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

Antoine Becker-Scarpitta*[1,2,3], Diane Auberson-Lavoie[1], Raphael Aussenac[4], Mark Vellend[1]

1: Département de Biologie, Faculté des Sciences, Université de Sherbrooke, Sherbrooke, Québec, Canada.

2: Spatial Foodweb Ecology Group, Faculty of Agriculture and Forestry, Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland.

3: Institute of Botany of the Czech Academy of Sciences, Lidická 971, 60200, Brno, Czech Republic.

4: Univ. Grenoble Alpes, INRAE, LESSEM, 2 rue de la Papeterie-BP 76, St-Martin d'Hères, F-38402, France

Contact: *Corresponding author: Antoine Becker-Scarpitta, Spatial Foodweb Ecology Group, Faculty of Agriculture and Forestry, Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland. antoine.becker.scarpitta@gmail.com

ORCID

Antoine Becker-Scarpitta: 0000-0001-9241-091X

Running title

Temporal change in forest plant communities

Abstract

Despite many studies showing biodiversity responses to warming, the generality of such responses across taxonomic groups remains unclear. Very few studies have tested for evidence of bryophyte community responses to warming, even though bryophytes are major contributors to diversity and functioning in many ecosystems. Here we report an empirical study comparing long-term change of bryophyte and vascular plant communities in two sites with contrasting long-term warming trends, using "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 trend, and that vascular plant communities, with narrower climatic niches, would be more sensitive than bryophyte communities to climate warming. For each taxonomic group in each site, we quantified the magnitude of changes in species' distributions along the elevation gradient, species richness, and community composition. We found contrasted temporal changes in bryophyte vs. vascular plant communities, which only partially supported the warming hypothesis. In the area with a stronger warming trend, we found a significant increase of local diversity and beta-diversity for vascular plants, but not for bryophytes. Presence absence data did not provide sufficient power to detect elevational shifts in species distributions. The patterns observed for bryophytes 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. Thus, to assess overall biodiversity responses to global change, abundance data from different taxonomic groups and different community properties need to be synthesized.

Key words

Community ecology, global change ecology, vascular plant, bryophyte, warming, elevational gradient, historical ecology, legacy data, resurvey, biodiversity, forest, understory vegetation, temporal dynamics

Introduction

Ecological impacts of global changes on biodiversity can take many different forms (McGill et al. 2015, Vellend et al. 2017b). 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 (favoring warm-adapted species) along elevation gradients. The many studies to date have focused on relatively few taxonomic groups, in particular vascular plants, invertebrate and vertebrates (Lenoir et al. 2008, Chen et al. 2011, Pauli et al. 2012, Stockli et al. 2012, Rumpf et al. 2018, 2019), and there is now a need for more exhaustive multi-taxonomic syntheses (Lenoir and Svenning 2015, Lenoir et al. 2020). The few studies of bryophyte responses to climate warming suggest that results might be different than those for vascular plants (Walker et al. 2006, Bergamini et al. 2009, Hudson and Henry 2010, Raabe et al. 2010, Vanneste et al. 2017, Becker-Scarpitta et al. 2017).

Understanding variation among taxonomic groups in their responses to environmental change is crucial for identifying priorities in conservation. However, the spatial variability of climate change complicates comparisons between studies of different taxa in different regions, and it is difficult to predict *a priori* differences between taxonomic groups. 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.

69 To assess long-term responses of ecological communities to environmental change, "legacy"
70 ecological records have been used to provide baselines for comparison with contemporary resurveys
71 (Vellend et al. 2013, Chytrý et al. 2014, Verheyen et al. 2017, Hédl et al. 2017). However, historical
72 botanical studies are strongly biased towards vascular plants, with few data on bryophytes, due in
73 part to the difficulty of identification (Gignac 2001; He, He, and Hyvönen 2016; Möls et al. 2013 but
74 see Becker-Scarpitta et al., 2017; Bergamini et al., 2009; Delgado & Ederra, 2013; Outhwaite, Gregory,
75 Chandler, Collen, & Isaac, n.d.; Vanneste et al., 2017). This is despite the fact that bryophytes are
76 significant contributors to diversity in many temperate ecosystem, and a major component of the
77 vegetation cover in boreal or alpine ecosystems. Bryophytes play a crucial role in ecosystem
78 functions, such as biomass accumulation, water retention, nutrient cycling, and food web dynamics
79 (Turetsky 2003, Rydin 2008, Lindo and Gonzalez 2010, Tuba et al. 2011, Patiño and Vanderpoorten
80 2018).

81 For several reasons we might expect vascular plants and bryophytes to show different responses to
82 various sources of environmental change (Lee and La Roi 1979, Möls et al. 2013, Bagella 2014,
83 Vanneste et al. 2017, Becker-Scarpitta et al. 2017). Compared to vascular plants, bryophytes are
84 distinguished by their small size, high sensitivity to the moisture and chemistry of their immediate
85 microenvironment (i.e., they are poikilohydric), lower temperature optima for growth, absence of
86 roots and an efficient vascular system, and dispersal via spores (Glime 2007). These two groups can
87 show contrasted spatial patterns of diversity (Lalanne et al. 2008, Mateo et al. 2016). For instance,
88 vascular plants show a clear latitudinal diversity gradient of decreasing species richness with
89 increasing latitude, while this is not true for bryophytes, for which temperate latitudes are equally
90 diverse as tropical latitudes (Geffert et al. 2013, Mateo et al. 2016). Some studies have also observed
91 different patterns of community β-diversity (Kraft et al. 2011, Mateo et al. 2016) with vascular plant
92 communities sometimes showing higher β-diversity along elevation gradients than bryophytes,

93 suggesting a broader tolerance of bryophyte species to temperature (Lee and La Roi 1979, Vittoz et
94 al. 2010, Glime 2013, Vanneste et al. 2017) or differences in dispersal ability (Lenoir et al. 2012).

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

109 As in many parts of the world, eastern Canada has shown a general warming trend over the past ~50
110 years, but with a strong east-west gradient in the magnitude of warming in the province of Québec
111 (Yagouti et al. 2008). Becker-Scarpitta, Vissault, and Vellend (2019) showed that the magnitude of
112 temporal changes of vascular plant communities in three protected areas generally increased from
113 east to west in southern Québec, with greater changes in areas of stronger warming in recent decades.
114 For two of these three parks, the historical data also included bryophytes, thus presenting an
115 opportunity to test for differential sensitivity among taxonomic groups to warming. Forillon National
116 Park is located at the eastern tip of the province of Québec where warming has been less pronounced

than in Mont-Mégantic Provincial Park, which is in central Québec where the warming trend has been stronger (Savage & Vellend, 2015; Yagouti et al., 2008 & Supporting Information 1).

