LETTER

Climate change-associated tree mortality increases without decreasing water availability

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Abstract

Temporal increases of tree mortality have been observed in regions where global warming has decreased long-term water availability and/or induced droughts. However, temporal decreases in water availability are not a global phenomenon. Understanding how water deficit-free forests respond to the recent effects of climate change is paramount towards a full appreciation of the impacts of climate change on global forests. Here, we reveal temporally increasing tree mortality across all study species over the last three decades in the central boreal forests of Canada, where long-term water availability has increased without apparent climate change-associated drought. In addition, we find that the effects of conspecific tree-to-tree competition have intensified temporally as a mechanism for the increased mortality of shade-intolerant tree species. Our results suggest that the consequences of climate change on tree mortality are more profound than previously thought.

Keywords

Climate change, global warming, neighbourhood analysis, tree mortality, water deficit.

Ecology Letters (2015)

INTRODUCTION

Climate change-associated increases in tree mortality have global implications for forest structure, function and biosphere-atmosphere interactions (Anderegg *et al.* 2013). Temporal increases of tree mortality have been observed in regions where global warming has either decreased long-term water availability (van Mantgem *et al.* 2009; Peng *et al.* 2011; Luo & Chen 2013), or induced droughts (Breshears *et al.* 2005, 2009; Michaelian *et al.* 2011; Williams *et al.* 2013). Water scarcity has been considered as the climatic driver of these temporal increases in tree mortality as it may lead to tree mortality directly through a cascade of interrelated failures of carbon metabolism and plant hydraulics (McDowell *et al.* 2008; Hartmann *et al.* 2015) and/or indirectly through their increased vulnerability to forest pests (Hogg *et al.* 2008; McDowell *et al.* 2011; Gaylord *et al.* 2013). However, temporal decreases in water availability have not been a global phenomenon (Sheffield *et al.* 2012; Dai 2013). In areas where temporal decreases in water availability are absent, rising temperatures might have positive effects on trees via the release of soil nutrients and through extending the growing season (Myneni *et al.* 1997; Peñuelas *et al.* 2009). Furthermore, as a major contributor to global warming, CO_2 increases could improve photosynthetic uptake and the efficacy of water-usage (Keenan *et al.* 2013). Elucidating how water deficit-free forests respond to recent climate change is paramount towards a full appreciation of the impacts of climate change on global forests.

Increases in tree mortality might also result from the intensification of tree-to-tree competition due to positive climatic effects on tree growth (Phillips *et al.* 2004). Although this process has been proposed as a potential mechanism of climate change-associated tree mortality (Phillips *et al.* 2004), no study to date has explicitly tested it. Such knowledge is required to better understand how trees die and to provide for improved predictions of tree mortality in future climatic scenarios (Anderegg *et al.* 2012; Cook *et al.* 2014). At the community level, trees are not isolated from each other; they compete for resources such as soil water, nutrients, light (Muller-Landau *et al.* 2006) and living space (Coates *et al.* 2009). As a result of this competition, trees may die from the lack of access to already limited resources (Luo & Chen 2011). This competition effect may vary among neighbouring tree species, and is generally more robust between conspecific neighbours because of possible occupation of the same ecological niche and negative density-dependent effects (Janzen 1970; Silvertown 2004; Luo & Chen 2011). However, the quantification of plant competition can be complicated (Weigelt & Jolliffe 2003). Neighbourhood analyses have proven to be a powerful analytical tool for describing how trees interact with their neighbours (Uriarte *et al.* 2004; Canham *et al.* 2006; Das *et al.* 2008; Coates *et al.* 2009).

Here, we sought to test the hypothesis that there was a systematic increase in climate change-associated tree mortality in a region that has not experienced a temporal decrease in water availability (Sheffield *et al.* 2012), and temporal increases in tree mortality might be associated with alterations in the effects of tree-to-tree competition. We utilised 146 plots, which were repeatedly measured from 1986 to 2010 in Manitoba, Canada (Fig. S1). We conducted individual tree mortality analyses for three major boreal tree species: *Pinus banksiana* Lamb, *Populus tremuloides* Michx and *Picea mariana* (Mill.) BSP. Of a total of 19 982 trees that were monitored, 4215 trees died over the course of the study period (Table S1 and Fig. S2). The spatial configurations of each tree were recorded since the plots were established, making it possible to compile a spatial neighbourhood competition index

for each tree at each census. As the temporal variations in tree mortality are attributable to both forest development and recent climate change (Luo & Chen 2011, 2013), our models account for endogenous factors such as competition, forest ageing and exogenous climate change factors.

MATERIALS AND METHODS

Study area and forest inventory plot data

The study area was located in Manitoba, Canada, ranging from 49°04′ to 56°99′ N in latitude and from 95°30′ to 101°68′ W in longitude (Fig. S1). The mean annual temperature and mean annual precipitation between 1983 and 2010 varied from −3.09 °C to 2.95 °C and from 443 mm to 674 mm respectively. Elevations ranged from 212 m to 675 m above sea level (a.s.l). Wildfire is the dominant stand-replacing disturbance with fire return intervals varying temporally and spatially, from 25 to 90 years (Weir *et al.* 2000).

