Examining boreal forest resilience to temperature variability using bryophytes: forest type matters

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Abstract. The capacity of individual species to tolerate environmental changes is a major driver of ecosystem resilience. This subject has been a hot topic in boreal forests due to the greater effect of climate change anticipated at northern latitudes. However, to date it has been mainly examined for trees, with comparatively little emphasis on other species groups. In this study, bryophytes were sampled in the boreal forest of Québec (Canada) using a stratified sampling design allowing us to separate the effect of dominant canopy composition (two types: coniferous and mixedwood) and of the spatial climatic gradient (relatively warm and relatively cold sites) on bryophyte community structure (species richness and composition). The results indicated that bryophyte composition was different between coniferous and mixedwood stands. The impacts of spatial variation in climate were more visible in mixedwood than coniferous stands, indicating an interaction between stand type and climate. Specifically, bryophytes from mixedwood stands, and particularly specialist communities associated with deadwood and live tree bases, were climate-sensitive and represent a potential target group to investigate the effects of climate change. In contrast, bryophyte communities from coniferous stands are stand structure-sensitive, with little response to climate, presumably partly because coniferous canopies buffer climatic variations. Since bryophyte community sensitivity to regional variations in climatic conditions depends on dominant canopy characteristics and microhabitat availability, we suggest that adapted forest management practices could play a role in attenuating climate change impacts on these organisms.

Key words: boreal forests; climate change; generalist bryophytes; liverwort; mixed stands; mosses; resilience; specialist bryophytes.

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INTRODUCTION

Several recent studies have suggested that North American boreal forests will be relatively resilient to climate change (Price et al. 2013, Gauthier et al. 2015). This view is mostly based on the fact that boreal forests are disturbance-adapted ecosystems (Schmiegelow et al. 2006) and that the regional tree species pool has been largely unmodified over thousands of years, suggesting no loss in function despite past disturbances and changes in climate (Johnstone et al. 2010, Blarquez et al. 2014).

This assertion can, however, be questioned on several levels. First, the impact of cumulative disturbances, such as logging and mining in addition to climate change, has probably not been sufficiently addressed (Steffen et al. 2015). Moreover, the arctic amplification results in greater anticipated climate change in northern ecosystems (IPCC 2007): From 1961–1990 to 2071–2100, mean
annual temperatures are expected to increase by between 3.3°C and 5.8°C in across North American boreal ecozones (Price et al. 2013) but by between 5°C and 10°C in northern Québec (Ouranos 2015). The expected speed and magnitude of climatic change exceed known paleoclimate rates of change, and coupled with cumulative disturbances, might overwhelm the capacity for resilience of boreal forests (Hansen et al. 2006).

Second, boreal regions include other forest types in addition to the iconic coniferous stands that have been examined in the past. In many regions of the boreal forest, mixedwood stands (where deciduous and coniferous trees co-dominate) represent a significant proportion of the landscape (Bergeron et al. 2004, Saucier et al. 2009) and offer valuable habitats that increase landscape diversity (Drapeau et al. 2001, Reich et al. 2001). Because coniferous and broadleaved species tend to be phylogenetically and functionally different, it is expected that stands dominated by these species will offer contrasting conditions for understory species such as bryophytes (Ross et al. 1986, Barbier et al. 2008).

Finally, the resilience and vulnerability of boreal forests are typically investigated for trees, because they are assumed to be keystone ecosystem components (Mallik 2003, Lindenmayer et al. 2014) and because of their short-term economic value (Price et al. 2013, Gauthier et al. 2015). The response of the myriad of non-tree species potentially sensitive to climate variation is comparatively little investigated. Bryophytes (herein, liverworts, mosses, and sphagna) are a fundamental ecosystem component in this respect, both because they are conspicuous elements of boreal ecosystems in terms of richness (Turetsky et al. 2012), and because they are functionally important (Chapin 2010). Indeed, abundant and diverse forest bryophyte communities fulfill various ecosystem services such as water filtration, carbon sequestration, soil thermoregulation, and permafrost stabilization (Turetsky et al. 2012). Given the functional roles of bryophytes in forest ecosystems, a change in the bryophyte community in response to climate change or other disturbances could reduce the resilience of the overall boreal system even if the tree species remain the same.

