ among hummocks as a function of burn severity regardless of the peatland that the hummock was located in, where hummocks with a lower burn severity would have a larger resilience zone that was present longer throughout the winter. The second objective was to evaluate how the environmental factors that influence the resilience zone vary in a burn severity gradient. We predicted that differences in snow depth, vegetation characteristics, and hummock volume and height among hummocks of different burn severities would alter the depth of the 0°C isotherm. Finally, our third objective was to assess the interannual variability in resilience zone dynamics over two winters, two- and three-years after wildfire. We predicted that if there were differences in interannual weather conditions between winters, then there would be an impact on resilience zone dynamics.

Methodology

Study area

The Georgian Bay Biosphere Mnidoo Gamii (GBB) is a freshwater archipelago spanning 175 km along the eastern coast of Georgian Bay, Ontario, Canada. Located on Anishinaabek Territory, the landscape consists of a complex mosaic of peatlands, upland rock barrens, and mixed forest. The GBB is a United Nations Educational, Scientific and Cultural Organization (UNESCO)

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Biosphere Reserve and is considered an area of global ecological significance (Georgian Bay Biosphere, 2021) supporting the highest concentration of reptiles and amphibians in Canada (Jalava et al., 2005). The region is characterized by a cool-temperate and humid climate (Crins, 2009) with 1118 mm of average annual precipitation, an average annual temperature high of 18.9°C in July and an average annual low of -11.1°C in January (Environment and Climate Change Canada, 2020).

Peatlands within the GBB are underlain by the granitic bedrock of the Precambrian Shield, which influences their development and ecohydrological properties (Didemus, 2016). Peatland morphology is constrained by the bedrock basin in which it develops which may restrict microtopographic complexity (Markle et al., 2020b). Additionally, many peatlands are not connected to regional groundwater systems and receive inputs solely from precipitation and surface runoff. Hydrological connectivity is intermittent and characterized by fill-and-spill dynamics (Spence and Woo, 2003). Peatlands are dominated by bryophytes (e.g., *Sphagnum spp.*) and diverse vascular plants including sedges (*Carex spp.*), trees (e.g., *Pinus banksiana, Larix laricina, Pinus strobus*) and other vegetation (e.g., *Chamaedaphne calyculata, Rhododendron groenlandicum, Kalmia angustifolia*). They also support faunal species, some of which are at-risk, including the eastern massasauga rattlesnake.

Macrohabitat (peatland) selection

Our study was conducted at six peatlands within the GBB and spanned two winters (2019–2020 and 2020–2021). The first winter (1 November 2019 – 31 May 2020) had an average temperature of 0.1° C and received 428 mm of precipitation while the second winter (1 November 2020–31 May 2021) was warmer than the first, receiving 410 mm of precipitation with an average

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temperature of 1.0°C (ECCC, 2021). We selected three burned peatlands (B1–B3) within the Parry Sound #33 (PS33) wildfire footprint which burned over 11,000 ha of land along the coast of Georgian Bay in 2018. Peatland B1 was relatively small and geographically isolated from other wetlands and was dominated by woody vegetation (i.e., *C. calyculata, R. groenlandicum, K. angustifolium*) and burned black spruce trees (*Picea mariana*). Peatland B2 was relatively large and permanently connected to a larger wetland complex. It was dominated by woody vegetation and burned black spruce trees. Peatland B3 was relatively small and geographically isolated from other wetlands. It was dominated by graminoids and had few trees. All three peatlands experienced similar burn severity and were surrounded by rock barrens uplands that were also burned during the fire.

The remaining three unburned peatlands (U1–U3) were located approximately 15, 35, and 60 km south of the fire footprint, respectively. Peatland U1 was a small, treed peatland dominated by woody vegetation (i.e., *C. calyculata, K. angustifolium*). Peatland U2 was a small peatland dominated by graminoids, while peatland U3 was relatively large and dominated by woody vegetation (i.e., *C. calyculata*) and pine trees (i.e., *P. banksiana*, *P. strobus*). All three unburned peatlands were relatively isolated from other wetlands on the landscape. One burned peatland (B2) was confirmed as overwintering habitat for the massasauga in May 2019 and two unburned peatlands (U1 and U2) were confirmed as overwintering habitat by local biologists. Two burned peatlands (B1 and B3) and one unburned peatland (U3) were not confirmed as overwintering habitat for the massasauga sighting and thus are considered critical habitat essential to the conservation of the species (*Species at Risk Act*, SC 2002 c29; Parks Canada Agency, 2015; OMNRF, 2016).

Microhabitat (hummock) selection

Table 2.1. Hummock burn severity metric for hummocks 0–3 years post-fire. The hummock burn severity metric categorizes hummocks based on a visual assessment of the ground cover on the surface of the hummock, hummock shape, the average depth of burn (the difference between estimated pre-fire and remnant peat depth), and whether the hummock is in a burned or unburned peatland (macrohabitat).