We used permanent sampling plots, which were established in stands (>4 ha in area) that were visually homogeneous in structure and composition, and were located at least 100 m from any openings to minimise edge effects. The plots were circular with an area of 500 m^2, and were remeasured every 5 years, from 1985 until 2010. To detect possible systematic changes of climate change-associated mortality and to examine climate change-altered competition effects on tree mortality, we selected the plots based on the following three criteria. First, stands were naturally established subsequent to fires and were not managed. Second, plots were measured for at least three consecutive censuses. Third, the spatial location of the plot was recorded such that climate data could be obtained. As a result, 146 plots were selected for our analysis (Fig. S1). The initial census year varied from 1986 to 2000 (mean = 1991, whereas the final census year ranged from 1996 to 2010 (mean = 2008). The monitoring length ranged from 10 to 20 years, averaging 16.6 years. The number of censuses ranged from three to five times (mean 4.3) (Fig. S2). Rather than including all measured trees in this study (i.e. all trees with heights exceeding 1.5 m), we analysed only those trees that were greater than 5 cm in diameter at breast height (DBH, 1.3 m above root collar) to eliminate mortality uncertainties associated with understory disturbances, such as mammal browsing and damage imparted from large falling neighbouring trees. A total of 19 982 trees were measured for three major tree species, *Pinus banksiana*., *Populus tremuloides* and *Picea mariana* (Table S1).

Explanatory variables

Stand age (SA) for each plot was determined according to records of a known fire, or by coring three dominant/co-dominant trees of each tree species that resided within or outside the plot at the time of plot establishment. With coring, the average ring count of tree samples for the species with the oldest ages was utilised to determine time since fire via species-specific relationships between forest age and time since fire developed in the boreal forests (Gutsell & Johnson 2002; Vasiliauskas & Chen 2002).

Because competition among neighbouring trees is critical to their mortality (Luo & Chen 2011), we employed Hegyi competition index (H) to quantify a tree's competitiveness for resources (Hegyi 1974), which takes into account the distances of the competitors to the subject tree as well as the dimensions of the trees.

$$H_{ijk} = \sum_{n \neq i} \frac{DBH_{njk}}{DBH_{ijk} \times \left((Distance_{in})_{jk} + 1 \right)} \tag{1}$$

where H_{ijk} is competition index of subject tree i at jth census period in kth plot; DBH_{njk}, DBH_{ijk} and $(Distance_{in})_{jk}$ are DBH of nth neighbour tree, DBH of the subject tree i and distance between tree i and n at jth census period in kth plot respectively. For each census period j of two measurements, H_{ijk} was calculated based on the initial measurement.

Since all plots were circular with a radius of 12.6 m, we calculated H based on the distance of 12.6 m between the subject tree and its neighbours. To correct for edge effects, H was weighted using an area-weighted edge correction (Das *et al.* 2008). For instance, if only 50% of the 12.6 m radius circle centred around a given tree was within the plot, the raw H for that tree was divided by 0.5. In addition, we calculated the Hegyi index from conspecific neighbouring trees (Hc) and the Hegyi index from interspecific neighbouring trees (Hi) (Table S2). Our analyses suggested that our plots were located in homogeneous forests in terms of tree size and composition, and that tree's locations in the sample plot had a little effect towards estimating the Hegyi competition index (Fig. S3).

We derived mean annual temperature (MAT), annual precipitation (AP) and annual climate moisture index (CMI) from BioSIM software (Régnière *et al.* 2012) (https://cfs.nr-can.gc.ca/projects/133), which generates regional historical scale-free climate data, interpolated from nearby weather stations, based on plot locations (latitude, longitude and elevation). The annual climate moisture index (CMI) comprised the sum of monthly CMI, which is the difference between monthly precipitation minus monthly potential evapotranspiration (PET). PET was computed using a simplified form of the Penman–Monteith equation (Hogg 1997). Lower CMI values indicated drier conditions (Hogg 1997). Annual climate anomalies are defined as departures of annual climate values from their long-term means (Clark *et al.* 2011). The long-term climate mean was defined as the average of each climate variable between 1953 and 2010. We employed mean annual temperature anomaly (ATA), annual precipitation anomaly (APA) and annual climate moisture index anomaly (ACMIA).

