Different temporal trends in vascular plant and bryophytes communities along elevational gradients over four decades of warming

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Database

Data are stored in *forestREplot* database (http://www.forestreplot.ugent.be/) under the code: N_AM_005 for Mont-Mégantic and N_AM_008 for Forillon. All plant specimens identified at the species level were deposited in the Marie-Victorin herbarium (Université de Montréal, Canada.) and all locations were entered into the GBIF database (GBIF - https://www.gbif.org/).

Abstract

1: Despite many studies showing biodiversity responses to warming, the generality of such responses across taxa remains unclear. Very few studies have tested for evidence of bryophyte

community responses to warming, despite the fact that bryophytes are major contributors to diversity in many ecosystems, playing a central role in ecosystem functions. Understanding variation among taxa in their responses to warming is crucial for identifying priorities in conservation.

2: We report an empirical study comparing long-term change of bryophyte and vascular plant communities in two sites with contrasting long-term warming trends. To assess long-term responses of ecological communities to warming, we used "legacy" botanical records as a baseline for comparison with contemporary resurveys.

We hypothesized that ecological changes would be greater in sites with a stronger warming trends, and that vascular plant communities would be more sensitive than bryophyte communities to climate warming. For each taxon in each site, we quantified the magnitude of changes in species' distributions along the elevation gradient, species richness, and community composition.

3: Temporal changes in vascular plant communities were consistent with the warming hypothesis, but this was not the case for bryophytes. We also did not find clear support for the hypothesis that vascular plants would show greater sensitivity than bryophytes to warming, with results depending on the metric of community change. As predicted for sites with a strong warming trend, we found a significant upward shift in the distributions of vascular plants but not bryophytes.

Synthesis: Our results are in accordance with recent literature showing that local diversity can remain unchanged despite strong changes in composition. Regardless of whether one taxon is systematically more or less sensitive to environmental change than another, our results suggest that vascular plants cannot be used as a surrogate for bryophytes in terms of predicting the nature and magnitude of responses to warming. In sites that experienced the same environmental changes, we found that communities of bryophytes and vascular plants did not predictably change

in the same ways. Thus, to assess overall biodiversity responses to global change, data from different taxonomical groups and community properties need to be synthesized.

Key words

Plant population and community dynamics, Global change ecology, vascular plant, bryophyte, warming, elevational gradient, historical ecology, legacy data, biodiversity, forest, understory vegetation, resurvey, temporal dynamic,

Introduction

Ecological impacts of global changes on biodiversity can take many different forms (McGill, Dornelas, Gotelli, & Magurran, 2015; Vellend, Baeten, et al., 2017). In the context of climate warming, montane ecosystems have received considerable attention due to clear predictions of changes in species' distributions (upslope shifts) and community composition (favouring warm-adapted species) along elevation gradients, although such studies have focused on relatively few taxa, in particular vascular plants and vertebrates (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Lenoir, Gegout, Marquet, de Ruffray, & Brisse, 2008; Pauli et al., 2012; Rumpf et al., 2018; Stockli, Wipf, Nilsson, & Rixen, 2012). Thus, despite many studies showing biodiversity responses to warming, the generality of such responses across taxa remains unclear. For instance, very few studies have reported clear empirical evidence of bryophyte community responses to climate warming (He, He, and Hyvönen 2016; Hudson and Henry 2010, but see Becker-Scarpitta et al. 2017; Bergamini, Ungricht, and Hofmann 2009; Outhwaite et al. 2020; Raabe et al. 2010; Vanneste et al. 2017).

Understanding variation among taxa in their responses to environmental change is crucial for identifying priorities in conservation. For example, even if one taxonomic group (e.g., vascular plants) is relatively insensitive to environmental change, other co-occurring taxa (e.g., bryophytes and lichens) might be very sensitive (Hudson & Henry, 2010), with potentially important

consequences for ecosystem functions (Lindo & Gonzalez, 2010; Turetsky, 2003). Thus, our limited knowledge base with which to identify the most relevant set of metrics or the taxonomic groups most sensitive to environmental change constrains our ability to set efficient conservation priorities. We operationally define "sensitivity" here as responsiveness: i.e., the degree to which a given community property changes in the face of environmental change.

To assess long-term responses of ecological communities to environmental change, "legacy" ecological records have been used to provide baselines for comparison with contemporary resurveys (Chytrý, Tichý, Hennekens, & Schaminée, 2014; Hédl, Bernhardt-Römermann, Grytnes, Jurasinski, & Ewald, 2017; Vellend, Brown, Kharouba, McCune, & Myers-Smith, 2013). However, historical botanical studies are strongly biased towards vascular plants, with few data on bryophytes, due in part to the difficulty of identification (Gignac 2001; He, He, and Hyvönen 2016; Möls et al. 2013 but see Becker-Scarpitta et al., 2017; Bergamini et al., 2009; Delgado & Ederra, 2013; Outhwaite, Gregory, Chandler, Collen, & Isaac, n.d.; Vanneste et al., 2017). This is despite the fact that bryophytes are major contributors to diversity and vegetation cover in many temperate, boreal or alpine ecosystems, playing an important role in ecosystem functions, such as biomass accumulation, water retention, nutrient cycling, and food web dynamics (Lindo & Gonzalez, 2010; Patiño & Vanderpoorten, 2018; Rydin, 2008; Tuba, Slack, & Stark, 2011; Turetsky, 2003).

For several reasons we might expect vascular plants and bryophytes to show different responses to various sources of environmental change (Bagella, 2014; Becker-Scarpitta et al., 2017; Lee & La Roi, 1979; Möls et al., 2013; Vanneste et al., 2017). Compared to vascular plants, bryophytes are distinguished by their small size, high sensitivity to the moisture and chemistry of their immediate microenvironment (i.e., they are poikilohydric), lower temperature optima for growth, absence of roots and an efficient vascular system, and dispersal via spores (Glime, 2007). These two groups can show contrasted spatial patterns of diversity (Lalanne, Bardat, Lalanne-Amara, Gautrot, & Ponge, 2008; Mateo et al., 2016). For instance, vascular plants show a clear latitudinal diversity

94 gradient of decreasing species richness with increasing latitude, while this is not true for
95 bryophytes, for which temperate latitudes are equally diverse as tropical latitudes (Geffert, Frahm,
96 Barthlott, & Mutke, 2013; Mateo et al., 2016). Some studies have also observed different patterns
97 of community β-diversity (Kraft et al., 2011; Mateo et al., 2016) with vascular plant communities
98 sometimes showing higher β-diversity along elevation gradients than bryophytes, suggesting a
99 broader tolerance of bryophyte species to temperature (Glime, 2013; Lee & La Roi, 1979; Vanneste
100 et al., 2017; Vittoz et al., 2010).

