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*Research Article*

# Initial Effects of Wildfire on Freshwater Turtle Nesting Habitat

**CHANTEL E. MARKLE**,[1] *School of Geography and Earth Sciences, McMaster University, 1280 Main Street W, Hamilton, Ontario, L8S 4K1, Canada*

**SOPHIE L. WILKINSON**, *School of Geography and Earth Sciences, McMaster University, 1280 Main Street W, Hamilton, Ontario, L8S 4K1, Canada*

**JAMES M. WADDINGTON**, *School of Geography and Earth Sciences, McMaster University, 1280 Main Street W, Hamilton, Ontario, L8S 4K1, Canada*

**ABSTRACT** Natural wildfire regimes are important for ecosystem succession but can have negative ecological effects depending on fire characteristics. A portion of a granite rock barrens landscape that extends along the eastern shoreline of Georgian Bay, Lake Huron to eastern Ontario, Canada, burned in 2018 during a wildfire that affected >11,000 ha. This landscape is a biodiversity hotspot providing habitat for many species at risk where freshwater turtles nest in soil deposits in cracks and crevices in the bedrock dominated by moss (*Polytrichum* spp.) and lichen (*Cladonia* spp.) cover. To assess the initial effect of wildfire on freshwater turtle nesting habitat, we measured soil depths and estimated moss, lichen, and vascular plant cover at 2 morphology types (crevice, flat) in burned and unburned areas of the landscape. The probability that burned flat plots supported soil was near zero; the burned flat plots had 98% less soil volume compared to unburned flat plots. Although crevices were more resistant to soil loss, burned crevices still had a 15% lower probability of having soil and 35% less soil volume compared to unburned crevice plots. We estimated nest site availability by calculating the number of locations with shallow (5–10 cm), intermediate (10–20 cm), and deep (>20 cm) soils required for a small (5 cm × 5 cm) or medium (10 cm × 10 cm) nest chamber. Overall, the burned open rock barrens had 71–73% fewer sites with suitable soil depth and volume for a nest chamber of either size. Furthermore, burned plots had almost no lichen and moss cover but were dominated by bare soil, forbs, and jack pine (*Pinus banksiana*) seedlings. Although the loss of tree cover in previously forested areas may increase nest site availability for freshwater turtles in newly open areas, we suggest that organic soil combustion and soil erosion may require restoration activities in the post-fire landscape to support successful nesting of at-risk turtles. 

**KEY WORDS** *Emydoidea blandingii*, fire, freshwater turtle, habitat, nesting, reptile, restoration, rock barrens.

Natural disturbances such as wildfire are key influences of ecosystem succession. For some ecosystems, vegetation composition and structure are influenced by natural fire regimes where successional response is typically related to fire characteristics (e.g., intensity, duration; Van Sleeuwen 2006). Jack pine (*Pinus banksiana*), for example, is a characteristic species of rock barrens ecosystems that are fire adapted and benefit from occasional, low-intensity fires (Gauthier et al. 1996). Fire, however, can have negative ecological consequences depending on severity and frequency (Van Sleeuwen 2006).

To classify the effect of wildfire, burn severity (mainly a function of soil organic matter consumed) is often assessed (Keeley 2009). Soil loss can occur through smouldering combustion causing near-total consumption of the organic component (Rein et al. 2008) and through erosion (Robichaud et al. 2016). Soil-limited landscapes that occur in rock barrens landscapes are particularly sensitive to high burn severity because a small absolute consumption of soil represents a relatively larger proportional loss compared to landscapes with deeper soils (e.g., the Canadian Boreal Plains ecozone). Furthermore, rock barrens landscapes covered by moss (*Polytrichum* spp.) and lichen (*Cladonia* spp.) are vulnerable to burning because mosses and lichens lack developed root systems and therefore dry out rapidly (Moore et al. 2019). Because the degree of soil loss affects ecosystem post-fire recovery rate (Lukenbach et al. 2017) and recovery trajectories in some systems (Kettridge et al. 2015), it is important for conservation and management biologists to assess the effect of wildfire across rock barrens landscapes, especially with respect to availability and suitability of habitat for species at risk.

Wildfire can increase canopy openness, creating diverse microhabitats for reptiles (Litzgus and Mousseau 2004, Dovčiak et al. 2013) and temporary turtle nesting habitat (Beaudry 2010); some species, such as the spotted turtle

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[1]*E-mail: marklece@mcmaster.ca*

(*Clemmys guttata*), prefer early-successional vegetation (Ernst 1976). Although wildfire can negatively affect habitat that turtles rely on for aestivation (e.g., junipers [*Juniperus* spp.] on rock outcrops; Litzgus and Brooks 2000), overwintering (e.g., peatlands; Markle and Chow-Fraser 2014), and travel corridors (e.g., vernal pools; Markle and Chow-Fraser 2014), shallow-soil nesting sites are likely to be the most severely influenced because of substantial soil loss.

From 18 July until 31 October 2018, the Parry Sound 33 wildfire burned >11,000 ha of rock barrens landscape along the northeast shoreline of Georgian Bay, Lake Huron in Ontario, Canada. This granite rock barrens landscape extends in a horseshoe shape along the eastern shoreline of Georgian Bay, Lake Huron to the Kaladar area in Ontario (Catling and Brownell 1999) and is characterized by a mosaic of wetlands, forested uplands, and open barrens. The rock barrens landscape, specifically the landscape along eastern Georgian Bay, is considered a biodiversity hotspot supporting rare plants and providing habitat for >50 species considered at-risk at the provincial or national level (State of the Bay 2018), including the Blanding's turtle (*Emydoidea blandingii*), spotted turtle, eastern musk turtle (*Sternotherus odoratus*), snapping turtle (*Chelydra serpentina*), northern map turtle (*Graptemys geographica*), and midland painted turtle (*Chrysemys picta marginata*). Although stand-replacing wildfires (that remove all or most tree cover and initiate forest succession) are common across other parts of the Canadian boreal forest (e.g., the Boreal Plains ecozone; Kurz et al. 1995), this wildfire was unprecedented in recent records (since 1950) for the Ontario Shield ecozone (Stocks et al. 2002, Natural Resources Canada 2018). There are records of previous fires in the Georgian Bay rock barrens (e.g., the 1877 fires in the Parry Sound region, and the 1864 and 1871 fires north of the French River; Hambly 2013), which overlap with historical and current distributions of reptile species. Therefore, given the increasing severity of summer droughts across the Canadian boreal forest (Wang et al. 2014), the extreme fire-danger rating in the Georgian Bay region before the 2018 fire (Natural Resources Canada 2018), and the recent history of fire suppression (Ward and Mawdesly 2000) that led to the build-up of wildfire fuels, the Parry Sound 33 wildfire may have resulted in unusually high burn severity and had a disproportionately negative effect on nesting habitats of at-risk turtle species.

