

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

³

⁴ **Running title:** Tree community responses to climate change

⁵ **Abstract**

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

¹¹ **Location** Québec, Canada

¹² **Time period** 1970–2016

¹³ **Taxa studied** Trees

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

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

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

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

³² **Keywords**

³³ Beta diversity, Climate change, Community temperature index, Community temporal change,

³⁴ 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 β diversity (Legendre, 2019) over 6000 resurveyed communities between
112 a historical (1970–1980) and a contemporary (2000–2016) period. Temporal β 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 β 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 52nd parallel, since 1970 by
123 the Ministère des forêts, de la Faune et des Parcs (Fig. 1; MFFP, 2016). For each plot, we compared the
124 tree composition between the first and last surveys. To maximize the time interval between surveys, only
125 plots that were inventoried in two distinct time periods (historical period: 1970–1980; contemporary period:
126 2000–2016) were retained for analysis. We disregarded plots that were subjected to active reforestation
127 during the study period as we were interested in compositional changes resulting from natural
128 post-disturbance recolonization. We also eliminated plots without trees (due to a disturbance) either at
129 their first or last year of sampling. This yielded a subset of 6281 plots analyzed (Fig. 1), with a median of
130 35 years between surveys (1st quartile: 33 and 3rd quartile: 41 years).

131 Within each circular plot (400 m²), trees larger than 9 cm in diameter at breast height (DBH) were
132 identified to species, measured and their vitality noted (MFFP, 2016). The selected plots included a total
133 of 51 tree species, from which we eliminated introduced and planted species as well as species with a single
134 occurrence, yielding 45 analyzed species (Table S1). Rare species were included in the analyses because
135 even the rarest can contribute to temporal changes; their identity does not bias our analyses and, contrary
136 to mobile species, there is little detection bias in tree surveys. Each species was assigned according to their

137 functional traits to one of three species groups of interest: boreal (6 species), pioneer (9 species) and
138 temperate (30 species; see Table S1 for details).

139 Environmental variables

140 The annual past climatic conditions, covering a period from 1960 to 2013, were extracted using a 2 km² (60
141 arc sec) resolution grid for the entire study area using the ANUSPLIN climate modeling software
142 (<http://cfs.nrcan.gc.ca/projects/3/8>; McKenney *et al.*, 2011). Bioclimatic variables hypothesized to
143 influence tree survival were intercepted at plot locations: the mean temperature and total precipitation
144 during the growing season, minimum temperature of the coldest period, maximum temperature of the
145 warmest period and the annual climate moisture index (CMI; difference between annual precipitation and
146 potential evapotranspiration). From these bioclimatic variables, we derived different predictors (see Table 1
147 for details). Over the past four decades, growing season temperature and precipitation have increased by
148 0.14 °C/decade and 9.5 mm/decade, respectively, while CMI has decreased by 1.2 cm/decade (Fig. S1).

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

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

162 Analysis

163 β diversity

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

168 $\beta = (B + C)/(A + B + C)$ where, for n species:

169 $A = \sum_{j=1}^n a_j$: unscaled similarity. a_j represents the abundance of species j that is common between t_1 and
170 t_2 ;

171 $B = \sum_{j=1}^n b_j$: unscaled species abundance losses. b_j represents the abundance of species j present at t_1 but
172 not at t_2 ; when species j increases in abundance, $b_j = 0$;

173 $C = \sum_{j=1}^n c_j$: unscaled species abundance gains. c_j represents the abundance of species j present at t_2 but
174 not at t_1 ; when species j decreases in abundance, $c_j = 0$;

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

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

183 $\beta_{\text{boreal}} = (B_{\text{boreal}} + C_{\text{boreal}})/(A + B + C)$, with $(A + B + C)$ the denominator computed over all tree
184 species. As a consequence, β can be decomposed as follows:

185 $\beta = \beta_{\text{boreal}} + \beta_{\text{pioneer}} + \beta_{\text{temperate}}$

186 Assessing the relative importance of drivers of community changes

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

191 In order to quantify the variation explained by climate change and disturbances, while controlling for the
192 baseline climate gradient and different time intervals, we classified our predictor variables into three
193 subsets: baseline conditions, climate change and disturbances (see Table 1). We then generated regression
194 models predicting β , gains and losses, for each of the three subsets. We also tested relevant interactions
195 between disturbance and climate predictors: Natural (old and recent) $\times \Delta\text{CMI}$ and Natural (old and
196 recent) $\times \Delta\text{Temp}$, because drought and heat stress can increase natural disturbance frequency; Harvest
197 (old and recent) $\times \Delta\text{Temp}$, because the effect of harvest was hypothesized to be influenced by warmer
198 temperatures. A forward selection of explanatory variables based on two stopping criteria (significance
199 level α and global R^2_{adj} ; Blanchet *et al.*, 2008) was performed to obtain parsimonious regression models for

200 each of the three subsets. The predictors had been previously standardized to z -scores to allow comparison
201 of their slope coefficients. We also ensured that residuals met the assumptions of normality and
202 homoscedasticity.

203 We assessed the unique contributions of each predictor subset (baseline conditions, climate change and
204 disturbances) as well as their shared effect on forest community changes using variation partitioning
205 analysis on the parsimonious regression models.