101 General predictions for the effects of warming on vascular plants include declines in the abundance
102 of cold-adapted species, an upward expansion of elevational range limits for warm-adapted
103 species (Rumpf et al., 2018), and an increase of local species richness in area without water-stress
104 (Harrison, 2020; Vellend, Baeten, et al., 2017). Compared to vascular plants, some studies have
105 suggested that changes in bryophyte communities are more strongly influenced by stochastic
106 processes or by micro-environmental variation than macro-environmental conditions (Fenton &
107 Bergeron, 2013; Pharo & Vitt, 2000; Raabe et al., 2010). Because bryophytes have wider
108 temperature affinities and higher affinity to micro-environment than macro-environment, we
109 might expect bryophytes to show lower sensitivity to global warming than vascular plants. The
110 consequences of warming for β-diversity are more difficult to predict given a paucity of studies on
111 this topic (Socolar et al. 2016 but see Nascimbene and Spitale 2017). However, numerical
112 simulations show that species with high dispersal capacity will be favored in areas experiencing
113 strong environmental changes, in which case we might predict a decrease of β-diversity (Mouquet
114 & Loreau, 2003) and thus biotic homogenization (Clavel, Julliard, & Devictor, 2011).

115 As in many parts of the world, eastern Canada has shown a general warming trend over the past
116 ~50 years, but with a strong east-west gradient in the magnitude of warming in the province of
117 Québec (Yagouti, Boulet, Vincent, Vescovi, & Mekis, 2008). Becker-Scarpitta, Vissault, and Vellend
118 (2019) showed that the magnitude of temporal changes of vascular plant communities in three

119 protected areas generally increased from east to west in southern Québec, with greater changes in
120 areas of stronger warming in recent decades. For two of these three parks, the historical data also
121 included bryophytes, thus presenting an opportunity to test for differential sensitivity among taxa
122 to warming. Forillon National Park is located at the eastern tip of the province of Québec where
123 warming has been minimal. In contrast, Mont-Mégantic Provincial Park is in central Québec were
124 the warming trend has been steeper (Savage & Vellend, 2015; Yagouti et al., 2008).

125 Here we report one of the first studies comparing long-term change of bryophytes and vascular
126 plants communities in sites with contrasting long-term warming trends. In each of the two parks,
127 we revisited ~50 legacy vegetation plots initially surveyed in the 1970s, applying the same
128 methods as the original surveys. To minimize potentially confounding factors, plots were selected
129 in mature forest ecosystems that have not experienced major natural or anthropogenic
130 disturbances during the time between surveys. We test two main hypotheses: (**i**) For both
131 bryophytes and vascular plants, the park with a stronger warming trend (Mont-Mégantic) has
132 experienced greater long-term community changes than the park with a weaker warming trend
133 (Forillon); (**ii**) Vascular plant communities are more sensitive than bryophyte communities to
134 climate warming. For each taxon in each park, we quantified the magnitude of changes in (a)
135 species' distributions along the elevation gradient, (b) species richness, and (c) community
136 composition.

137 **Methods**

138 ***Study site***

139 Our two study sites were located in eastern Canada: Forillon National Park in eastern Québec
140 (48°54′N, 64°21′W), and Mont-Mégantic Provincial Park in central Québec (45°27′N, 71°9′W).
141 Neither park has experienced logging or forest management over the last ~40 years. Forillon
142 National Park was created in 1970 and covers 245 km^2; our study plots ranged in elevation from

143 ~50 to 500 m a.s.l. The vegetation at Forillon is dominated by a mixture of northern tree species
144 such as *Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss and *Betula papyrifera* Marsh. at
145 higher elevations, and *Acer saccharum* Marsh. and *Betula alleghaniensis* Britt. at lower elevations
146 (Majcen, 1981). Mont-Mégantic Provincial Park was created in 1994 (logging ceased in the 1960s
147 during park planning) and covers ~55 km^2. Our study plots span an elevational gradient from
148 ~460 and 1100 m a.s.l., along which the vegetation gradient strongly resembles that in Parc
149 Forillon: from temperate deciduous forests dominated by *Acer saccharum*., *Fagus grandifolia* Ehrh.
150 and *Betula alleghaniensis*, to boreal forest dominated by *Abies balsamea,* and *Picea rubens* Sargent,
151 Silva. (Marcotte & Grandtner, 1974).

152 ***Data set***

153 Original vegetation surveys in both parks were conducted using phytosociological methods
154 (Majcen, 1981; Marcotte & Grandtner, 1974). In each plot, authors listed all species in different
155 strata (canopy trees, shrubs, herbs and ground bryophytes) and for each species assigned an
156 abundance coefficient following (Braun-Blanquet, Roussine, & Nègre, 1952). For vascular plants,
157 our analyses focused on shrubs and herbs, which were combined into a single "understorey"
158 stratum. All bryophyte species that were found on the ground were recorded (i.e. on organic litter
159 and soil surface mineral layers, not including deadwood, tree trunks and rocks); these surveys did
160 not involve intensive searches for individual stems of rare species within moss carpets (i.e., some
161 locally rare species were missed). After consulting with botanists active in Québec in the 1960s
162 and 1970s (C. Ansseau, Z. Majcen, personal communication, 2014), we are confident in comparing
163 Braun-Blanquet indices across time for vascular plants (*for further detail see* Becker-Scarpitta,
164 Vissault, and Vellend 2019) but not for bryophytes, given uncertainty in the definition of the area
165 over which percent cover was evaluated (microhabitats vs. entire plots). To maximize
166 comparability across time and taxa, we used presence-absence data for both vascular and
167 bryophyte species in all statistical analyses.

Our approach to plot relocation is described in Becker-Scarpitta et al., (2019). In short, original survey plots were not permanently marked, although locations were reported in maps and/or tables, such that plots are considered "semi-permanent". In both parks, original surveyors sampled mature forests where spatial heterogeneity was relatively low. We selected plot locations for recent surveys using original plot maps and environmental descriptions (elevation, slope, aspect), and observations in the field to maximize the match of current and historical abiotic conditions. In Mont-Mégantic, recent surveys included all plots within the current park boundary. Not all plot locations in Forillon were accessible, and plot selection for the recent surveys used the following criteria: (i) plots occurred in forest, excluding swamps or bogs; (ii) plots were accessible via <3-4 hours hiking off of established trails; (iii) plots had not obviously experienced major natural disturbances (e.g., storm, fire, or insect outbreak); (iv) in the original survey the plots were sampled in mature stands that have since maintained forest cover (i.e., no early successional dynamics in the intervening period) (Becker-Scarpitta et al., 2019).

