

# A drought-induced pervasive increase in tree mortality across Canada's boreal forests

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**Drought-induced tree mortality is expected to increase worldwide under projected future climate changes<sup>1-4</sup>. The Canadian boreal forests, which occupy about 30% of the boreal forests worldwide and 77% of Canada's total forested land, play a critical role in the albedo of Earth's surface<sup>5</sup> and in its global carbon budget<sup>6</sup>. Many of the previously reported regional-scale impacts of drought on tree mortality have affected low- and middle-latitude tropical regions<sup>2</sup> and the temperate forests of the western United States<sup>3</sup>, but no study has examined high-latitude boreal regions with multiple species at a regional scale using long-term forest permanent sampling plots<sup>7-9</sup>. Here, we estimated tree mortality in natural stands throughout Canada's boreal forests using data from the permanent sampling plots and statistical models. We found that tree mortality rates increased by an overall average of 4.7% yr<sup>-1</sup> from 1963 to 2008, with higher mortality rate increases in western regions than in eastern regions (about 4.9 and 1.9% yr<sup>-1</sup>, respectively). The water stress created by regional drought may be the dominant contributor to these widespread increases in tree mortality rates across tree species, sizes, elevations, longitudes and latitudes. Western Canada seems to have been more sensitive to drought than eastern Canada.**

Climatic warming during the past century has led to a variety of responses by terrestrial ecosystems, including changes in net primary productivity<sup>10,11</sup>, forest growth<sup>12</sup>, carbon balances<sup>7,13</sup>, plant phenology<sup>14</sup> and species distributions towards the poles<sup>15</sup>. These changes have been accompanied by increases in forest dieback and mortality around the world<sup>1-4</sup>. One of the greatest uncertainties in global climate change is predicting changes in the feedbacks between the biosphere and the atmosphere<sup>16</sup>. Forests exert strong controls on the global carbon cycle and influence regional hydrology and climatology directly through their effects on water and surface energy budgets<sup>5</sup>. Recent studies have indicated that forest mortality caused by rising temperatures and increased drought have rapidly increased around the world during the past decade<sup>1-4</sup>. So far, much progress has been made on quantifying the impacts of drought and increased water stress on forest mortality in tropical rainforests<sup>2,17</sup> and in temperate forests of the southwestern and western United States<sup>3,18</sup> and southern Europe<sup>4</sup>.

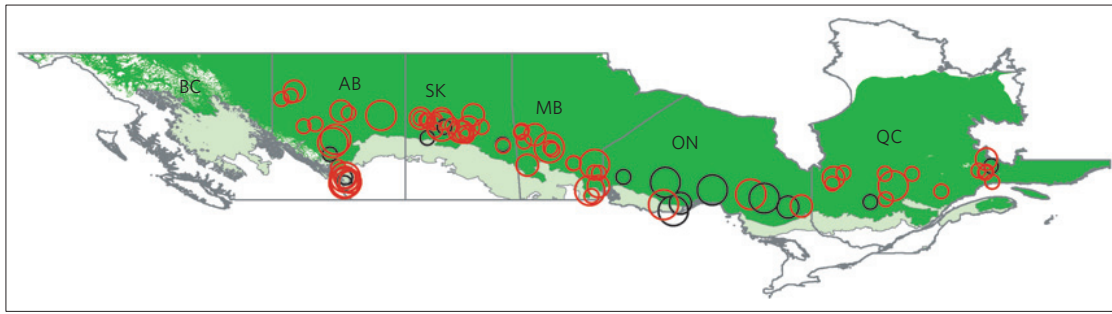
The possibility of increasing tree mortality in boreal forests is a particular concern because boreal forests have been identified as a critical 'tipping element' of the Earth's climate system and are believed to be more sensitive to drought than other forests<sup>19</sup>. Recent progress has been made in investigations of the impacts of

severe drought on trembling aspen (*Populus tremuloides*) mortality in western Canada<sup>8,9</sup>, suggesting that Canadian boreal forests may be vulnerable to rapid increases in tree mortality owing to a combination of warmer temperatures (that is, increased evapotranspiration) and more severe drought (that is, decreased water supply). However, to our knowledge, no comparable studies of chronic long-term changes in mortality rates have been conducted in natural (unmanaged) boreal forests using long-term forest permanent sampling plots (PSPs) across Canada.

