

## RESEARCH ARTICLE

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# Ecohydrological controls on lichen and moss CO<sub>2</sub> exchange in rock barrens turtle nesting habitat

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## Abstract

Lichens and mosses are among the first organisms to colonize the open bedrock of eastern Georgian Bay, Ontario making them essential for primary soil formation and ecosystem succession, while also providing nesting habitat for turtle species-at-risk. However, the slow growing nature of lichen and moss makes them vulnerable to ecohydrological stresses caused by climate and land-use change. In order to better understand how lichen and moss will respond to stressors, we examined which ecohydrological factors (e.g., near-surface soil moisture and temperature) control the CO<sub>2</sub> exchange of lichen (*Cladonia* spp.) and moss (*Polytrichum* spp.) on rock barrens, and the time of year growth primarily occurs. Net ecosystem productivity (NEP) was significantly greater in the wet period of the growing season than the dry, with an estimated difference of 0.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for lichen, 2.9  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for moss, and 2.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for a moss and lichen mix. These findings indicate that the wet portions of the growing season are critical for growth, while lichen and moss have little to no productivity during the dry period. Our results indicate that near-surface soil moisture is an indicator of the CO<sub>2</sub> exchange of lichen and moss, and this relationship varies among cover types. For the geographical regions where warm, dry conditions are expected to increase in duration and frequency with climate change, lichen and moss NEP will likely decrease, thus limiting the long-term availability of nesting habitat for turtle species-at-risk.

## KEYWORDS

*Cladonia*, *Polytrichum*, productivity, rock barrens, soil moisture, turtle habitat, turtle nesting

## 1 | INTRODUCTION

Lichen- and moss-dominated bedrock depressions and crevices within rock barrens landscapes are critical for ecosystem integrity and succession (Bowker, 2007; Lange, 2001). The initial colonization of bare rock by lichen and moss is vital for primary soil formation, the establishment of more complex vegetation, and the maintenance of open canopy habitats. These lichen- and moss-dominated areas with shallow soils also provide critical habitat for many reptile species-at-risk, including natural nesting habitat for turtles on the rock barrens

landscape (Beaudry, DeMaynader, & Hunter, 2010; Francis, Moldowan, Greischar, & Rollinson, 2019; Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014). Lichen and moss cover insulates and moderates soil temperature (Kershaw & Field, 1975; Lindo & Gonzalez, 2010; Moore, Smolarz, Markle, & Waddington, 2019) & retains soil moisture while maintaining sufficient drainage (Moore et al., 2019), therefore providing suitable soil conditions for successful egg incubation. However, lichen and moss mats are vulnerable to ecohydrological stresses from both direct (e.g., mining, road construction, and other infrastructure development) and climate-mediated

disturbance (e.g., drought and wildfire) because their relatively slow growth makes natural recovery difficult (Bowker, 2007; Smith, 1962; Smith, 2014). Knowledge of the ecohydrological controls on lichen and moss productivity and persistence is needed to inform conservation and restoration methods for these critical ecosystem components.

Rock barren vegetation is subject to harsh ecohydrological conditions including high temperatures, limited shade, and low water availability, which make it difficult for organisms to establish and for ecosystem succession to proceed (Burbanck & Platt, 1964; Keever, Oosting, & Anderson, 1951). Lichen and moss are the first to colonize open rock barrens as a result of their ability to succeed under these harsh conditions (Bowker, 2007; Keever et al., 1951; Lange, 2001). For example, crustose and foliose lichens are often the first to colonize because they can withstand high heat and low moisture, and they do not require a soil substrate (Keever et al., 1951; Lange, 2001). These pioneer lichens begin the process of breaking down the bedrock and forming mineral soil (Chen, Blume, & Beyer, 2000; Jackson, 2015). Subsequently, fruticose lichens, such as *Cladonia* spp., establish and begin to accumulate soil by contributing decaying organic matter (Keever et al., 1951), trapping soil particles (Burbanck & Platt, 1964), and weathering the bedrock (Jackson, 2015). With a growth rate of approximately 5 mm per year, lichens are relatively slow growing (Smith, 1962), and their growth is controlled by their metabolic response to ecohydrological conditions (e.g. water content, temperature, and light; Baldauf, de Guevara, Maestre, & Tietjen, 2018; Lange, 2001; Lechowicz, 1978; Sveinbjornsson & Oechel, 1983). Due to these ecohydrological controls and a low chlorophyll content, the photosynthetic rates of lichens are slower than more complex vegetation (Smith, 1962). Lichen photosynthesis and respiration will only occur when water is available (Baldauf et al., 2018; Lange, 2001), and as such, water content is critical in determining metabolic rates and where lichens are able to establish on a landscape (Lange, 2001; Smith, 1962). This is especially important for rock barrens where limited depression storage under lichen and moss mats and the fill-and-spill hydrological behaviour of these landscapes (Spence & Woo, 2002) have the potential to drive strong wet and dry period transitions. Temperature is another important control on lichen metabolic activity, although this remains understudied (Kershaw & Field, 1975; Lange, 2001).

The branched morphology of fruticose lichens means that moss spores can be trapped within the lichen mat, with this mat also providing the appropriate microclimate conditions for the growth of mosses, such as *Polytrichum* spp. (Burbanck & Platt, 1964; Shure & Ragsdale, 1977). Once established, mosses can further facilitate soil accumulation (Burbanck & Platt, 1964; Jackson, 2015) and moderate temperature and moisture conditions (Burbanck & Platt, 1964; Keever et al., 1951). The metabolic activity of *Polytrichum* spp. is controlled by water, light, and nutrient availability (Turetsky, 2003; Vitt, 1990; Zotz & Kahler, 2007). Similar to lichens, *Polytrichum* spp. relies more heavily on precipitation as a direct water source compared with vascular vegetation (Anderson & Bourdeau, 1955; Bayfield, 1973). Nonetheless, *Polytrichum* has the ability to transport water through internal

and external mechanisms from water stored in the near-surface soil. When water is unavailable or limited, *Polytrichum* leaves will adhere to the stem to reduce water loss (Anderson & Bourdeau, 1955; Bayfield, 1973; Corradini & Clément, 1999). As with lichens, moss is able to recover from desiccation, which means that growth can take place in the wetter spring and fall periods and is often limited in the drier summer (Corradini & Clément, 1999).

