

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 β diversity, gains and losses. The effects of climate and disturbances on temporal β 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 β diversity was mainly driven by disturbances, with harvesting as the most important factor. Despite the prevailing influence of disturbances, we revealed a generalized thermophilization ($\Delta\text{CTI} = +0.03^\circ\text{C}/\text{decade}$) of 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 ($+0.05^\circ\text{C}/\text{decade}$), a five-fold increase compared to minor disturbances ($+0.01^\circ\text{C}/\text{decade}$). The gains and losses of 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. However, this synergistic effect only benefited a few species, such as maples. Although accelerated by disturbances, tree responses still lag behind climate change.

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 species response is slow (Sittaro *et al.*, 2017) relative to the short duration of typical ecological studies (only a few years). 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 more easily detectable (Jump *et al.*, 2009). As such, there is a growing body of evidence for contemporary shifts in tree species distributions along altitudinal gradient 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). Though, because of the focus on range shifts, there has been little empirical work on the effect of climate change on tree community composition and abundance distribution within species range (e.g. Esquivel-Muelbert *et al.*, 2018; Searle & Chen, 2017). Worldwide increases in tree mortality rates triggered by droughts and heat stress 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), as opposed to short-lived herbaceous plants characterized by high community turnover (Savage & Vellend, 2015; Becker-Scarpitta *et al.*, 2019). Consequently, community-level response to climate change remains difficult to quantify and is probably underestimated at the moment.

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 (Gauthier *et al.*, 2015; Boucher *et al.*, 2017). 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 as 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). In addition, the frequency and intensity of natural disturbances can increase as an indirect effect of climate change (Seidl *et al.*, 2017).

Positive feedback between disturbances and climate change have already been observed locally on long temporal scales, over decades to centuries. 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. Conversely, Woodall *et al.* (2013) found little influence of disturbances on tree range limits in northern US during a 5-year interval from 1998 to 2003. Hence, there is still no clear consensus that positive synergy could influence contemporary tree community response at a large spatial scale. Yet, to anticipate and adapt to future forest changes, large-scale empirical studies are required in order to understand 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 (Savage & Vellend, 2015; Boucher *et al.*, 2017). Hence, analyzing shifts of relevant functional traits in communities using large-scale monitoring data should unravel 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). 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 responding 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 tree composition. We analyzed data from a long-term forest inventory program across meridional Québec, where vegetation ranges from northern hardwood forests dominated by sugar maple at low latitudes (up to 47°N) to mixed forests dominated by balsam fir (from 47°N to 48°N), to boreal forests dominated by black spruce at high latitudes (from 49°N to 52°N). Such dataset allowed us to compare community responses to recent climate change in plots that experienced different levels of disturbances along a large latitudinal gradient. As such, we can address four

questions: (1) how has the composition of forest communities changed during the last decades across different biomes? (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 β diversity (Legendre, 2019) over 6000 resurveyed communities between a historical (1970–1980) and a contemporary (2000–2016) period. Temporal β diversity, which describes the temporal dissimilarity in community composition, 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 β 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 Québec forest inventory plots, which have been sampled south of the 52nd parallel since 1970 by the Ministère des forêts, de la Faune et des Parcs (Fig. 1; MFFP, 2016). We compared the first and last years of the inventory and selected plots that were sampled both before 1980 and after 2000 so as to maximize the time interval. We disregarded plots that were subjected to active reforestation during the study period because 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 total of 6281 plots (Fig. 1) analyzed with a median of 35 years between surveys (1st quartile: 33 and 3rd quartile: 41 years).

Within each circular plot (400 m²), 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 47 tree species (Table S1), which were all 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 very little detection bias in tree surveys.

Environmental variables

The annual past climatic conditions, covering a period from 1960 to 2013, were extracted using a 2 km² (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). From these bioclimatic variables, we derived different predictors (see Table 1 for definitions). 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 mm/decade (Fig. S1).

To analyze the influence of disturbances, we collected information about fire, insect outbreak, windfall and harvesting from the forest inventory dataset (MFFP, 2016). At each plot measurement, disturbance type (23 types) and intensity were recorded. We reclassified disturbances according to four main types (fire, insect outbreak, windfall and harvesting), with 3 levels of intensity each (none, moderate or major; Table 1, Fig. S2). Major disturbances correspond to natural or anthropogenic events that have eliminated more than 75% of the total tree basal area of the previous forest stand, while moderate disturbances have eliminated between 25% and 75%. 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, as time interval between the first and last measurements varies among the forest plots, it was included as a predictor.

Analysis

β diversity

For each plot, we computed temporal β diversity (Legendre, 2019), which is the difference in species composition between two surveys of a given plot, by comparing local tree abundance in forest plots between the historical (before 1980, t_1) and contemporary (after 2000, t_2) periods. This dissimilarity index (β) was computed using the Ružička coefficient, which is one of the quantitative forms of the Jaccard dissimilarity:

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

$A = \sum_{j=1}^n a_j$: unscaled similarity — a_j represents the number of individuals of species j that is common between t_1 et t_2 ;

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

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

This temporal β 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 abundance. Throughout this paper, gains and losses refer to these relative metrics.

