1   **Title:** Boreal forests will be more severely affected by projected anthropogenic climate

2   forcing than mixedwood and northern hardwood forests in eastern Canada.

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4   **Authors:** Yan Boulanger[1]*, Jesus Pascual Puigdevall[1]

5   [1]Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre,

6   Québec, QC, Canada

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8   ***corresponding author** Yan Boulanger, Email : yan.boulanger@canada.ca; Phone:

9   (418) 648-5834

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10   **Abstract**

11   **Context**

12   Increased anthropogenic climate forcing is projected to have tremendous impacts on

13   global forest ecosystems, with northern biomes being more at risk.

14   **Objectives**

15   To model the impacts of harvest and increased anthropogenic climate forcing on eastern

16   Canada's forest landscapes and to assess the strong spatial heterogeneity in the severity,

17   the nature and direction of the impacts expected within northern forest regions.

18   **Methods**

19   We used LANDIS-II to project species-specific aboveground biomass (AGB) between

20   2020 and 2150 under three climate (baseline, RCP 4.5 and RCP 8.5) and two harvest

21   (baseline harvest, no harvest) scenarios within four forest regions (boreal west, boreal

22   east, mixedwood and northern hardwood).

23   **Results**

24   Climate change impacts within the boreal forest regions would mainly result from

25   increases in wildfires activity which will strongly alter total AGB. In the mixedwood and

26   northern hardwood, changes will be less important and will result from climate-induced

27   growth constraints that will alter species composition towards more thermophilous

28   species. Climate-induced impacts were much more important and swifter under RCP 8.5

29   after 2080 suggesting that eastern Canada's forests might cross important tipping points

30   under strong anthropogenic climate forcing.

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31 **Conclusions**

32 Boreal forest regions will be much less resilient than mixedwood or northern hardwoods

33 to the projected changes in climate regimes. Current harvest strategies will interact with

34 anthropogenic climate forcing to further modify forest landscapes, notably by

35 accelerating thermophilous species AGB gain in southernmost regions. Major changes to

36 harvest practices are strongly needed to preserve the long-term sustainability of wood

37 supply in eastern Canada. Adaptation strategies should be region-specific.

38 **Keywords**

39 Climate change, Harvest, Landis-II, boreal forests, mixedwood, northern hardwood,
40 eastern Canada

41

42 **Introduction**

43 Increased anthropogenic climate forcing is projected to have tremendous impacts on

44 global forest ecosystems (Heyder et al. 2011). Changes in temperature and precipitation

45 regimes since the last decades have already modified natural disturbances as well as

46 forest productivity in several forest regions worldwide. Among all forest biomes,

47 northern forests will probably be among the most impacted by climate change, with

48 temperatures projected to increase at much higher rates than elsewhere (Price et al. 2013).

49 In Canada, temperatures have already risen by 1.7 °C since 1948, a rate twice as fast as

50 the global average (NRCan 2019). During this time period, wildfire activity has

51 significantly increased (Hanes et al. 2019), boreal tree species productivity have declined

52 (Girardin et al. 2016) while warmer temperatures might be responsible for recent

53 modifications in forest insect outbreak regimes (Pureswaran et al. 2015). Tipping points

54 are likely to be crossed under aggressive anthropogenic climate forcing (e.g., RCP 8.5)

55 potentially resulting in biome shifts (Stralberg et al. 2018). No doubt that these alterations

56 of northern forest ecosystems will severely impact ecosystem services including carbon

57 storage (Kurz et al. 2008), timber supply (Gauthier et al. 2015; Boucher et al. 2019;

58 Brecka et al. 2020) and wildlife habitats (Tremblay et al. 2018; Cadieux et al. 2019,

59 2020).

60 Although alterations of northern forest ecosystems are projected to be significant, strong

61 spatial heterogeneity in the severity, the nature and direction of the impacts is to be

62 expected. Such heterogeneity would likely result from the complex interactions between

63 climate change and natural and anthropogenic disturbances, forest productivity, seed

64 dispersal and biophysical variables (e.g., soil conditions). Disturbance severity and types

65 strongly vary across the temperate to the boreal forest biomes and as such, are likely to

66 differently impact successional pathways, notably when interacting with climate change.

67 For instance, annual burned area is projected to strongly increase in central and western

68 Canadian boreal forests when compared to eastern boreal forests (Boulanger et al. 2014),

69 resulting in different impacts on productivity, biomass accumulation and successional

70 pathways (Boulanger et al. 2016; Cadieux et al. 2019). Moderate and potentially selective

71 disturbances (e.g., host-selective insect outbreaks) occurring at the temperate-boreal

72 ecotone could favor transitions to temperate forests while climate-induced increases in

73 severe stand-replacing disturbances would promote either transient or permanent

74 transitions to pioneer states within the boreal forest (Payette and Delwaite 2003,

75 Johnstone et al. 2016; Brice et al. 2020). Important modifications in species composition

76 are to be expected at the transition zones between boreal and temperate biomes where

77 several tree species are currently reaching either their southward or northward thermal

78 tolerance (Leithead et al. 2010; Brice et al. 2019). On one hand, one could expected that

79 projected increases in temperatures might favored the northward migration of e.g.,

80 thermophilous hardwood species at the expanse of boreal conifers, leading to a slow but

81 steady northward progression of the northern hardwood forest region either through

82 increased recruitment or better growth conditions (Duveneck et al. 2014). On the other

83 hand, more suitable growth conditions as projected in the short-term or under mild

84 climate forcing (D'Orangeville et al. 2018) could favor boreal species productivity in

85 northern locations leading to faster and larger biomass accumulation as well as to closed-

86 crown forest encroachment in sites where productivity is currently climate-limited.

87 Despite suitable recruitment and growth conditions, propagule availability might restrain

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88   the expansion of warmed adapted species, making virtually impossible for these species

89   to keep pace with the northward displacement of isotherms which would introduce a

90   migration lag in the southernmost part of the boreal forest (Sittaro et al. 2017; Taylor et

91   al. 2017). Furthermore, unsuitable, acidic soil conditions within the boreal forest could

92   also restrain the northward expansion of hardwood species (Brown and Velland 2014)

93   although recent analyses showed that soil characteristics represent a rather minor

94   impediment to such transitions (Brice et al. 2020). Yet, it is still unknown how these

95   agents of change will ultimately cumulate and interact at multiple spatial and temporal

96   scales to alter forest landscapes over areas experiencing distinct current and future

97   environmental conditions.

98   In commercial forests, anthropogenic impacts such as harvest are likely to cumulate with

99   climate change to further modify forest ecosystems (Boulanger et al. 2016; Cadieux

100 2019). Harvest-induced increases in disturbance rates might modify the system's inertia

101 and accelerate climate-induced changes by removing resident communities and providing

102 resources for warmed-adapted establishment and growth (Steenberg et al. 2013; Brice et

103 al. 2020). Indeed, it was shown that alike canopy gaps (Leithead et al. 2010), moderate

104 harvest-induced disturbance rates under warmer temperatures could favor co-occurring

105 thermophilous pioneer but also shade-tolerant species, and hasten their northward

106 migration within the boreal forest (Steenberg et al. 2013; Brice et al. 2019, 2020; Mina et

107 al. 2020). When cumulated with increasing natural disturbance rates, harvest could bring

108 total disturbance rates outside their range of natural variability (Bergeron et al. 2006; Cyr

109 et al. 2009), resulting in regeneration failures and long-term changes in successional

110 pathways (Splawinski et al. 2019). By favoring structural and compositional diversities,

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111   ecosystem-based forest management was suggested to promote forest resilience under

112   increasing climate warming (Duveneck et al. 2014, 2015a; Boulanger et al. 2019). Still,

113   this business-as-usual strategy that is now extensively applied throughout northern forests

114   might not be efficient in order to keep or restore functional diversity under climate

115   change (Boulanger et al. 2019; Mina et al. 2020). It has to be assessed how such a

116   strategy might interact with climate-induced changes and how it could affect forest inertia

117   within different forest ecosystems that will experience contrasting disturbance- and

118   climate regime changes. In this context, quantifying the effects as well as the importance

119   of harvest-induced impacts relative to those generated by climate change over different

120   forest regions should offer new insights about potential adaptation avenues (Messier et al.

121   2019).

122   Evaluating the spatial heterogeneity of future climate- and harvest-induced changes in

123   forest ecosystems is paramount in order to understand how specific drivers of forest

124   changes are projected to proceed. Furthermore, estimating the rate and nature of the shifts

125   as well as their overall impacts on harvest would help identify efficient and specific

126   adaptation measures, notably to ensure the continuous provision of forest ecosystem

127   services. Harvest and anthropogenic climate interactions on forest landscapes might be

128   realistically projected using spatially-explicit process-based model simulations. Forest

129   landscape models (FLM) were proven successful in order to project future changes in

130   forest composition and structure according to different climate and harvest scenarios

131   (e.g., Scheller and Mladenoff 2008; Steenberg et al. 2013; Duveneck et al. 2015a, 2015b,

132   Boulanger et al. 2019). Yet, FLM simulations are frequently conducted over territories

133   spanning less than 10M ha (with few notable exceptions, see Wang et al. 2014) which

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134   impeded the consideration of the heterogeneity in climate- and harvest- induced changes

135   over a wide range of environmental conditions.

136   In this study, we modeled the impacts of harvest and increased anthropogenic climate

137   forcing on the entire commercial forest (54.3M ha) of Quebec, Canada by using the

138   LANDIS-II FLM. Simulations were conducted in four forest regions (northern hardwood,

139   mixedwood, boreal east and boreal west) in eastern Canada and covered one of the

140   largest area ever simulated with a FLM. More specifically, our objectives were to i)

141   assess how and how much forest landscapes in each of these forest regions will be

142   specifically altered under different climate scenarios. Furthermore, ii) we explored how

143   harvest in the context of climate change, might differently affect forest inertia and the

144   nature of changes projected within those forest regions. We hypothesized that i) climate

145   change will severely altered forest landscapes with large changes driven by fire in the

146   boreal forest regions while changes in productivity will favored hardwoods over

147   coniferous species especially in the mixedwood region. Also ii) harvest will accelerate

148   climate induced-changes by favoring species turnover.

149   **2. Methods**

150   **2.1 Study regions**

151   We projected forest landscapes over the entire commercial forest in the province of

152   Québec (54.3 M ha, Figure 1). The area is bordered on the southeast by the northern

153   extent of the Appalachian Mountains. In this area, valleys covered by glacial till and

154   humo-ferric podzols are intermingled with broadly rolling mosaic of upland plateaus

155   sitting between 200 and 800 m above sea level. Most of the area located north of the St.

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156   Lawrence River belongs to the Canadian Shield. Landform and soils in this area are

157   dominated by uplands and wetlands, where Precambrian granitic bedrock outcrops

158   alternate with ridges encompassing coarse texture hummocky deposits of glacial origin.

159   Climate is more typical of the temperate continental region in the southernmost part of

160   the study area, whereas the northernmost part is typical of boreal regions. The study area

161   covers wide latitudinal and longitudinal temperature gradients (mean annual temperature

162   south MAT = 6.6°C; north MAT = -3.1°C and total annual precipitations west TAP = 600

163   mm; east TAP = 1200 mm, Robitaille and Saucier [1998]). A wide variety of forest

164   ecosystems occur within the area and as such, the study area was divided in four forest

165   regions based on the Quebec's bioclimatic subdomains, i.e., the northern hardwoods, the

166   mixedwoods as well as the boreal east and boreal west (Robitaille and Saucier 1998).

