Oecologia (2023) 202:55–67
https://doi.org/10.1007/s00442-023-05369-y

ORIGINAL RESEARCH

Diversity and assembly of lichens and bryophytes on tree trunks along a temperate to boreal elevation gradient

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Received: 14 February 2022 / Accepted: 2 April 2023 / Published online: 20 April 2023
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Abstract

Based on hypotheses related to environmental filtering vs. stochastic community assembly, we tested taxon-specific predictions regarding the relationships of alpha diversity, beta diversity and species composition of epiphytic macrolichens and bryophytes with elevation and the lateral gradient on trees (the different sides of the tree bole related to aspect and trunk inclination) at Parc national du Mont-Mégantic in Southeastern Québec, Canada. For lichens on firs, increasing elevation was associated with increasing alpha diversity, and a marked shift in community composition, at the scale of whole trees. In contrast, for bryophytes on maples, tree inclination and the lateral gradient had the strongest effects: more inclined trees had greater whole-tree alpha diversity and stronger within-tree contrasts in composition between the upper and lower bole surfaces. For lichens on maples, whole-tree alpha diversity showed a weak, negative relationship with inclination, and beta diversity increased slightly with elevation. Our results are consistent with theories predicting greater alpha diversity in more favorable environments (for lichens: high elevation with high relative air humidity and lower temperatures; for bryophytes: upper surfaces of tree boles with liquid water available), but support was weak for the prediction of greater beta diversity in more favorable environments. Overall, the important predictors of epiphytic cryptogam diversity vary more among the species of tree host (maple vs. fir) than focal taxa (lichens vs. bryophytes), with patterns likely related to different effects of water, temperature, and competition between lichens and bryophytes.

Keywords Lichen ecology · Bryophyte ecology · Alpha diversity · Beta diversity · Elevation gradients

Introduction

In community ecology, the degree to which deterministic or stochastic processes dominate assembly from the species pool is expected to have predictable consequences for patterns of species diversity and composition (Mittelbach and McGill 2019; Vellend 2016). In environments considered "challenging" for a particular group of organisms, such as ones with low productivity or a high rate of disturbance, deterministic environmental filters are expected to select for the relatively few species that tolerate these conditions (Chase 2003; Whittaker 1960). Therefore, in challenging environments, one would expect to see low diversity within sites (alpha diversity) and minimal differences in composition among sites (i.e., low beta diversity) (Chase 2003, 2010; Whittaker 1960). In contrast, in less challenging environments, more species are likely to be able to colonize a given site, and different community trajectories, depending on stochastic differences in colonization history, are expected to increase alpha and beta diversity among environmentally similar sites (Chase 2010).

For autotrophic organisms, most studies examining community patterns along environmental gradients are of vascular plants (Van der Maarel and Franklin 2012; Vellend et al. 2017). Whittaker (1960) mentions the tendency to find greater alpha diversity of vascular plants in more "favorable" conditions, e.g., warm and moist, and lower

Communicated by Anne Pringle.

We have revealed some surprising insights into the mechanisms of community assembly in an understudied group of organisms, pointing to the utility of this model system in studies in plant ecology.

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alpha diversity in "unfavorable" conditions, e.g., cold, arid, saline, or nutrient-poor. Harrison et al. (2011) re-analyzed Whittaker's dataset of vascular plants to quantitatively show that "structured" beta diversity (e.g., compositional turnover along one gradient) was higher in more productive (e.g., less stressful) areas. Although patterns of species diversity along environmental gradients are highly variable (Scheiner and Willig 2005), vascular plant biodiversity is often highest under warm and humid conditions (Vellend et al. 2017).

Lichens and bryophytes (collectively "cryptogams") are studied less frequently, despite playing major roles in ecosystem functioning, such as water and nutrient cycling, and as food and shelter for animals (Sillett and Antoine 2004). Lichens are an association between a fungus or fungi and an algal or cyanobacterial photobiont (Nash 2008); bryophytes are small spore-producing plants (Buck et al. 2009; Goffinet et al. 2009). Both taxa are poikilohydric, with little ability to regulate water internally; thus, their water status varies with surrounding environmental conditions (Proctor 2000; Nash 2008). Cryptogams are nonetheless desiccation-tolerant, able to dry to equilibrium with air humidity and then resume metabolic activity after rehydration (Proctor 2000; Nash 2008).

Lichens and bryophytes also have important differences. First, many species of lichens can obtain moisture from water vapor during periods of high relative air humidity (Lange et al. 1986, 1988; Phinney et al. 2019). In contrast, most bryophytes are reliant on liquid water (Proctor 2000; Proctor et al. 2007), mostly from rainfall (Proctor 2000), but also from dew (Csintalan et al. 1999), or cloud droplets (Leon-Vargas et al. 2006). Second, for lichens, oversaturation with water can limit photosynthesis via limited CO_2 diffusion (Lange et al. 1993, 2001), whereas most bryophytes can thrive under continuously wet conditions (Proctor 2000). Finally, net photosynthesis is positive at a lower and narrower range of temperatures for lichens (Palmqvist 2008) than for bryophytes (Furness and Grime 1982; Liu et al. 2001). As such, theory predicts different diversity patterns along environmental gradients for epiphytic bryophytes and lichens, with bryophyte diversity more sensitive to liquid water availability, and lichen diversity more sensitive to air humidity and temperature.

Elevation gradients offer a powerful means for testing ecological responses of organisms to environmental conditions (McCain and Grytnes 2010). Climatic conditions, particularly temperature and humidity, are correlated with elevation (McCain and Grytnes 2010); consistent with theory, alpha diversity of several taxa often declines under the challenging climatic conditions at the highest elevations (McCain and Grytnes 2010), as at our field site for vascular plants (Becker-Scarpitta et al. 2020; Savage and Vellend 2015). Elevation gradients of lichen alpha diversity vary among substrate(s) and regions. For epiphytic and/or corticolous lichens in temperate and boreal regions, alpha diversity appears to increase with elevation (Cobanaglu and Sevgi 2009; Bässler et al. 2015; Nascimbene and Marini 2015; Boch et al. 2019; Belguidoum et al. 2021), while some lichen studies on multiple substrates report mid-elevation peaks (Negi and Upreti 2000; Pinokiyo et al. 2008; Rapai et al. 2012). Lichen species composition varies with elevation, although we are aware of only a few studies that assess how beta diversity within a given elevation band varies across the elevation gradient. For arboreal epiphytes and/or corticolous bryophytes, alpha diversity is highest at mid-elevations (Wolf 1993; Ah-Peng et al. 2012; Spitale 2016; Boch et al. 2019; Marline et al. 2020) or low elevations (Mucina et al. 2000). For bryophytes on non-arboreal substrates, alpha diversity may increase with elevation (Lee and La Roi 1979a; Grau et al. 2007; Stehn et al. 2010) or show no relationship (Slack 1977; Grytnes et al. 2006). In our study area, alpha and beta diversity of terricolous bryophytes did not relate to elevation (Becker-Scarpitta and Vellend 2020). Rather, microclimatic patterns of moisture availability may better explain their diversity patterns (Lee and La Roi 1979b; Grytnes et al. 2006).

