Four decades of plant community change along a continental gradient of warming

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12   (with ABS as leader); ABS collected and analyzed the data; SV extracted climatic and
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Abstract

Many studies of individual sites have revealed biotic changes consistent with climate warming (e.g., upward elevational distribution shifts), but our understanding of the tremendous variation among studies in the magnitude of such biotic changes is minimal. In this study we re-surveyed forest vegetation plots 40 years after the initial surveys in three protected areas along a west-to-east gradient of increasingly steep recent warming trends in eastern Canada (Québec). Consistent with the hypothesis that climate warming has been an important driver of vegetation change, we found an increasing magnitude of changes in species richness and composition from west to east among the three parks. For the two mountainous parks, we found no changes in elevational species' distributions in the eastern most park where warming has been minimal (Forillon Park), and significant upward distribution shifts in the centrally located park where the recent warming trend has been marked (Mont-Mégantic). Community temperature indices (CTI), reflecting the average affinities of locally co-occurring to temperature conditions across their geographic ranges ("species temperature indices"), did not change over time as predicted. However, close examination of the underpinnings of CTI values suggested a high sensitivity to uncertainty in individual species' temperature indices, and so a potentially limited responsiveness to warming. Overall, by testing *a priori* predictions concerning variation among parks in the direction and magnitude of vegetation changes, we have provided stronger evidence for a link between climate warming and biotic responses than otherwise possible, and provided a potential explanation for large variation among studies in warming-related biotic changes.

<u>Introduction</u>

40   Climate is a dominant driver of large-scale plant distributions (Pearson & Dawson, 2003).

41   On smaller spatial and temporal scales, changes in local climatic conditions can lead to

42   modifications of species' abundances (Vellend *et al.*, 2017), risks of extinction (Parmesan

43   & Yohe, 2003; Rooney *et al.*, 2004; Urban, 2015), phenology (Menzel *et al.*, 2006;

44   Cleland *et al.*, 2007), distributions (Kelly & Goulden, 2008; Lenoir *et al.*, 2008; Bertrand

45   *et al.*, 2011) and local adaptation (Aitken *et al.*, 2008). Although many such changes have

46   been observed in previous studies, the magnitude of response varies tremendously from

47   study to study, and we have only a limited understanding of the processes underlying this

48   variation.

49   Most of the world's natural vegetation is dominated by long-lived perennials plants

50   (Grime, 1977), and so we expect vegetation responses to environmental change to occur

51   slowly relative to the time span of a few years (or less) typical of ecological studies

52   (Tilman, 1989). A key strategy used to assess longer-term temporal changes in plant

53   communities is the resurvey of plots initially surveyed decades ago, often referred to as

54   "legacy" studies (Vellend *et al.*, 2013a; Chytrý *et al.*, 2014; Hédl *et al.*, 2017; Perring *et

55   al.*, 2017). An important limitation of such studies is their constrained ability to test the

56   ecological mechanisms underlying temporal community change. Indeed, most legacy

57   studies pertain to a single site, meaning a set of plots within an area sharing a similar

58   climate and history, in which case community change might be caused by many local

59   changes, such as ongoing land use (Hermy & Verheyen, 2007; Kampichler *et al.*, 2012;

60   Newbold *et al.*, 2015), historical management legacies (Vanhellemont *et al.*, 2014;

61   Becker *et al.*, 2016; Perring *et al.*, 2017), nitrogen deposition (Becker-Scarpitta *et al.*,

62   2017) or grazing (Frerker *et al.*, 2014; Vild *et al.*, 2016).

63   Causes of community change at a single site are often assessed by comparing observed

64   changes in community composition across space or time with predictions based on

65   drivers of interest, such as the climate warming. For instance, as predicted by the climate

66   warming hypotheses, many species have experienced a shift in distribution towards

67   higher elevations (Gottfried *et al.*, 2012; Pauli *et al.*, 2012; Stockli *et al.*, 2012; Sproull *et*

68   *al.*, 2015) or latitudes (Parmesan *et al.*, 1999; Hickling *et al.*, 2006; Boisvert-Marsh *et al.*,

69   2014; but see VanDerWal *et al.*, 2012). Given that plant species richness tends to be

70   greater in warmer areas, a local-scale increase in richness is also predicted due to

71   warming, at least in the absence of severe moisture stress (Vellend *et al.*, 2017). Finally,

72   if each species is first characterized by its geographic affinity with different temperature

73   conditions (using a "Species Temperature Index"), then the average affinity across

74   species in a local community (the "Community Temperature Index") is predicted to

75   increase in response to warming (Devictor et al. 2008, 2012). Although there have been

76   considerable advances in testing these predictions in single-site studies (local scale),

77   explicit tests of predictions comparing multiple sites (regional scale) are needed to

78   improve our knowledge and ability to predict biodiversity responses to climate changes

79   (Verheyen *et al.*, 2017).

80   Here we report analyses of changes in forest plant communities over four decades at three

81   sites strategically chosen to be in areas covering a range of recent climate warming trends

82   in eastern North-America (Québec, Canada). To assess temporal changes, we have

83   revisited sites where botanical legacy data were collected in the 1970s, during the time

84   that many provincial parks were being planned and established in Québec. Plots were

85   widely distributed throughout each park and were typically placed in mature forest

86   stands. Since the time of the original surveys, these forests have not experienced any

87   major anthropogenic disturbances, thus minimizing possible confounding causes of

88   vegetation change.

89   The province of Québec (Canada) spans >1000 km east-west, over which there is a

90   marked gradient of warming over the past ~60 years (see Appendix S1 and Yagouti *et al.*,

91   2008). At the tip of the Gaspé Peninsula, the location of our most easterly site, Forillon

92   National Park (Fig. 1), warming has been least pronounced, likely due to the climatic

93   buffering effect of the Atlantic Ocean (see Appendix S1). In contrast, Gatineau Park in

94   continental western Québec has experienced marked warming, with Mont-Mégantic

95   Provincial Park in between both geographically and in terms of the magnitude of

96   warming (Fig. 1 and S1, Yagouti *et al.*, 2008). To the best of our knowledge, no study

97   has used legacy data to specifically test for contrasting vegetation responses in sites with

98   variable warming trends (but see Menzel *et al.*, 2006 for phenological responses to

99   different warming trends).

100   Our core hypothesis is that areas with greater warming will have experienced stronger

101   vegetation changes than areas with less warming (Chen *et al.*, 2011; Wang *et al.*, 2017).