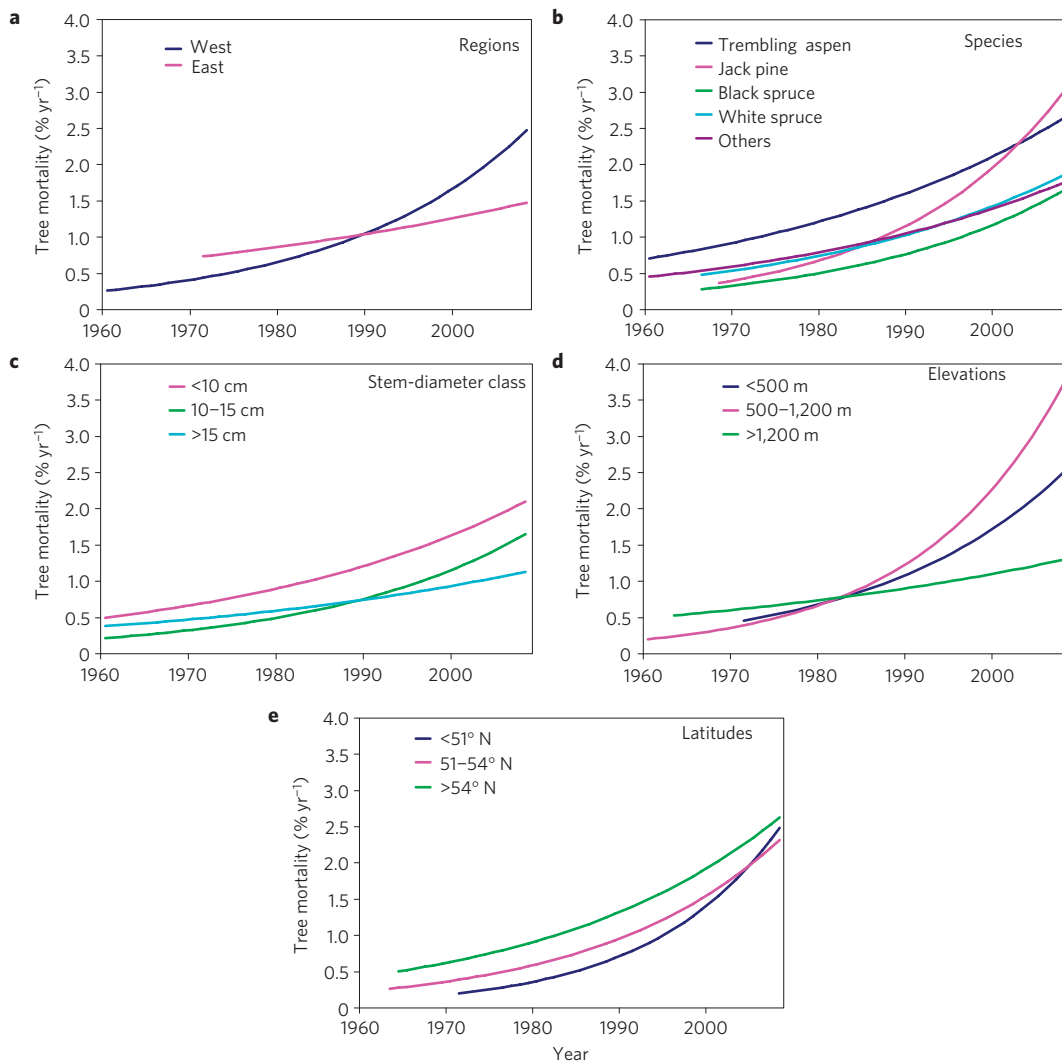
In the present study, we provide the first detailed analysis of long-term, annual-resolution tree recruitment and mortality in Canadian boreal forests at a national scale. We sought to determine whether systematic changes in tree recruitment and mortality have occurred in Canada's boreal forests, and, if any changes have occurred, whether they could be attributed to changes in climatic variables or in other potential contributing factors. We defined our study area based on the availability of long-term PSP data and the boundaries of Canada's boreal forest region. To minimize the effects of transient dynamics associated with stand development and succession, we limited our analyses to data from repeated censuses in undisturbed natural forest stands (that is, stands that had not undergone harvesting or any other silvicultural treatment) that were more than 80 years old (see Supplementary Information for details). Because old forests contain trees of all ages and sizes, any continuous long-term changes in stand demography are likely to be consequences of environmental changes<sup>3</sup>. In contrast, demographic changes in young forest stands are sometimes controlled by endogenous processes such as succession and self-thinning during stand development<sup>3</sup>, potentially obscuring the impacts of environmentally driven changes. To evaluate and quantify the impacts of climate change on tree mortality, it is therefore important to eliminate the effects of ecosystem disturbances such as fires and insect infestations because these phenomena are likely to show complex dynamics that have different degrees of dependence on climate change<sup>3</sup>.