Here we report one of the first studies comparing long-term change of bryophytes and vascular plants communities in sites with contrasting long-term warming trends. In each of the two parks, we revisited ~50 legacy vegetation plots initially surveyed in the 1970s, applying the same methods as the original surveys. To minimize potentially confounding factors, plots were selected in mature forest ecosystems that have not experienced major natural or anthropogenic disturbances during the time between surveys. We test two main hypotheses: (**i**) For both bryophytes and vascular plants, the park with a stronger warming trend (Mont-Mégantic) has experienced greater long-term community changes than the park with a weaker warming trend (Forillon); (**ii**) Vascular plant communities are more sensitive than bryophyte communities to climate warming. For each taxonomic group in each park, we quantified the magnitude of changes in (a) species' distributions along the elevation gradient, (b) species richness (alpha-diversity), and (c) temporal change in community composition. Note that these predictions were already tested for vascular plants in Becker-Scarpitta et al. (2019), to which we add data for bryophytes in this paper.

Methods

Study site

Our two study sites were located in eastern Canada: Forillon National Park in eastern Québec (48°54′N, 64°21′W), and Mont-Mégantic Provincial Park in central Québec (45°27′N, 71°9′W). Neither park has experienced logging or forest management over the last ~40 years. Forillon National Park was created in 1970 and covers 245 km^2; our study plots ranged in elevation from ~50 to 500 m a.s.l. The vegetation at Forillon is dominated by a mixture of northern tree species such as *Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss and *Betula papyrifera* Marsh. at higher elevations, and *Acer saccharum* Marsh. and *Betula alleghaniensis* Britt. at lower elevations (Majcen 1981). Mont-

141 Mégantic Provincial Park was created in 1994 (logging ceased in the 1960s during park planning) and
142 covers ~55 km^2. Our study plots span an elevational gradient from ~460 and 1100 m a.s.l., along
143 which the vegetation gradient strongly resembles that in Parc Forillon: from temperate deciduous
144 forests dominated by *Acer saccharum*., *Fagus grandifolia* Ehrh. and *Betula alleghaniensis*, to boreal
145 forest dominated by *Abies balsamea,* and *Picea rubens* Sargent, Silva. (Marcotte and Grandtner 1974).
146 Average temperatures at Mont-Mégantic shows an increase of ~0.90°C between 1960 and 2005 while
147 at Forillon the estimated increase is about ~0.55°C for the same period (Appendix S1).

148 ***Data set***

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

163 Our approach to plot relocation is described in Becker-Scarpitta et al., (2019). In short, original survey
164 plots were not permanently marked, although locations were reported in maps and/or tables, such
165 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 of 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 and 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 and subsetted to keep only species with at least two occurrences (see below). Raw data are stored in the *forestREplot* database (http://www.forestreplot.ugent.be) under the code: N_AM_005 for Mont-Mégantic and N_AM_008 for Forillon.

188 ***Taxonomical database***

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

192 Our data set was collected by four different survey teams: one for each of the two original surveys:
193 Forillon: Majcen, (1981); Mont-Mégantic: Marcotte & Grandtner, (1974); one for the recent Mont-
194 Mégantic vascular plant survey: Savage & Vellend, (2015); and one for the recent Mont-Mégantic
195 bryophyte survey and for the recent survey of both taxonomic groups at Forillon (A. Becker-Scarpitta
196 and assistants). Most plants were identified to the species level in the same way across surveys, so
197 for these species the only harmonization step was to standardize names. Coarser levels of taxonomic
198 resolution were used in some but not all surveys for certain species (e.g., a pair of similar species not
199 identified to the species level), and for other species (e.g., spring ephemeral species) the timing of
200 different surveys created doubt about the likelihood of comparable detection. In these situations,
201 comparability was maximized by using the coarser level of resolution applied to all data sets, or by
202 removing species (see Supplementary material S2 for details on taxonomic standardization). All
203 specimens identified at the species level were deposited in the Marie-Victorin herbarium (Université
204 de Montréal, Canada.) and all locations were entered into the GBIF database (GBIF -
205 https://www.gbif.org/).

206 ***Statistical analysis***

207 All statistical analyses were performed in R v.3.4.2 (R Foundation for Statistical Computing 2018). To
208 minimize the effect of potential bias due to uncertain species identification or very rare species, all
209 statistical analyses used the subset of species with at least two occurrences in each time period for
210 each park.

211 First, to test for upward elevational shifts in species distributions along the elevational gradients, we
212 calculated the mean elevation across occurrences for each species (Z), in each park, at each time. We
213 modelled main effects and two- and three-way interactions between park (P), time (Y) and taxonomic
214 group (T), each as a categorical variable. We thus tested for upward elevational shifts in species
215 distributions, and how these shifts depend on park and taxonomic group. The model was given by:

216 $$Z = \left(\beta_1 + b_{sp} + b_{park}\right) + \beta_2 P + \beta_3 T + \beta_4 Y + \beta_5 (P.T) + \beta_6 (P.Y) + \beta_7 (T.Y) + \beta_8 (P.T.Y) + \epsilon$$

217 Where Z is the mean species elevation, β_{1-8} are parameters to be estimated, b_{sp} and b_{park} are random
218 intercepts accounting for the effect of species and park, and ϵ is the model residuals assumed to be
219 normally distributed and independent. Following our first hypothesis, we expected the temporal
220 change at Mégantic to be stronger than at Forillon (significant β_6 parameter). The second hypothesis
221 predicted vascular plants to be more sensitive than bryophytes (significant β_7 parameter). All other
222 terms of the model that are not part of our hypotheses ensure accurate estimation of other
223 parameters in the model.

224 Second, we used the exact same model structure and hypotheses to analyze temporal trends of α-
225 diversity of both bryophytes and vascular plants in the two parks. All linear mixed effect models were
226 conducted in R, with the function *lmer*, package 'lme4' v.1.1-14, Bates, Mächler, Bolker, & Walker,
227 2015).

228 Third, we tested for temporal changes in community composition using two frameworks. In one
229 framework, we first tested the multivariate homogeneity of group dispersions - i.e. a multivariate
230 beta-diversity metric - using the Jaccard dissimilarity index (PERMDISP, function *betadisper*, package
231 'vegan' v.2.4-4; Anderson, Ellingsen, & McArdle, (2006)). Then, we quantified the change in
232 community composition over time using a permutational analysis of variance (PERMANOVA,
233 Anderson, 2001) with Jaccard distances using 999 permutations to (functions *adonis*, package 'vegan',
234 and *pairwise.adonis*, package 'pairwiseAdonis'). We first tested the significance of the three-way

235 interaction (park * taxonomic group * time) in a full model ($F=4.45$, $p<0.01$), and second, we ran
236 separate models for each combination of taxonomic group and park. The R^2 values computed from
237 these separate PERMANOVA models were used to compare the magnitude of temporal change
238 between groups. We used non-metric multidimensional scaling (nMDS) with Jaccard distances for
239 visualization (function *metaMDS*, package 'vegan').

240 In a second framework, to focus on the temporal component of change in species composition, we
241 calculated for each plot the temporal pairwise β-diversity using the binary Jaccard dissimilarity index
242 (for presence-absence data) between original and recent surveys (function *beta.temp,* package
243 'betapart' v.1.5.2, Baselga & Orme, 2012). This framework allowed us to decompose the Jaccard
244 dissimilarity into turnover i.e species replacement between plot and nestedness i.e. species loss
245 between plot, (Baselga 2010).