167   Species-rich northern hardwood forests dominated by deciduous mesophytic species are

168   located in the southern part of the study area. Forest gradually transitions to mixed in the

169   mixedwood forest region and finally to conifer-dominated forests with increasing latitude

170   in both boreal forest regions. Recurrent spruce budworm (SBW) outbreaks are the most

171   important natural disturbance in the mixedwood forest region (Boulanger et al. 2012),

172   and small windthrows and single-tree mortality drive natural forest succession in the

173   northern hardwood forest region. Wildfires are most prevalent within the boreal portion

174   of the study area with fire return intervals decreasing from *ca* 400 years in the east to *ca*

175   100 years in the drier, western part (Boulanger et al. 2014). Timber harvest occurs at

176   various rates over the entire study area, with cutblock size and proportion of biomass

177   harvested typically increasing with latitude. Single-tree and small-patch harvest are most

178   prevalent in the northern hardwoods, whereas clearcuts reaching more than 100 ha are

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179   more common in the boreal regions. These prescriptions follows ecosystem-based forest

180   management guidelines and aim at emulate natural disturbances in each of these regions.

181   **2.2 Climate data**

182   We produced monthly time series for baseline climate by interpolating data from climate

183   station records (McKenney et al. 2013). We obtained future climate projections from the

184   Canadian Earth System Model version 2 (CanESM2) for each of two different radiative

185   forcing scenarios, i.e. RCP 4.5 and RCP 8.5. Radiative forcing is assumed to stabilize at

186   4.5 W·m^{-2} after 2100 in the RCP 4.5 scenario, without an "overshoot" pathway. In the

187   RCP 8.5 scenario, the forcing reaches 8.5 W·m^{-2} in 2100 and keeps on increasing

188   afterwards. Under these scenarios, the CanESM2 projects mean annual temperature

189   increases of ca 3.9˚C (RCP 4.5) to ca 8.5˚C (RCP 8.5) throughout the study area by 2100

190   (compared to circa 2000), while average precipitation is projected to increase by 7%

191   (RCP 8.5) to 10% (RCP 4.5). We bias-corrected data from CanESM2 for the 1900 - 2100

192   period by expressing temperatures as differences and precipitations as ratios relative to

193   the CanESM2 monthly means for the 1961-1990 period.

194   **2.3 LANDIS-II forest landscape simulation model**

195   LANDIS-II is a spatially-explicit raster-based forest landscape model that simulates

196   disturbances, seed dispersal, and forest succession (Scheller et al. 2007). Species are

197   defined using unique life-history attributes and are represented in each grid cell as 10-

198   year age-cohorts. Forest composition and structure in each cell were initialized using

199   provincial ecoforestry maps and cohort data from provincial permanent and temporary

200   forest inventory plots (FIP). These maps were rasterized at a 250-m (6.25 ha) resolution.

201   Each of these cells was then assigned to a spatial unit (i.e., "landtype") with

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202   homogeneous soil and climate conditions. Grid cells with more than 50% of their area

203   covered with non-forest cover types were classified as inactive.

2.4 Forest succession and species growth potential

205   We used the LANDIS-II Biomass Succession extension v 3.2 (Scheller and Mladenoff

206   2004) to simulate forest succession in each 250-m cell. This extension simulates

207   modifications in cohort aboveground biomass (AGB) over time by taking into

208   consideration tree species' cohort age, life-history traits, and species-specific landtype

209   responses (Suppl. Mat. S1). We used species' life-history traits information collected

210   from various sources including several previous LANDIS-II publications conducted for

211   North American forest landscapes. Species were classified as either thermophilous or

212   boreal according to their thermal preference in growing degree-days (Suppl. Mat. S1).

213   We also classified species according to which successional stage, e.g., either pioneer or

214   mid-/late-successional, they are mostly associated consistent with their shade tolerance

215   and longevity.

216   We parameterized and calibrated three sets of dynamics inputs sensitive to soil and

217   climate conditions, i.e., i) species establishment probabilities (*SEP*), ii) maximum

218   possible aboveground net primary productivity (*maxANPP*), and iii) maximum

219   aboveground biomass (*maxAGB*). Parameterization was conducted using the individual

220   tree-based, forest patch model PICUS version 1.5 (Lexer and Honninger 2001; Taylor et

221   al. 2017). PICUS simulates the dynamics of individual trees on 10×10 m patches across

222   forest stand areas and accounts for spatially-explicit interactions among patches via a 3D

223   light module. PICUS simulates the effects of climate and soil properties on tree

224   population dynamics (Lexer and Honninger 2001). Using individual tree species

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225 parameters, we ran PICUS simulations for 17 tree species occurring in the study regions

226 (Suppl. Mat. S1). A complete description of the model and how it was parameterized and

227 validated can be found in Taylor et al. (2017). In order to determine the three dynamic

228 input parameters for Biomass Succession extension, we simulated mono-specific 1-ha

229 stands with PICUS for each of the 17 tree species. A factorial simulation design was used

230 to simulate all mono-specific stands for tree species and landtype, under climate

231 conditions for specific periods (2000-2010, 2011-2040, 2041-2070, 2071-2200) and

232 forcing scenarios (baseline, RCP 4.5, RCP 8.5). Simulations were run for 300 years,

233 starting from bare-ground and used the landtype-specific soil and the period- and climate

234 scenario specific climate data. Values for *SEP*, *maxANPP* and *maxAGB* were then

235 derived from these simulations (see Boulanger et al. 2016). Previous analyses (Boulanger

236 et al. 2016, 2017, 2019) have shown good agreement between successional pathways

237 predicted by LANDIS with those reported in the literature. Readers can refer to

238 Supplementary Material S2 for *maxAGB* maps.

239 **2.5 Forest harvest**

240 The Biomass Harvest extension (v3.0; Gustafson et al. 2000) was used to simulate forest

241 harvest. Relevant information regarding harvest parameters such as mean harvested patch

242 size and total harvested area, was summarized by forest management units (FMU).

243 Harvest was set to vary according to potential vegetation as defined by the Quebec's

244 Hierarchical System for Territorial Ecological Classification (Bergeron et al. 1992). This

245 system classifies forest stands according to their potential natural vegetation type, which

246 is a function of climatological and geomorphological constraints on vegetation growth

247 and succession. We simulated ecosystem-based forest management (EBFM), a harvest

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248   scenario that should closely mimic the historical disturbance regimes (wildfires, spruce

249   budworm outbreaks, single-tree mortality, small gap openings) occurring in the study

250   area. Rotation length time and biomass removal levels were fixed according to current

251   harvest regulations and expert advices as in Boulanger et al. (2019). Harvest rates were

252   held constant throughout the simulations unless not enough stands qualified for harvest.

253   In this latter case, harvest proceeded until there were no more stands available.

254   **2.6 Natural disturbances**

255   Fire, and spruce budworm (SBW, *Choristoneura fumiferana* [Clem.]) outbreaks, were

256   considered as natural disturbances in the LANDIS-II simulations. Both disturbances

257   historically had major impacts on Quebec' forest landscapes (e.g., Bouchard et al. 2006).

258   SBW outbreaks are mostly prevalent within the mixedwood region whereas fires are

259   more important within the boreal regions. The LANDIS-II Base Fire v3.0 extension was

260   used to simulate stochastic fire events dependent upon fire ignition, initiation and spread.

261   Fire regime data (annual area burned, fire occurrence, and mean fire size) were

262   summarized into "fire regions" corresponding to the intersection of the study area and the

263   Canadian Homogeneous Fire Regime zones of Boulanger et al. (2014). Baseline and

264   future fire regime parameters within each fire region were calibrated according to models

265   developed by Boulanger et al. (2014) and further updated for different RCP scenarios

266   (Gauthier et al. 2015). Annual area burned (AAB) will remain minimal within northern

267   hardwoods, regardless of climate scenarios whereas it will reach maximum values > 2%

268   after 2080 in boreal west under RCP 8.5 (Supplementary Material S3).

269   The Biological Disturbance Agent (BDA) v3.0 extension (Sturtevant et al. 2004)

270   modified to account for specific SBW parameters was used to simulate SBW outbreaks.

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271   From the most to least vulnerable, host tree species for SBW included balsam fir (*Abies*

272   *balsamea*), and white (*Picea glauca*), red (*P. rubens*) and black (*P. mariana*) spruces

273   (Hennigar et al. 2008). Outbreaks are simulated as probabilistic events at the cell level

274   with probabilities being a function of the site and neighborhood resource dominance

275   (e.g., host species occurrence within a 1-km radius) as well as regional outbreak status.

276   Outbreak-related tree mortality is contingent on these probabilities as well as on host

277   species- and age-specific susceptibility. SBW outbreak parameters were calibrated and

278   validated using various studies conducted within the boreal and mixedwood forests

279   (Hennigar et al. 2008). Regional outbreaks were calibrated at the highest severity level

280   possible were set to last one-time step (10 years) and to recur every 40 years in

281   accordance with historical regional cycles (Boulanger et al. 2012).

282   **2.7 Simulation design**

283   As the study area is one of the largest ever simulated with LANDIS-II, we had to split it

284   into five sub-areas that were simulated separately for computational reasons. In order to

285   consider some potential edge effect related to these zones pertaining to e.g., seed

286   dispersal or fire spread from nearby regions, we simulated each sub-area with an

287   additional 50-km buffer overlapping the adjacent sub-areas. Simulations were run

288   according to a factorial design, i.e., under the three climate projections, (corresponding to

289   baseline, and the RCP 4.5 and RCP 8.5 radiative forcing scenarios) and two harvest

290   scenarios. The two harvest scenarios were no harvest and a baseline, EBFM harvest

291   where current parameters described above were applied. Five replicates were run for 130

292   years for each harvest and climate change scenario combination, starting in the year

293   2020, and using 10-year time steps. Except for scenarios involving the baseline climate,

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294   we used the projected fire regime parameters projected for the 2011-2040 periods for the

295   2020-2040 simulated years. Also, fire regime parameters were allowed to change in

296   2041-2050 and 2071-2080 according to the average climate corresponding to each

297   forcing scenario. Fire regime parameters for 2071-2080 were held constant up to 2150.

298   Dynamic growth and establishment parameters (*SEP, maxANPP* and *maxAGB*), were

299   allowed to change according to each climate scenario following the same schedule used

300   for the fire regime parameters.

301   **2.8 Analyses**

302   We tested for the impacts of climate change and current harvest practices on forest

303   landscape by calculating dissimilarities between projected forest landscapes and those

304   under baseline climate. Analyses were performed by calculating Bray-Curtis dissimilarity

305   (d_{BC}) using species-specific AGB. First, species-specific AGB was averaged at the

306   landtype-level at each timestep among replicates. Dissimilarities were then calculated

307   relative to projections at time *t* as well as according to the harvest scenario under each

308   climate forcing scenario separately. Landtype-level dissimilarities were then area-weight

309   averaged at the forest region level.