102   We take advantage of this unique combination of original studies along a warming

103   gradient to perform a regional-scale analysis of temporal change of forest plant

104   communities. Results for Mont-Mégantic, including significant upward elevational

105   distribution shifts and increased local species richness, were reported in a previous paper

106   (Savage & Vellend, 2015), to which we here add data for Gatineau Park (stronger

107 warming trend) and Forillon Park (weaker warming trend). We tested the following

108 specific predictions: (1) Significant upward elevational distribution shifts have occurred

109 at Mont-Mégantic (already observed) but not at Forillon Park (tested in this paper).

110 (Elevational variation in Gatineau Park is minimal – insufficient to test for temporal

111 shifts in species distributions.) The magnitude of (2) the temporal change in species

112 richness, (3) the temporal change in community composition (R^2 from the "time" effect

113 in a multivariate analysis), and (4) the temporal change in Community Temperature

114 Index (CTI) vary in magnitude among parks as follows: Forillon < Mont-Mégantic <

115 Gatineau.

Materials and methods

Study region and sites

118 We studied vegetation change in three north-temperate forest sites in eastern Canada

119 (Québec), spanning ~1000 km from Forillon National Park in eastern Québec, to Mont-

120 Mégantic Provincial Park in central Québec and Gatineau National park in the western

121 part of the province (Fig. 1). For all three parks, there has been no logging or forest

122 management during the period of study.

123 Forillon National Park, located at the eastern extremity of the Gaspé peninsula (48°54′N,

124 64°21′W), was created in 1970 and covers 245 km^2, with our study plots ranging in

125 elevation from ~50 to 500 m a.s.l. The vegetation at Forillon is characterized in large part

126 by boreal species, such as *Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss and

127 *Betula papyrifera* Marshall. At low elevation, temperate deciduous or mixed forests are

128 dominated by *Acer saccharum* Marsh. and *Betula alleghaniensis* Britt. (Majcen, 1981).

129   Mont-Mégantic Provincial Park is located in the Eastern Townships region of Québec

130   (45°27′N, 71°9′W), about 650 southwest of Forillon Park and 15 km north of the U.S.

131   borders with New Hampshire and Maine. The park was created in 1994 (logging ceased

132   in the 1960s prior to park planning) and covers ~55 km^2. Our study plots range in

133   elevation between ~460 and 1100 m a.s.l. Vegetation patterns are very similar to Forillon,

134   with a somewhat more visually evident elevational gradient: at low elevations, temperate

135   deciduous forests are dominated by *Acer saccharum* Marsh., *Fagus grandifolia* Ehrh. and

136   *Betula alleghaniensis* Britt., while at high elevation boreal forests are composed largely

137   of *Abies balsamea* (L.) Mill. and *Picea rubens* Sar. (Marcotte & Grandtner, 1974).

138   Gatineau Park is located in southwestern Québec (45°35′N 76°00′W), in the Outaouais

139   region, 360 km west of Mont-Mégantic. The park was established in 1938, covers 361

140   km^2, with relatively little elevational variation compared to the other parks (250 m

141   elevational range). Contrary to Forillon and Mont-Mégantic, our vegetation sampling was

142   not spread throughout the entire park (access to certain sectors of the part is restricted).

143   Our study area (~30 km^2) is largely dominated by *Acer saccharum* Marsh and *Fagus*

144   *grandifolia* Ehrh., with a few more southerly tree species such as *Tilia americana* L.*,*

145   *Quercus rubra* L.*, Quercus alba* L. *or Fraxinus americana* L. as well.

146   **<u>Data set</u>**

147   All original vegetation surveys were conducted using phytosociological methods

148   (Marcotte & Grandtner, 1974; Chartrand, 1976; Majcen, 1981). In fixed-area plots (see

149   below), authors made a full list of vascular plant species in different strata (i.e. canopy

150   trees, shrubs, herbs) with abundance coefficients per species assigned following the scale

151   of Braun-Blanquet *et al.* (1952). In our analyses, we pooled shrubs and herbs into a single

152   "understorey" stratum and given the limited representation of the tree community in

153   smaller plots (90m^2, see below), we focused all analyses on the understorey data. For

154   analyses, Braun-Blanquet classes were converted to a percentage value representing the

155   mid-point of a given abundance class.

156   None of the original survey plots were permanently marked, but for all three parks plot

157   coordinates were reported in maps and/or tables. As such, plots are considered "semi-

158   permanent", which introduces the possibility of pseudo-turnover due to relocation

159   uncertainty (Stockli *et al.*, 2012; Vellend *et al.*, 2013a; Hédl *et al.*, 2017; Kapfer *et al.*,

160   2017). However, previous studies have shown that conclusions are robust to uncertainty

161   in plot relocation, which adds statistical noise but not systematic bias (Kopecký &

162   Macek, 2015). In our study, original surveyors tended to sample mature forest stands

163   where spatial heterogeneity was relatively low, thus reducing any effects of plot

164   relocation uncertainty. We used original plot maps and environmental descriptions

165   (elevation, slope, aspect) to select potential locations for resurvey plots in a GIS (QGIS

166   Development Team 2016, Open Source Geospatial Foundation Project). Potential

167   locations were visited in the field, with the final location of a given plot determined by

168   the best match to the original location and description. Logistical limitations prevented us

169   from resurveying all original plots in Forillon and Gatineau. At Mont-Mégantic, all plots

170   within the current park boundary were surveyed in 2012 (see Savage & Vellend, 2015).

171   Plot selection for our recent surveys followed several criteria: (i) plots occurred in forest,

172   excluding swamps or bogs; (ii) plots were accessible via <3-4 hours hiking off of trails

173   (abandonment of old forest roads and trails since the 1970s has reduced accessibility);

174 (iii) plots had not obviously experienced recent major natural disturbances (e.g., storms,

175 fire, or insect outbreaks); (iv) in the original survey the plots were sampled in mature

176 stands that have since maintained forest cover (i.e., no early successional dynamics in the

177 intervening period).

178 At Forillon, the original survey was conducted in June-September 1972 in 256 vegetation

179 plots of 500 m^2 distributed throughout the park (Majcen, 1981). We resurveyed 49 plots

180 during July and August of 2015. At Mont-Mégantic, the vegetation was originally

181 surveyed in 1970 in 94 plots, almost half of which were outside of the current park

182 boundaries. The plot size was 400 m^2 in coniferous forest and 800 m^2 in broadleaved

183 forests (Marcotte & Grandtner, 1974). Among the 94 original plots, 48 were revisited

184 within the current park limits at Mont-Mégantic in 2012, with results reported in Savage

185 & Vellend (2015). In Gatineau Park, surveys were conducted in 1973 in 33 plots of 90 m^2

186 during the summer in 1973 (Chartrand, 1976) and 28 plots were resurveyed in summer

187 2016. We harmonized taxonomy across all three parks and two time periods (see below),

188 so the Mont-Mégantic data are not precisely the same as reported in Savage & Vellend

189 (2015). The study design was perfectly balanced within parks for statistical analysis (i.e.,

190 the same number of plots in the original and recent surveys).