Burn Severity Category	Ground Cover	l Cover Depth of Shape Burn		Macrohabitat
Unburned Reference (UBR)	Sphagnum	0	Hummock shape intact	Unburned
Unburned (UB)	Sphagnum	0	Hummock shape intact	Burned
Lightly Burned (LB)	Singed <i>Sphagnum</i> , capitula intact	0	Hummock shape intact	Burned
Moderately Burned (MB)	Singed <i>Sphagnum</i> , capitula not intact	<0.1 m	Hummock shape partially intact	Burned
Severely Burned (SB)	No remaining Sphagnum	>0.1 m	No hummock shape remaining	Burned

We developed a hummock burn severity metric by assessing ground cover, depth of burn, and hummock shape to provide a rapid and qualitative indication of hummock burn severity (Table 2.1). At the microhabitat scale, 5–8 hummocks were selected within each of the six peatlands and categorized into five hummock burn severities (i.e., unburned reference, unburned, lightly burned, moderately burned, and severely burned) using the hummock burn severity metric. Unburned hummocks were located within a burned peatland (B1–B3), while unburned reference hummocks

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were in an unburned peatland (U1–U3). Lightly burned hummocks were characterized by singed *Sphagnum* moss with capitula still intact, while moderately burned hummocks also had singed *Sphagnum* but the capitula was not intact, and parts of the hummocks were combusted during the fire resulting in a depth of burn <0.1 m and irregular-shaped hummocks. Severely burned hummocks did not have *Sphagnum* cover and peat combustion during fire led to depths of burn >0.1 m. Severely burned hummocks were no longer raised peat microforms and often formed bowl-shaped structures on the peatland surface (Figure 2.1).

(a)

(b)



Figure 2.1. Photographs of an unburned reference hummock (UBR) in an unburned peatland (a), and unburned (UB), lightly burned (LB), moderately burned (MB) and severely burned (SB) hummocks in a burned peatland (b).

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For the first overwintering season, we compared hummocks among burn severity categories and between burned and unburned peatlands. Six hummocks were chosen at each burned peatland and ranged from lightly burned to severely burned. At each unburned peatland five unburned reference hummocks were selected haphazardly. For the second overwintering season two additional unburned hummocks were instrumented at each burned peatland. Five of the unburned reference hummocks were excluded from the study during the first winter and all unburned reference hummocks were excluded during the second winter due to large gaps in temperature data (Figure 2.2).



Figure 2.2. Conceptual model of the study design. In 2019–2020 (a), three burned and three unburned peatlands were instrumented with 2 severely burned (SB), 2 moderately burned (MB), 2 lightly burned (LB) and 2–4 unburned reference (UBR) hummocks. In 2020–2021 (b), three burned peatlands were instrumented with 2 severely burned (SB), 2 moderately burned (MB), 2 lightly burned (LB) and 2 unburned (UB) hummocks.

Resilience zone dynamics

For the purpose of this study, we defined the overwintering season between 1 November and 31 May. To capture temperature variability at the microhabitat scale, each hummock was instrumented with a thermocouple profile or an iBWetland temperature data logger (Alpha Mach, Ste-Julie, ON, Canada) installed at 5 depths (5, 10, 15, 25, and 50 cm below the hummock surface) at the burned peatlands, and 6 depths at the unburned peatlands (1, 5, 10, 15, 25, 50 cm below the surface). The temperature data were collected every 30 minutes and stored in a datalogger (Campbell Scientific Inc, Logan, UT, USA) when applicable. To measure water table dynamics, a groundwater well was installed at the deepest point of each peatland and was instrumented with a Levelogger Junior pressure transducer (Solinst, Georgetown, ON, Canada) that recorded the static water table position every 15 minutes. Another Levelogger Junior pressure transducer (Solinst, Georgetown, ON, Canada) was used to correct for atmospheric pressure changes. For analyses, water table depths were averaged to every 30 mins to match the frequency of the temperature measurements. We measured the vertical distance from the location of the groundwater well at the peat surface to the top of each hummock with a DISTO S910 laser distance meter (Leica, Richmond Hill, ON, Canada) or a Smart Leveler (Digital Leveling Systems, Smyrna, TN, USA) to account for differences in peatland surface elevation among hummocks.

Temperature and water table data were analyzed in RStudio 1.2.5001 (R Core Team, 2019). Five of the unburned reference hummocks were excluded from analysis (3 from U1, 1 from U2, and 1 from U3) due to large gaps in temperature data during the first winter and unburned reference hummocks were excluded fully from the analysis of the second winter because the unburned peatlands were inaccessible during COVID lockdowns (Table 2.2). We used linear interpolation

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to extract the 0°C isotherm from the raw temperature data. We applied a Gaussian low pass filter to reduce noise and manually removed spurious data points. We then subtracted the 0°C isotherm depth from the water table depth at 30-minute intervals to calculate the size (i.e., height) of the resilience zone in centimeters. Additionally, we calculated the number of times the resilience zone was lost (i.e., when the 0°C isotherm and water table intersect) and the timing and duration of the loss events. The resilience zone dynamics, including resilience zone size and the frequency and duration of loss events were compared among burn severities using a Kruskal-Wallis test with post-hoc comparisons (Dunn test with Bonferroni correction for multiple comparisons).

