

ECOHYDROLOGICAL CONTROLS OF NATURAL AND RESTORED LICHEN AND  
MOSS CO<sub>2</sub> EXCHANGE ON A ROCK BARRENS LANDSCAPE

ECOHYDROLOGICAL CONTROLS OF NATURAL AND RESTORED LICHEN AND  
MOSS CO<sub>2</sub> EXCHANGE ON A ROCK BARRENS LANDSCAPE

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TITLE: Ecohydrological controls of natural and restored lichen and moss CO<sub>2</sub> exchange on a rock  
barrens landscape

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## **Abstract**

Lichen and moss are the dominant ground cover on the Canadian Shield rock barrens of eastern Georgian Bay, and they provide many ecosystem services. Lichen and moss mats are essential for developing and accumulating soil on the bedrock landscape, and as the mats establish they moderate soil temperature and reduce soil water losses, thereby improving the microclimate for more complex vegetation. In addition to pioneering ecosystem succession, the lichen and moss mats provide essential nesting habitat for turtle species-at-risk. These lichen and moss mats are not well understood on rock barrens landscapes, and as such this thesis aims to increase knowledge of the growth, persistence and restoration approaches for these valuable ecosystem resources. We quantified the ecohydrological controls on the growth of lichen and moss mats by measuring the CO<sub>2</sub> exchange of lichen and moss under varying environmental conditions. From these results we determined that key growth periods for lichen and moss were during the wet portions of the growing season (spring and fall), and that growth was limited or non-existent during the dry period (summer). Further, we determined that soil moisture was the most important control on lichen and moss CO<sub>2</sub> exchange, and that this relationship differed among cover type (lichen, moss, mix of lichen and moss). Moss was able to continue CO<sub>2</sub> uptake at a lower water content than lichen, suggesting that lichen would have a greater decline in productivity under drier conditions. A decline in lichen and moss productivity would also likely lead to a decline in soil development through chemical weathering which, in turn, could affect the availability of turtle nesting habitat. We also used CO<sub>2</sub> exchange measurements to compare lichen and moss productivity between natural and transplanted mats. Transplanting in-tact patches of lichen and moss has not been widely studied, and as such we tested this approach on a rock barrens landscape. We determined that natural and transplant productivity did not differ for lichen, and that there were some differences

between treatments for mixed and moss plots. We also used the tea bag index method to compare relative decomposition rates between treatments (natural, transplant), where we found that decomposition rates did not differ. Our results indicate that it is feasible to remove lichen mats from the footprint of a planned disturbance such as construction and transplant them successfully to nearby undisturbed areas. This approach would restore the lichen cover and the ecosystem services that lichens provide immediately rather than waiting decades for natural regrowth or fragment establishment. As a whole, this thesis will increase knowledge of both the growth and persistence, as well as the restoration of lichen and moss on rock barrens landscapes. Given that lichens and mosses of these genera grow globally, our findings can be applied widely to enhance and protect lichen and moss mats, and the ecosystem services they provide.

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### List of Abbreviations and Symbols

ANOVA	Analysis of Variance
CI	Confidence Intervals
CO <sub>2</sub>	Carbon Dioxide
k	Decomposition rate
°C	Degrees Celsius
df	Degrees of Freedom
$\Delta$	Mean difference of transplant minus natural $\pm$ confidence intervals
ER	Ecosystem Respiration
GLMM	Generalized Linear Mixed Model
GPP	Gross Primary Productivity
$\alpha$	Initial slope of the modeled GPP and PPFD curve
LMM	Linear Mixed Model
LN	Lichen Natural
LT	Lichen Transplant
GPP <sub>max</sub>	Maximum GPP for the modeled GPP and PPFD curve
MN	Mixed Natural

MoN	Moss Natural
MoT	Moss Transplant
MT	Mixed Transplant
NE	North East
NEP	Net Ecosystem Productivity
NOBEL	Northern Ontario Barrens and Bog Ecosystems Landscape
K	Percent of mass lost
PPFD	Photosynthetic Photon Flux Density
PVC	Polyvinyl Chloride
Spp.	Species
S	Stabilization factor
TBI	Tea Bag Index
USA	United States of America
VWC	Volumetric water content
$\chi^2$	Chi Square

## **Declaration of Academic Achievement**

This thesis has been prepared in the “sandwich thesis” format, where chapters two and three are independent manuscripts. Chapter one and chapter four provide a general introduction and conclusion, respectively.

### **Chapter 1: General Introduction**

Author: Danielle T. Hudson

### **Chapter 2: Ecohydrological controls on rock barrens lichen and moss CO<sub>2</sub> exchange: Implications for primary soil formation and turtle nesting habitat**

Authors: Danielle T. Hudson, Chantel E. Markle, Lorna I. Harris, and James M. Waddington

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### **Chapter 3: CO<sub>2</sub> exchange of natural and restored lichen and moss patches on a rock barrens landscape: Applications for turtle species-at-risk nesting habitat**

Authors: Danielle T. Hudson, Chantel E. Markle, and James M. Waddington

Comments: D.T.H collected and analyzed all data and wrote the manuscript under the supervision of C.E.M and J.M.W. C.E.M and J.M.W provided insight on the methodology, analysis and preparation of manuscript for submission.



## **Chapter 4: General Conclusion**

Author: Danielle T. Hudson

## **Chapter 1: General Introduction**

### Rock barrens landscapes and ecosystem succession

Rock barrens landscapes are unique ecosystems which provide specialized habitat and support a wide diversity of flora and fauna (*e.g.* Withers & Edward, 1997). These rock outcrops are geological features which were formed by glacial erosion and have since evolved into a non-uniform surface of smooth rock, shallow depressions, and deeper crevices which provide specialized microhabitat for flora and fauna (*e.g.* Withers & Edward, 1997). Rock barrens landscapes also have a fill-and-spill hydrological regime (Spence & Woo, 2002). Depressions in the bedrock, which are often overlain by lichen and moss, act as storage units for overland flow, slowing runoff and reducing downslope flooding (Spence & Woo, 2002). As a result of this hydrological regime, the lichen and moss that dominate the bedrock depressions are subject to rapid wetting and drying cycles, and soil moisture is often limited.

Given the high temperatures, low moisture availability, and high light conditions characteristic of rock barrens landscapes, the organisms that can establish on bare rock are limited (Burbanck & Platt, 1964; Keever et al., 1951). Biological soil crust organisms such as lichen, moss, and microbial communities are the first to colonize open bedrock because they are desiccation resistant and do not require soil to establish (Burbanck & Platt, 1964; Keever et al., 1951). Once lichen and moss have established, they begin to accumulate soil by chemically weathering the bedrock (Jackson, 2015), decomposing and forming organic soil (Keever et al., 1951), and trapping soil particles from the wind (Burbanck & Platt, 1964). As the lichen and moss grow and accumulate soil, they moderate the temperature and moisture conditions on the landscape (Kershaw & Field, 1975; Moore et al., 2019), thus allowing more complex vegetation to survive (Shure & Ragsdale,

1977). Over time, the organic content of the soil, the vegetation biodiversity, and the ability of the soil to hold moisture all increase (Shure & Ragsdale, 1977)

### Lichen and moss on rock barrens

Lichens are among the first organisms to colonize granitic bedrock (Keever et al., 1951; Lange, 2001), where crustose and foliose lichens arrive first, as they can withstand high heat, low moisture and do not require soil to establish (Keever et al., 1951; Lange, 2001). Next, fruticose lichens (*e.g. Cladonia* spp.) begin to form mats on the bedrock and accumulate soil (Keever et al., 1951; Lange, 2001). Lichen growth is largely governed by their metabolic response to water availability, temperature and incoming solar radiation (Baldauf et al., 2018; Lange, 2001; Lechowicz, 1978; Sveinbjornsson & Oechel, 1983). However, there is a gap in knowledge with regards to the metabolic processes of lichen in situ on rock barrens landscapes. Lichens are slow growing, with growth rates of approximately 5 mm per year due to low carbon assimilation and a low chlorophyll content (Smith, 1962). Water content is critical in determining lichen metabolic rates, and moisture conditions will often determine where lichens establish across a landscape (Smith, 1962). Lichens have no mechanism for conserving water (Smith, 1962), but they are drought resistant as a result of their ability to go into a dormant state when water is unavailable (Lange, 1953; Smith, 1962). Temperature is also an important control on lichen metabolic activity (Kershaw & Field, 1975), but studies on the response of lichen and moss to changes in temperature are uncommon (Lange, 2001).

Mosses, particularly *Polytrichum* spp., supersede lichen in the succession of rock barrens ecosystems and are critical resources on the landscape. Mosses are able to withstand the low moisture and high temperatures of rock barrens ecosystems (Groeneveld & Rochefort, 2005) and

they are essential for facilitating growth of more complex vegetation as they regulate the microclimate and stabilize soil deposits (Groeneveld et al., 2007; Lindo & Gonzalez, 2010; Turetsky, 2003). Similar to lichens, the metabolic activity of moss is largely controlled by light, water, and nutrient availability (Turetsky, 2003; Zotz & Kahler, 2007). *Polytrichum* spp. mosses are adapted to withstand water stress and when water is unavailable *Polytrichum* spp. will close their leaves to limit photosynthesis and respiration during drought (Anderson & Bourdeau, 1955; Bayfield, 1973) and as such, growth of *Polytrichum* spp. will only occur when water is available (Vitt, 1990). Few researchers have considered the role temperature plays in moss growth (e.g. Corradini & Clément, 1999; Sveinbjornsson & Oechel, 1983). Sveinbjornsson and Oechel (1983) found that *Polytrichum* spp. had lower net photosynthesis under cooler temperatures, and Corradini and Clément (1999) found that the optimal growth rate of *Polytrichum commune* occurred within a temperature range of 7 to 15 °C. *Polytrichum* spp. are relatively rapid colonizers and researchers have found that it can take two to three growing seasons for the mosses to form a significant mat (Corradini & Clément, 1999; Groeneveld & Rochefort, 2005).

#### Lichen and moss vulnerability to disturbance and restoration methods

Despite the importance of lichen and moss to the integrity of rock barrens ecosystems, their low growth rate makes them vulnerable to disturbance. As a result of climate change, drought severity and frequency are expected to increase (Dai et al., 2004; Price et al., 2013; Trenberth et al., 2007), and in the northern hemisphere warm, dry conditions characteristic of summer weather, are predicted to become more common (Trenberth et al., 2007; Vrac et al., 2014; Walther et al., 2002). For lichen and moss, which rely on precipitation for moisture availability, this could mean reduced annual growth and greater respiration. Lichen and moss are further vulnerable to land use

change and disturbance. As development and resource extraction increase, lichen and moss are often not considered in restoration plans (Bowker, 2007). Since lichen and moss are slow growing, a loss of these mats from a given landscape can have long-term implications for the ecosystem.

Restoration approaches for lichen and moss have been considered, but are not widely studied (Bowker, 2007). One common thought is that lichen and moss take too long to recover and are not easily restored (Bowker, 2007). However, because lichen and moss provide critical habitat for key species and are essential for rock barrens succession, restoration of these resources can potentially jumpstart ecosystem recovery. Two common approaches for lichen and moss restoration are fragment dispersal and in-tact patch transplant. Fragment dispersal involves spreading fragments of the lichen or moss on a suitable substrate and allowing them to establish over time (*e.g.* Groeneveld & Rochefort, 2005; Groeneveld et al., 2007; Roturier et al., 2007). This method is reasonable for mosses which can form a mat in approximately three years (Graf & Rochefort, 2010; Roturier et al., 2007), but it is less feasible for lichens, which can take up to 45 years to form a mat from fragments (Carroll & Bliss, 1982; Crittenden, 2000; Dunford et al., 2006; Roturier et al., 2007). Furthermore, it is difficult for fragments to establish on a given substrate because there is a high potential for disturbance by animal movements, wind, and water (Duncan, 2015; Roturier et al., 2007; Roturier & Bergsten, 2009). The second known, but understudied, approach is transplanting patches of in-tact lichen and moss. Researchers have used this approach and have seen success (*e.g.* Groeneveld & Rochefort, 2005; Roturier & Bergsten, 2009), but these studies have not quantified the growth of these transplants in comparison to natural plots by measuring the CO<sub>2</sub> exchange. Transplanting in-tact patches of lichen and moss could potentially restore the ecosystem services of a natural mat, without having to wait the period of time required for fragments to establish.

### Turtle nesting on the eastern Georgian Bay landscape

Recruitment rates are declining in many turtle populations (Compton, 2007; Lesbarrères et al., 2014; Marchand & Litvaitis, 2004b; Steen & Gibbs, 2004), largely as a result of habitat loss (e.g. wetlands, upland nesting habitat) and degradation (Lesbarrères et al., 2014; Steen et al., 2012; Walton & Villeneuve, 1999), and the life history traits of turtles, such as delayed sexual maturity and low nest survival which constrain population recovery (e.g. Congdon et al., 1993; Congdon et al., 1994). Female turtles travel long distances on land to locate nesting sites (e.g. Blanding's turtle (*Emydoidea blandingii*), Edge et al., 2010), which increases their interaction with roads, and thereby increases their risk of mortality (Steen et al., 2006). Furthermore, females are often attracted to unpaved roads and the gravel shoulders of roads for nesting (Beaudry et al., 2010; Steen et al., 2006), which negatively impacts recruitment rates as roadside nests can lead to injury or mortality of both the nesting females and hatchlings (e.g. Aresco, 2004; Aresco, 2005; Steen et al., 2006). Nest predation is also a significant concern, as some turtle populations can have 90-100% of the nests depredated by mesopredators such as foxes, skunks, and raccoons (e.g. Aresco, 2004; Congdon et al., 1987). Given the impact of these stressors on the recruitment rates of turtle populations (Compton, 2007; Lesbarrères et al., 2014; Marchand & Litvaitis, 2004a; Steen & Gibbs, 2004), conservation efforts need to be undertaken. However, if conservation efforts are lacking sufficient research and understanding, management can be ineffective or potentially damaging (Congdon et al., 2000; Kolbe & Janzen, 2002). Globally, reptile species are declining (Gibbons et al., 2000), and in Ontario, all 8 native turtle species are classified as species-at-risk, indicating that there are significant threats to Ontario's turtle populations (Government of Canada, 2019). Species-at-risk protections are largely based on conserving the critical habitat used by the

species (e.g. habitat required for reproduction or overwintering; Government of Canada, 2019), and thus it is essential that we understand how these critical habitats function and persist on the given landscapes.