We found that 96 long-term forest PSPs from five provinces within two broad regions (western versus eastern Canada) met our criteria. The plots spanned 53° of longitude and 9° of latitude, and their elevations ranged from 59 to 2,609 m above sea level (asl) (Fig. 1, Supplementary Table S1). The plots ranged from 0.04 to 0.82 ha (mean = 0.12 ha), and collectively contained 22,425 living trees; the plot data included a total of 74,556 observations in these plots (Supplementary Information). As a result, these differences are unlikely to produce a single overall bias that would affect our study's goals. The selected plots were each censused three to five times (mean ± s.d. of 3.5 ± 0.6). The length of the census period

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**Figure 1 | Locations of the 96 forest PSPs in Canada's boreal forests.** The black and red circles represent plots with decreasing and increasing mortality rates, respectively. The circle size corresponds to the magnitude of the annual change in mortality rates (smallest symbols,  $<0.05\% \text{ yr}^{-1}$ ; largest symbols,  $>0.10\% \text{ yr}^{-1}$ ; medium symbols,  $0.05\text{--}0.10\% \text{ yr}^{-1}$ ), calculated using a generalized nonlinear model. The background colours of green and light green represent, respectively, Canada's boreal and hemiboreal regions. Of these plots, 70 were located in western Canada including Alberta (AB), Saskatchewan (SK) and Manitoba (MB), and 26 were located in eastern Canada including Ontario (ON) and Quebec (QC).



**Figure 2 | Simulated tree mortality dynamics in Canada's boreal forests.** Modelled trends in tree mortality rates for regions (a), tree species (b), stem-diameter classes (c), elevations (d) and latitudes (e).

ranged from 10 to 38 years ( $21.9 \pm 6.8$ ). The initial stand age of the plots ranged from 80 to 218 years ( $116.2 \pm 34.4$ ). The initial census years ranged from 1963 to 1994 and the final census year ranged from 1990 to 2008.

Our results showed that mortality rates increased significantly ( $P < 0.0001$ , two-tailed binomial test) in 83% of the PSPs,

including 91% of these plots (64/70) in western Canada and 62% of the plots (16/26) in eastern Canada (Fig. 1). Mortality rates increased significantly for all plots combined and in both regions analysed separately (Fig. 2, Table 1). Mortality rates also increased for small, medium and large trees (diameter at breast height  $<10$ ,  $10\text{--}15$ , and  $>15$  cm, respectively) and at low, medium

**Table 1 | Fixed effects in the generalized nonlinear mixed models describing annual tree mortality rate trends (for more details, see the Supplementary Information).**