Furthermore, we analysed temporal changes of the annual Palmer Drought Severity Index (PDSI) anomaly (APDSIA) in the study region. PDSI was used to quantify drought conditions based on antecedent and current precipitation and potential evaporation (Sheffield *et al.* 2012). Recently computed global self-calibrated monthly PDSI data sets, from 1948 to 2008, were obtained online (http://hydrology.princeton.edu/data.pdsi.php) (Sheffield *et al.* 2012). Annual PDSI was defined as an average of 12 monthly PDSIs, from January

to December. For the PDSI data set, potential evaporation was estimated using the Penman–Monteith equation (Maidment 1993) and precipitation was derived from four alternative precipitation products: CPC V1.0, CRU 3.10, GPCC V4 and Willmott–Matsuura V2.01. Twenty-six 1×1 degree grids were used, which covered our study area. Since PDSI demonstrated different trends during the study period among the four precipitation products (Fig. S4), we compared the precipitation data generated from these products with the regional historical precipitation data, which were derived from BioSIM (Régnière *et al.* 2012). The results indicated that CRU V3.10 and GPCC V4 provided better regional precipitation data than Willmott–Matsuura V2.01 and CPC V1.0, as indicated by higher Pearson correlation coefficients (Fig. S5). As a result, we reported PDSI data sets derived from CRU V3.10 and GPCC V4. Annual climate anomalies were utilised to detect regional climate changes.

To examine the systematic temporal trends of 5-year tree mortality, we used the middle calendar year of a census period (i.e. the period between two successive censuses), to represent recent trends of the climate as a whole (Luo & Chen 2013). The middle calendar year of the census period was denoted as Year. We further related the 5-year tree mortality probability to mean annual temperature over a census period.

Statistical analyses

For each of the three studied species, we examined the simultaneous influences of stand age, Hegyi competition index and climate changes as a whole (represented by calendar year), as well as their two-way interactions on mortality. The 5-year tree mortality probability was analysed at the individual tree level using hierarchical logistic regression since the competition index was tree-specific.

$$
\begin{aligned}
\mathrm{logit}(p_{ijk}) = {} & \alpha + \beta_1 \cdot \mathrm{H}_{ijk} + \beta_2 \cdot \mathrm{SA}_{ijk} + \beta_3 \cdot \mathrm{H}_{ijk} \times \mathrm{SA}_{ijk} \\
& + \beta_4 \cdot \mathrm{Year}_{ijk} + \beta_5 \cdot \mathrm{H}_{ijk} \times \mathrm{Year}_{ijk} \\
& + \beta_6 \cdot \mathrm{SA}_{ijk} \times \mathrm{Year}_{ijk} + \pi_k
\end{aligned} \tag{2}
$$

where p_{ijk} is 5-year mortality probability for ith tree of jth census period in plot k; H_{ijk}, SA_{ijk} and Year_{ijk} are Hegyi competition index (eqn 1), middle stand age (years) and middle calendar year of ith tree at jth census in kth plot; π_k is the random plot effect. To illustrate the extent to which mortality probability changed over the study period, we calculated the annual fractional change in mortality probability using the equation $\exp(\beta) - 1$, in which β is the fitted coefficient for Year (van Mantgem *et al.* 2009; Luo & Chen 2013). To assess how H effects change with Year, we calculated H effects as $\beta_1 + \beta_5 \times \mathrm{Year}$ (Cohen *et al.* 2013) by 2-year intervals. Moreover, we examined whether the effects of Hc and Hi on tree mortality might differ and change over time (Tables S3 and S4).

The Bayesian Markov Chain Monte Carlo methods were implemented using *JAGS* called from R with the *rjags* package. All independent variables were centred to expedite convergence. For each model, we evaluated convergence by running two independent chains with different initial values and by monitoring the Gelman–Rubin statistic. When conver-

gence was confirmed, an additional 10 000 iterations (with thinning by half) were used to calculate the mean, and 95% credible intervals for each coefficient from the posterior distribution. To prevent over-fitting, we used deviance information criterion (DIC) to select the most parsimonious models, which had fewer predictors when two models had similar DICs, i.e. the difference in DICs between the two models was <2. We verified their predictive performances by calculating the area under the receiver operation characteristic curve (AUC) and plotting the average predicted 5-year mortality probability against the observed 5-year proportion of dead trees (Fig. S6).

Since we were interested in the relative importance of endogenous and exogenous factors on mortality probability, similar to previous studies (Dietze & Moorcroft 2011; Luo & Chen 2013), we derived the sensitivity to each predictor. Similar to the sum of squares used to measure the influences of individual predictors on dependent variable in frequentist statistics, the sensitivity to each predictor was calculated as the absolute standard deviation between the predicted and the mean observed mortality probability. For example sensitivity score to Hegyi index (H): $\mathrm{Sensitivity\,score}_{\mathrm{H}} = \left| \sqrt{\sum_{i,j,k} \left(\mathrm{predicted\,P}_{ijk} - \bar{\mathrm{P}}_{ijk}\right)^2} \right|$, and predicted $\mathrm{P}_{ijk} = \frac{\exp(\alpha + \beta_1 \cdot \mathrm{H}_{ijk})}{1 + \exp(\alpha + \beta_1 \cdot \mathrm{H}_{ijk})}$, where predicated P_{ijk} for ith tree of jth census period in plot k was derived from the fitted coefficients in eqn 2; P_{ijk} is the mean observed mortality probability. We summed up sensitivity scores based on three groups (i.e. endogenous group that included the main and two-way interaction effects of endogenous factors, exogenous factors represented by year and interactive terms between the exogenous factor and endogenous factors). In addition, we also conducted analyses using linear mixed effect models and examined the sums of squares of individual predictors; the analyses produced qualitatively similar results and thus are not shown.