246 As a complementary analysis, we identified for each park separately the indicator species that
247 characterized each period using the IndVal procedure (function *multipatt*, package 'indicspecies'; De
248 Cáceres, Legendre, & Moretti, 2010).

249

250 **Results**

251 ***Species distributions along elevation gradients***

252 Among the four taxonomic group-site combinations, we failed to detect any significant upward shifts
253 in mean species elevations over time – i.e., none of the main effects or interaction terms including
254 time were significant (Table 1a). It is important to note that patterns reported here are not
255 quantitatively the same as in Becker-Scarpitta et al. (2019), who reported upward elevational shifts
256 of vascular plants at Mont Mégantic based on abundance-weighted mean elevations. The difference
257 in this paper is the use of presence-absence data, in addition to our selection of a subset of species
258 with at least two occurrences per survey.

259 Despite the lack of trends in mean species elevation for bryophytes, there was substantial variation
260 among species, more than for vascular plants (Table 1a, Fig. 1). This observation is reflected in the
261 strength of correlations between original and recent mean species elevations, which was lower for
262 bryophytes (Forillon Pearson *r* correlation = 0.33; Mont-Mégantic *r* = 0.61) than for vascular plants
263 (Forillon *r* = 0.52; Mont-Mégantic *r* = 0.73; see Supplementary material S2 for mean elevations and
264 sums of occurrences for each species in each survey).

265 ***Temporal changes in species richness***

266 At Forillon, the total number of bryophyte species across plots was greater in the recent survey (38
267 species) than in the original survey (25 species); 6 species from the original survey were not found
268 while 19 new species were observed, and the two surveys shared 19 species (Supplementary material
269 S3 for species occurrences). Similarly, at Mont-Mégantic, there was an increase in the overall number
270 of bryophytes species in the recent survey (original survey = 31 vs. recent = 39 species), with 6 species
271 lost, 14 gained while 25 species were shared between the two surveys.

272 Conversely, the total number of vascular plants at Forillon declined over time (original survey = 64
273 vs. recent = 44 species), with 22 original species not found in the recent survey, 2 new species added
274 and 42 shared species. While at Mont-Mégantic, the total number of vascular plant species increased
275 (from 72 species to 77 species), with 8 species lost, 13 gained and 64 shared species.

276 We detected a significant increase in mean plot-level species richness (α-diversity) only for vascular
277 plants at Mont-Mégantic (Table 1b). For bryophytes in both parks, and for vascular plants at Forillon
278 α-diversity showed no changes over time (Table 1b).

279 ***Temporal shift in community composition and heterogeneity***

280 We found significant temporal changes in vascular plant β-diversity and community composition at
281 Mont-Mégantic (Table 2, Fig. 2), where climate warming has been pronounced, as previously reported
282 (Becker-Scarpitta et al. 2019). However, we found an unexpected significant increase of multivariate

283 dispersion (β-diversity) over the past 40 years for bryophytes at Forillon but not at Mont-Mégantic
284 (Table 2, Fig. 2).

285 For both sites we found significant temporal shifts in bryophyte community composition; for vascular
286 plants there was significant compositional change only at Mont-Mégantic (Table 2, Fig. 2). As
287 predicted, the magnitude of the vascular plant compositional shift was greater for Mont-Mégantic
288 (R^2=0.037) than Forillon (R^2=0.019). However, bryophyte communities experienced an equal
289 magnitude of compositional shift for both Forillon and Mont-Mégantic (R^2=0.07 and 0.074
290 respectively). Moreover, compositional shifts were greater for bryophytes than for vascular plants at
291 both sites (Table 2).

292 Temporal beta-diversity showed contrasted patterns between taxonomic groups. Jaccard
293 dissimilarity between original and recent surveys was higher for bryophytes than for vascular plants.
294 The greater change in temporal beta diversity for bryophytes in the two parks is consistent with the
295 PERMANOVA results for changes in community composition. For all combinations of taxonomic
296 group and park, species turnover contributed more than nestedness to overall changes. However,
297 nestedness was considerably higher for vascular plants than for bryophytes (Table 2). In support of
298 the beta-diversity analysis, Table 3 shows the indicator species list that characterized each time
299 period in each park. All combinations of park and time show a complete change in the indicator
300 species assemblage. Even in the absence of beta-diversity change for bryophytes at Mégantic or for
301 vascular plants at Forillon, we detected changes in certain species frequencies. Several species
302 associated with recent time periods suggest possible non-climatic drivers of community change (e.g.,
303 Dennstaedtia punctilobula and Carex spp. are resistant to deer herbivory), a point we develop further
304 in the discussion.

305 **Discussion**

306 Most long-term legacy studies have been conducted on vascular plant communities (Verheyen et al.
307 2017), so it remains unclear whether bryophytes show similar or different responses to
308 environmental changes. Here we quantified community changes over ~40 years for both bryophytes
309 and vascular plants in two protected natural areas in eastern Canada with contrasting recent warming
310 trends. Temporal changes in vascular plant communities contrasted with the warming hypothesis.
311 As predicted for the area with a strong warming trend (Mont-Mégantic), we found a significant
312 increase of local diversity of vascular plants but no change for bryophytes (Table 1b), and a stronger
313 change in β-diversity and community composition for vascular plans as well (Table 2). However, we
314 did not detect any shift in species distribution along the elevation gradient (Table 1a, Fig. 1) and the
315 higher magnitude of changes in bryophyte community composition at both sites was not expected
316 (Table 2, Fig. 2).

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

318 At Mont-Mégantic, where the warming trend has been strongest, we found a significant increase of α-
319 diversity (Table 1b), a significant decrease of β-diversity and a stronger shift in community
320 composition than in Forillon (Table 2, Fig. 2). At Forillon, where the warming trend has been weaker,
321 we found neither shifts in elevational distributions (Table 1a, Fig. 1) nor changes of α-diversity for
322 either vascular plants or bryophytes (Table 1a). The lack of upward shift in elevation of vascular
323 plants in response to warming is clearly explained by the use of presence/absence data, and contrasts
324 with our previous results using abundance data (Becker-Scarpitta et al. 2019) in addition to studies
325 from other sites (Lenoir et al. 2008, Chen et al. 2011, Bertrand et al. 2011),. The temporal increase of
326 diversity of vascular plants at Mont-Mégantic is also consistent with the prediction that warming
327 should lead to increased local diversity in areas without severe moisture stress (Vellend et al. 2017b,
328 Harrison 2020).