Original surveys in Forillon Park were conducted in June-September 1972 in 256 vegetation plots (500 m^2) (Majcen, 1981). We resurveyed 49 plots during July and August of 2015. Original surveys in Mont-Mégantic were conducted in 1970 in 94 plots, roughly half of which fall outside the current park boundaries. Plots were 400 m^2 in coniferous forest and 800 m^2 in broadleaved forests (Marcotte & Grandtner, 1974). We resurveyed the 48 plots falling within the current park limits at Mont-Mégantic for vascular plants in 2012 (see Becker-Scarpitta et al., 2019) and for bryophytes during June and July 2014 (reported in the present study). We harmonized the taxonomy across both parks and periods (see below), so the Mont-Mégantic data are not precisely the same as reported in Savage & Vellend, (2015), but they are exactly the same as in Becker-Scarpitta et al., (2019) except transformed into presence-absence. Data are stored in *forestREplot* database (http://www.forestreplot.ugent.be/) under the code : N_AM_005 for Mont-Mégantic and N_AM_008 for Forillon.

193 ***Taxonomical database***

194 Our taxonomical reference was the Taxonomic Name Resolution Service v4.0 (assessed in Feb
195 2017: http://tnrs.iplantcollaborative.org) for vascular plants and Flore des bryophytes du
196 Québec-Labrador (Faubert, 2012, 2013, 2014) for bryophytes.

197 Our data set was collected by four different survey teams: one for each of the two original surveys:
198 Forillon: Majcen, (1981); Mont-Mégantic: Marcotte & Grandtner, (1974); one for the recent Mont-
199 Mégantic vascular plant survey: Savage & Vellend, (2015); and one for the recent Mont-Mégantic
200 bryophyte survey and for the recent survey of both taxa at Forillon (A. Becker-Scarpitta and
201 assistants). Most plants were identified to the species level in the same way across surveys, so for
202 these taxa the only harmonization step was to standardize names. Coarser levels of taxonomic
203 resolution were used in some but not all surveys for certain species (e.g., a pair of similar species
204 not identified to the species level), and for other species (e.g., spring ephemeral species) the timing
205 of different surveys created doubt about the likelihood of comparable detection. In these
206 situations, comparability was maximized by using the coarser level of resolution applied to all data
207 sets, or by removing species (see Appendix S1 for details on taxonomic standardization). All
208 specimens identified at the species level were deposited in the Marie-Victorin herbarium
209 (Université de Montréal, Canada.) and all locations were entered into the GBIF database (GBIF -
210 https://www.gbif.org/).

211 ***Statistical analysis***

212 All statistical analyses were performed in R v.3.4.2 (R Foundation for Statistical Computing 2018).
213 To test for upward elevational shifts in species distributions at Forillon and Mont-Mégantic, we
214 calculated the mean elevation across all occurrences of a given species in each time period. For
215 vascular plants and bryophytes separately, we then conducted linear mixed effect models (LMM,
216 function *lmer*, package 'lme4' v.1.1-14, Bates, Mächler, Bolker, & Walker, 2015) testing the effect

217 of time on mean elevation; each species was weighted by the sum of its occurrences in each survey,
218 and species was included as a random effect to account for the paired sampling structure of the
219 data (i.e. each species observed in each time period).

220 To test for differences between taxa and parks in terms of the temporal change in plot-level species
221 richness (α-diversity) we first calculated the log ratio, *ln*(recent richness/original richness), for
222 each taxa-park combination, and ran an ANOVA model with each combination of park and taxa as
223 factors. Secondly, we explored separately the temporal trend of α-diversity of both bryophytes
224 and vascular plants within parks using LMMs with time, elevation and the time*elevation
225 interaction (if significant) as fixed effects and with plot ID as a random effect.

226 We then explored temporal change in β-diversity using two different frameworks. First, we
227 assessed the multivariate homogeneity of group dispersions using an asymmetric binary Jaccard
228 dissimilarity (used for presence-absence data), with significance testing via permutation
229 (PERMDISP, function *betadisper*, package 'vegan' v.2.4-4; Anderson, Ellingsen, & McArdle, (2006)).
230 A decrease in the multivariate distance between plots and the time-specific centroid is interpreted
231 as biotic homogenization, while an increase indicates biotic differentiation. Second, to explore the
232 components of temporal change in species composition, we calculated the temporal pairwise β-
233 diversity as the binary Jaccard dissimilarity between the recent and original surveys for each plot.
234 Temporal β-diversity was decomposed into two components: turnover due to species
235 replacements (T) and nestedness (N) (function *beta.temp*, package 'betapart'; Baselga, 2012;
236 Baselga & Leprieur, 2015).

237 To examine changes in community composition over time, we used permutational analysis of
238 variance (PERMANOVA, Anderson, 2001) with Jaccard distances using 999 permutations (function
239 *adonis*, package 'vegan'). We used the R^2 values from the PERMANOVA models as a quantification
240 of the magnitude of temporal change in order to compare among parks. We used non-metric

241 multidimensional scaling (nMDS) with Jaccard distances for visualization (function *metaMDS*,
242 package 'vegan'). Finally, within each park, we identified indicator species for each time period
243 using the IndVal procedure (function *multipatt*, package 'indicspecies'; De Cáceres, Legendre, &
244 Moretti, 2010).

245 **Results**

246 ***Species distributions along elevation gradients***

247 Among the four taxa-park combinations, vascular plants at Mont-Mégantic was the only one
248 showing a significant upward shift in mean species elevations over time (Table 1a, Fig. 1). Data
249 for vascular plants at Mont-Mégantic were already presented in Becker-Scarpitta et al., (2019), and
250 it is important to note that patterns reported here are not quantitatively the same, given the use
251 of the presence-absence data in this study.

252 Consistent with our hypothesis, we detected no elevational distribution shift for either vascular
253 plants or bryophytes in Forillon, where the warming trend has been weak, nor for bryophytes at
254 Mont-Mégantic. Despite the lack of trends in average elevation for bryophytes, there was
255 substantial variation among species (less so than for vascular plants) (Table 2, Fig. 1). This
256 observation is reflected in the strength of correlations between original and recent mean species
257 elevations, which was lower for bryophytes (Forillon Pearson r correlation = 0.327; Mont-
258 Mégantic r = 0.577) than for vascular plants (Forillon r = 0.518; Mont-Mégantic r = 0.729). See
259 Appendix S2 for mean elevations and sums of occurrences for each species in each survey.

