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

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

4 Running title: Tree community responses to climate change

5 Abstract

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

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

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3 ²⁶ gains and losses of a few tree species contributed to this community-level shift.
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5 **Conclusions** Our study provides evidence that disturbances can strongly modify tree community
6 responses to climate change. Moderate disturbances, such as harvesting, may reduce competition and
7 facilitate gains of warm-adapted species, which then accelerate thermophilization of tree communities
8 under climate change. Although accelerated by disturbances, community thermophilization was driven by
9 the gains and losses of a small number of species, notably gains of maples.
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14 **Keywords**
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17 ³³ Beta diversity, Climate change, Community temperature index, Community temporal change,
18 ³⁴ Disturbances, Forest, Québec, Temperate-boreal ecotone, Thermophilization.
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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,

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3 70 the frequency and intensity of natural disturbances can increase as an indirect effect of climate change
4 71 (Seidl *et al.*, 2017).
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7 72 Although it is widely assumed that positive synergy between disturbances and climate warming should play
8 73 a key role in contemporary tree community changes, empirical studies have reached conflicting conclusions.
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10 74 For example, comparison of early industrial (early 1900) to contemporary forests in the Bas-Saint-Laurent
11 75 region of Québec showed that logging practices turned old-aged conifer forests into young mixed and
12 76 deciduous forests (Boucher *et al.*, 2006, 2009). Leithead *et al.* (2010) also observed that the establishment
13 77 of southern temperate species in the temperate-boreal ecotone of northern Ontario increased with the size
14 78 and age of canopy gaps. While Boisvert-Marsh *et al.* (2019) found that climate change outweighs
15 79 disturbances in explaining latitudinal shifts of tree saplings in Québec in the last decades, Danneyrolles *et*
16 80 *al.* (2019) found larger impacts of anthropogenic disturbances than climate warming on forest
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18 81 compositional changes in southern Québec over the last centuries. Hence, to anticipate and adapt to future
19 82 forest changes, large-scale empirical studies are required in order to unravel individual and aggregated
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21 83 impacts of multiple stressors on forest composition.
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25 84 Even though disturbances may mask slow community responses to climate change, these two drivers leave
26 85 distinguishable signatures on communities. Climate warming should favor warm-adapted species at the
27 86 expense of cold-adapted species, leading to a “thermophilization” of communities (De Frenne *et al.*, 2013;
28 87 Savage & Vellend, 2015). Conversely, disturbances should increase the prevalence of young forests
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30 88 dominated by shade-intolerant species (Boucher & Grondin, 2012; Savage & Vellend, 2015). Hence,
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32 89 analyzing shifts of relevant functional traits **and ecological affinities** in communities using large-scale
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34 90 monitoring data should disentangle the role of different environmental drivers in shaping communities
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36 91 (Violle *et al.*, 2007). For instance, the Community Temperature Index (CTI) has been used to measure
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38 92 thermophilization in various communities, such as plants, trees, birds and fishes (Devictor *et al.*, 2008;
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40 93 Cheung *et al.*, 2013; De Frenne *et al.*, 2013; Feeley *et al.*, 2013; Gaüzère *et al.*, 2015; Becker-Scarpitta *et al.*,
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42 94 2019; Danneyrolles *et al.*, 2019). The CTI is a community abundance-weighted average of the Species
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44 95 Temperature Indices (STI; proxy for species thermal preference computed as the mean temperature of a
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46 96 given species distribution). Because CTI reflects the relative abundance of warm-adapted (high STI) vs
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48 97 cold-adapted species (low STI), it is expected to increase following climate warming if species are moving
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50 98 according to their temperature requirements.
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54 99 Here, we quantify the temporal shifts in tree community composition in the temperate-boreal ecotone, and
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56 100 test whether recent climate change is impacting forest composition. We analyzed data from a long-term
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58 101 forest inventory program across meridional Québec, where vegetation ranges from northern hardwood
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60 102 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

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3 experienced different levels of disturbances along a broad latitudinal gradient. We address four questions:
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5 (1) how has the composition of forest communities changed during the last decades across different
6 bioclimatic domains? (2) What is the relative contribution of climate change and disturbances to these
7 temporal community changes? (3) Have forest communities experienced a thermophilization during the last
8 decades? And can disturbances accelerate community thermophilization? (4) How do gains and losses of
9 specific tree species contribute to thermophilization?
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12 Specifically, we measured temporal β diversity (Legendre, 2019) over 6000 resurveyed communities between
13 a historical (1970–1980) and a contemporary (2000–2016) period. Temporal β diversity, which describes the
14 temporal dissimilarity in community composition between survey times, was decomposed into gains and
15 losses to investigate the underlying mechanisms of change. Then, we quantified the effects of climate
16 change and disturbances on temporal β diversity using multiple regressions and variation partitioning.
17 Using community indices for temperature (CTI) and shade tolerance (CSI), we quantified community-level
18 changes associated with thermophilization and succession and compared these changes among levels of
19 disturbances. We finally quantified the species-specific contributions to thermophilization.
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25 Methods

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27 Study area

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29 To analyze large-scale temporal changes in forest community composition, we used the Québec forest
30 inventory plots that have been sampled in six bioclimatic domains, south of the 52nd parallel, since 1970 by
31 the Ministère des forêts, de la Faune et des Parcs (Fig. 1; MFFP, 2016). **For each plot, we compared**
32 **the tree composition between the first and last surveys. To maximize the time interval**
33 **between surveys, only plots that were inventoried in two distinct time periods (historical**
34 **period: 1970–1980; contemporary period: 2000–2016) were retained for analysis.** We
35 disregarded plots that were subjected to active reforestation during the study period as we were interested
36 in compositional changes resulting from natural post-disturbance recolonization. We also eliminated plots
37 without trees (due to a disturbance) either at their first or last year of sampling. This yielded a subset of
38 6281 plots analyzed (Fig. 1), with a median of 35 years between surveys (1st quartile: 33 and 3rd quartile:
39 41 years).

40 Within each circular plot (400 m²), trees larger than 9 cm in diameter at breast height (DBH) were
41 identified to species, measured and their vitality noted (MFFP, 2016). **The selected plots included a**
42 **total of 51 tree species, from which we eliminated introduced and planted species as well as**
43 **species with a single occurrence, yielding 45 analyzed species (Table S1).** Rare species were
44 included in the analyses because even the rarest can contribute to temporal changes; their identity does not
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3 bias our analyses and, contrary to mobile species, there is little detection bias in tree surveys. **Each**
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5 **species was assigned according to their functional traits to one of three species groups of**
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7 **interest: boreal (6 species), pioneer (9 species) and temperate (30 species; see Table S1 for**
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details).

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11 **Environmental variables**

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

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

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

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3 **167 Analysis**

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6 **168 β diversity**

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8 **169** For each plot, we computed temporal β diversity (Legendre, 2019), which is the dissimilarity in species
9 composition between two surveys of a given plot, by comparing local tree abundance (**i.e. number of**
10 **170 individuals**) in forest plots between the historical (1970-1980, t_1) and contemporary (2000-2016, t_2)
11 **171** periods. The dissimilarity (β) was computed using the Ružička coefficient (**Fig. S3**):
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13 **173** $\beta = (B + C)/(A + B + C)$ where, for n species:

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15 **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
16 **175** t_2 ;

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18 **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
19 **177** not at t_2 ; when species j increases in abundance, $b_j = 0$;

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21 **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
22 **179** not at t_1 ; when species j decreases in abundance, $c_j = 0$;

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24 **180** This temporal β diversity varies from 0 (community compositions at t_1 and t_2 are exactly the same) to 1
25 **181** (communities have no shared species). The use of this dissimilarity index enabled us to decompose the
26 **182** compositional change into relative gains ($C/(A + B + C)$) and losses ($B/(A + B + C)$) in tree abundances
27 **183** (**Fig. S3**). Throughout this paper, gains and losses refer to these relative metrics.

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29 **184** This additive framework allowed us to partition further the different components contributing to β
30 **185** diversity. Temporal dissimilarity in tree community can be decomposed into the dissimilarity (gains and
31 **186** losses) of different species groups of interest, here boreal, pioneer and temperate species (Table S1). The
32 **187** temporal dissimilarity of a given group, for instance boreal, relative to all species is simply:

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34 **188** $\beta_{\text{boreal}} = (B_{\text{boreal}} + C_{\text{boreal}})/(A + B + C)$, with $(A + B + C)$ the denominator computed over all tree
35 **189** species. As a consequence, β can be decomposed as follows:

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37 **190** $\beta = \beta_{\text{boreal}} + \beta_{\text{pioneer}} + \beta_{\text{temperate}}$

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39 **191 Assessing the relative importance of drivers of community changes**

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41 **192 We evaluated the effects of multiple drivers on temporal β , gains and losses using multiple**
42 **193 regressions, in combination with variation partitioning analyses (Borcard *et al.*, 1992;**
43 **194 Peres-Neto *et al.*, 2006).** For these analyses, we used a logit transformation $y' = \log(y/(1 - y))$
44 **195 of the response variables (β , gains, losses) as they were all in the standard unit range [0, 1].**

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46 **196 In order to quantify the variation explained by climate change and disturbances, while**

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3 197 controlling for the baseline climate gradient and different time intervals, we classified our
4 198 predictor variables into three subsets: baseline conditions, climate change and disturbances
5 199 (see Table 1). We then generated regression models predicting β , gains and losses, for each of the three
6 200 subsets. We also tested relevant interactions between disturbance and climate predictors:
7 201 Natural (old and recent) $\times \Delta\text{CMI}$ and Natural (old and recent) $\times \Delta\text{Temp}$, because drought
8 202 and heat stress can increase natural disturbance frequency; Harvest (old and recent) \times
9 203 ΔTemp , because the effect of harvest was hypothesized to be influenced by warmer
10 204 temperatures. A forward selection of explanatory variables based on two stopping criteria (significance
11 205 level α and global R^2_{adj} ; Blanchet *et al.*, 2008) was performed to obtain parsimonious regression models for
12 206 each of the three subsets. The predictors had been previously standardized to z-scores to allow comparison
13 207 of their slope coefficients. We also ensured that residuals met the assumptions of normality and
14 208 homoscedasticity.
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18 209 We assessed the unique contributions of each predictor subset (baseline conditions, climate change and
19 210 disturbances) as well as their shared effect on forest community changes using variation partitioning
20 211 analysis on the parsimonious regression models.
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23 212 Functional index of community change 24 25

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27 213 To test whether or not climate warming contributed to community changes, we examined the temporal
28 214 changes in the distribution of species temperature values within every plot. We quantified
29 215 such changes by the shift in the mean (Community Temperature Index or CTI; Devictor *et*
30 216 *al.*, 2008), as well as the lower 10th percentile and the upper 90th percentile of this plot-level
31 217 distribution (De Frenne *et al.*, 2013).
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34 218 To compute these metrics, we first combined climate and tree occurrence data to obtain
35 219 species temperature distributions. Specifically, we overlaid interpolated climate data (mean annual
36 220 temperature averages for 1970–2000 at a spatial resolution of 1 km², available online
37 221 <http://worldclim.org/version2>; Fick & Hijmans, 2017) and occurrence data from multiple forest inventory
38 222 databases of eastern North America (collected in the QUICC-FOR project;
39 223 <https://github.com/QUICC-FOR>) for the focal species. The mean annual temperature for each occurrence
40 224 was extracted to infer species temperature distributions. Following Devictor *et al.* (2008), we used the
41 225 mean of these temperature values as a proxy for species thermal preference (Species Temperature Index,
42 226 STI, in Celsius; Table S1). For each plot in each time period, the CTI was then calculated as the mean of
43 227 the STI values weighted by the abundances of the species present in that plot.
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46 228 Following De Frenne *et al.* (2013), we computed the 10th and 90th percentiles of the
47 229 plot-level temperature distributions, which correspond to the cold and warm tails of the
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3 230 distribution. To do so, for every plot and every species, we sampled 1000 temperature values
4 231 per individual from the species' temperature distribution. The plot-level temperature
5 232 distributions corresponds to the combination of the temperature values for all individuals in
6 233 a given plot. From these distributions, which accounted for species composition and their
7 234 relative abundances, we computed the 10th and 90th percentiles. Note that contrary to De Frenne
8 235 *et al.* (2013), we used the entire distribution for each species instead of modeling species thermal response
9 236 curves because numerous species distributions were not Gaussian.
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14 237 To evaluate the directionality of the changes in communities between the historical (t_1) and contemporary
15 238 (t_2) periods, we computed the temporal shift in the mean CTI, the cold tail and the warm tail (in °C per
16 239 decade) as follows:
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$$\Delta CTI = \frac{CTI_{t_2} - CTI_{t_1}}{t_2 - t_1} \times 10$$

