1 **Reorganization of tree assemblages over the last century in the northern hardwoods**

2 **of eastern Canada**

3 Running title: Post-settlement tree assemblages

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29   **Abstract**

30   **Question:** How has European settlement of Eastern North America modified tree species

31   assemblages?

32   **Location:** The northern temperate forests of the Lower St. Lawrence region (Québec,

33   Canada).

34   **Methods:** Changes in relative prevalence of tree taxa were reconstructed with early land

35   survey records (1821-1900) and modern forest inventories (1980-2010). Forest

36   composition reconstructions were then used to analyse changes in tree taxa assemblages

37   at the landscape scale and test for potential landscape homogenization.

38   **Results:** Our results show important maples (*Acer saccharum* and *A. rubrum*) and poplar

39   (*Populus tremuloides* and *P. balsamifera*) encroachment, shifting from the 6th to the 2nd

40   positions of relative prevalence and from the 7th to the 5th positions, respectively,

41   resulting in a significant shift in tree assemblage. Maples have spread throughout the

42   whole landscape and have tended to become the most abundant taxa in community where

43   it was already present in pre-settlement times. Poplars also widely spread throughout the

44   landscape but rarely became the most abundant taxa. Accordingly, deciduous

45   encroachment clearly engendered a spatial homogenization of composition at the

46   landscape scale.

47   **Conclusion:** Considering that both red maple and trembling aspen are opportunist early-

48   successional species, the increased relative prevalence of both species, as well as the

49   consequent reorganization of tree taxa assemblages and landscape homogenization

50   probably, resulted from the regional convergence toward an early successional state.

51   Along with restoration of long-lived shade-tolerant conifer populations, land and forest

52   managers should aim to increase heterogeneity of forest stand composition to improve

53   forests resilience to future global changes.

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56   **Keywords:** conifer decline, early land survey records, encroachment of deciduous

57   species, landscape homogenization, post-settlement forest composition, relative taxa

58   prevalence, eastern Canadian temperate forest

Introduction

In North America, settlement has caused major changes in the composition, structure, and dynamics of forested landscapes. Several studies have shown that an increase in the frequency and spatial extent of disturbances rejuvenated forests and modified their composition toward a more homogeneous landscape (White, & Mladenoff 1994; Jackson, Pinto, Malcolm, & Wilson, 2000; Black, & Abrams, 2001; Schulte, Mladenoff, Crow, Merrick, & Cleland, 2007; Thompson, Carpenter, Cogbill, & Foster, 2013). Small-scale disturbances, such as windthrow and insect epidemics (Lorimer, 1977; Lorimer, & White, 2003; Boulanger, & Arseneault, 2004), were replaced by larger disturbances that were more severe at the site scale such as logging and anthropogenic fires (Boucher, Arseneault, & Sirois, 2006; Boucher, Arseneault, & Sirois, 2009a; Boucher, Arseneault, Sirois, & Blais, 2009b; Dupuis, Arseneault, & Sirois, 2011; Boucher, Grondin, & Auger, 2014).

In the northern temperate forests of eastern North America, the presettlement forests were often dominated by long-lived, shade tolerant species, most notably conifers such as white, black and red spruce (*Picea glauca* (Moench) Voss; *P. mariana* (Mill.) BSP and *P. rubens* Sarg), white cedar (*Thuja occidentalis* L) and balsam fir (*Abies balsamea* (L) Mill). Deciduous species, including sugar and red maple (*Acer saccharum,* Marsh; *A. rubrum* L), and white and yellow birch (*Betula papyrifera* Marsh*; B. alleghaniensis* Britt) were also present, but were less frequent and less dominant than conifers (Lorimer 1977, Cogbill, Burk, & Motzkin, 2002; Dupuis et al. 2011; Danneyrolles, Arseneault, & Bergeron 2016a). In contrast, the present-day forested landscapes possess a much greater proportion of deciduous trees (White, & Mladenoff, 1994; Foster, Motzkin, & Slater, 1998; Jackson et al. 2000, Black, & Abrams, 2001; Dupuis et al. 2011; Danneyrolles et al. 2016a). This encroachment is characterized by an increase in opportunist pioneer species that take advantage of openings in the forest canopy and include red and sugar maples, as well as shade-intolerant species that are favoured by stand-replacing disturbances, such as trembling aspen (*Populus tremuloides,* Michx) and white birch (Siccama 1971; Schulte et al. 2007; Dupuis et al. 2011; Thompson et al. 2013;

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88   Danneyrolles et al. 2016a). In contrast, amongst the conifers, cedar appears to be one of

89   the most vulnerable species to human disturbances and has shown strong decreases in

90   frequency and dominance in eastern Canada (Jackson et al. 2000; Dupuis et al. 2011;

91   Danneyrolles et al. 2017) and in northern Maine (Lorimer 1977; Thompson et al. 2013).

92   In the context of the ecosystem-based forest management, an evaluation of the changes

93   that occurred over the 20th century is required, to help understand how to maintain or