329 Our results suggest that a temperature increase of ~0.9 °C (over the last 45 years at Mont-Mégantic)
330 does not have as strong an impact on the local diversity of bryophytes as it does for vascular plants,
331 assuming that the richness increase at Mégantic was indeed due to warming. This interpretation is
332 also supported by the absence of any relationship between bryophyte richness and elevation in the
333 two parks (Forillon estimate= 0.0042 ± (SE) 0.0024, t=1.8, p=0.079 ; Mégantic estimate= 0.0022 ±
334 (SE) 0.0014, t=1.6, p= 0.11) and consistent with previous results in the literature (Bruun et al., 2006;
335 Grytnes, Heegaard, & Ihlen, 2006; Odland, Reinhardt, & Pedersen, 2014 but see Vittoz et al., 2010).
336 The decrease of β-diversity over time for vascular plants at Mont-Mégantic is consistent with the
337 hypothesis that warming might cause biotic homogenization (Urban 2015, Socolar et al. 2016). Note
338 that this result using presence-absence data was different to the result in Becker-Scarpitta et al.,
339 (2019) using untransformed abundance data (for which we found no homogenization), but similar to
340 the finding of homogenization using fourth-root transformed abundances in Savage & Vellend,
341 (2015). These results collectively illustrate that the locally dominant species – whose influence is
342 minimized or eliminated via fourth-root or presence-absence transformation – can mask
343 homogenization created by species of lower abundance. This result highlights how ecological
344 conclusions are dependent on the data transformation, even with widely used diversity metrics.

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

346 We cannot draw strong conclusions about which of bryophytes or vascular plants is more or less
347 sensitive to environmental change in eastern Canada: results depended on which community
348 dimension was being investigated. Vascular plants showed more prominent richness increases
349 (Tables 1b) and a decrease in β-diversity, while bryophytes experienced stronger shifts in community
350 composition and no difference in the magnitude of compositional changes between the two parks
351 (Table 2, Fig. 2). We did not detect (with presence-absence data) shifts in distribution along the
352 elevational gradient for either taxonomic group (Table 1a, Fig. 1), while we previously found a clear
353 shift in elevation when using vascular plant abundance data at Mont-Mégantic (Becker-Scarpitta et

354 al. 2019). Our results for elevational shifts here are thus inconclusive, in that we do not know if
355 analyses using abundance data for bryophytes would have also shown a change in elevation.

356 ***<u>Potential non-climatic drivers of vegetation change</u>***

357 Our sites were chosen specifically due to their contrasting warming trends and lack of other obvious
358 major drivers of vegetation change, but there are certainly other possible drivers of ecological change
359 that might play a role in this region. Among the indicator species of recent surveys (Table 3), two
360 were non-native: *Galeopsis tetrahit* and *Epipactis helleborine*, the latter of which has increased
361 considerably in recent decades throughout its North American range, even in western Canada (Marie-
362 Victorin 1997, McCune and Vellend 2013). As such, some vegetation changes might be due simply to
363 protracted periods of non-native species expansions, regardless of local environmental change.
364 Another potential factor is changes in white-tailed deer browsing, which has increased over the past
365 century in much of North America (Côté et al. 2004). The indicator species of the recent survey at
366 Mont-Mégantic (Table 3) include species known to benefit from high levels of deer browsing:
367 *Dennstaedtia punctilobula* and *Carex* spp. (de la Cretaz and Kelty 2002, Augustine and Decalesta 2003,
368 Rooney 2009, Frerker et al. 2014). Interestingly, at Forillon deer are actually thought to have
369 decreased in abundance due to the expansion of the coyote population in the 1970s (UQCN 2005),
370 and we found no such species associated with recent surveys in Forillon Park.

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

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

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

399 There is also the possibility that changes in bryophyte communities resulted from interactions with
400 changing vascular plant communities. Studies have shown that bryophyte diversity and abundance
401 can be negatively correlated with total vascular plant biomass (Virtanen et al. 2017), cover (Jiang et
402 al. 2015) or abundances (Jägerbrand et al. 2012). While we have documented an increase of vascular
403 plant species richness at Mont-Mégantic (Tables 1b), we do not have data on vascular plant biomass.

404 If bryophytes are highly sensitive to vascular plant community properties, subtle changes for vascular
405 plants could translate into larger changes in bryophyte communities. This hypothesis is open to
406 testing via observational and experimental studies of the effect of vascular plants on bryophytes
407 communities under warming or other environmental changes. Understanding temporal changes in
408 one component of the community may require more consideration of interactions with other
409 components (Chesson 2000, HilleRisLambers et al. 2012).

410 ***Conclusion and conservation implications***

411 Overall, we found a significant temporal shift in the composition of both taxonomic groups in both
412 parks but only one significant change in α-diversity. This study shows the limitation of using presence
413 absence data to detect shift in distribution. While abundance data provide the necessary power to
414 detect changes in species distributions along the elevational gradient (Becker-Scarpitta et al. 2019),
415 presence/absence data clearly do not. Our results are in accordance with recent meta-analyses and
416 syntheses showing that local diversity can remain unchanged (or increase or decrease with equal
417 likelihood) despite strong changes in composition (Dornelas et al. 2014, Vellend et al. 2017a, Gotelli
418 et al. 2017, Spaak et al. 2017, Magurran et al. 2018, Blowes et al. 2019). Finally, regardless of whether
419 one taxonomic group is systematically more or less sensitive to environmental change than another,
420 our results suggest that one taxonomic group (e.g., vascular plants) cannot be used as a surrogate for
421 others (e.g., bryophytes) in terms of predicting the nature and magnitude of responses to
422 environmental change (Bagella 2014, Becker-Scarpitta et al. 2017, Outhwaite et al. 2020). In the same
423 plots that experienced the same environmental changes, we found that communities of bryophytes
424 and vascular plants did not predictably change in the same ways (Slack 1977, Lalanne et al. 2008,
425 Odland et al. 2014, Bagella 2014, Becker-Scarpitta et al. 2017). Thus, to assess overall biodiversity
426 responses to global change abundance data from different taxonomical groups and different
427 community properties need to be synthesized.

Acknowledgements

We would like to thank the field assistants who greatly contributed to the collection of data in the field, the identification of species in the laboratory and the realization of the herbarium: Melissa Paquette and Sara Gaignard. This work was made possible thanks to the support of park managers, especially Camille-Antoine Ouimet (at Mont-Mégantic) and Daniel Sigouin (at Forillon). We also thank Guillaume Blanchet, Michael Belluau and Willian Vieira for constructive discussion on this project. The project was funds by the Natural Sciences and Engineering Research Council, Canada and field mission were support by the Quebec Center for Biodiversity Sciences (QCBS).

Data Accessibilty Statement

Data are stored in the *forestREplot* database (http://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/).

Supplementary Materials

- Appendix S1 – Climatic temporal trends of the two parks.
- Supplementary material S2 – Taxonomic standardization of bryophytes species
- Supplementary material S3 – Species occurrences and mean species elevations

References

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. - Austral Ecol. 26: 32–46.

Anderson, M. J. et al. 2006. Multivariate dispersion as a measure of beta diversity. - Ecol. Lett. 9:

683–693.

Augustine, D. J. and Decalesta, D. 2003. Defining deer overabundance and threats to forest communities: From individual plants to landscape structure. - Écoscience 10: 472–486.