Model	Data	$\beta$	$a = \exp(\beta) - 1$	s.e.m.	$P$	$n$
Overall mortality trend	All	0.0458	0.0469	0.002	<0.0001	96
Mortality trends by longitude (region)	West (119° W–97° W)	0.0476	0.0488	0.002	<0.0001	70
	East (94° W–65° W)	0.0191	0.0193	0.008	0.0227	26
Mortality trends by latitude	<51° N	0.0686	0.0710	0.006	<0.0001	38
	51° N–54° N	0.0489	0.0501	0.003	<0.0001	24
	>54° N	0.0380	0.0387	0.003	<0.0001	34
Mortality trends by elevation	<500 m	0.0469	0.0480	0.005	<0.0001	35
	500–1200 m	0.0625	0.0645	0.003	<0.0001	26
	>1200 m	0.0204	0.0206	0.003	<0.0001	35
Mortality trends by species	Trembling aspen	0.0280	0.0284	0.006	<0.0001	21
	Jack pine	0.0537	0.0552	0.017	0.0132	10
	Black spruce	0.0425	0.0434	0.004	<0.0001	45
	White spruce	0.0329	0.0334	0.005	<0.0001	21
	Others	0.0286	0.0290	0.004	<0.0001	31
Mortality trends by diameter class	<15 cm	0.0304	0.0309	0.003	<0.0001	94
	15–20 cm	0.0428	0.0437	0.005	<0.0001	74
	>20 cm	0.0229	0.0232	0.005	<0.0001	50

$a$  is the estimated annual change in mortality rate (% yr<sup>-1</sup>),  $n$  is the number of forest plots used in the model and s.e.m. is standard error of the mean.

and high elevations (<500, 500 to 1,200 and >1,200 m asl, respectively) (Fig. 2, Table 1). The four most abundant tree species in our plots (comprising 69% of all trees) were trembling aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), black spruce (*Picea mariana*) and white spruce (*Picea glauca*). All four showed increasing mortality rates (Fig. 2, Table 1), as did trees of all the remaining species (31% of all trees).

In contrast to mortality rates, recruitment rates increased in only 42% of the plots. This proportion was not significantly different from a random result ( $P = 0.13$ , two-tailed binomial test). There was no detectable trend in recruitment for all plots combined ( $P = 0.076$ ), but recruitment decreased significantly in western Canada ( $P = 0.002$ , generalized nonlinear mixed model (GNMM)) and increased significantly in eastern Canada ( $P = 0.006$ , GNMM) when the two regions were analysed separately (Supplementary Table S2).

We considered that regional drought would be the dominant contributor to the increases in tree mortality rates. Mean annual precipitation showed no directional trend over the study period ( $P = 0.11$ , linear mixed model), whereas both mean annual temperature and the annual moisture index (AMI) increased significantly ( $P < 0.0001$ , linear mixed model) and the climate moisture index (CMI) decreased significantly ( $P < 0.0001$ , linear mixed model; Supplementary Table S4). At our study sites, temperature and water deficits (which are represented using the parameters CMI and AMI, defined in Supplementary Information) were both significantly positively correlated with tree mortality rates for all plots combined and for western Canada, whereas the correlation was only significant for temperature in eastern Canada ( $P < 0.0001$ , GNMM; Table 2). Our results are consistent with recent findings of a widespread moisture-driven increase in tree mortality in tropical forests in the Amazon basin<sup>2,17</sup>, temperate forests in the western United States<sup>3</sup> and trembling aspen stands in western Canada<sup>8,9</sup>.