310   Dissimilarities between projected and baseline forest landscapes can arise from changes

311   in species-specific abundance (AGB), from changes in species composition *per se*, or

312   from both (Basega 2013). Separating these components helps to identify the empirical

313   patterns underlying changes in species composition (Basega 2013). We therefore

314   decomposed all d_{BC} values into their two additive components i.e., the fraction linked to

315   balanced variation in abundance (d_{BC-bal}) and the one linked to abundance gradients (d_{BC-}

316    $_{gra}$) (Basega 2013). d_{BC-bal} informs about change in species composition or species

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317   turnover whereas d_{BC-gra} is related to change in species abundance. We then assessed

318   trends in these two components according to climate and harvest scenarios in each of the

319   four forest regions. All d_{BC} components were calculated using the *betapart* v1.5.2

320   package (Basega et al. 2020) in R 3.6.2 (R Core Team 2019).
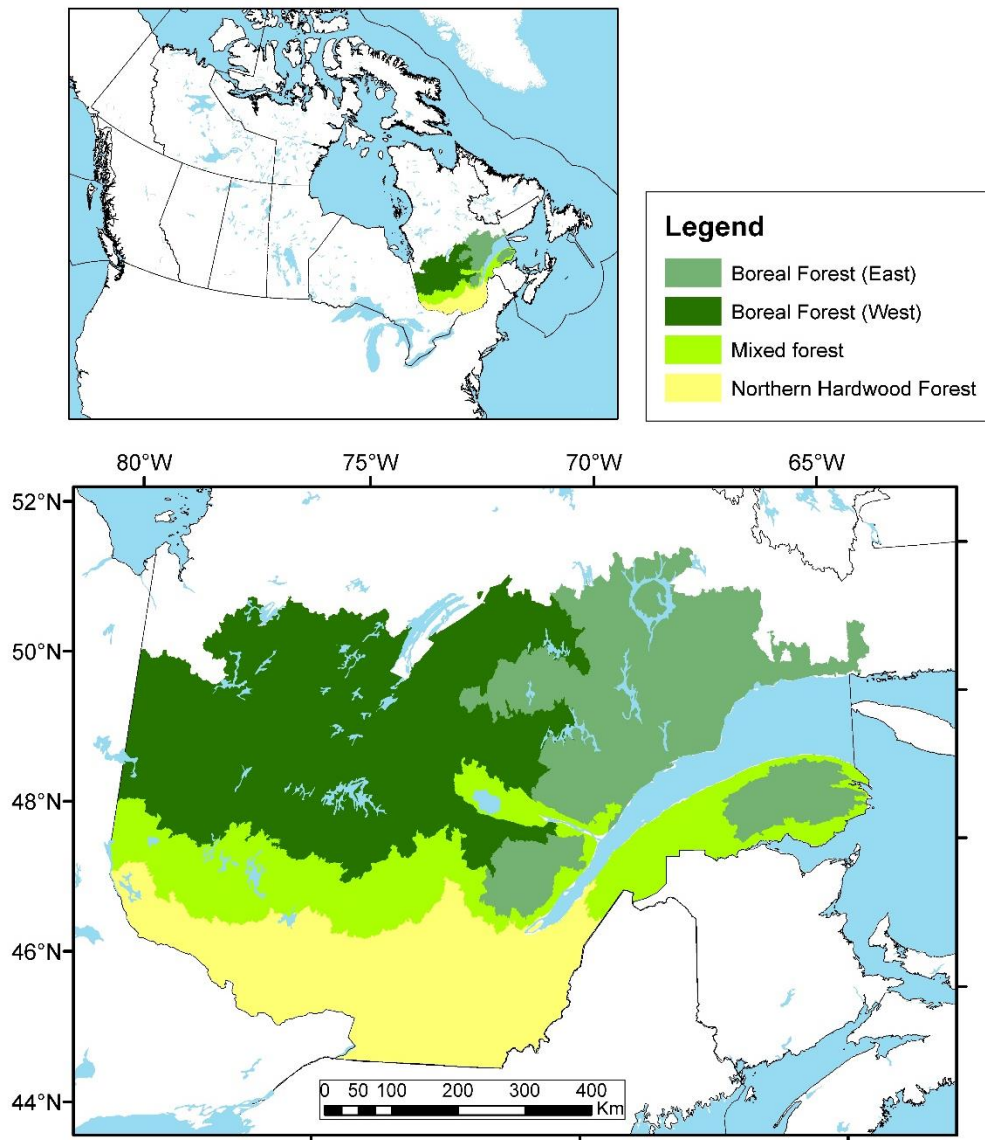
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322   **Figure 1.** Location of the study area as well as the four forest regions considered for

323   analyses.

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325 **Results**

326 **Climate change impacts across forest regions**

327 Generally speaking, dissimilarities were highest for boreal west and appeared sooner in the

328 simulations while being lowest for the northern hardwood throughout the simulated period,

329 regardless of the climate scenarios (Fig. 2). That being said, dissimilarities increased over

330 time and with increasing anthropogenic climate forcing in all regions (Fig. 2, see also

331 Suppl. Mat S4). Dissimilarities under RCP 4.5 and RCP 8.5 strongly diverged in all regions

332 in 2080-2100, showing a sharp increase under RCP 8.5 (Fig. 2).

333 With very few exceptions, dissimilarities with baseline climate forest landscapes were

334 mostly linked to gradients in abundance ($d_{BC\text{-}gra} > 50\%$) before 2100 rather than changes in

335 species composition ($d_{BC\text{-}bal}$) *per se*, regardless of forest regions and simulation scenarios

336 (Figure 3). However, there were important differences in $d_{BC\text{-}bal}$ trends between regions and

337 scenarios. $d_{BC\text{-}bal}$ tended to be higher in the mixedwood and northern hardwood forest

338 regions, especially under RCP 4.5, while being lowest in the boreal west where it never

339 exceeded 30% (Figure 3). In 2150 under RCP 4.5, more than 50% of the dissimilarities

340 were related to $d_{BC\text{-}bal}$ in the northern hardwood and mixedwood forest regions. Under RCP

341 8.5, $d_{BC\text{-}bal}$ never exceeded 50% in 2150 in any regions and was highest in the mixedwood

342 and boreal east (Figure 3). $d_{BC\text{-}bal}$ tended to increase with time in all scenarios except under

343 RCP 8.5 in both mixedwood and northern hardwood regions. In these regions, $d_{BC\text{-}bal}$ first

344 increased up to 2080-2100. From this point, $d_{BC\text{-}bal}$ sharply dropped under RCP 8.5 while

345 it continued to increase under RCP 4.5 (Figure 3).

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346   Dissimilarities linked to gradient in abundance can be associated with the strong climate-

347   induced decline in total AGB throughout the study under RCP 8.5, most notably after 2100

348   (Fig. 4). In boreal west, these declines would occur much sooner, i.e., as soon as 2050

349   under milder (RCP 4.5) anthropogenic climate forcing. Under RCP 8.5, the total decrease

350   in AGB relative to baseline climate was highest in this latter region (-54%) whereas AGB

351   decline in other regions would reach between 35 and 40% by 2150 (Fig. 4). AGB decreases

352   under RCP 4.5 would be much lower in any region. Under this scenario, total AGB in

353   mixedwood and northern hardwood forest regions would decrease by 10 to 15% relative to

354   baseline climate while differences in AGB between RCP 4.5 and the baseline climate

355   would be virtually nil (Fig. 4).

356   In all forest regions, decrease in total AGB is mostly associated with important declines in

357   boreal conifer AGB (Fig. 4, Suppl. Mat S5). These declines were more important with

358   increasing anthropogenic climate forcing and with decreasing latitude. AGB declines were

359   particularly important for white and black spruces regardless of the climate scenarios (Fig.

360   4). More notably, declines in black spruce in boreal west, which is by far the most common

361   species under current conditions in this region, would be dramatic as it would almost

362   completely disappear by 2150 under RCP 8.5 (Suppl. Mat S5). Balsam fir and red spruce

363   would also decline throughout the study area but mostly under RCP 8.5. Throughout the

364   study area, climate-induced decreases in boreal conifer AGB would not be compensated

365   by an increase in thermophilous species biomass which would rather maintain stable

366   biomass relative to baseline climate (Fig. 4). Notable exception includes red maple AGB

367   that would mostly increase under RCP 8.5 especially in the boreal east and mixedwood

368   forest regions (Fig. 4).

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369   As such, higher d_{BC-bal} in southernmost forest regions can be interpreted as gradual species

370   turnovers from boreal to thermophilous species (Fig. 5). Increases in thermophilous

371   proportions were highest in the mixedwood forest region (8 – 25% depending on scenarios

372   with increased forcing) and were likely due to an increase in the proportions of red and

373   sugar maples as well as American beech (Fig. 4). Overall increase in thermophilous

374   proportions were relatively small (< 10%) in both boreal forest regions compared with

375   baseline climate (Fig. 5). In these regions, changes in species composition were mostly

376   related to transition from mid-/late successional species to higher proportions of pioneer

377   species (Fig. 6). Pioneer species proportions strongly increased relative to baseline climate

378   in boreal (+10-50%) but also in mixedwood (+10-25%) forest regions while this increase

379   was much smaller in the northern hardwood region (Fig. 6). Increases were particularly

380   important under RCP 8.5, notably after 2100 and in the boreal west region. Increases in

381   pioneer proportions were mostly resulting from increased in trembling aspen (boreal

382   regions) and red maple (mixedwood) AGB (Fig. 4).

383   **Harvest impacts in the climate change context**

384   Harvest was projected to generate more dissimilarities (higher d_{BC}) between projected

385   forest landscape and those under baseline climate than when it is not included in the

386   simulations, for both the mixedwood and northern hardwood forest regions, regardless of

387   the climate scenario (Figure 2, see also Suppl. Mat S2). Although overall d_{BC} were low,

388   harvest had the most important impacts on dissimilarities in northern hardwoods when

389   compared with scenarios without harvest (Figure 2). As opposed, in both boreal regions,

390   virtually no difference in dissimilarities with baseline climate were projected between

391   scenarios with or without harvest with the exception of boreal west under RCP 4.5.

19

392   Moreover, harvest had little impacts on how climate induced dissimilarities with baseline

393   forest landscapes. Indeed, difference in $d_{BC\text{-}bal}$ values were rather small (Figure 3) with $d_{BC\text{-}bal}$

394   tending to be slightly higher under harvest than under no harvest.

395   Harvest promoted and accelerated the proportion of thermophilous species AGB within the

396   mixedwood forest region regardless of climate scenario, but most notably under RCP 8.5

397   (Fig. 5). In this region, thermophilous species proportions were at least 5 points of

398   percentage higher with harvest than no harvest under RCP 8.5. That being said,

399   thermophilous species also expanded with harvest when compared to simulation without

400   harvest, but at lower rates, under no or milder anthropogenic climate forcing in this forest

401   region. Harvest impacts in this regard were relatively small in other forest regions (+1-2

402   points of percentage). As expected, harvest also promoted pioneer species AGB virtually

403   everywhere (Fig. 6). Impacts were slightly more important under RCP 8.5 than under RCP

404   4.5 in the mixedwood and boreal west forest regions.