206 **Functional index of community change**

207 To test whether or not climate warming contributed to community changes, we examined the temporal
208 changes in the distribution of species temperature values within every plot. We quantified such changes by
209 the shift in the mean (Community Temperature Index or CTI; Devictor *et al.*, 2008), as well as the lower
210 10th percentile and the upper 90th percentile of this plot-level distribution (De Frenne *et al.*, 2013).

211 To compute these metrics, we first combined climate and tree occurrence data to obtain species
212 temperature distributions. Specifically, we overlaid interpolated climate data (mean annual temperature
213 averages for 1970–2000 at a spatial resolution of 1 km², available online <http://worldclim.org/version2>;
214 Fick & Hijmans, 2017) and occurrence data from multiple forest inventory databases of eastern North
215 America (collected in the QUICC-FOR project; <https://github.com/QUICC-FOR>) for the focal species.
216 The mean annual temperature for each occurrence was extracted to infer species temperature distributions.
217 Following Devictor *et al.* (2008), we used the mean of these temperature values as a proxy for species
218 thermal preference (Species Temperature Index, STI, in Celsius; Table S1). For each plot in each time
219 period, the CTI was then calculated as the mean of the STI values weighted by the abundances of the
220 species present in that plot.

221 Following De Frenne *et al.* (2013), we computed the 10th and 90th percentiles of the plot-level temperature
222 distributions, which correspond to the cold and warm tails of the distribution. To do so, for every plot and
223 every species, we sampled 1000 temperature values per individual from the species' temperature
224 distribution. The plot-level temperature distributions corresponds to the combination of the temperature
225 values for all individuals in a given plot. From these distributions, which accounted for species composition
226 and their relative abundances, we computed the 10th and 90th percentiles. Note that contrary to De Frenne
227 *et al.* (2013), we used the entire distribution for each species instead of modeling species thermal response
228 curves because numerous species distributions were not Gaussian.

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

$$232 \Delta CTI = \frac{CTI_{t_2} - CTI_{t_1}}{t_2 - t_1} \times 10$$

233 The shifts in the cold and warm tails were computed in the same way as for the shifts in mean CTI. A
234 positive value of Δ CTI indicates an overall thermophilization of the tree community in degrees per decade.
235 A positive shift of the cold tail indicates a decrease of cold-adapted species, while a positive shift of the
236 warm tail indicates an increase of warm-adapted species; both result in thermophilization.

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

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

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

255 Results

256 Temporal β diversity

257 The mean temporal β diversity was 0.56 over all sites in the study area ($n = 6281$), and these temporal
258 changes in composition were attributable to slightly more gains in abundances (52.5%) than losses (47.5%);
259 Fig. 2a). Temporal β diversity varied along a latitudinal gradient; it tended to decrease northward,
260 reaching its maximum at 48°N of latitude, which corresponds to the northern limit of the balsam fir-yellow
261 birch domain, the ecotone between boreal and deciduous forests. North of the 49°N of latitude, in the
262 spruce-moss domain, temporal β changes were dominated by losses whereas, south of this limit, gains
263 prevailed. Latitudinal patterns were also visible in the contributions of the three species groups to
264 temporal β (Fig. 2b). At minor disturbance level, community changes were mainly determined by gains in

265 temperate species south of 47°N and by gains in boreal species north of 47°N (where boreal species are the
266 most abundant species group).

267 The magnitude of compositional changes in forests was highly influenced by disturbances (Figs 2b-d, 3, S4).
268 In each domain, the β diversity values of highly disturbed forests are strongly skewed (Fig. 3). The mean
269 temporal β was 0.43 at minor disturbance level, whereas it was 0.53 at moderate disturbance level and
270 reached 0.74 at major disturbance level (all domains combined). Moreover, the fraction of changes
271 attributed to losses was generally lower at minor, than at moderate and major disturbance levels (minor:
272 41%; moderate: 48%; major: 50%, all domains combined), especially for the spruce-moss domain (minor:
273 40%; moderate: 73%; major: 64%; Fig. 3). At minor disturbance level, both boreal and temperate species
274 groups experienced more gains than losses (Fig. 2b), while at major disturbance level, we observed a strong
275 surge in losses of boreal tree species along with larger gains of pioneer species (Fig. 2d). In contrast, gains
276 in temperate species were higher at moderate disturbance level (Fig. 2c). Some species have experienced
277 great changes in abundance and occurrence throughout these domains, namely *Picea mariana*, *Acer*
278 *rubrum*, *Betula alleghaniensis*, *Fagus grandifolia* and *Populus tremuloides*, and likely contributed largely to
279 the pattern of temporal β diversity (Fig. S4).

280 Drivers of temporal changes

281 Once combined, predictors from the three subsets (baseline, climate change and disturbances; Table 1)

282 explained together 40% of the variation of temporal β diversity, and 30% for both gains and losses (Fig. 4).

283 As revealed by the variation partitioning analyses, community temporal changes were mainly driven by

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

286 Overall, disturbances enhanced temporal β diversity, with old major harvest (Old harvest₂) being the most
287 important driver, followed by old major natural disturbances (Old natural₂; Fig. 4a-c). Interestingly, while
288 recent disturbances (natural and harvest) promoted losses and reduced gains, old disturbances had the
289 opposite effect (Fig. 4b-c). As time-since-disturbance increased and the forests grew old (Age), forest
290 composition changed less and colonization by new individuals became less frequent (Fig. 4a-b).