191 **Taxonomy**

192 Our taxonomical reference for vascular plants was the Taxonomic Name Resolution

193 Service v4.0 (assessed in Feb 2017: http://tnrs.iplantcollaborative.org).

194 Our data set was collected by five different survey teams, one for each of the three

195 original surveys: Forillon: Majcen (1981); Mont-Mégantic: Marcotte & Grandtner

196   (1974); Gatineau: Chartrand (1976), one for the recent Mont-Mégantic survey: Savage &

197   Vellend (2015), and one for the recent Forillon and Gatineau surveys (A. Becker-

198   Scarpitta and assistants). Most plants were identified to the species level in the same way

199   across surveys, such that the only harmonization step for these taxa was to standardize

200   names, which may have changed over time. In many cases, however, coarser levels of

201   taxonomic resolution (e.g., a pair of similar species not identified to the species level)

202   were used in some but not all surveys, or the timing of different surveys created doubt

203   about the likelihood of comparable detection abilities (e.g., for spring ephemeral plants)

204   (see Appendix S2 for details on taxonomic standardization). In these cases, the coarser

205   level of resolution was applied to all data sets, or species were removed to maximize

206   comparability. We deposited all specimens identified at the species level to the Marie-

207   Victorin herbarium (Institut de Recherche en Biologie Végétale, Université de Montréal,

208   Canada) and all locations were entered into the GBIF database (GBIF -

209   https://www.gbif.org).

210   **Community Temperature Index (CTI)**

211   A predicted response of communities to warming is a temporal increase in the

212   Community Temperature Index (CTI), which we calculated for all plots in each survey.

213   CTI was calculated as the abundance-weighted average of the Species Temperature Index

214   (STI) across all species in a given plot. The STI for a given species is the median of the

215   long-term (1960-2010) mean annual temperatures calculated across all known

216   occurrences of the species (Devictor *et al.*, 2008). To calculate STIs, we compiled an

217   independent dataset by extracting all recorded occurrences for each species in the

218   Botanical Information and Ecology Network (BIEN - http://bien.nceas.ucsb.edu/bien/;

219   Enquist *et al.*, 2016) in eastern North America: 60˚ to 90˚W; 30˚ to 60˚N (red box of

220   Figure 1). We excluded occurrences further west, in order to control the range of

221   variation in precipitation (precipitation decreases markedly to the west of the deciduous

222   forest biome). Our STIs thus reflect temperature affinities under precipitation conditions

223   most comparable to those found in our study region. For each occurrence point, we

224   extracted the annual mean temperature from ANUSPLIN, a model developed by Natural

225   Resources Canada (http://cfs.nrcan.gc.ca/projects/3 ; McKenney et al. 2006). The

226   abundance-weighted version of CTIw was calculated for each plot *j* as:

227    $\text{eq1: } \text{CTIw}_j = \sum_{i=1}^{S}(\text{STI}_i * \text{RA}_{ij})$

228   The STI of species *i* is weighted by the relative abundance (RA) of species *i* in plot *j* (RA

229   = the species local abundance divided by the sum of all S species' abundances in that

230   plot). Given some surprising results concerning CTIw, we also explored analyses of the

231   unweighted version, CTIuw (median STI across species with no weighting for

232   abundance), thus focusing on which species were present in a given plot rather than their

233   relative abundances.

234   STI values were calculated only for species identified at the species level and with more

235   than 50 occurrences in the BIEN database (see Appendix S3 – Species Temperature

236   Index database). Note that compared to Savage & Vellend (2015) we used improved

237   climate data (ANUSPLIN instead of WORLDCLIM) and updated distribution data

238   (BIEN instead of GBIF), thus leading to the potential for different results.

239   **Statistical analysis**

240   All statistical analyses were performed in R v.3.4.2 (R Foundation for Statistical

241   Computing 2017). To test for upward elevational shifts in species distributions at

242   Forillon and Mont-Mégantic, we selected species occurring in at least four plots per

243   survey in a given park. For each species in each park we calculated the average

244   abundance-weighted elevation across occurrences. We then conducted linear mixed

245   effect models (LMM, function *lmer,* package 'lme4' v.1.1-14, Bates *et al.*, 2015) testing

246   for a fixed effect of time period on abundance-weighted mean elevation, with species as a

247   random effect to account for the paired sampling structure of the data (each species

248   observed in each time period).

249   We first studied the relationship between α-diversity (species richness) and time using

250   LMMs including time, elevation and the time*elevation interaction (if significant) as

251   fixed effects, and plot ID as a random effect. Because Gatineau has a negligible

252   elevation gradient, we used a model for this park with only time and plot ID as a random

253   effect. Coefficients of determination were expressed as marginal R^2 (R^2_m) and

254   conditional R^2 (R^2_c) using the function *r.squaredGLMM*, package 'MuMIn' v.1.40.0

255   (Nakagawa & Schielzeth, 2013).

256   We then explored temporal change in β-diversity (i.e. the variability in species

257   composition among communities) using permutational analysis of multivariate dispersion

258   (PERMDISP). This analysis assessed the multivariate homogeneity of group dispersions

259   based on Bray-Curtis distances (also called percentage-difference distance), with

260   significance testing via permutation (function *betadisper*, package 'vegan' v.2.4-4,

261   Anderson *et al.*, 2006). A decrease in the multivariate distance between plots and the

262 time-specific centroid is interpreted as biotic homogenization, while an increase indicates

263 biotic differentiation.

264 To examine changes in community composition over time, we used permutational

265 analysis of variance (PERMANOVA, with Bray-Curtis distances) using 999 permutations

266 (function *adonis*, package 'vegan') (Anderson, 2001). We used the R^2 values from the

267 PERMANOVA models as quantification of the magnitude of temporal change in order to

268 compare among parks. We used non-metric multidimensional scaling (NMDS) with

269 Bray-Curtis distances for visualization (function *metaMDS*, package 'vegan').

270 Temporal changes in the Community Temperature Index (CTI) were tested using LMMs

271 for both weighted and unweighted versions of CTI (CTIw and CTIuw, respectively).

272 Model structure was identical to the model for species richness. We included the

273 interaction between time and elevation only if significant.