Patterns in epiphytic lichen and bryophyte communities can also vary within individual host trees, due to "lateral" gradients around the tree bole (Ellis 2012). As one moves horizontally around a tree trunk, moisture and surface temperature change due to the influence of aspect or tree inclination. Lateral gradients present an opportunity for far greater replication than for other commonly studied gradients (e.g., elevation or latitude). In our study area, Parc national du Mont-Mégantic, Québec, Canada, deciduous and coniferous trees present different lateral gradients. Many deciduous trees have leaning boles and the angle of inclination influences microclimatic contrasts, typically resulting in an upper surface that receives more moisture via precipitation interception (Merrifield 2000) and stem flow (Ryan 1991) than the lower, drier surface (Fig. 1). Several studies suggest that stronger competitors dominate the upper (wetter) surfaces of the trunk (Barkman 1958)—in most cases faster growing and taller bryophytes—whereas lichens appear better able to withstand the lower, drier surfaces of the tree bole (Pike et al. 1975; Kenkel and Bradford 1986; Kuusinen 1994; McCune et al. 2000). In contrast, conifers grow mostly straight in our study area, and their architecture tends to channel water away from the trunk and inner canopy (Barkman 1958; Beier et al. 1993). Thus, aspect is likely a greater influence on the microclimate of the lateral gradient (Fig. 1). Some studies suggest that aspect plays a role in influencing lichen communities, specifically with greater frequencies, diversity, or cover of epiphytic species on the north aspect, where microclimatic conditions are cooler and more humid, and where sun exposure is lower (Gough 1975; Lang et al. 1980; Yarranton 1972).

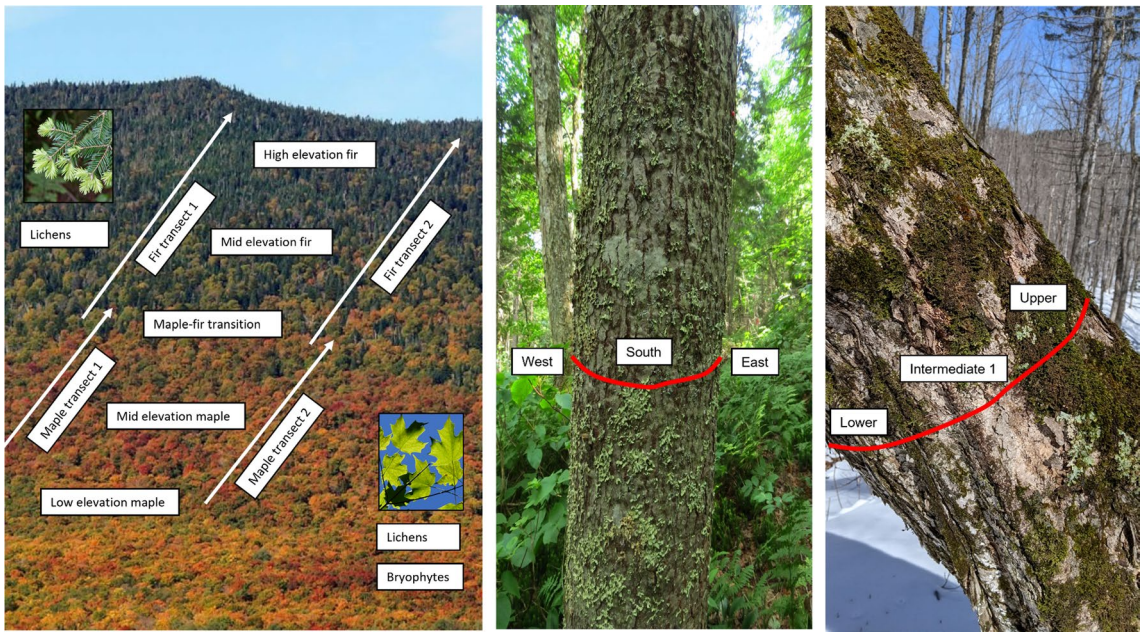


Fig. 1 Gradients and communities at Mont Mégantic. **a** The elevation gradient, divided into maple transects (low elevation to mid-elevation transition zone) and fir transects (mid-elevation transition zone–high-elevation coniferous forests). Three communities were studied: (i) lichens and (ii) bryophytes on maple trees and (iii) lichens on fir trees. Panels **b** and **c** show the lateral gradients of (**b**) firs (west, south, east, and north (not pictured)) and **c** maples (upper, intermediate 1, intermediate 2 (not pictured) and lower). The photo in (**a**) was taken in autumn, when sugar maple leaves turn orange and red

In this study, one of the few to examine diversity patterns in both lichens and bryophytes along multiple gradients, we report patterns of alpha diversity, beta diversity, and composition of three epiphytic communities (lichens on maples, bryophytes on maples, and lichens on firs) along elevation and lateral gradients at Parc national du Mont-Mégantic. Our predictions are based on the hypotheses that benign conditions favor alpha and beta diversity (Chase 2003, 2010; Whittaker 1960) and the contrasting physiologies between taxa (as described above): lichens are more sensitive to relative air humidity and temperature, whereas bryophytes are more sensitive to liquid moisture. We predicted that: (i) for lichens on both maples and firs, elevation is a stronger predictor of diversity and composition than tree bole inclination; we expected both whole-tree alpha and beta diversity to increase with elevation. Within trees, we expected lichen alpha diversity on firs to be greater on the cooler, northern aspects of boles, and on maples to be greater on the lower surfaces of inclined boles. (ii) For bryophytes on maples, inclination is a better predictor than elevation of diversity and composition. We expected whole-tree alpha diversity to increase with inclination, and we did not expect any relationship between beta diversity and elevation. Within trees, we expected alpha diversity of bryophytes to be greater on the upper (moister) surface of the bole. See also Table 1.