This additive framework allowed us to partition further the different components contributing to β diversity. Temporal dissimilarity in tree community can be decomposed into the dissimilarity (gains and losses) of different species groups of interest, here boreal (9 species), pioneer (11 species) and temperate species (27 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,

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

Assessing relative importance of drivers of community changes

We evaluated the effects of multiple drivers on temporal β , gains and losses using multiple regressions, which can be combined with variation partitioning analyses (Borcard *et al.*, 1992). Because the dependent variables (β , gains, losses) are in the standard unit range $[0, 1]$, we used a logit transformation $y' = \log(y/(1 - y))$.

We next quantify the influence of climate change and disturbances, while controlling for the baseline climate gradient and different time interval. To do so, we classified our predictor variables in three subsets: baseline conditions, climate change and disturbances (Table 1). We then generated global models predicting β , gains and losses, for each of the three subsets. We also tested relevant interactions between disturbance and climate predictors (fire ΔCMI ; *outbreak* $\Delta Temp$; harvest * $\Delta Temp$). A forward selection of explanatory variables based on two stopping criteria (α 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 and we ensured that residuals met 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 parsimonious models. The significance of each unique fraction was tested using 9999 permutations.

Functional index of community change

To test whether or not climate warming contributed to community changes, we combined climate and tree occurrence data to measure a Community Temperature Index (CTI) from species temperature distributions (Devictor *et al.*, 2008). Specifically, we overlaid interpolated climate data (mean annual temperature averages from 1970–2000 at a spatial resolution of 1 km², 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 all studied tree species. The mean annual temperature for each occurrence was extracted to infer species temperature distributions. The mean of these temperature values was used as a proxy for a species thermal preference (Species Temperature Index, STI, in degrees Celsius; Table S1). For each plot in each time period, CTI was then calculated as the mean of the STI weighted by the abundances of the species present in that plot. 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 CTI per decade:

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

A positive value of ΔCTI indicates an overall thermophilization of the tree community in degrees Celsius per decade.

To evaluate whether community thermophilization was caused by decreases of cold-adapted species or increases of warm-adapted species, we quantified the shift in the left (10th percentile) and right tails (90th percentile) of the plot-level distribution of species temperature preferences (see Fig.1 in De Frenne *et al.*, 2013). To do so, for each individual of a species present in a plot, we sampled 1000 temperature values from the temperature distribution of that species and summed the values across the individual stems present to obtain a plot-level temperature distribution. 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 were not following a Gaussian distribution; in particular, many southern species presented bimodal and skewed distributions. Then, we calculated the 10th (cold tail) and 90th percentiles (warm tail) of the plot-level temperature distributions. The shifts in the cold and warm tails of the temperature distributions were computed in the same way as for the shifts in mean. 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 ΔCTI through gain or loss in abundances. Species contributions were assessed following these steps: for each species, 1) we replaced the abundance at t_2 by its previous abundance at t_1 , as if the species abundance had not changed over time; 2) we computed a new CTI'_{t_2} ; 3) then we calculated $\Delta CTI'$ using CTI'_{t_2} and CTI_{t_1} as above; and finally 4) we measured the

difference between $\Delta CTI'$ and ΔCTI in each plot. A positive value indicates that the change (gain or loss) of a given species abundance increases thermophilization in a plot. We also determined the role of species gains and losses in ΔCTI by averaging their contributions for plots where they increased and where they decreased.

To test the alternative hypothesis that community changes are resulting from post-disturbance succession, we collected traits about shade tolerance (Niinemets & Valladares, 2006) to compute a Species Shade Index (SSI) that 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, ΔCSI , was computed in the same way as for ΔCTI , where a positive value indicates a progress in stand succession toward climax, in unit 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 S2. R scripts will be made available on GitHub upon manuscript acceptance.

Results

Temporal β diversity

Mean temporal β diversity was 0.56 for the whole study area ($n = 6281$), and these temporal changes in community composition were attributable to slightly more gains in abundances (52.5%) than losses (47.5%; Fig. 2a). Temporal β 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 β changes were dominated by losses whereas, south of this limit, losses prevailed.

For undisturbed forests, compositional changes were particularly notable in the southernmost domains (sugar maple-hickory and sugar maple-basswood; $\beta = 0.54$) and remained quite high from the sugar maple-yellow birch ($\beta = 0.46$) up in the balsam fir-white birch ($\beta = 0.49$), whereas the northernmost domain (spruce-moss) changed very little ($\beta = 0.32$; Fig. 3). This pattern reflects the latitudinal variation in the contribution of the three species groups to temporal β (Fig. 2b). 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). Some species have experienced great changes in abundance and occurrence throughout these domains, mainly black spruce, red maple, yellow birch, American beech and trembling aspen, and likely contributed largely to the pattern of temporal β diversity

(Fig. S3).

The magnitude of compositional change in forests was highly influenced by disturbances (Figs 2b-d, 3, S4).

The mean temporal β was 0.54 for moderately disturbed forests and 0.75 for highly disturbed forests, whereas it was only 0.43 for undisturbed forests (all domains combined). Yet, the fraction of changes attributed to losses was rather similar among the three levels of disturbance (none: 42.4%; moderate: 48.8%; major: 49.7%), except for spruce-moss forests where moderate and major disturbances resulted in considerably more losses than gains (71.9% and 63.7% respectively).

