

<sup>1</sup> Disturbances amplify tree community responses to climate change  
<sup>2</sup> in the temperate-boreal ecotone

<sup>3</sup>

<sup>4</sup> **Running title:** Tree community responses to climate change

## <sup>5</sup> **Abstract**

<sup>6</sup> **Aim** Climate change causes major shifts in species distributions, reshuffling community composition and  
<sup>7</sup> favoring warm-adapted species (“thermophilization”). Tree community response is likely to be affected by  
<sup>8</sup> major disturbances such as fire and harvest. Here, we quantify the relative contributions of climate change  
<sup>9</sup> and disturbances to temporal shifts in tree composition over the last decades and evaluate whether  
<sup>10</sup> disturbances accelerate community thermophilization.

<sup>11</sup> **Location** Québec, Canada

<sup>12</sup> **Time period** 1970–2016

<sup>13</sup> **Taxa studied** Trees

<sup>14</sup> **Methods** Using 6281 forest inventory plots, we quantified temporal changes in species composition  
<sup>15</sup> between a historical (1970–1980) and a contemporary period (2000–2016) by measuring temporal  $\beta$   
<sup>16</sup> diversity, gains and losses. The effects of climate and disturbances on temporal  $\beta$  diversity were quantified  
<sup>17</sup> using multiple regressions and variation partitioning. We compared how community indices of species  
<sup>18</sup> temperature preference (CTI) and shade tolerance (CSI) changed for forests that experienced different  
<sup>19</sup> levels of disturbance. We quantified the contribution of species gains and losses to change in CTI.

<sup>20</sup> **Results** Temporal  $\beta$  diversity was mainly driven by disturbances, with historical harvesting as the most  
<sup>21</sup> important predictor. Despite the prevailing influence of disturbances, we revealed a significant  
<sup>22</sup> thermophilization ( $\Delta$ CTI = +0.03°C/decade) throughout forests in Québec. However, this shift in  
<sup>23</sup> community composition was weakly explained by climate change and considerably slower than the rate of  
<sup>24</sup> warming (+0.14°C/decade). Importantly, thermophilization was amplified by moderate disturbances  
<sup>25</sup> (+0.044°C/decade), almost a three-fold increase compared to minor disturbances (+0.015°C/decade). The

<sup>26</sup> gains and losses of a few tree species contributed to this community-level shift.

<sup>27</sup> **Conclusions** Our study provides evidence that disturbances can strongly modify tree community  
<sup>28</sup> responses to climate change. Moderate disturbances, such as harvesting, may reduce competition and  
<sup>29</sup> facilitate gains of warm-adapted species, which then accelerate thermophilization of tree communities  
<sup>30</sup> under climate change. Although accelerated by disturbances, community thermophilization was driven by  
<sup>31</sup> the gains and losses of a small number of species, notably gains of maples.

<sup>32</sup> **Keywords**

<sup>33</sup> Beta diversity, Climate change, Community temperature index, Community temporal change,

<sup>34</sup> Disturbances, Forest, Québec, Temperate-boreal ecotone, Thermophilization.

## 35 Introduction

36 Climate warming over the past century has led to distribution shifts in many species (Parmesan & Yohe,  
37 2003). Despite the general trend of poleward and upward (in altitude) range shifts, the timing, magnitude  
38 and even direction of species shifts vary considerably among taxa and regions (VanDerWal *et al.*, 2013).  
39 Major reshuffling of community composition is therefore expected. Yet, we lack an understanding of the  
40 community-level consequences of climate-driven shifts. This knowledge gap is even greater in forests where  
41 tree response is slow (Sittaro *et al.*, 2017) relative to the short duration of typical ecological studies. So far,  
42 much of the emphasis has been placed on detecting species shifts at their range edge, where early signs of  
43 changes are expected to be readily detectable (Jump *et al.*, 2009). As such, there is a growing body of  
44 evidence for contemporary shifts in tree species distributions along altitudinal gradients in mountains  
45 (Beckage *et al.*, 2008; Lenoir *et al.*, 2008; Savage & Vellend, 2015), where ecotones are narrow and  
46 well-defined (Jump *et al.*, 2009). Similar evidence is also beginning to emerge for latitudinal shifts  
47 (Fisichelli *et al.*, 2014; Sittaro *et al.*, 2017; Boisvert-Marsh *et al.*, 2019). Though, because of the focus on  
48 shifts at range limits (e.g., leading and rearing edges of species ranges), there has been little empirical work  
49 on the effect of climate change on tree community composition and abundance distributions within the  
50 core of species range itself (e.g. Esquivel-Muelbert *et al.*, 2018; Searle & Chen, 2017).

51 Worldwide increases in tree mortality rates triggered by drought and heat stresses have been documented  
52 recently (Allen *et al.*, 2010). In the long term, even minor changes in demographic rates can modify the  
53 balance between local species gains and losses, leading to temporal change in community composition. Yet,  
54 as trees are long-lived species, mortality and recruitment rates are low (Iverson & McKenzie, 2013). Thus,  
55 tree community responses to contemporary climate warming are likely to be lagged, resulting in extinction  
56 debts (Svenning & Sandel, 2013; Talluto *et al.*, 2017). Consequently, tree community-level response to  
57 climate change remains difficult to quantify and is probably underestimated.

58 Furthermore, in northern temperate and boreal regions, natural disturbances (fires and insect outbreaks)  
59 and anthropogenic disturbances (timber harvesting) are major drivers of tree community dynamics  
60 (Goldblum & Rigg, 2010). These pulse disturbances are likely to dominate local, short-term biotic changes,  
61 resulting in increased prevalence of young forests dominated by early successional species. These  
62 short-term effects could easily mask climate-induced changes that are expected to occur on much longer  
63 time scales and broader spatial scales. For this reason, disturbances are often considered to be inconvenient  
64 confounding factors instead of an inherent part of contemporary ecosystems. Thus, numerous studies have  
65 searched for trends in relatively undisturbed systems (Parmesan & Yohe, 2003) rather than accounting for  
66 their effects. Yet, disturbances and climate change have a high potential for interactions, which can lead to  
67 synergistic or antagonistic ecological effects that are difficult to predict (Brook *et al.*, 2008). Indeed,  
68 disturbances create canopy openings that could facilitate the northward migration of temperate species  
69 (Leithead *et al.*, 2010; Xu *et al.*, 2012; Vanderwel & Purves, 2014; Boisvert-Marsh *et al.*, 2019). In addition,

70 the frequency and intensity of natural disturbances can increase as an indirect effect of climate change  
71 (Seidl *et al.*, 2017).

72 Although it is widely assumed that positive synergy between disturbances and climate warming should play  
73 a key role in contemporary tree community changes, empirical studies have reached conflicting conclusions.  
74 For example, comparison of early industrial (early 1900) to contemporary forests in the Bas-Saint-Laurent  
75 region of Québec showed that logging practices turned old-aged conifer forests into young mixed and  
76 deciduous forests (Boucher *et al.*, 2006, 2009). Leithead *et al.* (2010) also observed that the establishment  
77 of southern temperate species in the temperate-boreal ecotone of northern Ontario increased with the size  
78 and age of canopy gaps. While Boisvert-Marsh *et al.* (2019) found that climate change outweighs  
79 disturbances in explaining latitudinal shifts of tree saplings in Québec in the last decades, Danneyrolles *et*  
80 *al.* (2019) found larger impacts of anthropogenic disturbances than climate warming on forest  
81 compositional changes in southern Québec over the last centuries. Hence, to anticipate and adapt to future  
82 forest changes, large-scale empirical studies are required in order to unravel individual and aggregated  
83 impacts of multiple stressors on forest composition.

84 Even though disturbances may mask slow community responses to climate change, these two drivers leave  
85 distinguishable signatures on communities. Climate warming should favor warm-adapted species at the  
86 expense of cold-adapted species, leading to a “thermophilization” of communities (De Frenne *et al.*, 2013;  
87 Savage & Vellend, 2015). Conversely, disturbances should increase the prevalence of young forests  
88 dominated by shade-intolerant species (Boucher & Grondin, 2012; Savage & Vellend, 2015). Hence,  
89 analyzing shifts of relevant functional traits **and ecological affinities** in communities using large-scale  
90 monitoring data should disentangle the role of different environmental drivers in shaping communities  
91 (Viole *et al.*, 2007). For instance, the Community Temperature Index (CTI) has been used to measure  
92 thermophilization in various communities, such as plants, trees, birds and fishes (Devictor *et al.*, 2008;  
93 Cheung *et al.*, 2013; De Frenne *et al.*, 2013; Feeley *et al.*, 2013; Gaüzère *et al.*, 2015; Becker-Scarpitta *et al.*,  
94 2019; Danneyrolles *et al.*, 2019). The CTI is a community abundance-weighted average of the Species  
95 Temperature Indices (STI; proxy for species thermal preference computed as the mean temperature of a  
96 given species distribution). Because CTI reflects the relative abundance of warm-adapted (high STI) vs  
97 cold-adapted species (low STI), it is expected to increase following climate warming if species are moving  
98 according to their temperature requirements.

99 Here, we quantify the temporal shifts in tree community composition in the temperate-boreal ecotone, and  
100 test whether recent climate change is impacting forest composition. We analyzed data from a long-term  
101 forest inventory program across meridional Québec, where vegetation ranges from northern hardwood  
102 forests dominated by *Acer saccharum* at low latitudes (up to 47°N) to mixed forests dominated by *Abies*  
103 *balsamea* (from 47°N to 48°N), to boreal forests dominated by *Picea mariana* at high latitudes (from 49°N  
104 to 52°N). This dataset allowed us to compare community responses to recent climate change in plots that

105 experienced different levels of disturbances along a broad latitudinal gradient. We address four questions:  
106 (1) how has the composition of forest communities changed during the last decades across different  
107 bioclimatic domains? (2) What is the relative contribution of climate change and disturbances to these  
108 temporal community changes? (3) Have forest communities experienced a thermophilization during the last  
109 decades? And can disturbances accelerate community thermophilization? (4) How do gains and losses of  
110 specific tree species contribute to thermophilization?