94   improve resilience to disturbances and climate change (Millar and Stephenson 2015;

95   Johnstone et al. 2016), particularly in the regions that have been heavily logged/exploited

96   and transformed, such as the temperate forest zone of eastern North America (Boucher et

97   al. 2009a,b). Changes in the frequency and dominance of species, as well as the spatial

98   structure of the major types of forest stands (coniferous, mixed, deciduous) at the

99   landscape scale are well documented and show a rapid transformation of conifer-

100   dominated, uneven-aged forests to young even-aged forests with a larger proportion of

101   deciduous trees (White, & Mladenoff, 1994; Foster et al. 1998; Boucher et al. 2009b;

102   Dupuis et al. 2011). However, to what extent forest rejuvenation and deciduous

103   encroachment have impacted tree communities at the landscape scale is less evident.

104   More particularly, reorganization of relative taxon abundance as a consequence of maples

105   and poplars encroachment has not been specifically addressed. Forest composition

106   (Boucher, Auger, Noël, Grondin, & Arseneault, 2016; Flinn, Mahany, & Hausman, 2018)

107   and spatial structure (i.e. spatial homogenization or heterogenization; Schulte et al. 2007;

108   Hanberry, Palik, & He, 2012b; Thompson et al. 2013; Danneyrolles, Arseneault, &

109   Bergeron, 2018) represent decisive knowledge for ecosystem-based forest management

110   plan.

111   In North America, the pre-settlement forest composition has been mostly reconstructed

112   using archives of the earliest surveys conducted in order to divide the land for settlement,

113   particularly during the 19th century (Whitney 1994; Vellend, Brown, Kharouba, McCune,

114   & Myers-Smith, 2013). The most frequently used data type consists in species

115   determination of individual witness trees, systematically distributed at grid points

116   (Vellend et al. 2013). A second data type consists in taxon lists, which are ranked tree

117   species enumeration at point or along segments of surveyed lines (e.g., Jackson et al.

2000; Scull, & Richardson 2007; Flinn et al. 2018). In eastern Canada, tree taxon lists are generally the only available data type (Dupuis et al. 2011; Terrail, Arseneault, Fortin, Dupuis, & Boucher, 2014; Danneyrolles et al. 2016a; Laflamme, Munson, Grondin, & Arseneault, 2016) and recent studies pointed out that relative metrics (i.e. relative ranks) of taxon abundance obtained with taxon lists are more reliable than absolute metrics (Terrail et al. 2014; Larsen, Tulowiecki, Wang, & Trgovac, 2015). In this study, we use a dataset comprising 22555 tree taxon lists over an area of 8910 km^2 to reconstruct changes in position of relative order of prevalence for the principal tree taxa as a consequence of maple and poplar expansion. A portion of this dataset (8500 taxon lists from the western half of the study area) has already been analyzed for change in absolute metrics of taxa prevalence and dominance (Dupuis et al. 2011), but not for the reorganization of the relative order of taxa prevalence. We also analyse how deciduous encroachment impacted tree community assemblages at the landscape scale and assess potential homogenization or heterogenization of community composition.

Study region

The study area is located on the southern shore of the St. Lawrence River in eastern Canada (Fig. 1). This region is part of the Appalachian geological formation and is composed principally of sedimentary rocks (Robitaille, & Saucier, 1998). The Appalachian Plateau has a mean altitude of 500 m and is comprised of local summits up to 600 m along with valleys of variable depth. The surface deposits are primarily from glacial and alteration origins. The region is under a temperate continental climate, with mean annual temperatures of 3.1 °C (-12.3 °C in January and 17.5 °C in July), and a mean annual precipitation of 929 mm, with 37% falling in the form of snow. The growing season varies from 140 to 170 days and corresponds to 1500 degree-days above 5°C (Robitaille, & Saucier, 1998; Environment Canada, 2018).

The study region constitutes a transition zone between the northern temperate zone and the boreal zone of eastern North America. According to Québec's ecological land classification system, the forests in the west of the study area belong to the balsam fir-

147 yellow birch bioclimatic domain, while those in the easternmost section belong to the

148 balsam fir-white birch domain (Robitaille, & Saucier, 1998). Nowadays, the most

149 frequent tree species are balsam fir, white spruce, white birch, aspen, and red and sugar

150 maples.

151 <u>Forest history</u>

152 The European occupation of the Lower St. Lawrence region began in the 17th century

153 with the arrival of the first European settlers along the shores of the St. Lawrence River.

154 However, it was not until the start of the 19th century that forest industry developed and

155 triggered the true colonization of the region. Beginning in 1820, the Price Brothers

156 Company logged large timber species such as spruce and red pine (*Pinus resinosa*

157 (Aiton)). A significant development in agriculture accompanied logging and led to a

158 subsequent increase in the population starting around 1830 and a slow progression of

159 settlement from the St. Lawrence Lowlands towards the Appalachian Plateau in the

160 interior. The forest industry concentrated primarily on saw wood located within a few

161 hundred metres of the waterways up until the 20th century. The mechanization of the

162 forest industry and the construction of large pulp mills and sawmills then allowed logging

163 to rapidly develop inland (Fortin et al. 1993; Boucher et al. 2009b).