In eastern Georgian Bay, turtle species-at-risk, such as midland painted (*Chrysemys picta marginata*), Blanding's (*Emydoidea blandingii*), and snapping turtles (*Chelydra serpentina*) select nest sites in lichen- and moss-dominated soil deposits in bedrock depressions and crevices (e.g. Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014). The properties of lichen and moss cover enhance the suitability of these soil-filled bedrock depressions for nesting. Turtle nest sites must retain enough heat for embryo development while also keeping the soil cool enough to avoid egg desiccation (Gutzke & Packard, 1987; Packard et al., 1987; Standing et al., 1999). Lichen and moss moderate soil temperatures, thereby maintaining these conditions (Moore et al., 2019). Soil moisture is another important factor for nest success. If the soil is too dry it will collapse making nest construction difficult and dry soil could also lead to egg desiccation (Congdon et al., 2000). Second, if the soil does not allow sufficient drainage the nest could flood and the eggs would not survive (Congdon et al., 2000; Kiviat et al., 2004; Standing et al., 1999). Lichen and moss support the moisture regime needed for successful nests by reducing diffusive water losses from the soil (Moore et al., 2019). Further, successful nests require an open area with low canopy cover (Congdon et al., 2000; Schwarzkopf & Brooks, 1987), and lichen and moss mats maintain a short cover height. Therefore, to understand the persistence of nesting habitat on the rock barrens landscape we must also understand the growth and persistence of lichen and moss, a critical component of suitable turtle species-at-risk nesting habitat in eastern Georgian Bay.

## Thesis objectives

The objectives of this thesis are to first identify the key controlling variables on lichen and moss persistence on rock barrens landscapes, and second to investigate an understudied approach to restoring lichen and moss cover. To address the first objective, we measure the CO<sub>2</sub> exchange of lichen, mixed (lichen and moss), and moss plots, as well as environmental variables such as soil moisture, soil temperature, air temperature, and air relative humidity. We use statistical analyses to determine which of the measured ecohydrological variables has the strongest control on the net ecosystem productivity (NEP), ecosystem respiration (ER), and gross primary productivity (GPP) of lichen and moss. Further, we determine when lichen and moss growth primarily occurs between May and October. This research is critical for understanding the ecohydrological controls on the lichen and moss that dominate rock barrens landscapes. To address the second objective, we measure the CO<sub>2</sub> exchange and decomposition of natural and transplanted lichen and moss patches to quantify success in the first four months following transplant. We pair the transplanted lichen and moss patches with natural undisturbed patches and compare the NEP, ER and GPP. We use the decomposition of tea bags to compare relative differences in decomposition rates between transplant and natural treatments. These research findings are important because lichen and moss are essential for suitable turtle species-at-risk nesting habitat on rock barrens landscapes, and our transplant approach can be used to enhance restoration of these ecosystem resources.



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## **Chapter 2: Ecohydrological controls on rock barrens lichen and moss CO<sub>2</sub> exchange:**

### **Implications for primary soil formation and 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 identified which ecohydrological factors (*e.g.* 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. Our results indicate that soil moisture is a critical control on the CO<sub>2</sub> exchange of lichen and moss, and this relationship varies among cover types. 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. 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, resulting in a slower soil accumulation rate, thus limiting the availability of nesting habitat for turtle species-at-risk.

## 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 (Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014). Lichen and moss cover insulates and moderates soil temperature (Kershaw & Field, 1975; Lindo & Gonzalez, 2010; Moore et al., 2019) and 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, 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 barrens 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 et al., 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, 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 et al., 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 et al., 2018; Lange, 2001; Lechowicz, 1978; Sveinbjornsson & Oechel, 1983). Photosynthesis is the primary source of carbon for lichens, but due to ecohydrological controls and low chlorophyll content, their photosynthetic rates are lower 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 crevice water storage capacity and the fill-and-spill hydrological behaviour of these landscapes (Spence & Woo, 2002) have the potential to drive strong wet and dry period transitions. Moreover, temperature is another important control on lichen metabolic activity, although relatively little is known (Kershaw & Field, 1975; Lange, 2001).

The branched morphology of fruticose lichens enhances their ability to collect soil particles and can provide the appropriate microclimate conditions for the establishment of mosses, such as *Polytrichum* spp. (Burbanck & Platt, 1964; Shure & Ragsdale, 1977). Once established, mosses can further facilitate soil accumulation (Burbanck & Platt, 1964) and formation (Jackson, 2015), and moderate temperature and moisture conditions (Burbanck and 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). Despite having the ability to transport water through internal and external mechanisms, *Polytrichum* spp. largely rely on precipitation (Anderson & Bourdeau, 1955; Bayfield, 1973). When water is unavailable or limited, *Polytrichum* leaves will close and adhere to the stem to reduce water loss (Anderson & Bourdeau, 1955; Bayfield, 1973; Corradini & Clément, 1999). Due to the moss' ability to recover from desiccation, growth can take place in spring and fall, and is often limited in the summer (Corradini & Clément, 1999). Although lichens and mosses are the dominant cover type on the rock barrens of eastern Georgian Bay, the ecohydrological controls on their CO<sub>2</sub> exchange have not previously been examined.

The lichen and moss mats on the Canadian Shield bedrock of the eastern Georgian Bay rock barrens, in Ontario, Canada, are vulnerable to climate and land use changes. 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 et al., 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 on eastern Georgian Bay rock barrens through decreased productivity as a result of increasing frequency and duration of drought conditions (Dai et al., 2004; Price et al., 2013; Trenberth et al.,



2007) and increasing risk of wildfire (Braun et al., 2010; Wotton et al., 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 nesting habitat (Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014).

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

## Methods

### *Study area*

The Northern Ontario Barrens and Bog Ecosystems Landscape (NOBEL) in eastern Georgian Bay 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 et al., 2009). The valleys contain large wetland complexes or beaver ponds, while 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 which provide nesting habitat for turtle species-at-risk in the eastern Georgian Bay region (e.g. 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 (*Pinus 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 comparable 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 and 6.9 °C, respectively (Dunchurch station, ~45 km NE from site; Government of Canada, 2019). In 2019, the average air temperature from May through October was 15.2 °C, with a maximum of 33 °C and a minimum of -1.4 °C. The 26-year average cumulative rainfall from May to October is 563 mm (Government of Canada, 2019) and in 2019 the NOBEL 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).

### *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 m<sup>2</sup> and had minimal vascular plant

cover (< 30%). To ensure all plots could be considered potential turtle nesting habitat, average soil depth ranged from 8–15 cm (Markle et al., 2020) and canopy openness was  $\geq 65\%$  (e.g. Riley et al., 2014, Markle unpublished data).

Between May and October 2019, we measured CO<sub>2</sub> exchange at the nine plots using a closed static chamber (diameter = 10 cm, height = 15 cm, volume = 1.18 L) and an infrared gas analyzer (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-second period. CO<sub>2</sub> and photosynthetic photon flux density (PPFD;  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) were recorded every 5 seconds for 90 seconds. 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 seconds 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 8 May to 17 October 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<sup>2</sup> value less than 0.5 were checked for error and removed if necessary (13% of measurements removed; cf. Harris et al., 2018). Net ecosystem productivity (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 et al., 1998; Frohking et al., 1998). For each curve we determined the initial slope ( $\alpha$ ) and asymptote ( $GPP_{max}$ ) parameters.

### *Decomposition*

To estimate lichen and moss decay rates, samples were collected in spring 2015, cleaned of other litter and soil, dried, weighed, and placed into pre-sown 0.01 x 0.012 m nylon mesh litter bags (mesh size 300  $\mu$ m). Litter bags (n = 121) containing ~3 g (dry weight) of lichen (*Cladonia* spp.) or moss (*Polytrichum* spp.) were buried at a depth of 1 cm in rock barrens lichen and moss mats in June 2015. In June 2016, 79 of the litter bags were collected and weighed to determine the decomposition of the lichen and moss during this time period (12 months). The remaining 42 litter bags were collected in June 2017, to estimate decomposition over a 24-month period. We expressed decomposition as the percent of mass lost (K) over one or two years, respectively (Rocheffort et al., 1990). We also estimated relative differences in decomposition between cover types during the 2019 growing season using the tea bag method outlined by Keuskamp et al. (2013). We measured the initial weight of green and rooibos tea bags and then buried them 8 cm below the soil surface of each of our 9 plots. After 90 days we removed the tea bags, cleaned the outer bag of dirt and plant matter, and dried them at 60 °C for 48 hours. Once dry, we re-weighed them to determine percent of mass lost (K).

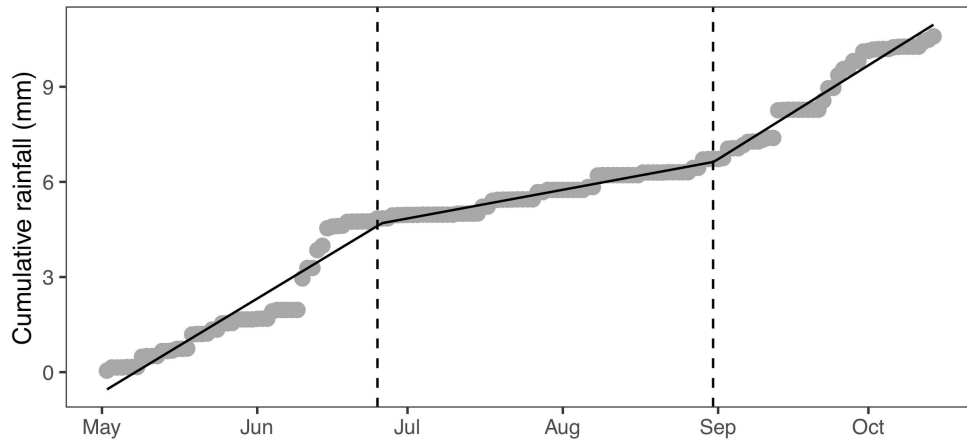
### *Soil moisture and temperature*

Continuous soil volumetric water content (VWC) and soil temperature were measured at a depth of 5 cm at all nine NEP (CO<sub>2</sub> exchange) plots during the 2019 growing season (8 May – 17

October). Soil VWC was measured every 15 minutes using a HOBO soil moisture smart sensor (0.05 m probe length, 0.3 L volume of influence, Onset HOBO S-SMxpM005, Massachusetts, USA) and logged using a HOBO Micro Station data logger (Onset HOBO H21-USB). Soil VWC probes were calibrated for NOBEL rock barrens soils according to Starr and Paltineanu (2002). Soil temperature was measured hourly using an iButton (iBWetland Type G). Temperature data were interpolated to 15-minute intervals to align with the soil VWC measurements. Air temperature, precipitation and relative humidity were measured every 30 minutes at a meteorological station within 100 m of the sites.

### *Analyses*

We conducted all statistical analyses in R 3.6.1 (R Core Team, 2019). We used a breakpoint analysis of cumulative rainfall (Figure S2.1) to define a wet and dry period within the study duration (8 May – 17 October 2019). Using this approach, we defined the wet season as the start of data collection (8 May) to 24 June and 1 September to the end of data collection (17 October). The dry season began 25 June and ended 31 August. 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 to the summer season (24 days).



**Figure S2.1.** Breakpoint analysis of cumulative rainfall (mm) indicating that the dry season began on 25 June 2019 and ended on 31 August 2019.

To determine if mean daily soil temperatures, NEP (n = 358), ER (n = 358), and GPP (n = 327) were different between season (wet, dry) and among cover types (lichen, mixed, moss), we fit a linear mixed effects model (LMM; *lme4*, Bates et al., 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 0-1) with season (wet, dry) and cover type (lichen, mixed, moss) as fixed effects and plot number as a random effect to account for repeated measurements. We used a Kruskal-Wallis test, and when necessary a pairwise Wilcox test, to identify significant differences in litter bag and tea bag decomposition.

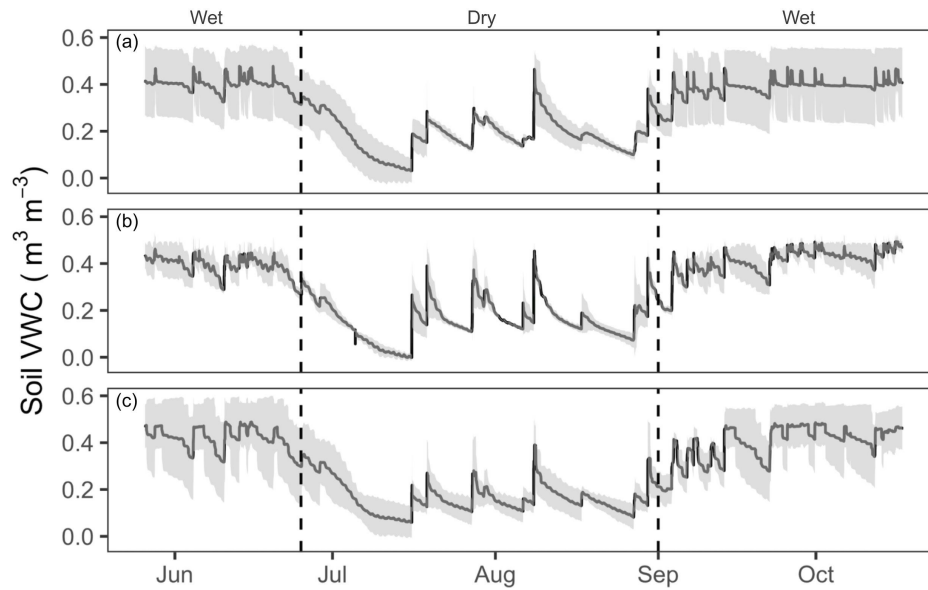
In order to determine which ecohydrological factors had the greatest effect on the fluxes we used linear mixed effects models. The NEP, ER and GPP data were approximately normally distributed and the Q-Q plots followed the straight line reasonably well. Generalized variance inflation factors for all fixed effects were less than three, therefore no parameters were excluded based on multi-collinearity. We tested linear mixed effect models with a combination of cover type (lichen, mixed, 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 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.