Bagella, S. 2014. Does cross-taxon analysis show similarity in diversity patterns between vascular plants and bryophytes? Some answers from a literature review. - C. R. Biol. 337: 276–282.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. - Glob. Ecol. Biogeogr. 19: 134–143.

Baselga, A. and Orme, C. D. L. 2012. betapart : an R package for the study of beta diversity. - Methods Ecol. Evol. 3: 808–812.

Bates, D. et al. 2015. Fitting Linear Mixed-Effects Models Using lme4. - J. Stat. Softw. 67: 1–48.

Becker-Scarpitta, A. et al. 2017. Long-term community change: bryophytes are more responsive than vascular plants to nitrogen deposition and warming. - J. Veg. Sci. 28: 1220–1229.

Becker-Scarpitta, A. et al. 2019. Four decades of plant community change along a continental gradient of warming. - Glob. Chang. Biol. 25: 1629–1641.

Bergamini, A. et al. 2009. An elevational shift of cryophilous bryophytes in the last century - an effect of climate warming? - Divers. Distrib. 15: 871–879.

Bertrand, R. et al. 2011. Changes in plant community composition lag behind climate warming in lowland forests. - Nature 479: 517–520.

Blowes, S. A. et al. 2019. The geography of biodiversity change in marine and terrestrial assemblages. - Science (80-.). 366: 339–345.

Braun-Blanquet, J. et al. 1952. Les Groupements Végétaux de la France Méditerranéenne (CNRS, Ed.). - CNRS.

473 Bruun, H. H. et al. 2006. Effects of altitude and topography on species richness of vascular plants,
474 bryophytes and lichens in alpine communities. - J. Veg. Sci. 17: 37–46.

475 Chen, I.-C. et al. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate
476 Warming. - Science (80-.). 333: 1024–1026.

477 Chesson, P. 2000. Mechanisms of maintenance of species diversity. - Annu. Rev. Ecol. Syst. 31: 343–
478 366.

479 Chytrý, M. et al. 2014. Assessing vegetation change using vegetation-plot databases: a risky
480 business. - Appl. Veg. Sci. 17: 32–41.

481 Clavel, J. et al. 2011. Worldwide decline of specialist species: toward a global functional
482 homogenization? - Front. Ecol. Environ. 9: 222–228.

483 Commission Joint International 2014. Canada - United States, Air quality agreement - progress
484 report.

485 Côté, S. D. et al. 2004. Ecological impacts of Deer overabundance. - Annu. Rev. Ecol. Evol. Syst. 35:
486 113–147.

487 De Cáceres, M. et al. 2010. Improving indicator species analysis by combining groups of sites. - Oikos
488 119: 1674–1684.

489 de la Cretaz, A. L. and Kelty, M. J. 2002. Development of tree regeneration in fern-dominated forest
490 understories after reduction of Deer browsing. - Restor. Ecol. 10: 416–426.

491 Delgado, V. and Ederra, A. 2013. Long-term changes (1982–2010) in the bryodiversity of Spanish
492 beech forests assessed by means of Ellenberg indicator values of temperature, nitrogen, light
493 and pH. - Biol. Conserv. 157: 99–107.

494 Dornelas, M. et al. 2014. Assemblage time series reveal biodiversity change but not systematic loss. -
495 Science (80-.). 344: 296–299.

496 Fenton, N. J. and Bergeron, Y. 2013. Stochastic processes dominate during boreal bryophyte
497 community assembly. - Ecology 94: 1993–2006.

498 Frerker, K. et al. 2014. Long-term regional shifts in plant community composition are largely
499 explained by local deer impact experiments. - PLoS One 9: e115843.

500 Geffert, J. L. et al. 2013. Global moss diversity: spatial and taxonomic patterns of species richness. - J.
501 Bryol. 35: 1–11.

502 Gignac, L. D. 2001. Bryophytes as indicators of climate change. - Bryologist 104: 410–420.

503 Glime, J. M. 2007. Bryophyte Ecology. Volume 1. Physiological Ecology. - Ebook sponsored by
504 Michigan Technological University and the International Association of Bryologists.

505 Glime, J. M. 2013. Life cycles : surviving change, Chap 2.2. In Bryophyte Ecology. Vol. 1 Physiology
506 and Ecology. - Ebook sponsored by Michigan Technological University and the International
507 Association of Bryologists.

508 Gotelli, N. J. et al. 2017. Community-level regulation of temporal trends in biodiversity. - Sci. Adv. 3:
509 e1700315.

510 Grytnes, J. A. et al. 2006. Species richness of vascular plants, bryophytes, and lichens along an
511 altitudinal gradient in western Norway. - Acta Oecologica 29: 241–246.

512 Harrison, S. 2020. Plant community diversity will decline more than increase under climatic
513 warming. - Philos. Trans. R. Soc. B Biol. Sci. 375: 20190106.

514 He, X. et al. 2016. Will bryophytes survive in a warming world? - Perspect. Plant Ecol. Evol. Syst. 19:
515 49–60.

516 Hédl, R. et al. 2017. Resurvey of historical vegetation plots: a tool for understanding long-term
517 dynamics of plant communities. - Appl. Veg. Sci. 20: 161–163.

518 Hember, R. A. 2018. Spatially and temporally continuous estimates of annual total nitrogen

519 deposition over North America, 1860–2013. - Data Br. 17: 134–140.

520 HilleRisLambers, J. et al. 2012. Rethinking community assembly through the lens of coexistence
521 theory. - Annu. Rev. Ecol. Evol. Syst. 43: 227–248.

522 Hudson, J. M. G. and Henry, G. H. R. 2010. High Arctic plant community resists 15 years of
523 experimental warming. - J. Ecol. 98: 1035–1041.

524 Jägerbrand, A. K. et al. 2012. Effects of neighboring vascular plants on the abundance of bryophytes
525 in different vegetation types. - Polar Sci. 6: 200–208.

526 Jiang, Y. et al. 2015. Diversity and distribution of ground bryophytes in broadleaved forests in
527 Mabian Dafengding National Nature Reserve, Sichuan, China. - Acta Ecol. Sin. 35: 13–19.

528 Kaufmann, S. et al. 2017. Comparing the plant diversity of paired beech primeval and production
529 forests: Management reduces cryptogam, but not vascular plant species richness. - For. Ecol.
530 Manage. 400: 58–67.

531 Kraft, N. J. B. et al. 2011. Disentangling the drivers of diversity along latitudinal and elevational
532 gradients. - Science (80-.). 333: 1755–1758.

533 Lalanne, A. et al. 2008. Opposite responses of vascular plant and moss communities to changes in
534 humus form, as expressed by the Humus Index. - J. Veg. Sci. 19: 645–652.

535 Lee, T. D. and La Roi, G. H. 1979. Bryophyte and understory vascular plant beta diversity in relation
536 to moisture and elevation gradients. - Vegetatio 40: 29–38.