164

165 **Materials and methods**

166 <u>Pre-settlement and modern data</u>

167 In Québec, the public land division was implemented in the form of townships of around

168 16 km × 16 km (10 miles × 10 miles), that were subdivided into parallel ranges 1.6 km

169 deep (1 mile) and lots 261 m (13 chains; 1 chain equals 20.1 m) wide. In total, the study

170 region includes 91 townships that were covered by 153 field surveys made by 58

171 surveyors between 1821 and 1900. Surveys were conducted along range lines and

172 township boundaries and included the precise measurement of distances between

173 successive observations. Various observations on forest composition can be found in the

174 surveyor's notebooks, such as taxon lists (e.g. spruce, fir, birch, cedar, and a few maple)

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175   and specific cover types (e.g. maple stand, cedar stand, etc.). In this study, specific cover

176   types were considered equivalent to pure stands of the corresponding taxon. General

177   cover types (e.g. mixed wood, hardwood) are also frequent but were not considered here.

178   For the analysis, we classified these observations into two geometric types, line or point,

179   according to the surveyors' notes. Lines could be clearly associated with both a starting

180   and an ending position along a range line whereas points could be clearly located, but

181   with no precise beginning or ending along a range line. When combining all observations

182   into the final database, each point observation was weighted by its mean spacing (mean

183   of the distances to the previous and next observations), whereas each line observation

184   was weighted by its length. Observations were georeferenced as points or lines over a

185   governmental cadastral map built from early land surveys.

186   In order to evaluate changes between the pre-settlement and present-day vegetation, we

187   used the last three decadal forest inventory programs conducted in the 1980s, 1990s, and

188   2000s by the provincial government. These inventories were conducted using 0.04 ha

189   sampling plots randomly stratified according to forest stand types (MFFP, 2016). Only

190   the plots located less than 1.6 km from a survey observation were considered, as this

191   distance also corresponds to the spacing between surveyed range lines. Each tree within a

192   plot was reported according to its species and diameter (using 2 cm DBH classes), which

193   allowed the total basal area (m^2 ha^{-1}) for each species in a plot to be calculated.

194   In total, over the entire study area, 22 555 taxon lists from the survey archives were

195   compared with 14 895 modern plots. Reclassification was required in order to compare

196   the two datasets. Spruces (white spruce, red spruce, black spruce), maples (sugar maple,

197   red maple) and poplars (trembling aspen, balsam poplar) were grouped to the genus level

198   for the two datasets as surveyors did not distinguish species for these genera. Only taxa

199   that occurred in more than 5% of survey observations or more than 5% of modern plots

200   were considered for this study, which includes four conifers (balsam fir, spruces, white

201   cedar, and pines) and four deciduous taxa (white and yellow birches, maples, and

202   poplars).

203   <u>Relative taxa prevalence and spatial analysis</u>

204   In a previous study, we have compared the reconstruction of forest composition obtained

205   with forest inventories from the early 20th century (i.e. reconstruction based on taxa basal

206   area) and early land survey taxon lists (Terrail et al. 2014). This showed that taxon lists

207   are highly accurate for reconstructing pre-settlement composition, and particularly when

208   using relative metrics (Terrail et al. 2014; Larsen et al. 2015). Thus, we computed relative

209   prevalence positions of the eight retained taxa in order to describe the vegetation for each

210   period. We first computed P_i, a measure of absolute taxa prevalence using the following

211   equation:

212 $$P_i = (n_i/M_i) \times 100 , \qquad\qquad (eq.1)$$

213   where n_i is the number of observations where the taxon i is present and M_i is the total

214   number of observations. The relative prevalence positions of taxa were then determined

215   from their absolute prevalence. The taxon with the highest absolute prevalence was

216   assigned a relative prevalence of 8, while a value of 1 was given to the taxon with the

217   lowest absolute prevalence. Taxa relative prevalence were firstly computed for the entire

218   study area and second, in order to analyse the spatial patterns of relative prevalence and

219   their reorganization between the two epochs, the relative prevalence was computed for

220   each cell of a grid with 412 cells of 5 km × 5 km (25 km^2) across the study area. Cells

221   containing less than 5 observations for either of the epochs were excluded from the

222   analysis. We tested several cell sizes and determined that a size of 25 km^2 permitted

223   retention of the maximum number of cells with well-distributed observations. On

224   average, the cells contained 50 taxon lists and 33 modern plots. We created relative taxa

225   prevalence maps for the 8 retained taxa (Appendix S1).

226   Taxa relative prevalence at the 25-km^2 grid scale were finally used to conduct two

227   distinct analyses. First, we regrouped cells according to community composition using a

228   k-means clustering analysis, which maximizes extra-group variance and minimizes

229   intergroup variance. We clustered data of each of the 412 cells from both periods in a

230   single run to allow direct comparison of communities between periods. An optimal

231   number of four groups was identified using a simple structure index (SSI) criterion.