Results

274

Species elevational distributions

275

276 In Forillon, where there has been the least warming in recent decades, there was no

277 significant temporal change, on average, in understorey species' elevational distributions

278 (original survey mean = 195.4 ± 12.3 (SE) m; recent = 206.8 ± 12.3 m, t = 0.85, p = 0.41,

279 Fig. 2a, see Appendix S4 for species-by-species data). In contrast, a significant upward

280 elevational shift was observed at Mont-Mégantic, which has experience marked warming

281 (original mean = 622.1 ± 10 m, recent mean = 660.94 ± 10 m, t = 4.67, p < 0.001, Fig.

282 2b). At Mont-Mégantic, on average species' distributions have shifted 39 m towards

283   higher elevations (~10 m.decade^{-1}), and this was consistent along the spatial gradient

284   (Fig. 2b; see also Savage & Vellend 2015).

Species richness

286   At Forillon, for plot-level species richness (α-diversity) we found no significant temporal

287   change (Table 1 and 2), and the weak negative trend of richness with elevation was not

288   significant (Fig 3d, Table 1). Across all plots we observed 18 fewer understorey species

289   in the recent survey (65 species) than in the original survey (83 species); 27 species

290   present in original survey were not found in the recent one, while we found 9 new species

291   (Table 2). It is important to note that these are not likely to be gains and losses to and

292   from the entire park, but only to and from this set of semi-permanent plots.

293   At Mont-Mégantic richness declined significantly with elevation in both time periods

294   (original: t = -6.97, p < 0.001; recent: t = -6.91, p < 0.001, Fig. 3e and Table 1). Similar

295   numbers of understorey plant species overall were found in the recent and original

296   surveys (92 and 87 species, respectively); 8 species from the original survey were not

297   found, while we recorded 13 new species in recent survey (Table 2). Mont-Mégantic

298   showed a significant increase over time in the plot-level richness of understorey species

299   (27% increase on average, see Fig. 3b and Tables 1 and 2), and this increase was

300   consistent across the elevational gradient (Fig. 3e).

301   Finally, in Gatineau Park, plot-level species richness increased significantly by an

302   average of 38% (t = 4.14, p < 0.001, Fig. 3c, Table 1 and 2). Overall, we found 20 more

303   species in the recent survey than in the original survey. Gatineau showed the largest

304   study-wide gain in species, with 32 new species observed in the recent survey and 12

305   species from the original survey not observed in recent one (Table 2).

Community composition and heterogeneity

307   At none of the three sites was there significant temporal change in β-diversity (Table 3).

308   However, we observed highly significant shifts in understorey community composition

309   for all study sites (Table 3), although in the two-dimensional NMDS ordinations the

310   shifts appear fairly subtle (Fig. 4). The magnitude of the understorey compositional shifts

311   (R^2) increased from Forillon (5%) to Mont-Mégantic (8%) to Gatineau (10%) (Table 3).

312   Appendix S5 reports the list of species frequencies and Appendix S6 shows an NMDS

313   ordination of all plots from all parks together.

Community temperature indices (CTI)

315   The only significant temporal change in Community Temperature Indices (CTIw) was

316   found at Mont-Mégantic, and the change was negative, the opposite of the predicted

317   direction. We detected no significant changes in CTI in Forillon or Gatineau (Fig. 5 and

318   Table 1). At Forillon, there was no significant relationship between CTI and elevation for

319   either the original or recent survey (Fig. 5d and Table 1), nor was there any relationship

320   for the original survey at Mont-Mégantic (Fig. 5e and Table 1). For the recent survey at

321   Mont-Mégantic, there was a significant negative relationship between CTIw and

322   elevation (t = -3.1, p = 0.003, Fig. 5e and Table 1), suggesting a decrease over time in the

323   CTIw at high elevations but not low elevations (Fig. 5e). When using the unweighted

324   CTI (CTIuw), results were qualitatively the same for Forillon and Gatineau. At Mont-

325   Mégantic, however, we found no effect of time and a clear and significant decrease in

326   CTIuw with elevation for both the original and recent surveys (see Appendix S7).

Discussion

327

328   Many studies at single sites have revealed temporal changes in species distributions,

329   community composition, or phenology that are consistent with predictions based on

330   climate warming (Lenoir *et al.*, 2009; Bertrand *et al.*, 2011; Bernhardt-Römermann *et al.*,

331   2015; Sproull *et al.*, 2015; Ash *et al.*, 2017; Rogora *et al.*, 2018). However, with

332   observational data (i.e., most long-term studies) it is always difficult to rule out

333   alternative causes of temporal community change, such that comparative multi-site

334   studies are needed to strengthen tests of the general hypothesis that biotic change over

335   time has been influenced by climate warming (Verheyen *et al.*, 2017). In this study, we

336   have taken advantage of a natural gradient in the degree of climate warming and of a

337   protected area network in eastern Canada, combining three re-survey efforts totaling

338   >100 plots to test whether greater warming has led to more marked changes in species

339   distributions and community properties. Results were mostly consistent with our

340   predictions, with the magnitude of biotic changes (i.e. elevational distributions, species

341   richness, composition) most often increasing from Forillon Park in eastern Québec,

342   where the warming trend has been relatively weak, to Mont-Mégantic where warming

343   has been moderate, to Gatineau Park in western Québec where the warming trend has

344   been the strongest. Results for community temperature indices were difficult to interpret,

345   as discussed further below.

346   **Species' elevational distributions**

347   As predicted, species' mean elevations shifted upward at Mont-Mégantic but not

348   Forillon. There is no elevational gradient in Gatineau Park. On average, species at Mont-

349   Mégantic moved toward higher elevations, as predicted if species are at least partially

350   spatially tracking their temperature optima in response to warming (Kelly & Goulden,

351   2008; Savage & Vellend, 2015; Sproull *et al.*, 2015).

352   The rate of elevational shift for the understorey plants at Mont-Mégantic (~10 m.decade^{-}

353   ^{1}) is close to the global average of 11 m.decade^{-1} reported in the meta-analysis of Chen *et*

354   *al.*, 2011), although individual studies have reported higher values (e.g., ~22 m.decade^{-1}

355   in southern California; Kelly & Goulden, 2008) and lower values (e.g., no shift in

356   elevation in Montana; Klasner & Fagre, 2002). However, direct comparison among

357   studies in different regions is complicated by different degrees of warming over the

358   relevant time frames in different places. Moreover, there has been relatively few studies

359   in North-America, making our study not only a novel general contribution to global

360   change biology, but also a valuable regional-scale contribution to our knowledge of

361   changes in species distributions along elevation gradients in eastern North-America.