Table 2.2. Characteristics of the six peatlands instrumented during the 2019–2020 and 2020–2021 overwintering seasons, including whether the peatland was burned or unburned, the percentage of hummocks within the peatland that were burned (visually estimated), and whether the peatlands were occupied during the overwintering season by massasaugas (conducted by local biologists completing field surveys). Peatland area (m²), catchment area (m²), and the ratio of catchment area to peatland area is also presented.

Peatland	Туре	% of Hummocks Burned	# Instrumented Hummocks	Occupied during overwintering season	Peatland area (m ²)	Catchment area (m ²)	Ratio of catchment area (m ²) to peatland area (m ²)
B1	Burned	75	2 UB (2020-2021 only) 2 LB 2 MB 2 SB	Unconfirmed	1,921	3,715	1.9
B2	Burned	90	2 UB (2020–2021 only) 2 LB, 2 MB, 2 SB	Confirmed	10,839	34,499	3.2
B3	Burned	85	2 UB (2020–2021 only) 2 LB, 2 MB 2 SB	Unconfirmed	1,320	46,013	34.9
U1	Unburned	0	2 UBR (2019– 2020 only)	Confirmed	1,500	6,505	4.3
U2	Unburned	0	4 UBR (2019–2020 only)	Confirmed	2,419	53,508	22.1
U3	Unburned	0	4 UBR (2019–2020 only)	Unconfirmed	9,159	79,286	8.7

Microhabitat characteristics

We measured hummock height, hummock surface elevation, hummock volume, snow depth, and conducted vegetation surveys at each hummock to assess the microhabitat characteristics that could potentially influence peatland water table position and peat thermal dynamics across a burn severity gradient. Hummock height was measured from the adjacent hollow whereas hummock surface elevation was measured from a reference point (i.e., where the groundwater well meets the peatland surface). We estimated hummock volume by measuring hummock circumference at 5–10 cm vertical intervals and then summed the volume of each frustum to calculate total hummock volume. Hummock height, surface elevation, and volume were compared among burn severity categories using a Kruskal-Wallis test with post-hoc comparisons (Dunn test with Bonferroni correction for multiple comparisons).

We measured snow depth at peatlands B1–B3 by installing a trail camera (Stealth Cam LLC, Grand Prairie, TX, USA) at each peatland to take photographs of the hummocks hourly between 10 am and 4 pm. Behind each hummock, an orange reference stake was installed where we marked a 50 cm section that was used to convert pixels from the photograph to the height of the stake. We chose one photograph per day (at a time of day that maximized photograph quality) and calculated daily snow depth at each hummock by subtracting the total stake length from the visible stake length in MATLAB (MATLAB, 2021). Peatland B1 was excluded from the analysis in 2020–2021 due to data loss during COVID lockdowns.

Vegetation surveys of the surface of each hummock were conducted once between July– September 2020. We recorded the percent cover and number of individuals for each species of both ground and vascular cover and compared vegetation composition among hummock burn

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severity categories and between burned and unburned peatlands using non-metric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM).

Macrohabitat characteristics

We compared macrohabitat characteristics to account for among-peatland differences that might influence microhabitat suitability. The percentage of hummocks within each peatland that were burned was estimated visually and we calculated peatland area, catchment area, and the ratio of peatland area to catchment area in ArcGIS Pro 2.7.0 using high resolution satellite imagery (COOP, 2016 or LiDAR, 2020).

Results

Water table dynamics

In general, peatland water table positions declined slightly throughout the winter, peaked in mid-March, and decreased more rapidly into late May (Figure 3). During the 2019–2020 winter, mean water table position varied by 0.19 m among peatlands. At all peatlands except U2, the mean water table position was below the peatland surface at the location the well was installed, and thus on average, the peat surface was not flooded. Although U2 had the highest mean water table position (0.04 ± 0.05 m above the surface; mean \pm SD), it had the second smallest water table range (0.28 m) after U1 (0.23 m). Conversely, U3 had the lowest mean water table position (-0.15 ± 0.07 m) but the highest range (0.42 m). Burned peatlands had a deeper mean water table position and smaller range (-0.10 ± 0.06 m; 0.42 m) than unburned peatlands (-0.05 ± 0.10 m; 0.57 m).

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Figure 2.3. Daily precipitation and peatland water table position relative to the peat surface in unburned (U1–U3) and burned (B1–B3) peatlands during the winter of 2019–2020 (a) and 2020–2021 (b).

During the 2020–2021 winter, the mean winter water table position varied by 0.05 m among burned peatlands. At peatlands B1 and B2, the mean water table position was -0.11 ± 0.04 m and -0.09 ± 0.04 m, respectively while at peatland B3 the mean water table position was -0.14 ± 0.04 m. Peatland B3 also had the largest water table range (0.43 m) while B1 and B2 had a smaller

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range (0.38 m and 0.39 m, respectively). The winter water table dynamics were comparable between overwintering seasons for the burned peatlands (Figure 2.3).