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21 241 The shifts in the cold and warm tails were computed in the same way as for the shifts in mean CTI. A
22 242 positive value of ΔCTI indicates an overall thermophilization of the tree community in degrees per decade.
23 243 A positive shift of the cold tail indicates a decrease of cold-adapted species, while a positive shift of the
24 244 warm tail indicates an increase of warm-adapted species; both result in thermophilization.
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27 245 We also quantified how each species contributed to ΔCTI through gain or loss in abundances. Species
28 246 contributions were assessed following these steps: for each species, (1) we replaced its abundance at t_2 by
29 247 its abundance at t_1 , as if this species abundance had not changed over time; (2) we computed a new CTI_{t_2}' ;
30 248 (3) then we calculated $\Delta CTI'$ using CTI_{t_2}' and CTI_{t_1} as above; and (4) we measured the difference
31 249 between $\Delta CTI'$ and ΔCTI in each plot. A positive value indicates that the change (gain or loss) of a given
32 250 species abundance increases thermophilization in a plot. Then, we determined the role of species gains and
33 251 losses in ΔCTI by averaging their contributions for plots where they increased and where they decreased.
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36 252 To test the hypothesis that community changes are resulting from post-disturbance succession, we collected
37 253 traits about species shade tolerance (Species Shade Index, SSI; Niinemets & Valladares, 2006), which
38 254 represents a species ability to grow in shade conditions. Shade tolerance indices ranged from 1 (very
39 255 intolerant to shade) to 5 (very tolerant) on a continuous scale. As for CTI, a Community Shade Index
40 256 (CSI) was computed for each plot as the mean of the SSI values weighted by the abundances of the species
41 257 present in that plot. Temporal shift in CSI **between the historical and contemporary time periods**,
42 258 ΔCSI , was computed in the same way as for ΔCTI , where a positive value indicates a progress in stand
43 259 succession toward climax, in units per decade.
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46 260 All analyses were performed using the R programming language version 3.5.1 (R Core Team, 2018). The
47 261 list of R packages that have been used throughout the analysis is provided in Table S3. R scripts will be
48 262 made available on GitHub upon final acceptance.
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1 2 3 263 Results 4 5

6 264 Temporal β diversity 7 8

9 265 The mean temporal β diversity was 0.56 over all sites in the study area ($n = 6281$), and
10 266 these temporal changes in composition were attributable to slightly more gains in
11 267 abundances (52.5%) than losses (47.5%; Fig. 2a). Temporal β diversity varied along a
12 268 latitudinal gradient; it tended to decrease northward, reaching its maximum at 48°N of
13 269 latitude, which corresponds to the northern limit of the balsam fir-yellow birch domain, the
14 270 ecotone between boreal and deciduous forests. North of the 49°N of latitude, in the
15 271 spruce-moss domain, temporal β changes were dominated by losses whereas, south of this
16 272 limit, gains prevailed. Latitudinal patterns were also visible in the contributions of the three
17 273 species groups to temporal β (Fig. 2b). At minor disturbance level, community changes were
18 274 mainly determined by gains in temperate species south of 47°N and by gains in boreal
19 275 species north of 47°N (where boreal species are the most abundant species group).

20 276 The magnitude of compositional changes in forests was highly influenced by disturbances
21 277 (Figs 2b-d, 3, S4). In each domain, the β diversity values of highly disturbed forests are
22 278 strongly skewed (Fig. 3). The mean temporal β was 0.43 at minor disturbance level, whereas
23 279 it was 0.53 at moderate disturbance level and reached 0.74 at major disturbance level (all
24 280 domains combined). Moreover, the fraction of changes attributed to losses was generally
25 281 lower at minor, than at moderate and major disturbance levels (minor: 41%; moderate: 48%;
26 282 major: 50%, all domains combined), especially for the spruce-moss domain (minor: 40%;
27 283 moderate: 73%; major: 64%; Fig. 3). At minor disturbance level, both boreal and temperate
28 284 species groups experienced more gains than losses (Fig. 2b), while at major disturbance
29 285 level, we observed a strong surge in losses of boreal tree species along with larger gains of
30 286 pioneer species (Fig. 2d). In contrast, gains in temperate species were higher at moderate
31 287 disturbance level (Fig. 2c). Some species have experienced great changes in abundance and
32 288 occurrence throughout these domains, namely *Picea mariana*, *Acer rubrum*, *Betula*
33 289 *alleghaniensis*, *Fagus grandifolia* and *Populus tremuloides*, and likely contributed largely to
34 290 the pattern of temporal β diversity (Fig. S4).

35 291 Drivers of temporal changes 36 37

38 292 Once combined, predictors from the three subsets (baseline, climate change and disturbances; Table 1)
39 293 explained together 40% of the variation of temporal β diversity, and 30% for both gains and
40 294 losses (Fig. 4). As revealed by the variation partitioning analyses, community temporal changes

were mainly driven by disturbances (R^2_{adj} for β : 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 β diversity, with old major harvest (Old harvest₂) being the most important driver, followed by old major natural disturbances (Old natural₂; 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 (Δ Precip) favored tree gains. Only one interaction was retained, which indicated that **stronger warming** (Δ Temp) mitigated the effect of recent moderate harvest (Recent harvest₁) 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 (Δ 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 (Δ 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 Δ CTI at moderate disturbance than at the other levels). Moreover, the latitudinal pattern of Δ 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.

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3 328 The analysis of ΔCSI revealed that major disturbances resulted in a large decrease in CSI
4 329 (Fig. 5c; mean $\Delta\text{CSI} = -0.037$), consistent with higher gains in pioneer species (Fig. 2),
5 330 while minor disturbances led to an increase in CSI (Fig. 5a; mean $\Delta\text{CSI} = +0.060$). Both
6 331 influenced by disturbances, ΔCTI and ΔCSI were negatively correlated (Pearson $r = -0.2$, p -value < 0.001)
7 332 indicating that the two ecological processes are intertwined. However, ΔCTI was more strongly correlated
8 333 to gains in temperate species and losses of boreal species than to gains in pioneer species (Fig. S6), which
9 334 suggests that thermophilization was not trivially driven by successional processes.
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14 335 Community thermophilization was asymmetrical and mainly driven by larger gains in warm-adapted
15 336 species, as indicated by the larger increases in the warm-tail of the temperature distributions than in the
16 337 cold-tail (Fig. 5d-f). Moderate disturbances exacerbated this effect from the sugar maple-yellow birch up
17 338 to the balsam fir-white birch domain (larger increase in the warm tail; Fig. 5e). The positive correlation
18 339 between ΔCTI and gains in temperate species in all domains, except in the spruce-moss, also corroborates
19 340 the role of warm-adapted species (Fig. S6).
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23 341 Only a few species contributed substantially to community thermophilization (Fig. 6). Gains of *Acer
24 342 rubrum* and *Acer saccharum*, as well as losses of *Abies balsamea* and *Picea mariana*, contributed strongly to
25 343 the thermophilization of all bioclimatic domains. In addition to the change of these four species, the losses
26 344 of *Betula papyrifera* and *Picea glauca* also played a key role in the thermophilization of ecotonal forests in
27 345 the balsam fir-yellow birch domain. Moreover, temperate species such as *Fagus grandifolia*, *Quercus rubra*
28 346 and *Fraxinus americana* contributed mostly to the thermophilization of southern domains (Fig. 6) where
29 347 their abundance has increased (Fig. S4). In contrast, the surge in CTI north of the 49°N (spruce-moss) in
30 348 highly disturbed forests (Fig. 5) was likely due to the replacement of boreal species by pioneer species (Fig.
31 349 S6), such as *Betula papyrifera* and *Salix spp.* (Fig. 6).
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37 350 Discussion

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41 351 Taken together, our results suggest that disturbances accelerate tree community responses to
42 352 climate change, revealing potential synergies that are yet to be investigated. Local and
43 353 short-term influences of disturbances mask long-term and lagging climate-induced changes in communities.
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45 354 Yet, we revealed a generalized thermophilization of forests throughout the temperate-boreal ecotone of
46 355 Québec, driven by a concurrent gain of temperate species and loss of boreal species. Moreover, we found
47 356 that moderate disturbances likely accelerated thermophilization. Hence, moderate disturbances, but not
48 357 major ones, could facilitate gains in warm-adapted species under climate change.
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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

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3 389 successional processes, highlighting that the observed thermophilization was not simply correlated with the
4 390 replacement of boreal by pioneer species. Our work provides a broad-scale community perspective on the
5 391 role played by disturbances in promoting northward migration of tree species, which is in agreement with
6 392 the conclusions of recent empirical (Boucher *et al.*, 2006; Leithead *et al.*, 2010) and simulation (Vanderwel
7 393 & Purves, 2014; Wang *et al.*, 2015) studies.
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11 394 Disturbances likely accelerate forest changes by reducing competition and providing establishment
12 395 opportunities to warm-adapted temperate tree species (Leithead *et al.*, 2010; Svenning & Sandel, 2013).
13 396 Indeed, in the absence of disturbances, trees grow slowly, their mortality rates are low and competition for
14 397 space and light is strong, thus preventing warm-adapted species from colonizing new areas, despite the
15 398 suitability of climatic conditions; community thermophilization is consequently very slow. Moderate
16 399 disturbances, however, remove individuals of resident species and reduce competition, which enhances the
17 400 replacement of boreal by temperate trees, thereby increasing the thermophilization rate. Furthermore,
18 401 moderate disturbances can also modify local microclimates (De Frenne *et al.*, 2013; Stevens *et al.*, 2015)
19 402 which may alter the survival rates of tree saplings. In contrast, major disturbances only favor early
20 403 successional species. Such findings echo the well-known intermediate disturbance hypothesis (Connell,
21 404 1978); as in the classical hypothesis, intermediate disturbances lower interspecific competition but here,
22 405 **not only do they increase local species richness (not shown)**, but they also accelerate ecological
23 406 transitions.
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27 407 Our complete set of predictors poorly explained the observed forest thermophilization, likely because this
28 408 process was highly variable among localities. Forest composition is thus changing as expected under
29 409 climate warming, but thermophilization does not appear to be directly driven by rising temperatures. As
30 410 suggested by Renwick & Rocca (2015), we surmise that, as climate warms up, moderate disturbances could
31 411 foster punctuated and episodic migration of warm-adapted species in localities where conditions are
32 412 otherwise favorable. However, it raises questions about the specific conditions in which the
33 413 thermophilization process can effectively take place. Further analyses are required to determine which
34 414 factors can trigger (e.g. type, size, frequency of disturbances) or constrain (e.g. soil type, competition,
35 415 precipitation) the invasion by warm-adapted species.
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39 416 **Our results contrast with those of Boisvert-Marsh *et al.* (2019) who found that climate was**
40 417 **more important than disturbances in explaining tree sapling recruitment at their northern**
41 418 **limit in Québec. This suggests that the pattern we uncovered might be primarily caused by**
42 419 **an increase in abundance of species already present rather than by new colonization.**
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44 420 **Danneyrolles *et al.* (2019) also found that forest compositional changes over the last**
45 421 **centuries (between 1790–1900 and 1980–2010) in deciduous forests of southern Québec were**
46 422 **largely driven by land-use changes, favoring more disturbance-adapted tree species, but did**
47 423 **not find any signs of thermophilization. In contrast to our study that covers a period of**
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3 424 pronounced climate warming, Danneyrolles *et al.* (2019) investigated a period dominated by
4 425 land-use and population changes which may explain the absence of thermophilization signal
5 426 in their results. In light of their results, we hypothesize that some of the thermophilization
6 427 we reported here in the sugar maple domains is in fact the result of secondary succession
7 428 after historical disturbances.
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12 429 **Species contributions to community thermophilization**