In the Georgian Bay rock barrens landscape, freshwater turtles nest in soil deposits in cracks and crevices in the bedrock (Litzgus and Brooks 1998, Markle and Chow-Fraser 2014), similar to features used in other rocky landscapes (e.g., ME, USA; Beaudry et al. 2010) but contrasting with nesting habitats from other parts of North America such as beaches (Bowen and Janzen 2008, Hughes et al. 2009, Markle and Chow-Fraser 2018) and fields (Mui et al. 2015, Piczak and Chow-Fraser 2019). Natural nest sites in open, rocky outcrops are often dominated by mosses and lichens with soil depths ranging from a few centimeters to >20 cm (Litzgus and Brooks 1998, Markle and Chow-Fraser 2014, Zagorski et al. 2019). Nesting sites are necessary for the survival or recovery of a species (Species at Risk Act [SARA] 2002; Environment and Climate Change Canada [ECCC] 2018*a*, *b*) and loss or degradation of such habitat is of concern for the recovery of at-risk turtle species (ECCC 2018*a*, *b*). If suitable nesting habitat is limited or unavailable, turtles may nest in unsuitable sites, which can have negative effects on hatch success and thus recruitment (Kolbe and Janzen 2002, Mui et al. 2015). Any further reduction in nest success could be detrimental to at-risk turtle populations, especially because nest success can approach zero in some Ontario populations (ECCC 2018*a*). In addition to suboptimal nest incubation conditions (Kolbe and Janzen 2002), low recruitment rates also result from delayed sexual maturity (Congdon et al. 1993) and high nest predation rates (Marchand and Litvaitis 2004). In Ontario rock barrens landscapes where soil depth is already limited and turtle populations occur at species' northern range limits, any further loss or alteration in suitable nesting habitat could have consequences for the persistence of turtle populations (ECCC 2018*a*, *b*).

Our main objective was to assess the initial effect of wildfire on freshwater turtle nesting habitat 8 months after the fire. We hypothesized that cumulative differences between a burned and unburned landscape would affect the availability and suitability of turtle nesting habitat. Here we define availability as the number of sites on the open rock barrens that have the required soil depth to be used as a nest site and suitable sites as the proportion of available sites that provide conditions necessary to support hatching such as appropriate temperature and moisture regimes. We predicted that locations on the unburned landscape would have a higher probability of having soil present on open rock barrens compared to the burned, and when soil was present, we predicted that the depth of remnant soil on the burned landscape would be shallower than soil on a comparable unburned area. As a result of reduced soil depths, we predicted that the burned landscape would have a lower soil volume compared to the unburned landscape, which would negatively affect the number of available nest sites in burned rock barrens. We also predicted that vegetation-cover composition on the burned landscape would differ from the unburned landscape. Lastly, we propose that the combination of reduced soil depth and alterations to vegetation cover in a rock barrens landscape after fire affects nesting habitat suitability directly and indirectly through a cascade of changes in soil properties that influence nest habitat conditions (e.g., soil temperature, moisture regime).

## STUDY AREA

The Georgian Bay ecoregion is underlain by granite bedrock and is characterized by a mosaic of wetlands, forested uplands, and rock barrens (Crins et al. 2009; Fig. 1). Land use in this ecoregion includes forestry, mining, recreation, and tourism. The topography along the eastern shoreline of Georgian Bay (Parry Sound ecodistrict) varies from ridges of exposed bedrock to valleys with wetlands, and ranges in elevation from 172–436 m above sea level (Wester et al. 2018). Located on the southern portion of the Canadian

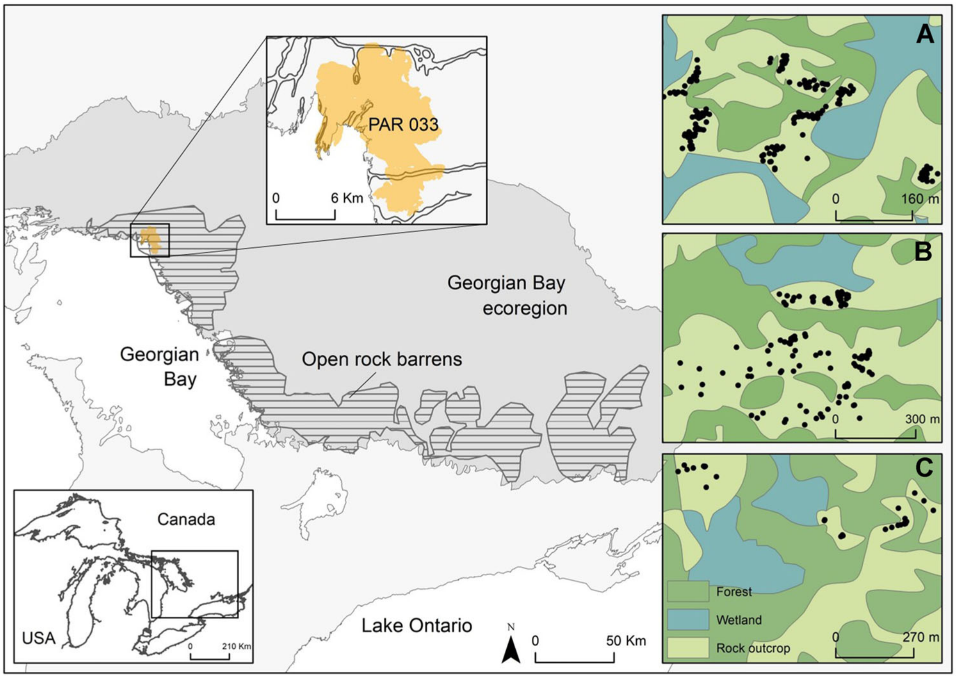


**Figure 1.** The Georgian Bay ecoregion on the southern portion of the Canadian Shield in Ontario, Canada, (Land Information Ontario 2015) and the approximate location of the open rock barrens landscape (estimated from Catling and Brownell 1999). The Parry Sound 33 (PAR 033) wildfire burned >11,000 ha of rock barrens along the northeast coast of Georgian Bay (inset; Land Information Ontario 2019). Plots (circles, surveyed Jul and Aug 2019) were located on burned (A) and unburned (B and C) rock barrens, and were within 500 m of wetlands occupied by turtles.