We further examined regional climate change utilising a linear mixed effect model (LME) with a plot as a random effect. To take into account the temporal autocorrelation of the time series data, we fitted models with a first-order autoregressive structure. These processes were implemented using the lme function in the "nlme" package in R (Pinheiro *et al.* 2013). We also examined whether our study area had experienced substantial drought events over the study period. A substantial drought event was defined in two ways. First, at relative
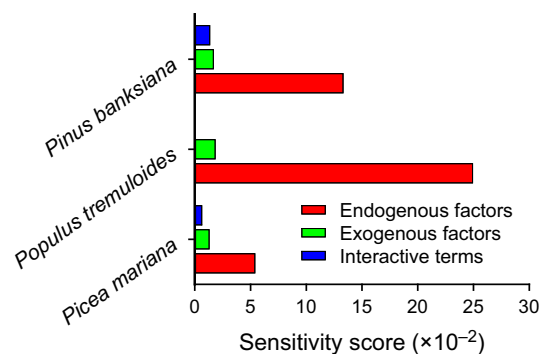

Figure 1 Sensitivity scores of the endogenous factors, exogenous factors and their interactive terms of the Year-based model in Table 1.

scale, a substantial drought event was defined as an occurrence of the drought indices (i.e. CMI or PDSI) of less than two standard deviation units below the long-term average (Williams *et al.* 2013). Second, at the absolute scale, a substantial drought event was defined as when the drought indices were less than a particular value, i.e. −10 cm for CMI and −3 for PDSI (Hogg *et al.* 2008; Sheffield *et al.* 2012).

Evaluation of potential methodology problems

Competition effects on tree mortality for initial and final census periods

To further examine how the effects of Hc and Hi on tree mortality changed over time, we compared the competition effects on tree mortality employing data from the first and final census periods (Table S5 and Fig. S7). We found that both the mean annual temperature anomaly and the mean annual climate moisture index anomaly over a census were significantly lower for the first census periods than for the final census periods, and competition effects are consistent with the effects of Year × Hc reported in Table S3.

Spatial autocorrelation testing

Our conclusion was not biased by sampling strategies such as plot sizes and measurement intervals since our plot sizes and measurement intervals were identical (i.e. plot sizes and measurement intervals were consistently 500 m^2 and 5 years respectively). Our plot size (i.e. 500 m^2) was a sound forest inventory sampling strategy in boreal forests for two reasons. First, our plots contained 164 trees per plot (on average) and represented the target forest (Fig. S2). Second, the mean mortality rates and annual fractional change in tree mortality rates were not altered significantly with the number of trees (Fig. S8). In addition, we examined spatial autocorrelations following previous studies (van Mantgem *et al.* 2009; Luo & Chen 2013). For all studied species, Mantel tests indicated no evidence of spatial autocorrelation among the plots for the mean 5-year mortality rate, annual fractional change in the
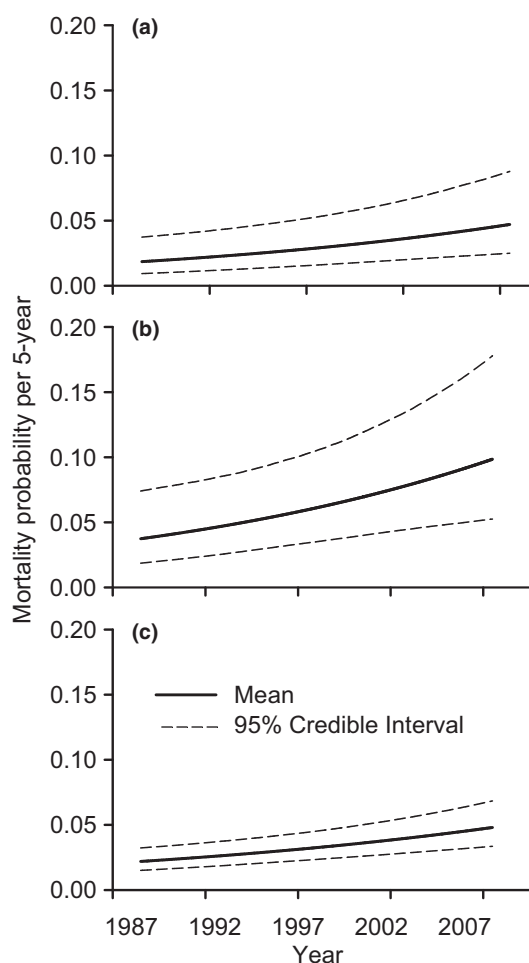

Figure 2 Modelled temporal trend of 5-year mortality probability with the effects of endogenous factors accounted. (a) *Pinus banksiana*. (b) *Populus tremuloides*. (c) *Picea mariana*. The mortality probability was modelled as logit(P) = log($\frac{P}{1-P}$), and thus $P = \frac{\exp(\alpha + \beta_4 \cdot \text{Year})}{1 + \exp(\alpha + \beta_4 \cdot \text{Year})}$, where α and β_4 are presented in Table 1. The solid and broken lines represent mean and 95% credible intervals respectively.