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15 430 We found that the observed community thermophilization was caused by gains and losses in abundance of
16 431 a restricted group of species. This differential rate of species response entails that other species lag even
17 432 more behind climate change and that larger reshuffling of communities is still ahead of us. The interaction
18 433 between climate and disturbances likely promotes generalist tree species adapted to disturbances with high
19 434 dispersal abilities (Aubin *et al.*, 2016). For instance, generalist species like *Acer sp.*, especially *Acer rubrum*,
20 435 have been expanding in eastern North America since the pre-industrial period (Boucher *et al.*, 2006;
21 436 Thompson *et al.*, 2013; Danneyrolles *et al.*, 2019) and recently established themselves in boreal forests
22 437 (Leithead *et al.*, 2010; Sittaro *et al.*, 2017) because they quickly take advantage from disturbances and
23 438 thrive in a wide variety of ecological conditions. In contrast, some species limited by dispersal, such as
24 439 *Carya sp.* and *Tilia americana*, or constrained to specific habitat, such as *Acer saccharinum*, might not
25 440 benefit from these opportunities.
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32 441 The magnitude of change in CTI varied by bioclimatic domains reflecting the spatial
33 442 patterns of species changes in response to climate warming and disturbances. The
34 443 thermophilization of the sugar maple domains was facilitated by the presence of a large pool
35 444 of warm-adapted species. When disturbed, these southernmost domains had lower
36 445 thermophilization because they gained pioneer species. We showed that the balsam fir-yellow
37 446 birch domain was particularly sensitive to moderate disturbances. The thermophilization of
38 447 this ecotonal zone was primarily due to increase in *Acer rubrum* and, to a lesser extent,
39 448 increase in *A. saccharum* and decrease in *Abies balsamea* and *Betula papyrifera*. Although
40 449 *A. rubrum* is already well established in this domain, our results suggest that it will continue
41 450 to thrive and spread, likely in response to a combination of climate warming, historical and
42 451 recent disturbances as well as natural forest dynamics. *A. saccharum* is presently
43 452 constrained on hilltops in the southern part of this domain (Gosselin, 2002), but our results
44 453 suggest that it could expand in nearby habitats. In contrast, the decrease in CTI in the
45 454 balsam fir-white birch and spruce moss domains could be explained by the fact that
46 455 temperate species are rare in these two northernmost domains, hence changes in CTI
47 456 resulted mostly from a dynamic of replacement between pioneer and boreal species in
48 457 response to disturbances. *A. rubrum* was the only temperate species to increase in the
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3 458 balsam fir-white birch domain (Fig. S4) and, when it did, it contributed to increase its CTI
4 459 (Fig. 6). Similarly to *A. saccharum*, *A. rubrum* distribution is spatially constrained within
5 460 the balsam fir-white birch domain (Blouin & Berger, 2008) and will likely expand from
6 461 existing existing patchy populations in the future.
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11 462 **Long-term perspectives for the temperate-boreal ecotone**
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14 463 Although the time period covered by our study (46 years) is sufficient to observe significant trends in forest
15 464 compositional changes, it is not long enough to test whether warm-adapted temperate species will persist
16 465 and thrive in these novel assemblages or if boreal species will out-compete them in the long run. Therefore,
17 466 an important question remains: does the current forest thermophilization indicates an ongoing ecosystem
18 467 shift or only a transient dynamic? Multiple studies suggest a persistence of these novel assemblages. For
19 468 instance, after a century of logging disturbances, temperate species were found to have increased and
20 469 persisted in forests formerly dominated by conifers (Boucher *et al.*, 2006). Furthermore, Fréchette & de
21 470 Vernal (2013) provided evidence that, during the last interglacial period (6-7°C warmer), the northern limit
22 471 of the temperate biome was located about 500 km north of its actual limit, suggesting that a northward
23 472 shift of the ecotone is possible. Hence, while climate warming erodes forest resilience by affecting
24 473 competitive advantages and generating colonization debt, our findings suggest that moderate disturbances
25 474 play a major role in promoting regime shift by speeding up the transition from one ecosystem state to
26 475 another. Such a conclusion stresses the importance of accounting for the synergistic effect of disturbances
27 476 and climate change in forest management strategies as well as in models of forest responses to climate
28 477 change.
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3 **600 Data Accessibility Statement**
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6 601 The complete forest inventory dataset used in this study is available online at
7 602 [https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-](https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui)
8 603 hui. All code required to repeat the analyses will be made available online on
9 604 GitHub.
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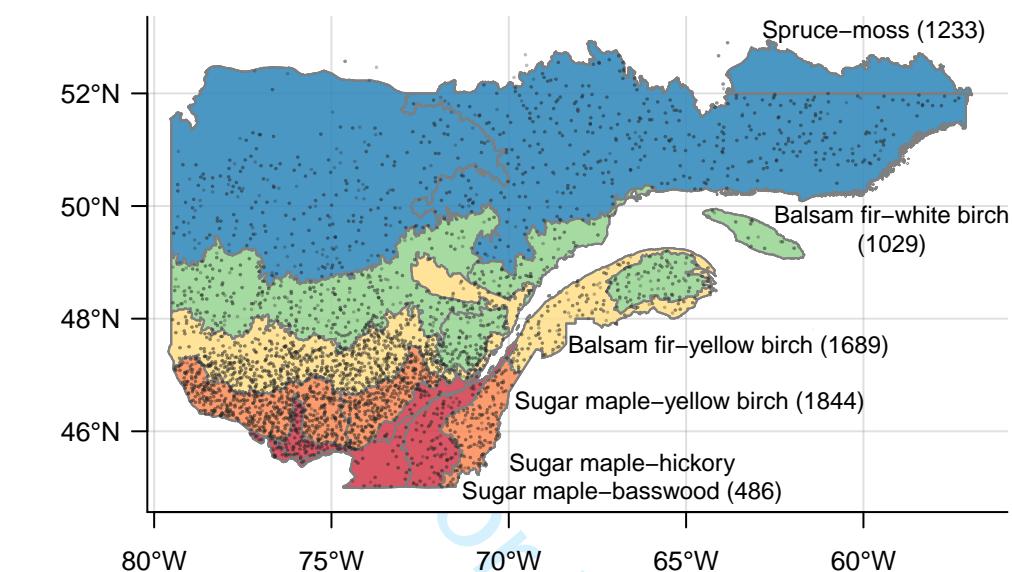
For Peer Review

Tables

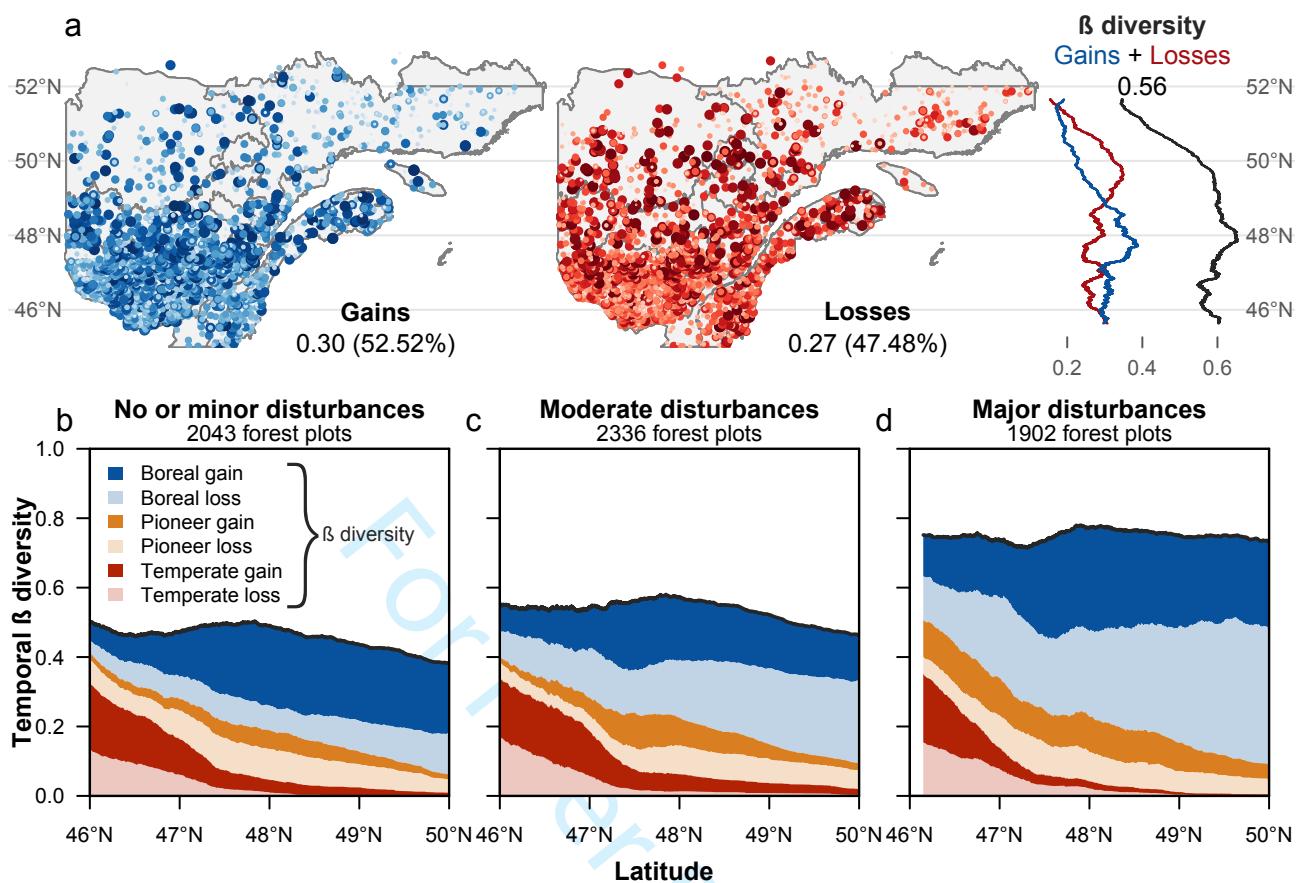
605 **Table 1.** Description of the predictors used in the multiple linear regression models. See Table S2 for
606 details about disturbance types.

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).