Shield, the climate in this region is cool-temperate and humid with mean annual precipitation ranging from 771 mm to 1,134 mm (Crins et al. 2009). In 2019, average daily temperatures ranged from –10.7°C in January to 21.4°C in July.

The open rock barrens on the eastern Georgian Bay landscape (Fig. 1) are characterized by bare rocky outcrops dominated by lichen, moss, juniper (*Juniperus communis*), and a few sparsely distributed coniferous trees (e.g., jack pine). A portion of this rock barrens landscape burned during the Parry Sound 33 fire (burned from 18 Jul 2018 until 31 Oct 2018; Fig. 1), an area known to support at-risk turtle species. In July and August 2019, 8 months after the fire, we surveyed turtle nesting habitat within the fire footprint (burned; Fig. 1A) and outside of the fire footprint (unburned; Fig. 1B, C).

# METHODS

To assess the effect of wildfire on the open rock barrens portion of the landscape burned during the Parry Sound 33 fire (Fig. 1), we surveyed burned and unburned plots (65 cm × 65 cm) located on 90 crevice and 90 flat bedrock morphologies (180 plots/landscape type, 360 plots total) spread across approximately 15 ha (Fig. 1). We selected the burned and unburned study areas because they support similar turtle species, have similar land cover composition (Fig. 1), and are both located within the Parry Sound eco-district, an area defined by a characteristic set of physiographic features (e.g., bedrock, geology, topography; Wester et al. 2018). We selected surveyed rock outcrops based on their proximity (<500 m) to confirmed turtle wetland habitat. Therefore, we classify our surveyed areas as potential nesting habitat because freshwater turtle nests are generally located within approximately 950 m of wetlands (Steen et al. 2012) and some turtles move many kilometers to nest (e.g., up to 6 km reported for Blanding's turtle; Edge et al. 2010). For plot selection, we randomly selected a point on the rock barrens and then surveyed the nearest flat or crevice morphology. Because crevices naturally accumulate deeper soil, we considered crevice and flat plots as 2 distinct bedrock morphologies to ensure we captured the natural variability of soil depths (Fig. 2).

Although a before-after control-impact study design is recommended to assess how landscape alterations affect a variable of interest (Christie et al. 2019), no pre-fire data on rock barrens soil depths exist within the fire footprint. In general, rock barrens in Ontario are not classified as ecosystems that experience regular, cyclical wildfire disturbance (Van Sleeuwen 2006). Fires in Ontario have been recorded since 1845 and the only large fire recorded in the coastal Georgian Bay area was in 1877, although no specific spatial data are available to confirm its exact location within the region (Hambly 2013). Hence, if we assume that the study area has been free of large fires since 1877, at the time of the Parry Sound 33 wildfire, all our sites represent a landscape ≥140 years after fire. Furthermore, in an unburned area south of the Parry Sound wildfire, radiocarbon analysis performed on shallow soil deposits underneath lichen and moss revealed that basal sample ages were between 665–730 and 551–663 calibrated years before present, respectively (J. M. Waddington, McMaster University, unpublished data). Therefore, soil accumulation rates are extremely slow

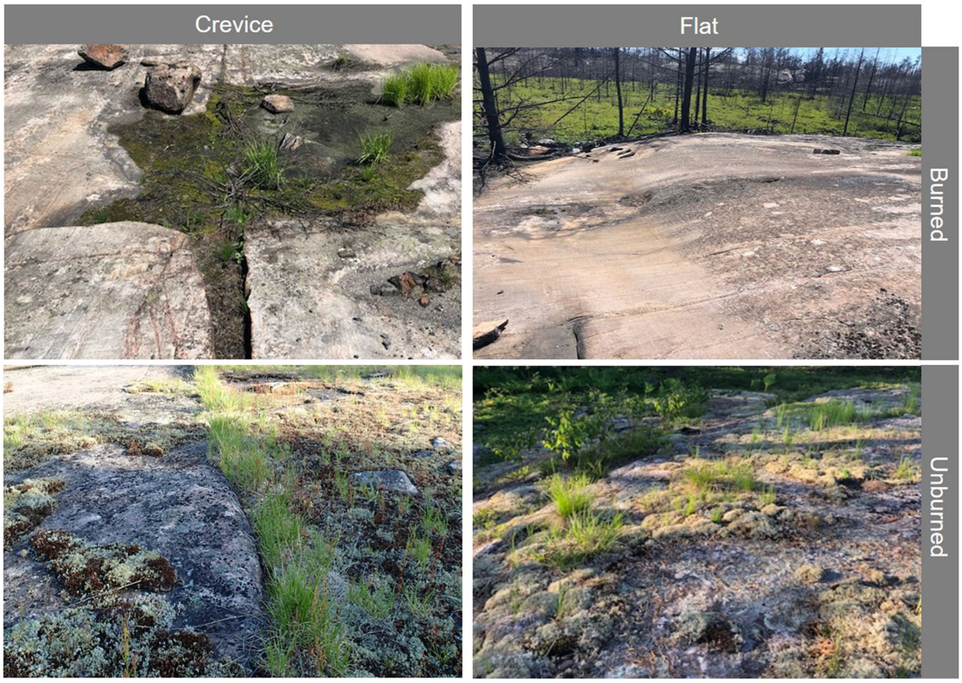


**Figure 2.** Examples of freshwater turtle nesting habitat surveyed in July and August 2019 in crevice and flat bedrock morphologies on a burned and unburned open rock barrens along the northeast coast of Georgian Bay, Ontario, Canada.

on the rock barrens landscape, and it is likely that pre-fire soil depths in 2018 were similar to soil depths at the control site in 2019.