232   Second, we tested for landscape homogenization or heterogenization using a multivariate

233 dispersion analysis (Anderson, Ellingsen, & McArdle, 2006). The relative prevalence of

234 taxa from each of the 412 cells from both periods were first used to compute a principal

235 coordinate analysis (PCoA), where the Bray-Curtis distance between cells was reduced to

236 eight principal coordinates (i.e., axes). PCoA analysis gives the advantage of using non-

237 Euclidian dissimilarity measures (e.g. Bray-Curtis dissimilarity). The multivariate

238 dispersion was calculated as the multivariate distance from each cell to its group

239 centroids (i.e. time periods). We performed a paired permutation test (999 permutations)

240 to detect significant homogenization or heterogenization between the two periods. This

241 approach is particularly well appropriate for assessing differences in β-diversity among

242 different areas or groups of samples (Anderson, Ellingsen, & McArdle, 2006). *k*-means

243 cluster and multivariate dispersion analyses were performed in R using the *cascadeKM*

244 and *betadisper* functions, respectively, which are both included in the vegan R package

245 (Oksanen et al. 2017).

246 **Results**

247 <u>Reorganization of relative taxa prevalence</u>

248 For the entire study area, conifers such as spruces, balsam fir, and cedar were the most

249 common taxa found on the pre-settlement landscape and occupied the highest relative

250 prevalence positions of 8, 7, and 5, respectively (Table 1). In contrast, the pines were

251 rare, occupying the position of 1 (Table 1). White birch was the most prevalent hardwood

252 and occupied the position of 6. Yellow birch, maples, and poplars occupied positions of

253 4, 3, and 2, respectively (Table 1).

254 The expansion of hardwoods since the pre-settlement period was characterized by an

255 increase in the absolute prevalence of maples by more than 45% and close to 25% for

256 poplars throughout the entire study region. Maples now occupy the second highest

257 position in relative prevalence, corresponding to an increase of 4 positions since the pre-

258 settlement era (Table 1). At the cell scale, maples have become the most abundant taxa in

259 more than the half of the cells (Fig. 2, Appendix S1). The relative prevalence of poplars

260 increased by two positions throughout the entire study region (from 2 to 4; 5.2% to

261 30.6%; Table 1) and is now ranked in positions 5 to 3 in 68% of cells (Fig. 2, Appendix

262 S1). While the absolute prevalence of white birch increased by 4.3 % during this

263 encroachment period, its relative prevalence decreased slightly from 6 to 5. Yellow birch

264 was the single hardwood species to experience a decrease in both absolute and relative

265 prevalence. Although these changes were slight at the regional scale (position 4 to 3;

266 Table 1), yellow birch underwent an important decrease in relative prevalence with more

267 than 50% of 25 km^2 cells that recorded a decrease of two or more positions of prevalence

268 (Fig. 2, Appendix S1).

269 Overall, the increase in the prevalence of hardwoods was counterbalanced by a decrease

270 in conifers. The most significant decrease was for cedar, with an absolute prevalence

271 decrease of 16 % and a loss of 3 positions in relative prevalence at the regional scale

272 (positions 5 to 2; Table 1). At the landscape scale, cedar occupied one of the four highest

273 position (i.e. positions 5 to 8) in 60 % of cells in pre-settlement times and is now ranked

274 positions equal or smaller than 3 in 83 % of the cells (Fig. 2, Appendix S1). The spruces

275 decreased by 10% in absolute prevalence and by 1 position in relative prevalence

276 throughout the entire study region (positions 7 to 6; Table 1). In pre-settlement times,

277 spruces ranked one of the two highest position in 70 % of the 25 km^2 cells while is now

278 ranked positions equal or smaller than 6 in 72 % of the cells (Fig. 2, Appendix S1). The

279 two remaining conifers, balsam fir and pines, were stable and were the most prevalent

280 (balsam fir; position 8 to 8; Table 1) and the less prevalent (pines; position 1 to 1; Table

281 1) taxa for the two periods.

282 Reorganization of tree taxa assemblages

283 Cluster analysis reveals that encroachment by maples and poplars resulted in an

284 important reorganization of tree taxa assemblage at the landscape scale (Fig. 3). While

285 the analysis identifies the existence of similar landscape assemblage in both periods (i.e.