To understand the different responses of tree mortality in eastern and western Canada to a warming climate, we examined two key variables that govern boreal forest growth and mortality: temperature and moisture. The changes in tree mortality rates differed significantly between boreal regions of western and eastern Canada (Fig. 2 and Table 1). The increase of tree mortality in western Canada ( $a = 0.0488 = 4.9\%$ ) was 2.6 times the rate in

eastern Canada ( $a = 0.0193 = 1.9\%$ ). This is probably because western Canada has experienced more severe and extensive droughts, such as the one in 2001–2002, than eastern Canada<sup>20</sup>. The average annual temperature (°C) was higher in western Canada than in eastern Canada and the CMI in western Canada has been much lower than that in eastern Canada since 1970 (Supplementary Fig. S3). Moreover, the summer water deficit has been considered to be the dominant factor that controls tree growth in western boreal Canada<sup>8,9</sup>, but this may not be the case for eastern Canada<sup>21</sup>. Although most areas of the Canadian boreal forest experienced some degree of drought in 2001–2002, trees in western Canada were most susceptible to mortality because these provinces experienced more serious and extensive droughts than eastern Canada<sup>20</sup>.

In western Canada, most available moisture for precipitation comes from the Pacific Ocean during the winter (November–March) and from the Gulf of Mexico during the summer (May–August)<sup>22</sup>. Thus, regional precipitation may be strongly connected to global sea surface temperature patterns<sup>23</sup>. For eastern Canada, Girardin *et al.*<sup>21</sup> showed that climate warming and increases in the amount and frequency of precipitation during the past century had no significant impact on the severity of summer drought. In addition, a long-term reduction in the amount of solar radiation in the Canadian Prairies between 1951 and 2005 (ref. 24) may also have increased the tree mortality due to a decline in forest productivity (that is, net photosynthesis) in western Canada<sup>8,9</sup>. Combined with the other aforementioned factors, this may explain the regional differences in tree mortality between western and eastern Canada.

As the predominant climate characteristic associated with mortality, drought could contribute to the increasing tree mortality rates by (1) hydraulic failure (through increasing water deficits and thus increasing the water stress in trees)<sup>25</sup>, (2) carbon starvation (failure to maintain metabolism and carbon balance)<sup>25</sup> or (3) outbreaks of biotic agents (such as the growth and reproduction of insects and pathogens that attack trees)<sup>25,26</sup>. The contribution to tree mortality from drought in the present study is consistent both with the apparent role of drought in episodes of recent mortality of trembling aspen forest in western Canada<sup>8,9</sup> and with the positive correlation observed between short-term variations in background mortality rates and drought-induced water stress observed in the Amazon rainforest<sup>2</sup> and temperate forests of the western United States<sup>3</sup>.

**Table 2 | Fixed effects in the generalized nonlinear mixed-effects models describing the relationship between annual tree mortality and climatic variables (see Supplementary Information for more details).**

Data	Models of tree mortality as a function of	$\beta$	s.e.m.	P	n
All plots	Annual mean temperature (°C)	0.3761	0.0217	<0.0001	96
	Annual CMI	-0.0318	0.0043	<0.0001	96
	AMI	0.0018	0.0002	<0.0001	96
West	Annual mean temperature (°C)	0.4445	0.0280	<0.0001	70
	Annual CMI	-0.0602	0.0049	<0.0001	70
	AMI	0.0023	0.0002	<0.0001	70
East	Annual mean temperature (°C)	0.0969	0.0554	0.0428	26
	Annual CMI	0.0083	0.0063	0.2020	26
	AMI	-0.0009	0.0006	0.1307	26

n is the number of forest plots used in the model and s.e.m. is standard error of the mean.

The widespread and unexpected increases in tree mortality rates across Canada's mature boreal forests are striking for several reasons. First, the increasing mortality rates demonstrate that ongoing, regional-scale changes in tree demography are not limited to the tropics<sup>2</sup> and temperate regions<sup>3,4</sup>. Second, some of the changes in the Canadian boreal forests contrast obviously with those in the tropics, where increasing mortality rates have been paralleled by increasing recruitment rates and basal area<sup>2</sup>, although the present results are consistent with those in the western United States<sup>3</sup>, where the recruitment rates have not changed significantly, although forest density and basal area have declined slightly<sup>3</sup>. Third, the present evidence is consistent with contributions from exogenous causes, with regional warming and the resulting moisture stress being the dominant drivers<sup>1-4</sup>.