291 Regression models provided only weak evidence of climate change effect on forest community changes.

292 Mainly, extreme minimum climate moisture index (CMI min) and extreme cold (Temp min) contributed to
293 community changes through losses in tree abundances (Fig. 4a,c). Increase in precipitation (Δ Precip)

294 favored tree gains. Only one interaction was retained, which indicated that stronger warming (Δ Temp)

295 mitigated the effect of recent moderate harvest (Recent harvest₁) on losses. Variables related to baseline
296 conditions were more important than climate change variables; the effects of mean temperature (Temp)

297 and total precipitation (Precip) likely reflect the latitudinal gradient in community change, while the effect

298 of time interval between surveys (Δ Time) reflects the fact that community change takes time.

299 **Changes in community temperature and shade indices**

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

305 Thermophilization was significantly larger in moderately disturbed forests (Δ CTI = +0.044 °C/decade)
306 than in undisturbed (+0.015 °C/decade) or highly disturbed forests (+0.018 °C/decade; ANOVA $F_{2,6278} =$
307 14.59, p -value < 0.001; a post-hoc Tukey test showed significantly higher Δ CTI at moderate disturbance
308 than at the other levels). Moreover, the latitudinal pattern of Δ CTI varied with the disturbance level: the
309 thermophilization in moderately disturbed forests extended further north than in undisturbed forests,
310 exceeding 48°N, up in the balsam fir-yellow birch domain (Fig. 5b,e), while at major disturbances,
311 thermophilization was more or less constant across the latitudinal gradient (Fig. 5c,f). Despite the
312 influence of disturbances on thermophilization, change in CTI was weakly explained by our complete set of
313 environmental predictors (R^2_{adj} ca. 3%). Moreover, the relationship between thermophilization and climate
314 change predictors was surprisingly weak ($R^2_{adj} < 1\%$), with no correlation at all with temperature change.

315 The analysis of Δ CSI revealed that major disturbances resulted in a large decrease in CSI (Fig. 5c; mean
316 Δ CSI = -0.037), consistent with higher gains in pioneer species (Fig. 2), while minor disturbances led to
317 an increase in CSI (Fig. 5a; mean Δ CSI = +0.060). Both influenced by disturbances, Δ CTI and Δ CSI
318 were negatively correlated (Pearson $r = -0.2$, p -value < 0.001) indicating that the two ecological processes
319 are intertwined. However, Δ CTI was more strongly correlated to gains in temperate species and losses of
320 boreal species than to gains in pioneer species (Fig. S6), which suggests that thermophilization was not
321 trivially driven by successional processes.

322 Community thermophilization was asymmetrical and mainly driven by larger gains in warm-adapted
323 species, as indicated by the larger increases in the warm-tail of the temperature distributions than in the
324 cold-tail (Fig. 5d-f). Moderate disturbances exacerbated this effect from the sugar maple-yellow birch up
325 to the balsam fir-white birch domain (larger increase in the warm tail; Fig. 5e). The positive correlation
326 between Δ CTI and gains in temperate species in all domains, except in the spruce-moss, also corroborates
327 the role of warm-adapted species (Fig. S6).

328 Only a few species contributed substantially to community thermophilization (Fig. 6). Gains of *Acer*
329 *rubrum* and *Acer saccharum*, as well as losses of *Abies balsamea* and *Picea mariana*, contributed strongly to
330 the thermophilization of all bioclimatic domains. In addition to the change of these four species, the losses

331 of *Betula papyrifera* and *Picea glauca* also played a key role in the thermophilization of ecotonal forests in
332 the balsam fir-yellow birch domain. Moreover, temperate species such as *Fagus grandifolia*, *Quercus rubra*
333 and *Fraxinus americana* contributed mostly to the thermophilization of southern domains (Fig. 6) where
334 their abundance has increased (Fig. S4). In contrast, the surge in CTI north of the 49°N (spruce-moss) in
335 highly disturbed forests (Fig. 5) was likely due to the replacement of boreal species by pioneer species (Fig.
336 S6), such as *Betula papyrifera* and *Salix spp.* (Fig. 6).

337 Discussion

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

345 Impact of disturbances on tree community changes

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

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

361 Climate-induced change in tree community

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

373 Feedback between climate change and disturbances

374 Our most striking finding is that community thermophilization was amplified by moderate disturbances.
375 Our combined analysis of change in CTI and CSI also allowed us to disentangle climate change effects from
376 successional processes, highlighting that the observed thermophilization was not simply correlated with the
377 replacement of boreal by pioneer species. Our work provides a broad-scale community perspective on the
378 role played by disturbances in promoting northward migration of tree species, which is in agreement with
379 the conclusions of recent empirical (Boucher *et al.*, 2006; Leithead *et al.*, 2010) and simulation (Vanderwel
380 & Purves, 2014; Wang *et al.*, 2015) studies.