Bryophyte species can be classified into two groups based on the strength of their association with specific microhabitats (defined as the smallest subunit of forest habitat, e.g., pieces of deadwood, rocks): (1) specialist species closely associated with one or a few well-defined microhabitats, with narrow ecological requirements and reduced dispersal abilities (Rambo 2001, Johansson et al. 2012); and (2) generalist species with broad ecological requirements and distribution ranges that have good dispersal abilities (During 1992).

The aim of this study was to separate the effects of variation in dominant canopy cover and mean annual temperature on bryophyte communities, in order to evaluate the potential sensitivity of this group to climate change. The study was done in two forest types (coniferous and mixedwood) sampled in landscapes located in the continuous boreal and mixed forest zones. Specifically, we asked two questions: (1) Do bryophyte communities in two types of boreal forest stands (coniferous and mixedwood) respond to a temperature shift by adjusting their composition? (2) And does the relative response of species to climate vary with their microhabitat associations and forest type?

In response to the first question, we predict that under a given type of canopy cover (coniferous or mixedwood forest type), a shift in bryophyte composition will be observed between northern (continuous boreal forest zone) and southern (mixed forest zone) locations, while taxonomic guild richness will remain stable. This shift will signal a community-level adjustment to temperature change (d’Orangeville et al. 2016) as a prerequisite for the maintenance of ecosystem functions in a changing climate. In response to the second question, based on Brown (1995) and Thuiller et al. (2005) who linked species climate sensitivity to their niche properties, we predict that specialist species inhabiting key boreal forest microhabitats (living trees and deadwood; Rambo 2001, Király et al. 2013) will be sensitive to climate. In contrast, generalist species inhabiting the forest floor will be less sensitive to spatial variation in climate (Brown 1995). We expect these relationships to hold true in both forest types (coniferous and mixedwood).

**MATERIALS AND METHODS**

**Study area**

The study area was located in eastern Canada and overlapped two vegetation zones: boreal and northern temperate (45°–51° N and 80°–64°
Six landscapes were selected: Three landscapes were selected in relatively cold locations well inside the boreal zone, and three landscapes were selected in warmer locations at the interface between the boreal forest and northern temperate forest zones. In each landscape, two types of stands were sampled: Two plots were in coniferous stands, and two plots in mixedwood stands, each plot separated by a distance of at least 500 m from one another. When establishing the plots, we made sure that the composition of the dominant canopy for each stand type was similar across landscapes: Coniferous stands were co-dominated by black spruce (*Picea mariana* Mill., Briton) and balsam fir (*Abies balsamea* (L.) Mill.), while mixedwood stands were dominated by a mix of those coniferous species with a significant element of white birch (*Betula papyrifera* var. *papyrifera* Marshall) and other deciduous species (Appendix S1: Table S1). Mean annual temperature was assessed at the landscape level and varied between −1.40°C and +2.30°C (Appendix S1). All plots were also established in stands on similar surficial deposits (and soil type), namely relatively deep (>1 m) tills with relatively gentle slopes. Ensuring that coniferous and mixedwood stands were similar in the different landscapes allowed us to separate the effects of dominant canopy composition and climate on understory communities in the analyses.

Environmental variables

Stand structure and climate variables are presented in Appendix S1: Tables S1 and S2. As most abiotic variables were controlled by the study design, abiotic characterization of the stands was limited to climatic variables. In the center of each stand, a 400-m² circular plot was placed to measure stand structure (tree species richness, density, mean DBH of living trees, density and decay class of snags and coarse woody debris). Coarse woody debris (diameter >8 cm) density was calculated from abundance data sampled with the line-intercept method (Van Wagner 1982) using three 10-m transect lines crossing each plot from the center to the edge. Decay classes of snags and coarse woody debris were determined using Hunter (1990).