Methods

Study area overview

We conducted this study in Parc-national du Mont-Mégantic, a 54.9 km^2 protected area in southeastern Québec. The park is located within the Northern Appalachian Mountains with the highest summit at 1105 m. The climate is northern temperate (PNdMM 2007). At a nearby weather station in Notre Dame des Bois (567 m), annual average temperature for 1980–2010 was 3.9 °C, and precipitation reached up to 980 mm each year (Government du Québec 2021). Natural disturbances in the park include spruce-budworm outbreaks (1974–1984), ice storm damage in 1998, and logging (until the 1960s). The location of our study area has either never been logged or has not been logged for more than a century (PNdMM 2007).

Environmental gradients and study trees

The elevation gradient, on the eastern slope of Mont St. Joseph, traverses ~ 300 m in elevation (720 m–1010 m) in the eastern portion of the park (Fig. 1). Precipitation increases and temperature decreases along the gradient

Table 1 Summary of hypotheses, predictions, and results for alpha diversity, beta diversity, and composition patterns for the three communities in this study: lichens on firs, lichens on maples, and bryophytes on maples

Community	Unit of observation	Prediction	Results
Lichens on firs	Whole-tree	Elevation is a strong predictor of alpha diversity (positive relationship) and composition	Supported
	Whole-tree	Elevation has a positive effect on beta diversity	Not supported
	Within-tree	Influence of aspect on composition and alpha diversity (greater on northern than southern aspects)	Not supported
Lichens on maples	Whole-tree	Elevation is a strong predictor of alpha diversity (positive relationship) and composition	Partially supported: weak effect of elevation on composition; alpha diversity predicted by inclination rather than elevation
		Elevation has a positive effect on beta diversity	Supported: weak effect
	Within-tree	Effect of lateral position on composition and alpha diversity (greater on the lower than upper surface)	Partially supported: no effect on composition, but alpha diversity greater on lower surface
		Beta diversity (among trees) greater on lower surfaces than upper surfaces	Not supported
Bryophytes on maples	Whole-tree	Inclination is a stronger predictor of alpha diversity (positive relationship) and composition	Partially supported: support for alpha diversity; composition influenced by both inclination and elevation
		Elevation not related to beta diversity	Supported
	Within-tree	Effect of lateral position on composition and alpha diversity (greater on the upper than lower surface)	Supported
		Beta diversity (among trees) greater on lower surfaces than upper surfaces	Not supported

The unit of observation refers to the spatial scale of the analysis. "Whole-tree" analyses compare one tree to another. "Within-tree" analyses refer to the lateral gradient. The lateral gradient was defined as the four cardinal aspects for firs and the differing surfaces of maple boles (upper, intermediate, and lower). See also Fig. 1

(PNdMM 2007). We studied epiphytic macrolichens and bryophytes (those occurring at least 1 m above ground level) on the two dominant tree species in the park: sugar maple (*Acer saccharum*) and balsam fir (*Abies balsamea*). Sugar maple occurs over roughly the lower half of the gradient (~ 720–825 m), where it is the dominant species. Balsam fir extends from the deciduous-coniferous transition zone up to the summit (~ 825–1010 m), dominating forests characterized by mixed stands of hardwoods, firs, and spruce. We analyzed data as three different communities: (i) bryophytes on sugar maples (ii) lichens on sugar maples and (iii) lichens on balsam fir trees. Bryophytes on firs could not be included as a distinct community, given very low frequency, which may be due to the unfavorable conditions of high acidity and low water holding capacity on fir bark (Barkman 1958). Focal sugar maples were located along two transects (three sites per transect), between the low elevation maple forest and the maple–fir transition zone. We also chose focal fir trees along two transects (three sites per transect), between the maple–fir transition zone (the uppermost maple plot) and the high-elevation coniferous forest.

Within each site, we randomly selected six healthy trees of a given species along a 50-m line. The trees we selected represented three diameter-at-breast-height size classes relatively evenly for maples (20–35 cm; 35–50 cm; ≥ 50 cm) and two size classes for balsam fir (20–35 cm; 35–50 cm). In total, we surveyed 72 trees (36 maples and 36 firs).

We defined contrasts along the lateral gradient differently for maples and firs, in all cases focusing on four different sides of a tree. On maples, which were often distinctly inclined, we defined the lateral gradient with reference to the incline: the upper surface, lower surface and two intermediates (Fig. 1). The inclination of the maple tree boles did not always follow the hill slope (e.g., west was not always the upper surface of the tree bole.). On firs, which are not noticeably inclined in our study area, we defined the lateral gradient with reference to aspects: the cardinal directions north, east, south, and west (Fig. 1).

Lichen and bryophyte surveys and identification

We conducted field surveys from 25 June to 05 August 2018. We inventoried epiphytic macrolichen and bryophyte

communities on each of four sides of each tree using a 10 cm × 50 cm sampling grid (based on Asta et al. 2002) subdivided into 10 sub-quadrants of 5 × 10 cm, with the lower side 1 m from the ground. We recorded the frequency of each taxon as the number of sub-quadrants where it was present.

We identified macrolichens and bryophytes in the field when possible and otherwise in the lichenology laboratory at the Canadian Museum of Nature (Gatineau, Québec) and at the University of Sherbrooke. We did not include crustose species (microlichens) or undeveloped lichens and bryophytes we could not accurately identify to species, such as those lacking identifiable features such as soredia, isidia, sporophytes, or unique morphological features (see Appendix A for *Usnea* chemical group identification).

Environmental variables

Our community analyses focused on the effects of elevation, the lateral gradient, and (for maples) tree inclination. We estimated elevation from a digital elevation model using GPS coordinates for each tree. For maples, we recorded the inclination of the tree bole and direction of the lean using a clinometer. To better understand potentially important environmental correlates of elevation and the lateral gradient, we also measured several environmental variables known to affect lichens and bryophytes (Green and Lange 1995; Green et al. 2011; Hauck 2011). Since microsite conditions (e.g., on a particular side of a tree) can deviate substantially from regional averages (Maclean et al. 2021), we collected our own climate data rather than relying on data from weather stations or models. At the site level, we measured air temperature and relative humidity from 04 July 2019 to 03 July 2021 across the entire elevation gradient. Our main interest was to assess the relative differences between sites rather than to capture absolute values of long-term averages. At the tree level, we recorded bark surface temperatures (on multiple occasions) and moisture content (once) on each side (see Appendix B).