Disturbances increased both gains and losses, and therefore β diversity, in each species group (Fig. 2b-d). At high disturbance level, we observed a strong surge in turnover of boreal tree species (both gains and losses) along with an increase in gains of pioneer species. In contrast, turnover in temperate species was slightly higher at moderate disturbance levels.

Drivers of temporal changes

Once combined, predictors from the three subsets (baseline, climate change and disturbances) explained together 32% of the variation of temporal β diversity, 21% of gains and 17% of losses (Fig. 4).

Community temporal changes were mainly driven by disturbances (R_{adj}^2 for β : 23%; gains: 12%; losses: 18%), whereas the impacts of climate change were significant but comparatively modest (R_{adj}^2 less than 1%; Fig. 5d-f). Overall, disturbances enhanced compositional changes, with major harvest being the most important driver. Interestingly, while most disturbances promoted losses and reduced gains, intense fires had the opposite effect (Fig. 4b-c). As time-since-disturbance increases and the forests grow old (Age), forest composition changes less and colonization of new individuals becomes scarcer (Fig. 4a-b).

Regression models provided only weak evidence of climate change effect on forest community change. Mainly, extreme minimum CMI (CMI min, i.e. drought) 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. Although the effect of climate warming alone (Δ Temp) was weak, we found strong interactions with disturbance variables. Increasing temperature amplified the effect of harvesting on losses and gains but mitigated the effect of insect outbreaks. Variables related to baseline conditions were more important than climate change, reflecting a latitudinal gradient in community change.

Changes in community temperature and shade indices

The community temperature index (CTI) increased significantly between the historical and contemporary period (paired t-test p -value < 0.001 ; mean of +0.03 °C/decade for all plots, ranging from -0.02 to +0.05 across domains), which indicates a generalized community thermophilization throughout the study area.

During the same period, the community shade index (CSI) also increased (+0.01 unit/decade), suggesting a transition towards late successional forests.

Thermophilization was significantly larger in moderately disturbed forests ($\Delta\text{CTI} = +0.05$ °C/decade) than in undisturbed (+0.01 °C/decade) or highly disturbed forests (+0.02 °C/decade; Anova $F(2, 6278) = 13.05$, p -value < 0.001 ; post-hoc Tukey tests showed that moderately disturbed forests had significantly higher ΔCTI than the other two levels). Moreover, the thermophilization in moderately disturbed forests extended further north, up to 48°N, in the balsam fir-white birch domain (Fig. 5b,e). Despite the influence of disturbances on thermophilization, change in CTI was weakly explained by our environmental predictors (R_{adj}^2 ca. 2% for all predictors in Table 1). Moreover, the relationship between thermophilization and climate change predictors was surprisingly weak ($R_{adj}^2 < 1\%$), with no correlation at all with temperature change.

The analysis of ΔCSI revealed that the higher the level of disturbances the more pronounced the decrease of CSI was (Fig. 5a-c), which was consistent with the gains in pioneer species (Fig. 2). The disparity between the ΔCTI and ΔCSI curves shown in Fig. 5, as well as the weak correlation between STI and SSI (Pearson $r = 0.15$, p -value = 0.26), suggest that thermophilization was not trivially driven by successional processes.

Community thermophilization was asymmetrical, with larger increases in the warm-tail of the temperature distributions than in the cold-tail (Fig. 5d-f), indicating that thermophilization was mainly driven by larger gains in warm-adapted species. The positive correlation between ΔCTI and gains in temperate species in all domains also corroborates this finding (Fig. S5). 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).

Only a few species contributed substantially to the community thermophilization (Fig. 6). Gains of red maple and sugar maple, as well as losses of balsam fir and black spruce, contributed strongly to the thermophilization of all forests. In addition to the change of these four species, the losses of white birch and white spruce also played a key role in the thermophilization of ecotonal forests in the balsam fir-yellow birch. Moreover, temperate species such as American beech, red oak and white ash contributed mostly to the thermophilization of southern domains (Fig. 6) where their abundance has increased (Fig. S3). 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. S5), such as white birch and willow spp. (Fig. 6).

Discussion

In this study, we found evidence of climate-induced shifts in tree community composition despite the prevailing influence of disturbances. Local and short-term influence of disturbances masks long-term and

lagging climate-induced changes in community. 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. Taken together, our results suggest that disturbances strongly modify tree community responses to climate change, revealing potential synergies that are yet to be studied.

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, this study underscores the prevalence of logging activities on the forest dynamics of the temperate-boreal ecotone. Tree harvesting was not only the type of disturbances with the highest impact on community changes, but also the most frequent: 24.2% (1521 out of 6281) of the plots were cut during the study period, which represents more than the frequency of insect outbreak, 20.3% and fire, 4.4% (Fig. S2). Natural disturbances and tree harvesting, however, impact forest composition and structure very differently. It has been shown that tree harvesting favored early successional stands to the detriment of old-growth forests (Boucher *et al.*, 2009; Boucher & Grondin, 2012). Such changes in forest age structure and composition jeopardize both forest resilience (Cyr *et al.*, 2009; Grondin *et al.*, 2018) and wildlife that only thrives in mature forests (Tremblay *et al.*, 2018).