286 cells within the four groups are found in each periods), there is a clear difference of

287 groups distribution between the two periods. In pre-settlement times more than 85 % of

288 cells belonged to groups 2 and 4, while in modern times 76 % of the cells are in group 3

289 and 18 % in group 1 (Fig. 3a). Balsam fir, spruces and white birch shows high and

290 comparable relative prevalence in all cluster groups, which are mostly differentiated by

291   the relative prevalence of cedar, yellow birch, maples and poplars (Fig. 3b). Pre-

292   settlement dominant groups (i.e. 2 and 4) showed higher relative prevalence of cedar and

293   yellow birch compared to modern dominant groups (i.e. 1 and 3). Groups 2 and 4 mostly

294   differentiated by higher prevalence of maples in groups 4 along with the almost complete

295   absence of this taxon in group 2. In addition, the relative prevalence of maples and

296   poplars is higher in modern dominant groups compared to pre-settlement dominant

297   groups 2 and 4 (Fig. 3b). Groups 1 and 3 are mostly separated by the prevalence of

298   maples and yellow birch. Maples is the most prevalent taxon (i.e. relative prevalence rank

299   of 8) in more than 50% of group 3 cells, which also show higher yellow birch prevalence

300   than to group 1. Yellow birch is almost totally absent in group 1 and relative prevalence

301   of poplars is slightly higher.

302   Results of groups transition (Fig. 3c) provide an important insight into the dynamic

303   trajectories of tree communities at the landscape scale. Very few cells in pre-settlement

304   dominant groups (i.e. groups 2 and 4) have maintained in the same groups in modern

305   times. Almost half of the study area (48 % of the cells) followed a transition from group

306   4, which exhibited an important relative prevalence of maples in pre-settlement times, to

307   group 3 in which maples is nowadays the most prevalent taxa. Nearly all cells in group 3

308   in pre-settlement times have stayed in groups 3 (10 % of the study area). Cells currently

309   in groups 1 mostly originated from groups 2 and 4 (8 % and 6% of the study area,

310   respectively). Together, these changes resulted in a significant landscape homogenization

311   (Fig. 4). During pre-settlement times, mean cells distance to centroid was 0.16 and has

312   decreased to 0.12 in modern times, indicating that composition of cells is more similar in

313   modern compared to pre-settlement times. Our permutation test shows that this

314   homogenization is significant ($p < 0.001$).

315

316   Discussion

317   The results of this study are consistent with the majority of similar studies conducted in

318   the temperate zone of eastern North America that recorded a significant encroachment by

319   maples and poplars as a result of land use activities since pre-settlement times (e.g.

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320   clearing for agriculture, anthropogenic fires, logging, farmland abandonment) (Whitney

321   1994; Jackson et al. 2000; Friedman, & Reich, 2005; Thompson et al. 2013; Danneyrolles

322   et al. 2016a; Flinn et al. 2018). Our study also agrees with works that recorded a

323   landscape homogenization as a consequence of these changes (Schulte et al. 2007;

324   Hanberry, Dey, & He, 2012; Hanberry, Palik, & He, 2012; Thompson et al. 2013). In this

325   context, our most important contribution here was to document the consequent

326   reorganization of relative taxon abundance. Although no taxon has been excluded or

327   introduced at the regional scale, the relative order of taxa prevalence has been reshuffled

328   for almost all taxa in all cells due to the regional expansion of maple and poplar

329   (Appendix S1). Because relative taxa prevalence condenses values of absolute prevalence

330   to a few discrete ranks, it provides easier to interpret and apply management targets for

331   ecosystem-based forest management. In the following sections we discuss the cause of

332   deciduous encroachment and resulting taxa reshuffling as well as the management

333   implications of our findings.

334   <u>Causes of maples and poplars encroachment</u>

335   Maples, the taxon that has increased the most throughout the study area corresponds to

336   both sugar and red maples since surveyors did not differentiated these two species. The

337   relative abundance of the two maples species in modern plots (Appendix S2) reveals that

338   red maple tends to be omnipresent across the modern landscape, while sugar maple is

339   more clustered. Red maple is known to be an opportunist early-successional, fast-

340   growing and short-lived species (Walter, & Yawney 1991; Abrams 1998) which has

341   benefited from disturbances and fire suppression in the eastern U.S.A. (Fei, & Steiner

342   2007, 2009; Nowacki, & Abrams 2008). Moreover, at its northern range limits, red maple

343   may even be favoured by stand-replacing fire (Zhang, Bergeron, Zhao, & Drobyshev,

344   2015). As such, it is very likely that red maple benefited from both stand-replacing and

345   partial disturbance (agricultural clearing, fire, clear-cutting, partial cutting, insect

346   outbreaks) from the last century in our study area. While sugar maple is generally

347   considered as very shade-tolerant late-successional species (Godman, Yawney, & Tubbs,

348   1991), studies near its northern range limit have shown that the species may also become

349   dominant quickly after stand-replacing disturbance such as clearcutting and fire (Nolet,

350 Bouffard, Doyon, Delagrange, 2008; Nolet, Delagrange, Bouffard, Doyen, & Forget,

351 2008; Pilon, & Payette 2015). By any means, sugar maple ability to maintain a vigorous

352 seedling banks and its strong response to canopy release allow it to take a substantial

353 advantage of low severity disturbances such as partial cutting and insect outbreaks

354 (Boucher et al. 2006; Danneyrolles, Arseneault, & Bergeron, 2016b).