Statistical analysis

We analyzed our data at two spatial scales (units of observation): whole-tree and within-tree (or "side"). For whole-tree analyses, we used species frequencies across the four different sides of a given tree as one unit. For within-tree analyses, we used side-specific species frequencies (Fig. 1). For maples, we averaged the two intermediate sides prior to analyses. Finally, we conducted all statistical analyses in R (v. 4.0.3; R Development Core Team, 2020).

Alpha diversity

To test for effects of elevation, inclination, and/or side on alpha diversity, we used linear mixed effects models (LMMs; lmer function in the lme4 package, v. 1.1–26; Bates et al. 2015) and generalized linear mixed effects models (GLMMs; package glmmTMB; v. 1.0.2.1; Brooks et al. 2017), then tested the significance of each predictor with an ANOVA. We used separate models for each tree species (lichens on firs in one model, and lichens and bryophytes on maples in another). We defined a priori models according to our hypotheses and predictions. We always retained variables that were part of our hypotheses and any significant interactions, dropping non-significant terms ($p > 0.05$) for variables not part of our hypotheses (Table S3 shows final models and results). In all models, we used the Hill-number version of the Shannon diversity index (Magurran 2004) to represent alpha diversity. "Site" was included as a random factor for whole-tree analyses and "tree" for within-tree analyses. We included inclination (maples only) and elevation (maples and firs) as continuous predictor variables. For lichens and bryophytes on maples, we included an interaction between taxon and elevation and taxon and inclination (whole-tree), and taxon and side (within-tree). For within-tree analyses, for the within-tree maple model, we included inclination as a covariate and used "dispformula" to capture the heteroscedasticity associated with this variable (e.g., the response variable, alpha diversity, is more variable relative to the mean, as inclination increases). Finally, we assessed pairwise comparisons using the estimated marginal means ("least-squares means") using the function "emmeans" (package emmeans, ver. 1.5.3; Lenth et al. 2018).

Composition

Here, we consider species composition as a multivariate concept: patterns of (dis)similarity among sites in terms of which species are present and at what abundance, with scores of plots on ordination axes illustrating differences in composition. We conducted the following tests in R with the vegan package, ver. 2.4-2 (Oksanen et al. 2013). To test for variation in whole-tree composition against elevation (maples and firs) and inclination (maples only), we first determined the most appropriate direct ordination method using a detrended correspondence analysis (DCA) with the decorana function. Given that the length of the first DCA axis was < 4, we then tested predictors of composition using redundancy analysis (RDA) (Lepš and Šmilauer (2003) with Hellinger transformations of species frequencies (Legendre and Gallagher 2001). We evaluated the significance of the entire RDA model and of the individual predictor variables using ANOVA with 999 permutations. To test for compositional variation

among sides within-trees, we used a PERMANOVA with 999 permutations with the adonis function in the vegan package. Finally, to partition variation among communities relating to different predictor variables, we used the "varpart" function, based on adjusted R^2 values, (Legendre and Legendre 2012).

We visualized our results from the compositional and beta diversity analyses using non-multi-dimensional scaling with the Bray–Curtis Index (NMDS), as this method reduces the "arch effect" (Legendre and Legendre 2012) and permits visual evaluation of "raw" site-to-site compositional differences in relation to environment (RDA axes are pre-defined to be maximally correlated with composition). To identify specific species associated with particular elevations or degrees of tree bole inclination, we also conducted indicator species analyses (ISA; multipatt function in the indicspecies package 1.7.12; Caceres and Legendre 2009) (Appendix C).

Given that maple and fir occupy different elevational ranges, we conducted two additional analyses. First, to test for compositional differences between the two focal host tree species independently of elevation, we conducted a permanova using only trees in the maple–fir transition zone (Appendix C). Second, because the fir transects covered a greater elevation range than the sugar maple transects (see Fig. 2), and could thus produce a stronger elevation signal, we repeated the key diversity and composition analyses for lichens on firs without the highest elevation site at > 1000 m (Appendix D).

Beta diversity

To test for changes in beta diversity according to (i) elevation and (ii) tree side, we used the betadisp function with the Bray–Curtis index of compositional dissimilarity in the vegan package (ver. 2.4-2; Oksanen et al. 2013) and a follow-up pairwise permutation test ($n = 999$ permutations). For whole-tree analyses (i.e., beta diversity represents differences in composition among whole trees), "site" was our predictor variable, and we then evaluated the index of multivariate dispersion for each site against elevation. Multivariate dispersion is the average dissimilarity between a given tree and the centroid in multivariate space defined by Bray–Curtis dissimilarities. For within-tree analyses (i.e., beta diversity represents tree-to-tree differences for a particular side), we used "side" as our predictor variable, coded as described previously.

Environmental variables

We used the bark surface temperature and moisture data to test whether greater tree bole inclination (maples) or aspect (firs) leads to a strong contrast in temperature among the sides of a tree bole. We also used our air temperature and relative humidity data to test whether there was a difference