111 Specifically, we measured temporal  $\beta$  diversity (Legendre, 2019) over 6000 resurveyed communities between  
112 a historical (1970–1980) and a contemporary (2000–2016) period. Temporal  $\beta$  diversity, which describes the  
113 temporal dissimilarity in community composition between survey times, was decomposed into gains and  
114 losses to investigate the underlying mechanisms of change. Then, we quantified the effects of climate  
115 change and disturbances on temporal  $\beta$  diversity using multiple regressions and variation partitioning.  
116 Using community indices for temperature (CTI) and shade tolerance (CSI), we quantified community-level  
117 changes associated with thermophilization and succession and compared these changes among levels of  
118 disturbances. We finally quantified the species-specific contributions to thermophilization.

## 119 Methods

### 120 Study area

121 To analyze large-scale temporal changes in forest community composition, we used the Québec forest  
122 inventory plots that have been sampled in six bioclimatic domains, south of the 52<sup>nd</sup> parallel, since 1970 by  
123 the Ministère des forêts, de la Faune et des Parcs (Fig. 1; MFFP, 2016). **For each plot, we compared**  
124 **the tree composition between the first and last surveys. To maximize the time interval**  
125 **between surveys, only plots that were inventoried in two distinct time periods (historical**  
126 **period: 1970–1980; contemporary period: 2000–2016) were retained for analysis.** We  
127 disregarded plots that were subjected to active reforestation during the study period as we were interested  
128 in compositional changes resulting from natural post-disturbance recolonization. We also eliminated plots  
129 without trees (due to a disturbance) either at their first or last year of sampling. This yielded a subset of  
130 6281 plots analyzed (Fig. 1), with a median of 35 years between surveys (1st quartile: 33 and 3rd quartile:  
131 41 years).

132 Within each circular plot (400 m<sup>2</sup>), trees larger than 9 cm in diameter at breast height (DBH) were  
133 identified to species, measured and their vitality noted (MFFP, 2016). **The selected plots included a**  
134 **total of 51 tree species, from which we eliminated introduced and planted species as well as**  
135 **species with a single occurrence, yielding 45 analyzed species (Table S1).** Rare species were  
136 included in the analyses because even the rarest can contribute to temporal changes; their identity does not

137 bias our analyses and, contrary to mobile species, there is little detection bias in tree surveys. **Each**  
138 **species was assigned according to their functional traits to one of three species groups of**  
139 **interest: boreal (6 species), pioneer (9 species) and temperate (30 species; see Table S1 for**  
140 **details).**

141 **Environmental variables**

142 The annual past climatic conditions, covering a period from 1960 to 2013, were extracted using a 2 km<sup>2</sup> (60  
143 arc sec) resolution grid for the entire study area using the ANUSPLIN climate modeling software  
144 (<http://cfs.nrcan.gc.ca/projects/3/8>; McKenney *et al.*, 2011). Bioclimatic variables hypothesized to  
145 influence tree survival were intercepted at plot locations: the mean temperature and total precipitation  
146 during the growing season, minimum temperature of the coldest period, maximum temperature of the  
147 warmest period and the annual climate moisture index (CMI; **difference between annual precipitation**  
148 **and potential evapotranspiration**). From these bioclimatic variables, we derived different predictors  
149 (see Table 1 for details). Over the past four decades, growing season temperature and precipitation have  
150 increased by 0.14 °C/decade and 9.5 mm/decade, respectively, while CMI has decreased by 1.2 cm/decade  
151 (Fig. S1).

152 We also collected information pertaining to natural and anthropogenic disturbances that  
153 have affected the forest plots both before and during the study period (Table 1, Fig. S2). At  
154 each plot, 21 disturbance types and their level of intensity (moderate or major) were  
155 recorded (Table S2; MFFP, 2016). The MFFP defined major disturbances as events that  
156 resulted in a loss of at least 75% of the tree basal area, whereas moderate disturbances have  
157 caused between 25% and 75% of loss. For our regression models, we differentiated two main  
158 types of disturbances: natural disturbances and harvest, with 3 levels of intensity each  
159 (minor, moderate or major) and 2 periods (old: occurred before the first inventory, and  
160 recent: occurred during the study period). To compare diversity measures among  
161 disturbance levels, we also assigned each forest to the level of intensity of the worst  
162 disturbance it experienced (regardless of the type or timing).

163 Core samples were also collected on selected trees during surveys to measure their age. Stand age was  
164 estimated as the mean of these measures to account for forest succession processes after disturbances.  
165 Finally, because the time interval between the first and last measurements varies among the forest plots, it  
166 was included as a predictor.

167 **Analysis**

168  **$\beta$  diversity**

169 For each plot, we computed temporal  $\beta$  diversity (Legendre, 2019), which is the dissimilarity in species  
170 composition between two surveys of a given plot, by comparing local tree abundance (**i.e. number of**  
171 **individuals**) in forest plots between the historical (1970-1980,  $t_1$ ) and contemporary (2000-2016,  $t_2$ )  
172 periods. The dissimilarity ( $\beta$ ) was computed using the Ružička coefficient (**Fig. S3**):

173  $\beta = (B + C)/(A + B + C)$  where, for  $n$  species:

174  $A = \sum_{j=1}^n a_j$  : unscaled similarity.  $a_j$  represents the abundance of species  $j$  that is common between  $t_1$  and  
175  $t_2$ ;

176  $B = \sum_{j=1}^n b_j$  : unscaled species abundance losses.  $b_j$  represents the abundance of species  $j$  present at  $t_1$  but  
177 not at  $t_2$ ; when species  $j$  increases in abundance,  $b_j = 0$ ;

178  $C = \sum_{j=1}^n c_j$  : unscaled species abundance gains.  $c_j$  represents the abundance of species  $j$  present at  $t_2$  but  
179 not at  $t_1$ ; when species  $j$  decreases in abundance,  $c_j = 0$ ;

180 This temporal  $\beta$  diversity varies from 0 (community compositions at  $t_1$  and  $t_2$  are exactly the same) to 1  
181 (communities have no shared species). The use of this dissimilarity index enabled us to decompose the  
182 compositional change into relative gains ( $C/(A + B + C)$ ) and losses ( $B/(A + B + C)$ ) in tree abundances  
183 (**Fig. S3**). Throughout this paper, gains and losses refer to these relative metrics.

184 This additive framework allowed us to partition further the different components contributing to  $\beta$   
185 diversity. Temporal dissimilarity in tree community can be decomposed into the dissimilarity (gains and  
186 losses) of different species groups of interest, here boreal, pioneer and temperate species (Table S1). The  
187 temporal dissimilarity of a given group, for instance boreal, relative to all species is simply:

188  $\beta_{boreal} = (B_{boreal} + C_{boreal})/(A + B + C)$ , with  $(A + B + C)$  the denominator computed over all tree  
189 species. As a consequence,  $\beta$  can be decomposed as follows:

190  $\beta = \beta_{boreal} + \beta_{pioneer} + \beta_{temperate}$

191 **Assessing the relative importance of drivers of community changes**

192 We evaluated the effects of multiple drivers on temporal  $\beta$ , gains and losses using multiple  
193 regressions, in combination with variation partitioning analyses (Borcard *et al.*, 1992;  
194 Peres-Neto *et al.*, 2006). For these analyses, we used a logit transformation  $y' = \log(y/(1 - y))$   
195 of the response variables ( $\beta$ , gains, losses) as they were all in the standard unit range [0, 1].

196 In order to quantify the variation explained by climate change and disturbances, while

197 controlling for the baseline climate gradient and different time intervals, we classified our  
198 predictor variables into three subsets: baseline conditions, climate change and disturbances  
199 (see Table 1). We then generated regression models predicting  $\beta$ , gains and losses, for each of the three  
200 subsets. We also tested relevant interactions between disturbance and climate predictors:  
201 Natural (old and recent)  $\times \Delta\text{CMI}$  and Natural (old and recent)  $\times \Delta\text{Temp}$ , because drought  
202 and heat stress can increase natural disturbance frequency; Harvest (old and recent)  $\times$   
203  $\Delta\text{Temp}$ , because the effect of harvest was hypothesized to be influenced by warmer  
204 temperatures. A forward selection of explanatory variables based on two stopping criteria (significance  
205 level  $\alpha$  and global  $R^2_{adj}$ ; Blanchet *et al.*, 2008) was performed to obtain parsimonious regression models for  
206 each of the three subsets. The predictors had been previously standardized to  $z$ -scores to allow comparison  
207 of their slope coefficients. We also ensured that residuals met the assumptions of normality and  
208 homoscedasticity.  
209 We assessed the unique contributions of each predictor subset (baseline conditions, climate change and  
210 disturbances) as well as their shared effect on forest community changes using variation partitioning  
211 analysis on the parsimonious regression models.