355 Concerning poplars, trembling aspen certainly accounts for a very large proportion of the

356 increase in poplar prevalence in our study area (Appendix S2). Trembling aspen is

357 considered as an early-successional, fast-growing and short-lived species (Perala, 1991).

358 More particularly, its capacity to vigorously regenerate by roots-suckering after

359 disturbance makes trembling aspen particularly adapted to the severe or frequent

360 disturbances that have followed European settlement (Bergeron, & Charron, 1994;

361 Boucher et al. 2014; Danneyrolles et al. 2016a).

362 Spatial reorganization of tree communities

363 Our cluster analysis also provides important insight into spatial reorganization of

364 community composition. One particularly striking pattern is that cells in which maples

365 are currently the most abundant taxa predominantly came from groups with the highest

366 abundance of maples in pre-settlement times. Indeed, maples have tended to become

367 dominant (i.e. taxon with the highest relative frequency) mainly in area where they were

368 already present (Appendix S3). Moreover, areas where maples became dominant

369 corresponds to area in which both sugar and red maples are currently present, while area

370 where maples became present but not dominant correspond to areas where only red

371 maple is currently present (Appendices S2 and S3). This is not surprising since red maple

372 produce each year a large amount of wind-dispersed seeds that easily colonize recently

373 disturbed area (Walter, & Yawney, 1991; Abrams, 1998) where population can establish

374 quickly (Fei, & Steiner 2009). By contrast, sugar maple seed production is more irregular

375 and the species has typically poorer abilities than red maple to colonize new area but has

376 better capacity to become dominant in stands where it is already present (Abrams, 1998;

377 Caspersen, & Saprunoff, 2005; Nolet et al. 2008b).

378   Trembling aspen has a high potential to colonize new area both by long seed dispersal

379   and vegetative reproduction (Perala, 1991), which explain its ubiquitous expansion across

380   the landscape (Figs 3, S1, S3). However, contrarily to maples, aspen is infrequently the

381   most abundant taxa in 25 km^2 cells. This may reflect the fact that aspen establishment is

382   more dependent to severe stand-replacing disturbance such as fire or clear-cut (Bergeron,

383   & Charron, 1994), and thus, within one cell, aspen may have become very abundant in

384   severely disturbed plots while remaining totally absent from others.

385   Spatial reorganization was also characterized by the landscape homogenization of forest

386   communities. Such a forest composition transformation in Northeastern North America

387   has been associated with the convergence of regional forest toward younger successional

388   states (Schulte et al. 2007; Hanberry et al. 2012b) and with a loss of influence of

389   environmental gradients in youngest forests (Hanberry et al. 2012a; Thompson et al.

390   2013). In our study area, landscape homogenization has been primarily driven by the

391   encroachment of maples and poplars. While balsam fir and spruces were omnipresent

392   across the pre-settlement landscape, heterogeneity was mainly determined by the

393   clustered distribution of maples (Appendix S1) that differentiated the two dominant

394   cluster groups in pre-settlement times (Fig. 3). Before European settlement maples

395   occurred mostly as small isolated stand on hilltops (Boucher et al. 2006; Dupuis et al.

396   2011). Conversely, maples tend to be omnipresent across the modern landscape, as

397   illustrated by the current large predominance of the maples-dominated group 3. This

398   ubiquitous distribution is likely linked to red maple present-day distribution (Appendix

399   S2). Considering than both red maple and trembling aspen are opportunist early-

400   successional species, landscape homogenization probably resulted from the regional

401   forest rejuvenation (i.e. convergence toward an early successional state). However,

402   because our analysis is limited to the 25 km^2 grid scale, it is not excluded that

403   disturbances of the last century have at the same time led to spatial heterogenization at a

404   finer scale (i.e. plot-to-plot variation within 25 km^2 cells; Thompson et al. 2013;

405   Danneyrolles et al. 2018).

406   Management implications

14

Spatial heterogeneity contributes to forest resilience to insect outbreaks and to broader global changes (Knops et al. 1999; Turner, Donato, & Romme, 2013) and has been weakened by landscape homogenization of the last century. Considering that ecosystem-based forest management has recently become a priority in the province of Québec (Gouvernement du Québec, 2015), our results (mainly Fig. 2) should be considered, along with additional criteria of sustainable forest management, to identify reference conditions of relative taxon abundance at large spatial scales (i.e., for spatial units of about 25 km^2) in order to restore heterogeneity and resilience. Because repeated disturbance associated with settlement and forest management is the most likely process that has increased and maintained high relative prevalence of maple and poplar, forest managers should avoid systematically increasing the prevalence of these two taxa at the expense of late-successional conifers. Maple and poplar dominance (i.e. frequency as the more prevalent taxon) and prevalence should be decreased and heterogenized among sites. Conversely, cedar and white and red spruces, as well as yellow birch, should be actively restored to higher ranks of relative prevalence through planting whenever possible. At the same time, it is encouraging that balsam fir, the most dominant and prevalent taxon of the study area, has been sufficiently resilient to high rates of anthropogenic disturbances and insect outbreaks of the 20th century that no specific action is needed to manage its relative prevalence.