381 Disturbances likely accelerate forest changes by reducing competition and providing establishment
382 opportunities to warm-adapted temperate tree species (Leithead *et al.*, 2010; Svenning & Sandel, 2013).
383 Indeed, in the absence of disturbances, trees grow slowly, their mortality rates are low and competition for
384 space and light is strong, thus preventing warm-adapted species from colonizing new areas, despite the
385 suitability of climatic conditions; community thermophilization is consequently very slow. Moderate
386 disturbances, however, remove individuals of resident species and reduce competition, which enhances the
387 replacement of boreal by temperate trees, thereby increasing the thermophilization rate. Furthermore,
388 moderate disturbances can also modify local microclimates (De Frenne *et al.*, 2013; Stevens *et al.*, 2015)
389 which may alter the survival rates of tree saplings. In contrast, major disturbances only favor early
390 successional species. Such findings echo the well-known intermediate disturbance hypothesis (Connell,
391 1978); as in the classical hypothesis, intermediate disturbances lower interspecific competition but here, not
392 only do they increase local species richness (not shown), but they also accelerate ecological transitions.

393 Our complete set of predictors poorly explained the observed forest thermophilization, likely because this

394 process was highly variable among localities. Forest composition is thus changing as expected under
395 climate warming, but thermophilization does not appear to be directly driven by rising temperatures. As
396 suggested by Renwick & Rocca (2015), we surmise that, as climate warms up, moderate disturbances could
397 foster punctuated and episodic migration of warm-adapted species in localities where conditions are
398 otherwise favorable. However, it raises questions about the specific conditions in which the
399 thermophilization process can effectively take place. Further analyses are required to determine which
400 factors can trigger (e.g. type, size, frequency of disturbances) or constrain (e.g. soil type, competition,
401 precipitation) the invasion by warm-adapted species.

402 Our results contrast with those of Boisvert-Marsh *et al.* (2019) who found that climate was more
403 important than disturbances in explaining tree sapling recruitment at their northern limit in Québec. This
404 suggests that the pattern we uncovered might be primarily caused by an increase in abundance of species
405 already present rather than by new colonization. Danneyrolles *et al.* (2019) also found that forest
406 compositional changes over the last centuries (between 1790–1900 and 1980–2010) in deciduous forests of
407 southern Québec were largely driven by land-use changes, favoring more disturbance-adapted tree species,
408 but did not find any signs of thermophilization. In contrast to our study that covers a period of
409 pronounced climate warming, Danneyrolles *et al.* (2019) investigated a period dominated by land-use and
410 population changes which may explain the absence of thermophilization signal in their results. In light of
411 their results, we hypothesize that some of the thermophilization we reported here in the sugar maple
412 domains is in fact the result of secondary succession after historical disturbances.

413 Species contributions to community thermophilization

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

425 The magnitude of change in CTI varied by bioclimatic domains reflecting the spatial patterns of species
426 changes in response to climate warming and disturbances. The thermophilization of the sugar maple

427 domains was facilitated by the presence of a large pool of warm-adapted species. When disturbed, these
428 southernmost domains had lower thermophilization because they gained pioneer species. We showed that
429 the balsam fir-yellow birch domain was particularly sensitive to moderate disturbances. The
430 thermophilization of this ecotonal zone was primarily due to increase in *Acer rubrum* and, to a lesser
431 extent, increase in *A. saccharum* and decrease in *Abies balsamea* and *Betula papyrifera*. Although *A.*
432 *rubrum* is already well established in this domain, our results suggest that it will continue to thrive and
433 spread, likely in response to a combination of climate warming, historical and recent disturbances as well as
434 natural forest dynamics. *A. saccharum* is presently constrained on hilltops in the southern part of this
435 domain (Gosselin, 2002), but our results suggest that it could expand in nearby habitats. In contrast, the
436 decrease in CTI in the balsam fir-white birch and spruce moss domains could be explained by the fact that
437 temperate species are rare in these two northernmost domains, hence changes in CTI resulted mostly from
438 a dynamic of replacement between pioneer and boreal species in response to disturbances. *A. rubrum* was
439 the only temperate species to increase in the balsam fir-white birch domain (Fig. S4) and, when it did, it
440 contributed to increase its CTI (Fig. 6). Similarly to *A. saccharum*, *A. rubrum* distribution is spatially
441 constrained within the balsam fir-white birch domain (Blouin & Berger, 2008) and will likely expand from
442 existing existing patchy populations in the future.

443 Long-term perspectives for the temperate-boreal ecotone

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

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⁵⁸¹ **Data Accessibility Statement**