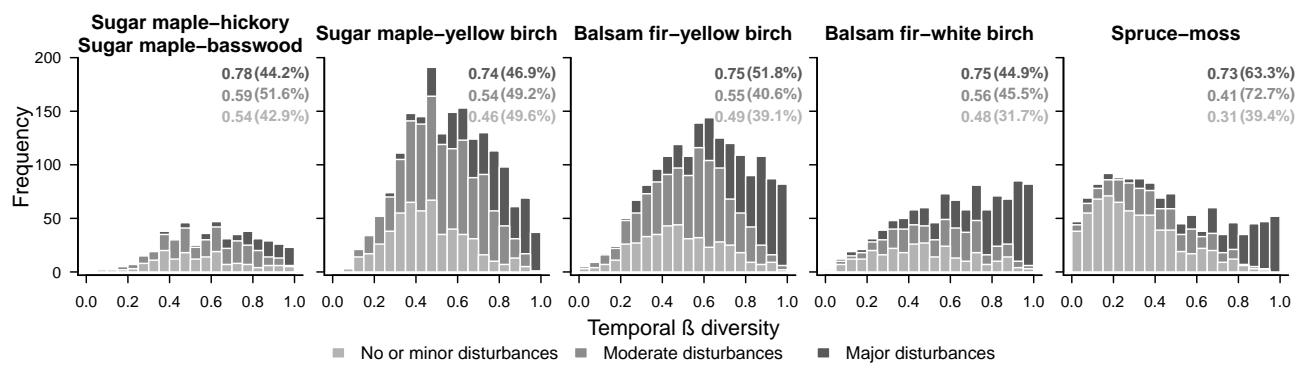
1
2
3 **Figures**



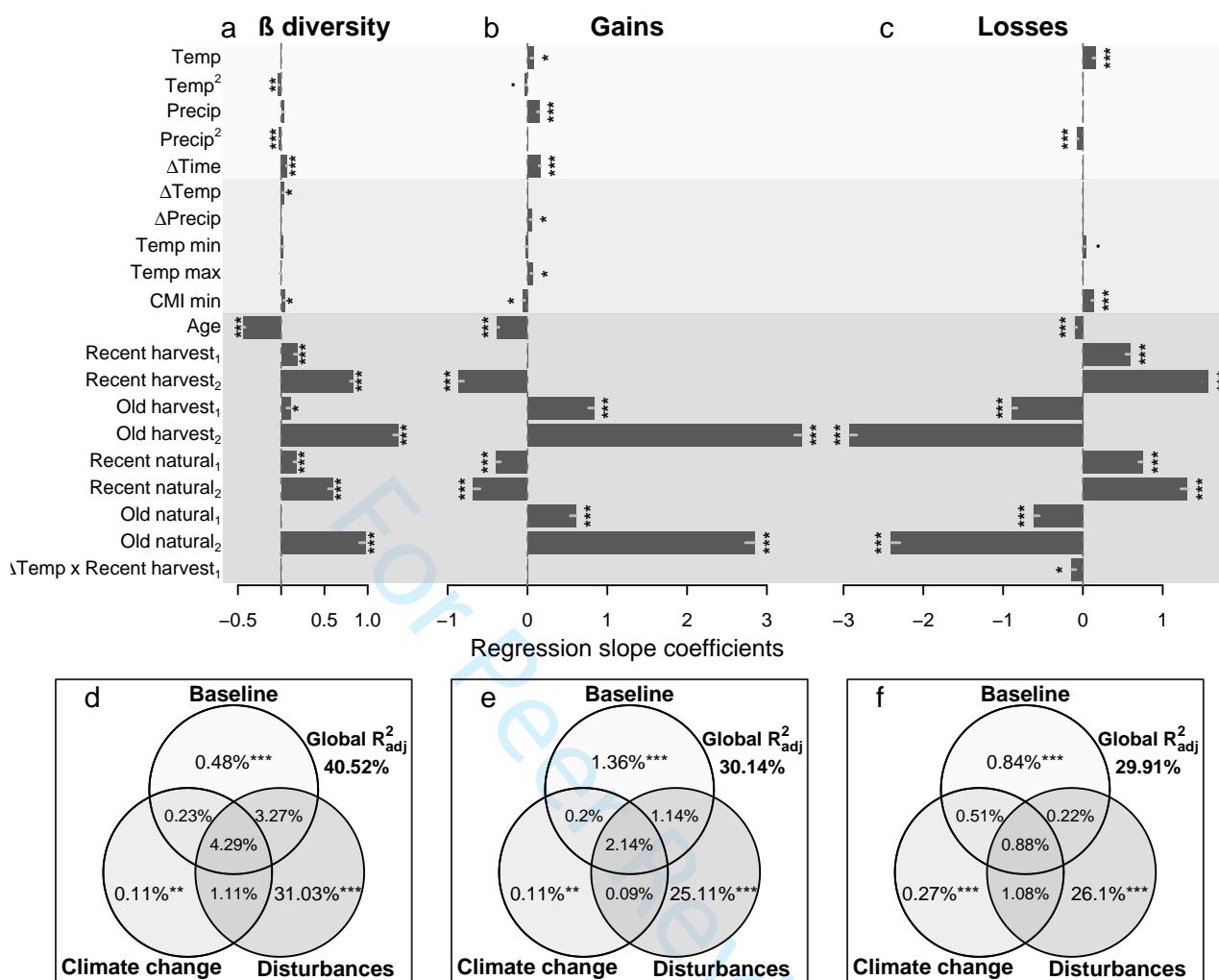
609 **Figure 1.** Locations of the 6281 forest inventory plots in meridional Québec, Canada. Colors delimit the
610 southernmost domains (orange) were combined in our analyses. The
611 number of forest plots in each domain is written in parentheses.
612



613
614 **Figure 2.** Maps of gains and losses in tree abundances (a) and latitudinal trends in temporal β 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 β 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.

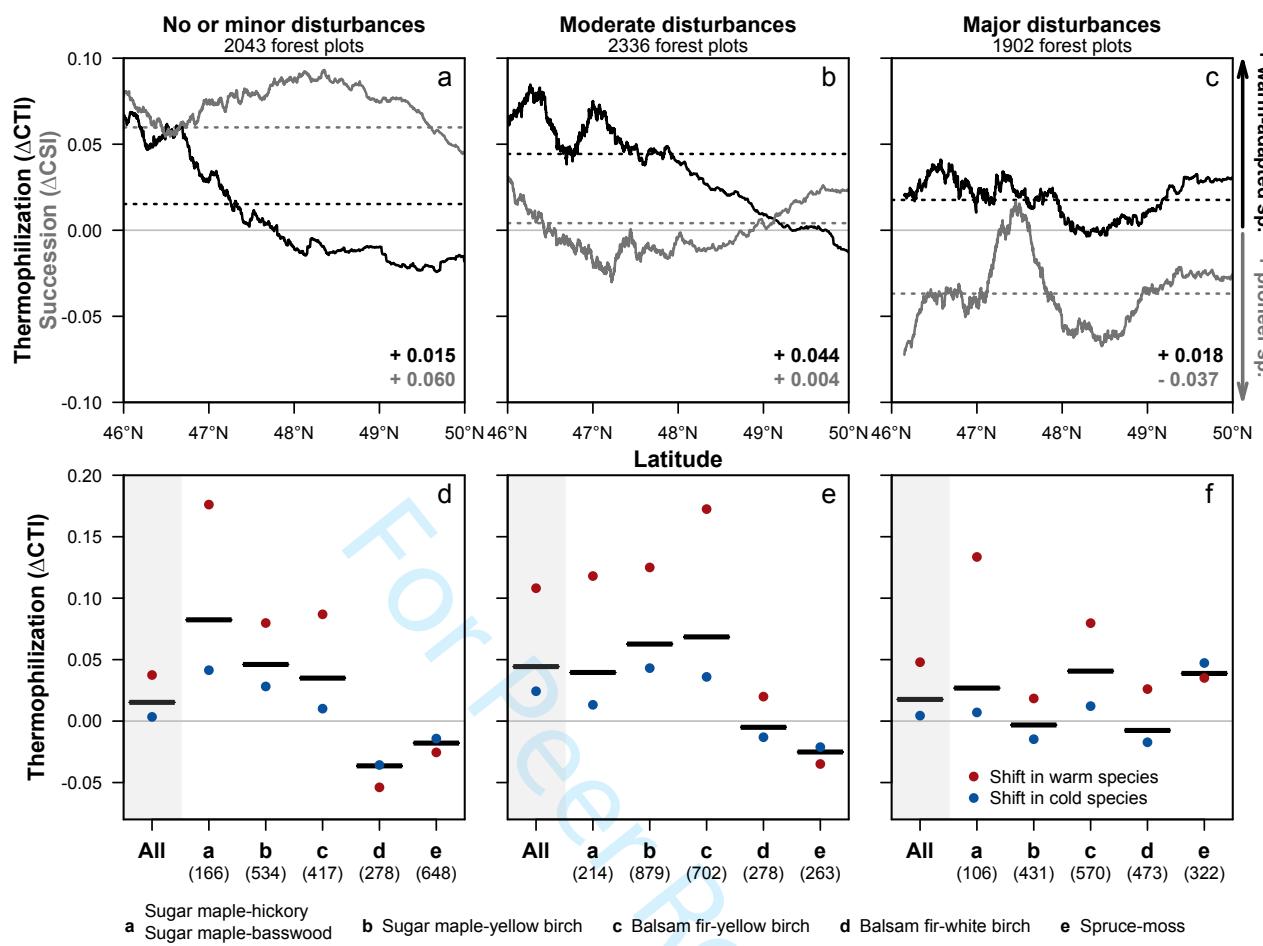


620
621 **Figure 3.** Frequency distributions of temporal β diversity in forests plots by bioclimatic domains. Forests
622 of different disturbance levels are stacked on top of each other. The values written in the panels are the
623 mean temporal β diversity values followed by the percentage of losses in parentheses. The distribution of β
624 diversity values is skewed to the right for higher disturbance levels.



626 **Figure 4.**

627 Slope coefficients from multiple regression models for (a) temporal β 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.**

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

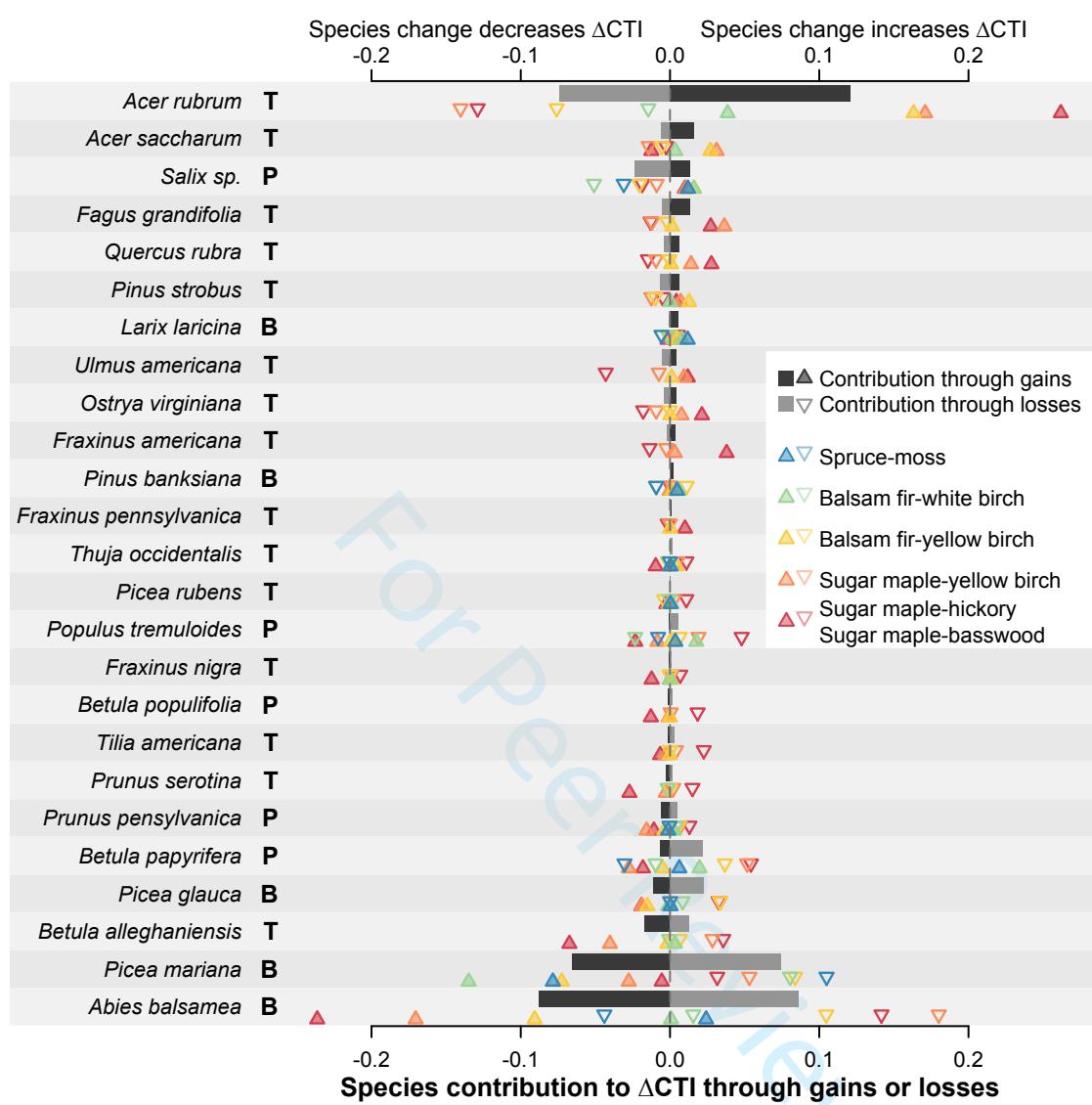


Figure 6.

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

Comments for reviewers and editor

Dear Dr Boucher-Lalonde,

Please find attached our revised manuscript entitled “Disturbances amplify tree community responses to climate change in the temperate-boreal ecotone” by Marie-Hélène Brice, Kevin Cazelles, Pierre Legendre, and Marie-Josée Fortin (GEB-2019-0064). We have revised and addressed our manuscript and incorporated all reviewers’ comments and concerns in the new version (changes are clearly indicated in bold in the manuscript). Please, find below our detailed reply. We will be happy to consider any other changes you deem necessary.

We would like to highlight three key points in the changes we made. First, thanks to a comment of reviewer 1, we made some modifications to our regression models. Reviewer 1 underscored that some forest communities come from fires of the 1910-1950 period. Hence, we decided that instead of using fire, outbreak, windfall and harvest as predictors, we would model the effect of recent vs old disturbances and only distinguish between natural disturbances and harvesting. Hence, our new variables are: old harvest 1 (moderate) and 2 (major), recent harvest 1 and 2, old natural 1 and 2 and recent natural 1 and 2. Our new regression models are now greatly improved by this new classification of disturbances (larger R^2_{adj} and easier interpretation).

Second, we slightly modified how disturbance categories were assigned to sites. In the original submitted version, to assign each forest to one of the three disturbance levels, we used the disturbance variables retrieved from the inventory dataset *in combination* with a variable describing the proportion of tree harvested in a plot. In this revised version of the manuscript, we only used the disturbance levels from the dataset to simplify the methods and to ensure that all disturbances are measured equivalently. This slightly changes the number of plots per group (before - minor: 2109, moderate: 2517, major: 1655; now - minor: 2043, moderate: 2336, major: 1902), but the conclusions drawn remain the same.

Last, we would like to point out that several modifications to the text have been made in order to reduce its length and save words for the requested revisions. Most of these modifications were minor, but one was more important: the last two paragraphs at the end of discussion were completely removed.