Peat temperature dynamics

For all hummocks, the position of the 0°C isotherm decreased from the fall into mid-February and then increased once more into the spring, although the depth of the 0°C isotherm and the duration of sub-zero peat temperatures differed along the hummock burn severity gradient (Figure 2.4). During the first winter, the mean 0°C isotherm depth did not differ between hummocks in burned (14.9 \pm 0.03 cm, n = 18, mean \pm SE) and unburned peatlands (12.0 \pm 0.03, n = 10, χ^2 = 1.3241, df = 1, p = 0.2499), however, severely burned hummocks had a shallower mean 0° C isotherm depth (8.8 ± 0.03 cm) than lightly burned (17.4 ± 0.05 cm, Z = -3.0180, p = 0.01527) and moderately burned hummocks (18.4 \pm 0.05 cm, Z = -3.1934739, p = 0.0084; Figure 2.4a). The maximum 0°C isotherm depth was 47.8 cm for unburned reference hummocks, 48.2 cm for lightly burned hummocks, 46.4 cm for moderately burned hummocks, and 26.3 cm for severely burned hummocks. In the second winter, unburned hummocks had a shallower mean 0°C isotherm position (0.1 ± 0.004 cm) than moderately burned (13.1 ± 0.05 cm, Z = -3.8025, p = 0.0008) and lightly burned (11.7 \pm 0.05 cm, Z = -3.2301, p = 0.0074) hummocks but not different than severely burned hummocks (3.7 ± 0.02 cm, Figure 2.4b). The maximum 0°C isotherm depth was 9.3 cm for unburned hummocks, 43.9 cm for lightly burned hummocks, 44.47 cm for moderately burned hummocks, and 23.22 cm for severely burned hummocks.



Figure 2.4. Air temperature (Air, °C) and mean 0°C isotherm depth for lightly burned (LB, n = 6), moderately burned (MB, n = 6), severely burned (SB, n = 6), unburned (UB, n = 6) and unburned reference (UBR, n = 10) hummocks in the winter of 2019–2020 (a) and 2020–2021 (b).

The 2020–2021 overwintering season was warmer (mean air temperature of 1.0° C vs 0.2° C) and the isotherm depths were shallower than the previous winter ($\chi^2 = 12.295$, df = 1, p-value =
0.0005). Unburned hummocks were the most effective at maintaining peat temperatures above 0°C. In fact, unburned hummocks provided peat temperatures above 0°C for 94.1–100% of the overwintering season. In contrast, both lightly burned and moderately burned hummocks were poor insulators during both overwintering seasons.

Resilience zone dynamics

The percentage of the overwintering season with unflooded and unfrozen conditions varied among hummock burn severities during both winters. In 2019–2020, unburned reference hummocks provided suitable conditions for approximately half of the winter ($54.5 \pm 21.5\%$, 17.7-87.4%; mean \pm SD, range) which was less than that of severely burned ($79.3 \pm 13.3\%$, 59.9-97.0%), moderately burned ($88.8 \pm 16.8\%$, 52.4-100%), and lightly burned ($81.1 \pm 21.1\%$, 48.6-100%) hummocks, which all provided unflooded and unfrozen conditions for the majority of the overwintering season (Figure 2.5a). Two lightly burned and two moderately burned hummocks provided a continuous resilience zone for the entire winter, and three were in the same peatland (B3).

During the subsequent winter, the percentage of the season with suitable overwintering conditions increased from the previous year. Severely burned and unburned hummocks provided suitable conditions for the greatest proportion of the winter (96.0 \pm 4.3%, 88.5–99.7% and 99.8 \pm 0.44%, 98.8–100%, respectively), while moderately burned and lightly burned hummocks provided suitable conditions for 94.5 \pm 10.6%, 70.9–100% and 90.4 \pm 13.4%, 68.7–100% of the overwintering season, respectively (Figure 5b). Nine hummocks maintained a resilience zone for the entire winter, including three moderately burned, one lightly burned, and five unburned

hummocks. Four of these hummocks were located in peatland B1, two were in peatland B2, and three were in peatland B3.



Figure 2.5. Percentage of the overwintering season where the resilience zone is present for severely burned (SB, n = 6), moderately burned (MB, n = 6), lightly burned (LB, n = 6), unburned (UB, n = 6) and unburned reference (UBR, n = 10) hummocks (a–b) and by peatland (c–d) in the winter of 2019–2020 (a, c) and 2020–20201 (b, d).

The size of the resilience zone (linear distance between the water table and the 0°C isotherm) was highly variable throughout the winter for all hummocks. The mean size of the resilience zone was 9.7 ± 9.1 cm, 0–40.1 cm (mean \pm SD, range) for severely burned hummocks, 21.9 ± 16.5 cm, 0–60.5 cm for moderately burned hummocks, 22.3 ± 17.6 cm, 0–69.4 cm for lightly burned hummocks and 5.8 ± 8.0 cm, 0–39.8 cm for unburned reference hummocks during the first winter.