362   Although the gradients in Forillon and Mont-Mégantic cover similar elevational ranges

363   (~500-600 m), the vegetation gradient is less pronounced in Forillon Park than at Mont-

364   Mégantic. For instance, Forillon's high elevation summits are not as predictably

365   dominated by boreal forest as they are at Mont-Mégantic. This can be seen in the weaker

366   relationships between plot richness and CTI with elevation at Forillon contrary to Mont-

367   Mégantic (Figs. 3d-e, 5 d-e, Appendix S7). Despite these differences, the clear absence of

368   any shift in elevational distributions in Forillon Park is consistent with the hypothesis that

369   climate warming is the probable cause of elevational distribution shifts at Mont Megantic

370   (and elsewhere).

Species richness, composition, and heterogeneity

372   Since warm areas tend to have higher local plant diversity than cold areas, climate

373   warming is predicted to increase local plant diversity in many regions (Vellend *et al.*,

374   2017). Consistent with our prediction, there was no significant temporal change in

375   species richness over ~40 years at Forillon but significant increases were found at Mont-

376   Mégantic and Gatineau. Some other studies in regions that have experienced warming

377   have also found increases of local vascular plant diversity (Klanderud & Birks, 2003;

378   Walther *et al.*, 2005; Stockli *et al.*, 2012; Steinbauer *et al.*, 2018), although temporal

379   changes in species richness are highly variable (Verheyen *et al.*, 2012; Vellend *et al.*,

380   2013b).

381   We found significant temporal shifts in understorey community composition in all three

382   parks, consistent with many studies in the literature showing species turnover through

383   time (Magurran *et al.*, 2010; Dornelas *et al.*, 2014; Shi *et al.*, 2015). Comparisons among

384   parks were consistent with our predictions, with the magnitude of community shifts (R^2)

385   following the gradient of warming: Forillon < Mont-Mégantic < Gatineau. However, we

386   found no evidence of biotic homogenization, in contrast to many studies in literature

387   (Jurasinski & Kreyling, 2007; Keith *et al.*, 2009; Zwiener *et al.*, 2018). In fact, our earlier

388   study of Mont Mégantic reported significant biotic homogenization (Savage & Vellend

389   2015), and the difference with the present study appears to be largely due to differences

390   in data processing and analysis. The raw community data were slightly different given

391   our taxonomic standardization across surveys in different parks and a few differences in

392   which woody plants were considered part of the understory vs. canopy (e.g., *Acer*

393   *spicatum* was included in the understory in the current study but not the earlier one).

394   More importantly, Savage & Vellend (2015) first used a fourth-root transformation of

395   abundance data prior to calculating Bray-Curtis differences (a recommendation in the

396   PRIMER software; Anderson *et al.*, 2008), whereas we saw no clear justification for this

397   in the present study. Applying the same transformation to our data revealed significant

398   biotic homogenization for Mont Mégantic, but not for the other two parks (results not

399   shown). This is of negligible consequence for the present study, given that we did not

400   have strong *a priori* predictions concerning beta diversity, although it is clear that the

401   earlier result of biotic homogenization was not robust to alternative methods of analysis.

402   All observational studies involve uncertainty in making inferences about the cause of

403   changes over space or time. Among potentially confounding factors that can underlie

404   temporal community changes, succession is of potentially high importance. However, our

405   study was designed specifically to minimize strong successional dynamics. We

406   resurveyed plots originally surveyed in mature stands that have maintained closed

407   canopies throughout the period of study. Importantly, we have no reason to suspect that

408   forest dynamics (driven by factors other than climate) varies among our three parks in a

409   way that aligns with the gradient of climate warming. As such, the best supported

410   hypothesis for explaining the temporal changes we observed along the east-west gradient

411   is that climate warming is a key driver.

412   Resurvey studies also raise questions about the comparability of surveys in different

413   years and in different parks (Vellend et al. 2013a). In this study, in order to minimize

414   differences between the six surveys, we paid close attention to taxonomic

415   homogenization, and we consulted with botanists active in the 1970s (e.g., Colette

416   Ansseau, a collaborator of M. Grandtner's, and Z. Majcen) in order to reproduce the

417   exact same field survey methods used in the original studies. One difference among parks

418   we could not avoid was plot size, with smaller plots in Gatineau than in Forillon and

419   Mégantic. It is predicted that in small communities, the importance of drift (stochastic

420   changes in abundance) in driving community dynamics should be relatively high

421   (Ricklefs & Lovette, 1999; Vellend, 2016). As such, all else being equal, one might have

422   expected reduced detectability of deterministic community change over time in Gatineau,

423   yet we found the opposite: a stronger temporal increase of α-diversity and a stronger

424   directional shift in composition. Thus, if anything, we may have underestimated the

425   difference between Gatineau and the other parks.

426   **Community temperature affinity (CTI)**

427   The results for Community Temperature Indices (CTI) diverged most strongly from our

428   predictions. Specifically, we failed to detect any temporal increase of CTI in Gatineau,

429   and contrary to our prediction, we found a significant decrease of CTIw for high

430   elevation plots at Mont-Mégantic (see Fig. 5e and Table 1). This result suggests a

431   "cooling" in terms of community affinities to temperature at high elevation, which has

432   actually been previously observed in the European Alps (Roth *et al.*, 2014). The fact that

433   there was no such trend when using unweighted community temperature indices (CTIuw)

434   indicates that changes in particular species' abundances drove the result for CTIw.

435   In particular, two of the most abundant species experienced major temporal changes: (i)

436   *Oxalis acetosella* L. (known also as *Oxalis montana* Raf.) decreased in average

437   abundance and (ii) *Dryopteris carthusiana* (Vill.) H.P. Fuchs increased in abundance (see

438   Appendix S8). *Oxalis acetosella* had a Species Temperature Index (STI) of 8.6 °C. This

439   species was often found at unusually high abundance in the original surveys at Mont-

440   Mégantic, especially at high elevation (>800 m). On average, *O. acetosella* contributed

441   ~74% to CTIw values for high elevation plots in the original survey, while contributing

442   only ~8% in the recent survey (see Appendix S8). Given abundance reductions at high

443   elevation, the abundance-weighted elevation of this species declined more than any other,

444   which represents an exception among the full set of species (*O. acetosella* is the right-

445   most point in Fig. 2b), but which has a major effect on CTIw values. In contrast,

446   *Dryopteris carthusiana* (STI = 7.6 °C) was not particularly abundant at high elevation in

447   the original surveys but became very abundant in the recent surveys. The contribution of

448   *D. carthusiana* to CTIw for plots at high elevation (>800 m) increased from 9.5% to

449   47%. At Mont-Mégantic, *O. acetosella* is more strongly associated with high elevation

450   forests (i.e., colder sites) than is *D. carthusiana*, and so their changes in abundance are in

451   one sense consistent with the hypothesis that warming is a major driver of vegetation

452   change. But since the estimated STI (using independent data) was actually higher for *O.*

453   *acetosella* than *D. carthusiana*, the changes in abundance caused a decline in high-

454   elevation CTIw. In sum, the high sensitivity of CTI to the dynamics of individual species,

455   combined with uncertainty in STI values (see also below), may reduce the degree to

456   which CTI acts as an indicator of climate warming.