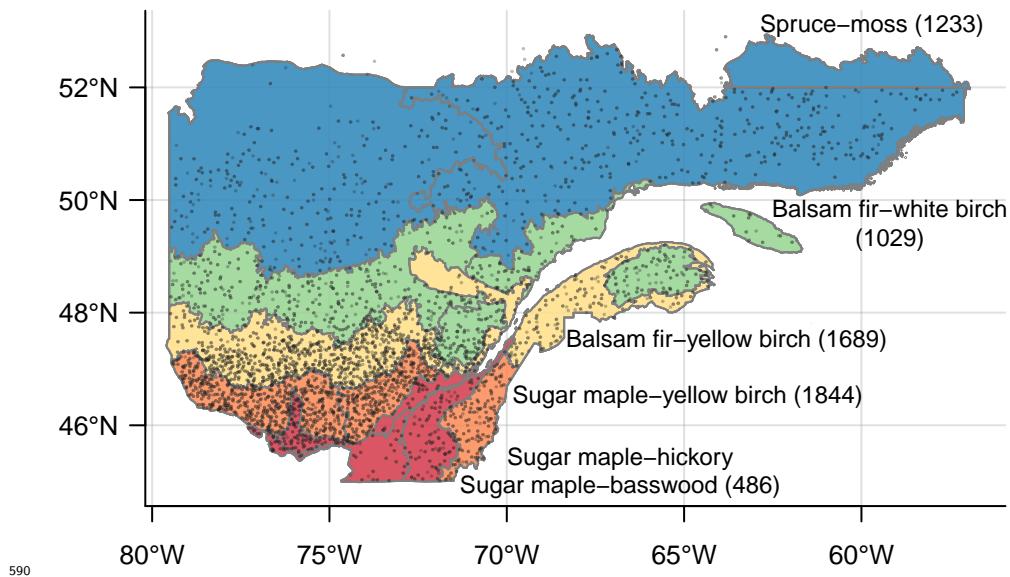
⁵⁸² The complete forest inventory dataset used in this study is available online at
⁵⁸³ <https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui>. All code required to repeat the analyses will be made available online on
⁵⁸⁴ GitHub.
⁵⁸⁵

586 **Tables**

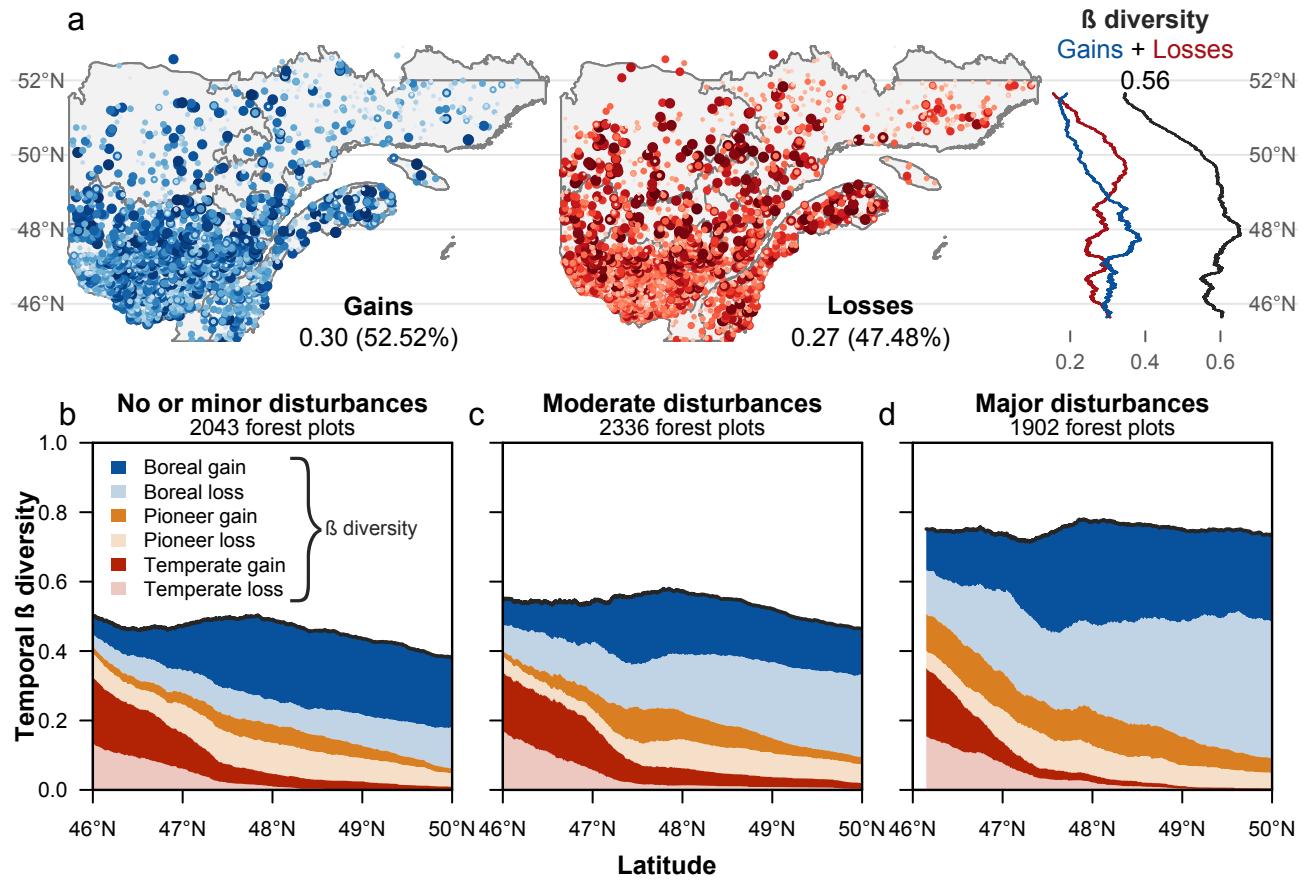
587 **Table 1.** Description of the predictors used in the multiple linear regression models. See Table S2 for
 588 details about disturbance types.