Table 1 - Analyses of temporal changes in (a) average species elevation, (b) plot-level species richness (α-diversity) along elevational gradients, and (c) multivariate β-diversity along elevation gradients (see Table 3 for other β-diversity analyses). For (a) and (b), results are shown for linear mixed models; in (a) species were weighted by the sum of occurrences across both original and recent surveys. In (c), β-diversity was measured as the distance of plots to time-specific centroids (space defined by Jaccard dissimilarities) and tested using PERMIDSP. The sign of the relation is indicated in brackets only for significant effect. R^2m is the marginal coefficient of determination, measuring the proportion of variance explained by fixed effects; R^2c is the conditional coefficient of determination, giving the proportion of variance explained by both fixed and random effects, $p < 0.05$.

		Effect		F	df	Pr(>F)	R^2_m	R^2_c
a) Average species elevation (m)								
Forillon								
	Bryophytes	Time		0.12	36	0.73	<0.01	<0.01
	Vascular plants			0.01	31	0.92	<0.01	<0.01
Mont-Mégantic								
	Bryophytes	Time		0.16	25	0.69	<0.01	0.09
	Vascular plants		(+)	8.54	55	**0.005**	<0.01	0.18
b) Species richness (α-diversity)								
Forillon								
	Bryophytes							
		Time		2.42	46	0.13	0.04	0.05
		Elevation		1.77	45	0.19		
	Vascular plants							
		Time		3.19	47	0.08	0.04	0.41
		Elevation		1.26	46	0.27		
Mont-Mégantic								
	Bryophytes							
		Time		0.01	46	0.92	0.01	0.32
		Elevation		0.85	45	0.36		
	Vascular plants							
		Time	(+)	26.77	47	**<0.001**	0.54	0.74
		Elevation	(-)	68.14	46	**<0.001**		
c) Heterogeneity (β-diversity)								
Forillon								
	Bryophytes							
		Time	(+)	7.14	45	**0.002**	0.17	0.26
		Elevation	(-)	10.75	46	**0.01**		
	Vascular plants							
		Time		0.92	47	0.27	0.02	0.51
		Elevation		1.25	46	0.34		
Mont-Mégantic								
	Bryophytes							
		Time		0.72	45	0.40	0.16	0.39
		Elevation	(-)	13.76	46	**<0.001**		
	Vascular plants							
		Time	(-)	22.30	46	**<0.001**	0.28	0.63
		Elevation	(+)	17.08	47	**<0.001**		

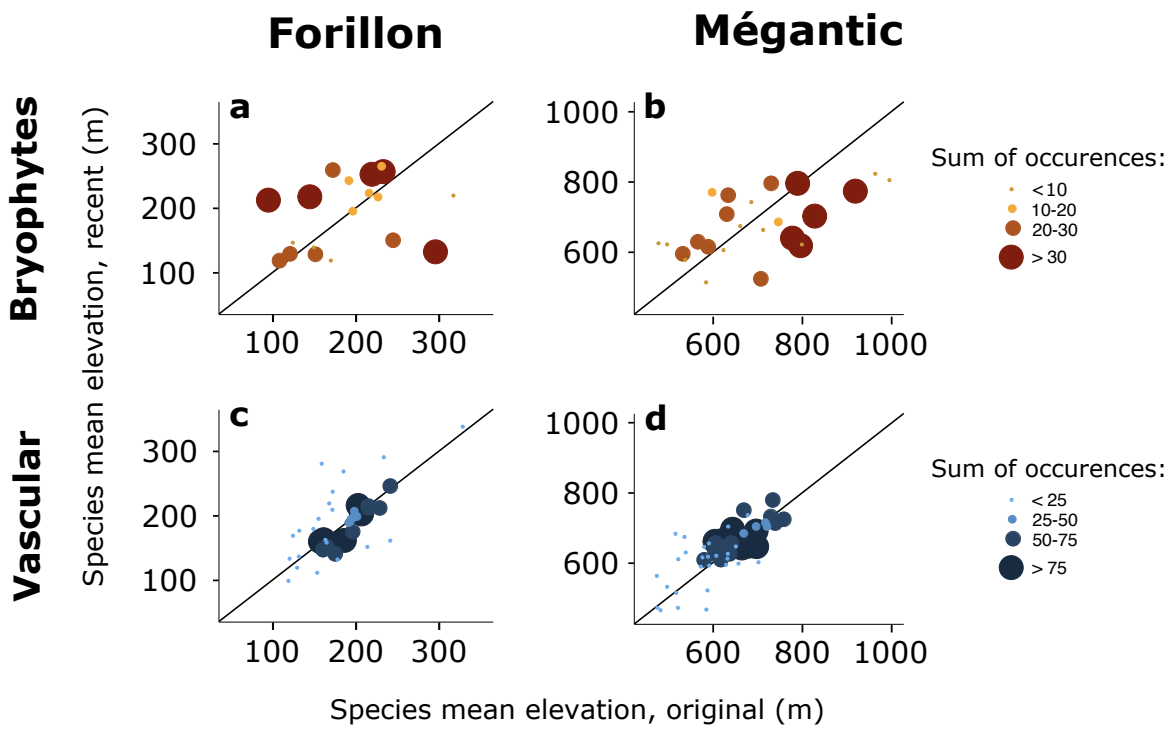

Figure 1 - Species distributions along elevation gradients in two-time periods. a) Bryophytes in Park Forillon (n = 19 species); b) Bryophytes at Mont-Mégantic (n = 25 species); c) Vascular plants in Park Forillon (n = 42 species); d) Vascular plants at Mont-Mégantic (n = 64 species). All species present in both original and recent surveys were included; the size of each point is proportional to the number of occurrences summed across the two survey years for a given species. Diagonals indicate 1:1 line (i.e. no changes over time). The only significant increase of mean species elevation over time was for vascular plants in Mont-Mégantic (panel d; see also Table 1a).

<u>Temporal changes in species richness</u>

At Forillon, the total number of bryophyte species across plots was greater in the recent survey (57 species) than in the original survey (42 species); 15 species from the original survey were not found while 30 new species were observed (Table 2 and Appendix S2 for species occurrences). Conversely, the total number of vascular plants at Forillon declined over time (original survey =

83 vs. recent = 65 species), with 27 original species not found in the recent survey and 9 new species added (Table 2).

At Mont-Mégantic we found similar trends between vascular plants and bryophytes. In the recent survey, there was an increase in the overall number of bryophytes species (original survey = 46 vs. recent = 55 species), with 16 species lost and 25 gained. The total number of vascular plant species also increased (from 87 species to 92 species), with 8 species lost and13 gained.