Lichens and mosses are the dominant cover type on the rock barrens of the Canadian Shield in eastern Georgian Bay, in Ontario, Canada, but the ecohydrological controls on their CO<sub>2</sub> exchange have not previously been examined. While the eastern Georgian Bay region is less developed than other parts of Ontario (Chow-Fraser, 2006; Cvetkovic & Chow-Fraser, 2011), increasing land use change (Baxter-Gilbert, Riley, Lesbarrères, & Litzgus, 2015; Walton & Villeneuve, 1999) will impact lichen and moss mats through altered hydrological flow paths and physical destruction. Furthermore, climate change is expected to impact lichen and moss mats in eastern Georgian Bay rock barrens through decreased productivity as a result of increasing frequency and duration of drought conditions (Croley, 1990; Mortsch et al., 2000; Price et al., 2013; Trenberth, 2011) and increasing risk of wildfire (Braun, Jones, Lee, Woolford, & Wotton, 2010; Wotton, Flannigan, & Marshall, 2017). These threats can have additional impacts on at-risk turtle species as they rely on lichen- and moss-dominated bedrock depressions and crevices for critical natural nesting habitat (Francis et al., 2019; Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014).

The objective of this research was to assess the primary ecohydrological controls (e.g., temperature, soil moisture, and relative humidity) on productivity and respiration for rock barren lichen and moss in order to advance our understanding of how they establish and persist on the landscape under varying conditions. We hypothesized that lichen and moss net ecosystem production (NEP) would be significantly greater in the wetter period of the growing season (spring and fall) than the drier period (summer). We also predicted that near-surface soil moisture and air temperature would be important indicators of the CO<sub>2</sub> exchange of lichen and moss mats on the rock barrens landscape.

## 2 | METHODS

### 2.1 | Study area

The eastern Georgian Bay region of Ontario, Canada, is characterized by wetlands and rock barrens, which provide unique ecosystems and habitat for species-at-risk. The Canadian Shield granitic bedrock of this region has an undulating surface with a pattern of valleys and uplands (Crins, Gray, Uhlig, & Wester, 2009). The valleys contain large wetland complexes and beaver ponds, whereas the uplands are dominated by lichen and moss mats, ephemeral wetlands, and smaller permanent wetlands. Wetlands on the landscape are primarily dominated by *Sphagnum* spp. and a variety of vascular vegetation including, but not limited to, leatherleaf (*Chamaedaphne calyculata*), jack pine (*Pinus*

*banksiana*), tamarack (*Larix laricina*), and sedges (*Carex* spp.). The upland bedrock is a non-uniform surface where small depressions and crevices in the rock have formed as a result of mechanical and chemical erosion (Fitzsimons & Michael, 2017). It is these shallow depressions and crevices that provide natural nesting habitat for turtle species-at-risk in the eastern Georgian Bay region (e.g., Francis et al., 2019; Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014). These upland rock barrens are dominated by lichen (*Cladonia* spp.), moss (*Polytrichum* spp.), blueberry (*Vaccinium angustifolium*), juniper (*Juniperus communis*), and jack pine (*P. banksiana*). Shallow soils on the rock barrens landscape have an average bulk density of  $781 \pm 18 \text{ kg m}^{-3}$  and an average organic matter content of  $12 \pm 0.5\%$ . The soils are similar under lichen ( $754 \pm 27 \text{ kg m}^{-3}$ ,  $11.7 \pm 1.0\%$ ) and moss ( $722 \pm 30.4 \text{ kg m}^{-3}$ ,  $14.2 \pm 1.1\%$ ; Sandler, unpublished data).

The region has a cool-temperate and humid climate with 26-year daily average maximum and minimum air temperatures for May–October of  $18.9^\circ\text{C}$  and  $6.9^\circ\text{C}$ , respectively (Dunchurch station, ~45 km NE from site; Government of Canada, 2019). In 2019, the average air temperature from May to October was  $15.2^\circ\text{C}$ , with a maximum of  $33^\circ\text{C}$  and a minimum of  $-1.4^\circ\text{C}$ . The 26-year average cumulative rainfall from May to October is 563 mm (Government of Canada, 2019), and in 2019, the region received 531 mm in that period. The region exhibits seasonal variation in precipitation, where the 26-year average precipitation for May–June is 167.9 mm, July–August is 166.7 mm, and September–October is 224.6 mm (Government of Canada, 2019).

## 2.2 | Production (CO<sub>2</sub> exchange)

We selected three lichen (*Cladonia* spp.), three mixed (*Cladonia* spp. and *Polytrichum* spp.), and three moss (*Polytrichum* spp.) plots in a confirmed turtle nesting area to assess ecohydrological controls on lichen and moss productivity and respiration. These plots were selected on lichen and moss mats, which were approximately  $1 \text{ m}^2$  and had minimal vascular plant cover (<30%). The mean soil depth was 9.4 cm, and the mean height of the lichen and moss above the surface was 4.6 cm. To ensure all plots could be considered potential turtle nesting habitat, average soil depth ranged from 8 to 15 cm (Markle, Wilkinson, & Waddington, 2020), and canopy openness was  $\geq 65\%$  (e.g., Riley, Freedberg, & Litzgus, 2014, Markle unpublished data).

Between May and October 2019, we measured CO<sub>2</sub> exchange at the nine plots using a closed dynamic chamber (diameter = 10 cm, height = 15 cm, volume = 1.18 L) and an infrared gas analyser (EGM-5, PP Systems, Massachusetts, USA) on permanent circular PVC collars (diameter = 10 cm, height = 15 cm). We measured the change in CO<sub>2</sub> concentration within the chamber over a 90-s period. CO<sub>2</sub> and photosynthetic photon flux density (PPFD;  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) were recorded every 5 s for 90 s. PPFD was measured using a quantum meter (MQ-200, Apogee Instruments, Utah, USA). Measurements were taken under full, dark, and half-light conditions using no shroud, opaque, or sheer shrouds, respectively. Chamber temperature and

relative humidity were measured every 10 s using an iButton (Type 23, Alpha Mach, Quebec, Canada). At each plot, measurements were taken on 41 different days between 8:00 and 16:00 from May 8 to October 17, 2019.

We calculated CO<sub>2</sub> flux using a linear regression of the change in CO<sub>2</sub> concentration over the measurement period as a function of chamber volume and collar area (Pirk et al., 2016). Measurements with an  $R^2$  value less than 0.5 were checked for error and removed if necessary (13% of measurements removed; cf. Harris, Moore, Roulet, & Pinsonneault, 2018). NEP was defined as the sum of ecosystem respiration (ER) and gross primary productivity (GPP). Here, we use the sign convention where a positive CO<sub>2</sub> flux represents uptake by the lichen and moss, and a negative flux represents a release of CO<sub>2</sub> to the atmosphere. ER was calculated from the CO<sub>2</sub> flux under dark conditions. GPP was calculated by subtracting ER from NEP. Negative GPP values were removed (31 of 358 measurements). We used SigmaPlot (V.14, Systat Software Inc.) to fit a rectangular hyperbola model to compare the GPP–PPFD relationship between cover type and season (Bubier, Crill, Moore, Savage, & Varner, 1998; Frolking et al., 1998). For each curve, we determined the initial slope ( $\alpha$ ) and asymptote (GPP<sub>max</sub>) parameters.