Table 1 Coefficients (mean with 95% Credible Intervals in brackets) of predictors on mortality probability of *Pinus banksiana*, *Populus tremuloides* and *Picea mariana*. Year- and mean annual temperature-based models included intercept (α) and coefficients β_s for predictors described in eqn 2. NA indicates that the variable is not included based on the variable selection from deviance information criterion

Term	Pinus banksiana	Populus tremuloides	Picea mariana
Year-based model			
α	−3.42 (−4.02 to −2.79)	−2.69 (−3.27 to −2.10)	−3.34 (−3.70 to −3.00)
β_1 (×10^{-2})	5.50 (5.07 to 5.94)	8.52 (8.01 to 9.04)	2.32 (1.92 to 2.73)
β_2 (×10^{-1})	1.19 (0.89 to 1.53)	0.71 (0.33 to 1.09)	0.28 (0.15 to 0.42)
β_3 (×10^{-3})	0.84 (0.52 to 1.17)	1.86 (1.47 to 2.25)	NA
β_4 (×10^{-2})	5.05 (1.65 to 8.11)	5.45 (1.57 to 9.42)	4.28 (2.41 to 6.04)
β_5 (×10^{-3})	0.71 (0.14 to 1.26)	NA	−0.98 (−1.53 to −0.42)
β_6 (×10^{-3})	−4.02 (−5.14 to −2.92)	NA	NA
Mean annual temperature-based model			
α	−3.29 (−3.76 to −2.80)	−2.70 (−3.19 to −2.19)	−3.23 (−3.65 to −2.83)
β_1 (×10^{-2})	5.26 (4.84 to 5.68)	8.58 (8.07 to 9.12)	2.25 (1.86 to 2.64)
β_2 (×10^{-1})	1.29 (1.16 to 1.41)	1.12 (0.97 to 1.28)	0.45 (0.32 to 0.58)
β_3 (×10^{-3})	1.39 (1.12 to 1.66)	1.88 (1.46 to 2.30)	NA
β_4 (×10^{-2})	3.64 (1.68 to 5.64)	2.70 (0.57 to 4.95)	1.81 (0.04 to 3.59)
β_5 (×10^{-3})	NA	NA	NA
β_6 (×10^{-3})	−2.71 (−4.12 to −1.33)	−4.36 (−6.36 to −2.35)	NA

5-year mortality rate, or the effects of plot identity on a 5-year mortality probability (Table S6).

Modelling strategy to deal with confounding factors
With all data pooled, there was a positive collinearity between SA and Year ($r = 0.099$, $P < 0.001$), but no collinearity between H and Year ($r = 0.0006$, $P = 0.88$). There were three possible approaches to disentangle their joint variations between endogenous factors and Year (Graham 2003). The first was to simultaneously model endogenous and Year effects. The second was to use residual and sequential regressions by assigning the priority to endogenous factors, and then modelling Year effects on the residuals. The third was to reverse the priority in the second approach. Regardless of priority settings, Year effects on tree mortality were positive for all tree species, and the simultaneous modelling approach yielded intermediate values (Table S7). We had no logical or theoretical basis to assign a variable as prior, in terms of a hypothetical causal structure of the data. We interpreted results from the simultaneous modelling as assigning priority to endogenous factors would marginalise the Year effect, and *vice versa* (Brown *et al.* 2011; Luo & Chen 2013).

RESULTS

Endogenous factors explained substantially more variation in tree mortality than exogenous factors (Fig. 1), indicating that tree mortality was predominantly driven by endogenous processes. After accounting for the endogenous processes, calendar year effects on tree mortality were significantly positive cross all species (Table 1; Fig. 2). The estimates of annual fractional changes (i.e. increases in the rate of tree mortality probability from previous year to current year), were 5.18% (Credible Interval (CI): 1.66–8.45%), 5.60% (CI: 1.58–9.88%) and 4.37% (CI: 2.44–6.23%) for *Pinus banksiana*, *Populus tremuloides* and *Picea mariana* respectively. The overlap in 95% CIs of annual fractional change indicated that the increases in tree mortality were not significantly different among the study species. Additional analyses, performed by partitioning conspecific and interspecific Hegyi indices, also revealed temporal increases of climate change-associated tree mortality across all study species (Table S3).