Climate variables were interpolated with BIOSIM 10 (Régnière et al. 2014), using data from the eight nearest weather stations from 1973 to 2016.
Interpolation was conducted using latitude, longitude, elevation, and slope/aspect as predictors, and the auto-select best model option to determine interpolation method (Régniere et al. 2014). Data are mean values measured during eight months per year (from April to November). Winter months were not considered because bryophytes are under snow cover during the winter, and no biological activity has been reported during this season (Longton and Greene 1967). The variables included were as follows: relative humidity (%), temperature (°C), maximum temperature (°C), precipitation (mm), the number of days <0°C, the number of days without precipitation, and the fire weather index (FWI, proxy of the stand moisture and dryness used to predict fire behavior; Van Wagner 1988).

**Bryophyte sampling**

Three rectangular 40-m² subplots (5 × 8 m), centered on the 400-m² circular plots, were established in each stand (n = 72). Within the subplots, all bryophyte species were sampled on all woody debris, snags, and living trees bases (>8 cm DBH, <1 m from the ground). In addition, three 1-m² quadrats were systematically placed at 0, 4, and 8 m in the center of the subplot and all forest floor bryophytes were collected. To ensure a balanced design, a target of at least five pieces of coarse woody debris and five live tree bases of each of black spruce, balsam fir, and white birch was established for each plot. When a sufficient number of microhabitats (downed woody debris, snags, or tree bases) was not found within the subplots, additional microhabitats were sampled outside the subplot, up to a maximal distance of 50 m from the center of the plot.

All the sampled bryophyte specimens were placed in individual marked paper bags (one bag per microhabitat) to be identified in the laboratory. Species presence in each of these samples was used in subsequent analyses. Nomenclature follows Faubert (2012–2014) except for *Sphagnum subtile* (Flora of North America Editorial Committee 2007). Validations were carried out using herbarium specimens from the Canadian Museum of Nature, Ottawa, Ontario, Canada.

**Data analyses**

Response of bryophyte communities in two forest types to climate.—We compared different bryophyte richness metrics between forest types (coniferous vs. mixedwood stands), and then, we compared the north–south difference within each forest type (northern vs. southern coniferous stands and northern vs. southern mixedwood stands). Bryophyte richness metrics were expressed as the mean number of species per forest type and were examined for all bryophyte species combined (total species richness), for each bryophyte life form individually (mean richnesses in liverwort, acrocarpous and pleurocarpous mosses, and sphagna; During 1992), and for the two bryophyte microhabitat associations: specialist species (deadwood, coarse woody debris, and snags, and living tree base communities) and generalist species (forest floor community; see Models below). The lm base function in the R software 3.3.3 (R Development Core Team 2017) was used to test differences among forest types and forest zones, at the forest plot level (n = 24). Square root transformations were applied when necessary to achieve normality, linear mixed models (lme; package nlme 3.1-131; Pinheiro and Bates 2017) if random factors representing the spatially nested nature of the design had a significant influence. We used post hoc tests to examine treatment differences with the package multcomp 1.4-7 (Hothorn et al. 2017). Finally, when data were not homoscedastic, the Kruskal-Wallis nonparametric tests were used, followed by post hoc multiple comparison tests (package pgirmess 1.6.7; Giraudoux 2017). In all statistical tests, a P value ≤ 0.05 was considered significant. Marginally significant results with P values between 0.10 and 0.05 are also discussed, as they suggest trends in the data associated with fine-scale biological responses (de Valpine 2014).