## 2.3 | Decomposition

To estimate the decay rates of lichen, moss, and soil, samples were collected in spring 2015. Lichen and moss samples were cleaned of external litter and soil and then all samples were dried, weighed, and placed into pre-sown  $10 \times 12 \text{ cm}$  nylon mesh litter bags (mesh size  $300 \mu\text{m}$ ). Litter bags containing ~3 g (dry weight) of lichen (*Cladonia* spp.;  $n = 42$ ), moss (*Polytrichum* spp.;  $n = 78$ ), or soil ( $n = 38$ ) were buried in the same material they were extracted from with lichen (moss) litter bags at a depth of 1 cm in lichen (moss) mats and soil litter bags 1 cm below the lichen/moss cover in June 2015. In June 2016, 109 of the litter bags were collected and weighed to determine the decomposition of the lichen, moss, and soil during this time period (12 months). The remaining 49 litter bags were collected in June 2017, to estimate decomposition over a 24-month period. We calculated decay constants using an exponential decay model (e.g., Moore et al., 2017; Olson, 1963).

## 2.4 | Near-surface soil moisture and temperature

Continuous near-surface soil volumetric water content (VWC) and temperature (hereafter referred to as soil VWC and soil temperature, respectively) were measured at a depth of 5 cm at all nine NEP (CO<sub>2</sub> exchange) plots during the 2019 growing season (May 8–October 17). Soil VWC was measured at a depth of 5 cm every 15 min using a HOBO soil moisture smart sensor inserted horizontally (5-cm probe length, 0.3-L volume of influence, Onset HOBO S-SMxpM005, Massachusetts, USA) and logged using a HOBO Micro Station data logger

(Onset HOB0 H21-USB). Soil VWC probes were calibrated for eastern Georgian Bay rock barrens soils according to Starr and Paltineanu (2002). While we did not take discrete destructive measurements of lichen and moss gravimetric water content (GWC) for this study due to the impact on nesting habitat, we use the VWC of the underlying soil as an indicator for the moisture conditions of the lichen and moss (Figure S1). Soil temperature was measured hourly using an iButton (iBWetland Type G), and data were interpolated to 15-min intervals to align with the VWC measurements. Air temperature, precipitation, and relative humidity were measured every 30 min at a meteorological station within 100 m of the sites.

## 2.5 | Analyses

We conducted all statistical analyses in R 3.6.1 (R Core Team, 2019). We used a breakpoint analysis of cumulative rainfall (Figure S2) to define a wet and dry period within the study duration (May 8–October 17, 2019). Using this approach, we defined the wet season as the start of data collection (May 8) to June 24 and September 1 to the end of data collection (October 17). The dry season began June 25 and ended August 31. We grouped spring and fall into a single wet season because we had a limited sample size for spring (10 days) and fall (7 days) individually, in comparison with the summer season (24 days).

To determine if mean daily soil temperatures, NEP ( $n = 358$ ), ER ( $n = 358$ ), and GPP ( $n = 327$ ), were different between season (wet and dry) and among cover types (lichen, mixed, and moss), we fit a linear mixed effects model (LMM; *lme4*, Bates, Maechler, Bolker and Walker, 2015) with plot number as a random effect to account for repeated measurements. We fit a generalized linear mixed effects model (GLMM, gamma distribution and log link; *lme4*, Bates et al., 2015) to compare mean daily soil VWC (values ranged between 0 and 1) with season (wet and dry) and cover type (lichen, mixed, and moss) as fixed effects and plot number as a random effect to account for repeated measurements. We used Kruskal–Wallis and Wilcoxon tests to identify significant differences in lichen, moss, and soil decomposition.

In order to determine which ecohydrological factors had the greatest effect on the fluxes, we used LMMs. The NEP, ER, and GPP data were approximately normally distributed, and the Q–Q plots followed the straight line reasonably well. Generalized variance inflation factors for all fixed effects were less than 3; therefore, no parameters were excluded based on multicollinearity. We tested LMMs with a combination of cover type (lichen, mixed, and moss), soil VWC, soil temperature, air temperature, and air relative humidity, as fixed effects, and included plot number as a random effect to account for repeated measures. The models were fit using maximum likelihood and compared using an analysis of variance (ANOVA). To select the best model, we considered the Akaike's information criterion, correlation of fixed effects, relative size of the estimates, and covariance of fixed effects. Unless otherwise stated, standard errors are reported.

## 3 | RESULTS

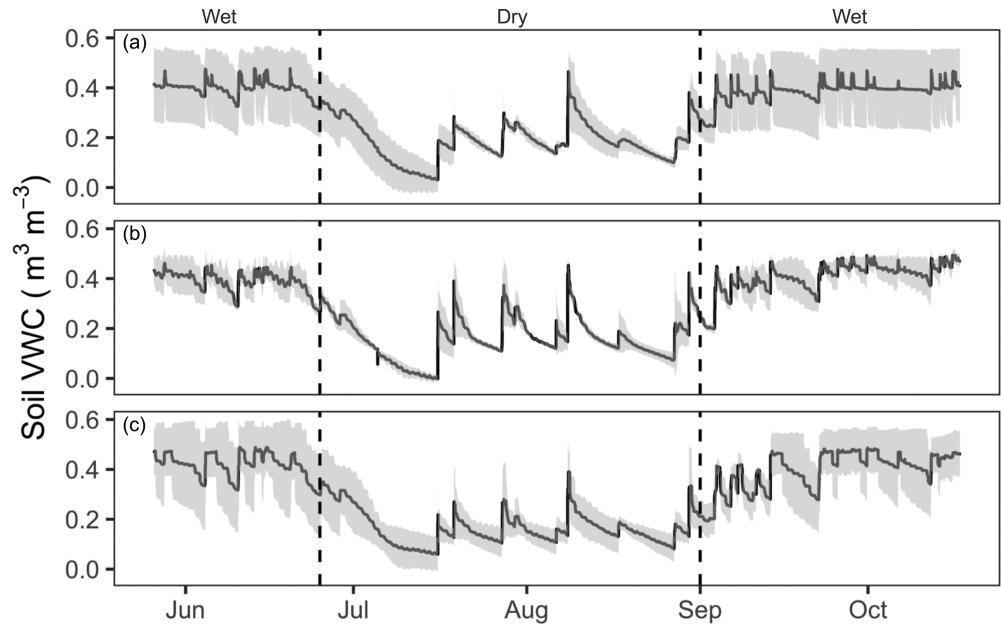
### 3.1 | Near-surface soil moisture and temperature