## Results

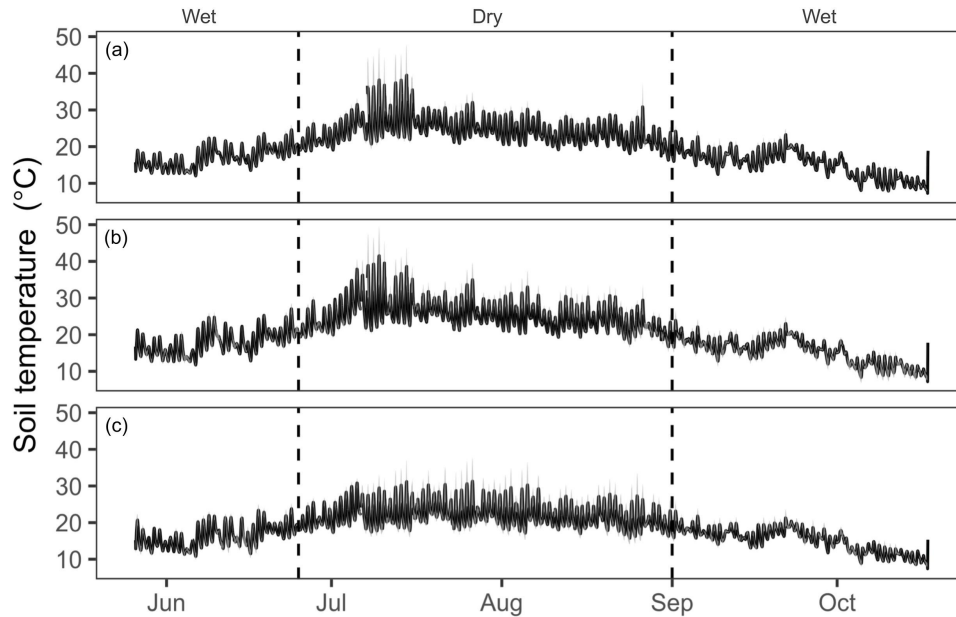
### *Soil moisture and temperature*

From May – June and September – October the soil VWC was consistently higher than July – August (Figure 2.1). In July and August soil VWC declined overall with peaks during rainfall followed by rapid drying (Figure 2.1). The soil VWC ranged from 0.12 to 0.58 m<sup>3</sup> m<sup>-3</sup> in the wet period (8 May – 24 June, 1 September – 17 October) and from 0 to 0.48 m<sup>3</sup> m<sup>-3</sup> in the dry period (25 June – 31 August). Soil VWC in the wet period was double the VWC in the dry period with a daily mean soil VWC of  $0.40 \pm 0.1$  m<sup>3</sup> m<sup>-3</sup> standard deviation in the wet season and  $0.17 \pm 0.09$  m<sup>3</sup> m<sup>-3</sup> standard deviation in the dry season (GLMM, estimate [est.] =  $0.8 \pm 0.02$ ,  $t = 35.5$ ,  $p \leq 0.001$ ). During both seasons, soil VWC was comparable between lichen and mixed (GLMM, est. =  $0.01 \pm 0.17$ ,  $t = 0.09$ ,  $p = 0.92$ ) and between lichen and moss plots (GLMM, est. =  $0.02 \pm 0.17$ ,  $t = 0.11$ ,  $p = 0.91$ ). Furthermore, soil VWC did not differ between mixed and moss plots (GLMM, est. =  $0.002 \pm 0.12$ ,  $t = 0.02$ ,  $p = 0.99$ ). Between 8 May and 17 October, the soil temperature was cooler in the wet periods (May – June, September – October) and warmer in the dry period (July – August; Figure 2.2). 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. =  $-7.95 \pm 0.15$ ,  $t = -51.06$ ,  $p \leq 0.001$ ) with a mean of  $15.9 \pm 3$  °C standard deviation and  $23.8 \pm 2.6$  °C standard deviation, respectively. Across both periods, the daily average soil temperature did not differ between lichen and mixed plots (LMM, est. =  $0.61 \pm 0.43$ ,  $t = 1.41$ ,  $p = 0.22$ ). The moss plots had a cooler mean soil temperature than lichen by 1.3 °C (LMM, est. =  $-1.27 \pm 0.43$ ,  $t = -2.92$ ,  $p = 0.03$ ) and mixed plots by 1.9 °C (LMM, est. =  $-1.88 \pm 0.42$ ,  $t = -4.47$ ,  $p = 0.01$ ).





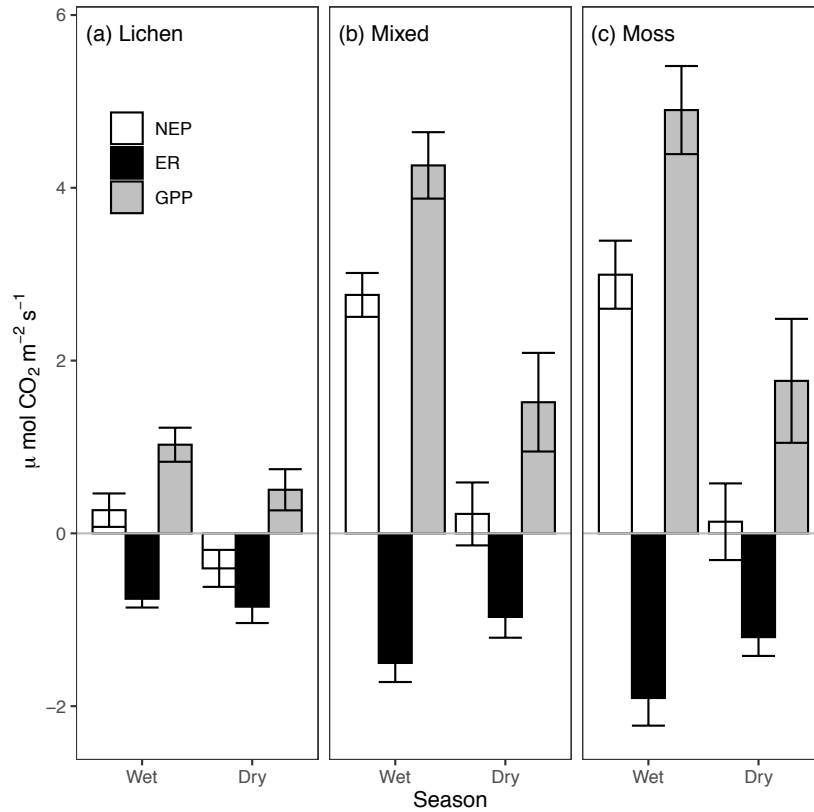
**Figure 2.1.** Mean soil volumetric water content (VWC;  $\text{m}^3 \text{m}^{-3} \pm$  standard deviation) measured every 15 minutes, at a depth of 5 cm, from May to October 2019 at lichen (a,  $n = 3$ ), mixed (b,  $n = 3$ ), and moss plots (c,  $n = 3$ ). Dashed lines denote the wet (8 May to 24 June; 1 September to 17 October) and dry (25 June to 31 August) seasons as determined by a breakpoint analysis of cumulative rainfall (Figure S2.1).



**Figure 2.2.** Mean soil temperature ( $^{\circ}\text{C} \pm$  standard deviation) measured hourly and interpolated to every 15 minutes, 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 (8 May to 24 June; 1 September to 17 October) and dry (25 June to 31 August) seasons as determined by a breakpoint analysis of cumulative rainfall (Figure S2.1).

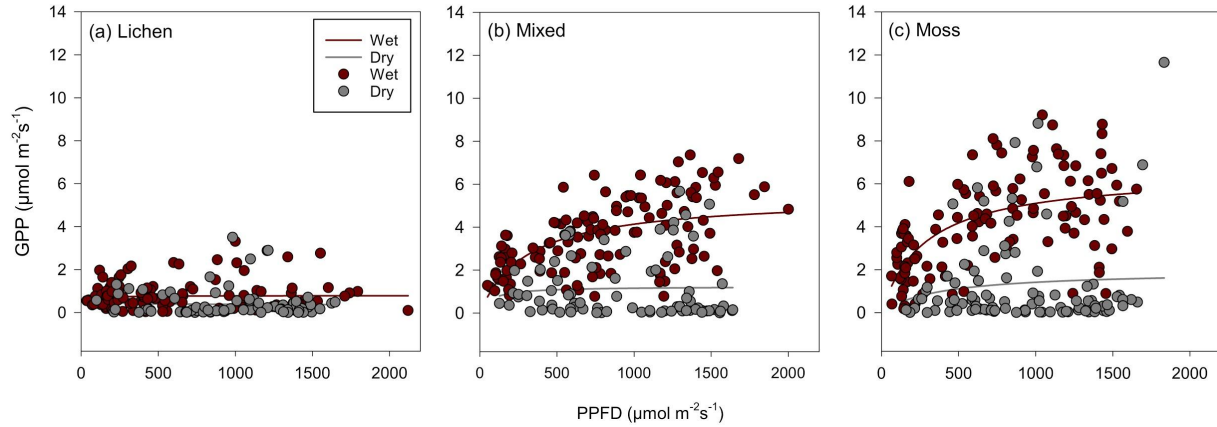
*Production (CO<sub>2</sub> exchange)*

The total mean NEP was greater in the wet season than the dry season for all cover types (Figure 2.3), 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,  $t = -5.1, p \leq 0.001$ ),  $2.5 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  for mixed (LMM,  $t = -11.7, p \leq 0.001$ ) and  $2.9 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  for moss (LMM,  $t = -9.95, p \leq 0.001$ ). 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,  $t = 0.9, p = 0.37$ ; Figure 2.3). 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,  $t = -3.25, p \leq 0.001$ ) and  $0.7 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  for moss plots (LMM,  $t = -3.8, p \leq 0.001$ ; Figure 2.3). 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,  $t = 3.6, p \leq 0.001$ ), mixed by  $2.7 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 8.31, p \leq 0.001$ ) and moss by  $3.2 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 7.6, p \leq 0.001$ ; Figure 2.3). In addition, across both seasons the CO<sub>2</sub> fluxes differed between cover types (Figure 2.3). Mixed and moss plots had a  $1.6 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 4.4, p \leq 0.001$ ) and  $1.4 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 3.91, p \leq 0.001$ ) difference in NEP respectively compared to lichens. Mixed ER was greater than lichen by  $0.4 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = -3.5, p \leq 0.001$ ) and moss ER was greater than lichen by  $0.7 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = -5.63, p \leq 0.001$ ). Finally, mixed plots had a difference in GPP of  $2.3 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 5.73, p \leq 0.001$ ) and moss had a difference of  $2.5 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LMM,  $t = 6.23, p \leq 0.001$ ) when compared to lichen plots. Mixed and moss plots did not have significantly different NEP, ER or GPP (Figure 2.3).



**Figure 2.3.** Mean net ecosystem productivity (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 8 May to 17 October 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.

The GPP-PPFD relationship had a worse fit under dry conditions compared to wet conditions for all cover types (Figure 2.4). During the wet period, the lichen plots had a smaller initial slope and maximum GPP ( $\alpha = 20.3$ ,  $GPP_{\max} = 0.79$ ) than both mixed ( $\alpha = 307.14$ ,  $GPP_{\max} = 5.41$ ) and moss ( $\alpha = 281.0$ ,  $GPP_{\max} = 6.52$ ). Under dry conditions, lichen maintained a smaller initial slope and maximum GPP ( $\alpha = -44.72$ ,  $GPP_{\max} = 0.37$ ) than mixed ( $\alpha = 69.1$ ,  $GPP_{\max} = 1.24$ ) and moss plots ( $\alpha = 372.42$ ,  $GPP_{\max} = 1.94$ ). The measured data vary greatly around the curve, which results in a poor curve fit in all instances (Figure 2.4).



**Figure 2.4.** 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 period (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 period (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 period (grey line,  $n = 97$ ,  $\alpha = 372.42$ ,  $\text{GPP}_{\text{max}} = 1.94$ ,  $R^2 = 0.01$ ). GPP and PPFD calculated from field  $\text{CO}_2$  and PPFD measurements for lichen (a), mixed (b), and moss (c) during the wet (red points) and dry (grey points) periods.