## 212 Functional index of community change

213 To test whether or not climate warming contributed to community changes, we examined the temporal  
214 changes in the distribution of species temperature values within every plot. We quantified  
215 such changes by the shift in the mean (Community Temperature Index or CTI; Devictor *et*  
216 *al.*, 2008), as well as the lower 10<sup>th</sup> percentile and the upper 90<sup>th</sup> percentile of this plot-level  
217 distribution (De Frenne *et al.*, 2013).  
218 To compute these metrics, we first combined climate and tree occurrence data to obtain  
219 species temperature distributions. Specifically, we overlaid interpolated climate data (mean annual  
220 temperature averages for 1970–2000 at a spatial resolution of 1 km<sup>2</sup>, available online  
221 <http://worldclim.org/version2>; Fick & Hijmans, 2017) and occurrence data from multiple forest inventory  
222 databases of eastern North America (collected in the QUICC-FOR project;  
223 <https://github.com/QUICC-FOR>) for the focal species. The mean annual temperature for each occurrence  
224 was extracted to infer species temperature distributions. Following Devictor *et al.* (2008), we used the  
225 mean of these temperature values as a proxy for species thermal preference (Species Temperature Index,  
226 STI, in Celsius; Table S1). For each plot in each time period, the CTI was then calculated as the mean of  
227 the STI values weighted by the abundances of the species present in that plot.  
228 Following De Frenne *et al.* (2013), we computed the 10<sup>th</sup> and 90<sup>th</sup> percentiles of the  
229 plot-level temperature distributions, which correspond to the cold and warm tails of the

230 distribution. To do so, for every plot and every species, we sampled 1000 temperature values  
231 per individual from the species' temperature distribution. The plot-level temperature  
232 distributions corresponds to the combination of the temperature values for all individuals in  
233 a given plot. From these distributions, which accounted for species composition and their  
234 relative abundances, we computed the 10<sup>th</sup> and 90<sup>th</sup> percentiles. Note that contrary to De Frenne  
235 *et al.* (2013), we used the entire distribution for each species instead of modeling species thermal response  
236 curves because numerous species distributions were not Gaussian.

237 To evaluate the directionality of the changes in communities between the historical ( $t_1$ ) and contemporary  
238 ( $t_2$ ) periods, we computed the temporal shift in the mean CTI, the cold tail and the warm tail (in °C per  
239 decade) as follows:

$$240 \Delta CTI = \frac{CTI_{t_2} - CTI_{t_1}}{t_2 - t_1} \times 10$$

241 The shifts in the cold and warm tails were computed in the same way as for the shifts in mean CTI. A  
242 positive value of  $\Delta CTI$  indicates an overall thermophilization of the tree community in degrees per decade.  
243 A positive shift of the cold tail indicates a decrease of cold-adapted species, while a positive shift of the  
244 warm tail indicates an increase of warm-adapted species; both result in thermophilization.

245 We also quantified how each species contributed to  $\Delta CTI$  through gain or loss in abundances. Species  
246 contributions were assessed following these steps: for each species, (1) we replaced its abundance at  $t_2$  by  
247 its abundance at  $t_1$ , as if this species abundance had not changed over time; (2) we computed a new  $CTI_{t_2}'$ ;  
248 (3) then we calculated  $\Delta CTI'$  using  $CTI_{t_2}'$  and  $CTI_{t_1}$  as above; and (4) we measured the difference  
249 between  $\Delta CTI'$  and  $\Delta CTI$  in each plot. A positive value indicates that the change (gain or loss) of a given  
250 species abundance increases thermophilization in a plot. Then, we determined the role of species gains and  
251 losses in  $\Delta CTI$  by averaging their contributions for plots where they increased and where they decreased.

252 To test the hypothesis that community changes are resulting from post-disturbance succession, we collected  
253 traits about species shade tolerance (Species Shade Index, SSI; Niinemets & Valladares, 2006), which  
254 represents a species ability to grow in shade conditions. Shade tolerance indices ranged from 1 (very  
255 intolerant to shade) to 5 (very tolerant) on a continuous scale. As for CTI, a Community Shade Index  
256 (CSI) was computed for each plot as the mean of the SSI values weighted by the abundances of the species  
257 present in that plot. Temporal shift in CSI **between the historical and contemporary time periods**,  
258  $\Delta CSI$ , was computed in the same way as for  $\Delta CTI$ , where a positive value indicates a progress in stand  
259 succession toward climax, in units per decade.

260 All analyses were performed using the R programming language version 3.5.1 (R Core Team, 2018). The  
261 list of R packages that have been used throughout the analysis is provided in Table S3. R scripts will be  
262 made available on GitHub upon final acceptance.

263 **Results**

264 **Temporal  $\beta$  diversity**

265 The mean temporal  $\beta$  diversity was 0.56 over all sites in the study area ( $n = 6281$ ), and  
266 these temporal changes in composition were attributable to slightly more gains in  
267 abundances (52.5%) than losses (47.5%; Fig. 2a). Temporal  $\beta$  diversity varied along a  
268 latitudinal gradient; it tended to decrease northward, reaching its maximum at 48°N of  
269 latitude, which corresponds to the northern limit of the balsam fir-yellow birch domain, the  
270 ecotone between boreal and deciduous forests. North of the 49°N of latitude, in the  
271 spruce-moss domain, temporal  $\beta$  changes were dominated by losses whereas, south of this  
272 limit, gains prevailed. Latitudinal patterns were also visible in the contributions of the three  
273 species groups to temporal  $\beta$  (Fig. 2b). At minor disturbance level, community changes were  
274 mainly determined by gains in temperate species south of 47°N and by gains in boreal  
275 species north of 47°N (where boreal species are the most abundant species group).

276 The magnitude of compositional changes in forests was highly influenced by disturbances  
277 (Figs 2b-d, 3, S4). In each domain, the  $\beta$  diversity values of highly disturbed forests are  
278 strongly skewed (Fig. 3). The mean temporal  $\beta$  was 0.43 at minor disturbance level, whereas  
279 it was 0.53 at moderate disturbance level and reached 0.74 at major disturbance level (all  
280 domains combined). Moreover, the fraction of changes attributed to losses was generally  
281 lower at minor, than at moderate and major disturbance levels (minor: 41%; moderate: 48%;  
282 major: 50%, all domains combined), especially for the spruce-moss domain (minor: 40%;  
283 moderate: 73%; major: 64%; Fig. 3). At minor disturbance level, both boreal and temperate  
284 species groups experienced more gains than losses (Fig. 2b), while at major disturbance  
285 level, we observed a strong surge in losses of boreal tree species along with larger gains of  
286 pioneer species (Fig. 2d). In contrast, gains in temperate species were higher at moderate  
287 disturbance level (Fig. 2c). Some species have experienced great changes in abundance and  
288 occurrence throughout these domains, namely *Picea mariana*, *Acer rubrum*, *Betula*  
289 *alleghaniensis*, *Fagus grandifolia* and *Populus tremuloides*, and likely contributed largely to  
290 the pattern of temporal  $\beta$  diversity (Fig. S4).

291 **Drivers of temporal changes**

292 Once combined, predictors from the three subsets (baseline, climate change and disturbances; Table 1)  
293 explained together 40% of the variation of temporal  $\beta$  diversity, and 30% for both gains and  
294 losses (Fig. 4). As revealed by the variation partitioning analyses, community temporal changes

were mainly driven by disturbances ( $R^2_{adj}$  for  $\beta$ : 31%; gains: 25%; losses: 26%), whereas the unique influence of climate change **as well as that of baseline conditions** were significant but comparatively modest ( $R^2_{adj} < 1\%$ ; Fig. 4d-f).

Overall, disturbances enhanced temporal  $\beta$  diversity, with old major harvest (Old harvest<sub>2</sub>) being the most important driver, followed by old major natural disturbances (Old natural<sub>2</sub>; Fig. 4a-c). Interestingly, while recent disturbances (natural and harvest) promoted losses and reduced gains, old disturbances had the opposite effect (Fig. 4b-c). As time-since-disturbance increased and the forests grew old (Age), forest composition changed less and colonization by new individuals became less frequent (Fig. 4a-b).

Regression models provided only weak evidence of climate change effect on forest community changes. Mainly, extreme minimum **climate moisture index** (CMI min) and extreme cold (Temp min) contributed to community changes through losses in tree abundances (Fig. 4a,c). Increase in precipitation ( $\Delta$ Precip) favored tree gains. Only one interaction was retained, which indicated that **stronger warming** ( $\Delta$ Temp) **mitigated the effect of recent moderate harvest** (Recent harvest<sub>1</sub>) on losses. **Variables related to baseline conditions were more important than climate change variables; the effects of mean temperature (Temp) and total precipitation (Precip) likely reflect the latitudinal gradient in community change, while the effect of time interval between surveys ( $\Delta$ Time) reflects the fact that community change takes time.**

## Changes in community temperature and shade indices

The community temperature index (CTI) increased significantly between the historical and contemporary periods (paired *t*-test *p*-value < 0.001; mean of +0.03 °C/decade for all plots **combined**, ranging from -0.02 to +0.05 across domains), which indicates a generalized community thermophilization throughout the study area. During the same **time** period, the community shade index (CSI) also increased (+0.01 unit/decade), suggesting a transition towards late successional forests (Fig. 5).

Thermophilization was significantly larger in moderately disturbed forests ( $\Delta$ CTI = +0.044 °C/decade) than in undisturbed (+0.015 °C/decade) or highly disturbed forests (+0.018 °C/decade; ANOVA  $F_{2,6278} = 14.59$ , *p*-value < 0.001; a post-hoc Tukey test showed significantly higher  $\Delta$ CTI at moderate disturbance than at the other levels). Moreover, the latitudinal pattern of  $\Delta$ CTI varied with the disturbance level: the thermophilization in moderately disturbed forests extended further north than in undisturbed forests, exceeding 48°N, up in the balsam fir-yellow birch domain (Fig. 5b,e), while at major disturbances, thermophilization was more or less constant across the latitudinal gradient (Fig. 5c,f). Despite the influence of disturbances on thermophilization, change in CTI was weakly explained by our complete set of environmental predictors ( $R^2_{adj}$  ca. 3%). Moreover, the relationship between thermophilization and climate change predictors was surprisingly weak ( $R^2_{adj} < 1\%$ ), with no correlation at all with temperature change.