Variable name	Variable description
Baseline conditions	
Temp, Temp ²	Mean temperature during growing season and its second order polynomial. 10-year average prior to first survey of each plot (°C).
Precip, Precip ²	Total precipitation during growing season and its second order polynomial. 10-year average prior to first survey of each plot (mm).
ΔTime	Time interval between first and last measurements (years).
Climate change	
ΔTemp	Slope between Temp and time (°C/y).
ΔPrecip	Slope between Precip and time (mm/y).
ΔCMI	Slope between Climate Moisture Index and time (cm/y).
Temp min	Extreme minimum temperature. Difference between minimum and mean temperature of the coldest period (°C).
Temp max	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 (cm), as a proxy of drought.
Disturbances	
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).

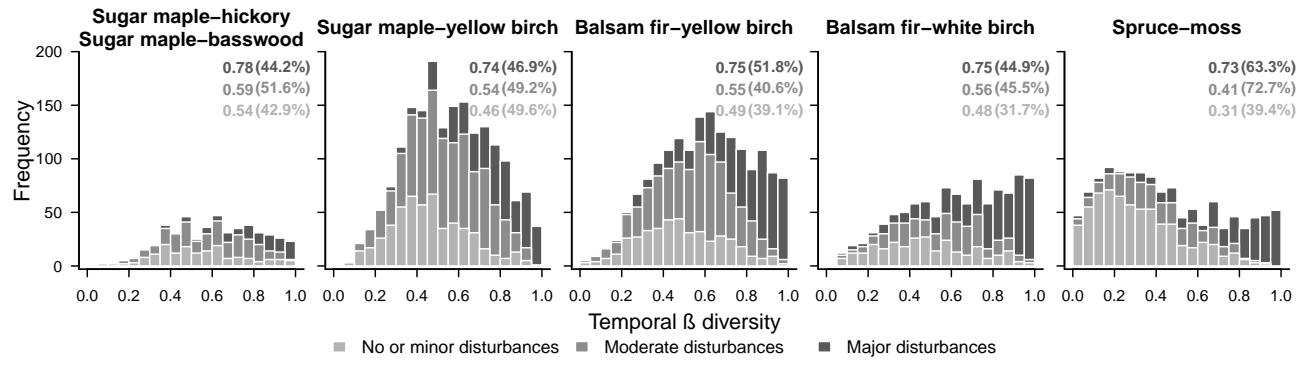
589 **Figures**



590 **Figure 1.** Locations of the 6281 forest inventory plots in meridional Québec, Canada. Colors delimit the
591 six bioclimatic domains. The two southernmost domains (orange) were combined in our analyses. The
592 number of forest plots in each domain is written in parentheses.
593