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). This corroborates 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), including recent studies showing no statistically significant response (Becker-Scarpitta *et al.*, 2019). The inertia of forest communities suggests ongoing extinction debts and colonization failures due to tree high longevity and low dispersal ability (Svenning & Sandel, 2013). Considering the velocity of predicted future climate change, this disequilibrium

is likely to grow, leading to biodiversity losses.

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 effects from climate change 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 that 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 disturbance, trees grow slowly, their mortality rates are low and competition for space and light is strong, thus preventing warm-adapted species from colonizing, despite the suitability of climatic conditions; community thermophilization is consequently very slow. Moderate disturbances, however, remove resident species and reduce competition, which enhances the replacement of boreal by temperate trees, thereby increasing the thermophilization rate. 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, instead of having a positive effect on local species richness, it accelerates ecological transition.

Furthermore, disturbances may also influence the compositional shift by modifying local abiotic conditions. For instance, it has been shown that forest canopy closure attenuates thermophilization of understory communities, likely by maintaining cool and wet local microclimates (De Frenne *et al.*, 2013; Stevens *et al.*, 2015). Therefore, as disturbances create canopy openings, they affect local microclimates which likely alter the survival rates of tree saplings as well as the understory plant communities.

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 in order 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.

Species contribution to community thermophilization

We found that the observed community thermophilization was caused by gains and losses in abundance of a restricted group of species which indicates that several species lag even more behind climate change. This differential rate of species response also entails that larger reshuffling of communities are still ahead. The interaction between climate and disturbances likely promotes generalist tree species adapted to disturbance with high dispersal abilities (Aubin *et al.*, 2016). For instance, generalist species like maples, especially red maple, have been expanding in eastern North America since the pre-industrial period (Thompson *et al.*, 2013; Boucher *et al.*, 2017) 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 hickories and basswood, or constrained to specific habitat, such as silver maple, might not benefit from these opportunities.

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 compositional changes in forests, 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 state 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 the northern limit of the temperate biome was located about 500 km north of its actual limit during the last interglacial period (6-7  C warmer), 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 results demonstrate that moderate disturbances play a major role in promoting regime shift by speeding up the transition from one ecosystem state to another (Johnstone *et al.*, 2016).

We show that the ecotonal zone is particularly sensitive to the combination of climate warming and moderate disturbances, where their interaction is likely to promote a patchy northward shift of the ecotonal zone into the balsam fir-white birch domain. Yet, change in composition may directly affect timber supply, especially in the ecotone where deciduous species replace conifers, and indirectly affect natural disturbance regime. Thus, major changes in forest management goals will become necessary to maintain ecological functions and processes (Williamson *et al.*, 2009; Daniel *et al.*, 2017). Our study provides valuable insights for potential adaptation measures in forest management. To help forest keep pace with climate change, planned selection cutting could be used to reduce competition in certain areas

and accelerate species range shifts. Such management is however a double-edged sword as it could bridge the gap between current species distribution and their optimal climate niche, but it could at the same time decrease forest diversity by promoting a narrow set of species. Hence, a combination of selection cutting with assisted migration might be necessary to maintain diverse forests (Iverson & McKenzie, 2013).

The frequency and severity of natural disturbances, such as fires, insect outbreaks, droughts and heat waves, are expected to increase in many regions of the world (Bergeron *et al.*, 2006; Seidl *et al.*, 2017). In the light of our results, this may lead to greater forest compositional changes over the next decades and potentially to permanent ecosystem shifts (Grondin *et al.*, 2018). However, if disturbances becomes too intense, they could merely promote early-successional pioneer species, thereby impoverishing forest communities. Our study focused on the forests of Québec, a straightforward avenue to investigate the generality of our findings is to compare our results with regions that are experiencing different disturbance and climate regimes. A natural candidate for such comparison is western Canada, which, over the last decades, has suffered an unprecedented outbreak of the mountain pine beetle, a severe drought (2001-2003) and extreme fire seasons (Williamson *et al.*, 2009; Michaelian *et al.*, 2011). If our results were to be confirmed, then we need to rethink current forest management strategies as well as models of forest responses to climate change in order to account for the synergistic effect of disturbances.

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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

598 **Table 1.** Description of the predictors used in the multiple linear regression models.

Variable name	Variable description
Baseline conditions	
Temp	Mean temperature during growing season, 10-year average prior to first measurement ($^{\circ}\text{C}$).
Precip	Total precipitation during growing season, 10-year average prior to first measurement (mm).
ΔTime	Time interval between first and last measurements (years).
Climate change	
ΔTemp	Slope between Temp and time ($^{\circ}\text{C}/\text{y}$).
ΔPrecip	Slope between Temp and time (mm/y).
ΔCMI	Slope between Climate Moisture Index and time (y^{-1}).
Temp min	Extreme minimum temperature. Difference between minimum and mean temperature of the coldest period ($^{\circ}\text{C}$).
Temp max	Extreme maximum temperature. Difference between maximum and mean temperature of the warmest period ($^{\circ}\text{C}$).
CMI min	Extreme minimum Climate Moisture Index (CMI). Difference between minimum CMI and mean CMI ($^{\circ}\text{C}$), as a proxy of drought.
Disturbances	
Age	Stand age (years)
Harvest	Tree harvesting. None (0), moderate (1) or major (2). Include clearcutting, selection cutting, shelterwood cutting, seed-tree cutting, etc.
Fire	Forest fires. None (0), moderate (1) or major (2).
Outbreak	Insect outbreaks. None (0), moderate (1) or major (2).
Windfall	Windfall or ice storm. None (0), moderate (1) or major (2).