At each 65-cm × 65-cm plot, we recorded soil depth (or remnant soil depth in the burned landscape) at the centroid of every 5-cm × 5-cm cell (169 measurements/plot). To compare soil depth between burned and unburned plots, we used a generalized linear mixed-effects model. We fit our model in R 3.6.2 (R Core Team 2019) using soil depth as the response variable, including the fixed effects of landscape type (burned or unburned), morphology (flat or crevice), and the interaction between these 2 effects, and a random effect of plot number (because we collected multiple points per plot). Because soil depth data were zero-inflated and overdispersed, we modeled soil presence-absence (binomial distribution) separately from soil depth >0 cm (gamma distribution) similar to a hurdle model (Brooks et al. 2017). We estimated soil volume by multiplying the soil depth measured at each of the 169 points/plot by the cell area (25 $cm^2$). We compared the estimated soil volume for crevice and flat plots between the burned and unburned landscape using estimation plots (Ho et al. 2019). We assessed the spatial distribution of soil by determining the number of measurements per plot that had soil present.

In each plot, we identified vegetation to species and recorded percent cover to the nearest 1%. To determine differences in surface cover and plant species composition between the burned and unburned landscape, we used nonmetric multidimensional scaling (NMDS) of a Bray-Curtis dissimilarity matrix calculated from percent surface-cover type (vegan package in R 3.6.2; Oksanen et al. 2019). We used an analysis of similarities to test for a significant difference in surface-cover composition between the burned and unburned landscape (significance accepted at $\alpha < 0.05$). We compared moss and lichen cover for crevice and flat plots between the burned and unburned landscape using estimation plots (Ho et al. 2019).

We quantified the number of available nest sites in each landscape by generally defining 2 nest chamber sizes (i.e., small [5 cm × 5 cm] and medium [10 cm × 10 cm]) based on the depth and sizes of nest chambers for small and medium-bodied turtle species previously recorded in a rock barrens landscape as part of another study (C. E. Markle, McMaster University, unpublished data). These data allowed us to estimate the minimum volume of soil required for a nest, and thus for a site to be classified as available nesting habitat (Fig. 3). In this landscape, soil depth ($D_s$; Fig. 3) from the surface to the bottom of the nest chamber can range from 7.5 cm (smaller-bodied turtle such as the spotted turtle) to 13.5 cm (medium-bodied turtle such as the Blanding's turtle). In addition to placing eggs at a certain depth below the surface, turtles also require a minimum volume of soil to contain eggs based on the nest chamber length ($C_l$), width ($C_w$), and height ($C_h$; Fig. 3). In this landscape, recorded nest chamber heights range from 3.0–3.5 cm for smaller-bodied turtles to 6 cm for medium-bodied turtles. Because soil depth required is greater than nest chamber height (i.e., $D_s > C_h$; Fig. 3), we examined the distribution of nest sites within shallow (5–10 cm), intermediate (10–20 cm), and deep (>20 cm) soils. Nest chamber width and length varies between 6.0 cm and 9.3 cm, so we operationally defined a small nest chamber as 5 cm × 5 cm and a medium nest chamber as 10 cm × 10 cm. We calculated the number of available sites for small and medium nest chambers at each

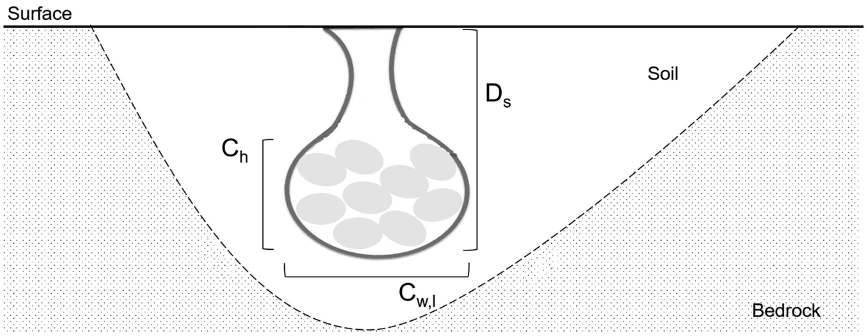


**Figure 3.** Conceptual diagram of a freshwater turtle nest chamber in an open rock barrens along the northeast coast of Georgian Bay, Ontario, Canada, 2019. The nest chamber size is defined by the chamber width ($C_w$), length ($C_l$), and height ($C_h$). The chamber is excavated by a turtle and eggs are laid below the soil surface ($D_s$); nest chambers can occur in shallow (5–10 cm), intermediate (10–20 cm), or deep (>20 cm) soils. For the purpose of estimating the number of available nesting sites, we classified $C_l$ and $C_w$ as small (5 cm × 5 cm) or medium (10 cm × 10 cm).

of the 3 soil-depth categories (shallow [5–10 cm], intermediate [10–20 cm], deep [>20 cm]). Because we collected soil depth data at a 5-cm resolution, we did not require interpolation when calculating availability of sites for small nest chambers; however, we interpolated data (bilinear interpolation in R 3.6.2) to a 10-cm resolution to estimate availability of sites for medium nest chambers.

## RESULTS

The probability of soil occurring on the landscape depended on bedrock morphology and whether the landscape was burned or unburned (interaction term, estimate [est.] ± SE = 3.06 ± 0.48, $Z = 6.3$, $P \leq 0.001$; Fig 4A; Table S1, available online in Supporting Information). The probability that burned flat plots supported soil was near zero compared to a 30% probability in the unburned flat plots (Fig. 4A). Crevices were more resistant to soil loss, but burned plots still had approximately 15% lower probability of having soil compared to unburned plots (Fig. 4A). Similarly, when soil was present, the interaction between landscape type and morphology significantly affected soil depth (est. = 1.16 ± 0.18, $t = 6.4$, $P \leq 0.001$; Fig. 4B; Table S1). Mean soil depths in unburned flat plots were almost double depths in burned flat plots according to the gamma mixed effects model (Fig. 4B). If soil was still present in a crevice, mean soil depth was comparable between burned and unburned plots (Fig. 4B); however, the occurrence of pockets of deep soils, and thus opportunities for nesting, was greatly reduced in the burned landscape (Fig. 4C).