457   The calculation and interpretation of CTI has several limitations. First, Species

458   Temperature Indices (STI) are calculated based on recorded species occurrences, but for

459   many species we have limited knowledge of geographic distributions, especially in

460   northern regions or at high elevation. Second, the assumption that median temperature

461   represents a species' optimum is unverified (Rodriguez-Sanchez *et al.*, 2012). As

462   mentioned above, STI is greater (warmer) for *Oxalis* than for *Dryopteris* due to the more

463   northern distribution of *Dryopteris*. However, in eastern North America *Oxalis* is known

464   to be more abundant in coniferous forests at high elevation while *Dryopteris* is more

465   widely distributed along elevation gradient. Thus, if we used data from occurrences along

466   elevational gradients (i.e., at Mont-Mégantic), *Oxalis* would have a *lower* STI than

467   *Dryopteris*. In other studies, CTI has been shown to increase as predicted by warming

468   (Devictor *et al.*, 2008; Lindström *et al.*, 2012; Bowler *et al.*, 2015). In our study system,

469   STIs and therefore CTIs come with considerable uncertainty.

470   In sum, we have provided empirical evidence of vegetation changes in eastern Canada

471   that are largely consistent with the east-west gradient in warming. Explicit comparisons

472   of community change among regions with variable climatic histories appears to be a

473   powerful method for increasing the confidence with which biotic trends can be attributed

474   to climate warming. Many unknowns remain, such as the functional attributes of "loser"

475   and "winner" species, and the extent to which adaptive changes within species might also

476   contribute to warming responses. Continuing to exploit historical data sources of all kinds

477   can help advance global change science.

Acknowledgements

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Appendices

684

685 • Appendix S1 - Climatic trends in three regions of Québec, Canada

686 • Appendix S2 - Taxonomic standardization between surveys

687 • Appendix S3 - Species Temperature Index (STI) database

688 • Appendix S4 - Mean abundance-weighted elevation and number of occurrences

689 per species per survey in Forillon and Mont-Mégantic

690 • Appendix S5 - Species occurrences per survey (number of plots where species

691 were recorded)

692 • Appendix S6 - Global ordination of community composition for all three parks in

693 both time-periods

694 • Appendix S7 - Results for unweighted Community Temperature Indices (CTIuw)

695 • Appendix S8 - Individual species contributions to Community Temperature

696 Indices (CTIw) for high elevation plots at Mont-Mégantic

697   Table 1 – Results of linear mixed models (LMMs) predicting species richness and
698   community temperature indices (CTIw). R^2m is the marginal R^2, measuring the
699   proportion of variance explained by fixed effects; R^2c is the conditional R^2, giving the
700   proportion of variance explained by both fixed and random effects.

	Effect	F value	df	Pr(>|t|)	R^2m	R^2c
a) Plot richness (α diversity)						
Forillon	Time	3.67	48	0.06	0.04	0.41
	Elevation	1.25	47	0.27		
Mégantic	Time	26.77	47	<0.001	0.54	0.74
	Elevation	68.14	46	<0.001		
Gatineau	Time	17.15	27	<0.001	0.16	0.50
b) Community Temperature Index (CTIw)						
Forillon	Time	0.01	47	0.74	0.01	0.16
	Elevation	0.57	48	0.46		
Mégantic	Time	7.02	46	0.01		
	Elevation	4.57	46	0.04	0.13	0.36
	Time * Elevation	9.57	46	0.003		
Gatineau	Time	1.49	27	0.23	0.01	0.56

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703   Table 2– Temporal changes in total species numbers and plot-level species richness (α-
704   diversity). The total number of species observed across all plots is broken down into
705   those shared, lost, or gained between the original and recent surveys. For plot-level
706   richness, means ± SE are reported. Shading indicates significant statistical differences
707   (p < 0.05, see Table 1 for statistical tests)

	Total species number					α-diversity	
	Original	Recent	Shared	Losted	Gained	Original	Recent
Forillon	83	65	56	27	9	18.2 ± 1	16.4 ± 0.8
Mégantic	87	92	79	8	13	21.2 ± 1.5	27.0 ± 1.5
Gatineau	70	90	58	12	32	11.6 ± 0.8	15.9 ± 0.8

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710   Table 3 – Tests for temporal shifts in β-diversity (PERMDISP) and community
711   composition (PERMANOVA) of understorey communities between original and
712   recent surveys. β-diversity is the mean distance between each plot and the time-
713   specific centroid in multivariate space (Bray-Curtis distances). R^2 is the proportion of
714   variation in community composition explained by time. Statistical significance levels
715   were calculated with 999 permutations.

|	β-diversity				Community composition		
	Original	Recent	F	Pr(<F)	R^2	F	Pr(<F)
Forillon	0.50	0.54	3.53	0.06	0.052	5.26	<0.001
Mégantic	0.53	0.50	2.56	0.11	0.076	7.78	<0.001
Gatineau	0.56	0.60	3.52	0.70	0.096	5.71	<0.001

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719   Figure 1: Location of study sites in (a) Canada and (b) the Province of Québec. The red

720   box in (a) shows the area used for extraction of species occurrences in the calculation

721   of Species Temperature Indices (STI): 60˚-90˚W; 30˚- 60˚N
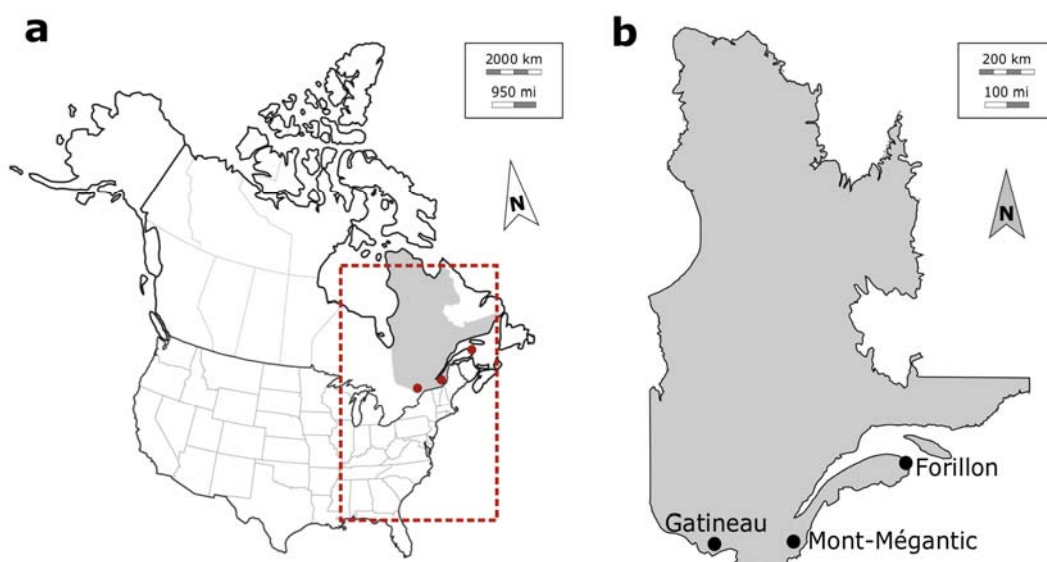
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723