Overall, the only strong significant temporal change detected in mean plot-level species richness was an increase for vascular plants at Mont-Mégantic (mean log ratio of species richness = 0.3; 95% CI [0.16, 0.44]; t = 4.40; df = 47; p<0.001), where richness significantly declined with elevation (Fig. 2d, Table 1b; see also (Becker-Scarpitta et al., 2019). For vascular plants at Forillon and for bryophytes in both parks, species richness at the plot level showed neither changes over time nor any relationship with elevation (Table 1a-b, Fig. 2 a-b-c).

Table 2 - Temporal changes in total species numbers, plot-level species richness (α-diversity) and mean species elevation for bryophytes and vascular plants in Forillon Park and Mont-Mégantic Park. The total number of species observed across all plots is divided into shared, lost, or gained species between the original and recent surveys. For plot-level richness and mean species elevation, mean ± SE are reported. Bold values indicate significant statistical differences (p < 0.05, see Table 1b for statistical tests). Temporal changes in "Total species number" were not tested statistically.

		Total species number					α-diversity			Mean species elevation		
		Original	Recent	Shared	Lost	Gained	Original	Recent	*n* plot	Original	Recent	*n* sp
Forillon												
	Bryophytes	42	57	27	15	30	5.4 ± 0.5	6.3 ± 0.4	47	208.8±9.5	204±9.8	19
	Vascular plants	83	65	56	27	9	18.2 ± 1	16.4 ± 1	48	186.3±5.5	186.8±5.6	42
Mégantic												
	Bryophytes	46	55	30	16	25	5.6 ± 0.4	5.5 ± 0.4	47	702.5±21.2	702.5±21.2	25
	Vascular plants	87	92	79	8	13	**21.2 ± 1**	**27 ± 1**	48	**629.2±7.3**	**642.5±7.1**	64

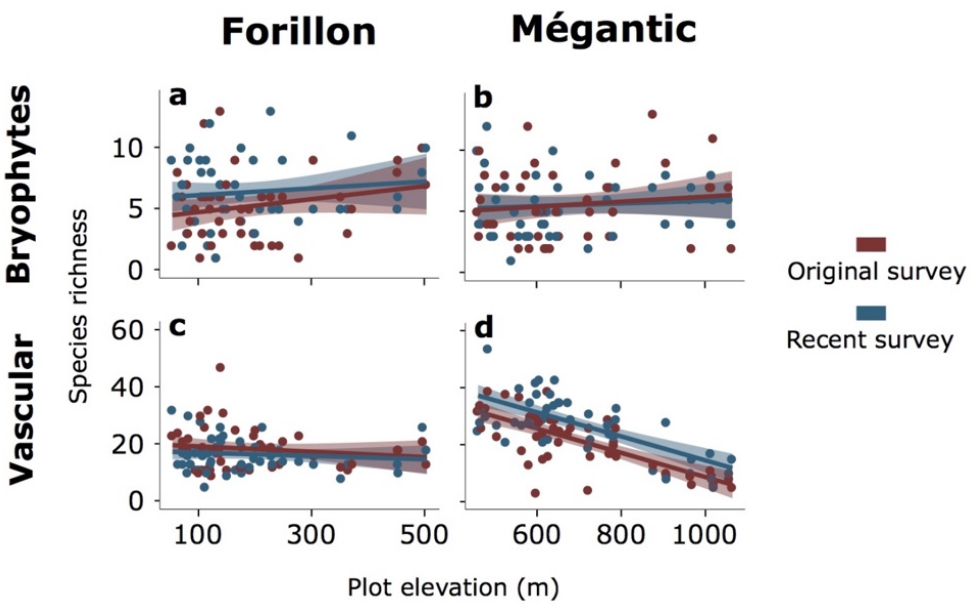

Figure 2 - Temporal changes of plot-level species richness (α-diversity) along elevation gradients. The only significant increase of α-diversity over time was for vascular plants in Mont-Mégantic (panel d; see also Table 1b).

<u>Temporal shift in community composition and heterogeneity</u>

Consistent with our hypotheses, we found significant temporal changes in vascular plant β-diversity and community composition at Mont-Mégantic (Figs. 3 & 4, Table 3), where climate warming has been pronounced, as previously reported (Becker-Scarpitta et al., 2019). However, we found unexpected results for bryophytes: a significant increase of multivariate dispersion (β-diversity) over the past 40 years at Forillon but not at Mont-Mégantic (Table 3, Fig. 3). The observed increase in the distance of plots from multivariate centroids at Forillon was consistent along the whole elevation gradient (Table 1c, Fig. 4). The decomposition of the temporal changes in bryophyte community composition showed a greater contribution of turnover (Forillon = 0.70, Mont-Mégantic = 0.86) than nestedness (Forillon = 0.11, Mont-Mégantic = 0.03, Table 3). For vascular plants at Mont-Mégantic but not at Forillon we found a significant decrease of β-diversity over time, consistent along the elevational gradient (Table

319 3, Figs. 3 & 4). Turnover was also the main driver of temporal community change for vascular plants
320 (Table 3).

321 For both sites and taxa, we found significant temporal shifts in community composition (Figs. 3 & 4,
322 Table 3), although the effect was weak in all analyses. As predicted, the magnitude of the vascular
323 plant compositional shift was greater for Mont-Mégantic (R^2 = 4%) than Forillon (R^2 = 2%, Table 3).
324 However, bryophyte communities experienced an equal magnitude of compositional shift for both
325 Forillon and Mont-Mégantic (R^2 = 7%). Moreover, compositional shifts were greater for bryophytes
326 than for vascular plants at both sites, contrary to our hypothesis (Table 3, Fig. 3).

327 Table 3 - Temporal changes in two β-diversity metrics and community composition between original
328 and recent surveys for vascular plants and bryophytes in Forillon Park and Mont-Mégantic Park.
329 "Multivariate dispersion" was calculated (based on Jaccard's dissimilarity) as the mean distance of
330 plots to time-specific centroids and analyzed using PERMDISP. "Temporal β-diversity" (βj) was
331 calculated as the pairwise Jaccard's dissimilarity between the recent and original survey and
332 decomposed into components of turnover (T) and nestedness (N). Changes in community
333 composition were analyzed using PERMANOVA. R^2 is the proportion of variation in community
334 composition explained by time. Statistical significance levels were calculated with 999 permutations,
335 $p < 0.05$.