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Mean resilience zone size was significantly smaller for unburned reference hummocks than lightly burned (Z = 3.5076, p = 0.0027) and moderately burned (Z = 3.7430, p = 0.0011) hummocks (Figure 2.6a). For the second winter, the mean resilience zone size did not differ between burn severities (Figure 2.6b). In general, unburned, unburned reference, and severely burned hummocks provided a smaller, but more stable resilience zone than lightly burned and moderately burned hummocks.



Figure 2.6. Mean resilience zone size for lightly burned (LB), moderately burned (MB), severely burned (SB), unburned (UB) and unburned reference (UBR) hummocks in the winter of 2019–2020 (a) and 2020–2021 (b).

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The frequency of resilience zone loss events during the first overwintering season was greatest for severely burned and unburned reference hummocks (23 ± 13 , 6–46; and 24 ± 8 , 10–38, respectively; mean \pm SD, range). Moderately burned hummocks had the fewest loss events (6 ± 7 , 0–18) while lightly burned hummocks had on average 15 \pm 11, 0–27 loss events during the first winter. The mean duration of a single loss event did not differ significantly between burn severities ($\chi^2 = 6.8325$, df = 3, p = 0.0774) and ranged from 5.5 to 220.0 hours. There were fewer resilience zone losses during the second winter than the first (6 ± 9 versus 17 ± 12 on average per hummock) and the duration of each loss event tended to be shorter the second winter (3.0 to 147.3 hours). Unburned hummocks had a shorter mean duration of resilience zone loss events (1.0 hours) than lightly burned (25.9 hours, Z = 2.3278, p = 0.0199) and severely burned (30.8 hours, Z = 2.8941, p = 0.0038) hummocks but the frequency of loss events did not differ among burn severities ($\chi^2 = 5.5801$, df = 3, p = 0.1339).

Microhabitat characteristics

Hummock height

Relative to the adjacent hollow or intermediate, mean hummock height was 9.5 ± 7.5 cm (mean \pm SD) for severely burned hummocks, 31.8 ± 4.9 cm for moderately burned hummocks, 32.8 ± 4.7 cm for lightly burned hummocks, 28.9 ± 6.9 cm for unburned hummocks, and 28.5 ± 6.2 cm for unburned reference hummocks (Figure 2.7a). Severely burned hummocks were also positioned at lower surface elevations (referenced to the location where the groundwater well and peatland surface meet) with a mean elevation of 7.0 ± 5.7 cm compared to 28.9 ± 13.3 cm for moderately burned hummocks, 26.4 ± 9.8 cm for lightly burned hummocks, 10.1 ± 7.3 cm for unburned hummocks, and 8.8 ± 7.5 cm for unburned reference hummocks (Figure 7b).



Figure 2.7. Hummock height (a) and surface elevation (b) of severely burned (n = 6), moderately burned (n = 6), lightly burned (n = 6), unburned (n = 6) and unburned reference (n = 10) hummocks.

There was a moderate correlation between hummock surface elevation and the percentage of the overwintering season with unflooded and unfrozen conditions during the first winter ($R^2 = 0.405$, F(1,26) = 17.69, p = 0.0003; Figure 2.8a) but not during the second winter ($R^2 = 0.082$, F(1,22) = 1.96, p = 0.1758; Figure 2.8b). There was also a strong correlation between hummock surface elevation and mean resilience zone size in 2019–2020 ($R^2 = 0.681$, F(1,26) = 55.55, p = <0.0001; Figure 2.9a) and 2020–2021 ($R^2 = 0.789$, F(1,22) = 82.50, p = <0.0001; Figure 2.9b).

There was no relationship between hummock height (measured from the adjacent intermediate) and the percentage of the winter with unflooded and unfrozen conditions for either winter, but hummock height was weakly correlated with mean resilience zone size in 2020–2021 (R^2 = 0.212, F(1,22) = 5.92, p = <0.0236).



Figure 2.8. Percentage of the overwintering season in 2019–2020 (a) and 2020–2021 (b) that conditions were unfrozen and unflooded within the hummocks.



Figure 2.9. Mean resilience zone size (cm) within hummocks during the overwintering season in 2019–2020 (a) and 2020–2021 (b).

Hummock volume

On average, hummock volume was greater in unburned peatlands $(1.89 \pm 1.04 \text{ m}^3)$ than in burned peatlands $(0.94 \pm 0.70 \text{ m}^3, \chi^2 = 5.1429, \text{df} = 1, \text{p} = 0.0233)$ and in general, hummock volume decreased as burn severity increased (Figure 2.10). Severely burned hummocks $(0.27 \pm 0.21 \text{ m}^3)$

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had significantly less volume than lightly burned hummocks $(1.38 \pm 0.64 \text{ m}^3, \text{Z} = -2.7539, \text{p} = 0.0589)$ and unburned reference hummocks $(1.87 \pm 1.04 \text{ m}^3, \text{Z} = -3.5975, \text{p} = 0.0032;$ Figure 2.10). Increased hummock volume was not associated with a greater resilience zone size or a greater percentage of the overwintering season with suitable conditions.