From May to June and September to October, the soil VWC was consistently higher than July–August (Figure 1). In July and August, soil VWC declined overall with peaks during rainfall followed by rapid drying (Figure 1). The soil VWC ranged from 0.12 to 0.58  $\text{m}^3 \text{m}^{-3}$  in the wet period (May 8–June 24, September 1–October 17) and from 0 to 0.48  $\text{m}^3 \text{m}^{-3}$  in the dry period (June 25–August 31). Soil VWC in the wet period was double the VWC in the dry period with a daily mean VWC of  $0.40 \pm 0.1 \text{m}^3 \text{m}^{-3}$  standard deviation in the wet season and  $0.17 \pm 0.09 \text{m}^3 \text{m}^{-3}$  standard deviation in the dry season (GLMM, estimate [est.] =  $0.8 \pm 0.02$ ,  $t = 35.5$ ,  $p \leq .001$ ). During both seasons, soil VWC was comparable between lichen and mixed (GLMM, est. =  $0.01 \pm 0.17$ ,  $t = 0.09$ ,  $p = .92$ ) and between lichen and moss plots (GLMM, est. =  $0.02 \pm 0.17$ ,  $t = 0.11$ ,  $p = .91$ ). Furthermore, soil VWC did not differ between mixed and moss plots (GLMM, est. =  $0.002 \pm 0.12$ ,  $t = 0.02$ ,  $p = .99$ ). Between May 8 and October 17, the soil temperature was cooler in the wet periods (May–June and September–October) and warmer in the dry period (July–August; Figure 2). Daily average soil temperature, at a depth of 5 cm, was approximately 8°C cooler in the wet period than the dry period (LMM, est. =  $-7.95 \pm 0.15$ ,  $t = -51.06$ ,  $p \leq .001$ ) with a mean of  $15.9 \pm 3^\circ\text{C}$  standard deviation and  $23.8 \pm 2.6^\circ\text{C}$  standard deviation, respectively. Across both periods, the daily average soil temperature did not differ between lichen and mixed plots (LMM, est. =  $0.61 \pm 0.43$ ,  $t = 1.41$ ,  $p = .22$ ). The moss plots had a cooler mean soil temperature than lichen by 1.3°C (LMM, est. =  $-1.27 \pm 0.43$ ,  $t = -2.92$ ,  $p = .03$ ) and mixed plots by 1.9°C (LMM, est. =  $-1.88 \pm 0.42$ ,  $t = -4.47$ ,  $p = .01$ ).

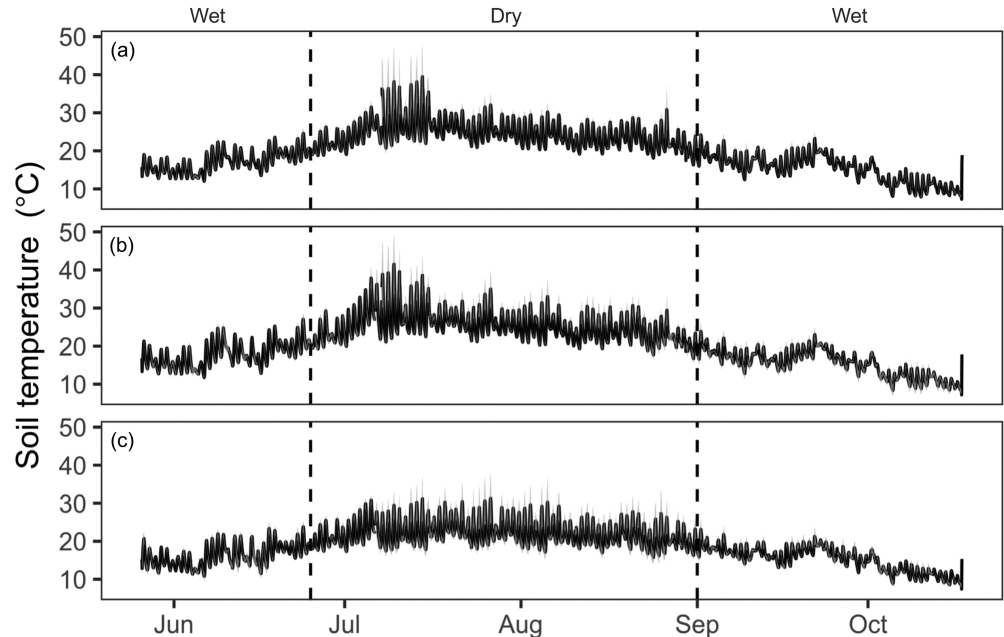
### 3.2 | Production (CO<sub>2</sub> exchange)

The total mean NEP was greater in the wet season than the dry season for all cover types (Figure 3), with an estimated difference (wet vs. dry) in NEP of  $0.7 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  for lichen (LMM,  $t = 5.1$ ,  $p \leq .001$ ),  $2.5 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  for mixed (LMM,  $t = 11.7$ ,  $p \leq .001$ ), and  $2.9 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  for moss (LMM,  $t = 9.95$ ,  $p \leq .001$ ). The ER of lichen plots was not significantly different between wet and dry seasons, with a difference of  $0.09 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 0.9$ ,  $p = .37$ ; Figure 3). For mixed plots and moss plots, the ER was greater in the wet season than the dry season, with a difference of  $0.5 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  for mixed plots (LMM,  $t = -3.25$ ,  $p \leq .001$ ) and  $0.7 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  for moss plots (LMM,  $t = -3.8$ ,  $p \leq .001$ ; Figure 3). All cover types had a greater mean GPP in the wet season than the dry season, where lichen differed by  $0.5 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 3.6$ ,  $p \leq .001$ ), mixed by  $2.7 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 8.31$ ,  $p \leq .001$ ), and moss by  $3.2 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 7.6$ ,  $p \leq .001$ ; Figure 3). In addition, between both seasons, the CO<sub>2</sub> fluxes differed among cover types (Figure 3). Mixed and moss plots had a  $1.6 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 4.4$ ,  $p \leq .001$ ) and

**FIGURE 1** Mean soil volumetric water content (VWC;  $\text{m}^3 \text{m}^{-3} \pm$  standard deviation) measured every 15 min, at a depth of 5 cm, from May to October 2019 at lichen (a,  $n = 3$ ), mixed (b,  $n = 3$ ), and moss plots (c,  $n = 3$ ). Dashed lines denote the wet (May 8–June 24; September 1–October 17) and dry (June 25–August 31) seasons as determined by a breakpoint analysis of cumulative rainfall (Figure S2)