Although climate change is likely to affect the ability of forest management to reduce gaps between current and pre-settlement forest composition, our results would still provide functional targets for forest management (Boulanger et al. 2019). For example, growth rate, longevity, and shade-tolerance of species can be considered in order to maintain functionally diverse and spatially heterogeneous stands and landscape, similar to the ones that prevailed before European settlement.

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Authors' contributions

All authors designed the study and methodology. RT and VD analyzed the data and wrote
the manuscript with inputs from DA, MJF and YB.

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Data accessibility

Historical data are available from the corresponding author upon request. Modern forest
data are freely available from the Ministère des Forêts, de la Faune et des Parcs du
Québec website: (https://mffp.gouv.qc.ca/le-ministere/acces-aux-donnees-gratuites/).

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643   **List of appendices**

644

645   **Appendix S1**: Position of relative prevalence for the eight taxa in each 5 km × 5 km cell for

646   the preindustrial and modern time periods.

647

648   **Appendix S2**: Relative ranks of basal area in each modern plot (1980-2010) for species that

649   were regrouped at the genus level.

650

651   **Appendix S3**: Changes in taxa presence and dominance status between preindustrial and

652   modern times.

653 Table 1. Absolute and relative prevalence of the tree taxa across the entire study area for
654 the two-time periods and their differences (Modern minus Archives). Ap: Absolute
655 prevalence; Rp: Relative prevalence.

656

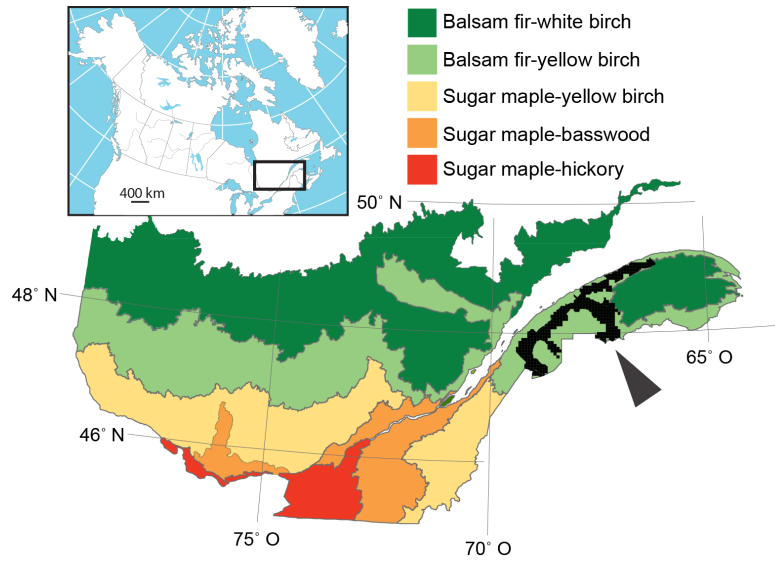| Taxa	Survey archives (1820-1900)		Modern inventory (1980-2010)		Difference	
	Ap	Rp	Ap	Rp	Ap	Rp
Maples	15.7	3	61.7	7	46.0	4
Poplars	5.2	2	30.6	4	25.3	2
Balsam fir	74.6	8	78.0	8	3.4	0
Pines	1.0	1	1.4	1	0.4	0
Spruces	67.7	7	57.7	6	-10.0	-1
White birch	50.5	6	54.8	5	4.3	-1
Yellow birch	32.9	4	27.2	3	-5.8	-1
Cedar	36.3	5	19.5	2	-16.7	-3