Effects of Hegyi on tree mortality were stronger for *Populus tremuloides* and *Pinus banksiana* than for *Picea mariana*, particularly the conspecific Hegyi effect (Table 1 and Table S3). Hegyi effects on tree mortality increased temporally for *Pinus banksiana*, did not change for *Populus tremuloides*, and decreased for *Picea mariana* (Fig. 3a–c). When Hegyi was separated into conspecific and interspecific components, we found that the effects of conspecific Hegyi on tree mortality increased for *Pinus banksiana* and *Populus tremuloides*, but decreased for *Picea mariana*. The effects of interspecific Hegyi decreased for *Pinus banksiana*, but did not change for the other two species (Fig. 3). The greater conspecific Hegyi effects on tree mortality than interspecific Hegyi effects on tree mortality indicated that temporal changes of Hegyi effects on tree mortality were primarily driven by the temporal changes of conspecific Hegyi effects. We also found that temporal increases of tree mortality were more rapid in young forests than in aged forests for *Pinus banksiana*, but not for the other two species (Table 1).
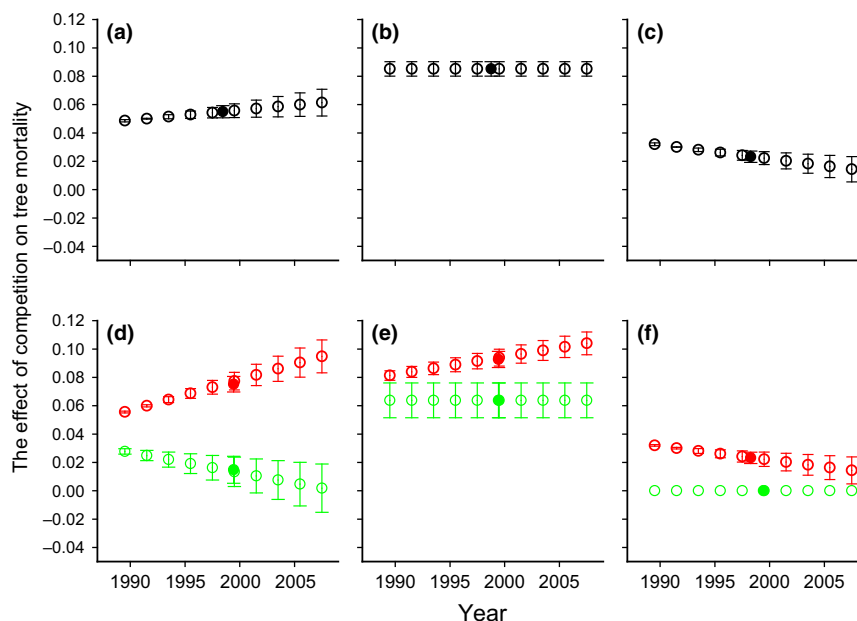

Figure 3 Calendar year-dependent effects of Hegyi competition index on tree mortality probability (logit(P)). (a), (b), (c) The effects of total competition (sum of conspecific and interspecific competition) on tree mortality probability for *Pinus banksiana*, *Populus tremuloides* and *Picea mariana* respectively. (d), (e), (f) The partitioned effects of conspecific competition (red) and intraspecific competition (green) on tree mortality probability for *Pinus banksiana*, *Populus tremuloides* and *Picea mariana* respectively. Values (means and 95% credible intervals) represent the effects of competition once the effect of stand age has been accounted for. Filled symbols represent the average effects of all sample plots for each species. The overall competition effects are presented in Table 1 and the conspecific and interspecific competition effects are in Table S3.

Over the study period, the annual temperature anomaly (ATA), annual precipitation anomaly (APA) and annual climate moisture index anomaly (ACMIA) increased by 0.042 °C year^{-1}, 3.91 mm year^{-1} and 0.369 cm year^{-1} respectively (Fig. 4a–c). The increases of these climate variables were consistent with long-term trends (i.e. 1953–2010) (Fig 4a–c). By employing a global data set from the Palmer Drought Severity Index (PDSI) (Sheffield *et al.* 2012), we also discovered a temporal increase in PDSI for both the long-term (1948–2008) and for the majority of the study period (1985–2008) (Fig. 4d). Collectively, these results suggested that the study region did not experience temporal water deficit increases, although regional warming was clearly evident. Furthermore, the study area did not experience significant drought events over the study period, although drought indices were lower in ~1988 and 2001–2002 (Fig. 5). Across all study species, models including ATA as a predictor indicated that the temporal increase in tree mortality was positively associated with ATA across all studied species (Table 1).