Sincerely yours, Marie-Hélène Brice, on behalf of all the authors

Answer to handling editor' comments

The reviewers provided comments that I think could be addressed in a modified version of the manuscript. In particular, please revise the text on Line 245-249, provide details for the classification of species into boreal and temperate, use scientific names more consistently throughout the manuscript and address the species-specific concerns of Reviewer #1. Please do carefully consider all comments provided by the reviewers, but I am aware that many comments involve providing more details such that you won't necessarily be able to accommodate them all in the manuscript (e.g., I don't think that a longer justification of the logit transformation is necessary).

Response: We corrected the mistake on Line 245-249. We now specify in the legend of Table S1 how we classified species into boreal, temperate, and pioneer. We also made most of the changes suggested by Reviewer #1 regarding the classification of some species. The scientific names are now used for species throughout the manuscript, except for the bioclimatic domains, which remain the same.

- **Line 123** Please change to “selected all plots” (else, please give more details)

Response: Done.

Line 146 I think that a Table in the Appendix with the 23 original disturbance type and how they were reclassified into the four types used for analyses would be useful.

Response: Done. We also clarified the paragraph according to the new predictors (L. 152-161). The number of original disturbance types changed to 21 because some of the original codes in the dataset corresponded to the same disturbances.

Line 186 Do you reach the same conclusions if you use those criteria on all possible subsets of the global model?

Response: If we perform the selection using all variables together, instead of selecting them by subsets, we obtain slightly different results: some climate variables are not selected. As stated in Borcard et al. (2011; Numerical ecology with R) “If one wants to estimate how much of the variation [in the response variable] is explained jointly by the [different] explanatory data sets, it is important to carry out forward selection separately on [each set] of explanatory variables.” Therefore, we performed the variable selection for each subset independently.

- **Line 313** all “domains” instead of “forests”?

Response: We kept “all forests” because we refer to all forests in Quebec in general.

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3 **Line 301** The pattern is qualitatively inconsistent across disturbance level, so I am not sure what the
4 “decrease” measures exactly and whether that’s particularly informative.
5
6

7 **Response:** We clarified this, the new sentence now reads (L. 328-330): “The analysis of ΔCSI
8 revealed that major disturbances resulted in a large decrease in CSI (Fig. 5c; mean $\Delta\text{CSI} =$
9 -0.037), consistent with higher gains in pioneer species (Fig. 2), while no or minor disturbances
10 led to an increase in CSI (Fig. 5a; mean $\Delta\text{CSI} = +0.060$).”
11
12

13 **Line 354** I don’t think that “leading to biodiversity losses” is a substantiated claim here. As long as lags
14 in losses are at least as great as lags in gains, alpha diversity won’t go down.
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16

17 **Response:** We agree with the editor’s comment and modified to (L. 383-385): “Considering
18 the velocity of the predicted future climate change, the gap between species distributions and
19 their optimal climate niches will likely widen and lead to greater reshuffling of biodiversity.”
20
21

- 22 • **Table 1** Please fix the description of delta Precipitation; shouldn’t the units for delta CMI be in
23 mm/y and for CMI min in mm?
24

25 **Response:** Done.
26

27 **Figure 4** Is there a missing delta Temp x Harvest 1 term?
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29

30 **Response:** No, because Temp x Harvest 1 was not selected in the model. Note that in the new
31 version of the manuscript Harvest 1 and Harvest 2 have been split into old harvest 1 / recent
32 harvest 1 and old harvest 2 / recent harvest 2, respectively.
33

34 **Line 186** Please make it explicit that these are the only three considered interaction terms, add
35 multiplication signs between the individual variables and justify this choice; I don’t see it as self-evident.
36
37

38 **Response:** We now explicitly describe the 3 interactions included in the model and justify this
39 choice (L. 200-204): “We also tested relevant interactions between disturbance and climate
40 predictors: Natural (old and recent) $\times \Delta\text{CMI}$ and Natural (old and recent) $\times \Delta\text{Temp}$, because
41 drought and heat stress can increase natural disturbance frequency; Harvest (old and recent) \times
42 ΔTemp), because the effect of harvest was hypothesized to be influenced by warmer
43 temperatures.”
44
45

46 **Line 422** Was alpha diversity higher at intermediate disturbance levels within the dataset?
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49 **Response:** Yes, alpha diversity is higher at intermediate disturbance levels as illustrated in the
50 Figure below. However, this paragraph was completely removed from the revised version of our
51 manuscript (because we add to cut in order to add some of the requested revisions).
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53

54 We modified the sentence “as in the classical hypothesis, intermediate disturbances lower
55 interspecific competition but here, instead of having a positive effect on local species richness, it
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accelerates ecological transition” to (L. 404-406) “as in the classical hypothesis, intermediate disturbances lower interspecific competition but here, not only do they increase local species richness (not shown), but they also accelerate ecological transitions”.

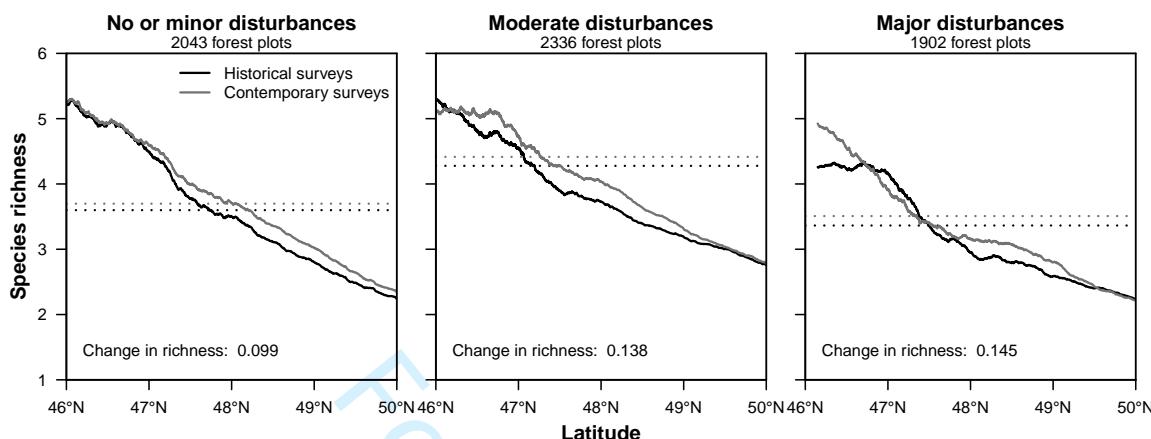


Figure S2 Please add the no disturbance plots.

Response: We made the change to Figure S2.

Answer to reviewer #1 comments

This study is well presented and is based on an original numerical ecology approach. Using permanent plots from the Ministère des forêts, de la faune et des parcs, the authors developed indices (CTI, CSI) to demonstrate that the thermophilization of communities was amplified by moderate disturbances. This original study provides new insights into our understanding of species migration (gains and losses).

We would like to thank the team of reviewers that have provided a very detailed review of our study that was of great help to clarify our manuscript.

Introduction and discussion

These two sections are excellent, but we propose to the authors to complete their review of the literature on the changes in the forest composition in a context of climate.

Response: As suggested, we added Boisvert-Marsh *et al.* (2019) which was closely related to our topic. We also added a reference to a recently published paper Danneyrolles *et al.* (2019) that address a similar topic. We however refrain from adding the two studies by D’Orangeville as they are dealing with a slightly different topic that would have required us to elaborate on new ideas while we were trying to shorten the paper.

Methods

L122-128. We propose to give more information about the method used to define the abundance of trees in forest plots. Does tree abundance correspond to the relative abundance of basal area for each forest species in a plot? Do plots used after year 2000 have the same position (geographical coordinates) as those before 1980? We think this is not always the case, because plots have been added after 2000.

Response: Tree abundance corresponds to the number of tree individuals/stems, not basal area. It is now explicitly written in the analysis section (L. 169-172) : “For each plot, we computed temporal β diversity (Legendre, 2019), which is the dissimilarity in species composition between two surveys of a given plot, by comparing local tree abundance (i.e. number of individuals) in forest plots between the historical (1970-1980, t_1) and contemporary (2000-2016, t_2) periods.”

Yes, the plots after 2000 and before 1980 have the same coordinates because we specifically selected plots that were surveyed at both time periods. We clarified the method in the manuscript (L. 123-126): “For each plot, we compared the tree composition between the first and last survey. To maximize the time interval between surveys, only plots that were inventoried in two distinct time periods (historical period: 1970–1980; contemporary period: 2000–2016) were retained for analysis.”

L151. Many authors used the oldest cored tree because this tree is most likely to identify the true year of origin.

Response: We chose to use the mean as the core samples were collected on selected trees representative of the plot. We agree with the reviewer that the oldest cored tree could have been used as well, but it would not make a big difference in the result as they were highly correlated (Pearson’s $r = 0.92$, p -value < 0.001).

L160-166. The description of A, B and C is difficult to understand. The description proposed by Legendre (2019) seems better.

Response: We added a supplementary figure (Fig. S3) to illustrate how to compute the temporal β diversity index using the component A, B and C.

L171-176 and table S1. We propose to use only Latin names in your article, because people who do not know the tree species of Quebec must learn two names for each species. *Alnus rugosa* on table S1 and *Alnus incana* on Figure 6? Your classification of boreal-temperate pioneer species is not at the same level: one is climate-related and the other concerns the forest dynamics. When both classifications are considered, some species do not appear to be properly characterized. For example, *Pinus strobus* and *Pinus resinosa* are mainly temperate species. For many Quebec ecologists, *Picea rubens* is a temperate (and maritime)

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3 species, not a boreal. May be all species with a temperature index greater than 4.25 could be considered as
4 temperate. We also think that *Thuya occidentalis* (4.30), *Populus deltoides* and *P. grandidentata* are
5 temperate species. *Malus sp.* could be remove (very rare introduce species without ecological signification).
6 *Salix sp.* is a general name for some species and we think this species brings confusion in your results. The
7 result presented on Figure 6 concerning these species is difficult to interpret on an ecological basis. We
8 propose to remove this species. Where is *Abies balsamea*? We don't see it on Table S1. The best
9 classification could be : A- temperate vs boreal and B- temperate pioneer (*Populus grandidentata*, *Pinus*
10 *resinosa*...) vs boreal pioneer (*Populus tremuloides*, *Betula papyrifera*, *Pinus banksiana*...). Why NA to
11 *Sorbus decora*. The two *Sorbus* species could be agglomerated to *Sorbus spp.* Most of the forest
12 technicians are not able to distinguish these species.
13
14

15 **Response:** Following the reviewers' comment, we changed all species names to latin names.
16
17 We corrected to *Alnus incana* in Table S1 and added *Abies balsamea* in Table S1.
18
19 We changed *Pinus strobus*, *P. resinosa*, *Picea rubens*, and *Thuja occidentalis* to the temperate
20 group.
21
22 We kept *Populus deltoides* and *P. grandidentata* in the pioneer group.
23
24 We removed *Malus sp.*, but kept *Salix sp.*, which are mostly shade intolerant species.
25
26 We combined the two *Sorbus* species under *Sorbus spp.*
27
28 We did not change the classification to separate pioneer species in temperate-pioneer and
29 boreal-pioneer because in this case we are mostly interested in the changes of temperate and
30 boreal species related to climate changes. The prevalence of pioneer species is here interpreted
31 as a sign of a successional transition and a subdivision of two groups of pioneer species would
32 add unnecessary complexity to the interpretation.
33
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35 **L178-181.** May be these 4 lines should be more popularized. We have difficulties to understand the
36 second sentence. When this transformation has been realized ? We propose : Before the variation
37 partitioning, we used a logit... because the dependent variables are in the standard unit range. And what is
38 the goal of this transformation ? May be try to give just a little bit more information to the reader... this
39 commentary concerns all the article.
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42 **Response:** We slightly modified this section for clarity (L. 192-195): "We evaluated the effects
43 of multiple drivers on temporal β , gains and losses using multiple regressions, in combination
44 with variation partitioning analyses (Borcard *et al.*, 1992; Peres-Neto *et al.*, 2006). For these
45 analyses, we used a logit transformation $y' = \log(y/(1 - y))$ of the response variables (β , gains,
46 losses) as they are in the standard unit range [0, 1]."