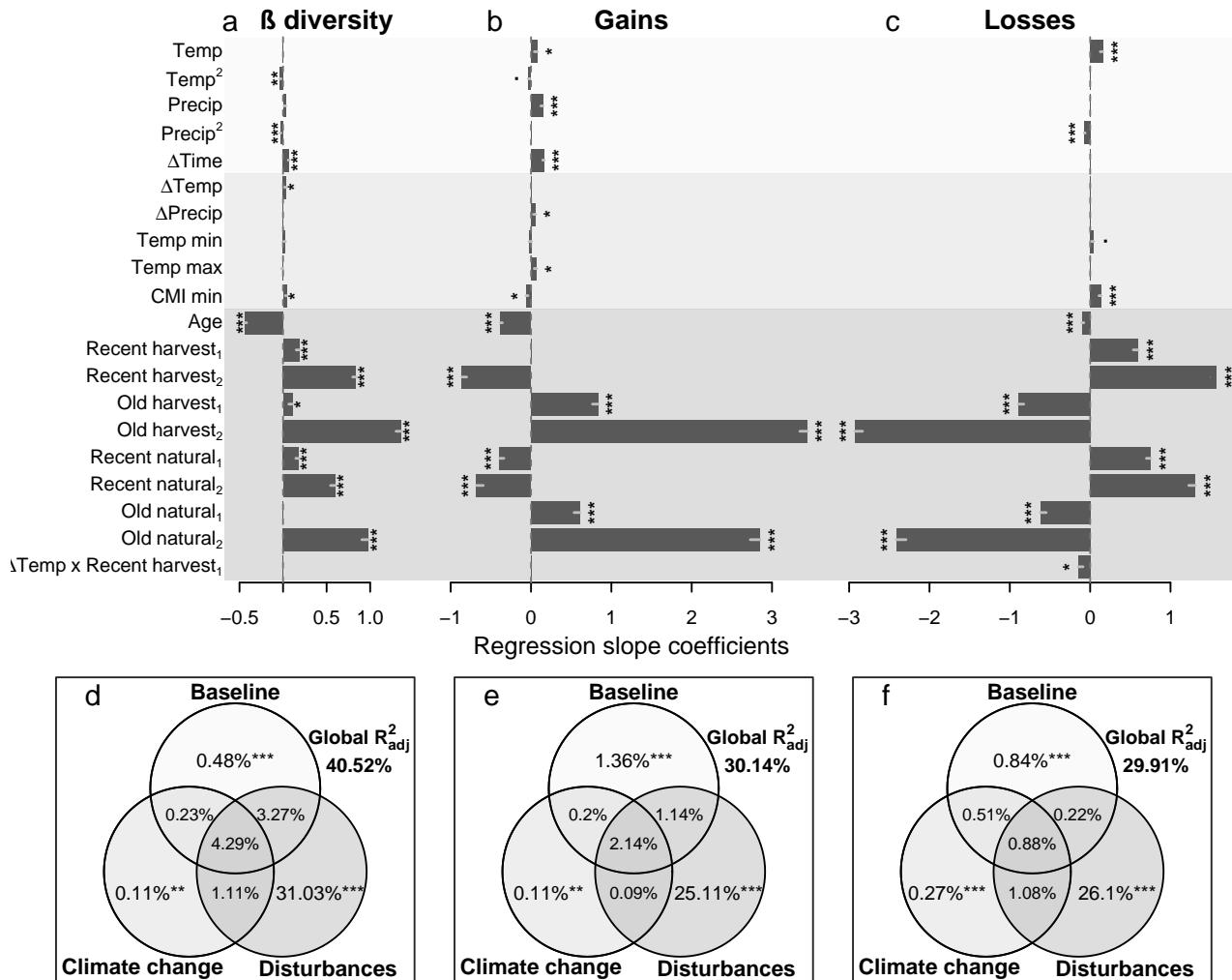


594 **Figure 2.** Maps of gains and losses in tree abundances (a) and latitudinal trends in temporal β diversity,
595 decomposed into gains (blue) and losses (red) of boreal, pioneer and temperate trees, for different levels of
596 disturbance (b-d). The sizes and colors of the points on the maps are proportional to the values of interest.
597 The latitudinal trends in temporal β in a-d are based on moving averages computed on each index against
598 latitude (window size of 500 plots in panel a and 400 plots in panels b-d), to smooth out local-scale
599 fluctuations and highlight broad-scale trends.
600



601

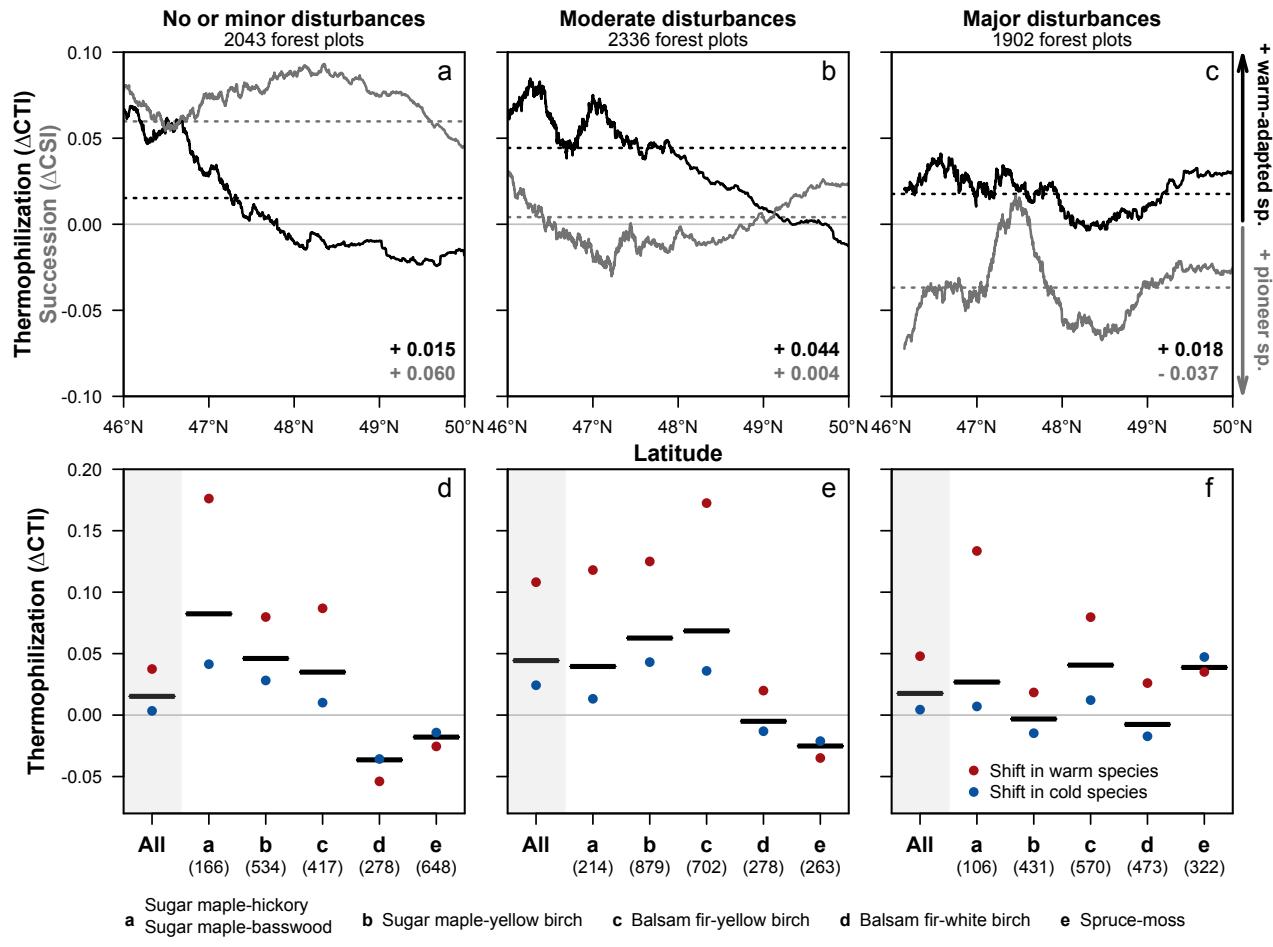
602 **Figure 3.** Frequency distributions of temporal β diversity in forests plots by bioclimatic domains. Forests
 603 of different disturbance levels are stacked on top of each other. The values written in the panels are the
 604 mean temporal β diversity values followed by the percentage of losses in parentheses. The distribution of β
 605 diversity values is skewed to the right for higher disturbance levels.