**FIGURE 2** Mean soil temperature ( $^{\circ}\text{C} \pm$  standard deviation) measured hourly and interpolated to every 15 min, at a depth of 5 cm, from May to October 2019 at lichen (a,  $n = 2$ ), mixed (b,  $n = 3$ ), and moss plots (c,  $n = 3$ ). Dashed lines denote the wet (May 8–June 24; September 1–October 17) and dry (June 25–August 31) seasons as determined by a breakpoint analysis of cumulative rainfall (Figure S2)



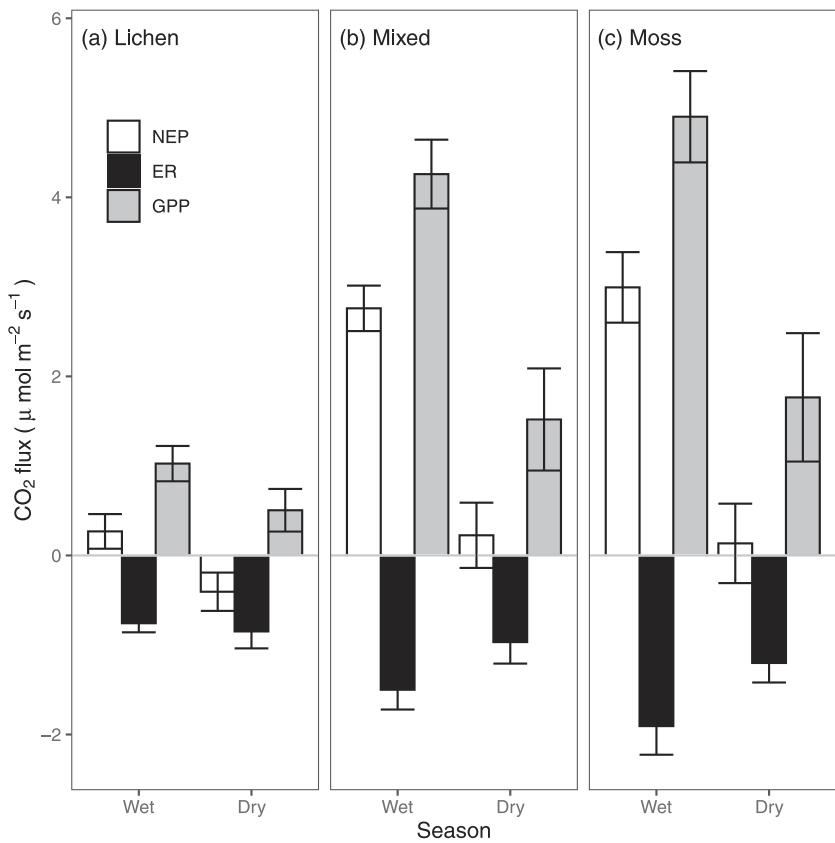
$1.4 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 3.91$ ,  $p \leq .001$ ) difference in NEP, respectively, compared with lichens. Mixed ER was greater than lichen by  $0.4 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = -3.5$ ,  $p \leq .001$ ), and moss ER was greater than lichen by  $0.7 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = -5.63$ ,  $p \leq .001$ ). Finally, mixed plots had a difference in GPP of  $2.3 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 5.73$ ,  $p \leq .001$ ), and moss had a difference of  $2.5 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 6.23$ ,  $p \leq .001$ ) when compared with lichen plots. Mixed and moss plots did not have significantly different NEP, ER, or GPP (Figure 3).

The GPP–PPFD relationship had a worse fit under dry conditions compared with wet conditions for all cover types (Figure 4). During the wet period, the lichen plots had a smaller initial slope and

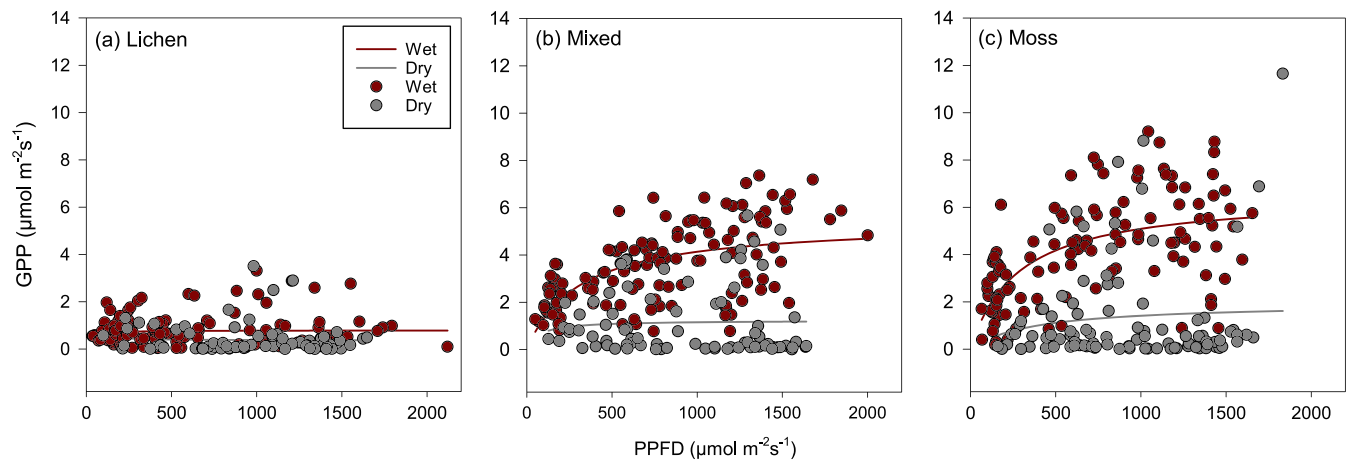
maximum GPP ( $\alpha = 20.3$ ,  $\text{GPP}_{\text{max}} = 0.79$ ) than both mixed ( $\alpha = 307.14$ ,  $\text{GPP}_{\text{max}} = 5.41$ ) and moss ( $\alpha = 281.0$ ,  $\text{GPP}_{\text{max}} = 6.52$ ). Under dry conditions, lichen maintained a smaller initial slope and maximum GPP ( $\alpha = -44.72$ ,  $\text{GPP}_{\text{max}} = 0.37$ ) than mixed ( $\alpha = 69.1$ ,  $\text{GPP}_{\text{max}} = 1.24$ ) and moss plots ( $\alpha = 372.42$ ,  $\text{GPP}_{\text{max}} = 1.94$ ).