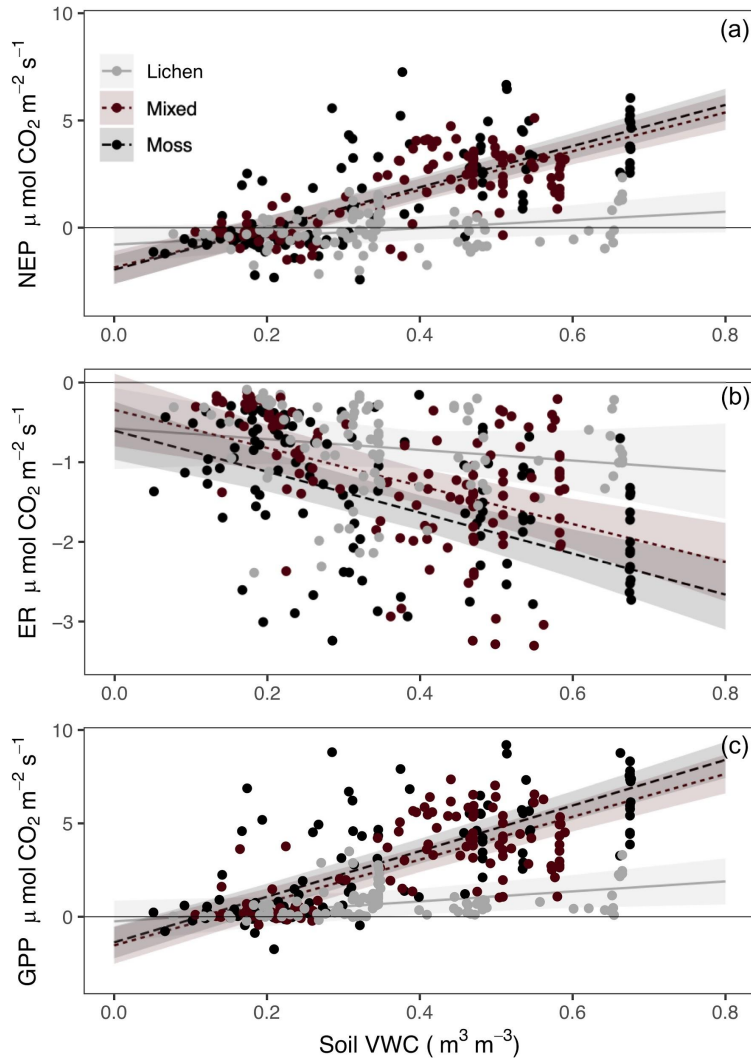
### *Ecohydrological controls*

Cover type, soil VWC and their interaction had the greatest effect on NEP, ER and GPP (Table 2.1). The slope of the predicted response of NEP to increasing soil VWC was greater by  $7.1 \pm 1.2$  (LMM,  $t = 5.96$ ,  $p \leq 0.001$ ) for mixed than lichen,  $7.7 \pm 1.1$  (LMM,  $t = 6.92$ ,  $p \leq 0.001$ ) for moss than lichen, and  $0.6 \pm 1.1$  (LMM,  $t = 0.56$ ,  $p = 0.58$ ) for moss than mixed (Figure 2.5). The predicted response of ER to increasing soil VWC had a greater slope of  $-1.7 \pm 0.8$  (LMM,  $t = -2.06$ ,  $p = 0.041$ ) for mixed when compared to lichen,  $-1.9 \pm 0.8$  (LMM,  $t = -2.46$ ,  $p = 0.02$ ) for moss when compared to lichen, and of  $-0.2 \pm 0.8$  (LMM,  $t = -0.24$ ,  $p = 0.81$ ) for moss when compared to mixed (Figure 2.5). 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,  $t = 5.65$ ,  $p \leq 0.001$ ), moss was greater than lichen by  $9.5 \pm 1.4$  (LMM,  $t = 6.58$ ,  $p \leq 0.001$ ), and moss was greater than mixed by  $0.75 \pm 1.4$  (LMM,  $t = 0.52$ ,  $p = 0.60$ ; Figure 2.5).

**Table 2.1.** Results from the linear mixed effects models for net ecosystem productivity (NEP), ecosystem respiration (ER), and gross primary productivity (GPP, n = 336).

	<i>Fixed effects</i>	<i>Estimate</i>	<i>Std. error</i>	<i>df</i>	<i>t value</i>	<i>p (&gt;  t )</i>
NEP	Intercept	-0.8	0.4	31.6	-1.80	0.08
	Mixed	-1.1	0.6	28.4	-1.82	0.08
	Moss	-1.2	0.5	22.8	-2.11	0.05
	VWC	1.9	0.9	297.9	2.06	0.04
	Mixed: VWC	7.1	1.2	320.7	5.96	≤ 0.001
	Moss: VWC	7.7	1.1	314.4	6.92	≤ 0.001
ER	Intercept	-0.6	0.3	50.6	-2.23	0.03
	Mixed	0.2	0.3	61	0.67	0.5
	Moss	-0.02	0.3	44.2	-0.09	0.93
	VWC	-0.7	0.6	173.4	-1.04	0.30
	Mixed: VWC	-1.7	0.8	246.1	-2.06	0.04
	Moss: VWC	-1.9	0.8	215.9	-2.46	0.01
GPP	Intercept	-0.2	0.6	33.3	-0.44	0.66
	Mixed	-1.3	0.7	30.2	-1.70	0.1
	Moss	-1.1	0.7	24.2	-1.58	0.12
	VWC	2.7	1.2	292.4	2.21	0.03
	Mixed: VWC	8.8	1.5	318.4	5.65	≤ 0.001
	Moss: VWC	9.5	1.4	311.1	6.58	≤ 0.001

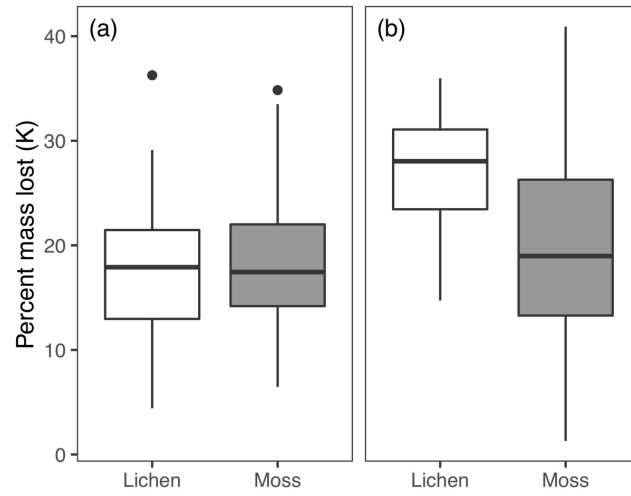




**Figure 2.5.** Predicted response of (a) net ecosystem productivity (NEP), (b) ecosystem respiration (ER), and (c) gross primary productivity (GPP) to increasing soil volumetric water content (VWC;  $\text{m}^3 \text{m}^{-3} \pm 95\%$  confidence intervals) according to the linear mixed effects models for lichen (grey solid line), mixed (red dotted line), and moss plots (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).

### *Decomposition*

After one year of decomposition, the average mass lost (K) was not significantly different between cover types, where lichen K was  $18.0 \pm 1.2$  % and moss K was  $18.6 \pm 0.8$  % ( $\chi^2_{1,79} = 0.24, p = 0.62$ ; Figure 2.6). Conversely, the set of litter bags that were removed after two years had a significantly greater K value for lichen ( $27.4 \pm 1.7$  %) than for moss ( $20.5 \pm 1.9$  %;  $\chi^2_{1,42} = 5.64, p = 0.02$ ; Figure 2.6). Lichen had a significantly greater mean K value after two years ( $27.4 \pm 1.7$  %) when compared to one year ( $18.0 \pm 1.3$  %;  $\chi^2_{1,42} = 13.17, p \leq 0.001$ ; Figure 2.6), while moss had similar mean K values after one ( $18.6 \pm 0.8$  %) and two ( $20.5 \pm 1.9$  %) years ( $\chi^2_{1,79} = 0.81, p = 0.37$ ; Figure 2.6). From the 2019 tea bag data, we determined that K was not significantly different between cover types ( $\chi^2_{3,14} = 0.93, p = 0.82$ ).



**Figure 2.6.** Mass lost (%) between (a) 2015-2016 and (b) 2015-2017 for lichen (2016, n = 28; 2017, n = 14) and moss (2016, n = 51; 2017, n = 28) fragments.

## Discussion

We determined that the wetter portion of the growing season (May – June, September – October; Figure 2.1) was critical for CO<sub>2</sub> uptake by lichen and moss on the rock barrens landscape. In the wet season lichen, mixed and moss plots had a difference in NEP of +0.68, +2.57 and +2.87  $\mu\text{mol m}^{-2} \text{s}^{-1}$  when compared to the dry season, respectively (Figure 2.3). GPP was greater in the wet season than the dry season by 0.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for lichen, 2.8  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for mixed and 3.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for moss (Figure 2.3). Ecosystem respiration (ER) was also greater in the wet season for mixed and moss but did not differ for lichen plots (Figure 2.3). The differences in CO<sub>2</sub> 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 2.3).

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; Froking 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 barrens soil 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 CO<sub>2</sub> uptake (Heijmans et al., 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 (although none were *Polytrichum* spp.) and found that CO<sub>2</sub> exchange was largely seasonal, with the highest uptake in fall and neutral CO<sub>2</sub> exchange in the summer.

In our study area of eastern Georgian Bay, air temperature and precipitation are expected to increase with climate change (Mortsch et al., 2000; Notaro et al., 2015; Price et al., 2013; Trenberth et al., 2011). The warm dry conditions, which are characteristic of summer months (July and August; Figure 2.1, Figure 2.2) in the northern hemisphere, are beginning earlier and finishing later in the year (Trenberth et al., 2007; Vrac et al., 2014; Walther et al., 2002). Furthermore, drought frequency and severity are expected to increase (Dai et al., 2004; Price et al., 2013; Trenberth et al., 2007). As our findings illustrate, dry conditions can result in a net loss of CO<sub>2</sub> for lichens and a lower or neutral CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> exchange that we found can be largely explained by the fact that lichen and moss productivity on the rock barrens landscape was controlled by cover type and

soil volumetric water content (VWC; Figure 2.5). As expected, the predicted response of net ecosystem productivity (NEP), ecosystem respiration (ER) and gross primary productivity (GPP) to changes in soil VWC differs between lichen, mixed and moss mats (Figure 2.5). Our results show that the predicted response of lichen to increasing soil VWC is significantly different from that of mixed and moss (Table 2.1), while the mixed and moss plots are not different from each other (Figure 2.5; Table 2.1). Our findings are consistent with trends in other landscapes, where researchers have shown that the CO<sub>2</sub> fluxes of lichen and moss are controlled by soil water and temperature (Baldauf et al., 2018; Grote et al., 2010; Lechowicz, 1978). Furthermore, our finding of lichen and moss responding differently is supported in the literature. Previous studies have found that lichens have lower carbon assimilation rates relative to mosses and vascular plants (Smith, 1962), which can explain the lower increase in CO<sub>2</sub> flux as soil VWC increases (Figure 2.5). Mosses are also better able to transport water (Bayfield, 1973; Moore et al., 2019), which explains why we saw greater CO<sub>2</sub> fluxes at lower soil VWC for mosses than lichens. These model results are further supported by our analysis of the GPP-PPFD relationship, which illustrates lichen's lower light-use efficiency when compared to mixed and moss plots (Figure 2.4). The GPP-PPFD relationship also illustrates our finding of soil moisture being an important control on GPP since the curves are lower for the dry period than the wet period for all cover types (Figure 2.4).

Climate change is expected to alter moisture conditions globally, and as such we can expect that the CO<sub>2</sub> fluxes of lichen and moss will also change (Baldauf et al., 2018; Grote et al., 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 eastern Georgian Bay region we expect

lichens will have a neutral or negative NEP, while mosses would maintain a small positive or neutral NEP. Our findings suggest that mosses will be able to maintain CO<sub>2</sub> uptake at a lower soil VWC 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 et al., 2002; Smith, 2014). If the soil VWC dries to a point where lichens become dormant and mosses remain productive, the mosses would be able to continue growing while the lichens would not. If lichen growth is limited, while mosses are still able to take up CO<sub>2</sub>, we would 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 nesting habitat for turtle species-at-risk (Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014). In addition, lichen and moss both play a critical role in primary soil development and a decline in metabolic activity could reduce the available soil on the landscape, further limiting suitable nesting habitat.

#### *Implications for primary soil formation and nesting habitat*

The differences in CO<sub>2</sub> response to changing soil VWC between cover types are important to consider under future climate scenarios and with regards 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 et al., 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; Mortsch et al., 2000; Notaro et al., 2015; d'Orgeville et al., 2014), 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. Since lichens play a key role in moderating soil temperatures and soil 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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### **Chapter 3: CO<sub>2</sub> exchange of natural and restored lichen and moss patches on a rock**

#### **barrens landscape: Applications for turtle species-at-risk nesting habitat**

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#### Abstract

Lichen and moss play a critical role in ecosystems globally as they often initiate ecosystem succession, stabilize soil and improve soil quality, and provide habitat for species-at-risk. Lichen and moss colonize landscapes with high temperatures, low moisture availability and limited soil. Once established, the lichen and moss improve the microclimate and develop soil, facilitating establishment of more complex vegetation. In boreal and tundra regions lichens are an important food source for caribou and reindeer, and in arid regions lichen and moss reduce soil erosion and improve soil quality. On the rock barrens landscape of eastern Georgian Bay, lichen and moss provide nesting habitat for turtle species-at-risk. Lichen and moss are essential ecosystem resources, but they are vulnerable to impacts from climate change and development due to their slow-growing nature. As a result, restoration methods must be considered to increase or maintain lichen and moss cover. Two common restoration approaches are fragment dispersal and in-tact patch transplants, but the latter is understudied. In this study we aimed to determine whether the in-tact transplant approach would be feasible for lichen and moss on rock barrens landscapes. We quantified the success of lichen and moss transplants by measuring their CO<sub>2</sub> exchange with a closed chamber and infrared gas analyzer at nine transplanted and six natural plots from July to October 2019. Furthermore, we quantified the decomposition under transplant and natural cover.

We found that there were no differences in productivity and decomposition between natural and transplant lichen patches, and there were some differences between that of mixed and moss patches. Our findings suggest that the in-tact patch transplant approach can be used to increase lichen cover on a given landscape, and specifically it can be used to improve constructed turtle nest sites on rock barrens landscapes.