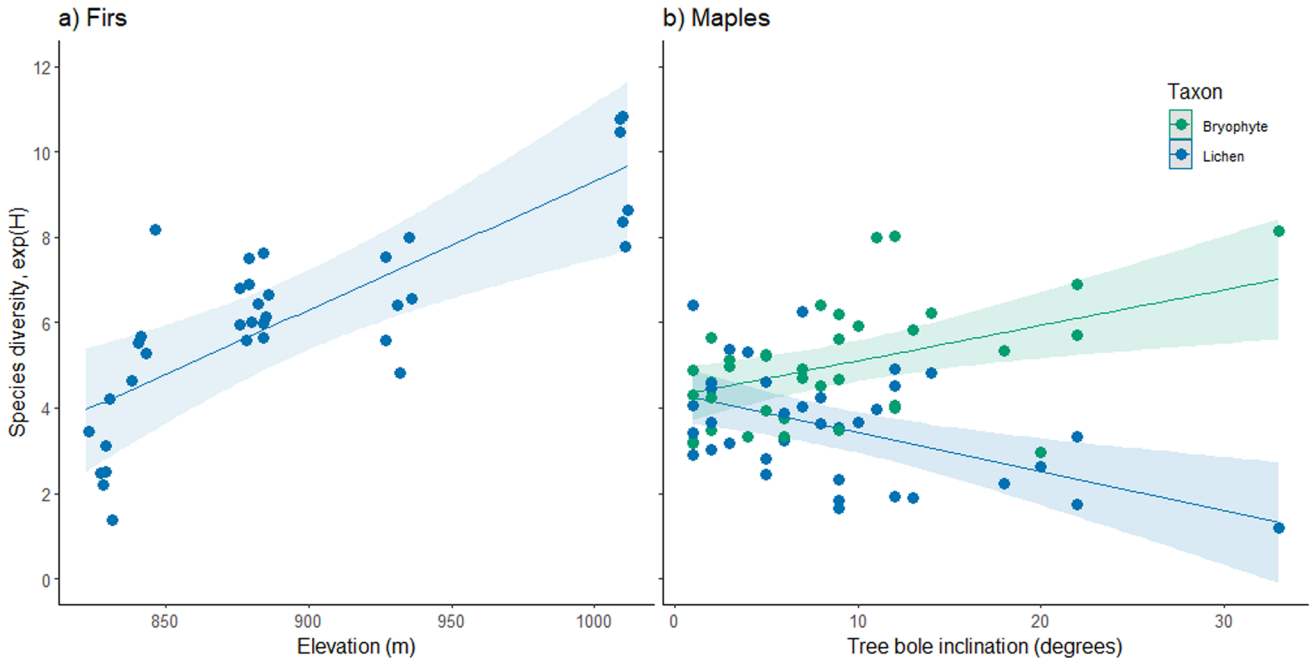


Fig. 2 Linear mixed effects model showing relationships between **a** elevation and tree-level alpha diversity (Hill-number version of Shannon diversity) of lichens on firs and **b** tree bole inclination and alpha diversity of lichens and bryophytes on maple. Lines show modeled predictions with 95% confidence intervals; points represent alpha diversity values for each tree

among elevations. Finally, we tested whether the environmental contrasts (relating to bark surface temperature and moisture) were different between maples and firs by comparing the coefficient of variation for each variable. See Appendix B.

Results

General results

Overall, we recorded 69 taxa (43 lichens and 26 bryophytes) on 72 trees (36 maples and 36 firs; Appendix E). Maple and fir trees shared six lichen taxa. For bryophytes, we observed 23 mosses and 3 liverworts (no hornworts). On firs, there was an average of nine lichen taxa per tree. On maples, there was an average of five lichen and seven bryophyte taxa. Permanova analysis of only trees in the maple–fir transition zone revealed that the tree hosts had significantly different lichen communities (Fig. S1).

Air temperature in all seasons decreased linearly and significantly along the elevation gradient (Fig. S2a, Table S1). The annual average difference in air temperature between the lowest and highest elevation sites was 2.1 ℃ (Table S2). Relative humidity increased with elevation for all seasons but summer (Fig. S2b, Table S1). The high-elevation coniferous forest had the greatest number of days with relative humidity above 82% (Table S2), the threshold above which chlorolichens (most lichens in our study) activate photosynthesis (Phinney et al. 2019). Bole inclination significantly affected surface temperature and moisture contrasts on maple trees, with the upper surfaces tending to be cooler and moister than the other surfaces (Fig. S3; Table S1). For fir trees, aspect significantly influenced bark surface temperature but not moisture (Fig. S4; Table S1). The within-tree coefficient of variation for bark moisture and temperature differed significantly between maples and firs (Table S1), with variation for bark moisture greater on maples (0.19) than on firs (0.13; see Appendix B for more details).

Whole-tree alpha diversity, composition and beta diversity

Whole-tree alpha diversity of lichens on firs increased with elevation. For lichens and bryophytes on maples, alpha diversity correlated more strongly to tree bole inclination, interacting with taxon (Fig. 2a, b; Table S3). On maples, inclination had a negative effect on lichen alpha diversity, but a positive effect on bryophyte alpha diversity. The difference between tree species in terms of elevation effects on alpha diversity (and composition) remained qualitatively the same when using a shortened elevation range (Appendix C; Fig S5). See also Table 1 for a summary of all results.

Redundancy analysis (RDA) (Fig S6, Table S4) revealed significant effects of elevation and inclination on species composition at the whole-tree level, though the magnitudes varied among communities. For lichens on firs, there was an especially strong distinction between communities at the highest elevation and those at lower elevations (Fig. 3a; Fig S6a), with elevation accounting for 38% of the variance in species composition (Table S4). For lichens on maples, elevation, and inclination had smaller effects on composition, with elevation accounting for 5.8% of variation and inclination 4.8% (Fig. 3b, c; FigS6b-c; Table S4). For bryophytes on maples, communities on the most inclined trees appeared distinct (Fig. 3d; Fig S6d-e), with inclination (11%) explaining a greater percentage of the variation than elevation (9%) (Table S4).

The indicator species analysis (ISA) for lichens on firs (Table S5), revealed that eleven species were significantly associated with high elevations, with *Platismatia glauca*, *Evernia mesomorpha*, and *Usnea* spp. with salazinic acid as the most abundant (Fig. 3a; Table S5). Fewer species were associated with the mid- and low elevations (Fig. 3a; Table S5). For lichens on maples, only *Myelochroa aurulenta* was associated with mid and low elevations, and *Melanelixia subaurifera* with slight and intermediately inclined tree boles (Fig. 3b, c; Table S5). Finally, bryophytes on maples had two species associated with strongly inclined tree boles, one a new record for the park (*Brachythecium rotaeanum*) and one an indicator of old growth forests (*Neckera pennata*) (Fig. 3d, e; Table S5).

Among the three combinations of taxon and tree species, we found a significant relationship between whole-tree beta diversity (differences among trees within a site) and elevation only for lichens on maples ($df = 5$; $F = 3.0374$; $p = 0.02$; Table S6), for which the effect was positive (Fig. S7).

Within-tree alpha diversity, composition and beta diversity

For lichens on firs, there was no relationship between bole aspect and within-tree alpha diversity, composition, and beta diversity (Tables S3, S6, and S7).