### 3.3 | Ecohydrological controls

Cover type, soil VWC, and their interaction had the greatest effect on NEP, ER, and GPP (Table S1). The slope of the predicted response of NEP to increasing soil VWC was greater by  $7.1 \pm 1.2$  (LMM,  $t = 5.96$ ,



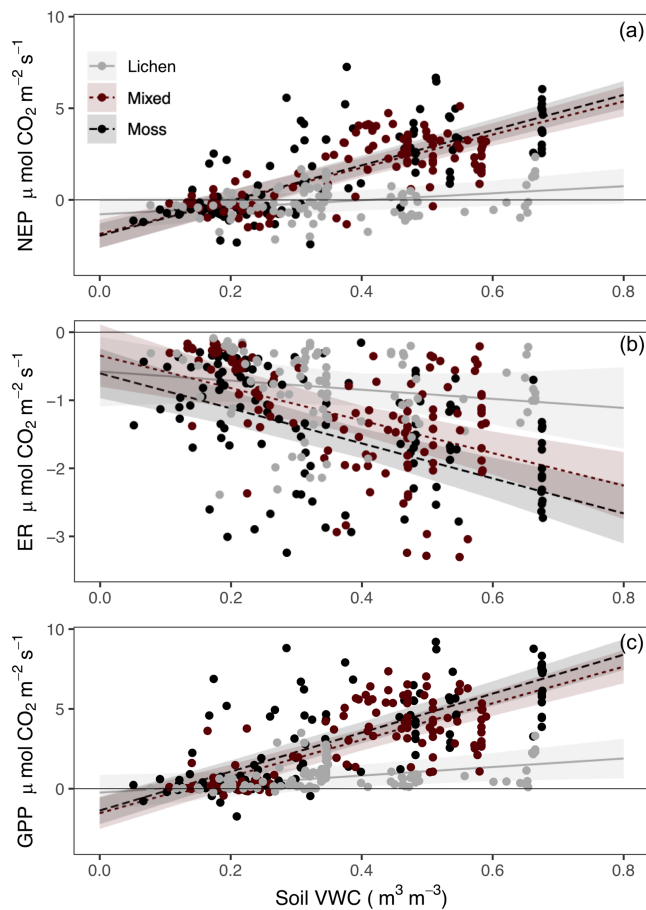
**FIGURE 3** Mean net ecosystem production (NEP), ecosystem respiration (ER), and gross primary productivity (GPP) fluxes ( $\pm 95\%$  confidence intervals) for lichen (a), mixed (b), and moss (c) plots in the wet (lichen  $n = 59$ , mixed  $n = 63$ , moss  $n = 58$ ) and dry (lichen  $n = 49$ , mixed  $n = 55$ , moss  $n = 74$ ) periods from May 8 to October 17, 2019. GPP sample size differed from NEP and ER for the wet (lichen  $n = 59$ , mixed  $n = 63$ , moss  $n = 58$ ) and dry (lichen  $n = 44$ , mixed  $n = 44$ , moss  $n = 59$ ) periods after removal of negative values



**FIGURE 4** Relationship between incoming photosynthetic photon flux density (PPFD,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and gross primary productivity (GPP,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) for lichen (a) during the wet (red line,  $n = 125$ ,  $\alpha = 20.3$ ,  $\text{GPP}_{\text{max}} = 0.79$ ,  $R^2 = 0.006$ ) and dry season (grey line,  $n = 82$ ,  $\alpha = -44.72$ ,  $\text{GPP}_{\text{max}} = 0.37$ ,  $R^2 = 0.004$ ), mixed (b) during the wet (red line,  $n = 122$ ,  $\alpha = 307.14$ ,  $\text{GPP}_{\text{max}} = 5.41$ ,  $R^2 = 0.3$ ) and dry season (grey line,  $n = 79$ ,  $\alpha = 69.1$ ,  $\text{GPP}_{\text{max}} = 1.24$ ,  $R^2 = 0.003$ ), and moss (c) during the wet (red line,  $n = 113$ ,  $\alpha = 281.02$ ,  $\text{GPP}_{\text{max}} = 6.52$ ,  $R^2 = 0.4$ ) and dry season (grey line,  $n = 97$ ,  $\alpha = 372.42$ ,  $\text{GPP}_{\text{max}} = 1.94$ ,  $R^2 = 0.01$ ). GPP and PPFD calculated from field CO<sub>2</sub> and PPFD measurements for lichen (a), mixed (b), and moss (c) during the wet (red points) and dry (grey points) periods

$p \leq .001$ ) for mixed than lichen,  $7.7 \pm 1.1$  (LMM,  $t = 6.92$ ,  $p \leq .001$ ) for moss than lichen, and  $0.6 \pm 1.1$  (LMM,  $t = 0.56$ ,  $p = .58$ ) for moss than mixed (Figure 5). The predicted response of ER to increasing soil VWC had a greater slope of  $-1.7 \pm 0.8$  (LMM,  $t = -2.06$ ,  $p = .041$ ) for mixed when compared with lichen,  $-1.9 \pm 0.8$  (LMM,  $t = -2.46$ ,  $p = .02$ ) for moss when compared with lichen, and of  $-0.2 \pm 0.8$  (LMM,  $t = -0.24$ ,

$p = .81$ ) for moss when compared with mixed (Figure 5). The slope of the predicted response of mixed GPP to increasing soil VWC was greater than that of lichen by  $8.8 \pm 1.6$  (LMM,  $t = 5.65$ ,  $p \leq .001$ ), moss was greater than lichen by  $9.5 \pm 1.4$  (LMM,  $t = 6.58$ ,  $p \leq .001$ ), and moss was greater than mixed by  $0.75 \pm 1.4$  (LMM,  $t = 0.52$ ,  $p = .60$ ; Figure 5).



**FIGURE 5** Predicted response of (a) net ecosystem production (NEP), (b) ecosystem respiration (ER), and (c) gross primary productivity (GPP) to increasing soil volumetric water content (VWC;  $\text{m}^3 \text{m}^{-3} \pm 95\%$  confidence intervals) according to the linear mixed effects models for lichen (grey solid line), mixed (red dotted line), and moss (black dashed line). NEP (a), ER (b), and GPP (c) calculated from field  $\text{CO}_2$  measurements for lichen (grey points), mixed (red points), and moss plots (black points)