### Introduction

On rock barrens landscapes, lichen and moss are the dominant bedrock cover and are integral to the succession and function of these ecosystems. Lichen and moss are the first organisms to colonize granitic bedrock landscapes as they are able to withstand high temperatures, low moisture, and do not require soil for establishment (Keever et al., 1951; Lange, 2001). Once established, lichen and moss facilitate ecosystem succession by improving microclimate conditions (Burbanck & Platt, 1964), moderating soil temperatures (Kershaw & Field, 1975), and reducing soil water losses (Moore et al., 2019). Lichen and moss also play an essential role in soil formation in rock barrens ecosystems. Soil is limited on these landscapes and only accumulates in shallow bedrock depressions. Lichen and moss are able to enhance soil accumulation through chemical weathering of bedrock (Jackson, 2015), trapping particles carried in the wind (Bowker, 2007; Burbanck & Platt, 1964) and stabilizing existing soil deposits (Aguilar et al., 2009; Belnap & Gillette, 1998; Chamizo et al., 2017). Further, lichen and moss play a key role in non-rock barrens ecosystems. For example, lichens (primarily *Cladonia* spp.) are an essential winter food source for caribou and reindeer populations in Boreal and tundra regions (Bergerud, 1972; Danell et al., 1994; Inga, 2007). In desert ecosystems lichen and moss form soil crusts which improve soil quality (Maestre et al., 2011) by reducing erosion (Aguilar et al., 2009; Belnap & Gillette, 1998;

Chamizo et al., 2017) and improving soil nutrients (*e.g.* Chamizo et al., 2012). Furthermore, lichen and moss crusts can provide habitat for desert fauna, such as arthropods (*e.g.* Lalley et al., 2006). On rock barrens landscapes, the ability of lichen and moss to moderate soil moisture and temperature, as well as to accumulate soil, makes lichen- and moss-dominated soil deposits suitable for turtle nesting (*e.g.* Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014). Despite their importance for ecosystem function, lichen and moss can take decades to form a sufficient mat (Carroll & Bliss, 1982; Crittenden, 2000; Dunford et al., 2006; Roturier et al., 2007) and they are vulnerable to climate change impacts (Dai et al. 2004; Price et al., 2013; Trenberth et al., 2007; Wotton et al., 2017) and increasing disturbances such as development and resource extraction (*e.g.* Baxter-Gilbert et al., 2015; Belnap & Eldridge, 2001; Duncan, 2015). As a result of the slow growth rates of lichen and moss (Bowker, 2007; Smith, 1962), and the harsh conditions of the ecosystems they inhabit (Bowker, 2007; Keever et al., 1951; Lange, 2001), natural recovery is delayed. Thus, disturbance of lichen and moss mats can have long-term impacts on ecosystems, and restoration approaches must be considered.

Lichen and moss mats are essential to ecosystems globally, yet they are understudied and often ignored in restoration literature (Bowker, 2007). Two methods used to restore lichen and moss mats on a given landscape are fragment dispersal (*e.g.* Groeneveld & Rochefort, 2005; Groeneveld et al., 2007; Roturier et al., 2007) and in-tact patch transplants (*e.g.* Groeneveld & Rochefort, 2005; Roturier & Bergsten, 2009) with the former being the most common. Fragment dispersal involves spreading small fragments of lichen or moss across a suitable substrate and allowing them to establish over time (*e.g.* Groeneveld & Rochefort, 2005; Groeneveld et al., 2007; Roturier et al., 2007). Research has shown that while moss fragments can establish after two to three years because of their greater net primary productivity (Graf & Rochefort, 2010; Roturier et

al., 2007), it can take lichens up to 45 years to form a sufficient cover (Carroll & Bliss, 1982; Crittenden, 2000; Dunford et al., 2006; Roturier et al., 2007). Furthermore, the success of fragment restoration for lichen or moss can be hindered by wind, runoff and animals (Duncan, 2015; Roturier et al., 2007; Roturier & Bergsten, 2009). Transplanting in-tact patches of lichen or moss with a thin layer of substrate attached is a less common approach in restoration literature and few studies have been conducted on this method of restoring lichen or moss mats (*e.g.* Groeneveld et al., 2007; Roturier & Bergsten, 2009). Groeneveld et al. (2007) transplanted in-tact patches of *Polytrichum strictum* and found that the moss patches moderated temperatures, retained more moisture and trapped particles and seeds more effectively than bare peat. Roturier and Bergsten (2009) successfully transplanted 0.25 m<sup>2</sup> patches of lichen, and other studies have observed lichen establishment following transplanting in-tact patches between different environments (*e.g.* Gilbert, 2001; Sonesson et al., 2007). On non-rock barrens landscapes, lichen and moss restoration has been undertaken for various purposes. Groeneveld and Rochefort (2005) showed that transplanted *Polytrichum strictum* patches and fragments can reduce frost heaving, while Groeneveld et al. (2007) found that transplanting *Polytrichum strictum* patches can improve microclimate conditions and encourage growth of other target species. On arctic and alpine landscapes, fragments and patches of lichen have been used to restore reindeer and caribou habitat following soil disturbance from overgrazing, mining or forestry (Duncan, 2015; Roturier et al., 2007). Nevertheless, there is a lack of research examining the restoration of lichen and moss on rock barrens landscapes, and while patch transplanting is understudied, this approach can potentially increase lichen and moss cover quicker than other methods, thereby more rapidly restoring the ecosystem functions that lichen and moss mats provide.

The landscape of eastern Georgian Bay, Ontario is characterized by Canadian Shield rock barrens where there is an increasingly urgent need for lichen and moss restoration research. While lichen- and moss-dominated mats in this region are essential to the integrity of rock barrens ecosystems (*e.g.* Burbanck & Platt, 1964; Keever et al., 1951), they are vulnerable to climate change impacts (see Chapter 2; Davidson et al., 2002; Smith, 2014) and increasing disturbances from development (*e.g.* Baxter-Gilbert et al., 2015; Belnap & Eldridge, 2001; Duncan, 2015). This research need is especially important because the lichen- and moss-dominated bedrock uplands also represent critical nesting habitat for turtle species-at-risk (*e.g.* Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014). Across their range turtles are experiencing habitat loss and degradation of both wetlands and upland nesting habitat as a result of climate change (Lesbarrères et al., 2014) and increasing human development (Lesbarrères et al., 2014; Walton & Villeneuve, 1999). Female turtles often make large terrestrial movements to locate nesting sites (*e.g.* Edge et al., 2010), which increases their road interactions and thus, their risk of mortality (Steen et al., 2006). Furthermore, females are often attracted to gravel road shoulders or unpaved roads for nesting (Beaudry et al., 2010; Steen et al., 2006). Roadside nests have negative implications for recruitment as there is high potential for injury or mortality of the nesting females and the hatchlings (*e.g.* Aresco, 2004; Aresco, 2005; Steen et al., 2006). Nest predation is another significant concern for turtle species-at-risk (Congdon et al., 1987; Marchand & Litvaitis, 2004a), as increasing human populations support a higher density of mesopredators such as foxes, skunks, and raccoons (*e.g.* Christiansen & Gallaway, 1984; Engeman et al., 2005; Riley & Litzgus, 2013), and some turtle populations can have 90-100% of the nests depredated (*e.g.* Aresco, 2004; Congdon et al., 1987). As a result of these challenges and the life history traits of turtles (*e.g.* Congdon et al., 1993; Congdon et al., 1994), recruitment rates are low or declining in many turtle



populations (Compton, 2007; Lesbarrères et al., 2014; Marchand & Litvaitis, 2004b; Steen & Gibbs, 2004). In an effort to mitigate these issues, researchers have constructed artificial nest sites to increase the availability of nesting habitat and reduce the distance turtles must travel to locate suitable sites (*e.g.* Kiviat et al., 2000; Paterson et al., 2013). Constructed nest sites have been designed for regions where turtles primarily nest in sand and gravel (*e.g.* Kiviat et al., 2000; Paterson et al., 2013). However, on rock barrens, sand and gravel deposits are not common, instead turtles nest in the lichen- or moss-dominated shallow soil deposits in bedrock depressions (Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014). Lichen and moss are critical for nest success because they moderate temperatures (Kershaw & Field, 1975), retain moisture (Moore et al., 2019), and reduce soil erosion (*e.g.* Aguilar et al., 2009; Belnap & Gillette, 1998; Chamizo et al., 2017), therefore in-tact patches of lichen and moss could be transplanted to enhance a novel constructed nest design for rock barrens landscapes.

Given that lichen and moss are necessary for the function of rock barrens ecosystems and turtle nesting habitat, we address a critical research gap by assessing the initial viability of transplanted in-tact patches of lichen and moss as a restoration approach. Considering that transplant viability depends greatly on the ability of the moss and lichen to sequester CO<sub>2</sub>, the first objective of our study was to determine whether the CO<sub>2</sub> exchange differed between natural and transplant lichen and moss plots. Our second objective was to determine whether the key functional relationships, including the gross primary productivity response to photosynthetic photon flux density, and the CO<sub>2</sub> flux response to soil volumetric water content, differed between natural and transplant plots. Our final objective was to quantify the decomposition rate under natural and transplant cover to determine whether this differs between treatments. We predicted that there would not be significant differences between natural and transplant patches, which would suggest

that transplant patches could persist on the landscape. Furthermore, we predicted that transplanting patches of lichen and moss would be a suitable approach for restoring lichen and moss cover and enhancing suitability of constructed turtle nesting habitat on rock barrens landscapes.

## Methods

### *Study area*

The eastern Georgian Bay landscape is characterized by wetland-filled valleys and bedrock-exposed uplands. Wetlands in this region are dominated by *Sphagnum* spp. and diverse vascular vegetation, including but not limited to leatherleaf (*Chamaedaphne calyculata*), jack pine (*Pinus banksiana*), tamarack (*Larix laricina*), and sedges (*Carex* spp.). The Canadian Shield granite upland rock barrens (Crins et al., 2009) have been shaped by erosion and currently exhibit a varying surface of shallow bedrock depressions, deeper crevices and smooth bedrock. The vegetation on the upland rock barrens include lichen (*Cladonia* spp.), moss (*Polytrichum* spp.), blueberry (*Vaccinium angustifolium*), juniper (*Juniperus communis*), and jack pine (*Pinus banksiana*). Species such as the snapping turtle (*Chelydra serpentina*), midland painted turtle (*Chrysemys picta marginata*), spotted turtle (*Clemmys guttata*), and Blanding's turtle (*Emydoidea blandingii*) are known to nest on this landscape (e.g. Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014).

The eastern Georgian Bay region has a cool-temperate and humid climate. The 26-year daily average maximum and minimum air temperatures for July – October are 18.9 and 6.9 °C, respectively (Government of Canada, 2019). In 2019, the average air temperature from July through October was 16.8 °C, with a maximum of 33 °C and a minimum of -0.6 °C. The 26-year

average cumulative rainfall from July – October is 394.6 mm (Government of Canada, 2019) and in 2019 the study area received 270.9 mm in that period.

### *Transplant and natural sites*

As part of another ongoing study, we constructed turtle nesting habitat using a novel approach specifically designed for the Canadian shield rock barrens of eastern Georgian Bay (Markle, unpublished data). The completed constructed sites had a soil depth of 0.2 m at the deepest point and an approximate area of 0.6 m<sup>2</sup>. With the soil in place, three lichen (*Cladonia* spp.), three mixed (*Cladonia* spp. and *Polytrichum* spp.), and three moss (*Polytrichum* spp.) patches from donor sites were transplanted to constructed nest sites (herein referred to as transplant sites; Table 3.1). Donor sites had a soil depth of less than 0.05 m to ensure that we were not disturbing existing nest habitat. Donor patches were removed from the bedrock by sliding our hands under the mat and carefully lifting it in one piece. The donor patches were then placed on the constructed nest site.

To evaluate the success of the transplanted lichen and moss patches, transplant sites were paired with undisturbed natural sites and were located within 10 m of each other (herein referred to as natural sites; Table 3.1). Natural sites were immediately adjacent to confirmed turtle nests to provide a direct assessment of suitable turtle nesting habitat. In total, six natural nest sites were monitored with varying cover types: three lichen- (*Cladonia* spp.), two mixed- (*Cladonia* spp. and *Polytrichum* spp.) and one moss-dominated (*Polytrichum* spp.).

**Table 3.1.** Site description and depths of both soil moisture and temperature probes (m).

Pair	Treatment	Cover	Depth of probes
1	Natural	Mixed	0.055
1	Transplant	Mixed	0.055
2	Natural	Mixed	0.05
2	Transplant	Mixed	0.05
3	Natural	Lichen	0.045
3	Transplant	Lichen	0.045
4	Natural	Lichen	0.055
4	Transplant	Lichen	0.055
5	Natural	Moss	0.05
5	Transplant	Moss	0.05
6	Natural	Lichen	0.075
6	Transplant	Lichen	0.075
7	Transplant	Moss	0.045
7	Transplant	Mixed	0.045
7	Transplant	Moss	0.045

### *CO<sub>2</sub> exchange*

Between July and October 2019, we measured CO<sub>2</sub> exchange at the 15 plots (six natural and nine transplant plots) using a closed static chamber (diameter = 10 cm, height = 15 cm, volume = 1.18 L) and an infrared gas analyzer (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-second period. CO<sub>2</sub> and photosynthetic photon flux density (PPFD;  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) were recorded every 5 seconds for 90 seconds. 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, and sheer shrouds, respectively. Chamber temperature and relative humidity were measured every 10 seconds using an iButton (Type 23, Alpha Mach, Quebec, Canada). Measurements were taken on 29 different days between 8:00 and 16:00 from 3 July to 17 October 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<sup>2</sup> value less than 0.5 were checked for error and removed if necessary (13% of measurements removed; cf. Harris et al., 2018). Net ecosystem productivity (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. We used SigmaPlot (V.14, Systat Software Inc.) to fit a rectangular hyperbola model to compare the GPP-PPFD relationship between treatment (natural, transplant), cover (lichen, mixed, moss) and season (wet,

dry; Bubier et al., 1998; Frohking et al., 1998). For each curve we determined the initial slope ( $\alpha$ ) and asymptote ( $GPP_{max}$ ) parameters.

### *Soil moisture and temperature*

From 3 July 2019 until 17 October 2019 continuous soil volumetric water content (VWC) and soil temperature were measured at all 15 plots. The VWC and temperature measurement depths were equivalent between paired plots but varied among pairs with a range of 0.045 to 0.075 m below the soil surface (in accordance with another ongoing study; Table 3.1). Soil VWC was measured every 15 minutes using a HOBO soil moisture smart sensor (0.05 m probe length, 0.3 L volume of influence, Onset HOBO S-SMxpM005, Massachusetts, USA) and logged using a HOBO Micro Station data logger (Onset HOBO H21-USB). Soil VWC probes were calibrated for the rock barrens soil according to Starr and Paltineanu (2002). Soil temperature was measured hourly using an iButton (iBWetland Type G). Temperature data were interpolated to 15-minute intervals to align with the soil VWC measurements. Air temperature was measured every 30 minutes at a meteorological station 1100 m from the sites.

### *Decomposition rates*

We used the Tea Bag Index (TBI) method to estimate relative differences in the decomposition rate and stabilization factor between each of our plots (Keuskamp et al., 2013). We measured the initial weight of non-woven polypropylene green (Lipton Indonesian tea Sencha tradition: EAN 87 22700 05552) and rooibos tea bags (Lipton Herbal infusion Rooibos - Rooibos and hibiscus: EAN 87 22700 188438) and buried them at an average soil depth of 0.064 m directly adjacent to the CO<sub>2</sub> collar. After 101 days the tea bags were removed and cleaned of external

debris. We dried the tea bags in an oven at 60 °C for 48 hours and then re-weighed the tea bags to determine final weight.