DISCUSSION

In this study, we once again pointed out the dominant role of endogenous factors on tree mortality in boreal forests (Luo & Chen 2011, 2013; Zhang *et al.* 2015). However, we have established that tree mortality after accounting for endogenous processes has increased over the last three decades across all study species in the region where climate change has resulted in increases in temperature, precipitation and water availability. Studies conducted in western North America suggested that the temporal increases of tree mortality were attributable to temporal water deficit increases (van Mantgem *et al.* 2009; Peng *et al.* 2011; Luo & Chen 2013) or climate change-associated drought (Breshears *et al.* 2005; Michaelian *et al.* 2011; Huang & Anderegg 2012; Williams *et al.* 2013). In this study,
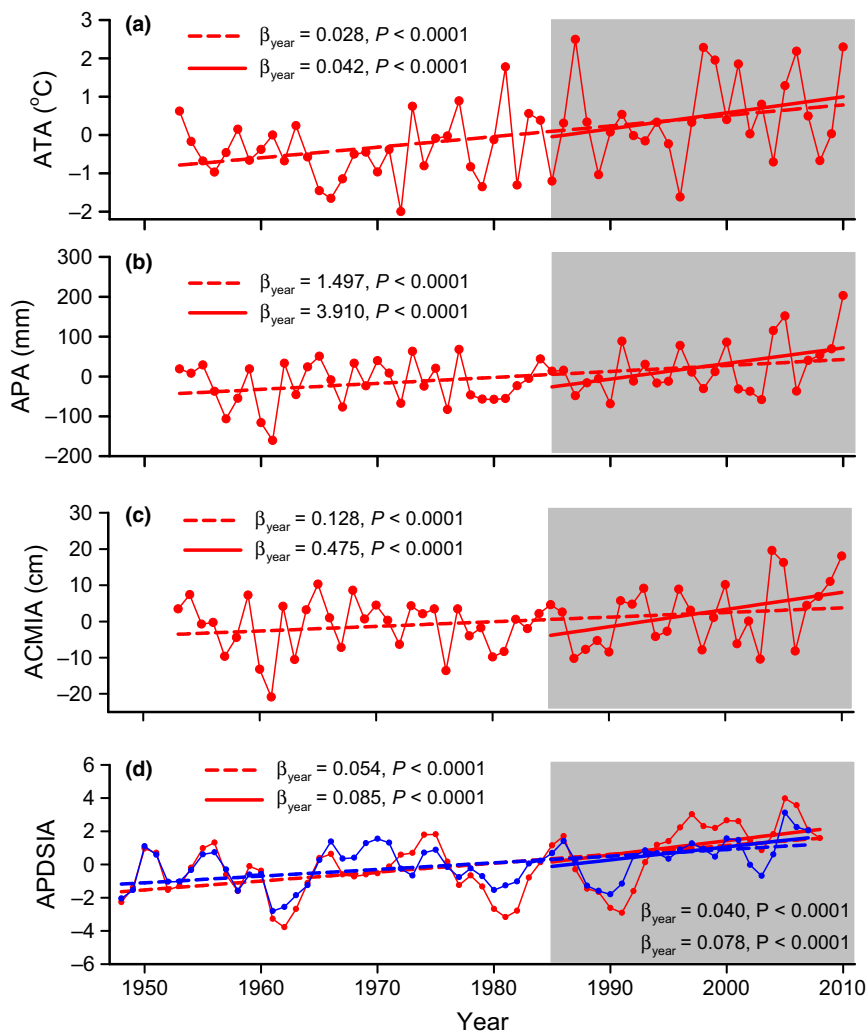

Figure 4 Temporal trends of climate variables. (a) Annual temperature anomaly (ATA, °C). (b) Annual precipitation anomaly (APA, mm). (c) Annual climate moisture index anomaly (ACMIA, cm). (d) Annual Palmer Drought Severity Index anomaly (APDSIA) that derived from CRU V3.10 (red lines) and GPCC V4 (blue lines). Dots represent the annual means of all study plots. Dash and solid lines were fitted with long-term trends and trends over the study period (grey area) respectively. β_{year} is the slope fitted in the linear mixed effect model with the first-order autoregressive structure. Note that APDSIA does not cover the entire study period due to the lack of data availability.
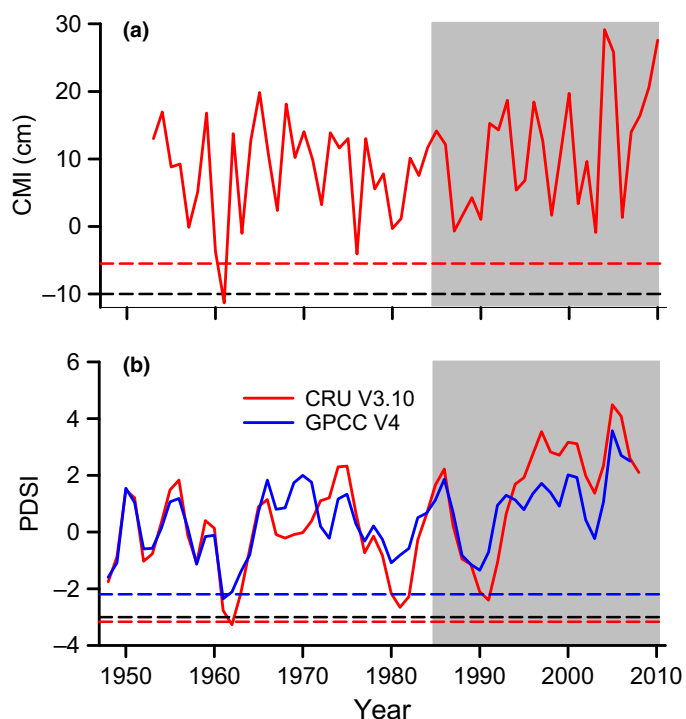
Figure 5 Significant drought events in the study area. (a) Annual climate moisture index (CMI, cm). (b) Palmer Drought Severity Index (PDSI) derived from CRU V3.10 (red lines) and GPCC V4 (blue lines). Dashed red and blue lines represent the value of 2 units of standard deviation below long-term means. Black dashed lines represent the threshold of an absolute value −10 cm for CMI and −3 for PDSI.

we found no long-term decrease in water availability and that the severity of droughts in recent decades seems to have been less severe than earlier droughts. These results indicated that temporal increases of tree mortality were not the result of decreasing water availability or drought events (Allen *et al.* 2010).