		Multivariate dispersion				Temp. β-diversity			Community composition		
		Original	Recent	F	Pr(<F)	βj	T	N	R^2	F	Pr(<F)
Forillon											
	Bryophytes	0.54	0.59	4.32	**0.04**	0.81	0.70	0.11	0.07	6.57	**<0.001**
	Vascular plants	0.45	0.44	0.55	0.47	0.52	0.37	0.16	0.02	1.74	0.05
Mégantic											
	Bryophytes	0.62	0.61	0.44	0.52	0.90	0.86	0.03	0.07	7.02	**<0.001**
	Vascular plants	0.50	0.44	9.23	**0.003**	0.54	0.39	0.16	0.04	0.43	**0.002**

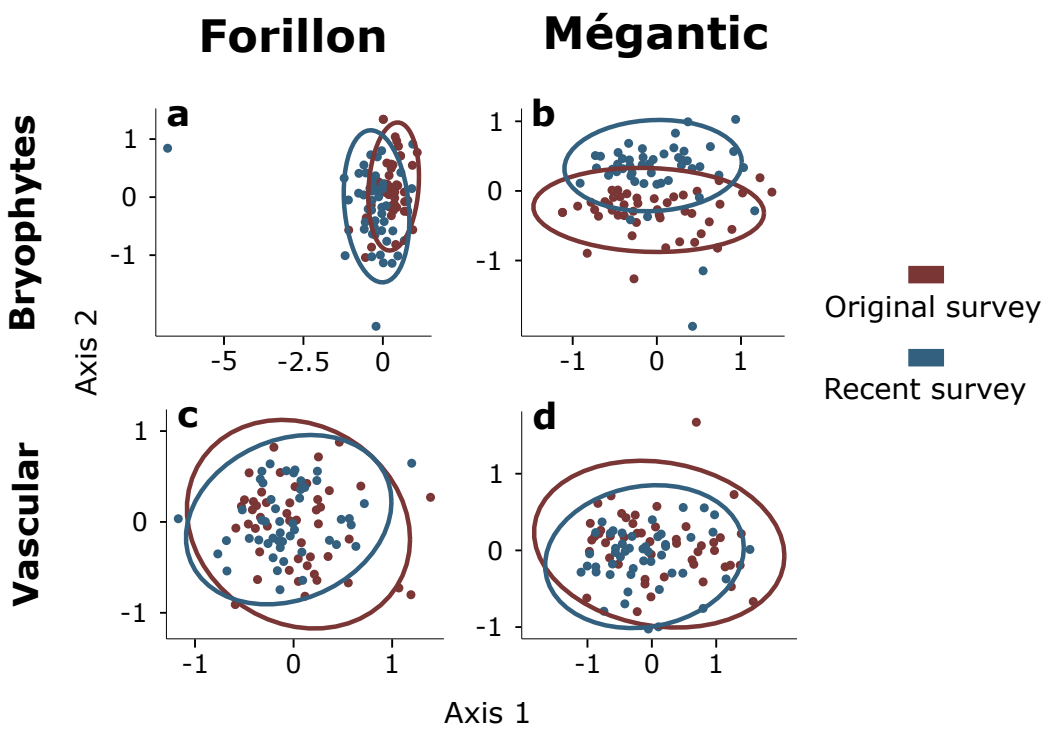

Figure 3 - nMDS ordinations (based on Jaccard's dissimilarity) of vascular plant and bryophyte communities across time in Forillon and Mont-Mégantic. In panel (a), the left-most plot was composed of a single unique species very rare elsewhere; PERMDISP and PERMANOVA results were qualitatively similar with and without this plot. Bryophytes at Forillon (panel a) show significant increase in beta-diversity while vascular plant in Mont-Megantic (panel d) show significant decrease of beta-diversity (see also Table 1c).

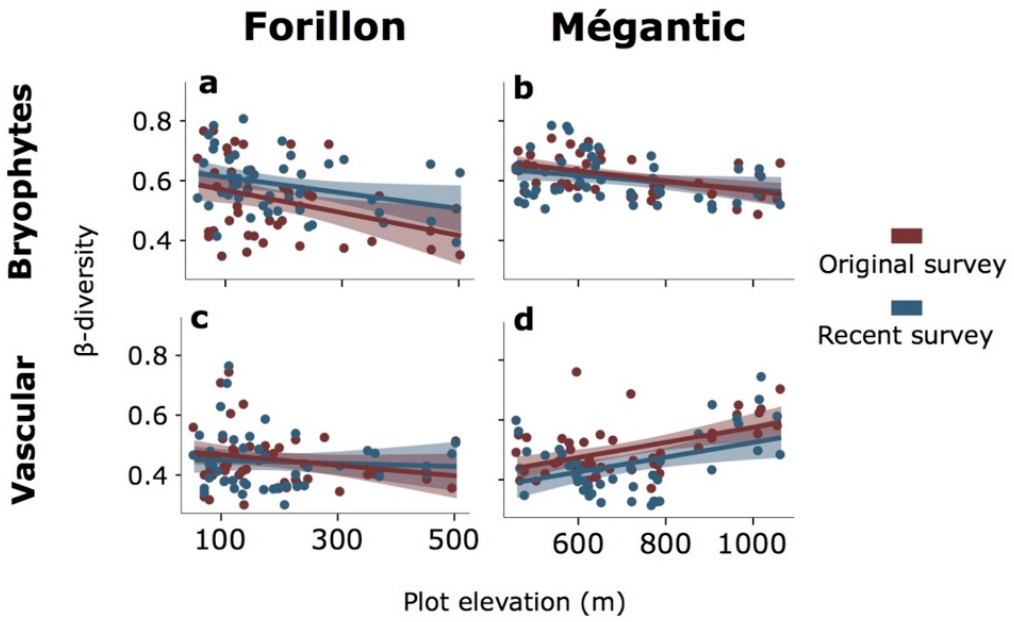

Figure 4 - Temporal changes of β-diversity along elevational gradients for bryophytes (a-b) and vascular plant communities (c-d) at Forillon and Mont-Mégantic. β-diversity is here calculated for each plot as the multivariate distance to time-specific centroids (Jaccard's dissimilarity; see Table 1c for statistical analyses).

In terms of bryophyte indicator species, *Dicranum fuscescens* was associated with original surveys for both parks, while *Dicranum polysetum* was associated with the two recent surveys (Table 4). These two species are morphologically very different to confuse them. Other indicator bryophytes for either time period were unique to one or the other park. For vascular plants, recent surveys were associated with two of only three non-native species in the data set: *Galeopsis tetrahit* (only at Mont-Mégantic) and *Epipactis helleborine* (both parks) (Table 4). Recent surveys at Mont-Mégantic were also associated with two species of *Carex* and the fern *Dennstaedtia punctilobula.*

356 Table 4 - Indicator species of bryophytes and vascular plants associated with original and recent
357 surveys at Forillon and Mont-Mégantic. Indicator values were considered significant if $p<0.05$
358 (calculated with 999 permutations).

