

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

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

## 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.

**Location** Québec, Canada

**Time period** 1970–2016

**Taxa studied** Trees

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

**Results** Temporal  $\beta$  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

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

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

## Keywords

Beta diversity, Climate change, Community temperature index, Community temporal change, Disturbances, Forest, Québec, Temperate-boreal ecotone, Thermophilization.

## Introduction

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

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

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

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

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

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

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

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

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

## Methods

### Study area

To analyze large-scale temporal changes in forest community composition, we used the Québec forest inventory plots that have been sampled in six bioclimatic domains, south of the 52<sup>nd</sup> parallel, since 1970 by the Ministère des forêts, de la Faune et des Parcs (Fig. 1; MFFP, 2016). For each plot, we compared the tree composition between the first and last surveys. 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. We disregarded plots that were subjected to active reforestation during the study period as we were interested in compositional changes resulting from natural post-disturbance recolonization. We also eliminated plots without trees (due to a disturbance) either at their first or last year of sampling. This yielded a subset of 6281 plots analyzed (Fig. 1), with a median of 35 years between surveys (1st quartile: 33 and 3rd quartile: 41 years).

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

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

## Environmental variables

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

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

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

## Analysis

### $\beta$ diversity

For each plot, we computed temporal  $\beta$  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. The dissimilarity ( $\beta$ ) was computed using the Ružička coefficient (Fig. S3):

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

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

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

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

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

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

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

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

## Assessing the relative importance of drivers of community changes

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

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

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

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

## Functional index of community change

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

To compute these metrics, we first combined climate and tree occurrence data to obtain species temperature distributions. Specifically, we overlaid interpolated climate data (mean annual temperature averages for 1970–2000 at a spatial resolution of 1 km<sup>2</sup>, available online <http://worldclim.org/version2>; Fick & Hijmans, 2017) and occurrence data from multiple forest inventory databases of eastern North America (collected in the QUICC-FOR project; <https://github.com/QUICC-FOR>) for the focal species. The mean annual temperature for each occurrence was extracted to infer species temperature distributions. Following Devictor *et al.* (2008), we used the mean of these temperature values as a proxy for species thermal preference (Species Temperature Index, STI, in Celsius; Table S1). For each plot in each time period, the CTI was then calculated as the mean of the STI values weighted by the abundances of the species present in that plot.

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

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

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



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

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

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

All analyses were performed using the R programming language version 3.5.1 (R Core Team, 2018). The list of R packages that have been used throughout the analysis is provided in Table S3. All the data used in the study as well as R scripts to reproduce the analyses and the figures can be found online at <https://github.com/mhBrice/thermophilization> (<https://doi.org/10.5281/zenodo.3242773>).

## Results

### Temporal $\beta$ diversity

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

temporal  $\beta$  (Fig. 2b). At minor disturbance level, community changes were mainly determined by gains in temperate species south of 47°N and by gains in boreal species north of 47°N (where boreal species are the most abundant species group).

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

## Drivers of temporal changes

Once combined, predictors from the three subsets (baseline, climate change and disturbances; Table 1) explained together 40% of the variation of temporal  $\beta$  diversity, and 30% for both gains and losses (Fig. 4). As revealed by the variation partitioning analyses, community temporal changes were mainly driven by disturbances ( $R^2_{adj}$  for  $\beta$ : 31%; gains: 25%; losses: 26%), whereas the unique influence of climate change as well as that of baseline conditions were significant but comparatively modest ( $R^2_{adj} < 1\%$ ; Fig. 4d-f).

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

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

and total precipitation (Precip) likely reflect the latitudinal gradient in community change, while the effect of time interval between surveys ( $\Delta$ Time) reflects the fact that community change takes time.

## Changes in community temperature and shade indices

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

Thermophilization was significantly larger in moderately disturbed forests ( $\Delta$ CTI =  $+0.044$  °C/decade) than in undisturbed ( $+0.015$  °C/decade) or highly disturbed forests ( $+0.018$  °C/decade; ANOVA  $F_{2,6278} = 14.59$ ,  $p$ -value  $< 0.001$ ; a post-hoc Tukey test showed significantly higher  $\Delta$ CTI at moderate disturbance than at the other levels). Moreover, the latitudinal pattern of  $\Delta$ CTI varied with the disturbance level: the thermophilization in moderately disturbed forests extended further north than in undisturbed forests, exceeding  $48^\circ\text{N}$ , 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.