For within-tree alpha diversity on maples, there was a significant interaction between bole position and taxon (Table S3), with lichens and bryophytes displaying different alpha diversity trends among the surfaces of the tree (Fig. 4). Lichen diversity was greatest on the lower surface of the bole, decreasing slightly (but not significantly) towards the upper surface (least squared means pairwise test upper and lower surfaces; $p = 0.3$). In contrast, bryophyte diversity was greatest on the upper surfaces of the boles, decreasing markedly and significantly towards the lower surface

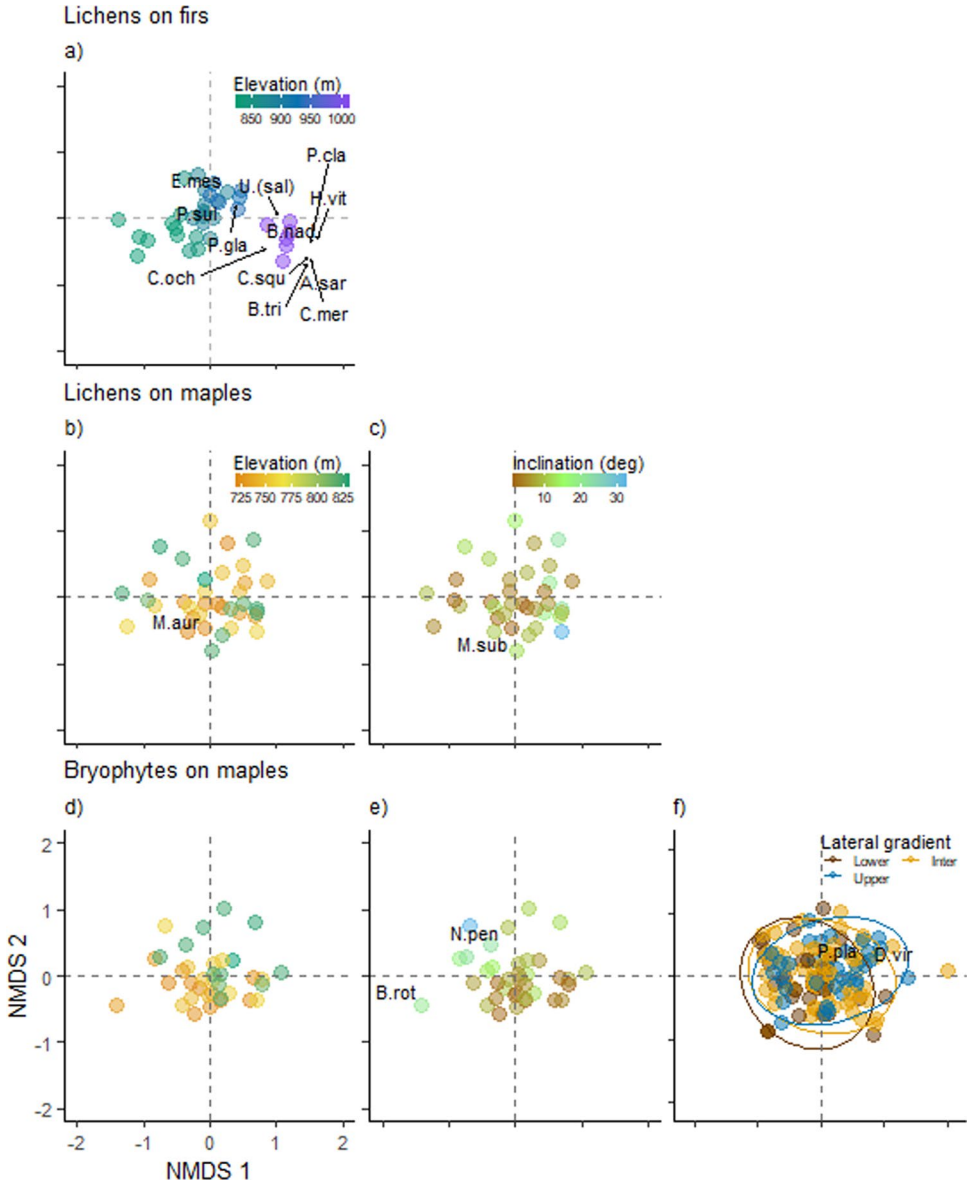


Fig. 3 Non-metric multidimensional scaling (NMDS) analyses showing relationships between **a** species composition of lichens on firs and elevation, **b** lichens on maples and elevation, and **c** inclination, and bryophytes on maples and **d** elevation, **e** inclination, and **f** the lateral gradient. We generated solutions for two dimensions. The text refers to species that were significantly associated with a community and predictor variable from the Indicator Species Analysis (Table S5). Names are abbreviated as the first letter for genus, followed by a period, and the last three letters of the species. In panel **a** A.sar = *Alectoria sarmentosa*, B.nad = *Bryoria nadvornikiana*, B.tri = *Bryoria trichodes*, C.mer = *Cladonia merochlorophaea*, C.och = *Cladonia ochrochlora*, C.squ = *Cladonia squamosa*, E.mes = *Evernia mesomorpha*, H.vit = *Hypogymnia vittata*, P.sul = *Parmelia sulcata*, P.gla = *Platismatia glauca*, P.cla = *Pseudevernia cladonia*, U.(sal) = *Usneas* with salazinic acid. In panel **b** M.aur = *Myelochroa aurulenta.* In panel **c** M.sub = *Melanelixia subaurifera.* In panel **e** B.rot = *Brachythecium rotaeanum*, N.pen = *Neckera pennata.* In panel **f** D.vir = *Dicranum viride* and P.pla = *Porella platyphylla*

(least squared means pairwise test upper and lower surfaces; $p = 0.004$; Fig. 4).

For lichens on maples, the evidence for within-tree effects of aspect on composition was weak ($p = 0.06$), but composition varied significantly among the surfaces of the tree bole for bryophytes on maples (Table S7; Fig. 3e). Finally, within-tree beta diversity did not vary significantly for either lichens or bryophytes on maples (Table S6).

Discussion

We tested predictions based on the hypotheses that benign conditions favor diversity (alpha and beta) and that air humidity and temperature (which covary with elevation) principally influence lichen diversity, while the availability of liquid water (which differs among sides of inclined trees) principally influences bryophyte diversity. We based our predictions largely on the different physiologies of lichens and bryophytes (Table 1); however, our results indicate that the most prominent differences were between tree species as substrates, rather than between the two focal taxa. The general idea that benign conditions favor biodiversity (Whittaker 1960; Chase 2003, 2010) clearly requires system-specific nuances in its application, as described below.