	Bryophytes	Vascular plants
Forillon		
Original	*Dicranum fuscescens*	*Lycopodium annotinum*
		Galium triflorum
Recent	*Dicranum montanum*	*Gymnocarpium disjunctum*
	Dicranum polysetum	*Sambucus racemosa*
	Brachythecium campestre	*Epipactis helleborine*
	Pseudoleskeella tectorum	
Mégantic		
Original	*Brotherella recurvans*	*Osmunda claytoniana*
	Dicranum fuscescens	*Botrychium virginianum*
	Paraleucobryum longifolium	
	Hypnum pallescens	
	Bryhnia novae-angliae	
	Brachythecium reflexum	
Recent	*Atrichum altecristatum*	*Dennstaedtia punctilobula*
	Hylocomiastrum umbratum	*Carex arctata*
	Dicranum polysetum	*Carex deweyana*
	Hypnum curvifolium	*Circaea alpina*
		Galeopsis tetrahit
		Epipactis helleborine

359 **Discussion**

360 Most long-term legacy studies have been conducted on vascular plant communities (Verheyen et al.,
361 2017), so it remains unknown whether bryophytes show similar or different responses to shared
362 environmental changes. More broadly, we have limited knowledge of how different taxonomic groups
363 respond to long-term environmental change. Thanks to an extensive resurveying of plots with legacy
364 data we quantified community changes over ~40 years for both bryophytes and vascular plants in
365 two protected natural areas in eastern Canada with contrasting recent warming trends. Temporal
366 changes in vascular plant communities were consistent with the warming hypothesis, but this was
367 not the case for bryophytes. We also did not find clear support for the hypothesis that vascular plants
368 would show greater sensitivity to environmental change (assumed to be dominated by climate
369 warming at Mont-Mégantic), with results depending on the metric of community change. As predicted

370 for the area with a strong warming trend (Mont-Mégantic), we found a significant upward shift of
371 vascular plant distributions but no change for bryophyte distributions (Table 1a, Fig. 1). However,
372 the higher magnitude of changes in bryophyte community composition at both sites was contrary to
373 our prediction (Table 3, Fig. 3).

374 ***Patterns along the gradient of warming trends***

375 Consistent with the abundance-based results in Becker-Scarpitta et al., (2019), for vascular plants we
376 found support for the hypothesis that areas with greater warming should experience stronger
377 community changes than areas with weaker warming trends. At Mont-Mégantic, where the warming
378 trend has been strongest, we found a clear pattern for vascular plants of upward shifts in elevational
379 distributions (Table 1a, Fig. 1), a significant increase of α-diversity (Tables 1b & 2, Fig. 2), a stronger
380 shift in community composition than in Forillon (Table 3, Fig. 3) and a significant decrease of β-
381 diversity (Table 3, Fig. 4). At Forillon, where the warming trend has been weaker, we found neither
382 shifts in elevational distributions nor changes of α-diversity for either vascular plants or bryophytes
383 (Table s1a-b & 2, Figs. 1 & 2). The upward shift in elevation of vascular plants in response to warming
384 is in line with many other studies (Bertrand et al., 2011; Chen et al., 2011; Lenoir et al., 2008). The
385 temporal increase of diversity of vascular plant in Mont-Mégantic is also coherent with the prediction
386 that warming should lead to increased local diversity in areas without severe moisture stress
387 (Harrison, 2020; Vellend, Baeten, et al., 2017).

388 Our results suggest that a temperature increase of 1-2 °C does not have as strong an impact on the
389 local diversity and distributions of bryophytes as it does for vascular plants. This interpretation is
390 also supported by the absence of any relationship between bryophyte richness and elevation in the
391 two parks (Table 1b, Fig. 2) and consistent with previous results (Bruun et al., 2006; Grytnes,
392 Heegaard, & Ihlen, 2006; Odland, Reinhardt, & Pedersen, 2014 but see Vittoz et al., 2010). The
393 decrease of β-diversity over time for vascular plants at Mont-Mégantic supports the hypothesis that

394 warming might cause biotic homogenization (Socolar et al., 2016; Urban, 2015). Note that this result
395 using presence-absence data was different to the result in Becker-Scarpitta et al., (2019) using
396 untransformed abundance data (for which we found no homogenization), but similar to the finding
397 of homogenization using fourth-root transformed abundances in Savage & Vellend, (2015). These
398 results collectively illustrate that the locally dominant species – whose influence is minimized or
399 eliminated via fourth-root or presence-absence transformation – can mask homogenization created
400 by species of lower abundance. This result highlights how ecological conclusions are dependent on
401 the data transformation, even with widely used diversity metrics.

402 ***Sensitivity of bryophytes vs. vascular plants***

403 We cannot draw strong conclusions about which of bryophytes or vascular plants is more or less
404 sensitive to environmental change in eastern Canada: results depended on which community
405 property was being investigated. Vascular plants showed more prominent upward elevational
406 distribution shifts and richness increases (Tables 1a-b & 2, Figs. 1 & 2) while bryophytes experienced
407 stronger shifts in community composition and no difference in the magnitude of compositional
408 changes between the two parks with contrasting warming trends (Table 3, Fig. 3).

409 The lack of directional shifts in bryophytes' elevational distributions at either site (Table 1a, Fig. 1) is
410 coherent with other results showing that bryophyte species have broader elevation ranges – and
411 therefore presumably reduced sensitivity to temperature change – compared to vascular plants (Lee
412 & La Roi, 1979; Vanneste et al., 2017; Vittoz et al., 2010). This may be due to the ability of bryophytes
413 to photosynthesize under larger ranges of temperature than vascular plants (Glime, 2013) and their
414 frequent occurrence in microhabitats (e.g., defined by micro-topography) buffered from macro-
415 environmental changes (Raabe et al., 2010). The decrease of bryophyte β-diversity with elevation in
416 both parks (Table 1, Fig. 4) suggests that bryophyte species found at high elevation (i.e. in boreal
417 forests) tend to be common along the entire gradient, while bryophytes occurring at low elevation

418 are absent from high elevations which is coherent with other patterns (Lee & La Roi, 1979; Slack,
419 1977).