537 Lenoir, J. and Svenning, J.-C. 2015. Climate-related range shifts - a global multidimensional synthesis
538 and new research directions. - Ecography (Cop.). 38: 15–28.

539 Lenoir, J. et al. 2008. A significant upward shift in plant species optimum elevation during the 20th
540 century. - Science (80-.). 320: 1768–1771.

541 Lenoir, J. et al. 2012. Dispersal ability links to cross-scale species diversity patterns across the

542 Eurasian Arctic tundra. - Glob. Ecol. Biogeogr. 21: 851–860.

543 Lenoir, J. et al. 2020. Species better track climate warming in the oceans than on land. - Nat. Ecol.
544 Evol. in press.

545 Lindo, Z. and Gonzalez, A. 2010. The bryosphere: An integral and influential component of the
546 Earth's biosphere. - Ecosystems 13: 612–627.

547 Magurran, A. E. et al. 2018. Divergent biodiversity change within ecosystems. - Proc. Natl. Acad. Sci.
548 115: 1843–1847.

549 Majcen, Z. 1981. Les forets du parc national Forillon, Gaspésie, Québec, étude phytosociologique.

550 Marcotte, G. and Grandtner, M. 1974. Étude écologique de la végétsation forestière du Mont
551 Mégantic.

552 Marie-Victorin, F. 1997. Flore laurentienne. Troisième édition mise à jour et annotée par L. Brouillet,
553 SG Hay, I. Goulet, M. Blondeau, J. Cayouette et J. Labrecque. - Les Presses de l'Université de
554 Montréal.

555 Mateo, R. G. et al. 2016. The mossy north: an inverse latitudinal diversity gradient in European
556 bryophytes. - Sci. Rep. 6: 25546.

557 McCune, J. L. and Vellend, M. 2013. Gains in native species promote biotic homogenization over four
558 decades in a human-dominated landscape. - J. Ecol. 101: 1542–1551.

559 McGill, B. J. et al. 2015. Fifteen forms of biodiversity trend in the Anthropocene. - Trends Ecol. Evol.
560 30: 104–113.

561 Möls, T. et al. 2013. Global gradients in moss and vascular plant diversity. - Biodivers. Conserv. 22:
562 1537–1551.

563 Mouquet, N. and Loreau, M. 2003. Community patterns in source-sink metacommunities. - Am. Nat.
564 162: 544–557.

565 Nascimbene, J. and Spitale, D. 2017. Patterns of beta-diversity along elevational gradients inform
566 epiphyte conservation in alpine forests under a climate change scenario. - Biol. Conserv. 216:
567 26–32.

568 Odland, A. et al. 2014. Differences in richness of vascular plants, mosses, and liverworts in southern
569 Norwegian alpine vegetation. - Plant Ecol. Divers. 00: 1–11.

570 Outhwaite, C. L. et al. 2020. Complex long-term biodiversity change among invertebrates,
571 bryophytes and lichens. - Nat. Ecol. Evol. 4: 384–392.

572 Patiño, J. and Vanderpoorten, A. 2018. Bryophyte Biogeography. - CRC. Crit. Rev. Plant Sci. 37: 175–
573 209.

574 Pauli, H. et al. 2012. Recent Plant Diversity Changes on Europe's Mountain Summits. - Science (80-.).
575 336: 353–355.

576 Pharo, E. J. and Vitt, D. H. 2000. Local variation in bryophyte and macro-lichen cover and density in
577 diversity in montane forests of western Canada. - Bryologist 103: 455–466.

578 Raabe, S. et al. 2010. Drivers of bryophyte diversity allow implications for forest management with a
579 focus on climate change. - For. Ecol. Manage. 260: 1956–1964.

580 Rooney, T. P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic
581 homogenization of forest ground-layer vegetation. - Plant Ecol. 202: 103–111.

582 Rumpf, S. B. et al. 2018. Range dynamics of mountain plants decrease with elevation. - Proc. Natl.
583 Acad. Sci. 115: 1848–1853.

584 Rumpf, S. B. et al. 2019. Elevational rear edges shifted at least as much as leading edges over the last
585 century (J Lenoir, Ed.). - Glob. Ecol. Biogeogr. 28: 533–543.

586 Rydin, H. 2008. Population and community ecology of bryophytes. - In: Bryophyte Biology.
587 Cambridge University Press, pp. 393–444.

588 Savage, J. and Vellend, M. 2015. Elevational shifts, biotic homogenization and time lags in vegetation
589 change during 40 years of climate warming. - Ecography (Cop.). 38: 546–555.

590 Slack, N. G. 1977. Species diversity and community structure in bryophytes: New York State studies.
591 - New York State Museum, The University of the State of New York.

592 Socolar, J. et al. 2016. How should beta-diversity inform biodiversity conservation? - Trends Ecol.
593 Evol. 31: 67–80.

594 Spaak, J. W. et al. 2017. Shifts of community composition and population density substantially affect
595 ecosystem function despite invariant richness. - Ecol. Lett. 20: 1315–1324.

596 Steinbauer, M. J. et al. 2018. Accelerated increase in plant species richness on mountain summits is
597 linked to warming. - Nature 556: 231–234.

598 Stockli, V. et al. 2012. Using historical plant surveys to track biodiversity on mountain summits. -
599 Plant Ecol. Divers. 4: 415–425.

600 Tuba, Z. et al. 2011. Bryophyte ecology and climate change. - Cambridge University Press.

601 Turetsky, M. R. 2003. The role of Bryophytes in carbon and nitrogen cycling. - Bryologist 106: 395–
602 409.

603 UQCN 2005. Rapport de synthèse - Parc National de Forillon. Importance et impacts des pressions
604 périphériques sur le maintien de l'intégrité écologique des aires protégées au Québec.

605 Urban, M. C. 2015. Accelerating extinction risk from climate change. - Science (80-.). 348: 571–573.

606 Vanneste, T. et al. 2017. Impact of climate change on alpine vegetation of mountain summits in
607 Norway. - Ecol. Res. 32: 579–593.

608 Vellend, M. et al. 2013. Historical ecology: Using unconventional data sources to test for effects of
609 global environmental change. - Am. J. Bot. 100: 1294–1305.

610 Vellend, M. et al. 2017a. Estimates of local biodiversity change over time stand up to scrutiny. -
611 Ecology 98: 583–590.

612 Vellend, M. et al. 2017b. Plant biodiversity change across scales during the anthropocene. - Annu.
613 Rev. Plant Biol. 68: 563–586.

614 Verheyen, K. et al. 2017. Combining biodiversity resurveys across regions to advance global change
615 research. - Bioscience 67: 73–83.

616 Virtanen, R. et al. 2017. Comparing the responses of bryophytes and short-statured vascular plants
617 to climate shifts and eutrophication (S Power, Ed.). - Funct. Ecol. 31: 946–954.