328 The analysis of  $\Delta\text{CSI}$  revealed that major disturbances resulted in a large decrease in CSI  
329 (Fig. 5c; mean  $\Delta\text{CSI} = -0.037$ ), consistent with higher gains in pioneer species (Fig. 2),  
330 while minor disturbances led to an increase in CSI (Fig. 5a; mean  $\Delta\text{CSI} = +0.060$ ). Both  
331 influenced by disturbances,  $\Delta\text{CTI}$  and  $\Delta\text{CSI}$  were negatively correlated (Pearson  $r = -0.2$ ,  $p$ -value < 0.001)  
332 indicating that the two ecological processes are intertwined. However,  $\Delta\text{CTI}$  was more strongly correlated  
333 to gains in temperate species and losses of boreal species than to gains in pioneer species (Fig. S6), which  
334 suggests that thermophilization was not trivially driven by successional processes.

335 Community thermophilization was asymmetrical and mainly driven by larger gains in warm-adapted  
336 species, as indicated by the larger increases in the warm-tail of the temperature distributions than in the  
337 cold-tail (Fig. 5d-f). Moderate disturbances exacerbated this effect from the sugar maple-yellow birch up  
338 to the balsam fir-white birch domain (larger increase in the warm tail; Fig. 5e). The positive correlation  
339 between  $\Delta\text{CTI}$  and gains in temperate species in all domains, except in the spruce-moss, also corroborates  
340 the role of warm-adapted species (Fig. S6).

341 Only a few species contributed substantially to community thermophilization (Fig. 6). Gains of *Acer  
342 rubrum* and *Acer saccharum*, as well as losses of *Abies balsamea* and *Picea mariana*, contributed strongly to  
343 the thermophilization of all bioclimatic domains. In addition to the change of these four species, the losses  
344 of *Betula papyrifera* and *Picea glauca* also played a key role in the thermophilization of ecotonal forests in  
345 the balsam fir-yellow birch domain. Moreover, temperate species such as *Fagus grandifolia*, *Quercus rubra*  
346 and *Fraxinus americana* contributed mostly to the thermophilization of southern domains (Fig. 6) where  
347 their abundance has increased (Fig. S4). In contrast, the surge in CTI north of the 49°N (spruce-moss) in  
348 highly disturbed forests (Fig. 5) was likely due to the replacement of boreal species by pioneer species (Fig.  
349 S6), such as *Betula papyrifera* and *Salix spp.* (Fig. 6).

## 350 Discussion

351 Taken together, our results suggest that disturbances accelerate tree community responses to  
352 climate change, revealing potential synergies that are yet to be investigated. Local and  
353 short-term influences of disturbances mask long-term and lagging climate-induced changes in communities.  
354 Yet, we revealed a generalized thermophilization of forests throughout the temperate-boreal ecotone of  
355 Québec, driven by a concurrent gain of temperate species and loss of boreal species. Moreover, we found  
356 that moderate disturbances likely accelerated thermophilization. Hence, moderate disturbances, but not  
357 major ones, could facilitate gains in warm-adapted species under climate change.

358 **Impact of disturbances on tree community changes**

359 Our results suggest that disturbances (e.g., clear-cutting, insect outbreaks, fires) are the primary drivers of  
360 forest community changes in the temperate-boreal ecotone. Such findings are in agreement with previous  
361 work showing that disturbances alter rapidly and profoundly tree communities that otherwise respond  
362 slowly to environmental changes (Vanderwel *et al.*, 2013).

363 Furthermore, our study underscores the importance of historical disturbances, particularly harvesting  
364 activities, on the forest dynamics of the temperate-boreal ecotone. Disturbance effects on communities may  
365 persist from decades to centuries (Johnstone *et al.*, 2016) and, here, the effects of historical disturbances  
366 even superseded that of recent disturbances. Such findings stress that disturbances cannot be ignored when  
367 modeling the future of forests with climate change, as they not only drive community changes, but also  
368 have long-lasting impacts. Tree harvesting was the most frequent type of disturbance (Fig. S2) and alone  
369 accounted for 24.7% of all tree mortality during the study period, thus impacting severely all components  
370 of temporal community changes. **However, in contrast to natural disturbances, tree harvesting**  
371 **has been shown to disrupt the relationship between vegetation and local environmental**  
372 **conditions and, because of its short return interval, to favor young even-aged stands to the**  
373 **detriment of old-growth forests (Boucher *et al.*, 2009; Boucher & Grondin, 2012).**

374 **Climate-induced change in tree community**

375 Our findings highlight an ongoing shift toward more warm-adapted tree species in forests across the  
376 temperate-boreal ecotone. This overall thermophilization trend of tree communities is consistent with the  
377 hypothesis of climate-induced range shift, expanding on earlier findings that forests are responding to  
378 climate warming (e.g. Sittaro *et al.*, 2017; Leithead *et al.*, 2010; Fisichelli *et al.*, 2014). However, the  
379 observed increase of tree community temperature of +0.03 °C/decade is considerably smaller than the  
380 rising trend in growing season temperature of 0.14 °C/decade (Fig. S1). **Although these measures**  
381 **have different origins and should thus be compared cautiously**, our findings support the  
382 conclusion of numerous studies that tree responses often lag behind environmental changes (Svenning &  
383 Sandel, 2013; Renwick & Rocca, 2015; Sittaro *et al.*, 2017; Talluto *et al.*, 2017). Considering the velocity of  
384 the predicted future climate change, the gap between species distributions and their optimal climate niches  
385 will likely widen and lead to **greater reshuffling of biodiversity**.

386 **Feedback between climate change and disturbances**

387 Our most striking finding is that community thermophilization was amplified by moderate disturbances.  
388 Our combined analysis of change in CTI and CSI also allowed us to disentangle climate change effects from

389 successional processes, highlighting that the observed thermophilization was not simply correlated with the  
390 replacement of boreal by pioneer species. Our work provides a broad-scale community perspective on the  
391 role played by disturbances in promoting northward migration of tree species, which is in agreement with  
392 the conclusions of recent empirical (Boucher *et al.*, 2006; Leithead *et al.*, 2010) and simulation (Vanderwel  
393 & Purves, 2014; Wang *et al.*, 2015) studies.

394 Disturbances likely accelerate forest changes by reducing competition and providing establishment  
395 opportunities to warm-adapted temperate tree species (Leithead *et al.*, 2010; Svenning & Sandel, 2013).  
396 Indeed, in the absence of disturbances, trees grow slowly, their mortality rates are low and competition for  
397 space and light is strong, thus preventing warm-adapted species from colonizing new areas, despite the  
398 suitability of climatic conditions; community thermophilization is consequently very slow. Moderate  
399 disturbances, however, remove individuals of resident species and reduce competition, which enhances the  
400 replacement of boreal by temperate trees, thereby increasing the thermophilization rate. Furthermore,  
401 moderate disturbances can also modify local microclimates (De Frenne *et al.*, 2013; Stevens *et al.*, 2015)  
402 which may alter the survival rates of tree saplings. In contrast, major disturbances only favor early  
403 successional species. Such findings echo the well-known intermediate disturbance hypothesis (Connell,  
404 1978); as in the classical hypothesis, intermediate disturbances lower interspecific competition but here,  
405 **not only do they increase local species richness (not shown)**, but they also accelerate ecological  
406 transitions.

407 Our complete set of predictors poorly explained the observed forest thermophilization, likely because this  
408 process was highly variable among localities. Forest composition is thus changing as expected under  
409 climate warming, but thermophilization does not appear to be directly driven by rising temperatures. As  
410 suggested by Renwick & Rocca (2015), we surmise that, as climate warms up, moderate disturbances could  
411 foster punctuated and episodic migration of warm-adapted species in localities where conditions are  
412 otherwise favorable. However, it raises questions about the specific conditions in which the  
413 thermophilization process can effectively take place. Further analyses are required to determine which  
414 factors can trigger (e.g. type, size, frequency of disturbances) or constrain (e.g. soil type, competition,  
415 precipitation) the invasion by warm-adapted species.

416 **Our results contrast with those of Boisvert-Marsh *et al.* (2019) who found that climate was**  
417 **more important than disturbances in explaining tree sapling recruitment at their northern**  
418 **limit in Québec. This suggests that the pattern we uncovered might be primarily caused by**  
419 **an increase in abundance of species already present rather than by new colonization.**  
420 **Danneyrolles *et al.* (2019) also found that forest compositional changes over the last**  
421 **centuries (between 1790–1900 and 1980–2010) in deciduous forests of southern Québec were**  
422 **largely driven by land-use changes, favoring more disturbance-adapted tree species, but did**  
423 **not find any signs of thermophilization. In contrast to our study that covers a period of**

424 pronounced climate warming, Danneyrolles *et al.* (2019) investigated a period dominated by  
425 land-use and population changes which may explain the absence of thermophilization signal  
426 in their results. In light of their results, we hypothesize that some of the thermophilization  
427 we reported here in the sugar maple domains is in fact the result of secondary succession  
428 after historical disturbances.

## 429 Species contributions to community thermophilization

430 We found that the observed community thermophilization was caused by gains and losses in abundance of  
431 a restricted group of species. This differential rate of species response entails that other species lag even  
432 more behind climate change and that larger reshuffling of communities is still ahead of us. The interaction  
433 between climate and disturbances likely promotes generalist tree species adapted to disturbances with high  
434 dispersal abilities (Aubin *et al.*, 2016). For instance, generalist species like *Acer sp.*, especially *Acer rubrum*,  
435 have been expanding in eastern North America since the pre-industrial period (Boucher *et al.*, 2006;  
436 Thompson *et al.*, 2013; Danneyrolles *et al.*, 2019) and recently established themselves in boreal forests  
437 (Leithead *et al.*, 2010; Sittaro *et al.*, 2017) because they quickly take advantage from disturbances and  
438 thrive in a wide variety of ecological conditions. In contrast, some species limited by dispersal, such as  
439 *Carya sp.* and *Tilia americana*, or constrained to specific habitat, such as *Acer saccharinum*, might not  
440 benefit from these opportunities.