724   Figure 2 – Changes over time in species' elevational distributions at (a) Forillon, n=35

725   species, F=0.70, p=0.41 – no significant shift in elevation, and (b) Mont Mégantic,

726   n=50 species, F=22.72, p<0.001 – significant upward shift in elevation. The diagonal

727   line (1:1) represents no elevational change over time. Each point represents one

728   species (occurring in minimum four plots per survey); see Appendix S4 for data.
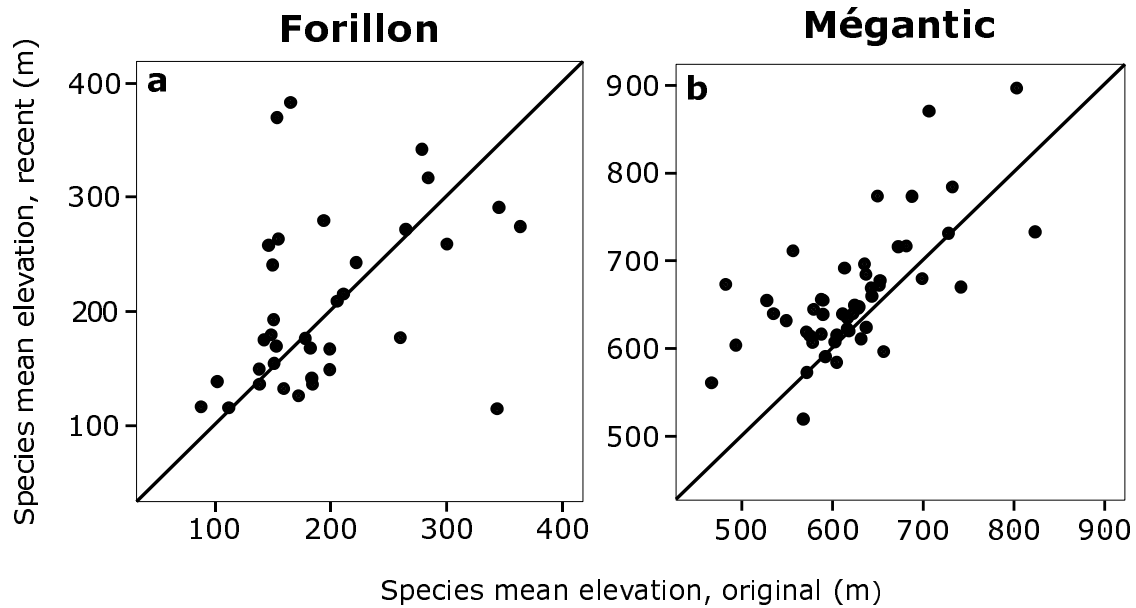