The effects of Hegyi on tree mortality were more robust for shade-intolerant *Pinus banksiana* and *Populus tremuloides* than for shade-tolerant *Picea mariana*. Hegyi effect increased temporally for *Pinus banksiana*, which were driven primarily by temporal increases in conspecific Hegyi index. Similarly, conspecific Hegyi effect on tree mortality increased temporally for *Populus tremuloides*. These results indicated that the effects of conspecific Hegyi on tree mortality have intensified over time for the two shade-intolerant species. Tree growth increased temporally at the stand level and for the two shade-intolerant species (Fig. S9). Furthermore, the Hegyi index increased temporally for the two shade-intolerant species (Fig. S10), and Hegyi index was positively associated with growth rate (Fig. S11). If Hegyi index can indeed quantify tree–tree competition (Uriarte *et al.* 2004; Canham *et al.* 2006; Das *et al.* 2008; Coates *et al.* 2009), these results, collectively, suggested that the effects of competition on tree mortality may have intensified over time as a result of growth enhancement, probably due to positive climate changes such as rising atmospheric CO_2 concentration, and regional warming-associated increases of growing season length and soil nutrient

availability (Myneni *et al.* 1997; Peñuelas *et al.* 2009) (Fig. S12). Despite a similar level of temporal mortality increases in *Picea mariana*, temporal mortality increases of *Picea mariana* were less associated with the effect of Hegyi. Heat stress, which is a proposed mechanism for climate change induced mortality (Allen *et al.* 2010; Anderegg *et al.* 2013), might be felt more predominantly by this more northerly distributed species than *Pinus banksiana* and *Populus tremuloides*. In addition to direct heat stress, warming might result in increased respiration, which draws down carbon reserves and consequently leads to higher tree mortality.

Over the study period, growth rate increased temporally (Fig. S9), suggesting that recent climate changes, i.e. rising atmospheric CO_2 and warming casted positive effect on tree growth where climate change-associated drought is absent. Our results are consistent with the findings in Amazon forests (Brienen *et al.* 2015) and those of the early successional forests in the region west of our study area (Chen & Luo 2015), in which tree mortality increased accompanied increased growth. There are two potential mechanisms to explain the coupled temporal increases of tree mortality and growth. First, the increase in growth shortens tree longevity (Brienen *et al.* 2015). Alternatively, faster growth intensifies tree–tree competition, as previously hypothesised (Phillips *et al.* 2004). While the first mechanism remains to be tested, we find the evidence for temporally increased conspecific competition effect on tree mortality for the two shade-intolerant species. In the same study area, Zhang *et al.* (2015), however, did not find a temporal increase in growth. The different findings on growth responses between Zhang *et al.* (2015) and this study possibly resulted from different stand ages and tree sizes: Zhang *et al.* (2015) used 50 plots with stand age ≥ 50 years and trees ≥ 9 cm in DBH, whereas this study included 146 plots with stand age ≥ 10 years old and all trees ≥ 5 cm. However, it remains to be tested whether tree growth responses to climate change differ with stand age and tree size.

Our results are quite striking. First, temporal increases of climate change-associated mortality do not occur only in regions with temporal water deficit increases, but also in areas without temporal water deficit increases. Given that temporal water deficit increases are not a global phenomenon (Sheffield *et al.* 2012; Dai 2013), our results call for more studies to examine the impacts of recent climate changes on forest dynamics beyond those regions with temporal water deficit increases (Breshears *et al.* 2005, 2009; van Mantgem *et al.* 2009; Michaelian *et al.* 2011; Peng *et al.* 2011; Luo & Chen 2013; Williams *et al.* 2013). Second, our results reveal that climate change may intensify the effects of conspecific competition, while reducing the effects of interspecific competition on tree mortality for shade-intolerant tree species. If water availability does not change in these forests, although some projections suggest it may (Cook *et al.* 2014), this could potentially lead to a positive effect on species coexistence, since higher conspecific competition, rather than interspecific competition, constitutes a primary mechanism for species coexistence in forest ecosystems (Condit *et al.* 2006; Comita *et al.* 2010). However, the temporal increases in both mortality and growth could lead to faster carbon pool turnover and less carbon

storage in the boreal forests, as indicated in tropical forests (Brienen *et al.* 2015).

AUTHORSHIP

Y.L. and H.Y.H.C. designed the project; Y.L. performed data compilation and analysis; and Y.L. and H.Y.H.C. wrote the manuscript.

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