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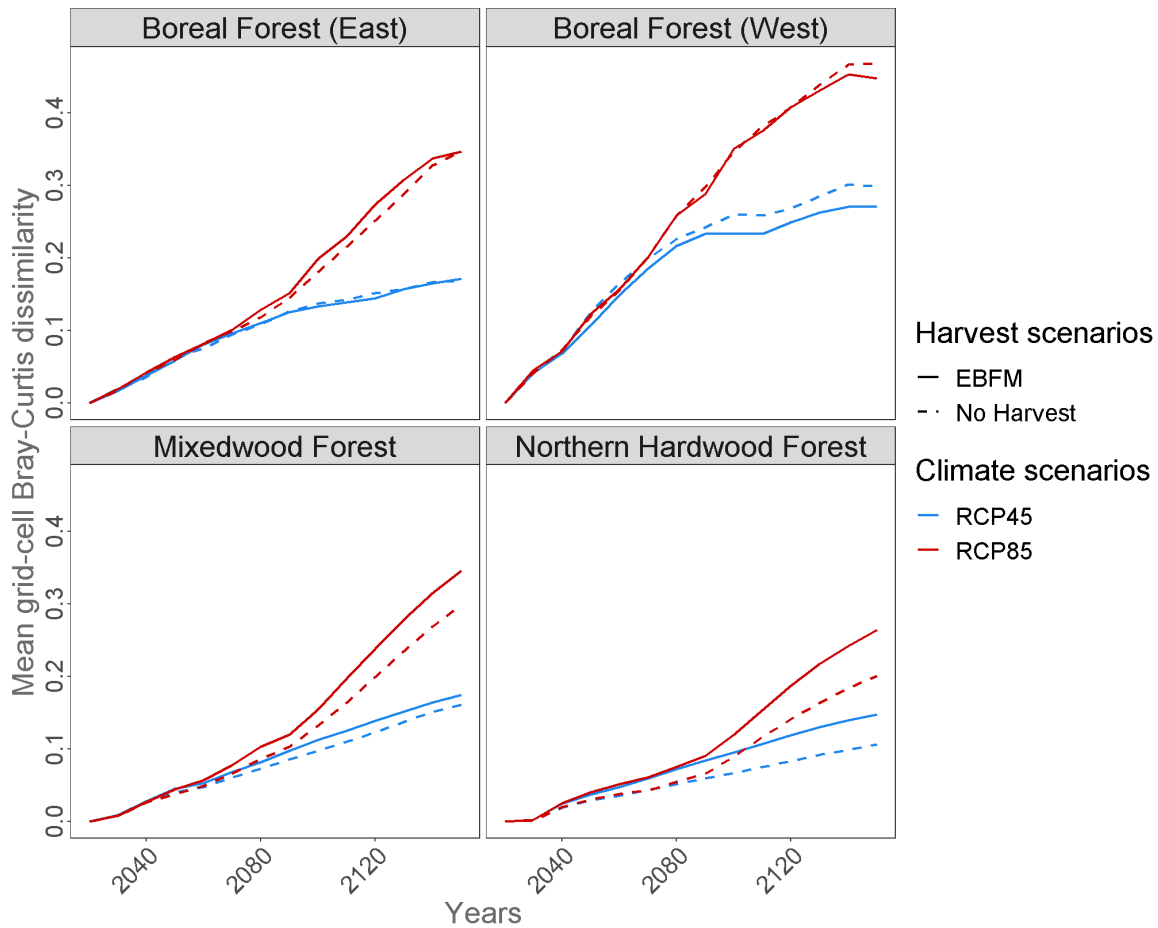
Figure 2. Temporal trends in Bray-Curtis dissimilarities (d_{BC}) under RCP 4.5 and RCP 8.5

and the two harvest scenarios (EBFM = Ecosystem-based forest management; No harvest).

Dissimilarities were calculated against the respective harvest scenario under baseline

climate.

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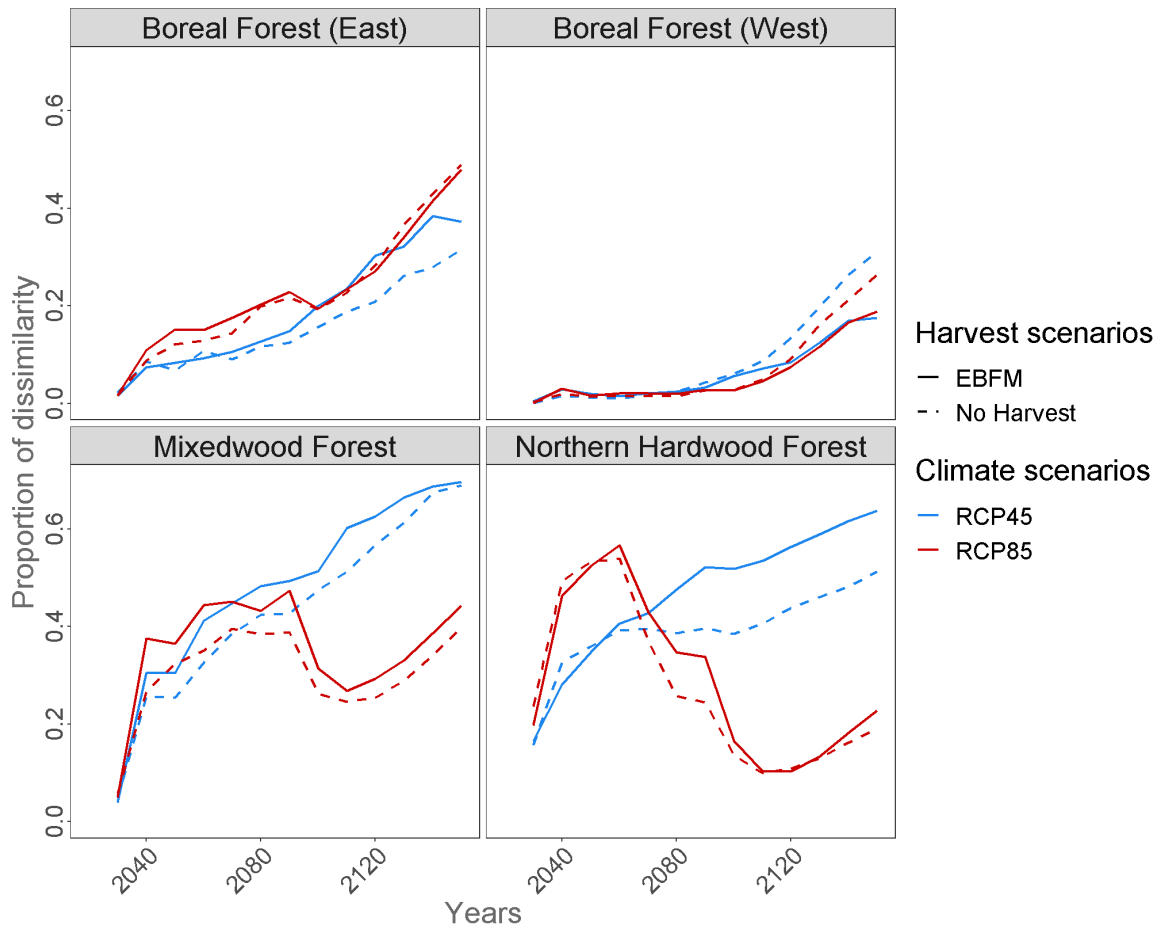
Figure 3. Temporal trends in the proportion of Bray-Curtis dissimilarities shown in figure 2 linked to balanced variation in species abundance ($d_{BC\text{-}bal}$, Baselga 2013). Recall that $d_{BC\text{-}bal}$ is the inverse of the variation in Bray-Curtis dissimilarity linked to abundance gradient, i.e, $d_{BC\text{-}gra} = 1\text{-}d_{BC\text{-}bal}$ under RCP 4.5 and RCP 8.5 and the two harvest scenarios. Results are shown for the two climate and two harvest scenarios separately.

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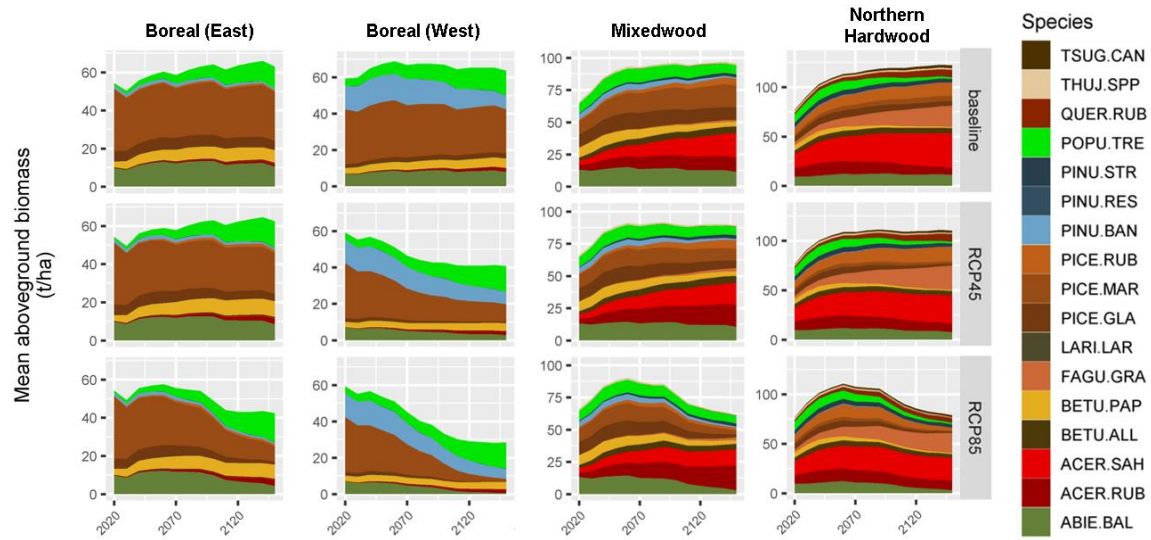
Figure 4. Stacked trends in species AGB for each of the four forest regions simulated under either baseline, RCP 4.5 or RCP 8.5 climate scenarios. See Suppl. Mat. S1 for species abbreviations. Only simulations considering baseline harvest are considered here.

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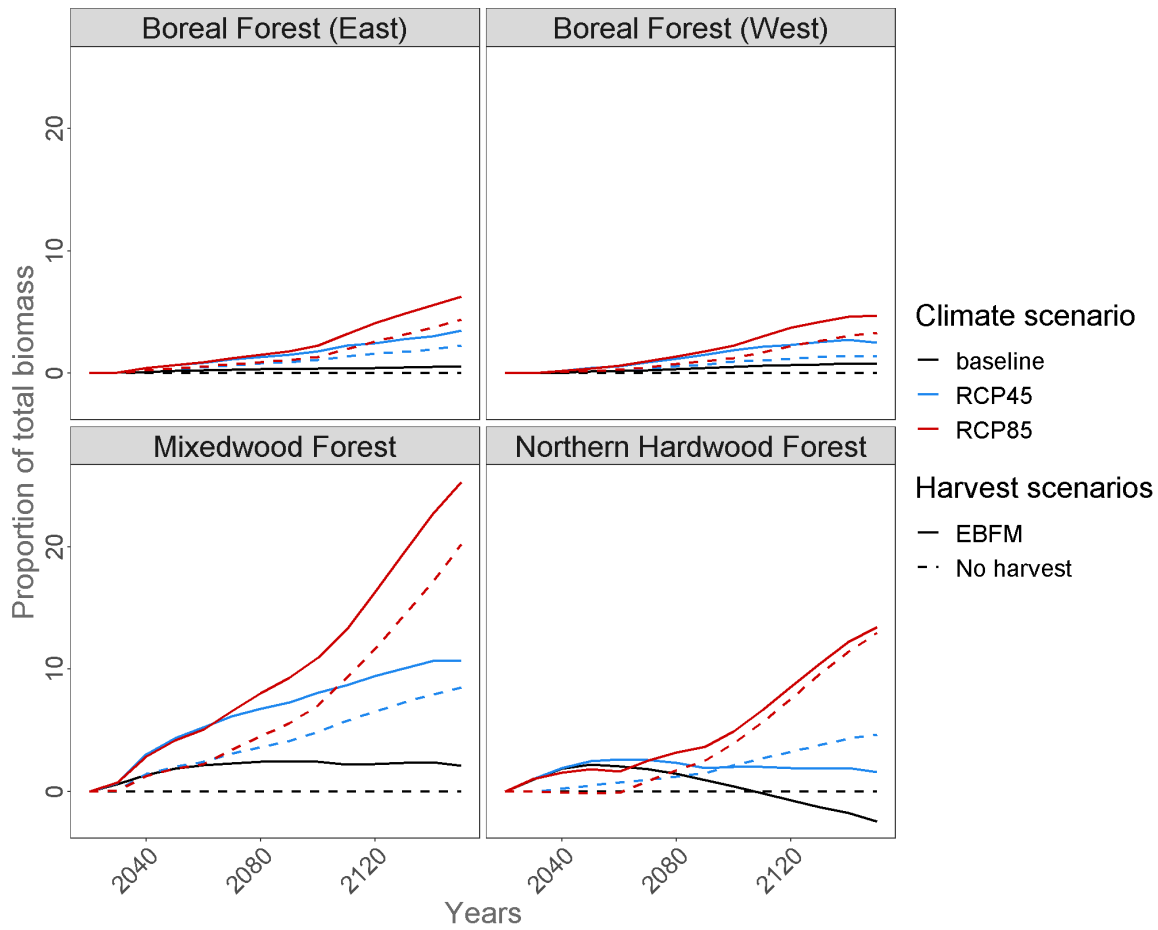
Figure 5. Temporal trends in proportions of thermophilous species (see table 1 for definition) under the three climate and two harvest scenarios. Results are expressed as differences with simulations conducted under baseline climate and no harvest at time *t*.