47 **L182.** We quantify the influence of climate change... What is the goal of the variation partitioning ? is it
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3 to measure an influence ?... or it is to quantify the variation explained by all subsets of the variables when
4 controlling for the effect of the other subsets (Borcard et al. 2011, page 180) or to apportioning the
5 variation of variable y among sets of explanatory variables. We think we don't quantify an influence but
6 measure a variation explained ?
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10 **Response:** We think that both formulations are correct, but to clarify we modified as
11 suggested (L. 196-199): "In order to quantify the variation explained by climate change and
12 disturbances, while controlling for the baseline climate gradient and different time interval, we
13 classified our predictor variables in three subsets: baseline conditions, climate change and
14 disturbances (see Table 1)."
15
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18 **L182-186.** Baseline climate gradient : These variables are presented on table 1 (Temps. Precip). Why do
19 you use Δ Time between first and last measurement (years) as a climate baseline condition. You used
20 Δ Time on figure 4 but you don't comment this result in the article.
21
22

23 **Response:** Δ Time between first and last measurement was included in the subset "baseline
24 conditions" because we wanted to control for difference in time interval. We expected that the
25 longer the time interval between surveys, the larger the change in temporal β diversity. It is
26 true that we did not comment the result about baseline conditions in the paper, primarily
27 because of word constraints. However, we made some additions in the results (L. 294-297): "As
28 revealed by the variation partitioning analyses, community temporal changes were mainly
29 driven by disturbances (R^2_{adj} for β : 31%; gains: 25%; losses: 26%), whereas the unique influence
30 of climate change as well as that of baseline conditions were significant but comparatively
31 modest ($R^2_{adj} < 2\%$; Fig. 4d-f)."
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36 (L. 308-311) "Variables related to baseline conditions were more important than climate change
37 variables; the effects of mean temperature (Temp) and total precipitation (Precip) likely reflect
38 the latitudinal gradient in community change, while the effect of time interval between surveys
39 (Δ Time) reflects the fact that community change takes time."
40
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42
43 **Table 1 A.** - what is exactly the meaning of : 10-year average prior to first measurement. Do these 10
44 years correspond to 1970-1980 ? **B-** Temp min is mentionned twice as name of a variable in the section
45 Climate change. **C-** May be define what are the variables Temp2 and Precip2 presented on figure 4. **D-**
46 May be insert in the table 1 the variables : fire Δ CMI; outbreak Δ Temp; harvest * Δ Temp defined on line
47 186 and also the variables defined at the base of the first part of figure 4 (Δ Temp X Harvest2). Overall, we
48 propose to define all the variables used in your study on table 1.
49
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52 **Response: A and C.** For each plot, we computed the average of temperature (or precipitation)
53 measurements in the 10 years before its first survey. Hence, if a given plot was surveyed in 1977,
54 we gathered the values of the mean temperature during the growing season from 1968 to 1977
55
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3 and computed the average of those values. Temp² and Precip² are second order polynomial.
4
5 Regarding these two points, we added in Table 1: "Mean temperature during growing season
6 and its second order polynomial. 10-year average prior to first survey of each plot (°C)".
7
8

9 B. We corrected Table 1 and replaced Temp min with Temp max where required.

10 D. We did not add the interactions in Table 1, but the explanations in the methods are now
11 more explicit (L. 200-2-4): "We also tested relevant interactions between disturbance and
12 climate predictors: Natural (old and recent) × ΔCMI and Natural (old and recent) × ΔTemp,
13 because a drought and heat can increase natural disturbance frequency; Harvest (old and
14 recent) × ΔTemp), because the effect of harvest was hypothesized to be influenced by warmer
15 temperature."

16 **L178-194.** In this paragraph, we understand that you present information on multiple regressions and
17 variation partitioning in alternance. Maybe it will be easier for the reader to understand this section if you
18 present A. information on regressions (first part on figure 5) and B. information on variation partitioning
19 (second part of figure 5). We understand that both analyses are closely related.

20 **Response:** The description of the two analyses are already presented in different paragraphs
21 (Second paragraph of the section, L.182-190, presents the regression models while third
22 paragraph, L.191-194, presents the variation partitioning). In the first paragraph, we think that
23 it is better to present the complete workflow to better understand the following steps. However,
24 to clarify that the second paragraph is about the regression models we added a minor precision
25 (L. 199): "We then generated regression models predicting β, gains and losses, for each of the
26 three subsets."

27 **L210-222.** We have difficulties to understand this paragraph. Why ? A- On lines 211 and 219, we don't
28 understand the meaning of : we quantified the shift in the left and right tail. B- line 213 when you mention
29 : for each individual of a species, we understand that we are using each tree of the plots instead the
30 abundance of the species. Do you really work at the tree level ? The use of individual is ambiguous. C-
31 Lines 211 and 218 give the same information about the percentiles. L220 : we don't understand : were
32 computed in the same way as for the shifts in mean. Is this sentence related to line 202 ?. D. At the end of
33 this paragraph (L210-222) we are supposed to understand the figure 5d-e, but that's not quite the case. We
34 propose to improve this section.

35 **Response:** We made important changes to this section. Mainly, we combined the methods
36 about the CTI with the ones about the 10th and 90th percentiles as they are closely related.
37 We also added some details about the computation of the warm and cold tails. We think that
38 with these changes, the section will be easier to understand.

39 **A-B-C** The section now reads as follows (L. 213-244):

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3 "To test whether or not climate warming contributed to community changes, we examined the
4 temporal changes in the distribution of species temperature values within every plot. We
5 quantified such changes by the shift in the mean (Community Temperature Index or CTI;
6 Devictor *et al.*, 2008), as well as the lower 10th percentile and the upper 90th percentile of this
7 plot-level distribution (De Frenne *et al.*, 2013).
8
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10 To compute these metrics, we first combined climate and tree occurrence data to obtain species
11 temperature distributions. Specifically, we overlaid interpolated climate data (mean annual
12 temperature averages for 1970–2000 at a spatial resolution of 1 km², available online
13 <http://worldclim.org/version2>; Fick & Hijmans, 2017) and occurrence data from multiple forest
14 inventory databases of eastern North America (collected in the QUICC-FOR project;
15 <https://github.com/QUICC-FOR>) for the focal species. The mean annual temperature for each
16 occurrence was extracted to infer species temperature distributions. Following Devictor *et al.*
17 (2008), we used the mean of these temperature values as a proxy for species thermal preference
18 (Species Temperature Index, STI, in Celsius; Table S1). For each plot in each time period, the
19 CTI was then calculated as the mean of the STI values weighted by the abundances of the
20 species present in that plot.
21
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23 Following De Frenne *et al.* (2013), we computed the 10th and 90th percentiles of the plot-level
24 temperature distributions, which correspond to the cold and warm tails of the distribution. To
25 do so, for every plot and every species, we sampled 1000 temperature values per individual from
26 the species' temperature distribution. The plot-level temperature distributions corresponds to
27 the combination of the temperature values for all individuals in a given plot. From these
28 distributions, which accounted for species composition and their relative abundances, we
29 computed the 10th and 90th percentiles. Note that contrary to De Frenne *et al.* (2013), we used
30 the entire distribution for each species instead of modeling species thermal response curves
31 because numerous species distributions were not Gaussian.
32
33

34 To evaluate the directionality of the changes in communities between the historical (t_1) and
35 contemporary (t_2) periods, we computed the temporal shift in the mean CTI, the cold tail and
36 the warm tail (in °C per decade) as follows:
37
38

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

39 The shifts in the cold and warm tails were computed in the same way as for the shifts in mean
40 CTI. A positive value of ΔCTI indicates an overall thermophilization of the tree community in
41 degrees per decade. A positive shift of the cold tail indicates a decrease of cold-adapted species,
42 while a positive shift of the warm tail indicates an increase of warm-adapted species; both result
43 in thermophilization."
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3 D. We hope that with these modifications, the interpretation of Figure 5 is clearer.
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6 **L223-230.** Can you explain how the methodology described allows to define the change (gain or losses) in
7 each species and each plot. You cancel the effect one species by one species to evaluate its contribution to
8 the change ?. At the end of this paragraph we are supposed to understand the figure 6. But that's not the
9 case; we think that something is missing. **A-** We understand for example that *Acer rubrum* will increase
10 (mean value of 0.12) and this increase will mainly characterize the sugar maple-basswood domain (red
11 triangle), **B-** At the opposite, the negative value of *Abies balsamea* (close to -0.8) indicate that this species
12 can decrease and this decrease is mainly important in the sugar maple-basswood domain (red triangle).
13 However the dark grey color of the rectangle indicate a gain for *Abies* (according to the legend of figure 6).
14
15 There is something that we don't understand.
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18 **Response:** **A-** For *Acer rubrum*, the Figure 6 should be read as follows: When *Acer rubrum*
19 increases in abundance in a plot, it will generally increase the ΔCTI value by an average of
20 ~0.12 for all Québec (dark grey bar) and an average of ~0.25 for the sugar maple
21 basswood/bitternut hickory domains (red solid up-pointing triangle). Conversely, when *Acer*
22 *rubrum* decreases in abundance in a plot, it will lead to a decrease in ΔCTI by an average of
23 ~-0.08 for all Québec (light grey bar), and an average of ~-0.14 for the sugar maple-yellow birch
24 domain (orange empty down-pointing triangle).
25
26

27 **B-** When *Abies balsamea* increases in abundance in a plot, it will lead to a decrease in CTI, by
28 an average of ~-0.09. We added an example of interpretation in the figure's legend: "For
29 example, the ΔCTI increased by an average of 0.12 for all plots where *Acer rubrum* has
30 increased in abundance (dark grey bar), whereas the ΔCTI also increased by an average of 0.09
31 for all plots where *Abies balsamea* has decreased in abundance (light grey bar)."
32
33

34 **L250-259.** We propose in this section on Temporal B diversity, to make A- a first paragraph on Figure 2a
35 (L243-249, L 253-258), B- a second paragraph on figure 2b-2d (L260-269) and C- a third paragraph
36 considering changes in species levels (Figure S3).
37
38

39 **Response:** We made several changes to this section to improve the flow following the
40 reviewers' recommendation (L.265-290). However, we did not write a complete paragraph about
41 Figure S3, as this figure is used only to support our results about beta diversity, and it would
42 require a lot of words to detail this supplementary figure.
43
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45 **L273.** We propose to begin this section with : As revealed by variation partitioning... to help the reader to
46 understand that the paragraph 273-278 brings information on variation partitioning and the paragraph
47 279-285 on Regression models.
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50 **Response:** We applied the suggested change and changed the paragraph division.
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3 **L283-284.** Sentence beginning by Increasing temperature : We understand that the harvest is more
4 important in the south and we don't understand : but mitigated the effect of insects outbreaks. May be
5 the information on harvest don't have to be consider, mainly because the variation partitioning shows no
6 significant relation between climate change and disturbances, whatever the element considered (B diversity,
7 gains, losses).
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11 **Response:** The results are now different, but we modified the sentence as we realized that it
12 was not clear (L. 306-307): "Only one interaction was retained, which indicated that stronger
13 warming (Δ Temp) mitigated the effect of recent moderate harvest (Recent harvest1) on losses."

14
15
16 When you write "the variation partitioning shows no significant relation between climate
17 change and disturbances", we think you refer to the absence of stars in the shared fractions in
18 the variation partitioning. However, this absence is not related to an absence of relation
19 between the subsets: the shared fractions cannot be tested for significance because it is only
20 obtained by subtraction. We added a precision in Fig. 4 legend: "In each variation partitioning,
21 significance of each unique fraction was tested using 9999 permutations, while shared fractions
22 cannot be tested."
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27 **L284-285.** Variables related to baseline conditions... We don't understand this sentence. The baseline
28 conditions are presented in the upper part of Figure 4 and the climate change just below. How can we
29 interpret these result in the sense that they reflect the latitudinal gradient in community change ?
30
31 Something is missing in our understanding.
32

33 **Response:** The baseline conditions subset contains Temp (mean temperature during the
34 growing season) and Precip (total precipitation during the growing season) which reflect the
35 latitudinal gradient in climate. We clarified the sentence (L. 308-311): "Variables related to
36 baseline conditions were more important than climate change variables; the effects of mean
37 temperature (Temp) and total precipitation (Precip) likely reflect the latitudinal gradient in
38 community change, while the effect of time interval between surveys (Δ Time) reflects that
39 community change takes time."
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44 **L287-291.** It is difficult for the reader to understand all this information without reference to any figure.
45
46 At the end of this section please put Figure 5... into parentheses. We think you need to explain that if you
47 take all your average CTI on figures 5c, 5d, 5f you will obtain +0,03. We don't understand the by decade.
48
49 At the beginning of L290, it is difficult to understand : During the same period. May be write : From the
50 first to the second period...
51

52 **Response:** We added the reference to Fig. 5.
53

54 The Δ CTI of +0.03 is the mean for all plots. We added a minor precision (L.314): "mean of
55 +0.03 °C/decade for all plots combined".
56
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The unit of Δ CTI is in °C per decade because we divided the change in CTI by time interval and multiplied it by 10, as explained in the methods. We chose to report Δ CTI in °C per decade because it is often how climate warming is reported, hence it is easier to compare.