Figures

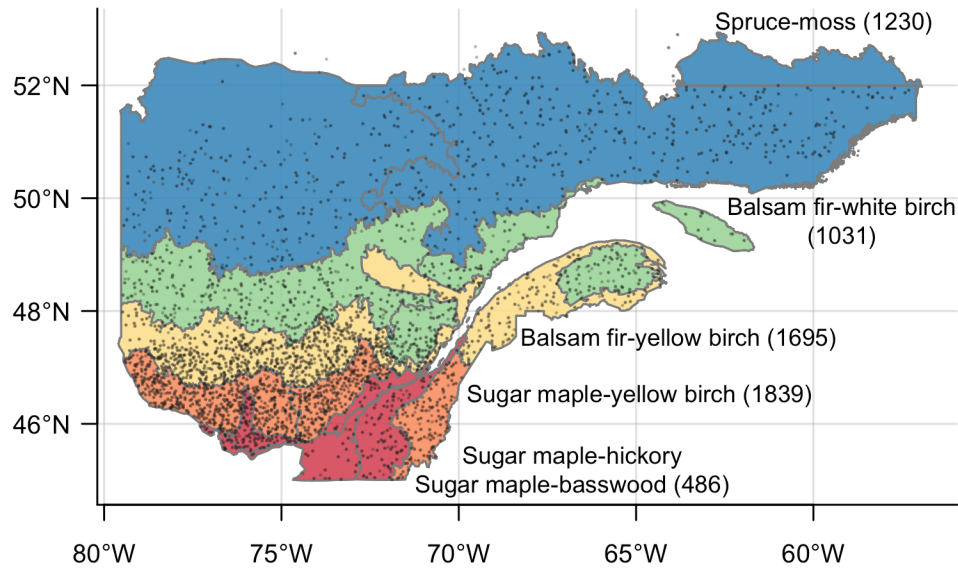


Figure 1. Locations of the 6281 forest inventory plots in meridional Québec, Canada. Colors delimit the six bioclimatic domains. The two southernmost domains (orange) were combined in our analysis. The number of forest plots in each domain is written in parentheses.