Burned and unburned crevices almost always had some soil (89 and 90 plots with soil, respectively). Burned crevices had an average of 32 ± 14% ($\bar{x} \pm$ SD) of the plot surface covered in soil, with a maximum of 77%, compared to unburned crevices, which had an average of 44 ± 21% coverage, with a maximum

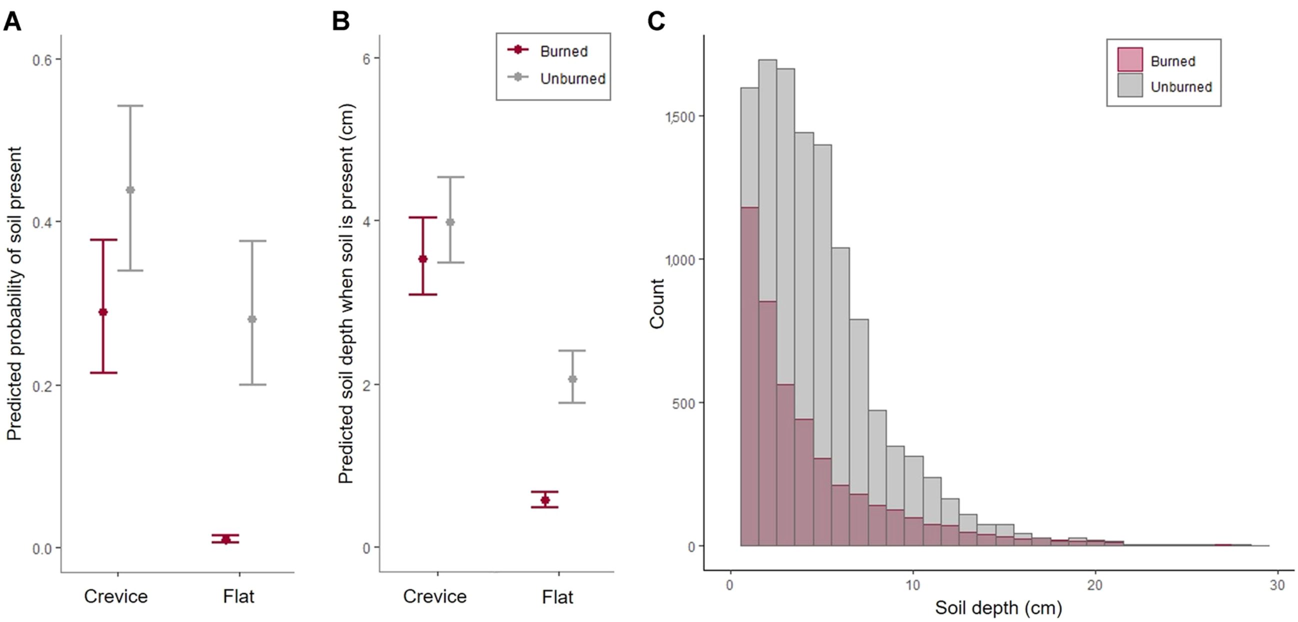


**Figure 4.** The predicted probability ($\bar{x} \pm$ 95% CI) that soil is present (depth >0 cm) in crevices or on flat bedrock in a burned (red) and unburned (grey) rock barrens landscape (A) in July and August 2019 along the northeast coast of Georgian Bay, Ontario, Canada. The predicted soil depth ($\bar{x} \pm$ 95% CI) when soil is present (depth >0 cm) in crevices or on flat bedrock in a burned (red) and unburned (grey) rock barrens landscape (B), and the observed distribution of soil depths (cm) when soil is present (depth >0 cm) in 180 burned (90 crevice, 90 flat) and 180 unburned (90 crevice, 90 flat) plots (C). There were 18 points in burned crevice plots and 9 in unburned crevices plots with soil depth >30 cm (burned maximum = 56 cm, unburned maximum = 86 cm).

of 98% (Fig. S1). Of the unburned flat plots, 73% had some soil compared to 62% of the burned flat plots. Moreover, unburned flat plots had an average of $53 \pm 40\%$ soil coverage, with some plots completely covered in soil, compared to the burned flat plots, which had on average only $6 \pm 8\%$ soil coverage. No burned flat plots had more than 50% soil coverage, with most not exceeding 20% (Fig. S1).

The difference in spatial coverage of soil between the burned and unburned landscapes was also reflected in the difference in soil volume, which was much lower in the burned landscape. On average, burned crevices had 35% lower soil volume than unburned crevices (Fig. S2). Burned flat plots were almost completely devoid of soil with 98% lower soil volume than the unburned flat plots (Fig. S2). In total, burned plots had an estimated $0.52\,m^3$ of soil and unburned plots had $1.45\,m^3$ of soil across $152\,m^2$ of surveyed rock barrens, almost a 3-fold difference in the total estimated volume of soil. If we expand this difference in soil volume to the 3,100 ha of open rock barrens estimated to have burned during the Parry Sound 33 fire (P. Rupasinghe, McMaster University, unpublished data), this represents a loss of roughly 190,000 $m^3$ of soil from the rock barrens via combustion or erosion.

Of the 30,420 depth locations measured (i.e., sites) in each landscape to determine availability of nesting habitat for small nest chambers (5 cm × 5 cm), 16% of sites (4,729) were appropriate for nesting in the unburned landscape, but the majority of the sites were available in shallow soil (5–10 cm; Table 1). Although almost 1,400 sites were still available for small nest chambers in the burned landscape, this only represented 5% of all surveyed sites (Table 1). Availability of intermediate and deep soil was limited in both landscapes, but there was a 56% and 9% difference in available nest habitat for intermediate (956 vs. 419) and deep (68 vs. 62) sites in the unburned compared to the burned landscape, respectively, for small nest chambers (Table 1). Nesting site availability for medium nest chambers was comparable to small nest chambers; 15% of surveyed sites (1,352) were available for nesting in the unburned landscape and only 4% of surveyed sites (371) were available for nesting in the burned landscape (Table 1). For small and medium nest chambers in shallow and intermediate soil depths, there was an approximately equal distribution of available nest sites in unburned crevices and flat areas (Table 1). In contrast, available nesting locations were almost exclusively found in crevices in the burned landscape. Overall, the unburned landscape offered almost 3.5 times the number of small (4,729 vs. 1,368) or medium (1,352 vs. 371) nesting sites, representing a 71–73% difference in available nest habitat based on soil depth alone (Table 1).