We changed to (L. 316): "During the same time period".

L292-295. Is it possible to avoid long portion of sentences into parentheses?

Response: Unfortunately, it is not possible as the details about these post-hoc test is important.

L298-300. Is this information duplicated with that shown in Figure 4d-4e-4f? These 3 figures indicate that the unique value of Baseline climate and climate change is significant but very low. If this is the case, it is not important to repeat the information in another way

Response: This information is actually different, here we are talking about the effects of climate change on Δ CTI, not β .

L305-318. This section is probably the most important of the study. **A.** On lines 311-313 we estimate that increase in *Acer rubrum* in all the temperate domains, is not necessarily linked to the thermophilization because *Acer rubrum* is a temperate species and its increase in abundance after a disturbance is part of the natural dynamics. **B.** On Lines 313-314 you mention *Betula papyrifera* and *Picea glauca* but the losses of *Prunus pensylvanica* and *Betula alleghaniensis* are also important. Why did you not mention these 2 last species ? According to your results, - B1. *Acer rubrum* will be the only temperate species which will increase in the Balsam fir-white birch domain. This species is nowadays present in the southern part of this domain and these communities will continue to expand. - B2. *Acer rubrum* will also increase in the balsam fir-yellow birch domain, but this species is already well represented in this domain. - B3. *Acer saccharum* will increase in the balsam fir-yellow birch domain. In this domain, *Acer saccharum* communities are mainly located in the upper part of the hills, and your study indicated that *Acer saccharum* has the potential to migrate down the hills. - B4. *Pinus strobus* also will increase in the balsam fir-yellow birch domain, but not in the balsam fir-white birch domain. - B5. *Fagus grandifolia*, *Quercus rubra*, *Ulmus americana*, *Ostrya virginiana* and *Fraxinus americana* will increase in the sugar maple domains. We suggest that you provide this information or a part of it in your results. **C.** On the figure 5c, section d (Balsam fir-White birch domain), can you clarify why the red dot is negative? - We repeat that we don't understand the signification of the dark grey rectangles (gains ?) in the section of species change decreases. How these gains can be interpreted as species change decreases ? We have difficulties to understand the lower part of the figure 6.

Response: A. Our results (Fig. 6) show that the increase in *Acer rubrum* is the most important contributor to the thermophilization of communities. It is very plausible that its increase might not be caused by climate change but by disturbances. That being said, the key

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3 result remains the same, *Acer rubrum* is causing thermophilization. We added a paragraph in
4 the discussion (L. 440-460) about the thermophilization in each domain (in response to this
5 comment and others) where the specific case of *Acer rubrum* is detailed.
6
7

8 **B.** Unfortunately, we cannot discuss the specific results of every species in the main text
9 because of the word constraints, but the supplementary Figure S4 (formerly S3) provides
10 detailed information for every species that will hopefully be of interest for some readers. Figure
11 6 shows how the change of each species contributes to ΔCTI . It should be clearer with the
12 example provided in the legend.
13
14

15 **C.** We assume you are referring to Figure 5d. When not disturbed, the ΔCTI of plots in the
16 balsam fir-white birch domain decreased (i.e. “coldiphilization” as the reviewer 2 said). The
17 cold tail (blue dot) is negative because there is a gain in cold-adapted species and the warm tail
18 (blue dot) is even more negative because there is a larger loss of warm-adapted species.
19 Therefore, it seems that the “coldiphilization” of the balsam fir-white birch domain is
20 principally caused by a loss of warm-adapted.
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23 Discussion

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27 **L324.** we found that moderate disturbances likely accelerated thermophilization : We agree with this idea
28 but the information that we presented just before L313-314, stratified by domain is important. We are
29 greatly interested by the migration potential of temperate species in the balsam fir-yellow birch and in the
30 balsam fir-white birch domains. We think that the increase of *Acer rubrum* in the balsam fir-white birch
31 domain will be mainly enhanced by the extension of actual communities. These communities come from
32 fires of the 1910-1950 period. This process belongs to your no disturbance category. See Fig A4 of
33 Boisvert-Marsh et al. 2014.
34
35

36 **Response:** Our disturbance levels include both old and recent disturbances. The manuscript
37 now includes a paragraph in the discussion with a detailed interpretation of our results
38 stratified by domain (L. 440-460).
39
40

41 **L339-341.** May be try to nuance this section. Tree harvesting, if done well, does not necessarily mean loss
42 of resilience.
43
44

45 **Response:** We removed the last sentence and added a few details about the differences
46 between natural stand replacing disturbances and forest harvesting (L. 370-373): “However, in
47 contrast to natural disturbances, tree harvesting has been shown to disrupt the relationship
48 between vegetation and local environmental conditions and, because of its short return interval,
49 to favor young even-aged stands to the detriment of old-growth forests.”
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3 **L347-348.** Can you really compare these two results (temperature of the community vs temperature
4 increase of the season) that do not have the same origin?
5

6 **Response:** The reviewers rightfully question whether the comparison is meaningful. Here, this
7 comparison is used as an indicator of the lag in response. We do not expect the CTI to change
8 at exactly the same pace as climate change, but we could expect that if trees followed they
9 climate niche, the Δ CTI would be closer to the Δ Temp. We modified this passage to take into
10 account the reviewer's comment (L. 378-382): "However, the observed increase of tree
11 community temperature of +0.03 °C/decade is considerably smaller than the rising trend in
12 growing season temperature of 0.14 °C/decade (Fig. S1). Although these measures have
13 different origins and should thus be compared cautiously, this corroborates the conclusion of
14 numerous studies that tree responses often lag behind environmental changes."
15
16

17 **L356-377.** All this section is very interesting. But when we read it, we have in mind our comments
18 presented on L313-314 and L324. We don't see the link between the moderate disturbance and the increase
19 of Acer rubrum in the balsam fir-white birch domain.
20

21 **Response:** It is a general hypothesis to explain our results shown in Fig. 5. We did not test
22 specifically if recent disturbances promoted *A. rubrum* in the balsam fir-white birch domain.
23 We now discuss about the natural expansion of *A. rubrum* from existing communities in the
24 new paragraph in the discussion (L. 440-460; in response to this comment and others).
25

26 **L394.** We do not really think that *Acer rubrum* has recently established in the Quebec's boreal forest, and
27 especially in the southern part of the western Balsam fir-White birch subdomain. We believe that the
28 stands dominated by this species and probably other temperate species (*Betula alleghaniensis*) are residues
29 of a warm Holocene period. During this warm period, the stands dominated by *Acer rubrum* were probably
30 larger in superficy and occupied by others temperate species, not only *Acer rubrum*. May be consult :
31 Vegetation and climate history of Quebec's mixed boreal forest suggests greater abundance of temperate
32 species during the early-and mid- Holocene by Larochelle, Lavoie, Grondin and Couillard, Botany 2018.
33

34 **Response:** We agree with the reviewers and, as stated in the answer above, we added more
35 detail about the expansion of *A. rubrum*. However, we did not changed this specific sentence as
36 it was reporting the results of other papers.
37

38 **L396.** Hickories is not in your Table S1.
39

40 **Response:** *Carya cordiformis* is included, but *Carya ovata* is not as it only has a single
41 occurrence in our selected plots.
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43 **L403.** Can you give a reference and elaborate on the notion of state shift. May be see Barnosky et
44 al. 2018. <https://www.nature.com/articles/nature11018>
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3 **Response:** We changed “state shift” to “ecosystem shift”, and we think that the concept is
4 popular enough among ecologists that it does not require the addition of a reference.
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7 **L405-406.** Frechette et al. 2018 also demonstrate that the northern limit of temperate species was in the
8 past located north of their actual limit.
9
10 <https://mffp.gouv.qc.ca/documents/forets/recherche/Memoire179.pdf>

11 **Response:** We think that the study by Frechette and colleagues we include in our list of
12 reference is adequate.
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18 **Answer to reviewer #2 comments**
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21 The authors test the contributions of climate change and disturbances to temporal shifts in tree community
22 compositions over the last decades in Quebec. They also evaluate whether disturbances modulate tree
23 community thermophilization.
24
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26 This is an impressive work, with an interesting conclusion and strong methodological developments. I do
27 appreciate the diversity of methods used to test the hypotheses. Authors developed different methods to
28 disentangle the drivers underlying changes in community diversity and the shift in community temperature
29 affinities. The paper shows a wide diversity of results, but they are well presented and discussed.
30
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32 Authors show clear results and tested few alternative hypotheses to explain the patterns found e.g. the link
33 between CTI and CSI, the analysis showing the driver of thermophilization (shift in warm or cold species)
34 or the species contributions to CTI. These show the high quality of analyses and the robustness of the
35 paper’s conclusions.
36
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38 The discussion is very rich and explores the results with an interesting perspective for forest management.
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41 We are grateful to the reviewer for the constructive comments he formulated that contribute to
42 improve our manuscript.
43
44

45 For each species’ names used in the manuscript, could you give the Latin name, which is the official
46 language for taxonomy.
47
48

49 **Response:** The species names were changed throughout the manuscript. The only exceptions
50 are the names of the bioclimatic domains.
51
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53 **L89-91** Semantical issue: Careful, CTI is not a functional trait, it is an Index of ecological affinity. Please
54 adjust this sentence because the term “functional trait” is misused. You can just say that CTI is an index
55 of ecological affinity.
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3 **Response:** We added a precision in this sentence (L. 89-90): “Hence, analyzing shifts of
4 relevant functional traits and ecological affinities in communities using large-scale monitoring
5 data should unravel the role of different environmental drivers in shaping communities.”
6
7

8 **L95** mean or median? Usually, we use the median.
9

10 **Response:** We used the mean temperature of a given species distribution to measure STI,
11 following the initial paper by Devictor *et al.* (2008). We tested our analyses using the median
12 and found that the results are qualitatively similar. We added this information in the sentence
13 (L. 224-225): “Following Devictor *et al.* (2008), we used the mean of these temperature values
14 as a proxy for species thermal preference”.
15
16

17 **L305-310** Question to authors: I found very interesting the result of Figure 5d: there is a
18 thermophilization in Sugar maple domains and Balsam fir-yellow birch but a “coldiphilization” at high
19 latitudes for Balsam fir-white birch and Spruce moss domains. The same pattern as for beta diversity
20 (dominated by losses north of the 49° and by gains south of this limit). Do you have any hypothesis or
21 ideas explaining these results? I wonder if authors find these results interesting enough to discuss?
22
23

24 **Response:** We agree with the reviewer that this pattern is quite interesting: thermophilization
25 in sugar maple domains and balsam fir-yellow birch, but a “coldiphilization” at high latitudes
26 for balsam fir-white birch and spruce moss domains. We think that it could be explained by the
27 fact that temperate species are rare in these two northernmost domains, hence their change in
28 CTI may result from the replacement of pioneer species by boreal species in response to old
29 disturbances. We added a paragraph in the discussion (L. 440-460) with more details about
30 interpretation of our results stratified by domain (in response to this comment and others from
31 reviewer #1).
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34 **Discussion:**
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37 The sentence starting your discussion “In this study, we found evidence of climate-induced shifts in tree
38 community composition...” is not really true since results show the exact opposite L274, L279, L282, L298.
39 It could be more honest to start your discussion with something close to L326-327.
40
41