### *Analyses*

We conducted all statistical analyses in R 3.6.1 (R Core Team, 2019). We used a breakpoint analysis of cumulative rainfall (see Figure S2.1) to define a wet and dry period over the entire growing season (8 May and 17 October 2019). Using this approach, we defined the wet period as the 8 May to 24 June and 1 September to 17 October. The dry season began 25 June and ended 31 August. For this study, CO<sub>2</sub> data was only collected during the dry season (25 June to 31 August) and the second part of the wet season (1 September to 17 October), and these periods will be herein referred to as the wet and dry periods.

We used the *dabestr* package to compare CO<sub>2</sub> exchange between treatment (natural, transplant), cover (lichen, mixed, moss), and season (wet, dry) using estimation plots (Ho et al., 2019). We created the estimation plots using a 99% confidence interval to account for small, uneven sample sizes between cover types and seasons. To determine if the response of CO<sub>2</sub> exchange ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) to changing soil VWC ( $\text{m}^3 \text{m}^{-3}$ ) differed between treatment (natural, transplant) and cover (lichen, mixed, moss) we used the *lme4* package (Bates et al., 2015) to fit a linear mixed effects model (LMM) for each cover type with treatment and soil VWC as fixed effects and plot number as a random effect to account for repeated measures. The models were fit using restricted maximum likelihood. We used the method outlined in Keuskamp et al. (2013) to calculate the decomposition rate (k) and the stabilization factor (S) for each plot. We used an unpaired two-sample t-test to compare the mean decomposition rate and stabilization factor between natural and transplant plots. The data were normally distributed and had homogeneous

variance, with the exception of the mixed decomposition rate which was not normally distributed. To account for this, we used an unpaired two-sample Wilcoxon test to compare the mixed plots between treatments. Unless otherwise stated the reported error represents 99% confidence intervals.

## Results

### *CO<sub>2</sub> exchange*

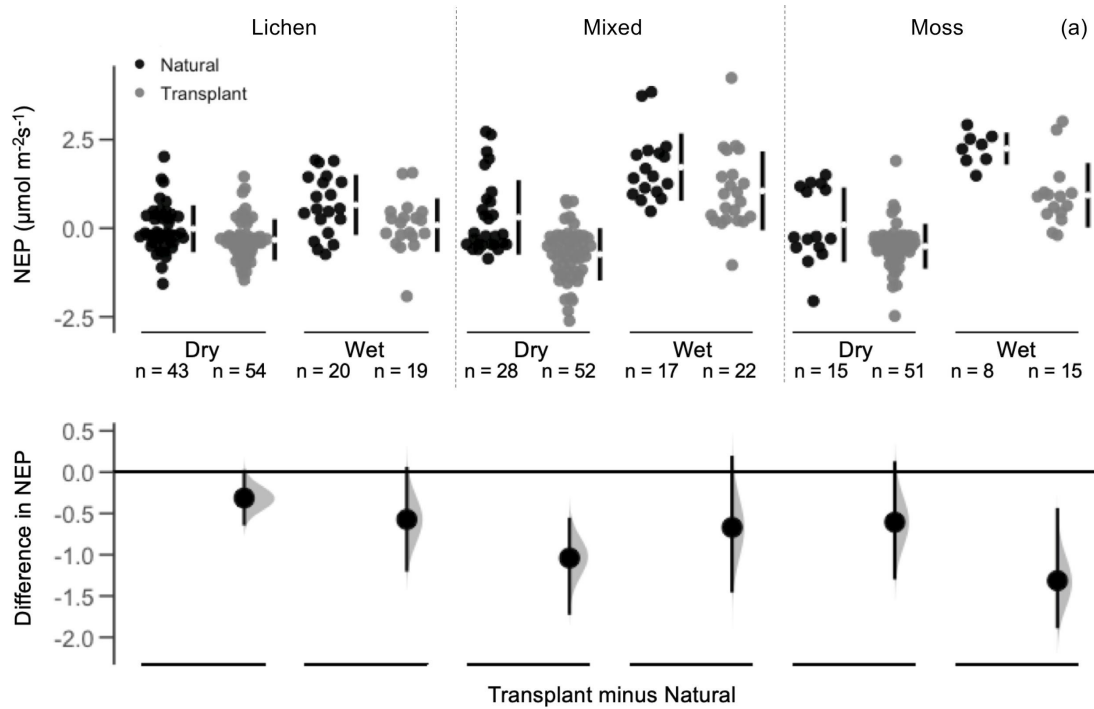
The natural and transplant lichen plots had a similar NEP for both the dry (mean difference of transplant minus natural  $\pm$  CI ( $\Delta$ ) =  $-0.31 \pm 0.34 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and wet ( $\Delta$  =  $-0.57 \pm 0.64 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) periods (Figure 3.1). Mixed transplants had a lower mean NEP than natural in the dry period ( $\Delta$  =  $-1.0 \pm 0.59 \mu\text{mol m}^{-2}\text{s}^{-1}$ ), while the NEP was similar between natural and transplant in the wet period ( $\Delta$  =  $-0.67 \pm 0.74 \mu\text{mol m}^{-2}\text{s}^{-1}$ ; Figure 3.1). The moss transplants had a similar NEP in the dry period ( $\Delta$  =  $-0.61 \pm 0.72 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and a lower NEP than natural plots in the wet period ( $\Delta$  =  $-1.31 \pm 0.73 \mu\text{mol m}^{-2}\text{s}^{-1}$ ; Figure 3.1).

Lichen ER was similar between transplant and natural plots in both the dry ( $\Delta$  =  $-0.11 \pm 0.2 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and wet ( $\Delta$  =  $-0.05 \pm 0.39 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) periods (Figure 3.2). Mixed transplant plots had a similar ER in the dry period ( $\Delta$  =  $-0.26 \pm 0.38 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and a greater ER in the wet period ( $\Delta$  =  $-0.30 \pm 0.26 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) when compared to the natural plots (Figure 3.2). Moss transplant plots were similar to natural plots in both the dry ( $\Delta$  =  $0.51 \pm 0.75 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and wet ( $\Delta$  =  $0.35 \pm 0.38 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) periods (Figure 3.2).

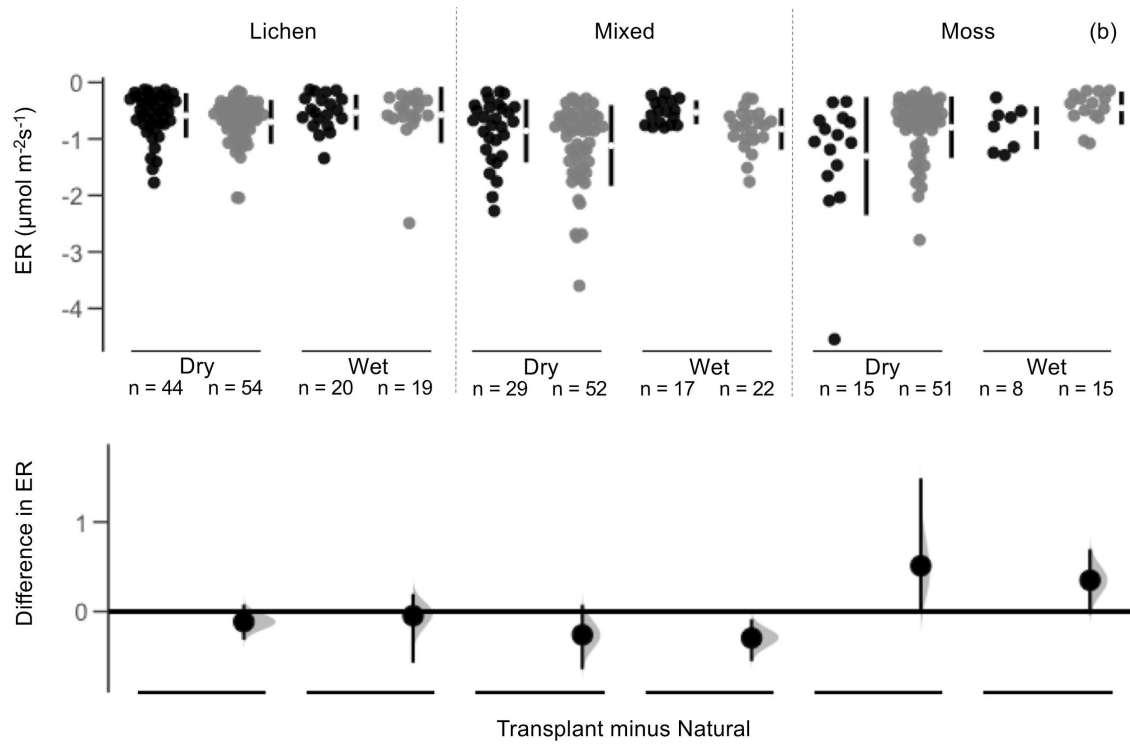
The lichen transplant plots had a similar GPP when compared to the natural plots in both the dry ( $\Delta$  =  $-0.21 \pm 0.34 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and wet ( $\Delta$  =  $0.60 \pm 0.62 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) periods (Figure 3.3). Mixed transplant plots had a lower GPP in the dry period ( $\Delta$  =  $-0.81 \pm 0.64 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and a



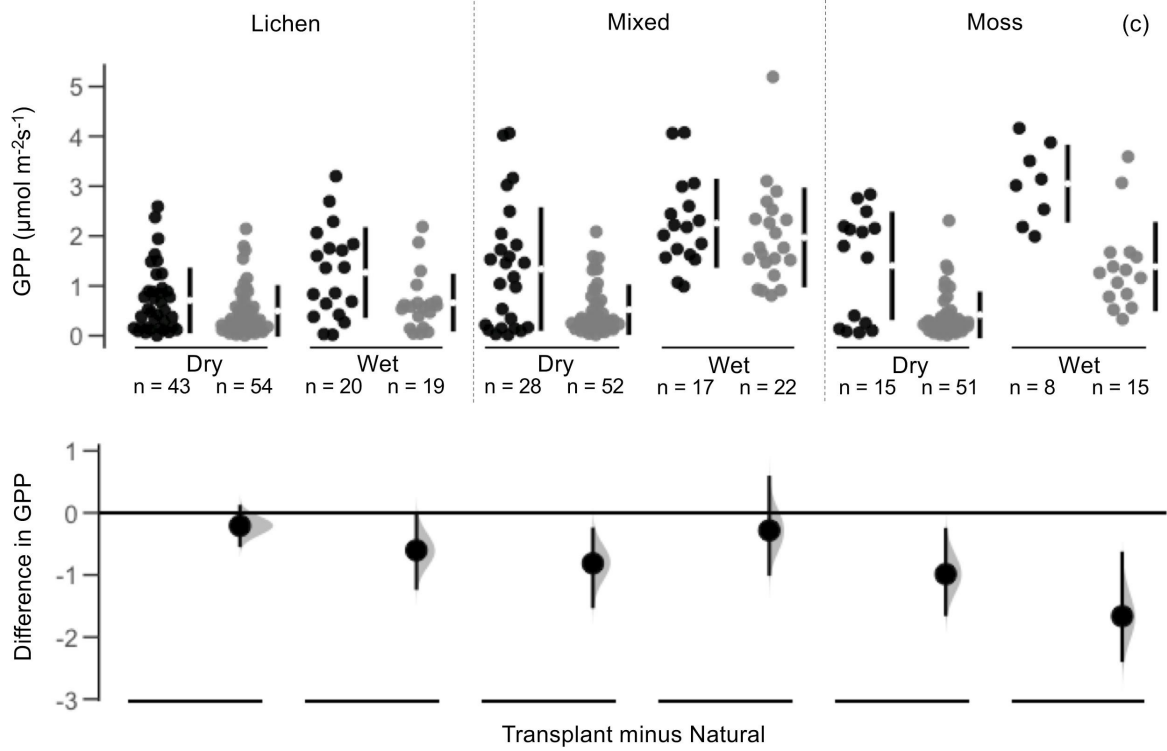
similar GPP in the wet period ( $\Delta = -0.28 \pm 0.8 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) when compared to natural plots (Figure 3.3). Moss GPP was lower in the transplant plots than natural plots during the dry period ( $\Delta = -0.99 \pm 0.71 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and the wet period ( $\Delta = -1.66 \pm 0.89 \mu\text{mol m}^{-2}\text{s}^{-1}$ ; Figure 3.3).



**Figure 3.1.** Mean differences in net ecosystem productivity (NEP) between transplant and natural plots ( $\pm$  99% confidence intervals) within season (wet, dry) and cover type (lichen, mixed, moss).