We also examined differences in overall community composition between forest types with a principal coordinates analysis (PCoA; Borcard et al. 2011) performed on binary data (i.e. presence/absence data) using the package vegan 2.3-0 (Oksanen et al. 2015). This analysis was performed on individual samples (n = 1075). Jaccard’s dissimilarity index was used as the distance measure. Negative eigenvalues were corrected using the Caillez correction (Gower and Legendre 1986). Species with less than six occurrences and microhabitats containing less than three species were removed from the ordination matrix, as analyses performed on matrices
comprising rare species tend to give less robust solutions. The resulting matrix contained 72 species and 1075 microhabitats (526 and 549 microhabitats in coniferous and mixedwood stands, respectively). Distance-based tests of multivariate differences between forest types and north–south (4 predefined groups: northern and southern coniferous stands, northern and southern mixedwood stands) from the PCoA were performed using multi-response permutation procedure (MRPP) in the package vegan 2.3-0 (Therneau and Atkinson 2004) on 9999 permutations. Within- and between-group dissimilarities based on species presence/absence data and Jaccard’s dissimilarity index were also extracted. The scores of each microhabitat were also extracted and used as response variables in further modeling.

**Relationship between microhabitat association and response to climate.**—The responses to climate of specialist species growing on deadwood or live tree bases and of generalist species growing on the forest floor were examined. To determine the relative importance of climate in shaping bryophyte community patterns, the weights of climate variables were compared to that of stand structure variables for the two types of species (specialists and generalists) using a model selection approach. Bryophyte community composition on each microhabitat (either deadwood, live tree bases, or forest floor) was represented univariately by the PCoA axis 1 sample score (one per microhabitat). The scores for deadwood, live tree base, and the forest floor were separated, generating three variables each representing community composition on one microhabitat type.

Only two key climate variables were included in the model selection procedure. The first variable (mean annual temperature) is widely available to scientists and decision makers, easy to interpret, and useful as a predictor because it facilitates comparison with other regions. The second variable (fire weather index) is widely used in Canada to infer humidity content in the duff layer (in the context of fire prediction systems) and was selected because it is highly relevant for bryophytes. Stand structure was summarized using a principal component analysis (PCA). The scores of the first two PCA axes were extracted and used as two variables representing stand structure (Appendix S2: Fig. S1). The first axis was negatively correlated with living tree variables (tree diversity, tree density, mean deadwood DBH, and mean tree DBH) and represented 59% of the variability explained, while the second axis was negatively correlated with deadwood variables (deadwood density and deadwood decay class) and represented 38% of explained variation. This method was used to balance the number of climate and stand structure variables.

Eight candidate models that included individual and combined models of the four variables (mean annual temperature, mean annual fire weather index, tree structure [PCA axis 1], and deadwood structure [PCA axis 2]) were evaluated for each response variable (deadwood, live tree base, and forest floor communities) in each forest type (Appendix S3: Table S1). As the two climate variables were correlated (Spearman’s rank correlation $r^2 = 0.91$), they were not included in the same model. Models were analyzed with a repeated-measures ANOVA (nlme 3.1-131; Pinheiro and Bates 2017) with landscape and plot as random effects to account for the spatial structure of the design. Candidate models were ranked based on Akaike’s information criterion corrected for small sample size (AICc; Burnham and Anderson 2002) using the package aicmodavg 2.1-1 (Mazerolle 2017). The model with the lowest AICc was considered the best compromise of parsimony and explanatory power. In the case where several models had a delta AICc < 2, evidence-ratio tests were performed to compare their respective explanatory weight. Subsequently, the effect of each explanatory variable of the best model or models was tested with multimodel inference. We obtained 95% confidence intervals and model predictions using the modavgShrink function of the package aicmodavg 2.1-1 (Mazerolle 2017). Variables with 95% confidence intervals excluding 0 had a significant effect on community composition, and their predicted values were plotted against the explanatory variable. An estimate of model adjustment was indicated by Spearman’s Rho.