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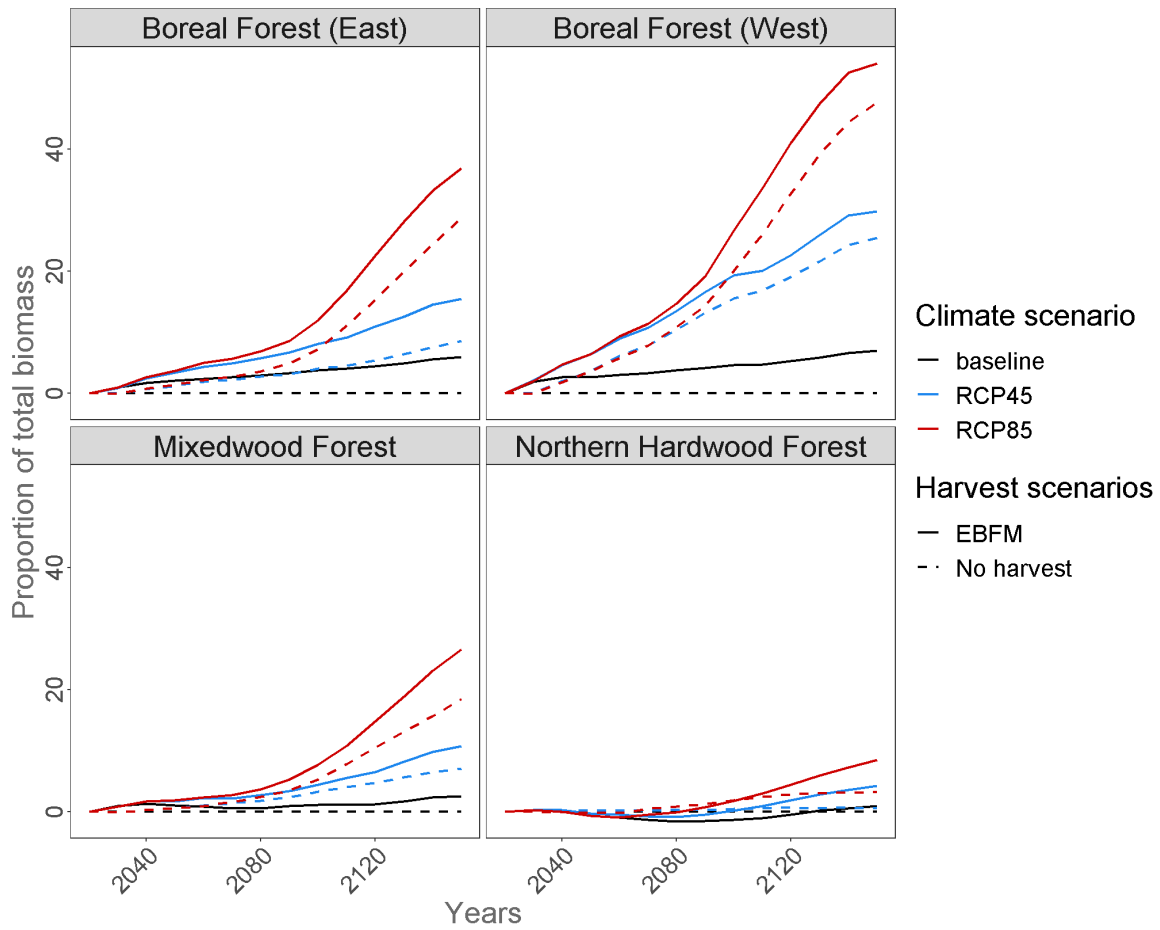
433   **Figure 6.** Same as figure 5 but for pioneer species proportions.

434

435   **Discussion**

436   Our results showed that climate change impacts will be striking in eastern Canada forest

437   regions. Simulated changes were most important within the boreal forest regions, where

438   they mainly translated into very sharp decreases in AGB. Important increase in wildfire

439   activity which could reach >2 % of area burned per year by 2100 under RCP 8.5 (Suppl.

440   Mat. S3) could explain these declines, most notably in boreal west. Increased annual area

441   burned will result in extensive conversion of old-growth boreal-dominated stands into

442   regenerating and young stands, which comprise much lower AGB (Boulanger et al.

443   2016). Very short fire intervals (< 30 years) under RCP 8.5 in boreal west could also

444   extensively preclude the regeneration of non-pyrophilous and late-successional species

445   such as white spruce and balsam fir, further contributing to this decline. Most

446   importantly, such an increase in wildfires could also impede black spruce regeneration by

447   preventing individuals to reach sexual maturity. Overall, such declines might cause large

448   areas in eastern Canada's boreal forests to experience "regeneration failures" which

449   would further decrease the long-term ability of the boreal forest to accumulate AGB

450   (Gauthier et al. 2015; Splawinski et al. 2019). This result is particularly dramatic as it

451   could lead to the widespread extirpation (Suppl. Mat. S5) of black spruce, the Canada's

452   boreal flagship species, in boreal west. As a corollary, increased disturbance rates under

453   more important climate forcing will favour pioneer species, most notably trembling

454   aspen, which were projected to mostly expand in boreal regions. Aspen was shown to

455   increase with more frequent anthropogenic disturbances, including fires, within the last

456   200 years in eastern Canada's boreal forest (Danneyrolles et al. 2016) and is also

26

457   projected to strongly increase with climate-induced changes throughout the boreal forest

458   (Boulanger et al. 2016, 2017; Brecka et al. 2020).

459   Increased natural disturbance rates within the boreal forest regions likely cumulated with

460   climate-induced growth constraints to most boreal species to further reduce total AGB.

461   Strong warming, especially under RCP 8.5, will gradually reduce the potential

462   productivity of several boreal species throughout eastern Canada, except in the

463   northernmost and most elevated lands (Suppl. Mat S2), as species will experience

464   conditions further from their optimal climate tolerance. Similar declines in productivity

465   have also been projected for boreal species within most of their range under aggressive

466   climate forcing (Girardin et al. 2016; D'Orangeville et al. 2019), primarily as a result of

467   increased metabolic respiration following more frequent and severe drought conditions

468   (Girardin et al. 2016). Lack of propagules of warm-adapted species within most of the

469   boreal range impeded potential AGB recovery from boreal conifer decline. In fact,

470   thermophilous species migration towards more northern, suitable conditions will be

471   strongly outpaced by the northward shift of the isotherms even under moderate forcing

472   (Brice et al. 2019; Prasad et al. 2020). Considering their limited dispersal abilities, we

473   projected that thermophilous species would colonize sites only few tens of km north of

474   their actual northern range (Suppl. Mat S5), although suitable conditions would expand

475   much further north under increased climate forcing (Suppl. Mat S2). Additionally, some

476   thermophilous species (e.g., sugar maple) might face important growth constraints,

477   presumably drought-induced (Taylor et al. 2017) even north of their current range under

478   aggressive climate forcing (Suppl. Mat S2), compromising their potential expansion

479   within the boreal forest. Notwithstanding the increased disturbance rates, thermophilous

27

480 species are therefore less likely to extensively compensate AGB losses by boreal species

481 by introducing a significant "migration lag" within the boreal forest (Taylor et al. 2017;

482 Prasad et al. 2020).

483 In the more southern mixedwood and northern hardwood regions, changes will be less

484 important than within boreal regions and will further result from alteration in species

485 composition. Thermophilous species proportions within those two forest regions will

486 strongly increase at the expanse boreal species. Climate-induced changes in growth

487 directly altered the competitive abilities of boreal species, making these more likely to be

488 outperformed by co-occurring thermophilous species (Fisichelli et al. 2014; Reich et al.

489 2015; Boulanger et al. 2016). As opposed to boreal forest regions, this co-occurrence

490 allows thermophilous species to partially compensate the decline in boreal species AGB

491 in the mixedwood and northern hardwood. Notably, reduced climate-induced recruitment

492 for balsam fir following SBW outbreaks could have allowed for co-occurring hardwood

493 species turnover, leading to permanent thermophilization of the ecotone (Brice et al.

494 2019, 2020). Combined with the boreal migration lag mentioned above, this suggests that

495 the mixedwood forest region might strongly contract in the upcoming decades, making

496 the ecotone between the northern hardwood and boreal forest much more abrupt.

497 Our results suggested that the boreal forest regions will be much less resilient than

498 northern hardwoods to the projected changes in climate regimes. The boreal forest is

499 known to have been particularly resilient to variations in climate and disturbance regimes

500 during the last several millennia (Carcaillet et al. 2010). Indeed, stand-replacing

501 disturbances (e.g., fires) that are mostly occurring within the boreal forests were

502 hypothesized to promote resilience by favoring the recovery of resident species (Liang et

28

503   al. 2018). However, projected disturbance rates in the boreal forest will likely fell outside

504   the range of natural variability, triggering potential important ecosystem shifts (Bergeron

505   et al. 2006). Cumulative impacts of wildfires and productivity decline within boreal west

506   could result in alternative stable states (Stralberg et al. 2018) toward landscapes more

507   reminiscent of open parklands or taiga (Girard et al. 2007). Therefore, this extensive

508   disturbance- and climate-induced biome shift projected for the next century would be

509   unprecedented since the last glaciation in this area. Similar transitions from boreal forest

510   to open parklands or prairie ecosystems is also projected for several regions in western

511   Canada as a result of increase drought and wildfire activity (Stralberg et al. 2018).

512   Diversified forests were shown to be more resilient under increased anthropogenic

513   climate forcing (Duveneck et al. 2014; Mina et al. 2020). Higher species diversity along

514   with diversified functional traits and low projected disturbance rates will help northern

515   hardwood forest landscapes being more resilient to climate-induced changes although

516   species turnover will likely occur.