With respect to differences between tree taxa, the elevation gradient strongly influenced the diversity and composition of lichens on balsam fir trees, whereas the lateral gradient (tree bole inclination) principally influenced bryophytes *and* lichens on sugar maples. The lichen communities on high-elevation firs were more diverse and compositionally unique from those at lower elevations, but we did not find

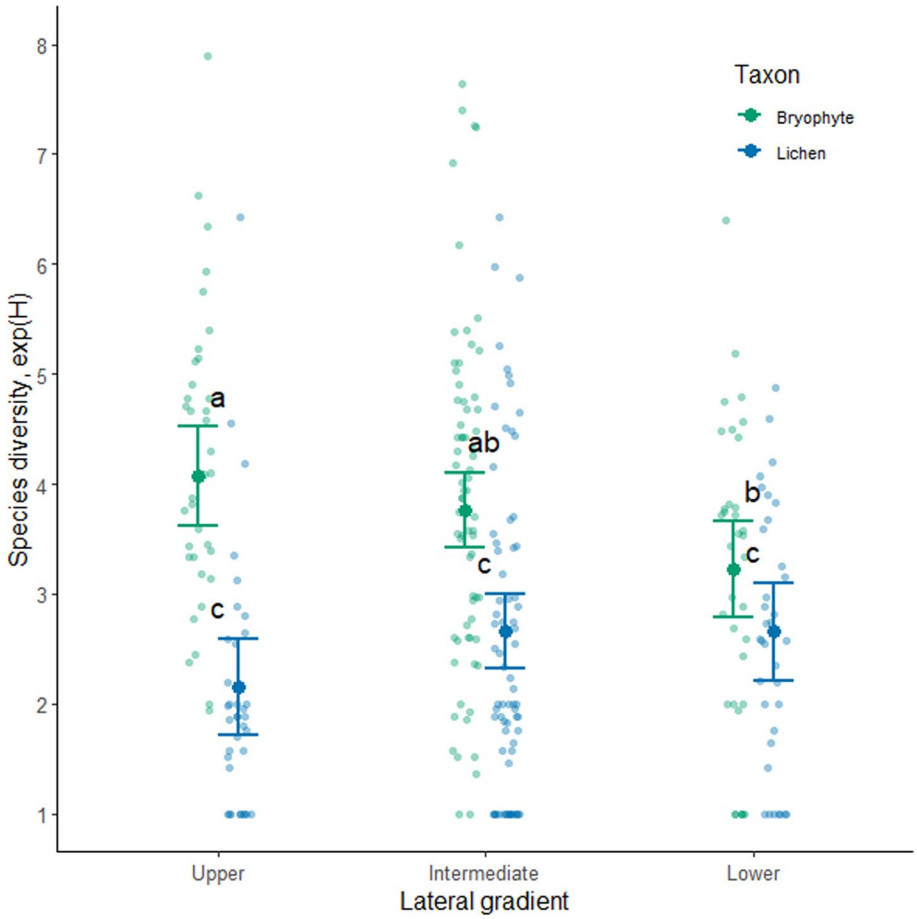


Fig. 4 The relationship between within-tree alpha diversity (Hill-number version of Shannon diversity) and the lateral gradient (upper, intermediate, and lower) for bryophytes (green) and lichens (blue) on maples. The bars represent the modeled results, and the points represent the raw data. The letters represent significant differences within each taxon

marked within-tree compositional variation. For lichens on maples, whole-tree alpha diversity decreased with bole inclination, but composition was unaffected, and we observed no significant within-tree changes. For bryophytes on maples, the upper surfaces of tree trunks had higher alpha diversity and distinct composition compared to lower surfaces, and communities on the most inclined trees were more diverse and compositionally distinct from those on straighter-trunked trees. Though it is difficult to disentangle the effects of elevation and tree species, given that our host trees occur at different elevations, the two tree species clearly host different communities at the same elevation (Fig. S1) and the maple–fir difference in the effect of elevation was robust to the length of the elevation gradient (see Appendix 3 and Fig S6). In addition to the clear tendency for inclination in maples but not firs, our results indicate important effects of tree species on how environmental variables influence cryptogam communities. In the following paragraphs, we argue that the key factors underlying the different results for maple vs. fir are as follows: (i) The increase in relative humidity and decrease in temperature along the elevation gradient is important for lichens on firs, with the mountain top during the spring particularly distinct, having an average relative humidity of > 82%, the minimum amount needed for the lichens in our study (see below for explanation) (Phinney, et al., 1990); (ii) the change in liquid water along the lateral gradient, particularly on inclined trees, is most important as a direct influence on bryophytes (rather than lichens) on maples; (iii) lichens on maples likely respond as much to competition from bryophytes as to the abiotic lateral gradient directly.

For lichens on firs, we observed an increase of alpha diversity with elevation (Fig. 2a), and a strong effect of elevation on composition, with a clear distinction of communities at the highest elevation from those from lower elevations (Fig. 3a). Although rare, an increase in alpha diversity with elevation agrees with our predictions that higher elevations are less stressful for lichens, given an increase in air relative humidity, and a decrease in temperature (Figs. S1, S2; Tables S2, S3). This result is also in agreement with other studies of epiphytic and/or corticolous lichens in temperate and boreal regions (Cobanaglu and Sevgi 2009; Bässler et al. 2015; Nascimbene and Marini 2015; Boch et al. 2019; Belguidoum et al. 2021). In our study, all lichen species are chloro and cephalolichens containing a trebouxioid green-algae photobionts, and for this group, Phinney et al. (2019) showed that many chlorolichens activate photosynthesis at ~ 82% relative humidity. Furthermore, 95% relative humidity is particularly

important for full photosynthetic activation of alectorid and shrubby fruticose growth forms, which are abundant at the high elevations in our study area. At Mon-Mégantic, average spring relative humidity was > 82%, and average fall relative humidity at least 95%, only at the highest elevation (Table S2). These results suggest that spring and fall may be important periods of growth for epiphytic lichens, with fall particularly important for the fruticose lichens. Furthermore, lichens absorb water vapor from the air when water potential is lower in the lichen than the air, which occurs when relative humidity is high (75–95%) and temperatures < 20 ℃ (Palmqvist 2008). Lower temperatures also reduce respiration relative to photosynthesis (Palmqvist 2008), such that high elevations likely provide favorable conditions for a greater diversity of lichens.