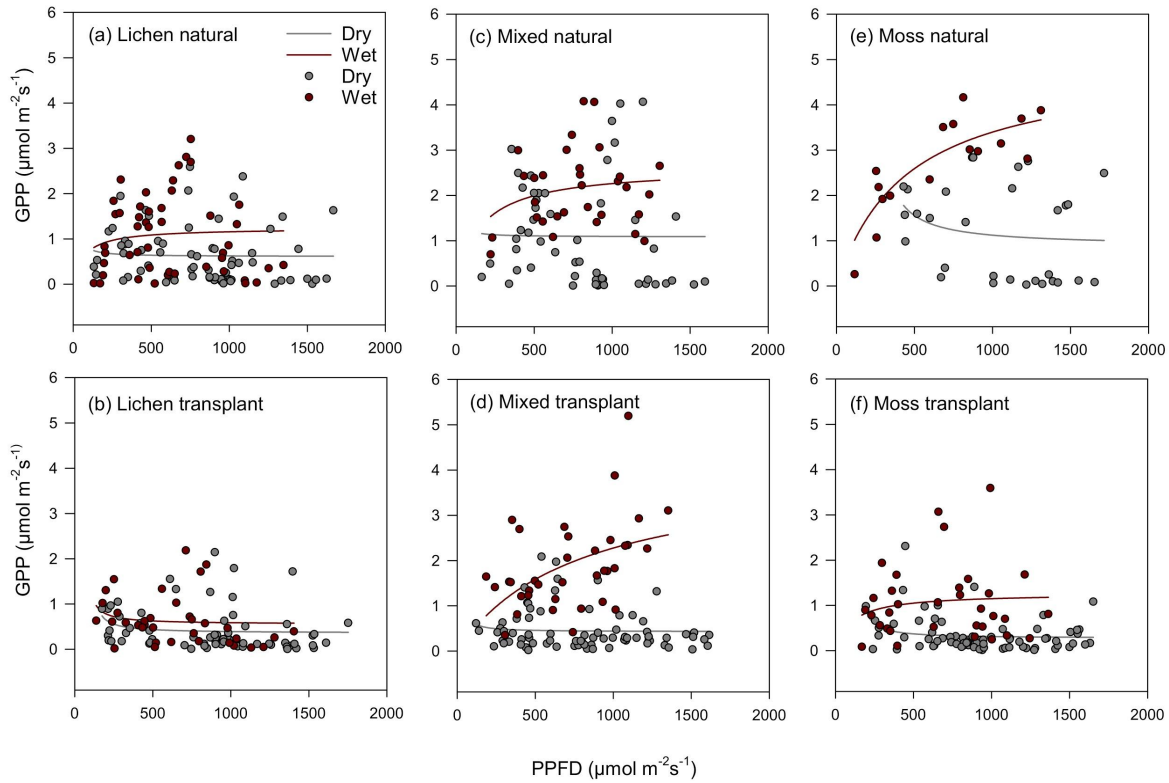


**Figure 3.2.** Mean differences in ecosystem respiration (ER) between transplant and natural plots ( $\pm 99\%$  confidence intervals) within season (wet, dry) and cover type (lichen, mixed, moss).



**Figure 3.3.** Mean differences in gross primary productivity (GPP) between transplant and natural plots ( $\pm$  99% confidence intervals) within season (wet, dry) and cover type (lichen, mixed, moss).

The GPP-PPFD relationship had a poor rectangular hyperbolic fit, due to highly variable measured data around the curve, for all cover types and seasons for both natural and transplant sites, with the exception of the moss transplant plots during the wet season (Figure 3.4). Lichen transplant plots (LT) had a lower initial slope ( $\alpha$ ) and  $GPP_{max}$  than natural (LN) in both the dry (LN:  $\alpha = -23.3$ ,  $GPP_{max} = 0.61$ ,  $R^2 = 0.002$ ; LT:  $\alpha = -89.84$ ,  $GPP_{max} = 0.36$ ,  $R^2 = 0.026$ ) and wet periods (LN:  $\alpha = 70.3$ ,  $GPP_{max} = 1.24$ ,  $R^2 = 0.018$ ; LT:  $\alpha = -58.73$ ,  $GPP_{max} = 0.55$ ,  $R^2 = 0.028$ ). Mixed transplant plots (MT) had lower initial slope ( $\alpha$ ) and  $GPP_{max}$  than natural (MN) in the dry period (MN:  $\alpha = -10.35$ ,  $GPP_{max} = 1.08$ ,  $R^2 = 0$ ; MT:  $\alpha = -33.93$ ,  $GPP_{max} = 0.43$ ,  $R^2 = 0.004$ ) and higher values in the wet period (MN:  $\alpha = 155.26$ ,  $GPP_{max} = 2.61$ ,  $R^2 = 0.072$ ; MT:  $\alpha = 778.25$ ,  $GPP_{max} = 4.05$ ,  $R^2 = 0.161$ ). Moss transplant plots (MoT) had lower initial slope ( $\alpha$ ) and  $GPP_{max}$  values than natural (MoN) in the dry period (MoN:  $\alpha = -218.06$ ,  $GPP_{max} = 0.88$ ,  $R^2 = 0.057$ ; MoT:  $\alpha = -136.36$ ,  $GPP_{max} = 0.27$ ,  $R^2 = 0.066$ ) and the wet period (MoN:  $\alpha = 451.68$ ,  $GPP_{max} = 4.93$ ,  $R^2 = 0.73$ ; MoT:  $\alpha = 103.92$ ,  $GPP_{max} = 1.27$ ,  $R^2 = 0.02$ ) when compared to the natural plots.

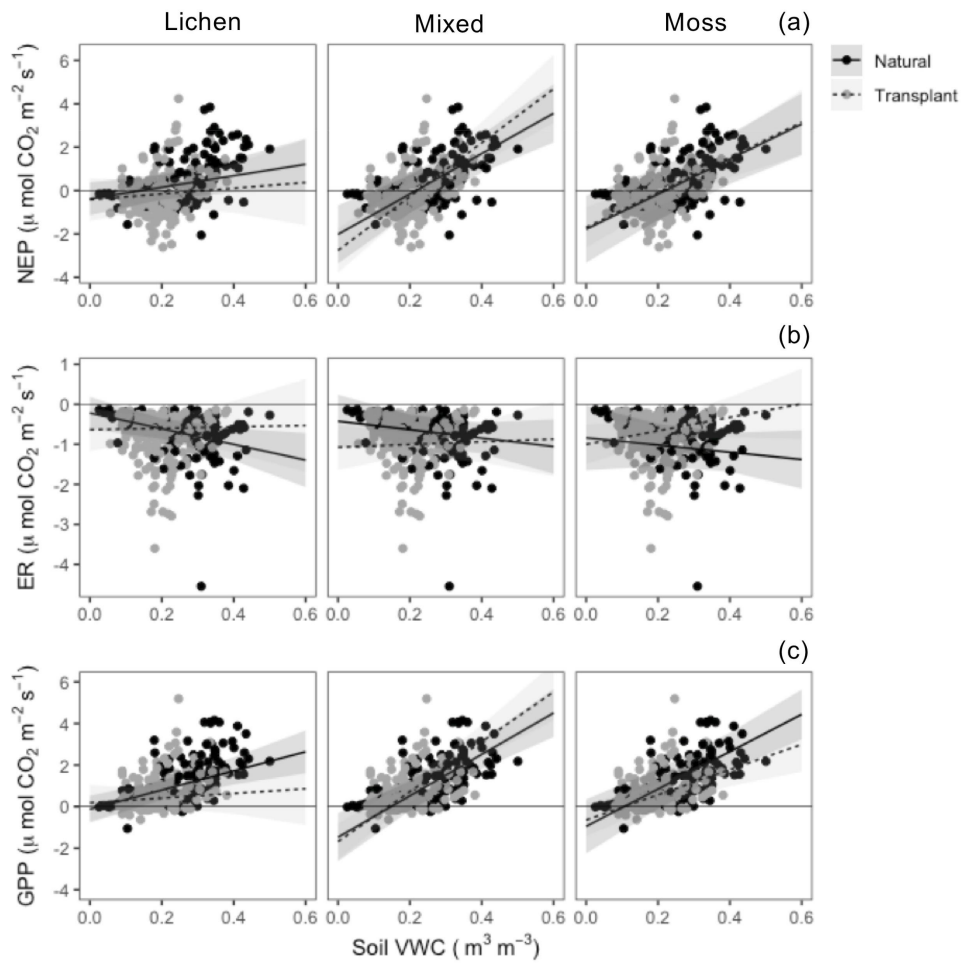


**Figure 3.4.** Relationship between incoming photosynthetic photon flux density (PPFD,  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) and gross primary productivity (GPP,  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) for natural lichen (a) during the wet ( $\alpha = 70.3$ ,  $\text{GPP}_{\text{max}} = 1.24$ ,  $R^2 = 0.018$ ) and dry period ( $\alpha = -23.3$ ,  $\text{GPP}_{\text{max}} = 0.61$ ,  $R^2 = 0.002$ ), transplant lichen (b) during the wet ( $\alpha = -58.73$ ,  $\text{GPP}_{\text{max}} = 0.55$ ,  $R^2 = 0.028$ ) and dry period ( $\alpha = -89.84$ ,  $\text{GPP}_{\text{max}} = 0.36$ ,  $R^2 = 0.026$ ), natural mixed (c) during the wet ( $\alpha = 155.26$ ,  $\text{GPP}_{\text{max}} = 2.61$ ,  $R^2 = 0.072$ ) and dry period ( $\alpha = -10.35$ ,  $\text{GPP}_{\text{max}} = 1.08$ ,  $R^2 = 0$ ), transplant mixed (d) during the wet ( $\alpha = 778.25$ ,  $\text{GPP}_{\text{max}} = 4.05$ ,  $R^2 = 0.161$ ) and dry period ( $\alpha = -33.93$ ,  $\text{GPP}_{\text{max}} = 0.43$ ,  $R^2 = 0.004$ ), natural moss (e) during the wet ( $\alpha = 451.68$ ,  $\text{GPP}_{\text{max}} = 4.93$ ,  $R^2 = 0.73$ ) and dry period ( $\alpha = -218.06$ ,  $\text{GPP}_{\text{max}} = 0.88$ ,  $R^2 = 0.057$ ); and transplant moss (f) during the wet ( $\alpha = 103.92$ ,  $\text{GPP}_{\text{max}} = 1.27$ ,  $R^2 = 0.02$ ) and dry period ( $\alpha = -136.36$ ,  $\text{GPP}_{\text{max}} = 0.27$ ,  $R^2 = 0.066$ ). GPP and PPFD calculated

from field CO<sub>2</sub> and PPFD measurements for natural lichen (a), transplant lichen (b), natural mixed (c), transplant mixed (d), natural moss (e), and transplant moss (f) during the wet (red points) and dry (grey points) periods.

*Predicted response to temperature and moisture*

The predicted slope of NEP and soil VWC, did not differ significantly between transplant and natural plots for lichen (LMM, estimate [est.]  $\pm$  standard error [SE] =  $-1.67 \pm 2.05$ ,  $t = -0.82$ ,  $p = 0.42$ ), mixed (LMM, est.  $\pm$  SE =  $3.23 \pm 2.95$ ,  $t = 1.1$ ,  $p = 0.27$ ) or moss (LMM, est.  $\pm$  SE =  $0.18 \pm 2.45$ ,  $t = 0.07$ ,  $p = 0.94$ ) plots (Figure 3.5). The predicted response of ER to changing soil VWC did not differ significantly between transplant and natural plots for lichen (LMM, est.  $\pm$  SE =  $2.09 \pm 1.14$ ,  $t = 1.83$ ,  $p = 0.07$ ), mixed (LMM, est.  $\pm$  SE =  $1.39 \pm 1.71$ ,  $t = 0.81$ ,  $p = 0.42$ ) or moss (LMM, est.  $\pm$  SE =  $2.6 \pm 1.8$ ,  $t = 1.45$ ,  $p = 0.15$ ) plots (Figure 3.5). The predicted response of GPP to changing soil VWC did not differ significantly between transplant and natural plots for lichen (LMM, est.  $\pm$  SE =  $-3.64 \pm 1.94$ ,  $t = -1.88$ ,  $p = 0.068$ ), mixed (LMM, est.  $\pm$  SE =  $2.2 \pm 2.68$ ,  $t = 0.82$ ,  $p = 0.41$ ) or moss (LMM, est.  $\pm$  SE =  $-2.82 \pm 2.0$ ,  $t = -1.41$ ,  $p = 0.16$ ) plots (Figure 3.5).

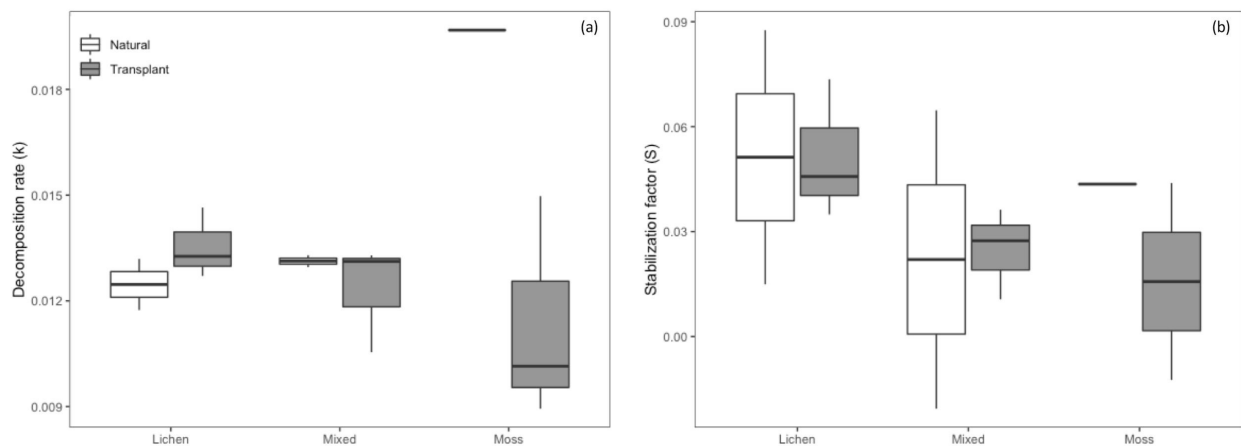


**Figure 3.5.** Predicted response of (a) net ecosystem productivity (NEP), (b) ecosystem respiration (ER), and (c) gross primary productivity (GPP) to increasing soil volumetric water content (VWC;  $\text{m}^3 \text{m}^{-3} \pm 95\%$  confidence intervals) according to the linear mixed effects models for natural (solid line) and transplant plots (dashed line). NEP (a), ER (b), and GPP (c) calculated from field  $\text{CO}_2$  measurements for natural (black points) and transplant plots (grey points).