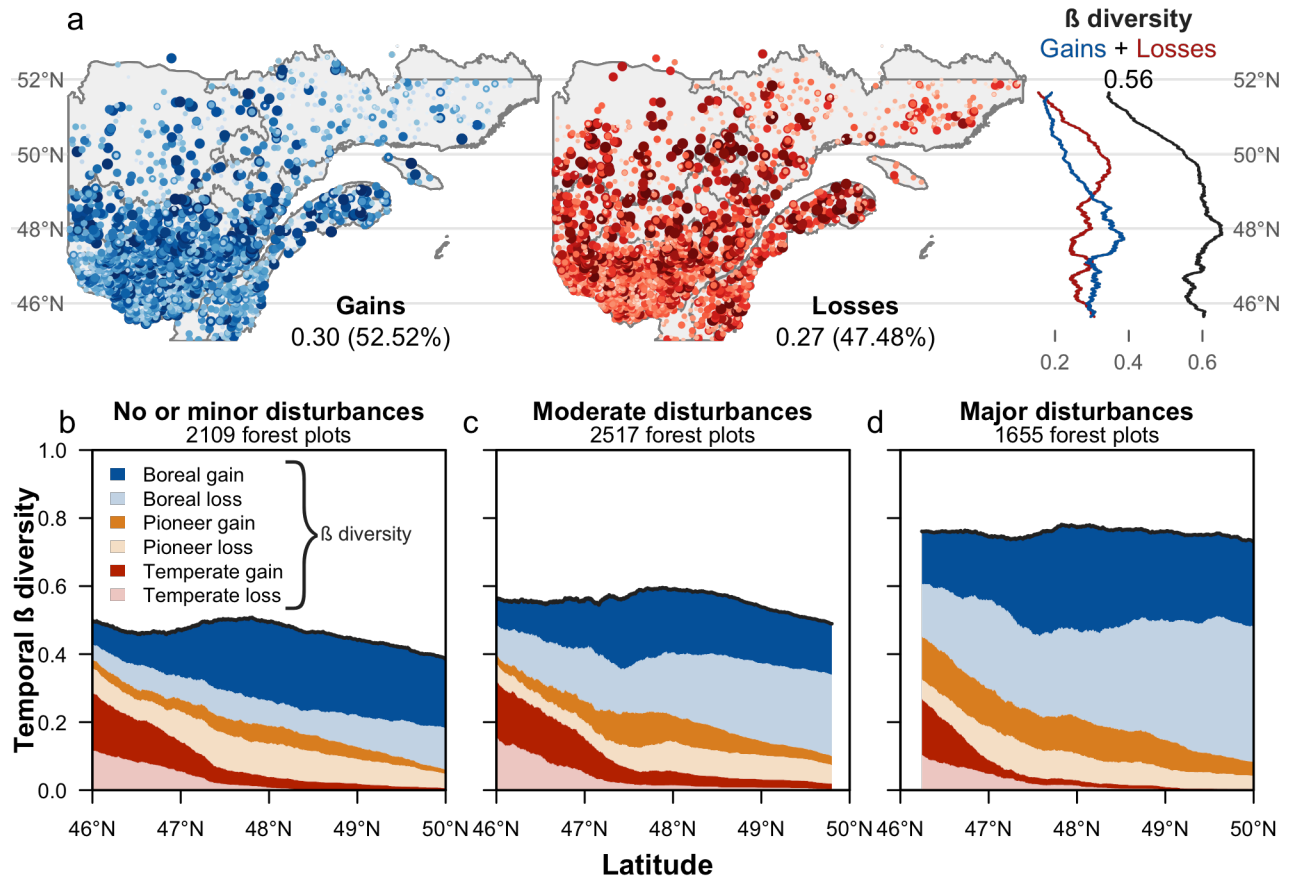


Figure 2. Maps of gains and losses in tree abundances (a) and latitudinal trends in temporal β diversity, decomposed into gains (blue) and losses (red) of boreal, pioneer and temperate trees, for different levels of disturbance (b-d). The sizes and colors of the points on the maps are proportional to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

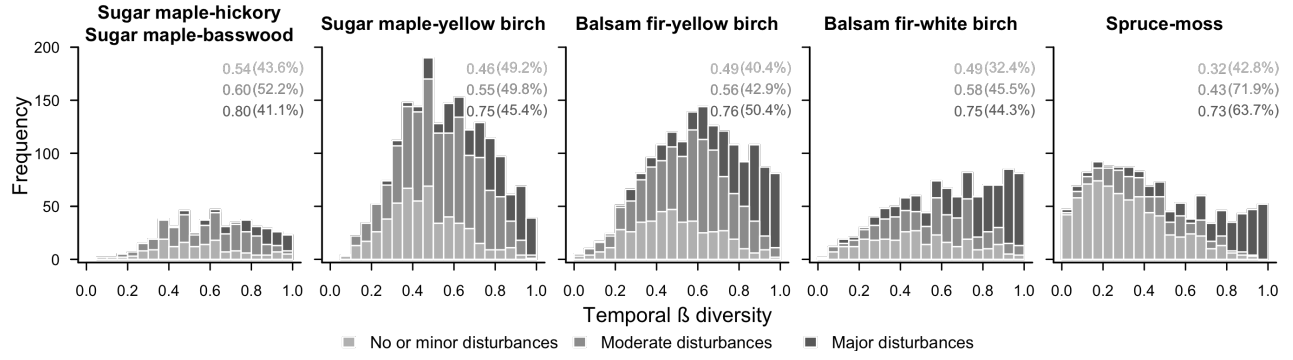


Figure 3. Frequency distributions of temporal β diversity in forests plots by bioclimatic domains. Forests of different disturbance levels are stacked on top of each other. The values written on the plots are the mean temporal β diversity values followed by the percentage of losses in parentheses.