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

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

Only a few species contributed substantially to community thermophilization (Fig. 6). Gains of *Acer rubrum* and *Acer saccharum*, as well as losses of *Abies balsamea* and *Picea mariana*, contributed strongly to

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

## Discussion

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

### Impact of disturbances on tree community changes

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

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

## Climate-induced change in tree community

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

## Feedback between climate change and disturbances

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

Disturbances likely accelerate forest changes by reducing competition and providing establishment opportunities to warm-adapted temperate tree species (Leithead *et al.*, 2010; Svenning & Sandel, 2013). Indeed, in the absence of disturbances, trees grow slowly, their mortality rates are low and competition for space and light is strong, thus preventing warm-adapted species from colonizing new areas, despite the suitability of climatic conditions; community thermophilization is consequently very slow. Moderate disturbances, however, remove individuals of resident species and reduce competition, which enhances the replacement of boreal by temperate trees, thereby increasing the thermophilization rate. Furthermore, moderate disturbances can also modify local microclimates (De Frenne *et al.*, 2013; Stevens *et al.*, 2015) which may alter the survival rates of tree saplings. In contrast, major disturbances only favor early successional species. Such findings echo the well-known intermediate disturbance hypothesis (Connell, 1978); 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.

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

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

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

## Species contributions to community thermophilization

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

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

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

## Long-term perspectives for the temperate-boreal ecotone

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

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## **Data Accessibility Statement**

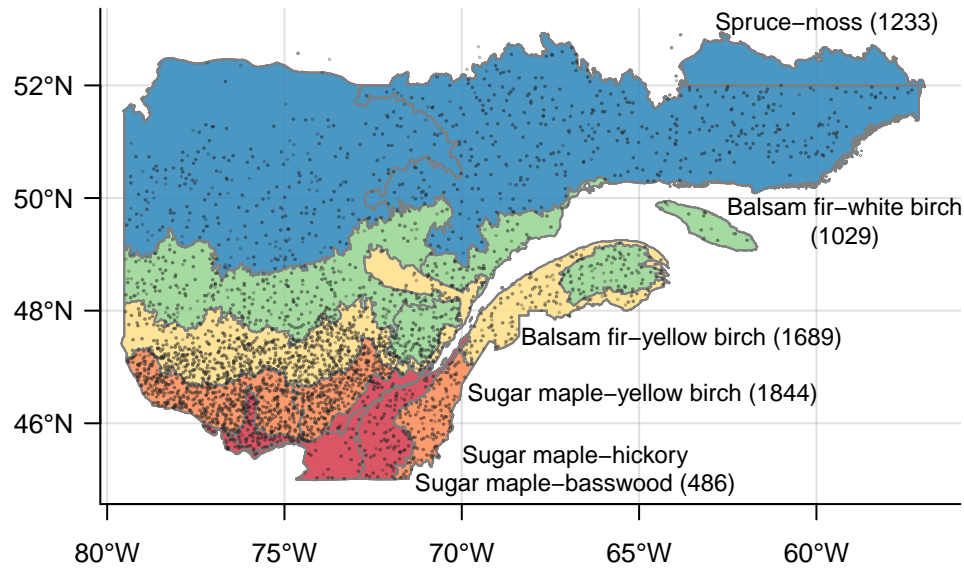
The complete forest inventory dataset used in this study is available online at <https://www.donneesquebec.ca/recherche/fr/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui>. All code required to repeat the analyses will be made available online on GitHub.