Quantifying the potential impacts of the increasing tree mortality on ecosystem processes requires research into the effects of this mortality on carbon, energy and water budgets at both site and regional levels. These impacts, however, have generally been ignored in large-scale carbon-cycle modelling studies<sup>1,7,10,16</sup> both because data on tree mortality over large areas are expensive to collect and are therefore not widely available<sup>1</sup>, and because the physiological mechanisms of drought-induced tree mortality at broad scales are still poorly understood<sup>1-4,8,9,25,26</sup>. This failure to account for the impacts of tree mortality in carbon-cycle modelling may have resulted in an overestimation of the carbon sinks in previous studies of the potential for forests to offset anthropogenic carbon dioxide under a warmer, drier environment with increased water stress<sup>6,27</sup>. Despite recent progress, the uncertainty around the responses of tree mortality to climate change limits our ability to forecast the likelihood and the impacts of this mortality<sup>1</sup>. Studies are needed to further explore the physiological mechanisms responsible for tree mortality in a wide variety of functional types<sup>1-4,25</sup>, to connect patterns of mortality with extreme climate events<sup>28</sup> and to forecast the potential impacts of tree mortality on carbon, energy and water fluxes<sup>1,5,7,10,11</sup>.

Under future global warming scenarios<sup>16</sup>, severe regional droughts are likely to become more frequent, and this trend is expected to continue for the foreseeable future. Drought-induced tree mortality in Canada may also co-occur with peaks of forest ecosystem disturbances such as insect outbreaks<sup>29</sup> and increased fire activity<sup>30</sup>. Such interactions among climatic warming, ecosystem disturbances and forest responses represent potential positive feedbacks that could dramatically alter future carbon sink-source relationships in boreal forests. If this tree mortality continues to increase more rapidly than growth in response to climate change<sup>16</sup>, this will reduce net forest growth, transform Canadian boreal forests from a net carbon sink<sup>31</sup> into a large net carbon source, weaken the terrestrial carbon sink and increase future atmospheric carbon dioxide levels during the twenty-first century.

## Methods

To assess the impacts of drought on tree mortality, we analysed data from 96 long-term PSPs that met nine criteria for natural (unmanaged) mature boreal forest stands in five Canadian provinces (including Alberta, Saskatchewan, Manitoba, Ontario and Quebec) (Supplementary Information). In total, 80 plots (83% of the total) were located in the boreal region and 16 (17% of the total) were located in the hemiboreal region. In addition, 91% of the plots (64/70) in western Canada and 62% of the plots (16/26) in eastern Canada experienced increasing mortality.

To obtain climatic data for these plots, we used Canada's daily 10 km raster-gridded climate dataset from 1961 to 2003, which contains data on daily maximum and minimum temperatures ( $T_{\max}$  and  $T_{\min}$ ) and precipitation (PRE) for latitudes south of 60° N. The climatic data for plots with census data after 2003 were downloaded from the nearest meteorological station (S10). We also calculated the CMI and the AMI from these data (Supplementary Information). Both CMI and AMI were used to measure climatic water deficits in this study.

We adopted the statistical models of ref. 3. We used generalized nonlinear models to regress the changes in recruitment and mortality as a function of time for specific plot; we used GNMMs with a normal random effect at plot level when several plots were analysed collectively. We estimated these changes by means of annual compounding over the census interval length. All parameters were estimated using the maximum-likelihood method. Full methods, data and associated references are available in Supplementary Information.

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### Author contributions

C.P. contributed to the study design, data collection, method development, result analysis and writing of the manuscript. Z.M. and X.L. conducted the data analysis and developed the statistical models. All authors contributed to the data analysis, result discussion and manuscript preparation.

### Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on [www.nature.com/natureclimatechange](http://www.nature.com/natureclimatechange). Reprints and permissions information is available online at <http://www.nature.com/reprints>. Correspondence and requests for materials should be addressed to C.P.