### 3.4 | Decomposition

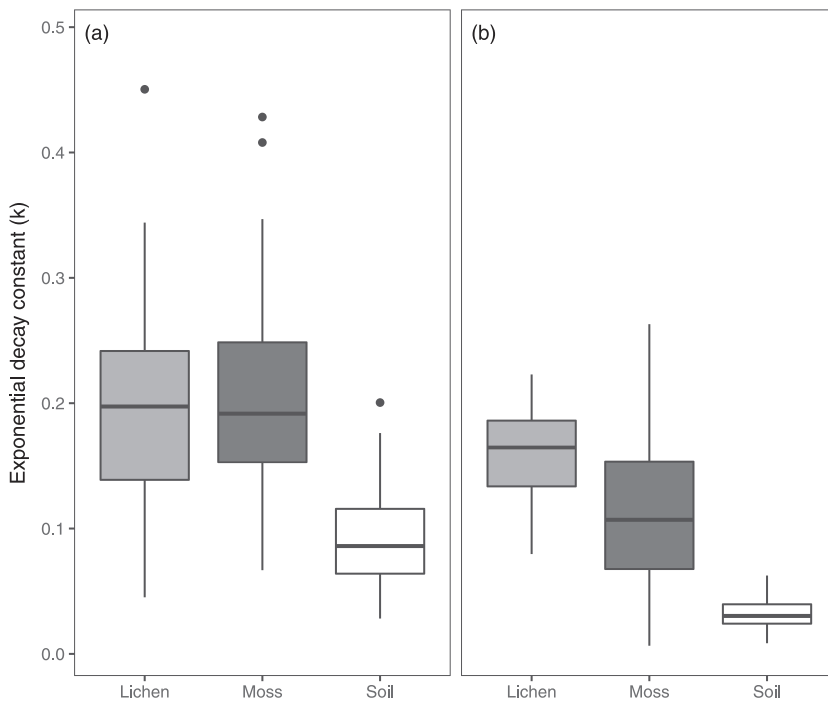
After 1 year of litter bag incubation, the exponential decay constant was not significantly different between cover types ( $\chi^2_{1,79} = 0.24$ ,  $p = .62$ ; Figure 6), where lichen had a mean decay constant of  $0.20 \pm 0.02$  and moss had a mean decay constant of  $0.21 \pm 0.01$ . Conversely, the lichen litter bags that were removed after 2 years ( $0.16 \pm 0.01$ ) had a significantly greater exponential decay constant than the moss litter bags removed after 2 years ( $0.12 \pm 0.01$ ;  $\chi^2_{1,41} = 5.21$ ,  $p = .02$ ; Figure 6). The decay constants of lichen litter bags removed after 1 ( $0.20 \pm 0.02$ ) and 2 years ( $0.16 \pm 0.01$ ) were not significantly different ( $\chi^2_{1,42} = 2.15$ ,  $p = .14$ ; Figure 6). The moss litter bags removed after 1 year ( $0.21 \pm 0.01$ ) had a greater decay constant than the bags removed after 2 years ( $0.12 \pm 0.01$ ;  $\chi^2_{1,78} = 21.7$ ,  $p < .01$ ; Figure 6). Soil litter bags had a mean decay constant of  $0.09 \pm 0.01$  after 1 year of incubation, and the mean decay constant

was  $0.03 \pm 0.005$  after 2 years of incubation ( $\chi^2_{1,38} = 14.13$ ,  $p < .01$ ; Figure 6). Following 1 year of incubation, soil had a significantly lower decay constant than both lichen ( $W = 766$ ,  $p < .001$ ) and moss ( $W = 1,445$ ,  $p < .001$ ). After 2 years of incubation, the decay constants of soil remained significantly lower than lichen ( $W = 112$ ,  $p < .001$ ) and moss ( $W = 199$ ,  $p < .001$ ).

## 4 | DISCUSSION

We determined that the wetter portion of the growing season (May–June and September–October; Figure 1) was critical for  $\text{CO}_2$  uptake by lichen and moss on the rock barrens landscape. The differences in  $\text{CO}_2$  fluxes between seasons indicate that the wet periods of the growing season (spring and fall) are critical for lichen and moss growth on the rock barrens landscape, while there is no growth in the dry period (summer; Figure 3). Furthermore, we determined that soil moisture is an important indicator of the  $\text{CO}_2$  fluxes of lichen and moss (Figure 5), which suggests that lichen and moss will become less productive if the proportion of warm and dry conditions increases relative to cool and wet conditions as a result of climate change in the eastern Georgian Bay region (d'Orgeville, Peltier, Erler, & Gula, 2014; Mortsch et al., 2000; Notaro, Bennington, & Lofgren, 2015).

Our findings highlight the unique water storage dynamics of lichen and moss on rock barrens landscapes. Vascular plants and *Sphagnum* moss in peatlands (Bubier et al., 1998; Carroll & Crill, 1997; Frohling et al., 1998) and forest floor species (Botting & Fredeen, 2006; Swanson & Flanagan, 2001) are able to maintain productivity throughout the growing season if water remains available. However, rock barren depressions have limited water storage capacity, and the lichen and moss have a high dependence on summer precipitation, whereas moss and lichen in peatlands and forests benefit from higher water storage capacity and more favourable climate conditions in these ecosystems. Timing of peak productivity for lichen and moss on rock barrens is more similar to cryptogams in desert ecosystems, where peak NEP is directly tied to precipitation (Kappen & Valladares, 1999). Our results confirm that the wet season (spring and fall) is critical for the productivity of lichen and moss on the rock barrens landscape. Previous research has shown that the ability of lichen and moss to recover from desiccation allows them to have two growth periods in a year (Corradini & Clément, 1999). Studies from other landscapes have found that fall can be a period of peak productivity, and summer can be a period of limited  $\text{CO}_2$  uptake (Heijmans, Arp, & Chapin, 2004; Kappen & Valladares, 1999; Lange, 2003; Zotz & Rottenberger, 2001), and this is supported by our findings from the eastern Georgian Bay rock barrens. Lange (2003) found lichens to have longer metabolically active periods in the autumn and shorter periods in the summer and winter. Similarly, Zotz and Rottenberger (2001) studied three species of moss (*Grimmia pulvinata*, *Schistidium apocarpum*, and *Tortula ruralis*) and found that  $\text{CO}_2$  exchange was largely seasonal, with the highest uptake in fall and neutral  $\text{CO}_2$  exchange in the summer.