Figure 2.10. Hummock volume of severely burned (SB, n = 6), moderately burned (MB, n = 6), lightly burned (LB, n = 6), unburned (UB, n = 6) and unburned reference (UBR, n = 10) hummocks.

Vegetation

Vascular vegetation composition did not differ among hummock burn severity categories (R = 0.0018, p = 0.445; Figure 2.11b) although there was a difference in vegetation composition between hummocks in burned and unburned peatlands (R = 0.2377, p = 0.0164; Figure 2.11d). All peatlands were dominated by woody vegetation (e.g., *C. calyculata*) except for peatland U2 and B3 that were dominated by graminoids. Burned peatlands were generally also colonized by species that are known to proliferate rapidly after wildfire such as *R. groenlandicum* and *K. angustifolia*,

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while these species were typically absent on hummocks in unburned peatlands. Ground cover (including bryophytes, lichens, peat, and litter) differed between burn severities (R = 0.6381, p = 0.0004) and between hummocks in burned and unburned peatlands (R = 0.3769, p = 0.0002; Figure 2.11a, c). Unburned hummocks were typically colonized by *Sphagnum* moss species, including *S. capillifolium* and *S. magellanicum*, while burned hummocks were typically composed of exposed peat or burned mosses. As hummock burn severity increased, the proportion of exposed peat increased, while live moss was reduced.



Figure 2.11. Non-metric multidimensional scaling for ground (a, c) and vascular vegetation (b, d) cover on hummocks among burn severities (a–b) and between burned and unburned peatlands (c–d).

Snow

In 2019–2020, the number of snow free days with mean daily temperature below 0°C ranged from 17–61 for severely burned hummocks, 28–51 for moderately burned hummocks, and 20–72 for lightly burned hummocks. All hummocks lost their snowpack in mid-March within 15 days of one another, which coincides with the abrupt increase in peatland water table position in March (Figure 2.3a). There was no difference in mean snow depth among burn severities nor among burned peatlands in 2019–2020. In 2020–2021, snow conditions were comparable to those in the previous winter. All hummocks lost their snowpack between 10 March and 20 March, 2021 which corresponds to increases in peatland water levels during this time (Figure 2.3b). However, the weather conditions were warmer than the previous winter and the number of snow free days with mean daily temperature below 0°C ranged from 17–22 for severely burned hummocks, 17–23 for moderately burned hummocks, and 18–22 for lightly burned hummocks. Mean snow depth did not differ among burn severities, however, peatland B3 had a greater mean snow depth than peatland B2 (8.1 cm vs. 4.4 cm, $\chi^2 = 5.7692$, df = 1, p = 0.0163).

Macrohabitat characteristics

The surface area of the burned peatlands ranged from 1,320 m² to 10,839 m² while the surface area of the unburned peatlands ranged from 1,500 m² to 9,159 m². The ratio of watershed size to peatland area ranged from 1.9 at B1 to 34.9 at B3, and in general, the catchment area was not proportional to peatland area. We estimated that 75%, 90%, and 85% of hummocks at peatlands B1, B2, and B3 were burned, respectively (Table 2.2). Catchment area and the ratio of catchment area to peatland area was not correlated with mean resilience zone size or the percentage of the overwintering period with unfrozen and unflooded conditions in 2019–2020 or 2020–2021.

Peatland area was negatively correlated with mean resilience zone size in 2019–2020 ($R^2 = 0.146$, F(1,26) = 4.43, p = 0.0452) and 2020–2021 ($R^2 = 0.291$, F(1,26) = 49.02, p = 0.0065) and with the percentage of unflooded and unfrozen conditions in 2020–2021 ($R^2 = 0.328$, F(1,22) = 10.72, p = 0.0035).

Discussion

Massasaugas have been considered fire specialists (Cross et al., 2015) although the suitability of massasauga overwintering habitat after wildfire has not been previously assessed in a rock barrens landscape. This remains a critical knowledge gap, particularly for massasaugas at the northern limit of the species range which may overwinter for more than half of the year (Harvey and Weatherhead, 2006). Our findings demonstrate that peatlands in the eastern Georgian Bay region can provide suitable habitat after wildfire regardless of hummock burn severity. We found that massasaugas overwintered in a burned peatland (B2) even when an unburned peatland was located nearby (<30 m). Since massasaugas demonstrate site fidelity by returning to the same general area each year (within ~100 m of the hibernacula from the previous year; Harvey and Weatherhead, 2006; Yagi et al., 2020), massasaugas are selecting burned peatlands for overwintering. Therefore, peatland hummocks appear to provide resilient overwintering habitat for the massasauga after wildfire.