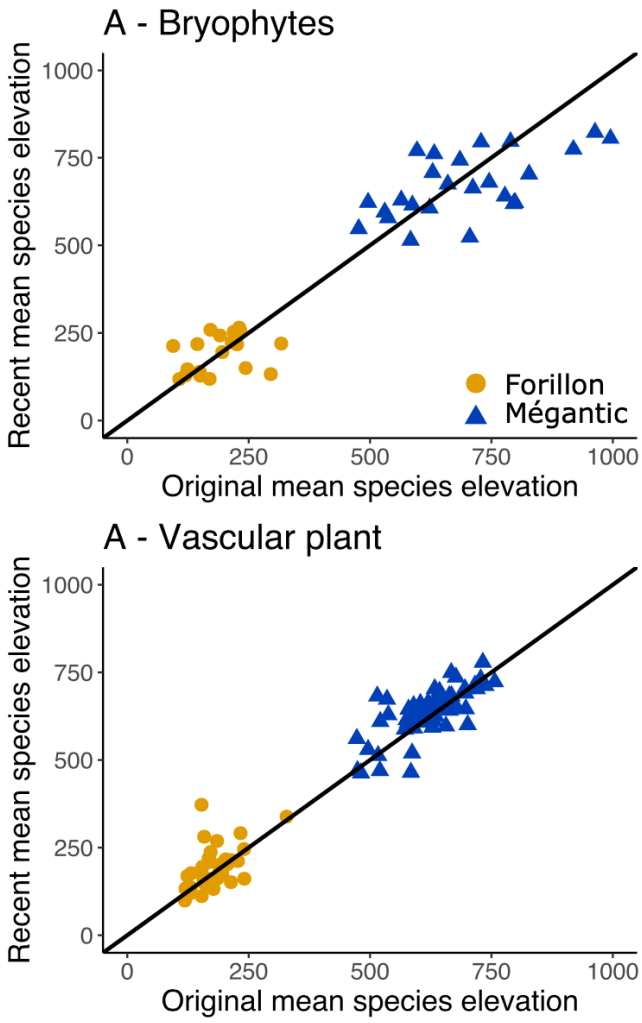
618 Vittoz, P. et al. 2010. Subalpine-nival gradient of species richness for vascular plants, bryophytes
619 and lichens in the Swiss Inner Alps. - Bot. Helv. 120: 139–149.

620 Walker, M. D. et al. 2006. Plant community responses to experimental warming across the tundra
621 biome. - Proc. Natl. Acad. Sci. U. S. A. 103: 1342–1346.

622 Yagouti, A. et al. 2008. Observed changes in daily temperature and precipitation indices for southern
623 Québec, 1960–2005. - Atmosphere-Ocean 46: 243–256.

624

625 **Figures and Tables**



626

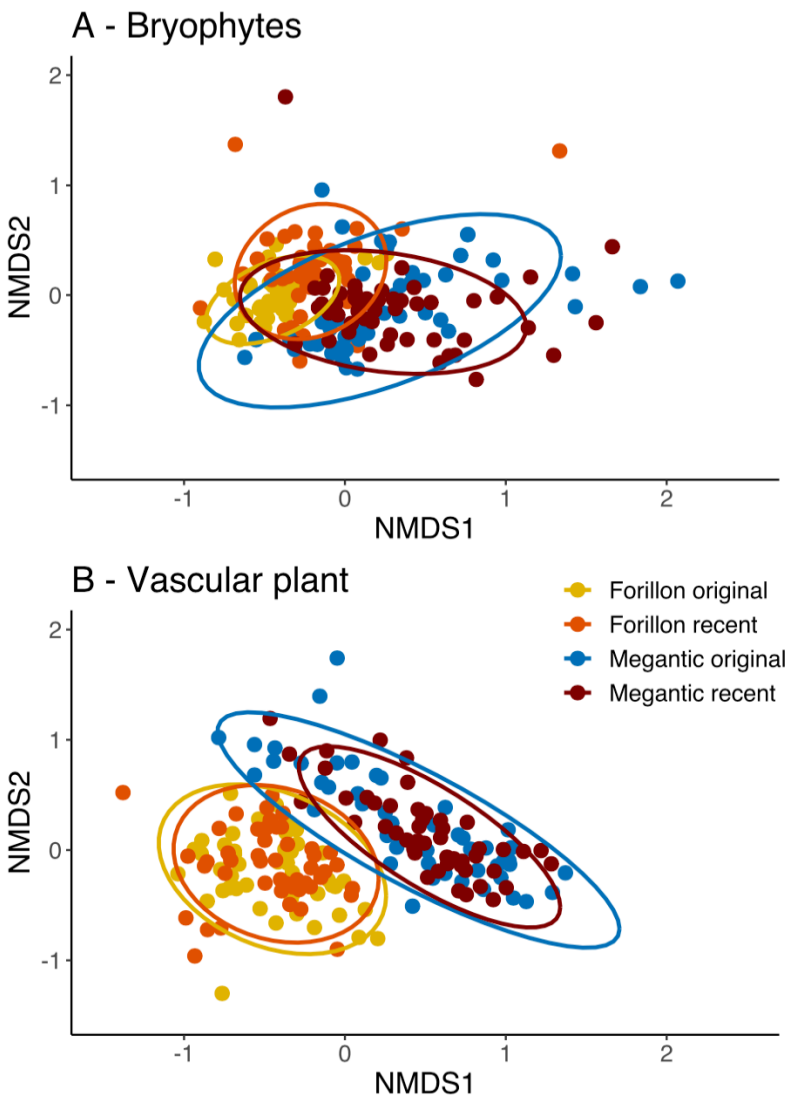
627 Figure 1 – Mean elevations of species' distributions in two time periods and two parks. A) Bryophytes,

628 Forillon = 19 species, Mégantic = 25 species); B) Vascular plants, Forillon = 42 species, Mégantic = 64

629 species. All species present in both the original and recent surveys were included. Diagonal lines

630 indicate 1:1 (i.e. no changes over time). See Table 1a for statistical analysis.

631



632

633 Figure 2 – Temporal changes in (A) bryophyte and (B) vascular plant community composition over
634 time in Forillon and Mont-Mégantic, based on Jaccard's dissimilarity and non-metric
635 multidimensional scaling (NMDS). At both sites, bryophytes showed significant shifts in composition
636 over time and a significant increase in beta diversity. For vascular plants significant shifts in
637 community composition and a significant decrease in beta diversity were found at Mont Mégantic but
638 not Forillon (Table 2).

639

Table 1 - Analyses of temporal changes in (a) mean species elevation, and (b) species richness. For both models, parameter estimates ± credible intervals (CI) are reported from linear mixed models. The baseline condition (Intercept) against which effects are tested was bryophytes at Parc Forillon in the initial survey. R^2m is the marginal coefficient of determination, measuring the proportion of variance explained by fixed effects i.e., time, park, and taxonomic group; R^2c is the conditional coefficient of determination, giving the proportion of variance explained by both fixed and random effects. Names in parentheses refer to the level of the variable tested. In categorical models, the Intercept is the reference level used to test the effect of other variables. Bold values indicate statistically significant differences ($p<0.05$).