517

518   Our analyses showed that current harvest strategies will strongly decrease forest inertia

519   and will interact with anthropogenic climate forcing to further modify forest landscapes

520   notably in the southernmost forest regions. In the mixedwood forest region for instance,

521   harvest will accelerate climate-induced changes by hastening the increase in

522   thermophilous species AGB, promoting a more rapid biome shift toward communities

523   more typical of the northern hardwoods than under no harvest. Increased disturbance

524   rates are known to catalyze changes toward more adapted species (Thom et al. 2017). We

525   showed that harvest will favour opportunistic species such as red maple, a species known

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526   as a "supergeneralist" for which historical harvest already contributed to its swift

527   expansion throughout northeastern North America (Danneyrolles et al. 2016), notably by

528   interacting with climate change (Brice et al. 2020). Harvest strategies likely played a role

529   to affect forest inertia differently between forest regions. Frequent and widespread partial

530   cutting (typically removing ~25-40% of total biomass over > 3% of the territory per year)

531   in the mixedwood and northern hardwood, as oppose to relatively infrequent but severe

532   clearcuts (removing 90-100% of the biomass over < 1% of the territory per year) in the

533   boreal forests, potentially affected forest inertia more severely over a large portion of the

534   territory, hence accelerating species turnover in these southern regions. Moderate

535   disturbances as these harvest strategies were shown to strongly decrease forest inertia and

536   favor species turnover by promoting hardwood species recruitment and growth at the

537   temperate-boreal ecotone (Brice et al. 2019, 2020). As after natural disturbances that

538   these harvest management strategies are emulating, climate-induced growth constraints

539   on boreal species make them less likely to recolonize small gaps in areas where they co-

540   occur with thermophilous species (Leithead et al. 2010). Furthermore, natural

541   disturbances are projected to remain stable and/or infrequent (wildfires, windthrow) or

542   even to decrease (SBW outbreaks) in the mixedwood and northern hardwood (Boulanger

543   et al. 2014, 2016). This makes harvest more likely to alter forest inertia in these regions

544   than within the two boreal forest regions, especially boreal west, where climate impacts

545   on disturbance rates will overwhelm those generated by harvest even in the short term.

546   The forest sector is currently one of the most important industry in eastern Canada,

547   representing $11.5 MM, i.e., 4.4% of Quebec's GDP in 2006 (MFFP 2016). Alterations

548   in biomass, age structure and species composition resulting from changes in natural

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549   disturbances and climate-induced growth constraints would likely reduce timber supply

550   (Gauthier et al. 2015; Daniel et al. 2017; Boucher et al. 2019; Brecka et al. 2020) which

551   would greatly affect supply value chains (Yemshanov et al. 2018). A posteriori analyses

552   showed that strong anthropogenic climate forcing will reduce harvested biomass by as

553   much as 40% by 2150 (Suppl. Mat. S6). Furthermore, concurrent with the overall decline

554   in harvested biomass, strong compositional shifts towards deciduous species in the

555   mixedwood could have serious economic implications as conifers are generally preferred

556   by the industry. The type and quality of wood products that companies can manufacture

557   (Brecka et al. 2020) could thus be seriously affected. In this context, increased costs,

558   timber supply shortages and important impacts on the supply value chains are to be

559   expected throughout the study area, with a potential collapse of timber harvest in some

560   regions (McKenney et al. 2016, Brecka et al. 2020). Major changes to harvest practices

561   that consider projected wildfire activities and changes in productivity (Irulappa Pillai

562   Vijayakumar et al. 2016; Boulanger et al. 2017) are thus strongly needed to preserve the

563   long-term sustainability of wood supply in eastern Canada. Adaptation strategies should

564   be region-specific as we showed that climate change will affect forest landscapes

565   differently throughout the study area. Reducing long-term harvest targets by lengthening

566   rotation periods could ensure steady, sustainable timber supplies by maintaining a stock

567   of timber that could buffer the effects of wildfire activity (Raulier et al. 2014; Brecka et

568   al. 2020). Furthermore, harvest strategies fostering natural transition to thermophilous

569   species in the mixedwood forest region could be favored (Pedlar et al. 2012;). In

570   combination with e.g., assisted migration, these strategies would help compensate

571   biomass loss in regions where boreal species growth will be strongly constrained.

31

572   Eastern Canada forest ecosystems might cross important tipping points leading to

573   significant changes under strong anthropogenic climate forcing. We showed that climate-

574   induced impacts were much more important and swifter under RCP 8.5, with great

575   divergence with baseline-climate forest landscapes occurring after 2080 throughout the

576   study area. We showed that significant forest landscape alterations, notably total AGB

577   declines, might be prevented under RCP 4.5 for most of eastern Canada (except boreal

578   west), presumably causing minimal impacts on ecosystem services. This should call for

579   strong mitigation measures in order to maintain anthropogenic climate forcing to lower

580   values than those expected by the end of the century under business-as-usual global

581   strategies (Hausfather and Peter 2020).

582   **Acknowledgements**

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Supplementary Material S1 – LANDIS-II and PICUS parameters

Table S1. LANDIS-II input data for tree species simulated within the study area.

Species	Species code	Longevity	Age at maturity	Shade tolerance†	Effective seed dispersal (m)‡	Maximum seed dispersal (m)	Vegetative regeneration	Post-fire regeneration	Growth curve shape parameter	Mortality curve shape parameter	Thermal preference*	Successional stage**
Abies balsamea	ABIE.BAL	150	30	5	25	160	No	Seeding	0	25	boreal	M/L- succ.
Acer rubrum	ACER.RUB	150	10	3	100	200	Yes	Resprout	0	25	Therm.	Pioneer
Acer saccharum	ACER.SAH	300	40	5	100	200	Yes	Resprout	1	15	Therm.	M/L- succ.
Betula alleghaniensis	BETU.ALL	300	40	3	100	400	Yes	Resprout	1	15	Therm.	M/L- succ.
Betula papyrifera	BETU.PAP	150	20	2	200	5000	Yes	Resprout	0	25	boreal	Pioneer
Fagus grandifolia	FAGU.GRA	250	40	5	30	3000	Yes	Seeding	1	15	Therm.	M/L- succ.
Larix laricina	LARI.LAR	150	40	1	50	200	No	Seeding	0	25	boreal	Pioneer
Picea glauca	PICE.GLA	200	30	3	100	303	No	Seeding	1	15	boreal	M/L- succ.
Picea mariana	PICE.MAR	200	30	4	80	200	No	Serotiny	1	15	boreal	M/L- succ.
Picea rubens	PICE.RUB	300	30	4	100	303	No	Seeding	1	15	boreal	M/L- succ.
Pinus banksiana	PINU.BAN	150	20	1	30	100	No	Serotiny	0	25	boreal	Pioneer
Pinus resinosa	PINU.RES	200	40	2	12	275	No	Seeding	1	15	boreal	Pioneer
Pinus strobus	PINU.STR	300	20	3	100	250	No	Seeding	1	15	Therm.	M/L- succ.
Populus tremuloides	POPU.TRE	150	20	1	1000	5000	Yes	Resprout	0	25	boreal	Pioneer

Quercus rubra	QUER.RUB	250	30	3	30	3000	Yes	Resprout	1	15	Therm.	M/L- succ.
Thuja occidentalis	THUJ.OCC	300	30	5	45	60	No	Seeding	1	15	boreal	M/L- succ.
Tsuga canadensis	TSUG.CAN	300	60	5	30	100	No	Seeding	1	15	Therm.	M/L- succ.

* Thermophilous (Therm.): minGDD $\geq$ 500 AND maxGDD $\geq$ 4000 (see table S2). All other species were considered boreal

** Pioneer: Shade tolerance $\leq$ 2 and Longevity $\leq$ 200 years. All other species were considered mid- to late-successional (M/L – succ.)

† Index of the ability of species to establish under varying light levels where 1 is the least shade tolerant and 5 is the most shade tolerant.

‡Distance within which 95 % of seeds disperse.

Table S2. Select input parameters specific to PICUS for species simulated within the study area.

Species	Soil nitrogen*	Minimum soil pH†	Maximum soil pH†	Minimum GDD (Base temp 5°C) ‡	Maximum GDD (Base temp 5°C) ‡	Maximum SMI§	Optimum SMI§
ABIE.BAL	2	2	9	150	2723	0.3	0
ACER.RUB	2	2	9.5	500	6608	0.5	0.05
ACER.SAH	2	1.7	9.9	450	5093	0.3	0
BETU.ALL	2	2	10	500	4517	0.5	0.05
BETU.PAP	2	2.2	9.4	150	3081	0.5	0.05
FAGU.GRA	2	2.1	9	500	5602	0.7	0.1
LARI.LAR	1	3	9.6	150	2548	0.3	0
PICE.GLA	3	2	10.2	150	2495	0.5	0.05
PICE.MAR	2	2	8.5	150	2495	0.3	0
PICE.RUB	2	2	7.8	450	3239	0.3	0
PINU.BAN	1	2.5	10.2	300	3188	0.7	0.1
PINU.RES	1	2.5	8	500	3300	0.7	0.1
PINU.STR	2	2	9.3	500	4261	0.7	0.1

QUER.RUB	2	2.3	11	150	3024	0.5	0.05
POPU.TRE	2	2.3	11	150	3024	0.5	0.05
THUJ.OCC	2	3	10	500	3383	0.7	0.1
TSUG.CAN	2	2.2	9	500	4660	0.5	0.05

* Nitrogen response curves: Three classes (1-3) with 1 being very tolerant

† USDA plant fact sheets (USDA, 2016) and the Ontario Silvics Manual (OMNR, 2000) were used to derive the widest optimum pH range possible.

‡ Growing Degree Days (GDD). We used McKenney et al. (2011) growing season model, specifically the minimum GDD for the 0°C and growing season window with degree days over 5°C. For the maximum GDD, we used GDD Maximum from McKenney's previous growing season model (McKenney et al. 2007).

§ Soil Moisture Index (SMI). Determines each species tolerance to drought (see Lexer and Honninger pg. 52). HighTolerance (0.1 to 0.7), MedTolerance (0.05 to 0.5), LowTolerance (0 to 0.3).

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Supplementary Material S2. Maps showing for each tree species the difference in landtype-level *maxAGB* (tons per ha) as assessed from PICUS under A) RCP 4.5 or B) RCP 8.5 for the 2071-2100 period with the one simulated under historical climate. Forest regions are outlined in black. *maxAGB* was one of the dynamic inputs used in the Biomass Succession extension in LANDIS-II. We only show *maxAGB* since other dynamic inputs (*SEP* and *maxANPP*) were highly correlated to *maxAGB* (data not shown). See the Material and Methods section for details regarding the calculation of *maxAGB*.
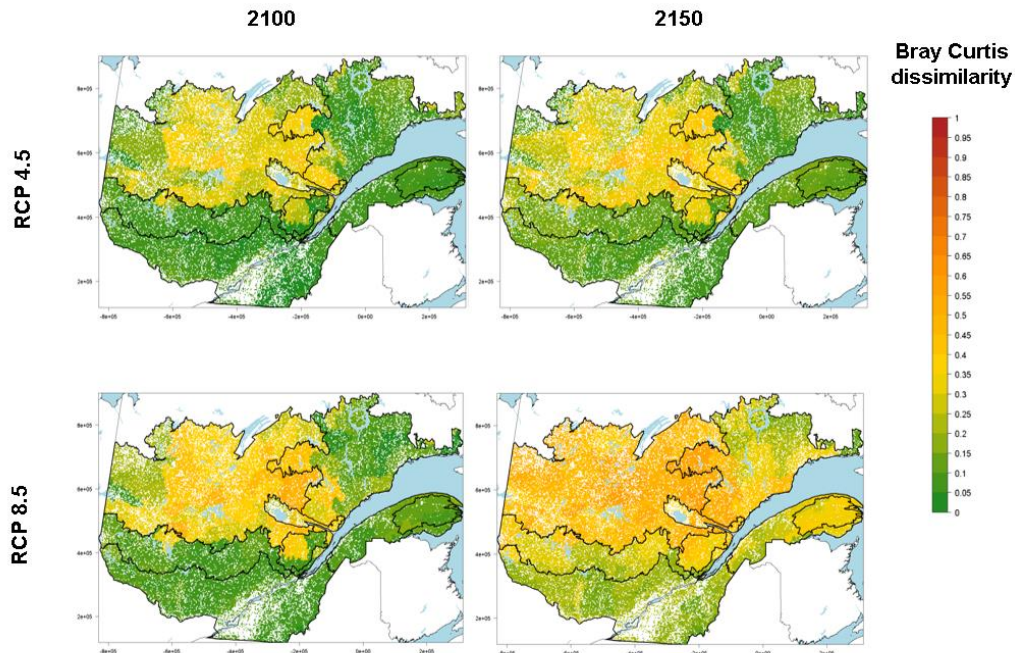
A) RCP 4.5