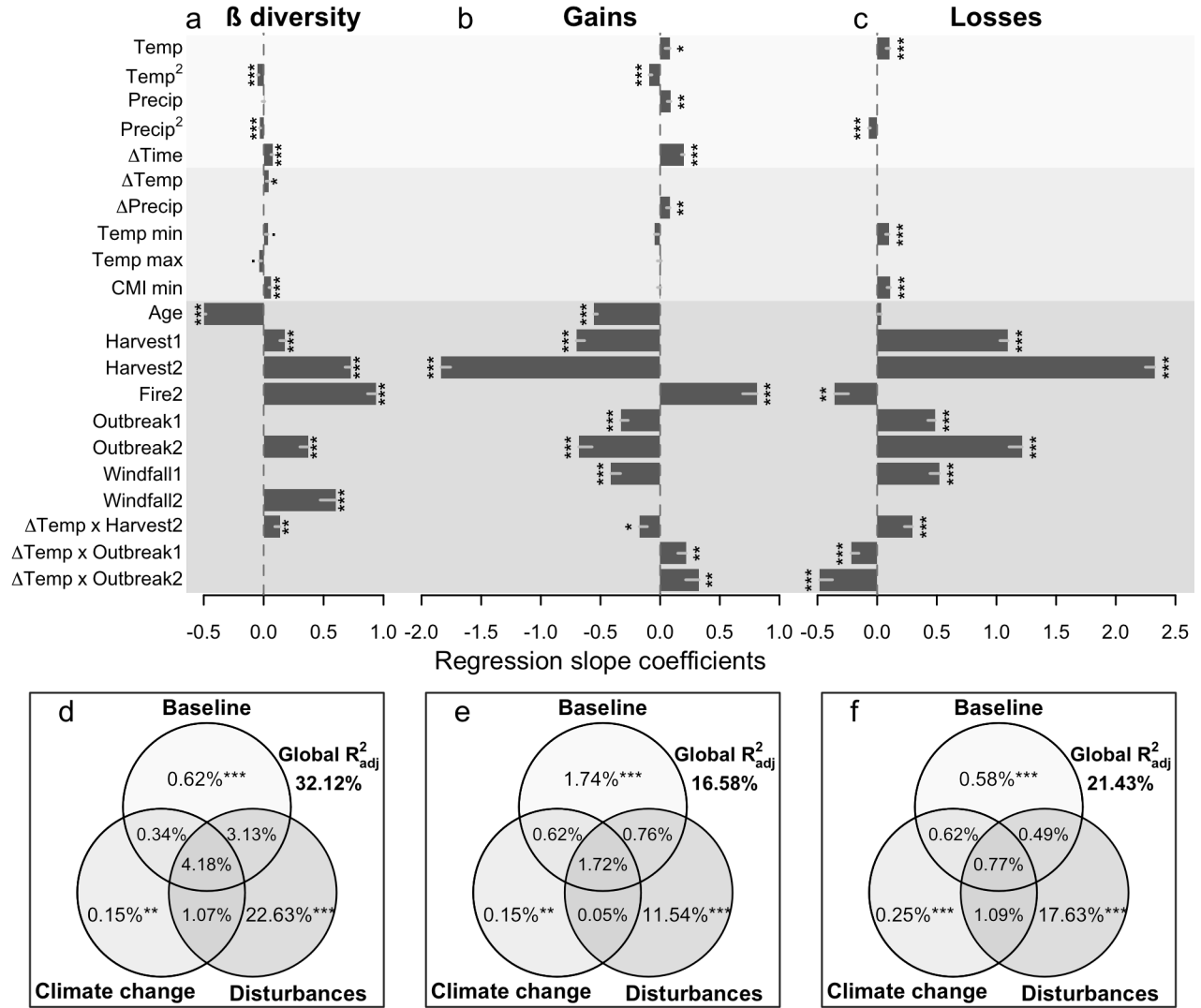


Figure 4.

Slope coefficients from multiple regression models for (a) temporal β 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 each model, only the selected predictors are shown, and stars correspond to the level of significance of the p-value (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). See Table 1 for description of the predictor variables.

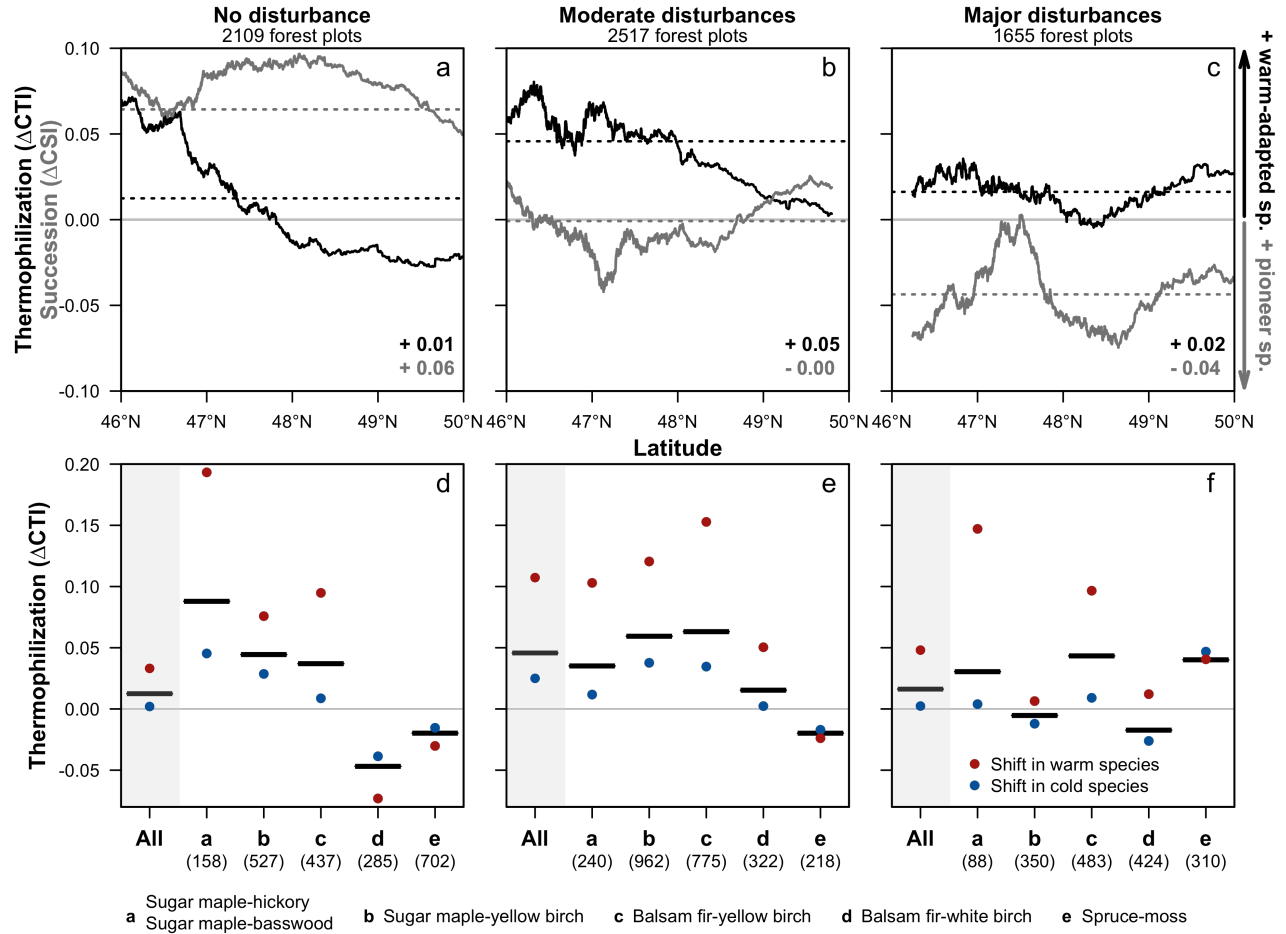


Figure 5.