## Tables

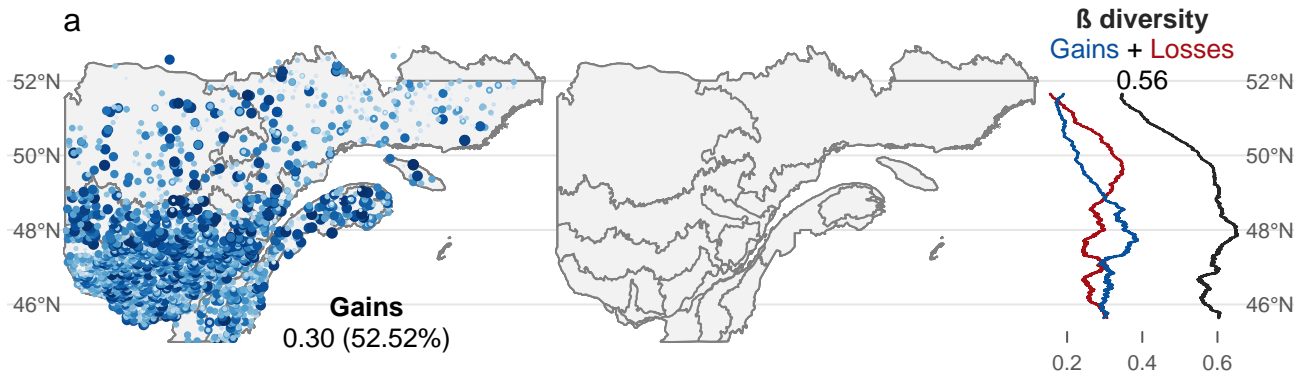
**Table 1.** Description of the predictors used in the multiple linear regression models. See Table S2 for details about disturbance types.

Variable name	Variable description
<b>Baseline conditions</b>	
Temp, Temp <sup>2</sup>	Mean temperature during growing season and its second order polynomial. 10-year average prior to first survey of each plot (°C).
Precip, Precip <sup>2</sup>	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).
<b>Climate change</b>	
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.
<b>Disturbances</b>	
Age	Stand age (years).
Old harvest	Tree harvesting (clearcutting, partial cutting, selection cutting, etc.) that occurred before the study period. 1. Minor (0), moderate (1) or major (2).
Recent harvest	Tree harvesting (clearcutting, partial cutting, selection cutting, etc.) that occurred during the study period. Minor (0), moderate (1) or major (2).
Old natural	Natural disturbances (fire, insect outbreak, windfall, etc.) that occurred before the study period. Minor (0), moderate (1) or major (2).
Recent natural	Natural disturbances (fire, insect outbreak, windfall, etc.) that occurred before the study period. Minor (0), moderate (1) or major (2).

## Figures

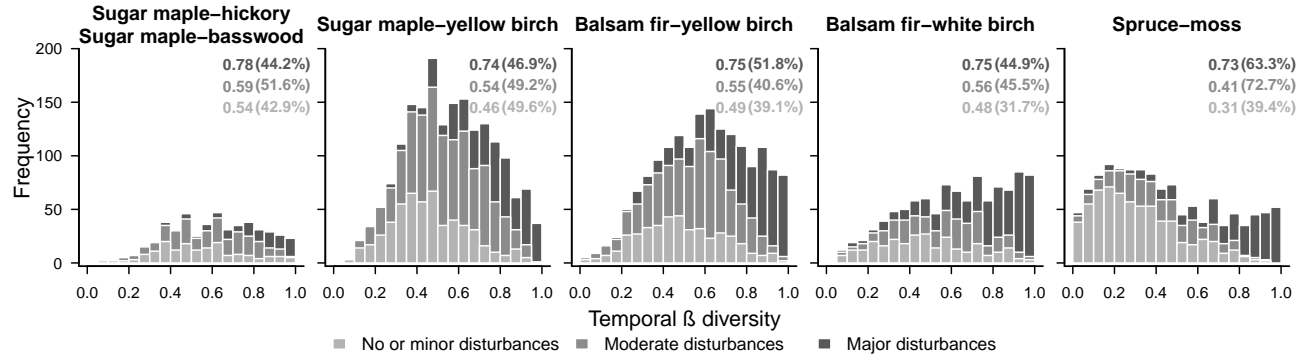


**Figure 1.** Locations of the 6281 forest inventory plots in meridional Québec, Canada. Colors delimit the six bioclimatic domains. The two southernmost domains (orange) were combined in our analyses. The number of forest plots in each domain is written in parentheses.