	Parameters	Estimates	CI	p	df
(a) Mean species elevation					
Intercept (Forillon, bryo, t0)	β1	189.28	156.35 – 222.22	**<0.001**	216.20
park (Mégantic)	β2	504.98	461.29 – 548.67	**<0.001**	216.20
group_taxo (Vascular)	β3	-8.94	-48.63 – 30.75	0.658	216.20
time (t1)	β4	1.50	-28.33 – 31.33	0.921	146.00
park (Mégantic) * group_taxo (Vascular)	β5	-65.38	-117.55 – -13.21	**0.014**	216.20
park (Mégantic) * time (t1)	β6	-23.48	-63.05 – 16.09	0.243	146.00
group_taxo (Vascular) * time (t1)	β7	9.67	-26.28 – 45.61	0.596	146.00
park (Mégantic) * group_taxo (Vascular) * time (t1)	β8	28.14	-19.11 – 75.39	0.241	146.00
Random Effects					
Variance $_{park:species}$	bpark, bsp	3141.17			
Variance residual		2163.68			
Marginal R^2 / Conditional R^2		0.905 / 0.961			
(b) Species richness					
Intercept (Forillon, bryo, t0)	β1	5.00	3.28 – 6.73	**<0.001**	348.96
park (Mégantic)	β2	0.28	-2.16 – 2.72	0.820	354.45
group_taxo (Vascular)	β3	12.83	10.61 – 15.05	**<0.001**	275.14
time (t1)	β4	0.89	-1.34 – 3.12	0.431	273.75
park (Mégantic) * group_taxo (Vascular)	β5	2.67	-0.49 – 5.83	0.098	287.09
park (Mégantic) * time (t1)	β6	-1.07	-4.20 – 2.07	0.504	276.07
group_taxo (Vascular) * time (t1)	β7	-2.81	-5.95 – 0.33	0.079	273.75
park (Mégantic) * group_taxo (Vascular) * time (t1)	β8	8.75	4.33 – 13.18	**<0.001**	274.91
Random Effects					
Variance $_{park:plot}$	bpark, bplot	6.13			
Variance residual		30.18			
Marginal R^2 / Conditional R^2		0.639 / 0.700			

650 Table 2 – Temporal changes in beta diversity and community composition. β-diversity was measured
651 as the multivariate distance of plots to the time-specific centroid in multivariate space. The R^2 of the
652 shift in community composition reflects the proportion of variation in community composition
653 explained by time. Jaccard temporal β-diversity values are decomposed into turnover and nestedness
654 between original and recent surveys. Bold values indicate significant statistical differences $p<0.05$.

		***β*-diversity**			**Composition**			**Temporal beta diversity**		
		Original	Recent	p	F	p.adj	R2	Jaccard	Turnover(%)	Nestedness(%)
Bryophytes										
	Forillon	0.53	0.58	**0.015**	6.93	**0.006**	0.070	0.80±0.02	85.5%	14.5%
	Megantic	0.61	0.60	0.93	7.64	**0.006**	0.074	0.89±0.02	96.4%	3.6%
Vascular plants										
	Forillon	0.45	0.43	0.80	1.86	0.126	0.019	0.52±0.02	69.9%	29.9%
	Megantic	0.50	0.43	**0.004**	3.60	**0.024**	0.037	0.53±0.02	70.8%	29.2%

655

656 Table 3 - Indicator species of bryophytes and vascular plants associated with original and recent
657 surveys at Forillon and Mont-Mégantic. Indicator values were considered significant if $p<0.05$
658 (calculated with 999 permutations).

Bryophytes			
Forillon, original	**stat**	**p.value**	
Dicranum fuscescens	0.74	0.001	***
Forillon, recent			
Dicranum montanum	0.625	0.002	**
Dicranum polysetum	0.554	0.001	***
Brachythecium campestre	0.484	0.001	***
Pseudoleskeella tectorum	0.413	0.009	**
Plagiochila porelloides	0.357	0.026	*
Mégantic, original			
Brotherella recurvans	0.729	0.001	***
Dicranum fuscescens	0.639	0.001	***
Paraleucobryum longifolium	0.531	0.001	***
Hypnum pallescens	0.484	0.001	***
Bryhnia novae-angliae	0.438	0.035	*
Brachythecium reflexum	0.386	0.006	**
Mégantic, recent			
Atrichum altecristatum	0.600	0.001	***
Hylocomiastrum umbratum	0.543	0.003	**
Dicranum polysetum	0.447	0.002	**
Hypnum curvifolium	0.447	0.001	***

Vascular plants			
Forillon, original	**stat**	**p.value**	
Mitella nuda	0.497	0.008	**
Lycopodium annotinum	0.479	0.002	**
Galium triflorum	0.476	0.021	*
Moneses uniflora	0.447	0.029	*
Carex arctata	0.382	0.012	*
Epilobium angustifolium	0.354	0.031	*
Forillon, recent			
Sambucus racemosa	0.476	0.011	*
Epipactis helleborine	0.433	0.003	**

Mégantic, original			
Osmunda claytoniana	0.433	0.004	**
Botrychium virginianum	0.408	0.006	**
Mégantic, recent			
Dennstaedtia punctilobula	0.677	0.001	***
Carex arctata	0.594	0.001	***
Carex deweyana	0.520	0.001	***
Circaea alpina	0.476	0.017	*
Osmundastrum cinnamomeum	0.424	0.049	*
Epipactis helleborine	0.408	0.007	**
Galeopsis tetrahit	0.408	0.008	**
Lycopodium annotinum	0.354	0.030	*
Habenaria sp	0.354	0.025	*

659

Appendix S1 - Climatic temporal trends

To model the mean annual temperature trend in both parks, we extracted temperature data from the ANUSPLINE model (McKenney et al. 2011). The relevant period to study the effect of temperature change on forest plant communities includes a lag of approximately ~10 years before the time of the survey. We thus considered the period 1960-2005, which aligns with a previous study showing a sharp warming gradient in the region (Yagouti et al. 2008). The model includes the effect of the categorical variable park (with two levels: Forillon and Mégantic), the continuous variable year from 1960 to 2005, and a random effect on the different measures within each park.

We only report results for annual mean temperature but found similar results for annual minimum and maximum temperatures, with no temporal change in annual mean precipitation. For the period 1960-2005, we find that Forillon experienced an increase of 0.12 °C ± 0.010°C/decade, while at Mégantic the increase per decade was almost twice as strong: 0.20 °C ± 0.014°C/decade.

	Mean annual temperature			
	Estimates	*Sdt.Error*	t	*p*
Intercept (Forillon)	-29.04	7.505	-3.87	**<0.001**
Year	0.012	0.0010	11.88	**<0.001**
Year : Mégantic	0.008	0.0014	5.49	**<0.001**
Random Effects				
Variance residual	0.436			
Variance $_{plot:park}$	0.429			
Variance $_{park}$	108.725			
Marginal R^2 / Conditional R^2	0.340 / 0.997			