In burned peatlands, 4 of the 18 hummocks in 2019–2020 and 9 of the 24 hummocks in 2020–2021 provided continuous unflooded and unfrozen conditions throughout the winter, compared to 0 hummocks in unburned peatlands. Although the environmental conditions of hummocks in burned peatlands were more suitable than those in unburned peatlands in 2019–2020, they were comparable to hummocks in unburned peatlands in previous studies. For example,

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6 of 16 hummocks in 2015–2016 and 3 of 18 hummocks in 2016–2017 provided a continuous resilience zone in basin peatlands occupied by massasaugas (Markle et al., 2020a) and in 2016, 16 monitored hummocks provided unflooded and unfrozen conditions for 77–96% of the winter (Smolarz et al., 2018). In general, hummocks in burned peatlands provided a larger resilience zone (17.0 \pm 10.0 cm vs 5.8 \pm 3.3 cm, mean \pm SD) and a higher percentage of unflooded and unfrozen conditions (83.2 \pm 17.8% vs 54.5 \pm 21.5%) than hummocks in unburned peatlands during the first winter. Despite providing less suitable habitat, both peatlands U1 and U2 were confirmed as overwintering habitat for the massasauga. Similarly, the peatland with the least suitable hummocks (B2) during the first winter was also occupied during the overwintering habitat.

Peatland surface topography within the eastern Georgian Bay region is spatially heterogeneous and topographic complexity is high, especially as peatland size increases (Markle et al., 2020b). Our research demonstrates that hummock surface elevation is an indicator of resilience zone size (Figure 2.9) and in 2019–2020 was also correlated with the percentage of unflooded and unfrozen conditions within the hummock (Figure 2.8a). While hummock height relative to the adjacent microtopography is considered an indicator of overwintering habitat suitability as taller hummocks have a greater capacity to buffer sub-zero temperatures and water table fluctuations (Smolarz et al., 2018), localized areas of high hummock surface elevation may be important to provide unfrozen and unflooded conditions, even in peatlands that are flooded under mean winter water table positions (e.g., Peatland U2; Markle et al., 2020b). Therefore, the interplay between surface topography and peatland processes is likely an important determinant of habitat suitability.

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The resilience zone quantifies the space within a hummock that remains unflooded and unfrozen throughout the winter (Smolarz et al., 2018) and thus habitat suitability is tightly coupled with peatland hydrological and thermal dynamics. These dynamics are shaped by a series of complex feedbacks and interactions that drive the function of suitable overwintering habitat for the massasauga and the presence and size of the resilience zone (Markle et al., 2020c). These feedbacks incorporate water storage and runoff, thermal, vegetation, and peat properties (Markle et al., 2020c). We predicted that these interactions would be altered across a hummock burn severity gradient, manifested through changes in hummock height, hummock volume, vegetation, and snow depth after wildfire. However, vascular vegetation composition did not differ significantly between burn severity categories (Figure 2.11b) and regrowth was rapid at all three burned peatlands. In particular, woody vegetation was prominent both two- and three-years postfire and this may have stabilized the thermal and hydrological feedbacks (Waddington et al., 2015; Markle et al., 2020c) within the peatland to maintain resilient overwintering habitat.

Snow depth also did not differ among burn severities in the burned peatlands, and the duration of time that an established snowpack was present on the hummocks was similar both among burn severities and between winters. However, hummocks during the 2019–2020 winter were exposed to temperatures below 0°C without a snowpack for a longer duration than the hummocks in 2020–2021 which may have contributed to the deeper isotherm depths across all hummocks in 2019–2020 compared to 2020–2021. Therefore, even small differences in interannual winter weather conditions can potentially change peat thermal dynamics, altering resilience zone size (Figure 2.6), the percentage of unflooded and unfrozen conditions (Figure 2.5) and the frequency of resilience zone loss events between winters.

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Our data demonstrate an inverse relationship between hummock volume and hummock burn severity (Figure 2.10). We did not find an association between hummock volume and resilience zone size nor the percentage of the overwintering season with suitable conditions. However, the loss of hummock volume due to peat combustion during wildfire may reduce the space within the hummock available for overwintering. While habitat suitability encompasses the environmental conditions of the habitat that allow for overwintering survival (e.g., unflooded and unfrozen conditions; Smolarz et al., 2018), habitat availability accounts for the accessibility and abundance of the habitat on the landscape (Krausman, 1999). Even small depths of burn may result in large losses in overwintering habitat at the peatland scale. For example, the average depth of burn from nine peatlands within the PS33 wildfire footprint was 0.02 ± 0.06 m (Wilkinson et al., 2020). If 2 cm of peat was removed from the entire peatland surface, it would result in the loss of 26 m³ of available habitat in a smaller peatland (e.g., B3, 1,320 m²) and 216 m³ of available habitat in a larger peatland (e.g., B2, 10,839 m²). While low severity wildfire can increase habitat complexity and may benefit massasaugas which rely on microhabitat diversity (Steen et al., 2015), high severity wildfire can result in homogenous burned area (Pastro et al., 2011). This is of particular concern as fire severity is expected to increase under warming climate conditions (Cassell et al., 2019) which may threaten habitat availability in a landscape where overwintering habitat is limited (Harvey and Weatherhead, 2006).