An NMDS ordination showed a distinct difference in surface cover composition between burned ($n = 180$) and unburned ($n = 164$) plots (Fig. 5; best solution reached after 20 runs with stress <0.15, indicating a good fit in 2-dimensional space). Furthermore, plots within the 2 landscape types supported comparable surface cover but burned versus unburned plots differed from each other ($R = 0.274$, $P = 0.001$, permutations = 999). The most notable difference in surface cover was the near complete absence of lichen and mosses on the burned landscape (burned $1 \pm 2.7\%$ coverage vs. unburned $24 \pm 23\%$; Fig. S3). If a burned plot did have moss cover, it was typically fire moss (*Ceratodon purpureus*). Instead, burned plots were dominated by forbs such as rock harlequin (*Corydalis sempervirens*), seedling jack pine, and bare soil. Both burned and unburned plots had some shrub cover and open bedrock.

# DISCUSSION

As predicted, the burned landscape had a lower probability of soil presence, lower soil volume and depth (Fig. 4A, B), and was characterized by a distinct surface and vegetation-cover composition compared to the unburned landscape (Fig. 5), supporting our hypothesis that cumulative differences between a burned and unburned landscape would

**Table 1.** The estimated number of available freshwater turtle nesting sites and the percentage of surveyed locations that met specified nest requirements in an unburned and burned rock barrens landscape in July and August 2019 along the northeast coast of Georgian Bay, Ontario, Canada, based on different turtle nest cavity classifications and bedrock morphologies. We classified a small nest chamber as having a width and length of 5 cm × 5 cm, and a medium nest chamber as 10 cm × 10 cm. Small and medium nest chambers can occur in shallow (5–10 cm), intermediate (10–20 cm), or deep (>20 cm) soils.

| Nest cavity type (chamber size, soil depth) | Available nesting sites | | | | % difference in number of sites available[b] (unburned − burned) | Available sites in crevice bedrock morphology (%) | |
|---|---|---|---|---|---|---|---|
| | Number | | %[a] | | | | |
| | Unburned | Burned | Unburned | Burned | | Unburned | Burned |
| Small, shallow | 3,705 | 887 | 12 | 3 | −76 | 48 | 98 |
| Small, intermediate | 956 | 419 | 3 | 1 | −56 | 61 | 99 |
| Small, deep | 68 | 62 | 0.2 | 0.2 | −9 | 99 | 100 |
| Small, all depths | 4,729 | 1,368 | 16 | 5 | −71 | 51 | 98 |
| Medium, shallow | 1,047 | 241 | 12 | 3 | −77 | 48 | 98 |
| Medium, intermediate | 279 | 121 | 3 | 1 | −57 | 63 | 100 |
| Medium, deep | 26 | 9 | 0.3 | 0.1 | −65 | 96 | 100 |
| Medium, all depths | 1,352 | 371 | 15 | 4 | −73 | 52 | 99 |

[a] We calculated percent available as the number of available sites divided by the number of surveyed sites (30,420 surveyed for small chambers and 8,820 surveyed for medium chambers) in each landscape type.

[b] We calculated percent difference as the percent decrease in the number of nest sites in the unburned compared to the burned landscape; for all cavity types the difference was negative because unburned locations supported more nest sites than burned locations.

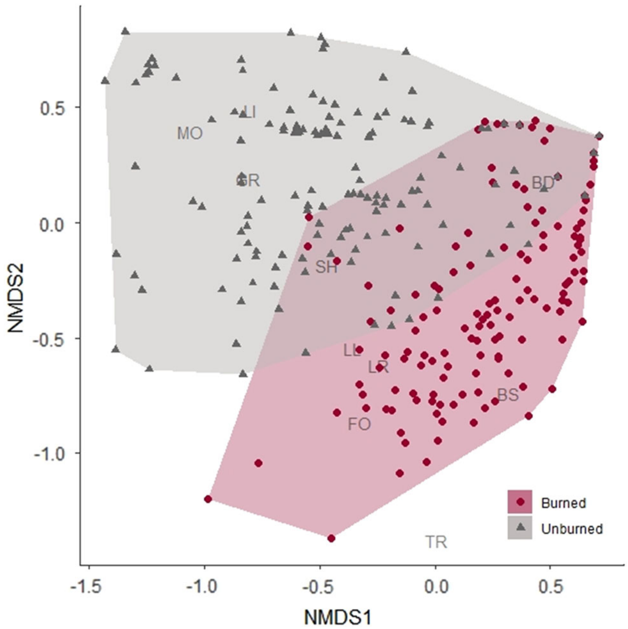


**Figure 5.** A non-metric multidimensional scaling (NMDS) ordination of a Bray-Curtis dissimilarity matrix generated from percent surface cover surveyed at 180 burned plots and 164 unburned plots in July and August 2019 on a rock barrens landscape along the northeast coast of Georgian Bay, Ontario, Canada. Convex hulls delineate the smallest polygon that encompasses all plots in the burned (grey) or unburned (red) landscapes; plots on the 2 landscape types overlap in vegetation and surface-cover composition. Unburned plots had a greater percent cover of lichen (LI) and mosses (MO), whereas burned plots were characterized by a greater percent cover of bare soil (BS), forbs (FO), and seedling jack pine (TR). Burned and unburned plots contained similar percent cover of open bedrock (BD) and shrubs (SH). Additional cover types included grasses (GR), litter (LR), and loose rocks (LR).