441 The magnitude of change in CTI varied by bioclimatic domains reflecting the spatial  
442 patterns of species changes in response to climate warming and disturbances. The  
443 thermophilization of the sugar maple domains was facilitated by the presence of a large pool  
444 of warm-adapted species. When disturbed, these southernmost domains had lower  
445 thermophilization because they gained pioneer species. We showed that the balsam fir-yellow  
446 birch domain was particularly sensitive to moderate disturbances. The thermophilization of  
447 this ecotonal zone was primarily due to increase in *Acer rubrum* and, to a lesser extent,  
448 increase in *A. saccharum* and decrease in *Abies balsamea* and *Betula papyrifera*. Although  
449 *A. rubrum* is already well established in this domain, our results suggest that it will continue  
450 to thrive and spread, likely in response to a combination of climate warming, historical and  
451 recent disturbances as well as natural forest dynamics. *A. saccharum* is presently  
452 constrained on hilltops in the southern part of this domain (Gosselin, 2002), but our results  
453 suggest that it could expand in nearby habitats. In contrast, the decrease in CTI in the  
454 balsam fir-white birch and spruce moss domains could be explained by the fact that  
455 temperate species are rare in these two northernmost domains, hence changes in CTI  
456 resulted mostly from a dynamic of replacement between pioneer and boreal species in  
457 response to disturbances. *A. rubrum* was the only temperate species to increase in the

458 balsam fir-white birch domain (Fig. S4) and, when it did, it contributed to increase its CTI  
459 (Fig. 6). Similarly to *A. saccharum*, *A. rubrum* distribution is spatially constrained within  
460 the balsam fir-white birch domain (Blouin & Berger, 2008) and will likely expand from  
461 existing existing patchy populations in the future.

462 **Long-term perspectives for the temperate-boreal ecotone**

463 Although the time period covered by our study (46 years) is sufficient to observe significant trends in forest  
464 compositional changes, it is not long enough to test whether warm-adapted temperate species will persist  
465 and thrive in these novel assemblages or if boreal species will out-compete them in the long run. Therefore,  
466 an important question remains: does the current forest thermophilization indicates an ongoing ecosystem  
467 shift or only a transient dynamic? Multiple studies suggest a persistence of these novel assemblages. For  
468 instance, after a century of logging disturbances, temperate species were found to have increased and  
469 persisted in forests formerly dominated by conifers (Boucher *et al.*, 2006). Furthermore, Fréchette & de  
470 Vernal (2013) provided evidence that, during the last interglacial period (6-7°C warmer), the northern limit  
471 of the temperate biome was located about 500 km north of its actual limit, suggesting that a northward  
472 shift of the ecotone is possible. Hence, while climate warming erodes forest resilience by affecting  
473 competitive advantages and generating colonization debt, our findings suggest that moderate disturbances  
474 play a major role in promoting regime shift by speeding up the transition from one ecosystem state to  
475 another. Such a conclusion stresses the importance of accounting for the synergistic effect of disturbances  
476 and climate change in forest management strategies as well as in models of forest responses to climate  
477 change.

478 **References**

- 479 Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... Cobb, N.  
480 (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks  
481 for forests. *Forest Ecology and Management*, **259**, 660–684.
- 482 Aubin, I., Munson, A., Cardou, F., Burton, P., Isabel, N., Pedlar, J., ... McKenney, D. (2016) Traits to stay,  
483 traits to move: A review of functional traits to assess sensitivity and adaptive capacity of temperate and  
484 boreal trees to climate change. *Environmental Reviews*, **24**, 164–186.
- 485 Beckage, B., Osborne, B., Gavin, D.G., Pucko, C., Sicama, T. & Perkins, T. (2008) A rapid upward shift  
486 of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the*  
487 *National Academy of Sciences*, **105**, 4197–4202.
- 488 Becker-Scarpitta, A., Vissault, S. & Vellend, M. (2019) Four decades of plant community change along a  
489 continental gradient of warming. *Global Change Biology*, **0**.
- 490 Blanchet, F.G., Legendre, P. & Borcard, D. (2008) Forward selection of explanatory variables. *Ecology*, **89**,  
491 2623–2632.
- 492 Blouin, J. & Berger, J.-P. (2008) *Guide de reconnaissance des types écologiques: région écologique 5b :*  
493 *côteaux du réservoir Gouin, région écologique 5c : collines du Haut-Saint-Maurice, région écologique 5d :*  
494 *collines qui ceinturent le lac Saint-Jean*, Division de la classification écologique et productivité des stations,  
495 Direction des inventaires forestiers, Forêt Québec, Ministère des ressources naturelles, Québec.
- 496 Boisvert-Marsh, L., Périé, C. & Blois, S. de (2019) Divergent responses to climate change and disturbance  
497 drive recruitment patterns underlying latitudinal shifts of tree species. *Journal of Ecology*, **0**.
- 498 Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological  
499 variation. *Ecology*, **73**, 1045–1055.
- 500 Boucher, Y., Arseneault, D. & Sirois, L. (2006) Logging-induced change (1930-2002) of a preindustrial  
501 landscape at the northern range limit of northern hardwoods, eastern Canada. *Canadian Journal of Forest*  
502 *Research*, **36**, 505–517.
- 503 Boucher, Y., Arseneault, D., Sirois, L. & Blais, L. (2009) Logging pattern and landscape changes over the  
504 last century at the boreal and deciduous forest transition in Eastern Canada. *Landscape Ecology*, **24**,  
505 171–184.
- 506 Boucher, Y. & Grondin, P. (2012) Impact of logging and natural stand-replacing disturbances on  
507 high-elevation boreal landscape dynamics (1950–2005) in eastern Canada. *Forest Ecology and Management*,  
508 **263**, 229–239.

- 509 Brook, B., Sodhi, N. & Bradshaw, C. (2008) Synergies among extinction drivers under global change.
- 510 *Trends in Ecology & Evolution*, **23**, 453–460.
- 511 Cheung, W.W.L., Watson, R. & Pauly, D. (2013) Signature of ocean warming in global fisheries catch.
- 512 *Nature*, **497**, 365–368.
- 513 Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.
- 514 Danneyrolles, V., Dupuis, S., Fortin, G., Leroyer, M., de Römer, A., Terrail, R., ... Arseneault, D. (2019)
- 515 Stronger influence of anthropogenic disturbance than climate change on century-scale compositional
- 516 changes in northern forests. *Nature Communications*, **10**, 1265.
- 517 De Frenne, P., Rodriguez-Sanchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., ... Verheyen,
- 518 K. (2013) Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National*
- 519 *Academy of Sciences*, **110**, 18561–18565.
- 520 Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008) Birds are tracking climate warming, but not fast
- 521 enough. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2743–2748.
- 522 Esquivel-Muelbert, A., Baker, T.R., Dexter, K.G., Lewis, S.L., Brienen, R.J.W., Feldpausch, T.R., ...
- 523 Phillips, O.L. (2018) Compositional response of Amazon forests to climate change. *Global Change Biology*.
- 524 Feeley, K.J., Hurtado, J., Saatchi, S., Silman, M.R. & Clark, D.B. (2013) Compositional shifts in Costa
- 525 Rican forests due to climate-driven species migrations. *Global Change Biology*, **19**, 3472–3480.
- 526 Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: New 1-km spatial resolution climate surfaces for global
- 527 land areas. *International Journal of Climatology*, **37**, 4302–4315.
- 528 Fisichelli, N.A., Frelich, L.E. & Reich, P.B. (2014) Temperate tree expansion into adjacent boreal forest
- 529 patches facilitated by warmer temperatures. *Ecography*, **37**, 152–161.
- 530 Fréchette, B. & de Vernal, A. (2013) Evidence for large-amplitude biome and climate changes in Atlantic
- 531 Canada during the last interglacial and mid-Wisconsinan periods. *Quaternary Research*, **79**, 242–255.
- 532 Gaüzère, P., Jiguet, F. & Devictor, V. (2015) Rapid adjustment of bird community compositions to local
- 533 climatic variations and its functional consequences. *Global Change Biology*, **21**, 3367–3378.
- 534 Goldblum, D. & Rigg, L.S. (2010) The Deciduous Forest - Boreal Forest Ecotone: Deciduous - boreal forest
- 535 ecotone. *Geography Compass*, **4**, 701–717.
- 536 Gosselin, J. (2002) *Guide de reconnaissance des types écologiques des régions écologiques 4b – Coteaux du*
- 537 *réservoir Cabonga et 4c – Collines du Moyen-Saint-Maurice.*, Division de la classification écologique et
- 538 productivité des stations, Direction des inventaires forestiers, Forêt Québec, Ministère des ressources
- 539 naturelles.