### Decomposition rates

When cover types (lichen, mixed, moss) were grouped into two treatments (natural, transplant), the mean decomposition rates did not differ between natural (0.014) and transplant (0.012) treatments ( $t = 1.28$ ,  $df = 12$ ,  $p = 0.22$ ; Figure 3.6). The mean stabilization factors were also similar between natural (0.038) and transplant (0.031) treatments ( $t = 0.42$ ,  $df = 12$ ,  $p = 0.68$ ; Figure 3.6). The natural and transplant treatments had similar decomposition rates within the lichen ( $t = -1.16$ ,  $df = 3$ ,  $p = 0.33$ ), mixed ( $W = 4$ ,  $p = 0.77$ ), and moss ( $t = 2.26$ ,  $df = 2$ ,  $p = 0.15$ ) cover types (Figure 3.6). Furthermore, the stabilization factors did not differ between natural and transplant treatments for lichen ( $t = -0.004$ ,  $df = 3$ ,  $p = 1.0$ ), mixed ( $t = -0.08$ ,  $df = 3$ ,  $p = 0.94$ ) or moss ( $t = 0.86$ ,  $df = 2$ ,  $p = 0.48$ ) plots (Figure 3.6).



**Figure 3.6.** Differences in decomposition rate (a) and stabilization factor (b) between natural and transplant within each cover type (lichen, mixed, moss).

## Discussion

Lichen CO<sub>2</sub> exchange was similar between natural and transplant plots in both the wet and dry season (Figures 3.1 – 3.3) suggesting that transplanting in-tact lichen patches does not significantly affect lichen productivity. Furthermore, we found that the CO<sub>2</sub> flux response to changing soil volumetric water content (VWC) did not differ between natural and transplant lichen mats (Figure 3.5) which is critical since soil VWC is a known control on the net ecosystem productivity (NEP), ecosystem respiration (ER) and gross primary productivity (GPP) of lichen and moss (see Chapter 2). Moreover, we found the relationship between GPP and photosynthetic photon flux density (PPFD) to be similar between natural and transplant lichen plots (Figure 3.4) which further supports our finding that in-tact lichen patches can be transplanted successfully. Our results are consistent with similar studies where researchers documented growth of in-tact lichen patches following transplant (*e.g.* Gilbert, 2001; Roturier & Bergsten, 2009; Sonesson et al., 2007). Roturier and Bergsten (2009) used repeated photographs to monitor the growth of transplant lichen patches over 6 years and found that the transplant patches maintained a higher lichen cover when compared to fragment dispersal plots. Furthermore, Sonesson et al. (2007) transplanted *Nephroma arcticum* lichens between elevations and found that lichens were able to effectively acclimate to new environmental conditions. In addition, the high-altitude lichen transplants had increased net photosynthesis when compared to the natural controls (Sonesson et al., 2007). Together, the previous literature from non-rock barrens ecosystems and our findings suggest that transplanting lichen patches should be a suitable approach for maintaining lichen cover on rock barrens landscapes.

We found that plots containing moss had greater differences in CO<sub>2</sub> exchange between the transplant and natural treatments, suggesting that the in-tact transplants of moss were less

successful than the lichen transplants with regards to productivity. Our finding contradicts previous studies which successfully transplanted *Polytrichum* spp. patches (e.g. Groeneveld et al., 2007; Groeneveld & Rochefort, 2005). It is possible that our moss transplants were less productive because two of the three transplant patches were from a partially shaded donor site with poor drainage. When the patches were transplanted to the receptor site, which had no canopy cover and drained well, they potentially became stressed and therefore less productive. Another possible explanation for the differences between natural and transplant moss plots could be the timing of transplant. Because we paired the transplant plots with confirmed turtle nests, we had to move the lichen and moss in late June. It is possible that the moss transplants were moisture stressed given the dry conditions for two months following transplant (see Chapter 2) and were unable to recover in the fall. Conversely, lichens become dormant under dry conditions and can rapidly return to productivity when water becomes available, which could explain the discrepancy between cover types. Moss has a higher growth rate than lichens (Smith, 1962) and previous research has shown that moss can establish from fragments in approximately three years (Graf & Rochefort, 2010). Given our results and existing literature, fragment dispersal is possibly a more effective long-term approach for increasing moss cover.

We further determined that both the decomposition rates and stabilization factors were similar in natural and transplant plots (Figure 3.6). We used the tea bag index method which allows us to compare the decomposition between plots without having to consider variation in litter, thus the method allows us to examine how decomposition varies under the different environmental conditions between sites (Didion et al., 2016; Keuskamp et al., 2013). Given the fact that decomposition is largely controlled by temperature and moisture conditions (Coûteaux et al., 1995; Trofymow et al., 2002), our tea bag index results provide support for our hypothesis that

transplanted lichen and moss patches can provide the same conditions that natural plots do. While our results may be unsurprising given that our sites are located within 300 m of each other, these findings still support our conclusion that, at least initially, transplanting lichen cover is a viable approach for restoring lichen mats on a landscape. Our observed decomposition rates and stabilization factors are on the lower end of the data presented for a range of ecosystems in Keuskamp et al. (2013) and are most similar to wet forest, pasture, and peat environments. This is surprising, as we expected that the relatively high temperatures of rock barrens landscapes (Keever et al., 1951; Lange, 2001) would lead to higher rates of decomposition. Decomposition varies under different environmental conditions and we found that it did not differ between our natural and transplant plots, thereby suggesting the transplant plots were providing similar environmental conditions to the natural plots. These results support our conclusion that transplanting lichen patches is a viable restoration approach.

Our results have important implications for maintaining the total area of lichen mats on rock barrens landscapes in an era of unprecedented natural and human disturbance. This is a critically important finding because not only are lichens essential for primary soil formation and ecosystem succession, they also provide suitable turtle nesting habitat on rock barrens landscapes in the eastern Georgian Bay region. As such, we suggest that a constructed turtle nest design for rock barrens regions should incorporate lichen as the dominant cover type.

The two common approaches for maintaining or increasing lichen cover through restoration are fragment dispersal and transplanting in-tact patches, as we did in this study. Fragment dispersal is less suitable for rock barrens landscapes as lichen fragments have slow growth rates (*e.g.* Carroll & Bliss, 1982; Crittenden, 2000; Dunford et al., 2006; Roturier et al., 2007) and there is high potential for disturbance by wind, runoff, and animals (Duncan, 2015;

Roturier et al., 2007; Roturier & Bergsten, 2009). Our findings are therefore critical, as they suggest that the in-tact transplant approach is viable for use on rock barrens landscapes. For example, this restoration method could be applied in a situation where a planned disturbance, such as highway expansion, is expected to disturb turtle species-at-risk nesting habitat by crushing lichen mats or disrupting the hydrologic regimes necessary for lichen growth. Our study has shown that instead of destroying the lichen mats, which take decades to form and are critical ecosystem resources, they can be transplanted out of the impact footprint to a nearby undisturbed area. In the case where there is not a suitable area nearby to receive the transplant patches, lichens can be stored for up to three years (Glaholt et al., 1997; Honegger, 2003) or propagated in a greenhouse for use in future restoration projects (Duncan, 2015).

Lichen patch restoration can be applied in various ecosystems and used to improve ecohydrological conditions. For example, caribou and reindeer populations rely on lichen (*e.g.* *Cladonia* spp.) for nutrition during the winter (Bergerud, 1972; Danell et al., 1994; Inga, 2007). The habitat used by caribou and reindeer is often disturbed by overgrazing or industry (*e.g.* forestry, mining; Berg et al., 2008; Duncan, 2015), and lichen restoration could mitigate the impact of these disturbances. In arid environments, lichen and moss transplants could be used to form or enhance soil crusts which can improve soil quality (Maestre et al., 2011) and provide habitat for fauna (*e.g.* Lalley et al., 2006). Wildfire significantly decreases the volume of soil available on rock barrens landscapes (Markle et al., 2020), and given that lichen and moss are essential for primary soil formation, restoration of lichen and moss mats could jumpstart ecosystem recovery. On bedrock landscapes, lichen and moss patches also provide an essential storage unit for runoff, thereby increasing infiltration and reducing surface runoff (Spence & Woo, 2002). When considering the application for turtle nesting, this in-tact patch transplant approach can be used to

restore suitable nesting habitat by enhancing artificial nest construction on rock barrens landscapes. In summary, we have found that transplanting lichen patches will not impact the productivity of the lichen, and as such this method can be used to rapidly increase lichen cover in a range of ecosystems, including the rock barrens landscape.

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## Chapter 4: General Conclusion

Lichen and moss are the dominant ground cover on the rock barrens of eastern Georgian Bay, and they play a crucial role in the ecosystem as pioneering organisms, which are among the first to colonize open bedrock and jumpstart ecosystem succession (Burbanck & Platt, 1964; Keever et al., 1951). When lichen and moss colonize, they begin to develop and accumulate soil by chemically weathering the rock to create mineral soil (Jackson, 2015), decaying and forming organic soil (Keever et al., 1951), and trapping particles from wind and runoff (Burbanck & Platt, 1964). Further, the lichen and moss are able to stabilize the soil deposits by reducing erosion (Aguilar et al., 2009; Belnap & Gillette, 1998; Chamizo et al., 2017). Another role lichen and moss play in the ecosystem is moderating and improving the microclimate, which allows more complex vegetation to establish (Burbanck & Platt, 1964; Keever et al., 1951). Beyond their function in ecosystem succession, lichen and moss also provide habitat for species-at-risk wildlife. For example, lichen are a critical food source for caribou and reindeer in boreal and tundra regions (Bergerud, 1972; Danell et al., 1994; Inga, 2007). In arid regions, lichen and moss form biological soil crusts which improve soil nutrients (*e.g.* Chamizo et al., 2012) and provide habitat for microfauna such as arthropods (*e.g.* Lalley et al., 2006). On the rock barrens landscape of eastern Georgian Bay, the lichen and moss provide nesting habitat for turtle species-at-risk (*e.g.* Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014). However, lichen and moss are vulnerable to climate change and disturbance, and as such understanding the growth and persistence of these ecosystem resources is a critical research need in order to effectively conserve turtle nesting habitat.

In chapter two we determined that the wet periods (spring and fall) of the growing season are critical for the growth of lichen and moss in rock barrens ecosystems. Furthermore, we

determined that soil moisture is the most important control on lichen and moss CO<sub>2</sub> exchange, and that lichen and moss do not respond in the same way to changes in soil moisture. These results have important implications when considering the impact of climate change on rock barrens landscapes. As the climate changes, drought frequency and severity are expected to increase (Dai et al., 2004; Price et al., 2013; Trenberth et al., 2007), and in the northern hemisphere summer-like conditions are expected to become more frequent (Trenberth et al., 2007; Vrac et al., 2014; Walther et al., 2002). If we begin to see drier conditions on the rock barrens, lichen and moss will have shorter periods where CO<sub>2</sub> uptake is possible and annual productivity will likely decline. Lichen will be more impacted than moss, as moss has a greater CO<sub>2</sub> uptake at lower soil moisture contents when compared to lichen. This difference could lead to a greater proportion of moss on the landscape relative to lichen. A lower proportion of lichen on the landscape would negatively impact turtles as they primarily select lichen-dominated soil deposits for nesting. Further, lower productivity of lichen and moss will likely lead to reduced chemical weathering, and therefore less soil development on the landscape. A decline in soil development will reduce available nesting habitat as smaller-bodied turtles nest in 8 – 15 cm of soil on a rock barrens landscape (Markle et al., 2020). In summary, we determined that lichen and moss productivity will likely decline as a result of increasingly limited soil moisture, and this will have negative implications for the integrity of rock barrens ecosystems.

In chapter three we determined that lichen productivity and decomposition were similar between transplant and natural patches, which suggests that transplanting in-tact patches of lichen is a feasible restoration approach. Conversely, we found some differences in moss productivity between transplant and natural patches which implies that fragment dispersal may be a better method for moss restoration. While fragment dispersal is feasible for moss, which can form a mat

from fragments in two to three seasons (Graf & Rochefort, 2010; Roturier et al., 2007), it is less reasonable for lichens which can take up to 45 years to form a mat (Carroll & Bliss, 1982; Crittenden, 2000; Dunford et al., 2006; Roturier et al., 2007). By transplanting in-tact patches of lichen out of an impact footprint, we can use the transplant patches to restore habitat and provide lichen cover. Transplanting patches allows us to immediately recover the ecosystem services that lichens provide, rather than having to wait decades for fragments to establish. On the eastern Georgian Bay rock barrens lichen mats are essential turtle nesting habitat (Litzgus & Brooks, 1998; Markle & Chow-Fraser, 2014) and restoration methods are often needed following disturbance from construction or wildfire. If we can transplant lichen and moss out of the footprint of a planned impact, we can move the transplants to an undisturbed portion of the landscape and restore nesting habitat in that area. This transplant approach can likely be applied in other ecosystems, such as boreal forests and tundra regions where caribou and reindeer rely on lichen as a food source (Bergerud, 1972; Danell et al., 1994; Inga, 2007), and in arid regions where lichen and moss are essential for stabilizing soil (Aguilar et al., 2009; Belnap & Gillette, 1998; Chamizo et al., 2017) and providing habitat for microfauna (*e.g.* Lalley et al., 2006). In chapter three we tested an understudied restoration approach for lichen and moss, and we determined that transplanting intact lichen patches is possible on rock barrens landscapes and can be applied prior to destruction from planned disturbances to preserve lichens.

In summary, this thesis has expanded the knowledge of lichen and moss on rock barrens landscapes. We have explored the ecohydrological controls that govern lichen and moss growth in eastern Georgian Bay, and we have defined peak growth periods. We then applied that knowledge and our understanding of the rock barrens landscape to transplant lichen and moss as in-tact patches. Through this experiment we have determined that transplanting lichen patches is a

feasible approach that can be applied to protect the slow-growing lichens and reduce long term impacts on turtle nesting habitat in the eastern Georgian Bay region. Lichen and moss grow around the world, and we believe that in addition to eastern Georgian Bay, our findings will be relevant for ecosystems globally. Our chapter two findings will add to the literature and understanding of lichen and moss growth, and our chapter three findings indicate that lichen transplants can be successful, and we believe they can be applied in other ecosystems as well. In terms of future work, the in-tact transplant approach should be studied for a longer time period and in a variety of ecosystems. Further, the moss transplant experiment should be repeated under higher moisture conditions to see if the moss transplants can maintain the same productivity as natural patches when water is more available. Overall, this thesis has contributed to the knowledge and understanding of lichen and moss persistence on rock barrens landscapes, and we have provided evidence of a restoration approach that could be used to restore surface cover characteristic of suitable turtle nesting habitat in rock barrens ecosystems.



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