affect the availability of turtle nesting habitat. We attribute these differences directly to the wildfire or indirectly through soil erosion after the fire (Robichaud et al. 2016). Because percent soil organic matter in the unburned open rock barrens ranges from 3–25% (Moore et al. 2019), the difference in soil volume and depths observed between burned and unburned plots is most likely a result of the combustion of the organic component and redistribution of the remaining soil on the landscape during rain events. The greatest soil loss occurred on the flat bedrock morphology with an almost 50% reduction in soil spatial coverage and 98% less soil volume in the burned landscape. Crevices seem to be more resistant to burning or tend to collect remnant soils during runoff events (Fig. 4B) because, on average, spatial coverage of soil was only 12% less, soil volume was 35% less, and available nest sites were almost exclusively in crevice morphologies in the burned landscape (Table 1). This substantial combustion or redistribution of soils in the burned landscape has reduced the number of available nest sites by 71–73% from solely the perspective of soil depth (Table 1). Overall, we estimated a 3-fold difference in soil volume between the burned and unburned landscape, which directly and indirectly reduces nesting habitat availability and suitability, respectively (Fig. 6). This reduction in nest site availability and suitability could affect up to 6 of the turtle species that occur in the Georgian Bay region. Although the turtle population size and thus the extent of the effect on local populations is unknown within our study area, similar land cover types (wetlands and rocky outcrops) within the ecoregion had the highest reported population density for Blanding's turtles in Ontario (Zagorski et al. 2019). The Endangered Species Act in Ontario considers Blanding's turtle nesting habitat essential and the least tolerant of alteration (Ontario Ministry of Natural Resources and Forestry [OMNRF] 2013); therefore, the loss of >70% of nesting habitat and alteration of remaining nesting sites is a significant loss.

The loss of lichen and moss in the burned landscape reduces suitability of nest habitat because this cover type plays a key role in reducing variability in soil temperature (Fig. 6) and acts as an evaporative barrier (Moore et al. 2019) to prevent egg desiccation. Furthermore, the loss of lichen and moss cover decreases albedo, leading to increases in soil temperature, more extreme temperatures, and greater fluctuations (Kershaw 1977; Fig. 6). Although pioneer moss species (e.g., fire moss) will likely dominate early post-fire succession (Benscoter and Vitt 2008), they would be expected to colonize crevices as opposed to bare rock because remnant soil is present (Fig. 4). As such, monitoring vegetation recovery trajectories can serve as a starting point to understand the natural recovery of turtle nesting habitat in the long term.

In addition to reducing soil depth and vegetation cover, wildfire likely influences the suitability of the remaining habitat because nest-site characteristics (e.g., canopy cover, soil organic matter, soil compactness) directly affect egg incubation conditions (Moore et al. 2019) and hatchlings (Wilson 1998, Weisrock and Janzen 1999). For example, the loss of deeper nest sites may negatively affect the quality of available nest sites because shallower nest sites (i.e., shallower soils) are subject to increased temperature fluctuations and increased likelihood of flooding (Fig. 6). If eggs are exposed to extreme temperature fluctuations, cooler temperatures can inhibit development and warmer temperatures can lead to female-skewed sex ratios or mortality (Valenzuela et al. 2019). Through combustion, wildfire also reduces soil organic matter content and increases soil bulk density (Neff et al. 2005; Fig. 6). A trade-off exists regarding bulk density, which reflects soil compactness, as looser, moist soils favor nest cavity excavation (Kinney et al. 1998, Congdon et al. 2000), but increased bulk density (at a given moisture content) reduces temperature fluctuations in nests (Abu-Hamdeh and Reeder 2000). Ultimately, although the accumulation of soil organic matter takes centuries on a rock barrens landscape, it is an important process for increasing soil depth and thereby availability of nesting habitat (Fig. 6).

Post-fire watershed drainage is greater than pre-fire drainage for similar rainfall events (Kinoshita and Hogue 2011) because of soil erosion (Robichaud et al. 2016) and reduced surface cover resulting in less surface water storage (Benavides-Solorio and MacDonald 2005; Fig. 6). Runoff can also increase because water infiltration into soil