- 540 Iverson, L.R. & McKenzie, D. (2013) Tree-species range shifts in a changing climate: Detecting, modeling,  
541 assisting. *Landscape Ecology*, **28**, 879–889.
- 542 Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., ... Turner, M.G.  
543 (2016) Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the  
544 Environment*, **14**, 369–378.
- 545 Jump, A.S., Mátyás, C. & Peñuelas, J. (2009) The altitude-for-latitude disparity in the range retractions of  
546 woody species. *Trends in Ecology & Evolution*, **24**, 694–701.
- 547 Legendre, P. (2019) A temporal beta-diversity index to identify sites that have changed in exceptional ways  
548 in space–time surveys. *Ecology and Evolution*, **9**, 3500–3514.
- 549 Leithead, M.D., Anand, M. & Silva, L.C.R. (2010) Northward migrating trees establish in treefall gaps at  
550 the northern limit of the temperate–boreal ecotone, Ontario, Canada. *Oecologia*, **164**, 1095–1106.
- 551 Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P. & Brisson, H. (2008) A Significant Upward Shift in  
552 Plant Species Optimum Elevation During the 20th Century. *Science*, **320**, 1768–1771.
- 553 McKenney, D.W., Hutchinson, M.F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., ... Owen, T.  
554 (2011) Customized Spatial Climate Models for North America. *Bulletin of the American Meteorological  
555 Society*, **92**, 1611–1622.
- 556 MFFP (2016) *Placettes-échantillons permanentes: normes techniques*, Ministère des Forêts de la Faune et  
557 des Parcs, Secteur des forêts, Direction des Inventaires Forestiers.
- 558 Niinemets, Ü. & Valladares, F. (2006) Tolerance to shade, drought, and waterlogging of temperate  
559 northern hemisphere trees and shrubs. *Ecological Monographs*, **76**, 521–547.
- 560 Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural  
561 systems. *Nature*, **421**, 37–42.
- 562 Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data  
563 matrices: Estimation and comparison of fractions. *Ecology*, **87**, 2614–2625.
- 564 R Core Team (2018) *R: A Language and Environment for Statistical Computing*, R Foundation for  
565 Statistical Computing, Vienna, Austria.
- 566 Renwick, K.M. & Rocca, M.E. (2015) Temporal context affects the observed rate of climate-driven range  
567 shifts in tree species: Importance of temporal context in tree range shifts. *Global Ecology and Biogeography*,  
568 **24**, 44–51.
- 569 Savage, J. & Vellend, M. (2015) Elevational shifts, biotic homogenization and time lags in vegetation  
570 change during 40 years of climate warming. *Ecography*, **38**, 546–555.

- 571 Searle, E.B. & Chen, H.Y.H. (2017) Persistent and pervasive compositional shifts of western boreal forest  
572 plots in Canada. *Global Change Biology*, **23**, 857–866.
- 573 Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., ... Reyer, C.P.O. (2017)  
574 Forest disturbances under climate change. *Nature Climate Change*, **7**, 395–402.
- 575 Sittaro, F., Paquette, A., Messier, C. & Nock, C.A. (2017) Tree range expansion in eastern North America  
576 fails to keep pace with climate warming at northern range limits. *Global Change Biology*, **23**, 3292–3301.
- 577 Stevens, J.T., Safford, H.D., Harrison, S. & Latimer, A.M. (2015) Forest disturbance accelerates  
578 thermophilization of understory plant communities. *Journal of Ecology*, **103**, 1253–1263.
- 579 Svenning, J.-C. & Sandel, B. (2013) Disequilibrium vegetation dynamics under future climate change.  
580 *American Journal of Botany*, **100**, 1266–1286.
- 581 Talluto, M.V., Boulangeat, I., Vissault, S., Thuiller, W. & Gravel, D. (2017) Extinction debt and  
582 colonization credit delay range shifts of eastern North American trees. *Nature Ecology & Evolution*, **1**, 0182.
- 583 Thompson, J.R., Carpenter, D.N., Cogbill, C.V. & Foster, D.R. (2013) Four Centuries of Change in  
584 Northeastern United States Forests. *PLOS ONE*, **8**, e72540.
- 585 VanDerWal, J., Murphy, H.T., Kutt, A.S., Perkins, G.C., Bateman, B.L., Perry, J.J. & Reside, A.E. (2013)  
586 Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature  
587 Climate Change*, **3**, 239–243.
- 588 Vanderwel, M.C., Coomes, D.A. & Purves, D.W. (2013) Quantifying variation in forest disturbance, and its  
589 effects on aboveground biomass dynamics, across the eastern United States. *Global Change Biology*, **19**,  
590 1504–1517.
- 591 Vanderwel, M.C. & Purves, D.W. (2014) How do disturbances and environmental heterogeneity affect the  
592 pace of forest distribution shifts under climate change? *Ecography*, **37**, 10–20.
- 593 Violette, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the  
594 concept of trait be functional! *Oikos*, **116**, 882–892.
- 595 Wang, W.J., He, H.S., Iii, F.R.T., Fraser, J.S., Hanberry, B.B. & Dijak, W.D. (2015) Importance of  
596 succession, harvest, and climate change in determining future composition in U.S. Central Hardwood  
597 Forests. *Ecosphere*, **6**, art277.
- 598 Xu, C., Gertner, G.Z. & Scheller, R.M. (2012) Importance of colonization and competition in forest  
599 landscape response to global climatic change. *Climatic Change*, **110**, 53–83.

600 **Data Accessibility Statement**

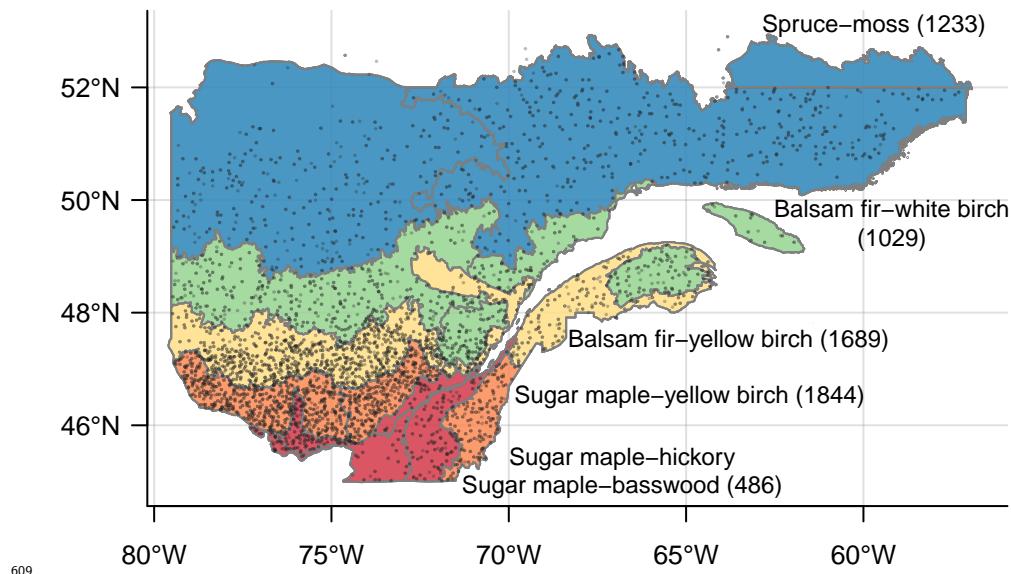
601 The complete forest inventory dataset used in this study is available online at  
602 <https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui>. All code required to repeat the analyses will be made available online on  
604 GitHub.

605 **Tables**

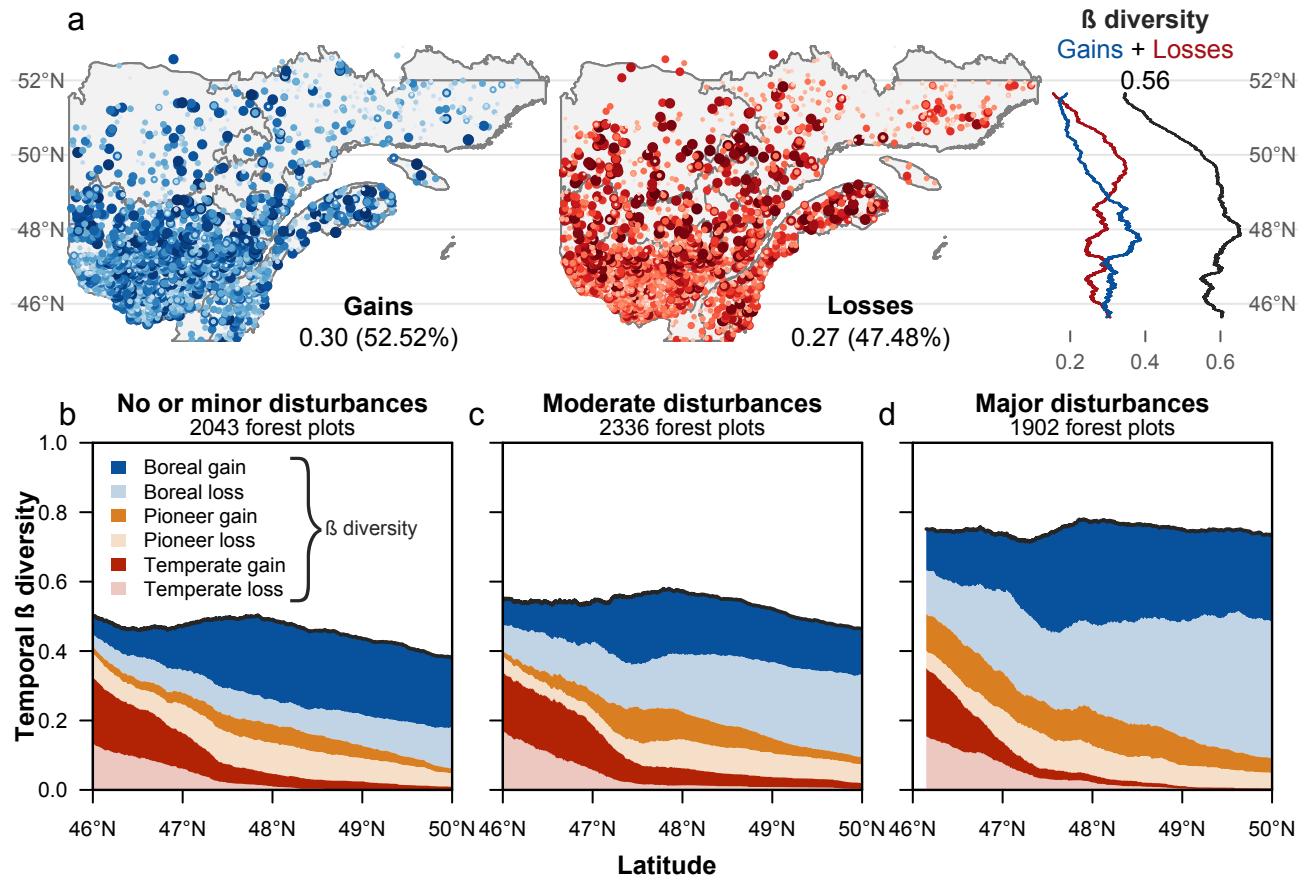
606 **Table 1.** Description of the predictors used in the multiple linear regression models. See Table S2 for  
 607 details about disturbance types.