**FIGURE 6** Exponential decay constants between (a) 2015–2016 and (b) 2015–2017 for lichen (2016,  $n = 28$ ; 2017,  $n = 14$ ), moss (2016,  $n = 51$ ; 2017,  $n = 27$ ), and soil (2016,  $n = 30$ ; 2017,  $n = 8$ )

In our study area of eastern Georgian Bay, air temperature and precipitation are expected to increase with climate change (d'Orgeville et al., 2014; Mortsch et al., 2000; Notaro et al., 2015). With warmer temperatures, evaporation and evapotranspiration are predicted to increase, and snowpack is expected to decline, which together will result in overall drier conditions (Croley, 1990; Mortsch et al., 2000; Notaro et al., 2015; Price et al., 2013; Trenberth, 2011). The warm dry conditions, which are characteristic of summer months (July and August; Figures 1 and 2) in the northern hemisphere, are beginning earlier and finishing later in the year (Trenberth et al., 2007; Vrac, Vaittinada Ayar, & Yiou, 2014; Walther et al., 2002). Furthermore, drought frequency and severity are expected to increase (Dai, Trenberth, & Qian, 2004; Trenberth et al., 2007). As our findings illustrate, dry conditions can result in smaller uptake or a net loss of  $\text{CO}_2$  for lichens and a lower or neutral  $\text{CO}_2$  uptake for moss and mixed plots. Given our results, we would expect that an increase in air temperatures and a decrease in water availability will lead to a decline in lichen and moss productivity on the eastern Georgian Bay rock barrens. The seasonal trends in the lichen and moss  $\text{CO}_2$  exchange suggest that lichens are more sensitive than mosses to low moisture conditions, and as a result, the decline in productivity would not be equal between cover types.

The seasonal pattern in  $\text{CO}_2$  exchange that we found can be largely explained by the fact that lichen and moss productivity on the rock barrens landscape was correlated with cover type and soil VWC (Figure 5). As expected, the predicted response of NEP, ER and GPP to changes in soil VWC differs between lichen, mixed, and moss mats (Figure 5). Our results show a weak relationship of lichen NEP and GPP to increasing soil VWC. While moisture content of the underlying soil is not expected to directly influence photosynthesis in the upper part of the lichen mats, it is nonetheless indicative of lichen moisture

status due to the shallow nature of the depressions and responsiveness of moisture content to rainfall and evaporative demand. The  $\text{CO}_2$  flux response of mixed and moss to increasing soil VWC is greater than lichen; however, the mixed and moss plots do not differ from each other (Figure 5; Table S1). Our findings are supported by previous studies that show that lichens have slower carbon assimilation rates relative to mosses and vascular plants (Smith, 1962) and that mosses are able to transport water to their upper photosynthetically active surface (Bayfield, 1973; Moore et al., 2019). These model results are further supported by our analysis of the GPP-PPFD relationship, which illustrates lichens' lower light-use efficiency when compared with mixed and moss plots (Figure 4). The GPP-PPFD relationship also highlights the importance of the wet period of the growing season for lichen and moss GPP (Figure 4). While we have found that soil VWC is an important indicator of the  $\text{CO}_2$  fluxes of lichen and moss, we acknowledge that we have not included data for the gravimetric moisture content of the lichen and moss, which is a known important controlling factor (e.g., Lange, 2001; Lechowicz, 1978; Lechowicz, 1982). However, Figure S1 demonstrates that soil VWC can be used as an indicator of the lichen and moss moisture content.

Climate change is expected to alter moisture conditions globally, and as such, we can expect that the  $\text{CO}_2$  fluxes of lichen and moss will also change (Baldauf et al., 2018; Grote, Belnap, Housman, & Sparks, 2010). On the rock barrens, this shift will be exacerbated by the limited water storage capacity of bedrock crevices (Spence & Woo, 2002). The fill-and-spill nature of the bedrock landscape leads to rapid drying and limited soil water during dry periods (Spence & Woo, 2002). Given these landscape properties and the predicted future climate conditions for the eastern Georgian Bay region, we expect lichens will have a neutral or negative NEP, whereas mosses would maintain a small positive or neutral NEP. Our findings suggest



that mosses may be able to better maintain CO<sub>2</sub> uptake in drier conditions than lichens. Consequently, as conditions become drier, the lichen mats will likely halt productivity earlier than the moss mats, reducing their annual growth. Moreover, a decline in precipitation events could further reduce the ability of lichen to recover from disturbance (Davidson, Bowker, George, Phillips, & Belnap, 2002; Smith, 2014). If lichen growth is limited, while mosses are still able to take up CO<sub>2</sub>, we may expect to see an increase in the extent of moss mats, and there would be a potential for mosses to become more dominant on the landscape. This shift could be problematic as lichens are often the first to colonize open rock and lichen mats provide suitable natural nesting habitat for turtle species-at-risk (Francis et al., 2019; Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014). In addition, lichen and moss both play a critical role in primary soil building, and a decline in metabolic activity could reduce the available soil on the landscape, further limiting suitable nesting habitat.

As lichen and moss decompose, they contribute organic matter to the soil. We found that lichen and moss decomposition did not differ following 1 year of incubation, whereas lichen decayed more rapidly than moss after 2 years (Figure 6). These results are similar to those found in the literature, where reported exponential decay constants typically range from 0.15 to 0.45 (e.g., Hagemann & Moroni, 2015; Lang et al., 2009). Our findings suggest that lichens contribute less organic matter to the soil, and combined with lichen's lower productivity, soil accumulation is likely to be slower in lichen mats than moss mats. As temperature and precipitation increase with climate change, decomposition rates are also expected to increase (Moore et al., 1999). However, this effect could be reduced on the rock barrens, where the soil deposits have a limited water storage capacity and the predicted increase in precipitation will be offset by the increase in evaporation and evapotranspiration, decline in snowpack, and increase in drought severity. As the temperature and moisture conditions shift with climate change and the decomposition rates of lichen and moss vary, the amount of organic matter contributed to the soil will also shift.

#### 4.1 | Implications for turtle nesting habitat

The variation in CO<sub>2</sub> response in wet and dry periods for the different cover types is important to consider under future climate scenarios and with regard to turtle species-at-risk habitat. While lichens and mosses respond differently to fewer precipitation events, CO<sub>2</sub> exchange will likely be reduced for both, and this has implications for primary soil formation on the rock barrens landscape. On granitic bedrock, lichens and mosses significantly increase the rate of chemical weathering and soil formation, but this is driven by their metabolic activity (Chen et al., 2000; Gehrmann, Krumbein, & Petersen, 1988; Jackson, 2015). A decline in metabolic activity with climate change would reduce both chemical weathering of bedrock and organic soil accumulation. A decrease in soil formation on the landscape would

hinder establishment of vascular vegetation and limit development of deeper soils required for turtle nesting sites. The predicted increase in air temperature and decrease in water availability (Croley, 1990; d'Orgeville et al., 2014; Mortsch et al., 2000; Notaro et al., 2015), combined with the low storage capacity of shallow bedrock depressions (Spence & Woo, 2002), could limit future increases in the extent of lichen mats on rock barrens landscapes. Because lichens play a key role in moderating soil temperatures and moisture retention (Moore et al., 2019; Shure & Ragsdale, 1977), changes in mat coverage and distribution could impact the suitability of shallow soil deposits as turtle nest sites.

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#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

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

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