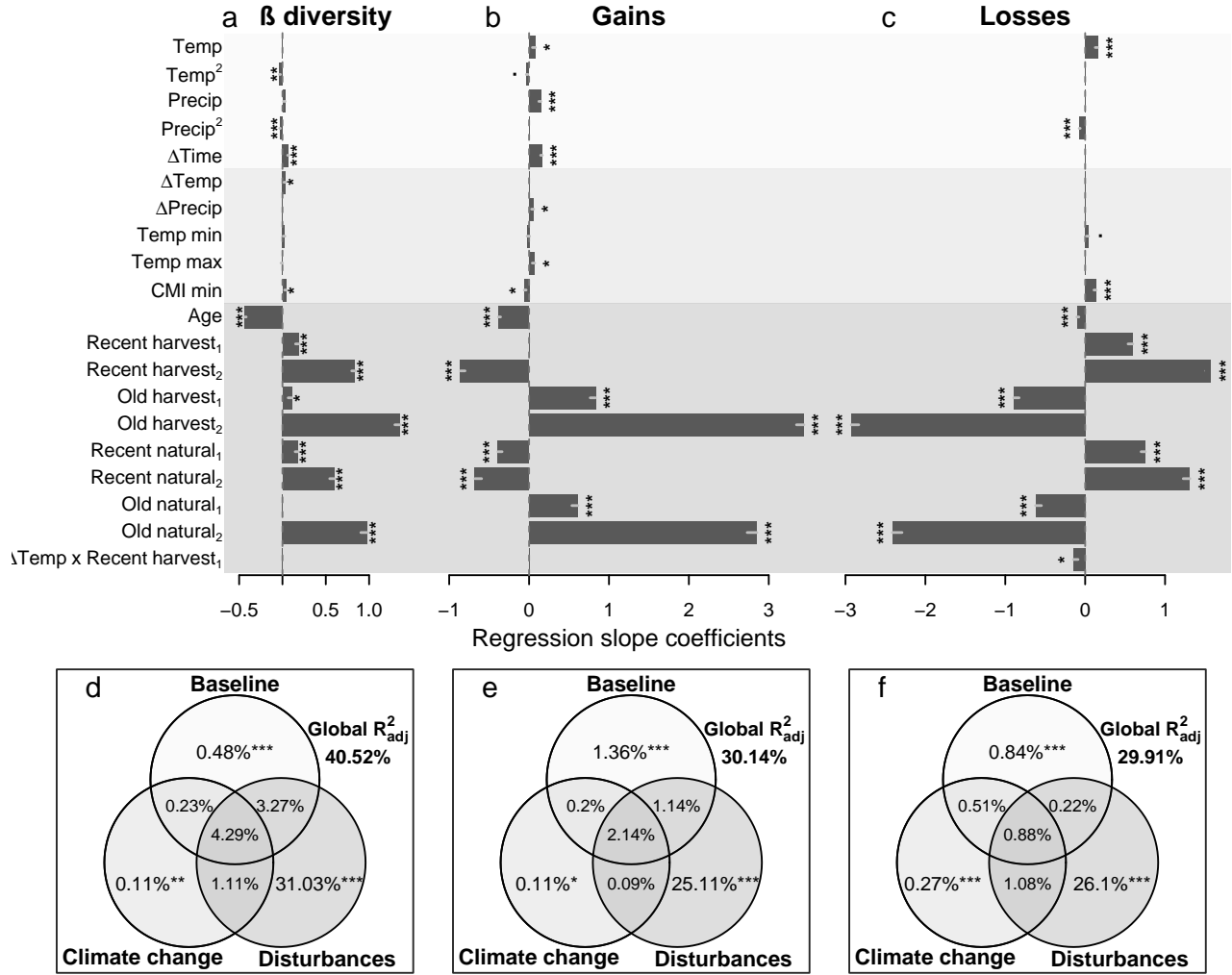
595

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



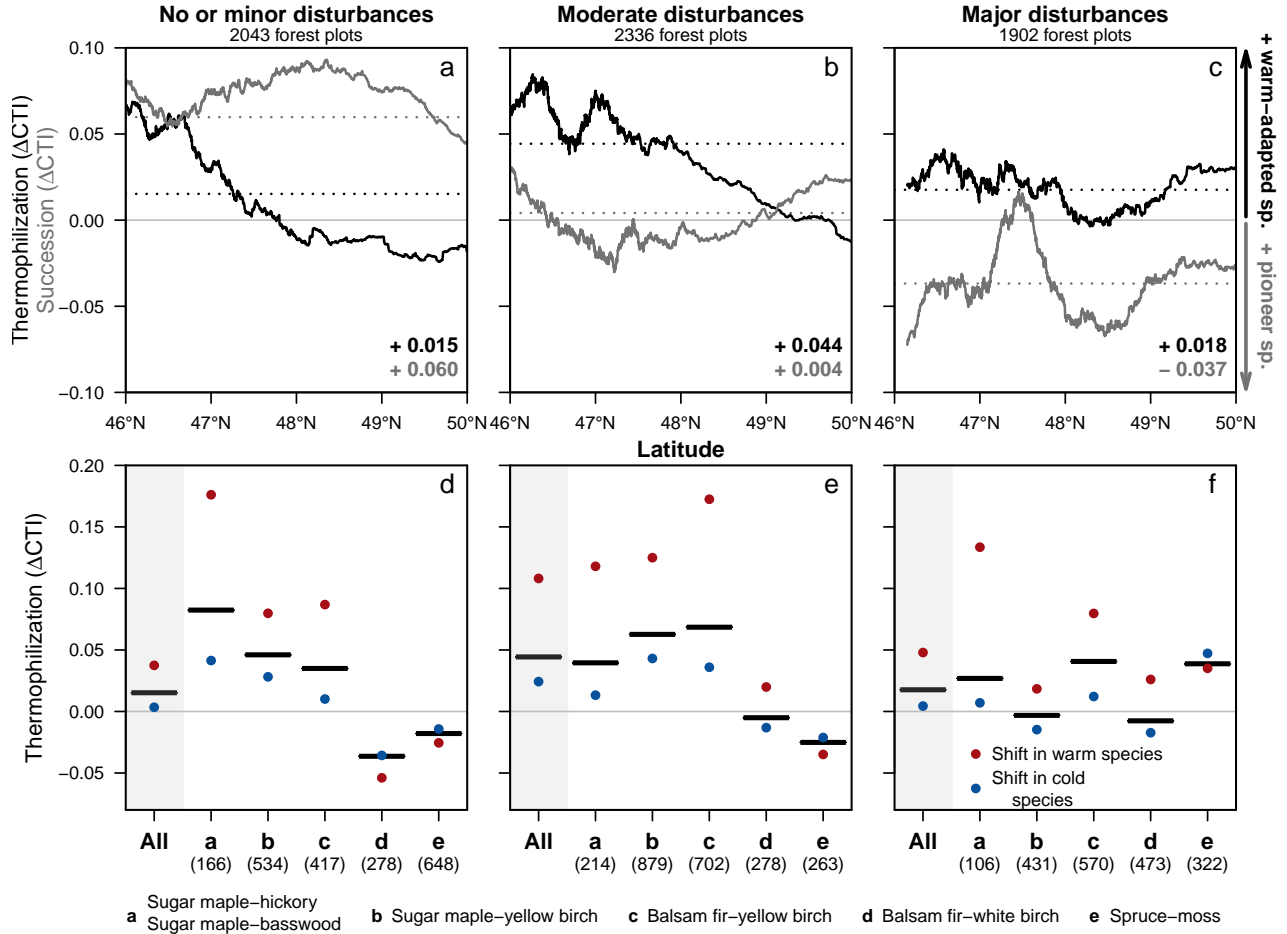
**Figure 3.** Frequency distributions of temporal  $\beta$  diversity in forests plots by bioclimatic domains. Forests of different disturbance levels are stacked on top of each other. The values written in the panels are the mean temporal  $\beta$  diversity values followed by the percentage of losses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