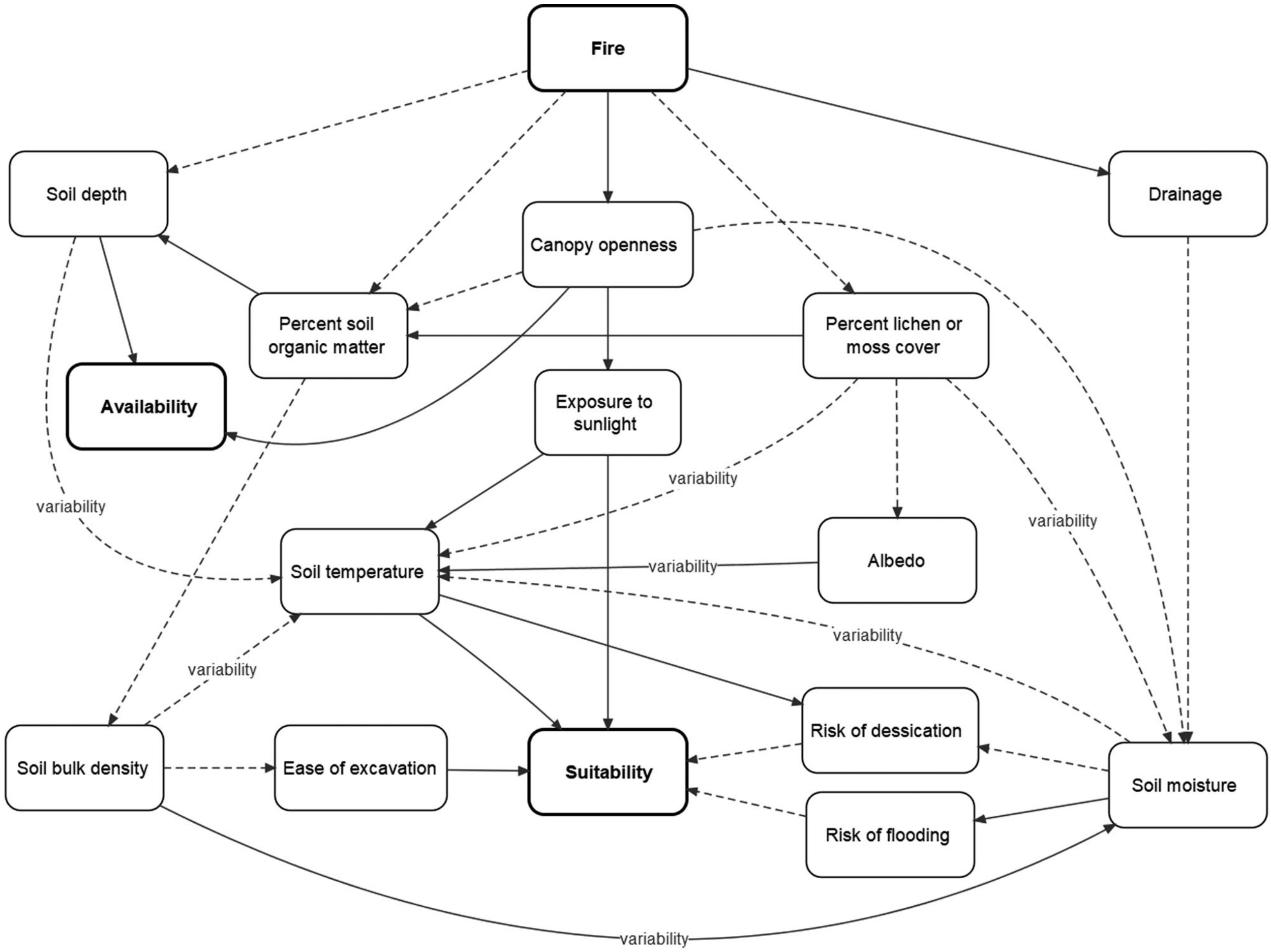


**Figure 6.** Conceptual model describing major environmental changes after fire on an open rock barrens landscape that directly and indirectly affect freshwater turtle nesting habitat availability and suitability. Negative effects are represented by a dashed line and positive effects are represented by a solid line. Variability refers to increased fluctuations in soil temperature or moisture conditions.

is initially lower in post-fire landscapes (Robichaud et al. 2016). As a result of altered watershed dynamics and soil properties, soil moisture in remnant shallow soil deposits are likely to fluctuate between flooded and dry states with more variability (Fig. 6). Such changes could have effects on egg hatching success because soil moisture must be maintained to balance the risk of egg desiccation and drowning (Packard et al. 1987, Packard 1999, Standing et al. 1999). Moreover, increased bulk density, or compactness, of remnant soil after fire also increases the risk of nest flooding because decreased soil pore-space results in large fluctuations in the water table position (Sherwood et al. 2013).

Despite fire negatively affecting turtle nesting habitat through changes in soil depth, soil organic matter, lichen and moss cover, and drainage (Fig. 6), wildfire can also increase nesting habitat availability through the creation of early-successional vegetation communities in burned areas. Burning of dense shrubs and trees may create additional nesting habitat because increased canopy openness may attract turtles (Litzgus and Mousseau 2004). Although loss of tree and shrub cover further decreases water storage capacity, increased canopy openness increases surface temperature of previously shaded areas (Webb et al. 2005; Fig. 6) and can provide more thermally diverse microhabitats (Litzgus and Mousseau 2004). The naturally deeper soils in forested areas should be more resistant to deep burning and newly open areas with intact soil could provide an opportunity for turtle nesting. The extent and effect of soil organic matter loss and soil erosion, however, can be severe in some upland forested areas (S. L. Wilkinson, McMaster University, unpublished data). Future research should quantify the trade-offs between decreases in habitat suitability and availability in open rock barrens nesting habitat and increases in nesting opportunities in previously forested areas after fire opens the canopy.

We suggest that, in the years following fire in a rock barrens landscape, turtles will have 3 options for nesting if no restoration actions occur. First, some species, such as Blanding's turtles, might seek unburned habitat by making long-distance movements; however, this may require individuals to migrate outside of their pre-disturbance home range. Second, turtles may nest in the remnant soil on burned open rock barrens, but associated changes in site suitability could be detrimental if turtles nest in patches of remnant soil that do not provide conditions suitable for incubation, resulting in an ecological sink (Mui et al. 2015; Fig. 6). Lastly, turtles may search for historical nesting sites on the burned rock barrens but because of greatly reduced soil depths may nest in newly open sites that were previously upland forest. Turtle nesting activity and hatch success should be monitored at burned nesting areas near occupied wetlands to assess turtle nesting behavior and incubation conditions at selected nest sites to investigate possible population-level effects.

Although wildfire is a natural process in maintaining open rocky landscapes, fires with high burn severity are predicted to increase in frequency under a changing climate (Flannigan et al. 2009), thereby increasing the loss of soil through extreme combustion and erosion. Given possible long-lasting effects on nesting habitat after wildfire through the potential dissociation between nesting habitat availability and suitability, restoration will likely play an increasingly important management role to provide suitable nesting habitat for turtles following wildfire. But traditional methods used to create nesting habitat such as sand mounds do not simulate natural habitat features and will erode on a rocky landscape. Moreover, sand mounds, although successful for incubation (Paterson et al. 2013), could attract predators (Quinn et al. 2015), especially if used in a rocky landscape where natural nests tend to be dispersed (Markle 2017, Zagorski et al. 2019) in comparison to other landscapes (Kell 2018).

## MANAGEMENT IMPLICATIONS

After an 11,000-ha fire in a rock barrens landscape, the availability of nesting habitat for freshwater turtles was lower at burned compared to unburned sites, and the suitability of remaining potential nest sites was likely negatively affected through alterations in soil properties. Extensive organic soil combustion and soil erosion, leading to loss and alteration of nesting habitat, may require restoration activities in post-fire landscapes to support successful nesting of at-risk turtles. We propose 3 general approaches to enhance nesting habitat availability and suitability on burned rock barrens landscapes. Although crevices contain some remnant soil following fire, restoration actions such as adding organic soil, and transplanting lichen and moss mats to increase surface cover, could improve crevices' suitability as nest sites. Because the flat bedrock morphology tends only to provide shallow nesting habitat appropriate for smaller-bodied species, more intensive restoration approaches, such as using barriers for soil retention (e.g., rocks or large logs), could create nesting areas with deeper soils in these locations. Transplanted organic soil and vegetation cover could create additional shallow nest sites on flat rock barrens subjected to extensive soil loss after fires.

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