48
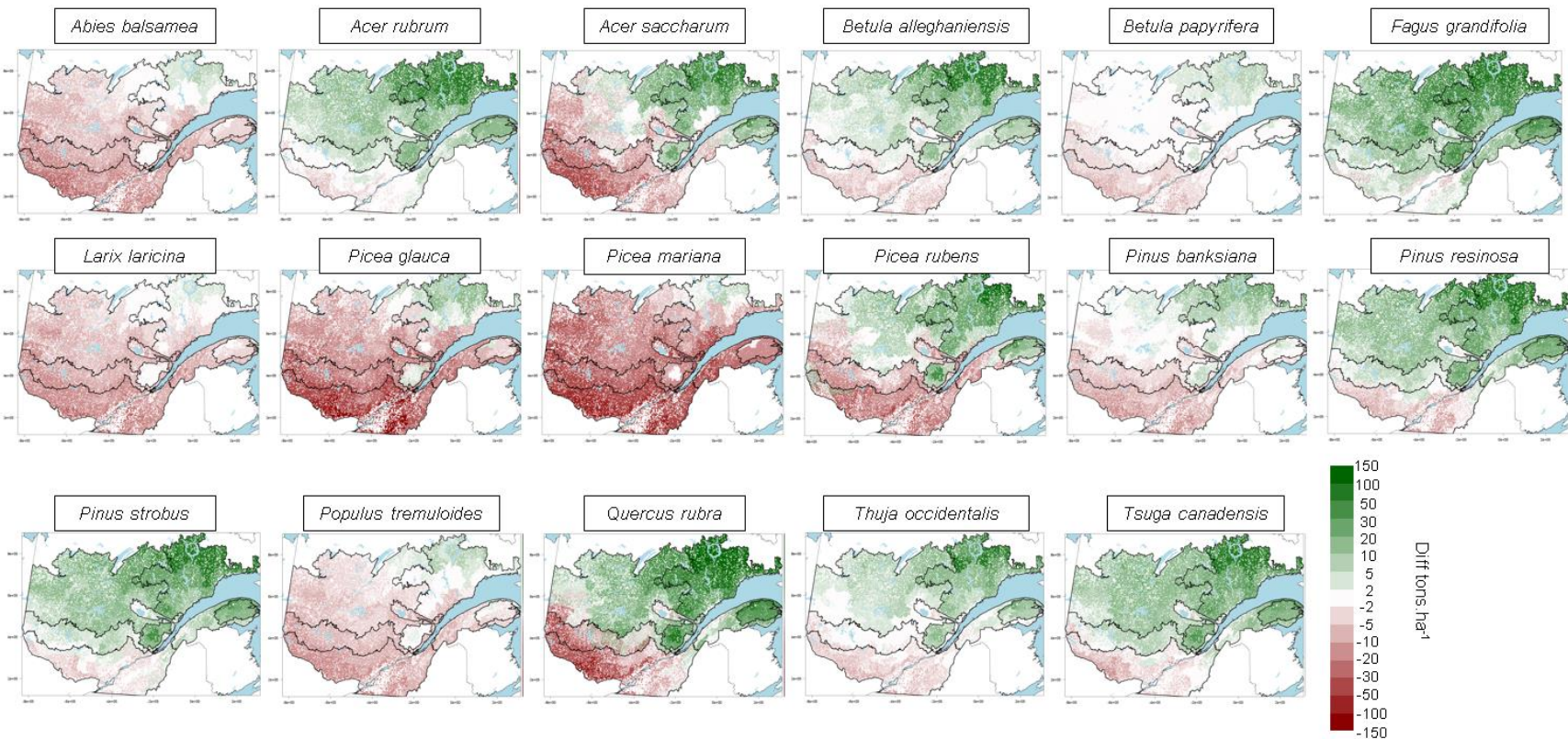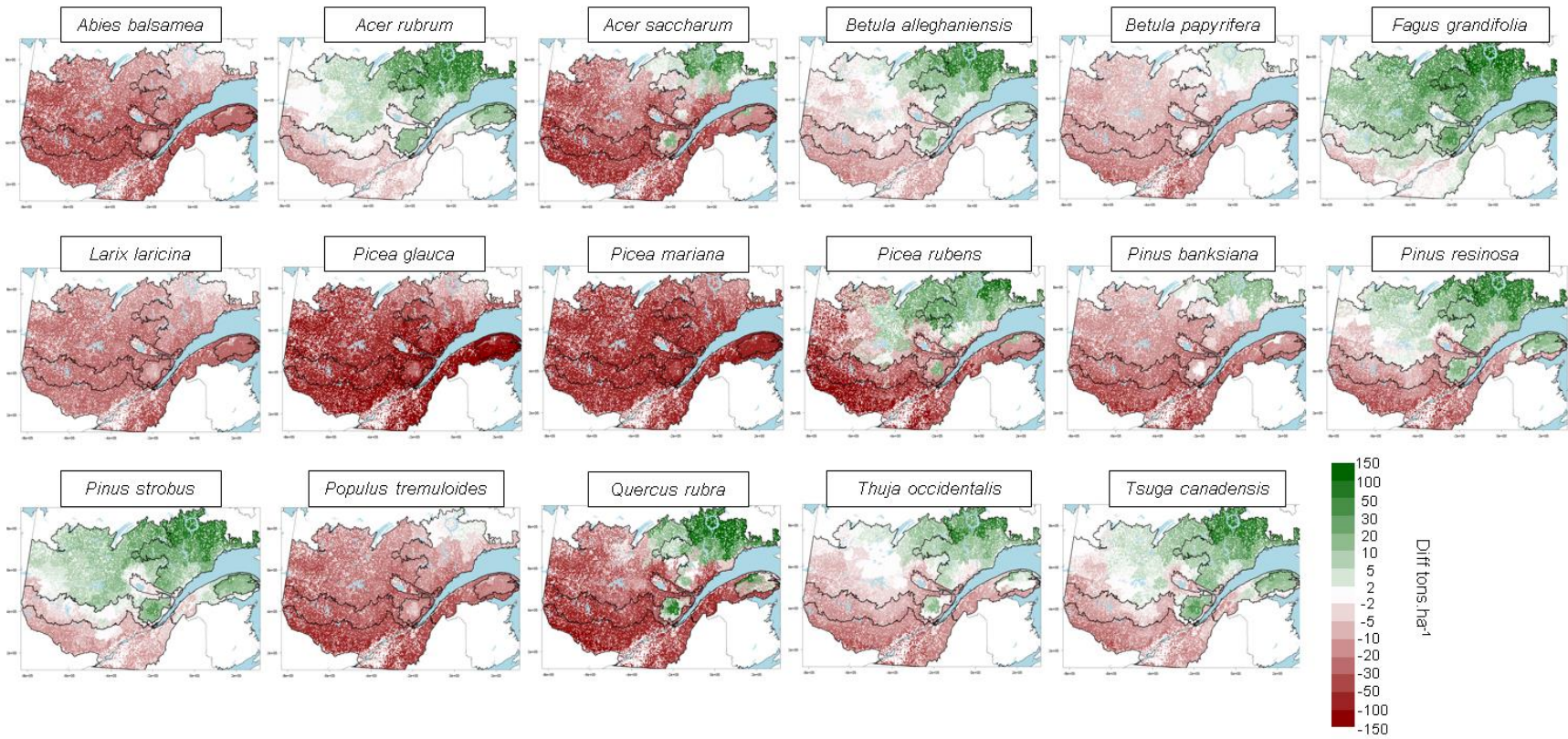
B) RCP 8.5