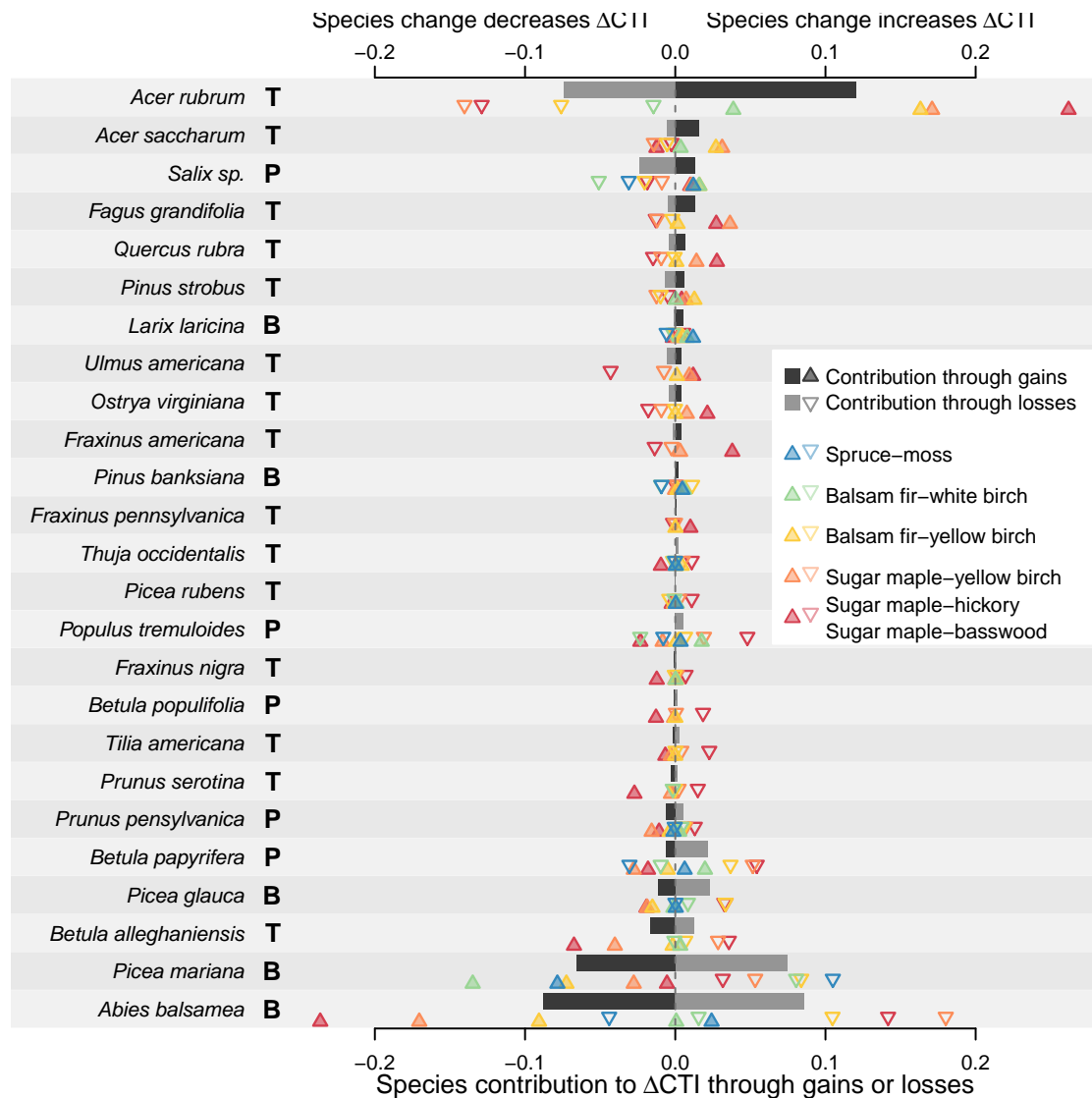
**Figure 4.**

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



**Figure 5.**

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



**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  $\Delta CTI$  increased by an average of 0.12 for all plots where *Acer rubrum* has increased in abundance (dark grey bar), whereas the  $\Delta CTI$  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)ioneer and (B)oreal species. Only species that contributed more than 0.01 in at least one domain are shown.