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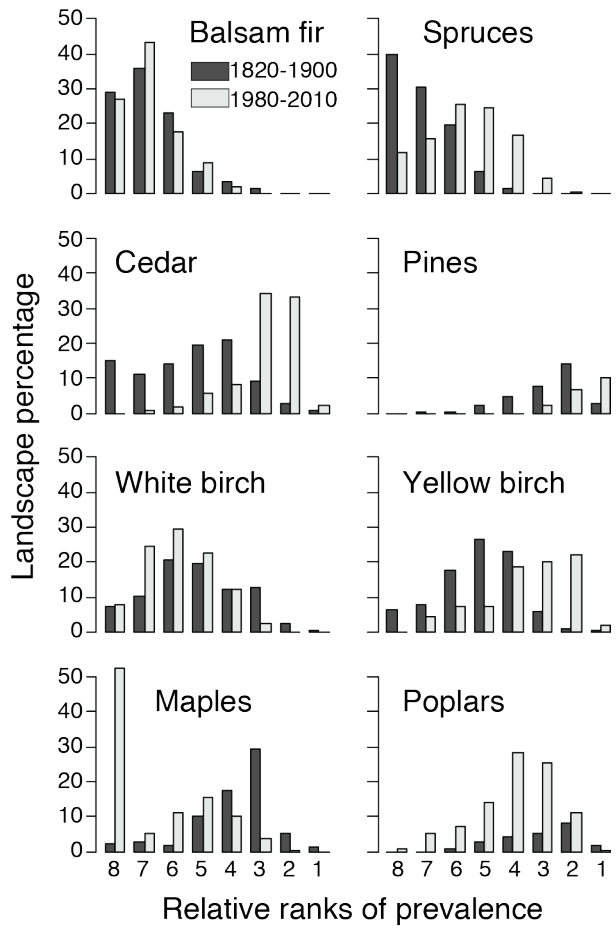
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Figure 1. Location of the study area in eastern Québec (black) in relation to the
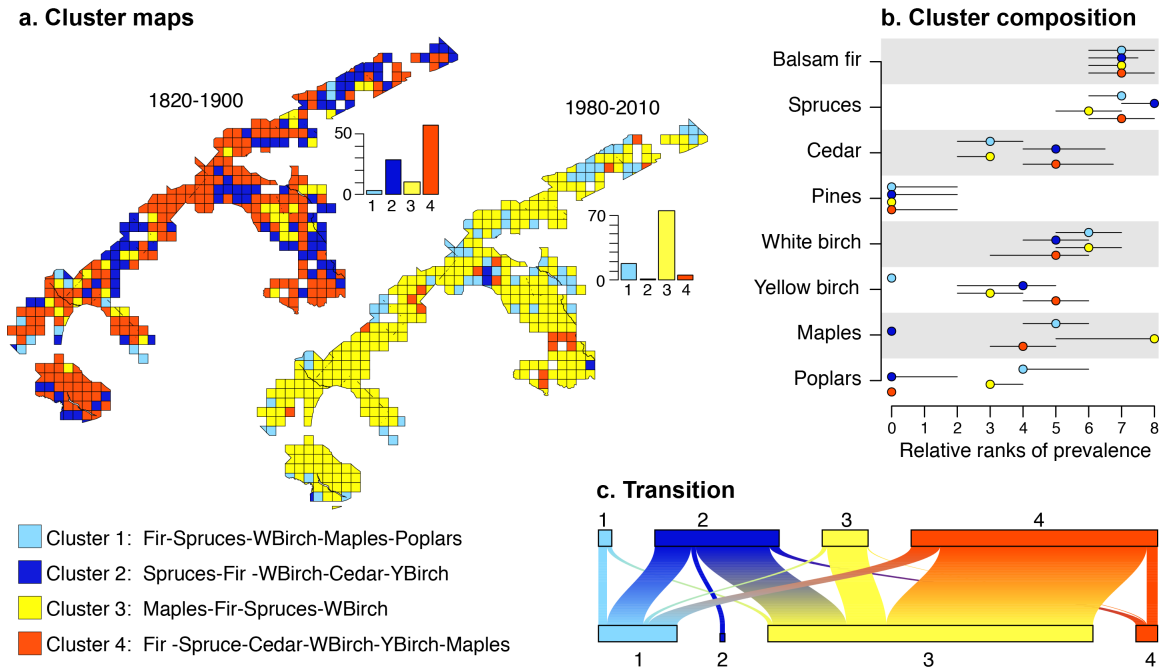bioclimatic domains.

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Figure 2. Percentage of cells occupied by each position of relative prevalence for each

taxon and each time period.

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a. Cluster maps

1820-1900

1980-2010

Cluster 1: Fir-Spruces-WBirch-Maples-Poplars
Cluster 2: Spruces-Fir -WBirch-Cedar-YBirch
Cluster 3: Maples-Fir-Spruces-WBirch
Cluster 4: Fir -Spruce-Cedar-WBirch-YBirch-Maples

b. Cluster composition

c. Transition

672

Figure 3. Forest communities identified by k-means clustering of the 25 km^2 grid cells. (a): Maps of the clusters for the two time periods with histograms showing the percent of cells in each cluster for the two periods; (b): diagram of cluster composition with points representing the median relative ranks of frequency and error bars displaying the first and third quartiles; (c): diagram quantifying cell transition among cluster groups from preindustrial (above) to modern (below) time periods (width of each box is proportional to the corresponding number of cells).

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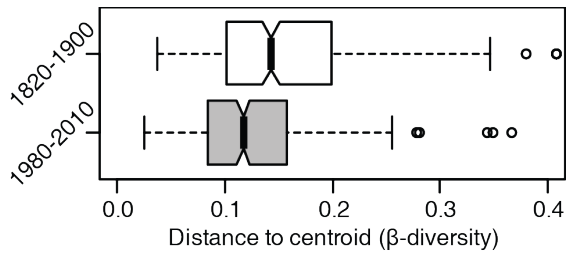
Figure 4. Landscape homogenisation as assessed by multivariate dispersion analysis. The lower the distance to the centroid, the more cells are similar in terms of composition, thus resulting in a more homogeneous landscape. A permutation test shows significant difference between the two times periods ($p<0.001$).