Supplementary Material S3. Annual area burned (%) simulated within each of the four forest regions under baseline, RCP 4.5 and RCP 8.5 climate respectively. Values are only showed for simulations including EBFM harvest and are averaged across the five replicates
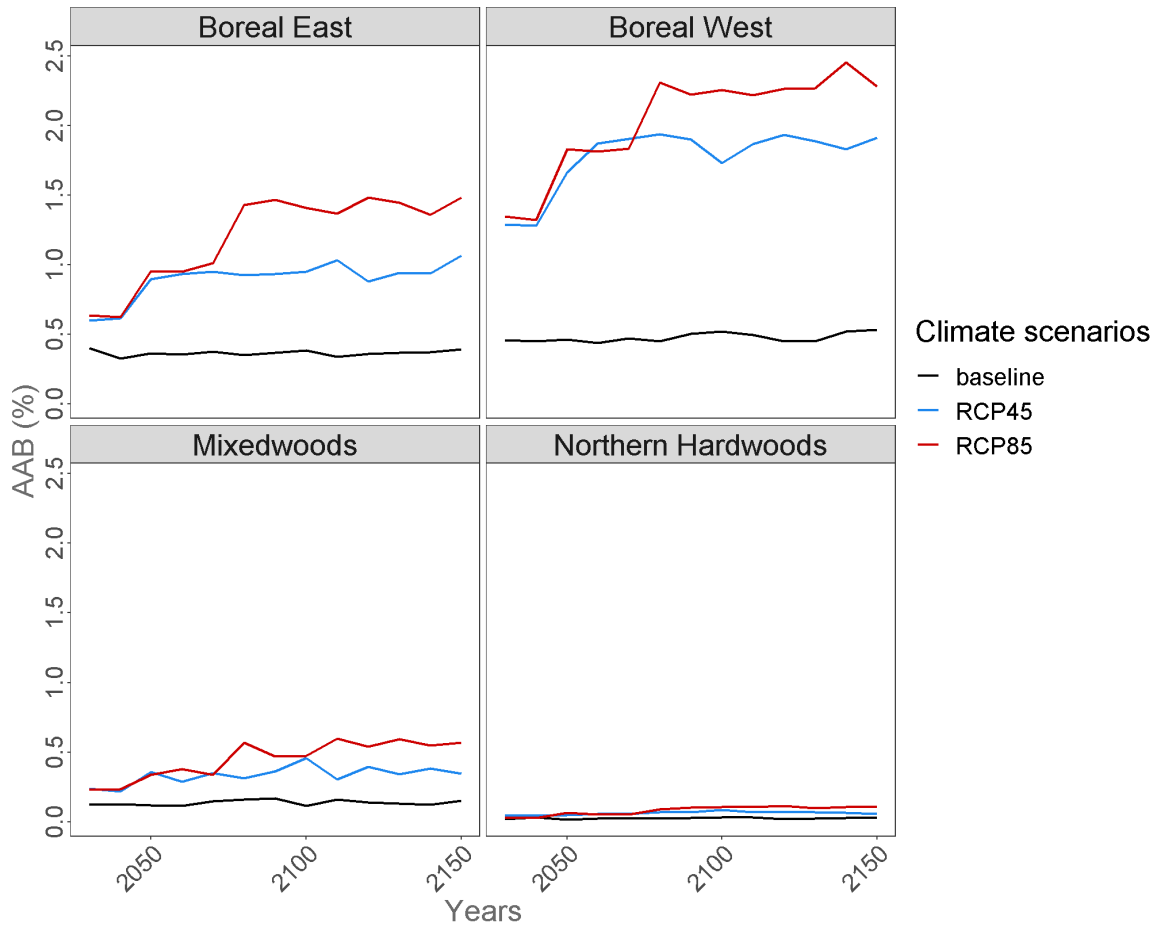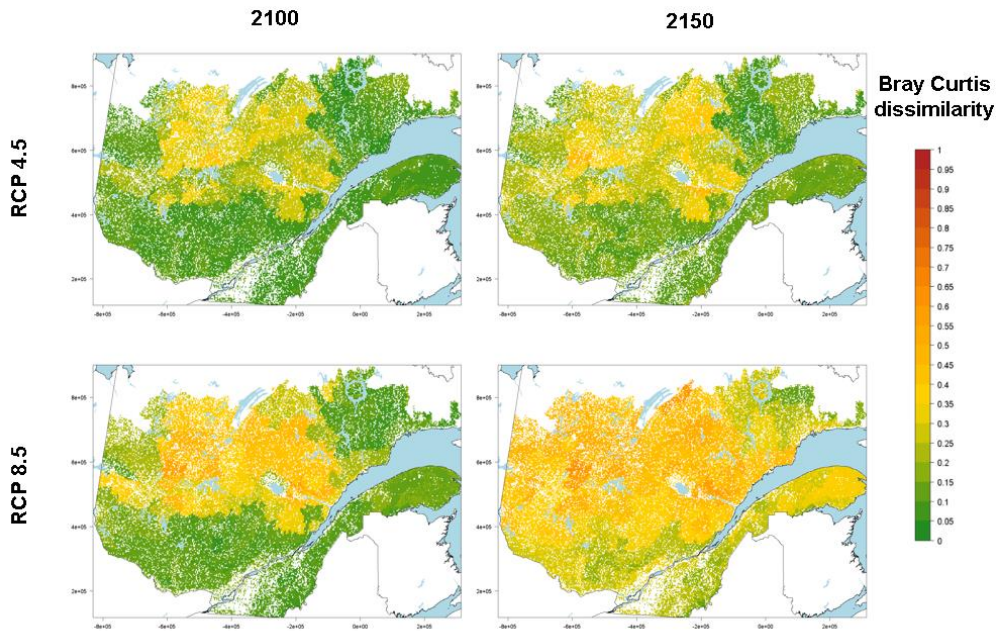
Supplementary Material S4. Maps showing Bray-Curtis dissimilarity at the landtype scale. Results are shown at years 2100 and 2150 for simulations ran under the RCP 4.5 and RCP 8.5 climate forcing separately. Forest regions are outlines in black.

A) Simulations without harvest

B) Simulations with harvest

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Supplementary Material S5. Maps showing for each tree species the difference in AGB (tons per ha) under A) RCP 4.5 or B) RCP 8.5 in 2150 with the one simulated under historical climate in 2150. We also show pixels where species either colonized (blue) or were extirpated (pink). To be extirpated, a species AGB in 2020 must be higher than its 1st percentile (as calculated from the 2020 maps) and drop to nil in 2150. For a pixel to be colonized, the species must be absent (AGB = 0) in 2020 and must be higher than its 1st percentile (as calculated from the 2020 maps) in 2150. We are only showing results where EBFM harvest was included. Forest regions are outlined in black.

A) RCP 4.5
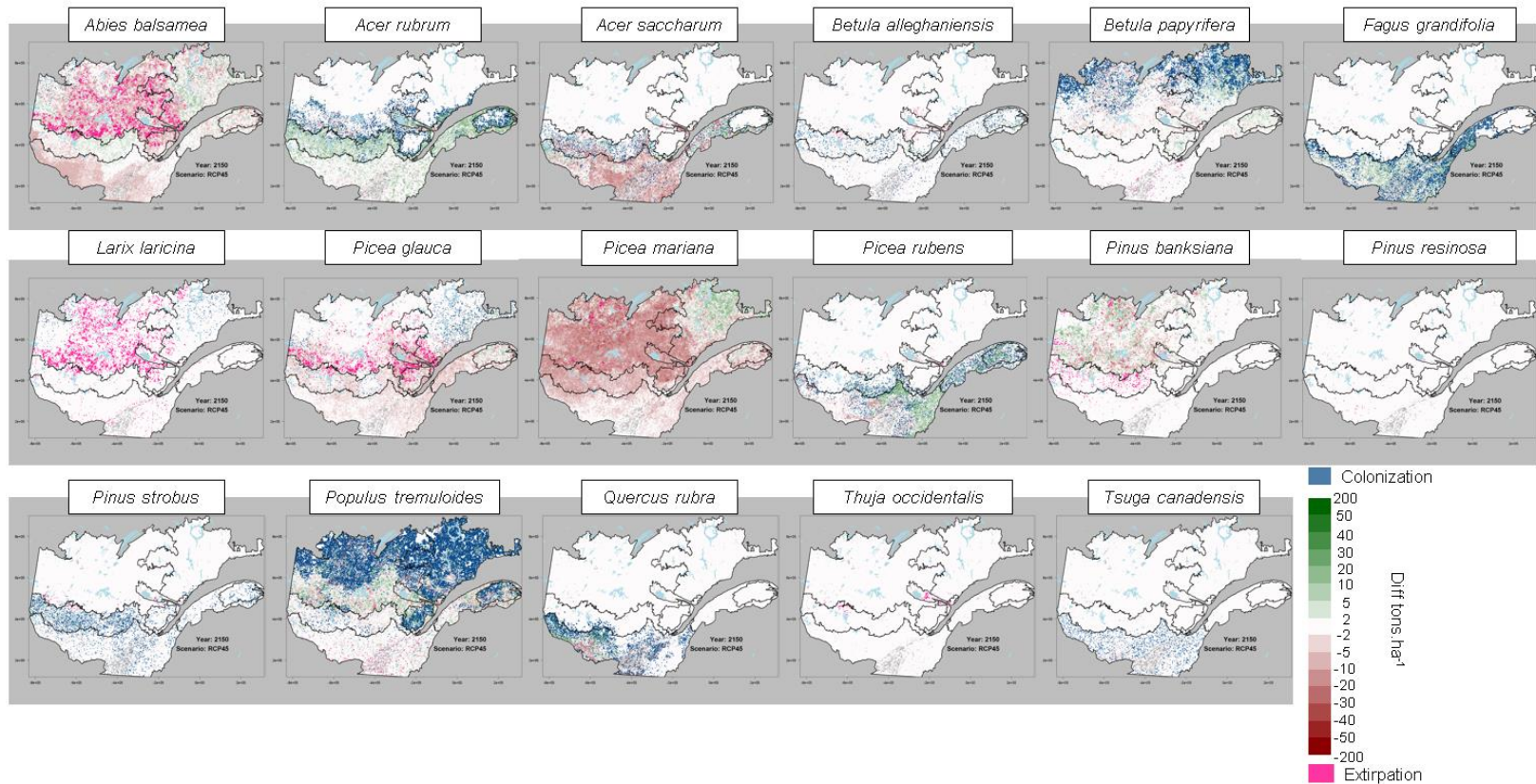
B) RCP 8.5
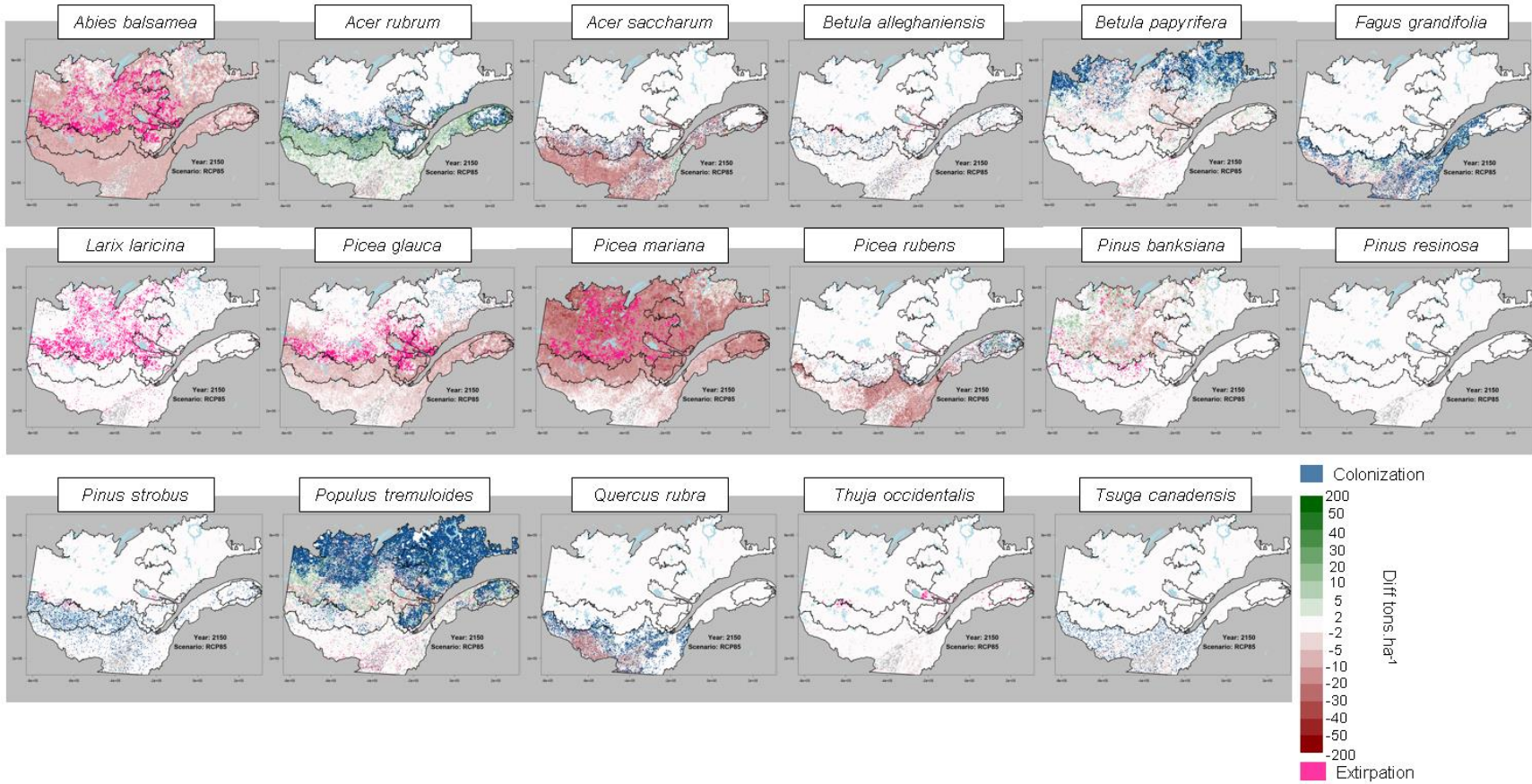
Supplementary Material S6. Temporal trends in AGB harvested under the three climate and two harvest scenarios. Results are expressed as differences (%) with AGB harvested at time *t* under baseline climate.