606

607 **Figure 4.**

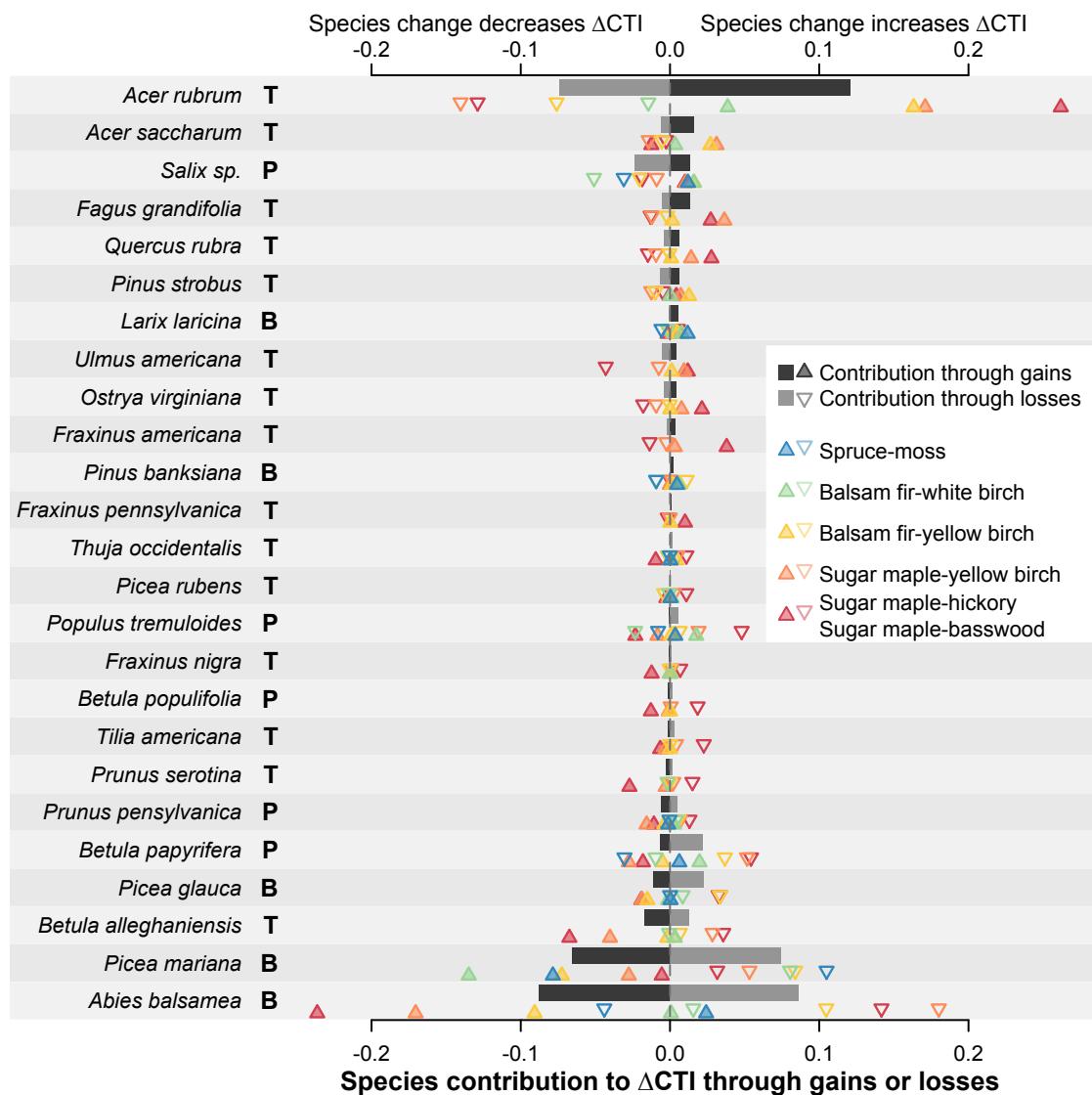
608 Slope coefficients from multiple regression models for (a) temporal β diversity, (b) species gains and (c)
 609 species losses and the corresponding variation partitioning diagrams (d, e, f). Error bars represent one
 610 standard error of the slope coefficient. For the regression models, only the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



615

616 **Figure 5.**

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



627

628 **Figure 6.**

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