Thermophilization (i.e., change in community temperature index, ΔCTI) and successional process (i.e., change in community shade index, ΔCSI) of forests for different levels of disturbance. In the upper panels (a, b, c), the latitudinal trends in ΔCTI (black curve) and ΔCSI (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 represent the mean ΔCTI (black) and ΔCSI (grey) 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; positive values indicate overall thermophilization, increases of warm-adapted and decreases of cold-adapted species, respectively.

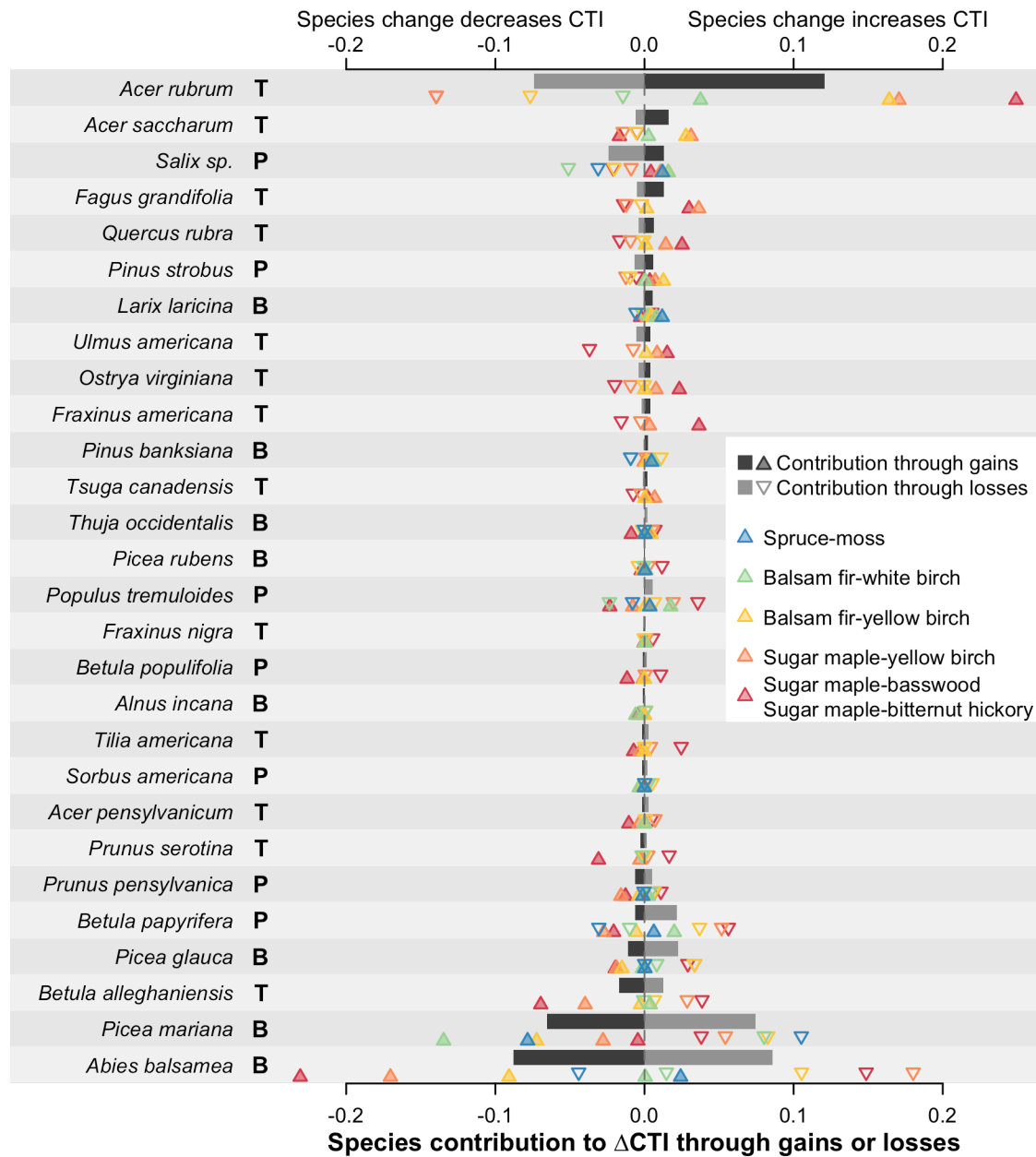


Figure 6.

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 points represent the mean contributions of given species through gains (solid) or losses (empty) by domain. Letters next to species names correspond to (T)emperate, (P)ioneer and (B)oreal species. Only species (28) that contributed more than 0.005 in at least one domain are shown.