729

730   Figure 0 – Temporal changes in understorey species richness. (a-c) Box plots of original
731   and recent species richness per plot in the three parks. (d-e) Linear relationships
732   between species richness and elevation in the original and recent surveys at Forillon
733   (n=49*2 plots, no significant relationship for either original or recent surveys, see
734   Table 1), and Mont-Mégantic (n=48*2 plots, significant relationship for both original
735   and recent surveys, see Table 1). The colored polygons around each regression line
736   represent 95% confidence intervals. *** p<0.001
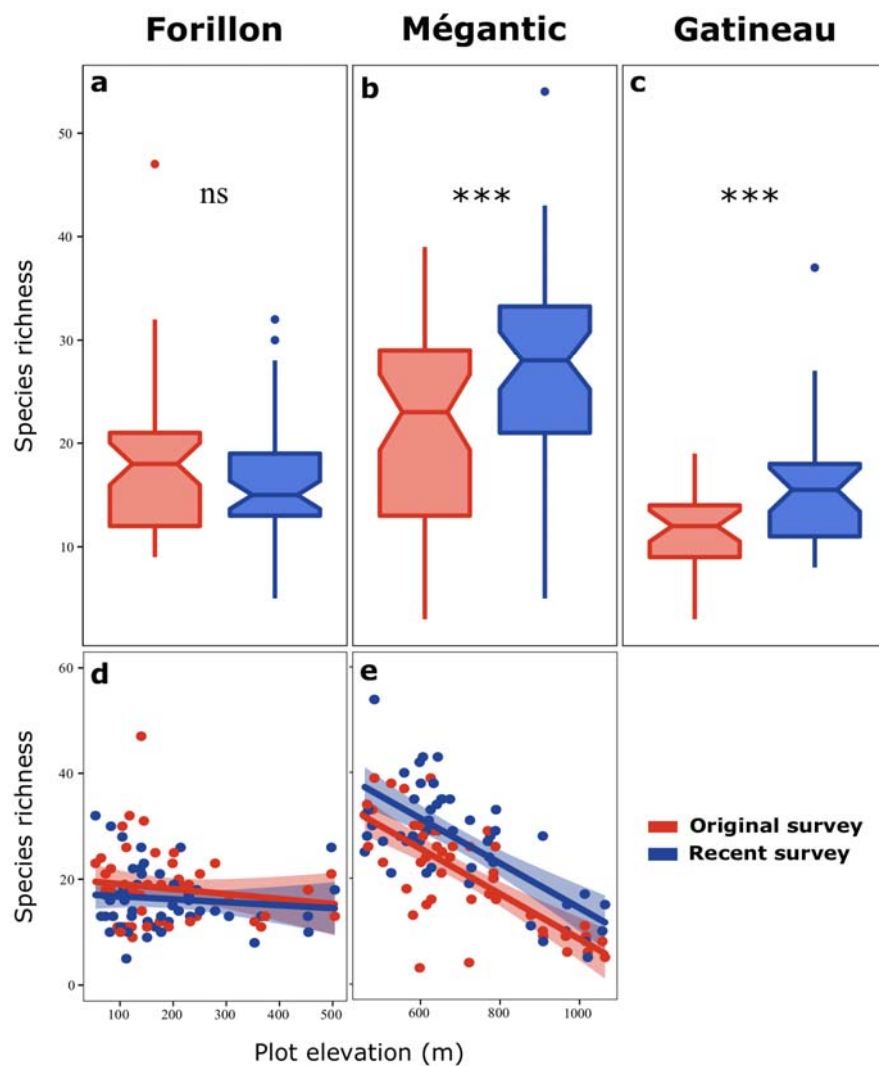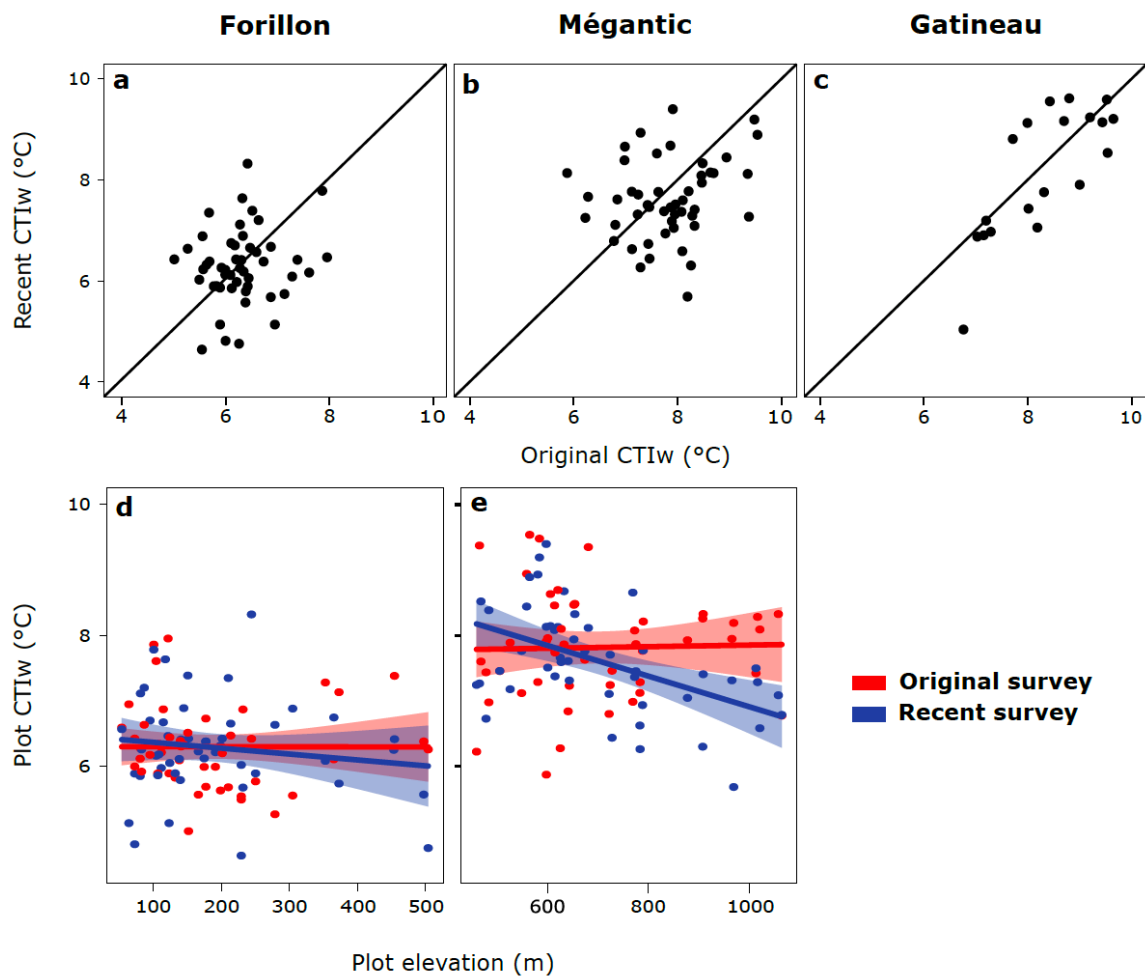

737

738   Figure 4 – Non-metric multidimensional scaling (NMDS) ordinations of understorey
739   communities across time for (a) Forillon, stress = 0.94; (b) Mont-Mégantic,
740   stress=0.97 and (c) Gatineau, stress=0.97. Each point represents a survey plot, and
741   colors refer to the time-period of surveys (red: original survey; blue: recent survey).
742   Ellipses show 75% confidence limits for each time-period. We used two dimensions
743   and Bray-Curtis distances. For a single ordination with species names see Appendix
744   S6.
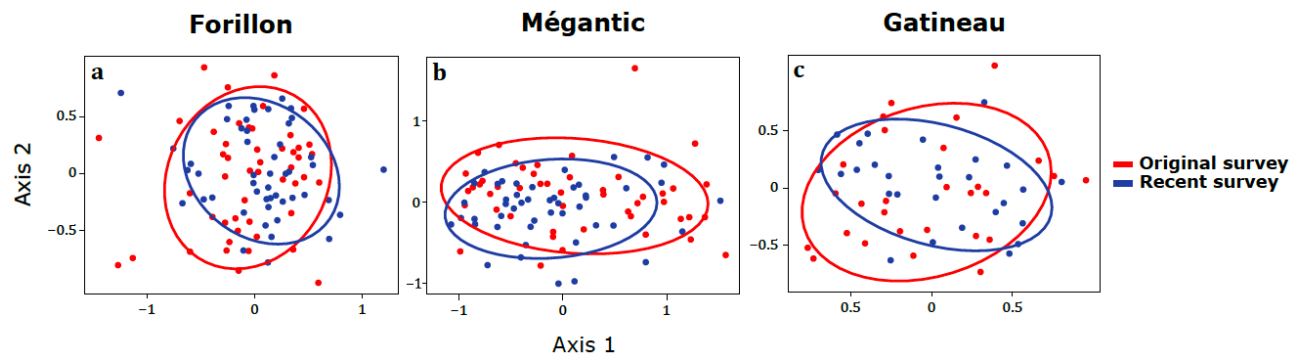
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746

747   Figure 5 – Community Temperature Indices (CTIw) during the two-time periods and
748   across the elevational gradient. (a-c) Abundance-weighted indices (CTIw) at Forillon,
749   Mont-Mégantic, and Gatineau, with the 1:1 line indicating no temporal change
750   between two times. (d-e) Relationships between CTIw and elevation for each time
751   period at Forillon and Mont-Mégantic. Red and blue illustrate original and recent
752   surveys, respectively. Each point is a plot in all panels.

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