One potentially important source of moisture input at high elevation—although not quantified in our study—comes from fog during the frequent days when clouds enshroud the mountain top (a "cloud cap") down to roughly the deciduous-boreal transition (PNdMM 2007; Vellend et al. 2021). For example, certain desert epiphytic species maximize photosynthesis rates more rapidly during fog events than via high relative humidity (Jung et al. 2020). The role of fog relating to lichen diversity patterns deserves further study.

Our conclusion that the lateral gradient plays a smaller role in predicting lichen distributions on fir trees agrees with other studies of conifers in the region. The markedly different temperatures on different aspects, most notably the cooler temperatures on the northern aspects, did not correlate with changes in diversity or composition in our study (Table S3; Fig S5; Fig. 5). On Whiteface Mountain in New York, the microclimate of fir and spruce boles correlated only weakly with epiphytic cover (Hauck et al. 2006). Finally, the water holding capacity of conifers seems to be limited; furthermore, differences in water holding capacity among living and dead spruces did not correlate with lichen diversity, as noted by Hauck et al. (2000). Nonetheless, in coniferous forests where the trees are more inclined, the lateral gradient may play a much greater role in determining diversity and composition, as found in the Pacific Northwestern United States (McCune et al. 2000).

For bryophytes on maples, we observed a strong effect of inclination and the lateral gradient on composition and diversity of more inclined trees (Fig. 2b) and upper surfaces (Fig. 4). We also observed that the upper surfaces of inclined maple boles were cooler and held more moisture than the lower surface (Figs. S3, S4). These results support our hypothesis that areas with more liquid water are more favorable to bryophytes, given their need of a greater and more constant supply of liquid water for recovery from desiccation (Greene and Lange 1995; Proctor 2000). Furthermore, the lower temperatures also observed on the upper surfaces may indicate lower evapotranspiration (Fig. S4). Although McGhee et al. (2019) did not quantify bark moisture content according to side as in our study, they did find that older sugar maples tended to have greater surface water availability, which correlated with increasing bryophyte species richness and cover. We did not quantify total bark water holding capacity, but we confirmed that variation in moisture is greater around the trunks of maples than firs (Table S3).

Our results are consistent with other studies showing that bryophytes tend to dominate over lichens in the presence of liquid water (Pike et al. 1975; Kuusinen 1994; Löbel et al. 2006; Ranius et al. 2008). Furthermore, the fact that the lateral gradient has a stronger influence on bryophyte composition than lichen composition is consistent with the idea that bryophytes are responding *directly* to the moisture gradient (Table S7). Lichens on maples may be responding largely *indirectly* via competition from bryophytes, which is stronger on the upper surfaces of inclined tree boles. Similarly, Löbel et al. (2006) reported a negative correlation between lichen diversity and tree bole inclination. Furthermore, several studies have noted the presence of drought tolerant (mostly crustose) lichens on the lower surfaces of tree boles, where there is less bryophyte cover (Pike et al. 1975; Kuusinen 1994; Ranius et al. 2008). Although we did not include crustose lichens in our study, we did observe that they occurred commonly on the lower surfaces of maple boles. The inclusion of crustose lichens in diversity studies warrants further attention.

As predicted and based on the hypothesis that beta diversity increases in more benign conditions (Chase 2003, 2010), we found an increase in beta diversity of lichens on maples with elevation. This weak relationship may indicate that the slightly more humid and cooler conditions at higher elevations create a more favorable environment for lichens on maples, potentially magnifying the potential for community differentiation between trees. However, we found no relationship between elevation and alpha diversity for lichens on maples, for which we do not have a clear explanation. Even with a shortened gradient for fir trees (Appendix 3), we still see a stronger relationship between elevation, alpha diversity, and composition of lichens on firs (Fig. 2a) compared to lichens on maples (Fig. S6).

The lack of relationship between beta diversity and elevation for lichens on firs and the lateral gradient and bryophytes on maples did not support our predictions. We can only speculate on causes, although beta diversity differences along environmental gradients can be relatively weak compared to alpha diversity patterns (Harrison et al. 2011; Vellend 2016). Perhaps the length of our gradient was too short to detect a clear beta diversity signal for lichens on firs. For bryophytes on maples, tree bark is not the main substrate in the forest, and it may act as strong environmental filter itself, limiting the species pool and thus potential tree-to-tree differentiation.

Conclusion

We have shown some clear effects of elevation and tree bole inclination on diversity and composition of epiphytic cryptogams, the presence and direction of which depend more on the tree species (substrate) than on the focal taxon. Elevation matters most on firs, where alpha diversity increased markedly with elevation. The lateral gradient was more important in explaining diversity on maples, with bryophytes being more responsive than lichens. Increasing relative humidity and cooler temperatures at high elevation appear advantageous for lichens on firs, while the presence of more liquid water on the upper surface of inclined maple trees favors bryophytes over lichens. Future studies that include specific characteristics of the host tree, the role of fog, and inclusion of crustose lichens, along with experimental manipulations of environmental conditions or individual transplants, could provide greater insight into the patterns of cryptogam diversity and composition.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-023-05369-y.

Acknowledgements We thank Parc national du Mont-Mégantic for letting us conduct research there. Jennifer Doubt provided much assistance with bryophyte identification. Dr. Nicole Fenton, Dr. Bill Shipley, Etienne Lacroix-Carignan, and Florence Normand-Boisseau provided input on the manuscript, study design, field work, or statistical analyses. An additional thank you to Anna Crofts, Ming Ni, Christine Wallis, Madelaine Anderson, and Hasanki Gamhewa for their support.

Author contribution statement CR, MV and TM conceived the ideas and designed the methodology; CR collected the data; CR and TM identified the specimens; CR, MV, and FR analyzed the data; CR and MV led the writing of the manuscript with critical inputs from TM and FR.

Funding The authors thank the Natural Sciences and Engineering Research Council of Canada and Fonds de Recherche Nature et Technologies Québec for their financial support.

Availability of data and materials The datasets used and/or analyzed during the current study will be available in the supplementary information.

Code availability Data were analyzed in R and are available as supplementary information.

Declarations

Conflict of interest Not applicable.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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