420 ***Potential non-climatic drivers of vegetation change***

421 Our sites were chosen specifically due to their contrasting warming trends and lack of other obvious
422 major drivers of vegetation change, but there are certainly other possible drivers of ecological change
423 that might play a role in this region. Among the indicator species of recent surveys, two were non-
424 native: *Galeopsis tetrahit* and *Epipactis helleborine*, the latter of which has increased considerably in
425 recent decades throughout its North American range, even in western Canada (Marie-Victorin, 1997;
426 McCune & Vellend, 2013). As such, some vegetation changes might be due simply to protracted
427 periods of non-native species expansions, regardless of local environmental change. Another
428 potential factor is changes in white-tailed deer browsing, which has increased over the past century
429 in much of North America (Côté, Rooney, Tremblay, Dussault, & Waller, 2004). The indicator species
430 of the recent survey at Mont-Mégantic include species known to benefit from high levels of deer
431 browsing: *Dennstaedtia punctilobula* and *Carex* spp. (Augustine & Decalesta, 2003; de la Cretaz &
432 Kelty, 2002; Frerker, Sabo, & Waller, 2014; Rooney, 2009). Interestingly, at Forillon deer are actually
433 thought to have decreased in abundance due to the expansion of the coyote population in the 1970s
434 (UQCN, 2005), and we found no such species associated with recent surveys in Forillon Park.

435 Our most difficult result to interpret was the strong species turnover of bryophyte communities at
436 Forillon, which has not experienced strong long-term trends in temperature, precipitation, or
437 atmospheric nutrient deposition (Commission Joint International, 2014; Hember, 2018). We can only
438 speculate and offer hypotheses about potential non-climatic drivers of bryophyte community change.
439 First, as in all legacy studies, there is the potential for observer biases due to (i) different sampling
440 effort between original and recent surveys, or (ii) species' identification errors. It seems highly likely
441 that detection probabilities and the potential for identification errors are greater for bryophytes than
442 for vascular plants, although we have no reason to suspect this caused systematic increases or

443 decreases of particular species frequencies (necessary to explain overall compositional shifts). We
444 paid very close attention to repeating the original survey methods, focusing on the visually obvious
445 species in a given microsite (i.e., not examining each individual moss stem closely on the field), and
446 the lack of any difference over time in local richness (Fig. 2a-b) suggests comparable species'
447 detection abilities in the two surveys. Although we cannot exclude the possibility that a real richness
448 change was cancelled out by a change in survey effort, we have no reason to suspect this rather
449 unlikely coincidence. Second, given uncertainty in the comparability of abundance estimates across
450 time for bryophytes, we also decided to use presence-absence data. In short, changes in observer
451 effort seem highly unlikely to account for the temporal change in species composition. Furthermore,
452 our procedure to homogenize taxonomy across data sets was quite conservative in order to reduce
453 bias due to misidentifications.

454 One potential hypothesis to explain compositional change over time in bryophyte communities
455 relates to the history of park protection. Forillon Park was established (and so protected) only two
456 years before the original survey was conducted, and parts of the park previously included homesteads
457 (i.e., non-forest land uses). Mont-Mégantic was established as a park more recently (1994), but
458 logging activities (the only prominent land use) ceased ~15 years before the original survey. Although
459 plot selection focused only on non-disturbed forests, metacommunity dynamics involving dispersal
460 of species from sites undergoing rapid succession may have caused local shifts in composition and
461 increased β-diversity. It has been previously shown that managed forests tend to have a lower β-
462 diversity than protected forests (Kaufmann, Hauck, & Leuschner, 2017). The increase in bryophyte β-
463 diversity might partially be due to the recovery of natural forest that occurring in the 1970s.

464 There is also the possibility that changes in bryophyte communities resulted from interactions with
465 changing vascular plant communities. Studies have shown that bryophyte diversity and abundance
466 can be negatively correlated with total vascular plant biomass (Virtanen, Eskelinen, & Harrison,
467 2017), cover (Jiang, Liu, Song, Yu, & Shao, 2015) or abundances (Jägerbrand, Kudo, Alatalo, & Molau,

468 2012). While we have documented an increase of vascular plant species richness at Mont-Mégantic
469 (Tables 1b & 2, Fig. 2), we do not have data on vascular plant biomass. If bryophytes are highly
470 sensitive to vascular plant community properties, subtle changes for vascular plants could translate
471 into larger changes in bryophyte communities. This hypothesis is open to testing via observational
472 and experimental studies of the effect of vascular plants on bryophytes communities under warming
473 or other environmental changes. Understanding temporal changes in one component of the
474 community may require more consideration of interactions with other components (Chesson, 2000;
475 HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012).

476 ***Conclusion and conservation implications***

477 Overall, we found a significant temporal shift in the composition of both taxa in both parks but only
478 one significant change in α-diversity. Our results are in accordance with recent meta-analyses and
479 syntheses showing that local diversity can remain unchanged (or increase or decrease with equal
480 likelihood) despite strong changes in composition (Blowes et al., 2019; Dornelas et al., 2014; Gotelli
481 et al., 2017; Magurran et al., 2018; Spaak et al., 2017; Vellend, Dornelas, et al., 2017). Finally,
482 regardless of whether one taxon is systematically more or less sensitive to environmental change
483 than another, our results suggest that one taxon (e.g., vascular plants) cannot be used as a surrogate
484 for others (e.g., bryophytes) in terms of predicting the nature and magnitude of responses to
485 environmental change (Bagella, 2014; Becker-Scarpitta et al., 2017; Outhwaite et al., n.d.). In the same
486 plots that experienced the same environmental changes, we found that communities of bryophytes
487 and vascular plants did not predictably change in the same ways (Bagella, 2014; Becker-Scarpitta et
488 al., 2017; Lalanne et al., 2008; Odland et al., 2014; Slack, 1977). Thus, to assess overall biodiversity
489 responses to global change data from different taxonomical groups and community properties need
490 to be synthesized.

491

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Authors' contribution

ABS and MV conceived the ideas, design methodology, and wrote the manuscript collaboratively with ABS as leader and DAL revising the manuscript; ABS and DAL collected and analyzed the data. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

All specimens identified at the species level were deposited in the Marie-Victorin herbarium (Université de Montréal, Canada.) and all locations were entered into the GBIF database (GBIF - https://www.gbif.org/). The dataset *per se* was deposit into the forestREplot database (http://www.forestreplot.ugent.be/) under the reference: N_AM_005 for Mont-Mégantic and N_AM_008 for Forillon.

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748 **<u>Supplementary Materials</u>**

749 - Appendix S1 - Taxonomic standardization of bryophytes species between surveys

750 - Appendix S2 - Mean species elevation and sum of occurrences for bryophytes for original and
751 recent survey in Forillon and Mont-Mégantic

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