Variable name	Variable description
<b>Baseline conditions</b>	
Temp, Temp <sup>2</sup>	Mean temperature during growing season and <b>its second order polynomial. 10-year average prior to first survey of each plot (°C).</b>
Precip, Precip <sup>2</sup>	Total precipitation during growing season and <b>its second order polynomial. 10-year average prior to first survey of each plot (mm).</b>
ΔTime	Time interval between first and last measurements (years).
<b>Climate change</b>	
ΔTemp	Slope between Temp and time (°C/y).
ΔPrecip	Slope between <b>Precip</b> and time (mm/y).
ΔCMI	Slope between Climate Moisture Index and time ( <b>cm/y</b> }).
Temp min	Extreme minimum temperature. Difference between minimum and mean temperature of the coldest period (°C).
<b>Temp max</b>	Extreme maximum temperature. Difference between maximum and mean temperature of the warmest period (°C).
CMI min	Extreme minimum Climate Moisture Index (CMI). Difference between minimum CMI and mean CMI ( <b>cm</b> ), as a proxy of drought.
<b>Disturbances</b>	
Age	Stand age (years).
Old harvest	Tree harvesting (clearcutting, partial cutting, selection cutting, etc.) that occurred before the study period. 1. Minor (0), moderate (1) or major (2).
Recent harvest	Tree harvesting (clearcutting, partial cutting, selection cutting, etc.) that occurred during the study period. Minor (0), moderate (1) or major (2).
Old natural	Natural disturbances (fire, insect outbreak, windfall, etc.) that occurred before the study period. Minor (0), moderate (1) or major (2).
Recent natural	Natural disturbances (fire, insect outbreak, windfall, etc.) that occurred before the study period. Minor (0), moderate (1) or major (2).

608 **Figures**

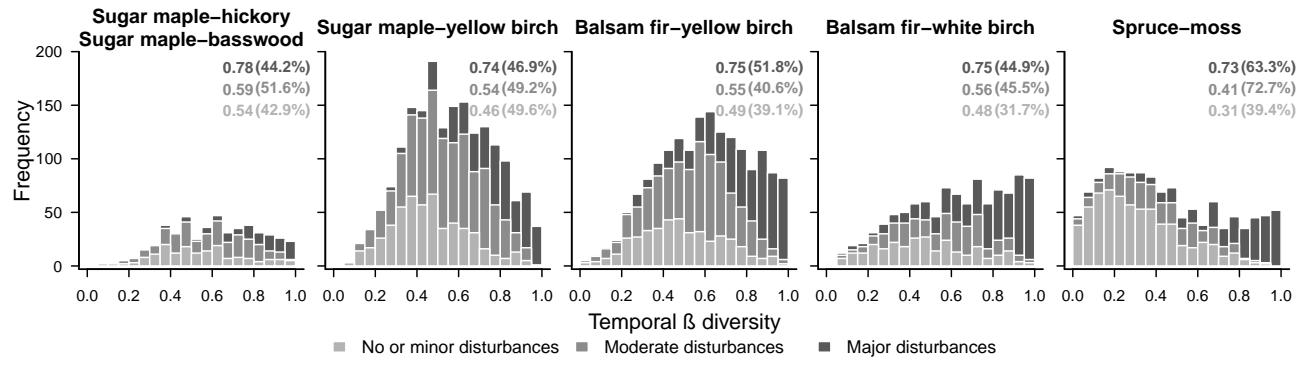


609  
610 **Figure 1.** Locations of the 6281 forest inventory plots in meridional Québec, Canada. Colors delimit the  
611 six bioclimatic domains. The two southernmost domains (orange) were combined in our analyses. The  
612 number of forest plots in each domain is written in parentheses.



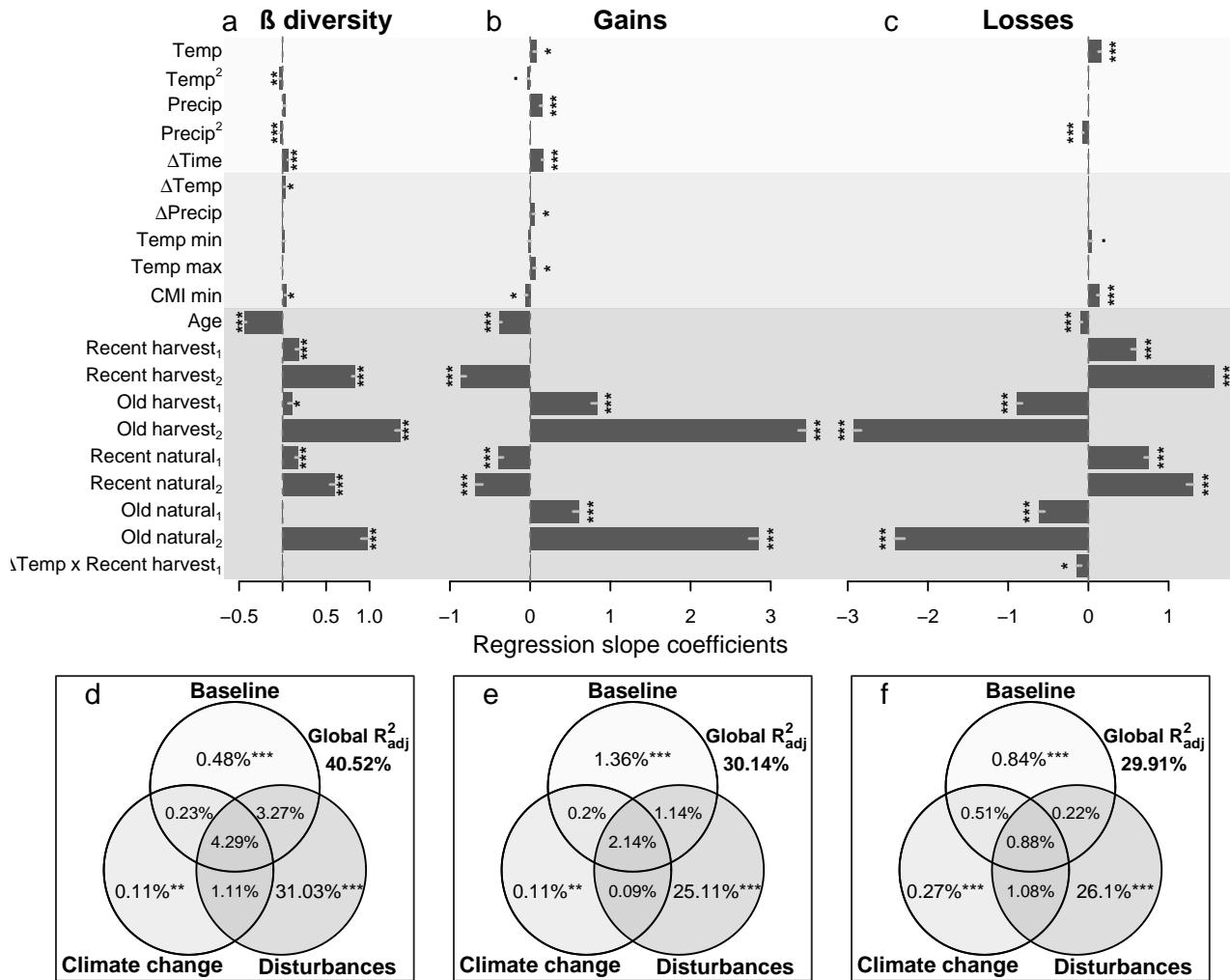
613

614 **Figure 2.** Maps of gains and losses in tree abundances (a) and latitudinal trends in temporal  $\beta$  diversity,  
 615 decomposed into gains (blue) and losses (red) of boreal, pioneer and temperate trees, for different levels of  
 616 disturbance (b-d). The sizes and colors of the points on the maps are proportional to the values of interest.  
 617 The latitudinal trends in temporal  $\beta$  in a-d are based on moving averages computed on each index against  
 618 latitude (window size of 500 plots in panel a and 400 plots in panels b-d), to smooth out local-scale  
 619 fluctuations and highlight broad-scale trends.