**Results**

**Bryophyte community: differences between north and south**

A total of 132 bryophyte species were identified, of which 60 can be considered rare
(<6 occurrences in the entire database). We found 108 species in coniferous forest of which 36% were rare, and 98 species in mixedwood stands of which 32% were rare (Appendix S4: Table S1). No significant differences in any species richness were found between northern and southern plots within a forest type (Fig. 2a, b; Appendix S5: Table S1). There were no significant differences in mean total and acrocarpous species richness between forest types (Fig. 2a; Appendix S5: Table S1). Only mean species richness of liverworts and sphagna was greater in coniferous than in mixedwood stands (marginally and significantly greater, respectively). The reverse was observed for mean species richness of pleurocarpous species, which was significantly higher in mixedwood than in coniferous stands. Mean richness of generalist species was marginally significantly higher in mixedwood than in coniferous stands, but no significant difference was found in mean richness of specialist species between forest types (Fig. 2b).

In terms of community composition, there was a gradient from northern coniferous to southern mixedwood stands along the first axis (32.6%) although there was significant overlap of the ellipses (Fig. 3a, b). The part of the variance explained by the second axis was low, and it was difficult to interpret (axis 2: 6.35%). While many species were shared between the two forest types (Herzogiella turfaea, Nowelia curvifolia, Plagiothecium cavifolium; Fig. 3b), many liverworts were associated with coniferous stands (Lophozia longidens, Polytrichum longifolium, Sphenolobus hellerianus) and several pleurocarps (Brachythecium campestre, Platygyrium repens, Plagiothecium

![Fig. 2. Mean richness of bryophytes per plot. Mean richness is presented by (a) bryophyte life forms and (b) niche characteristics and are compared by forest type (C, coniferous stands; M, mixedwood stands) and latitude (white boxes, north; gray boxes, south). Statistical significance is indicated between forest types (upper case) and between latitudes for a same forest type (lower case). Linear mixed models (lme) and Kruskal-Wallis tests were used. Levels of significance: † 0.01 < P < 0.05; *0.001 < P < 0.01; **0.001 < P < 0.0001; na, non-applicable; NS/ns, nonsignificant. The horizontal line of the box plot indicates the median, while the bottom and top of the box indicate the 25th and the 75th percentiles, respectively. The whiskers indicate 2SD. Dots above or below 2SD are outliers.](image-url)
denticulatum) were associated with mixedwood stands. Epiphytic acrocarps (Pylaisia polyantha, Ulota coactata) were particularly associated with southern mixedwood stands.

MRPP results confirmed this pattern as bryophyte composition differed both between forest types ($P < 0.001$, chance-corrected within-group agreement A 0.037) and between north and south sampling units ($P < 0.001$; A 0.058). Furthermore, bryophyte communities were more dissimilar between forest types (83.2% of Jaccard dissimilarity index between coniferous and mixedwood stands) than within forest types (76.8% for northern vs. southern coniferous stands and 80.5% for northern vs. southern mixedwood stands). Therefore, each forest type-latitude combination varied in its bryophyte community composition, and bryophyte communities under mixedwood canopies were slightly more dissimilar between the north and the south than they were under coniferous canopies.

**Role of microhabitat association and forest type in determining community response to climate**

Overall, forest type influenced model explanatory power for specialists as best models (with $\text{AIC}_c \leq 2$) were stronger for live tree bases and deadwood microhabitats in coniferous stands ($\rho > 0.73$) than in mixedwood stands ($0.34 > \rho > 0.52$), but not for generalists (forest floor; $0.33 > \rho > 0.57$ in coniferous and $0.33 > \rho > 0.36$ in mixedwood, respectively; Table 1). The best models differed not only between specialists and generalists but also between forest types for a microhabitat. This was particularly clear for specialists, as best models in coniferous stands included only forest structure variables (living and deadwood), while in mixedwood stands, the best models included climate variables (Table 1). Multimodel inference results interpreted in consideration of PCA and PCoA graphs (from which axes scores were used sampled and 84 species (Appendix S4: Table S1 for complete species names), and (b) microhabitats in function of forest stand type and latitude. The ellipses are the 95% confidence intervals of the mean position of groups (microhabitats of one forest type per latitude). From the darkest to the lightest gray: north-coniferous > south-coniferous > north-mixedwood > south-mixedwood forest. In the species plot (a), only the 59 most common species are shown, and + indicates positions of less common species.
as proxy of stand structure variables and community composition, respectively) indicate that less structurally complex stands (arrows of the PCA pointed toward negative values) have poorer specialist bryophyte communities (few species on the PCoA graph near ellipses of coniferous stands). For mixedwood stands, an increase in temperature was linked with a diversification of specialist communities (more species at the extreme right of the PCoA near southern mixedwood stands), especially for pleurocarpous and epiphytic species (Table 2). For the generalist community, none of the models explained the patterns as none of the intervals excluded 0. However, mean temperature was in the best models in both forest types for generalists.