42 **Response:** In this first sentence, the “climate-induced shifts in tree community composition”
43 was referring to thermophilization. However, to avoid confusion and reduce the length of the
44 paper, we simply replaced this first sentence by the last one (L. 351-352): “Taken together, our
45 results suggest that disturbances accelerate tree community responses to climate change,
46 revealing potential synergies that are yet to be studied.”
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49 **L333-341:** Even if you discuss this point later, could you discuss very briefly the possibility that the
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3 thermophilization you detected could be the result of secondary succession after harvesting rather than the
4 shift in forest community composition by competition effect.
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6 **Response:** We now discuss this possibility in the section *Feedback between climate change and*
7 *disturbances* (L. 416-427): “In contrast to our study that covers a period of pronounced climate
8 warming, Danneyrolles *et al.* (2019) investigated a period dominated by land-use and
9 population changes which may explain the absence of thermophilization signal in their results.
10 In light of their results, we hypothesize that some of the thermophilization we reported here in
11 the sugar maple domains is in fact the result of secondary succession after historical
12 disturbances.”
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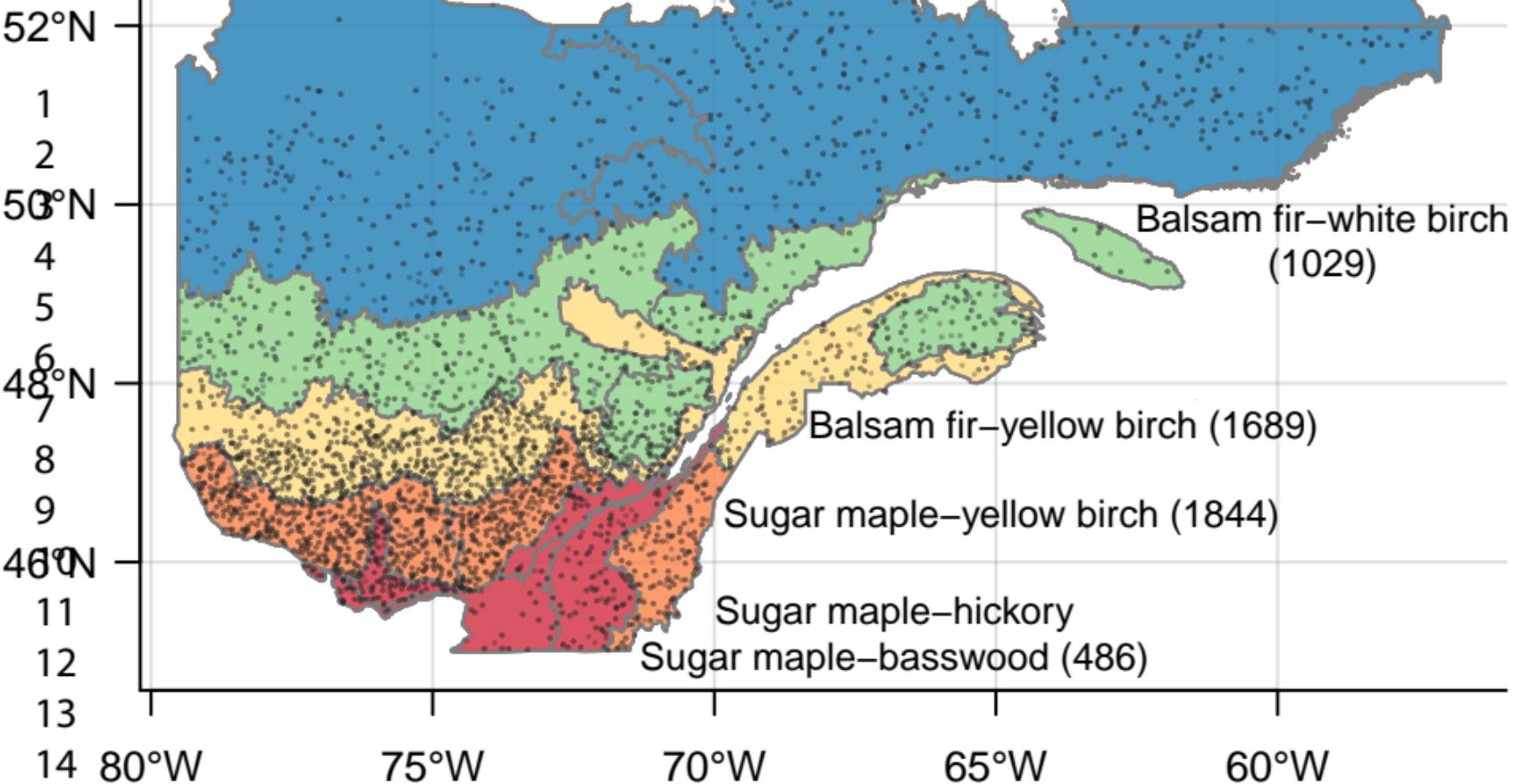
14 I also wonder if there is a plantation after harvesting. Which could also be a part of the explanation.
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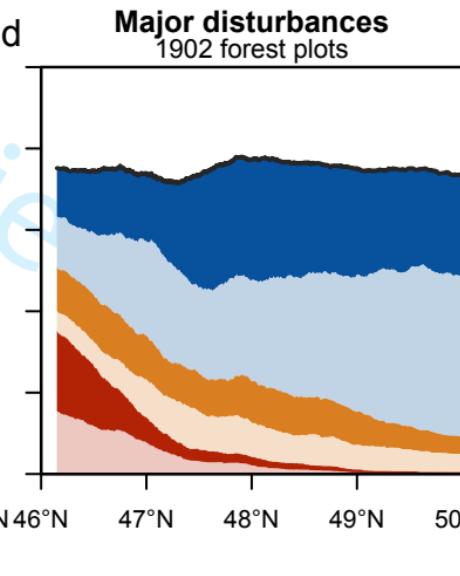
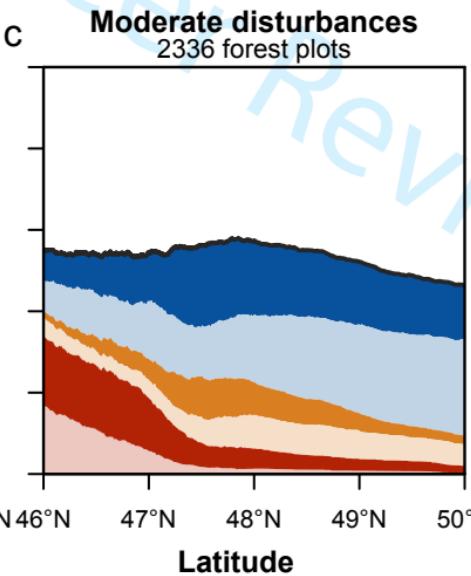
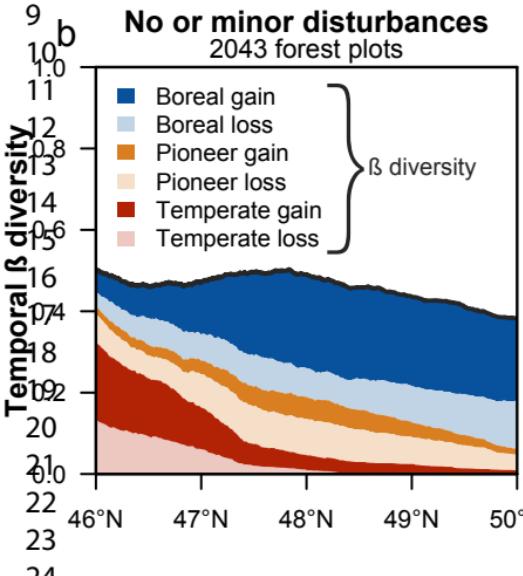
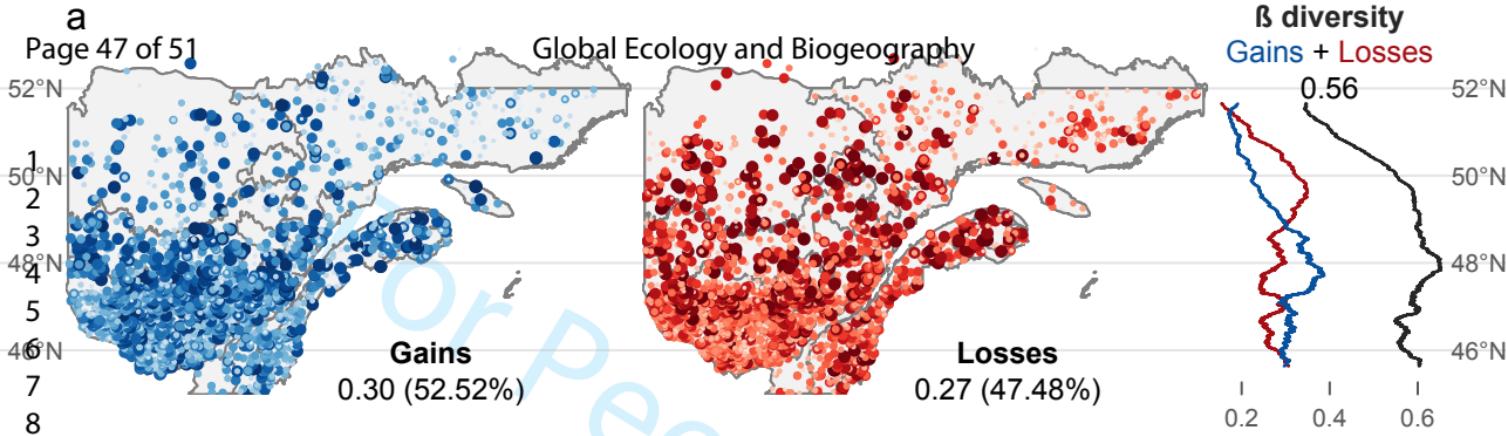
16 **Response:** We removed all plots where tree plantation was reported during the study period
17 (see methods), hence there should not be any effect of human plantation.
18

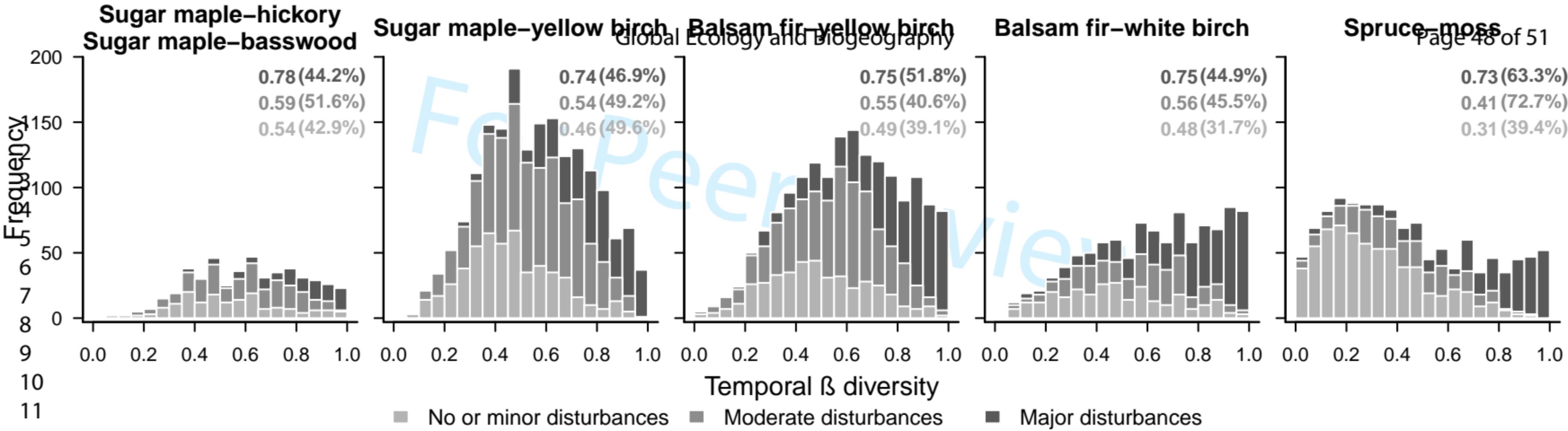
25 References

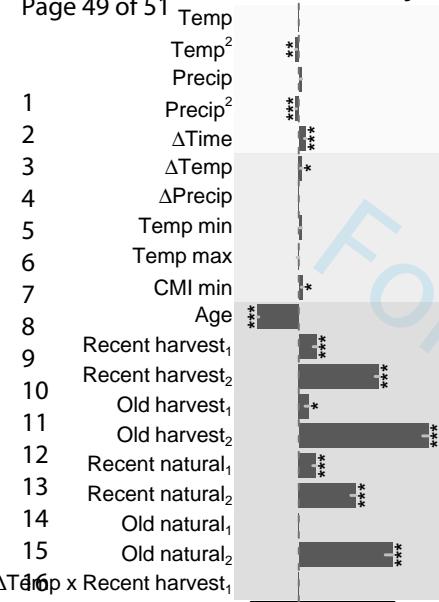
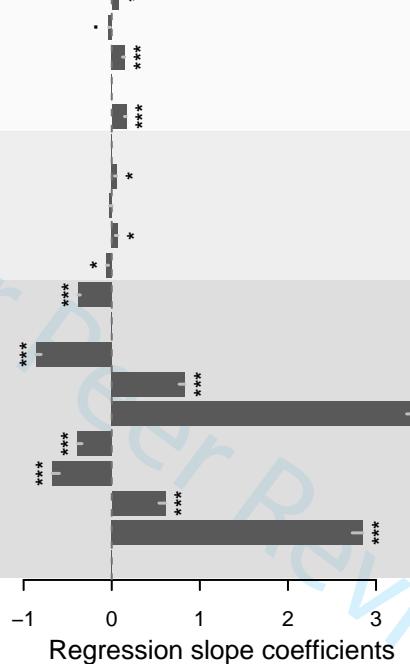
26

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42 matrices: Estimation and comparison of fractions. *Ecology*, **87**, 2614–2625.
- 43







a β diversity**b** Gains
Global Ecology and Biogeography**c** Losses