620

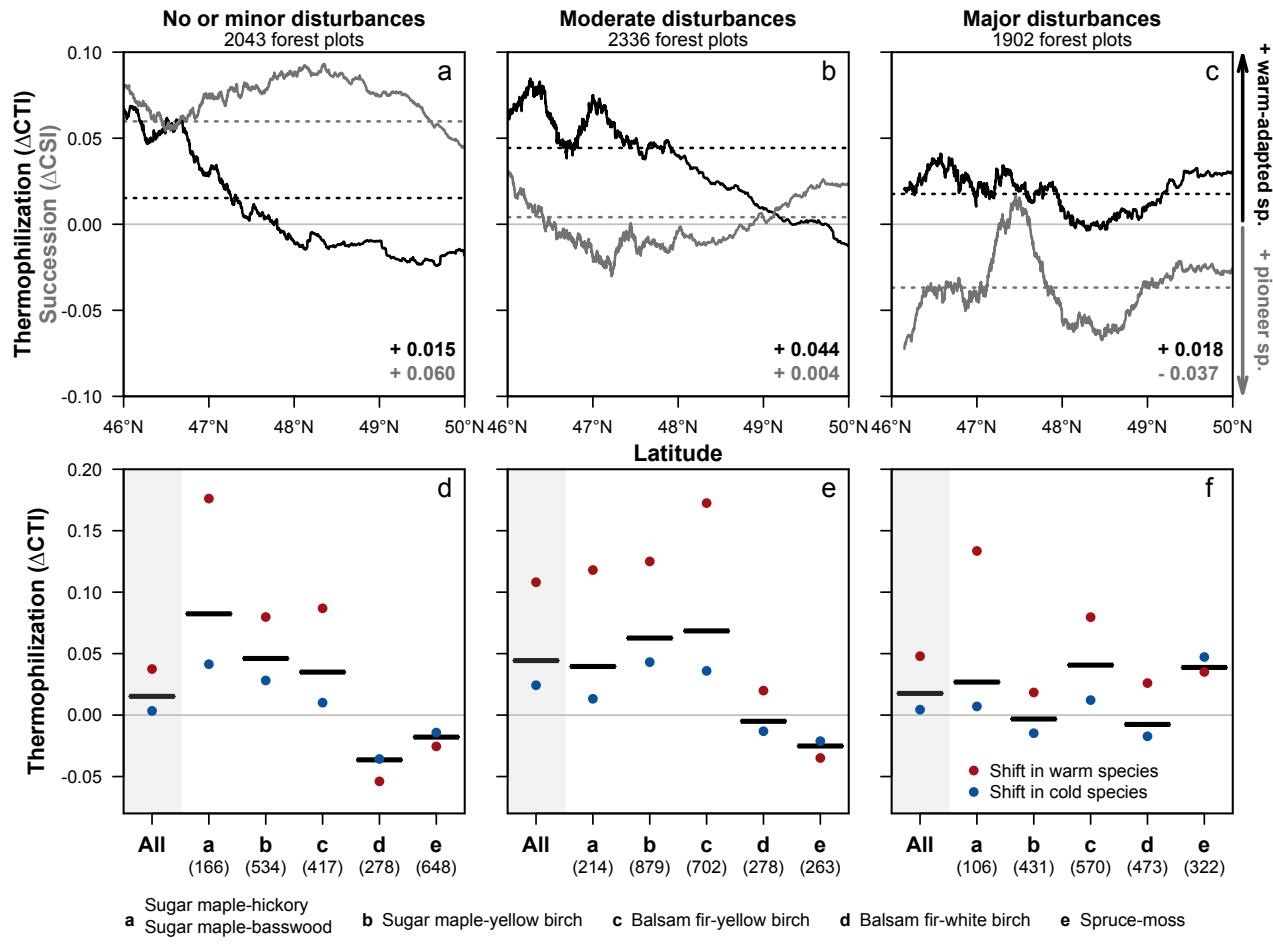
621 **Figure 3.** Frequency distributions of temporal  $\beta$  diversity in forests plots by bioclimatic domains. Forests  
 622 of different disturbance levels are stacked on top of each other. The values written in the panels are the  
 623 mean temporal  $\beta$  diversity values followed by the percentage of losses in parentheses. The distribution of  $\beta$   
 624 diversity values is skewed to the right for higher disturbance levels.



625

626 **Figure 4.**

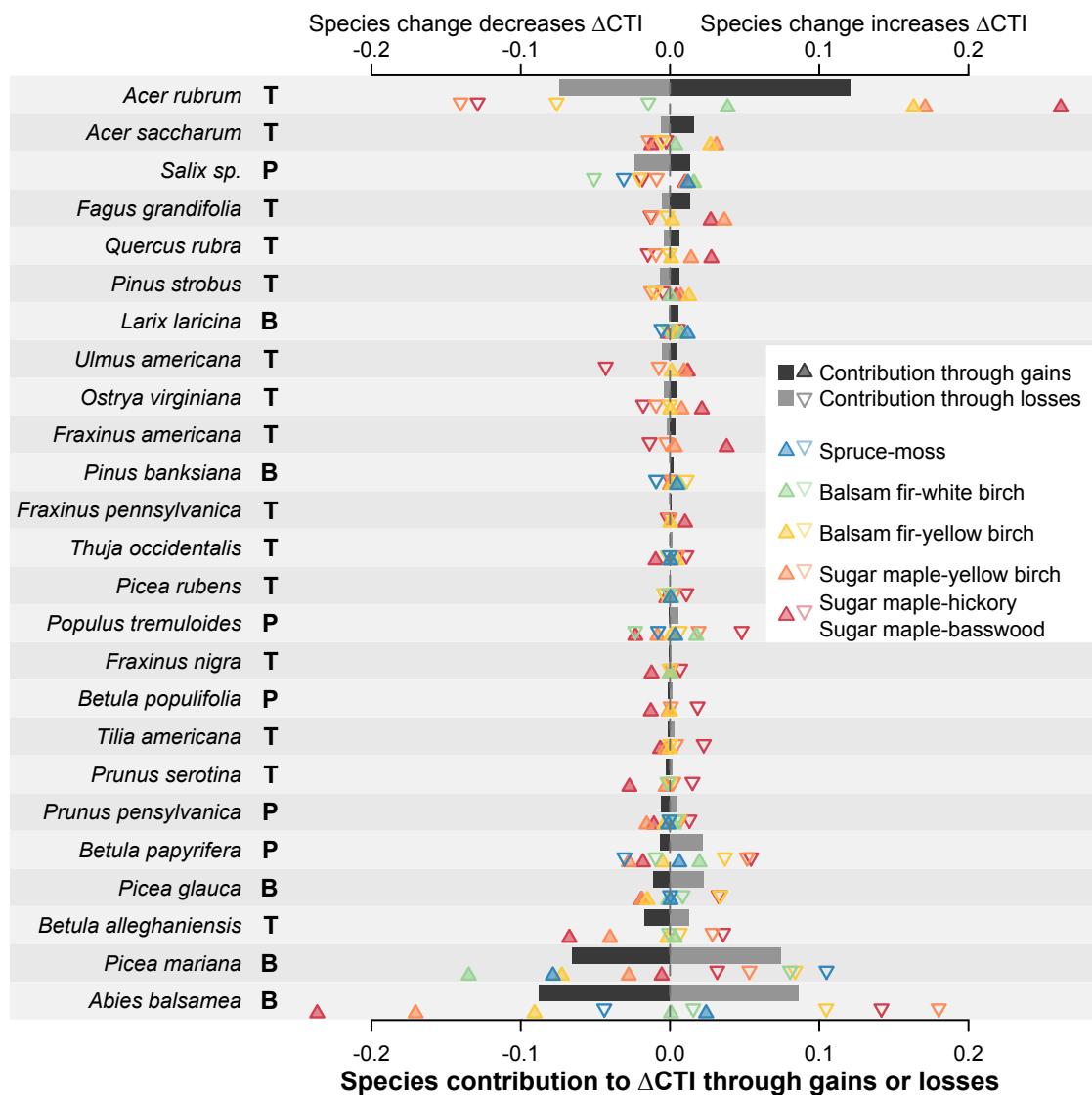
627 Slope coefficients from multiple regression models for (a) temporal  $\beta$  diversity, (b) species gains and (c)  
628 species losses and the corresponding variation partitioning diagrams (d, e, f). Error bars represent one  
629 standard error of the slope coefficient. For the regression models, only the selected predictors are shown.  
630 Subscripts following disturbance predictors indicate their levels of intensity: 1 Moderate and 2 Major. **In**  
631 **each variation partitioning, significance of each unique fraction was tested using 9999**  
632 **permutations, while shared fractions cannot be tested.** Stars indicate the level of significance of the  
633 p-values (\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ). See Table 1 for description of the predictor variables.



634

635 **Figure 5.**

Thermophilization (i.e., change in community temperature index,  $\Delta\text{CTI}$ ) and successional process (i.e., change in community shade index,  $\Delta\text{CSI}$ ) of forests for different levels of disturbance. In the upper panels (a, b, c), the latitudinal trends in  $\Delta\text{CTI}$  (black curve) and  $\Delta\text{CSI}$  (grey curve) are based on moving averages computed on the indices against latitude (window size of 400 plots). Positive values indicate an increase in warm-adapted species (black) or in late-successional species (grey) over time. The dotted lines in (a, b, c) represent the mean  $\Delta\text{CTI}$  (black) and  $\Delta\text{CSI}$  (grey) values for different levels of disturbance. In the lower panels (d, e, f), thermophilization of the forest plots across the study area (All) and by bioclimatic domain. Temporal shift of the mean (black line), left tail (red) and right tail (blue) of the distribution of CTI, for which positive values indicate overall thermophilization, increases of warm-adapted and decreases of cold-adapted species, respectively.



646

647 **Figure 6.**

648 Individual species contributions, through gains and losses, to thermophilization of forest communities  
 649 across the study area and for each bioclimatic domain. The rectangles represent the mean contributions of  
 650 given species through gains (dark grey) or losses (light grey) across the study area, while the colored  
 651 triangles represent the mean contributions of given species through gains (solid) or losses (empty) by  
 652 domain. **For example, the ΔCTI increased by an average of 0.12 for all plots where *Acer***  
**653 *rubrum* has increased in abundance (dark grey bar), whereas the ΔCTI also increased by an**  
**654 average of 0.09 for all plots where *Abies balsamea* has decreased in abundance (light grey**  
**655 bar).** Letters next to species names correspond to (T)emperate, (P)pioneer and (B)oreal species. Only  
 656 species that contributed more than 0.01 in at least one domain are shown.