**DISCUSSION**

Surprisingly, bryophyte responses to variation in climate were not similar in the two forest types. While there were no differences in total or guild species richness, communities from mixedwood stands were slightly more different between the north and the south than communities from coniferous stands. Consequently, the hypothesis that bryophyte communities will respond to climate was only upheld for the mixedwood stands. Specialist bryophyte community composition from woody microhabitats (i.e., deadwood and live tree bases) was influenced by climate in mixedwood stands but not in coniferous stands, where stand structure was the primary variable influencing specialist bryophyte community composition. Forest floor communities were little influenced by climate. Hence, our second hypothesis was only upheld for mixedwood stands. This suggests that response to spatial variation in temperature is both microhabitat-dependent (forest floor vs. woody microhabitats) and forest type-dependent (coniferous vs. mixedwood).

**Role of the forest type in species response to climate change**

The divergent bryophyte community responses to temperature change may be caused by differences in how coniferous and mixedwood canopies buffer climatic variation. For instance, seasonal variation in the canopy associated with deciduous tree leaf out and leaf fall

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**Table 1. Results of the multimodel selection procedure for bryophyte community composition (presented as species scores on PCoA first axis) for each microhabitat type per forest type tested with lme (see Appendix S3: Table S1 for details about models).**

| Forest type by microhabitat type | Model name         | Log-likelihood | K  | AICc   | ΔAICc | wiq | p      | Evidence-ratio |
|---------------------------------|--------------------|----------------|----|-------|-------|-----|--------|----------------|
| **Live tree bases**             |                    |                |    |       |       |     |        |                |
| Coniferous                      | Tree Structure     | 70.16          | 5  | −130.03 | 0.00 | 0.59 | 0.76 | 2.62          |
|                                 | Tree and DW Structure | 70.26          | 6  | −128.11 | 1.92 | 0.22 | 0.76 |               |
| Mixedwood                       | Temp               | 87.75          | 5  | −165.15 | 0.00 | 0.60 | 0.39 | 2.06          |
|                                 | Global2            | 89.18          | 7  | −163.71 | 1.45 | 0.29 | 0.34 |               |
| **Deadwood**                    |                    |                |    |       |       |     |        |                |
| Coniferous                      | Tree Structure     | 72.71          | 5  | −135.11 | 0.00 | 0.44 | 0.73 | 1.59          |
|                                 | Tree and DW Structure | 73.31          | 6  | −134.19 | 0.92 | 0.28 | 0.74 |               |
| Mixedwood                       | Global2            | 82.98          | 7  | −151.47 | 0.00 | 0.64 | 0.52 |               |
| **Forest floor**                |                    |                |    |       |       |     |        |                |
| Coniferous                      | Temp               | 34.45          | 5  | −57.78  | 0.00 | 0.29 | 0.33 | 1.29          |
|                                 | Tree Structure     | 34.19          | 5  | −57.28  | 0.51 | 0.22 | 0.46 |               |
|                                 | Tree and DW Structure | 34.93          | 6  | −56.28  | 1.50 | 0.14 | 0.57 |               |
| Mixedwood                       | ModTemp            | 20.77          | 5  | −30.52  | 0.00 | 0.63 | 0.36 | 2.77          |
|                                 | ModFWI             | 19.75          | 5  | −28.48  | 2.04 | 0.23 | 0.33 |               |