Our research found that resilience zone dynamics were highly variable both within and among peatlands, as well as interannually, however these dynamics did not scale in a consistent manner with increasing hummock burn severity (Figure 5). In fact, resilience zone dynamics were more consistent among hummocks within the same peatland than within the same burn severity category. This suggests that peatland and/or catchment-scale characteristics likely have a greater

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or overriding control on resilience zone dynamics than burn severity at the microhabitat scale. Both water table and peat thermal dynamics are closely linked with catchment-scale processes such as hydrological connectivity, runoff potential, and snow accumulation (Waddington et al., 2015, Markle et al., 2020c). For example, shallow soil deposits on upland rock barrens provide water storage on an otherwise impermeable surface (Moore et al., 2019). Soil combustion and erosion can reduce the volume of shallow soil deposits after wildfire (e.g., Markle et al., 2020d) and diminish the water storage capacity. The loss of soil and vegetation can increase surface runoff (Morales et al., 2000; Robichaud et al., 2007) and inflow into basin peatlands. Although we did not find a relationship between catchment size or the ratio of catchment area to peatland area and the percentage of the winter with suitable conditions or mean resilience zone size, our sample size was very small. Therefore, we recommend further research to examine how catchment-scale hydrological processes feedback to regulate resilience zone dynamics.

Management implications

Throughout their range, massasaugas demonstrate overwintering site fidelity (Smith, 2009) by returning to the same general area each year (Harvey and Weatherhead, 2006). Thus, in the eastern Georgian Bay region, the translocation of adult massasaugas may not be a feasible conservation strategy to compensate for overwintering habitat destruction (Rogers, 2015). We found that habitat suitability was highly variable both spatially and temporally in eastern Georgian Bay basin peatlands, though it appears that the complex ecohydrological feedbacks that regulate peat temperature and thermal dynamics (Waddington et al., 2015; Markle et al., 2020c) are able to maintain resilient massasauga overwintering habitat in the face of a moderate disturbance. For a landscape adapted to low severity fires (Anderson et al., 1995) these findings are not unexpected.

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However, under future projected climate conditions wildfire will become more prevalent and fire intensity and burn severity will increase (Wotton et al., 2010; Flannigan et al., 2015). While peatlands can provide climate change refugia (Strahlberg et al., 2020), high burn severities may threaten the availability of overwintering habitat on the landscape. Therefore, the identification and conservation of resilient peatland ecosystems should be prioritized to preserve critical massasauga overwintering habitat. Future research should investigate how habitat availability and habitat selection is impacted by wildfire and how catchment-scale ecohydrological feedbacks regulate microhabitat suitability for the massasauga.

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Chapter 3: General Conclusion

Across Canada, peatlands are at increased wildfire risk (Flannigan et al., 2009; Granath et al., 2016) which may expose declining reptile populations (Bohm et al., 2013; Gibbons et al., 2000) to potentially threatening conditions. In particular, the eastern Georgian Bay region is a reptile hotspot (Jalava et al., 2005), and some of these species rely on peatlands for part of their life cycle. In particular, the eastern massasauga rattlesnake uses peatland habitats extensively during both the active and overwintering seasons (Szymanski, 1998). Thus, understanding the threat of wildfire and other climate-mediated disturbances on massasauga habitat in this landscape is important to protect the critical habitat of an at-risk species.

Historically, low severity wildfires occurred regularly in the eastern Georgian Bay region (Cwynar, 1977; Terasmae and Weeks, 1979) and the Anishinaabek used shkode as a land management tool for hundreds of years (Lovisek, 1991; Dey and Guyette, 1996; Davidson-Hunt, 2003). However, this knowledge was largely lost due to colonization during European settlement (Crafts, 2020). At this time, fire suppression became the dominant land management technique (Forest History Society of Ontario, 2013) and has been used in this region throughout modern history (Ward and Mawdesly, 2000). Fire suppression, which often results in the accumulation of surface fuels (Ryan et al., 2013), paired with climate change may have led to the high burn severity of the Parry Sound 33 wildfire in 2018 (Markle et al., 2020).

Our research has improved the understanding of how the environmental conditions of massasauga overwintering habitat respond after wildfire. We determined that hummocks provided suitable overwintering habitat irrespective of hummock burn severity, suggesting that while natural variation in site suitability is high, the complex feedbacks that govern peatland

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hydrological and thermal dynamics maintain resilient overwintering habitat after wildfire. Particularly, peatland surface complexity is important to provide unflooded and unfrozen conditions during periods of hydrological and/or thermal variation. In addition, environmental conditions were more consistent among peatlands than among hummock burn severities, suggesting that catchment-scale characteristics, rather than burn severity, has an overriding control on microhabitat suitability. This relationship, between habitat suitability and catchment-scale processes, should be explored further.

Our research also suggests that habitat availability is likely more threatened by wildfire than habitat suitability. Therefore, a study directly exploring the loss of hummocks at a peatland or landscape scale after wildfire is warranted. Overall, this research is important to identify the regulators of overwintering habitat suitability after wildfire and inform the conservation and protection of overwintering habitat for a species-at-risk snake at the northern limit of its range.

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