Notes: Only models with ΔAICc ≤ 2 are presented, with number of parameters included (K), second-order Akaike information criterion (AICc), distance from the best model (ΔAICc), Akaike weight (wiq), estimate of model adjustment by Spearman’s Rho (p), and value of the evidence ratio between the best model and the second model. Full explanations of models are found in Appendix S3.
could affect bryophytes. This variation results in changes in temperature, moisture, irradiance, and wind in the understory (Barbier et al. 2008). Furthermore, the type, amount, and variability of irradiance reaching the forest floor vary between forest types during the growing season (Messier et al. 1998), resulting in overall cooler, darker, and more stable microclimatic conditions in coniferous stands than those found in mixedwood stands.

Bryophyte species present in mixedwood stands must therefore be able to tolerate conditions that are more fluctuating than species in coniferous stands. Mixedwood communities may have a greater tolerance to regional climatic conditions because the overstory, similar to a colander, lets regional climatic conditions penetrate to the understory. In contrast, the constant and relatively dense overstory of coniferous stands, which similar to a solid dome, buffers the effects of the regional climate on the understory. Based on the definitions of autogenic and allogenic mechanisms of Tansley (1935), allogenic mechanisms, such as external processes imposed by the environment, drive bryophyte community dynamics in mixedwood stands. Conversely, community dynamics under coniferous tree canopies are governed by local stand characteristics and processes and are therefore driven by autogenic dynamics.

**Role of microhabitat associations in determining species and community response to climate**

A shift in bryophyte composition could signal a community-level adjustment to temperature change (d’Orangeville et al. 2016), which could facilitate the maintenance of ecosystem functions in a changing climate. Such a shift was observed in mixedwood stands, but not in coniferous stands. Moreover, forest type also interacted with climate to influence bryophyte community composition at the microhabitat level. Consequently, our results only partially support Brown (1995) and Thuiller et al. (2005), since specialist communities seemed more affected by climate than generalist communities, but in a forest type-dependent manner.

In coniferous stands, specialist communities on woody microhabitats such as live tree bases and deadwood were positively related to stand structure with little relationship with climate. Based on the definitions of autogenic and allogenic mechanisms of Tansley (1935), allogenic mechanisms, such as external processes imposed by the environment, drive bryophyte community dynamics in mixedwood stands. Conversely, community dynamics under coniferous tree canopies are governed by local stand

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**Table 2. Model-averaged estimates of coefficients, unconditional standard error, and lower and upper 95% confidence intervals of parameters explaining bryophyte species composition for niche specialist and generalist species in function of forest type.**

| Forest stand by microhabitat type | Parameters of the best models | Estimate | SE  | Lower CI | Upper CI |
|----------------------------------|-------------------------------|----------|-----|----------|----------|
| **Live tree bases**              |                               |          |     |          |          |
| Coniferous                       | Stand structure (−)           | −0.3     | 0.05| −0.4     | −0.2     |
|                                  | Deadwood structure            | 0.00     | 0.01| −0.01    | 0.01     |
| Mixedwood                        | Mean temperature (+)          | 0.08     | 0.03| 0.01     | 0.15     |
|                                  | Stand structure               | 0.00     | 0.01| −0.03    | 0.02     |
|                                  | Deadwood structure            | −0.01    | 0.02| −0.05    | 0.03     |
| Deadwood                         |                               |          |     |          |          |
| Coniferous                       | Stand structure (−)           | −0.28    | 0.07| −0.42    | −0.14    |
|                                  | Deadwood structure            | −0.01    | 0.01| −0.03    | 0.02     |
| Mixedwood                        | Mean temperature (+)          | 0.11     | 0.05| 0.02     | 0.21     |
|                                  | Stand structure               | 0.00     | 0.01| −0.02    | 0.02     |
|                                  | Deadwood structure            | −0.04    | 0.03| −0.10    | 0.02     |
| Forest floor                     |                               |          |     |          |          |
| Coniferous                       | Mean temperature              | 0.04     | 0.05| −0.07    | 0.14     |
|                                  | Stand structure               | −0.06    | 0.06| −0.19    | 0.07     |
|                                  | Deadwood structure            | −0.01    | 0.02| −0.05    | 0.03     |
| Mixedwood                        | Mean temperature              | 0.07     | 0.05| −0.03    | 0.16     |
|                                  | Mean Fire Weather Index       | 0.03     | 0.05| −0.08    | 0.13     |

**Note:** Significant parameters are indicated in bold with the sign of the relationship indicated between parentheses.
Furthermore, tree density is linked with the deadwood volume (Moussaoui et al. 2016), another variable of prime importance for epiphytic species (Rambo 2001).

In contrast, in mixedwood stands, community composition on woody microhabitats depends on climatic variables, specifically temperature. Multiple direct and indirect pathways could explain this relationship, as the sensitivity of epiphytic species to variations in temperature is well known (Király et al. 2013), as it can affect tree bark characteristics (humidity and pH levels, adherence) differentially in coniferous and deciduous trees (Szövényi et al. 2004). Furthermore, fluctuating temperatures associated with mixedwood stands may enhance the action of wood decomposing fungi (Toljander et al. 2006) resulting in a higher volume in deadwood in advanced decay classes that are key microhabitats for various epixylic liverworts (Rambo 2001). This may explain the high species richness found in warmer sites but not the difference in bryophyte composition in northern mixedwood stands, which were richest in generalist species with a broad array of climatic tolerance.

The difference in community composition response between forest types may be caused by a mechanism suggested by Swihart et al. (2003): “species with requirements near the mean climate conditions of a studied area should be less sensitive than species with outlying niches defined as marginal species.” Following this rationale, the microclimatic conditions present in coniferous stand understories may be optimal for boreal bryophytes, while the conditions present in the understory of mixedwood stands may be suboptimal for boreal bryophytes.

The response of the generalist forest floor community did not uphold our hypothesis as they responded to none of the examined variables. The inclusion of additional variables such as humidity and irradiance may give a clearer picture of their potential sensitivity to climate as the explanatory power of the models was poor.

Conclusions

We partially reject all our hypotheses, shedding light on a nuanced bryophyte response to variables such as climate, microhabitat, and forest type. The response of bryophyte communities to climate is both forest type- and niche/microhabitat-dependent, which suggests that it would be difficult to use bryophytes in general to monitor the impacts of climate change without including co-variates, or focusing on subgroups of species, such as habitat specialists in mixedwood stands. Since bryophyte community sensitivity to regional variations in climatic conditions depends on dominant canopy characteristics and microhabitat availability, we suggest that adapted forest management practices could play a role in attenuating climate change impacts on these organisms.

Our study examined a 3.9°C spatial variation in mean annual temperature, which is significant but will probably be surpassed by the temporal temperature change in the mid-century (Ouranos 2015). The ability of coniferous stands to buffer the effects of climate may not hold true in a more distant future when temperature change becomes more extreme. This might lead, in the future, to a breakdown in the buffering capacity of coniferous stands, which could have negative consequences on ecosystem stability. The impact of future changes in temperature is also difficult to predict for mixedwood forest bryophytes because, even though these stands contain bryophyte communities that are apparently more sensitive to temperature change, we do not know whether some breakdown could happen beyond the temperature gradient examined here. The question is particularly important considering unprecedented speed and magnitude of anticipated climate changes.

The multiple elements influencing boreal forest response to temperature change (i.e., forest type, microhabitat association) emphasize the importance of scale, which may lead to surprisingly different conclusions about a similar topic. The use of bryophytes together with the segregation of the boreal forest into two sub-forest types revealed previously hidden patterns about forest dynamics. Our approach may be used with other organisms, especially from the understory, and in other ecosystem types to revisit the resilience and vulnerability concepts at a new and finer scale.

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