Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate

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Tree mortality, growth, and recruitment are essential components of forest dynamics and resiliency, for which there is great concern as climate change progresses at high latitudes. Tree mortality has been observed to increase over the past decades in many regions, but the causes of this increase are not well understood, and we know even less about long-term changes in growth and recruitment rates. Using a dataset of long-term (1958–2009) observations on 1,680 permanent sample plots from undisturbed natural forests in western Canada, we found that tree demographic rates have changed markedly over the last five decades. We observed a widespread, significant increase in tree mortality, a significant decrease in tree growth, and a similar but weaker trend of decreasing recruitment. However, these changes varied widely across tree size, forest age, ecozones, and species. We found that competition was the primary factor causing the long-term changes in tree mortality, growth, and recruitment. Regional climate had a weaker yet still significant effect on tree mortality, but little effect on tree growth and recruitment. This finding suggests that internal community-level processes—more so than external climatic factors—are driving forest dynamics.

boreal forest | climate change | forest dynamics | tree demographic rates | tree competition

Forests provide fundamental ecosystem services for sustaining the global environment, such as storing carbon and maintaining biodiversity. These services, however, are at risk for decline as evidence has increasingly shown that forests in many parts of the world are undergoing rapid changes (1–4). Climate at the regional or global scale is often presumed to be responsible for these changes (5–14), with surprisingly little attention being paid to the possible effects of endogenous processes despite the fact that competition is often an important force driving stand dynamics and succession (15–18). How climate change and competition interplay to affect the long-term change of demographic rates and what are their relative contributions to the change are unanswered questions (19, 20).

We addressed these questions by compiling data from 1,680 permanent sample plots (PSPs) that are located in undisturbed natural forests across western Canada (Fig. 1). The trees in these plots, which cover a wide geographic region spanning 32° of longitude and 10° of latitude primarily in the boreal zone, were censused over a period from 1958 to 2009 (Fig. 1). Within each plot, all standing trees with diameter at breast height (DBH) ≥ 9 cm were tagged, recorded, and remeasured at irregular time intervals (mean = 10 y) (*SI Appendix*, Fig. S1). Plot sizes ranged from 0.04 ha to 0.81 ha (mean = 0.14 ha). To reduce possible impact of plot sizes on our analyses, only the plots with at least 50 trees at their first census were selected. The plots have been censused three to eight times (mean of four times). In total, these plots contained 320,878 living trees over the study period (*SI Appendix*, Table S1).

We analyzed the changes of tree demographic rates (mortality, growth, and recruitment rates) over time at the species, stand, and regional levels and by stand age, tree size, and plot elevation

(*Methods*). Two major possible drivers of the changes, competition and regional climate, were considered in our analyses. To test the effect of competition on the demographic rates, we used stand basal area (BA), basal area of larger trees (BAL), and stand density index (SDI), all commonly used in forestry (6, 12) as indexes of competition. To assess the effect of climate change, we selected mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), and mean annual precipitation (MAP). We incorporated both competition and climatic variables simultaneously in the models, rather than separately as previous studies did (6, 11), and considered possible interactions between competition and climatic variables (21) in the models.

Results and Discussion

We found that tree mortality significantly increased over the last five decades (Fig. 2*A*). Increased mortality was consistently observed across all provinces, ecozones, elevations, and tree size classes (*SI Appendix*, Fig. S2). At the species level, a significant increase in tree mortality was found in seven of the nine most common tree species [Fig. 2*B*; $P < 0.0001$, generalized nonlinear mixed model (GNMM)].

For all plots combined, tree growth rates, calculated as relative growth in total basal area, were observed to decline significantly, regardless of ages [Fig. 2*C*; $P < 0.001$, linear mixed model (LMM)]. The decreased growth rates were consistently observed in all species except balsam fir (*Abies balsamea*) (Fig. 2*D*), across all provinces except Manitoba, at various elevations, and for various tree size classes (*SI Appendix*, Fig. S3). A significant decrease in growth rate ($P < 0.001$, LMM) was also detected in the boreal

Significance

Forests worldwide have undergone rapid changes; however, understanding the causes of the changes has been a challenge. Climate on the regional scale has been overwhelmingly presumed to drive these changes, with little attention paid to the possible effects of competition. We compiled a long-term forest dataset from western Canada to study the relative importance of climate change and competition on tree growth, mortality, and recruitment. We showed that competition was the primary factor causing the long-term changes. Regional climate had a weaker yet significant effect on tree mortality, but no effect on tree growth and recruitment. This finding suggests that forest studies focused solely on the effects of climate may overlook the effect of other processes critical to forest dynamics.
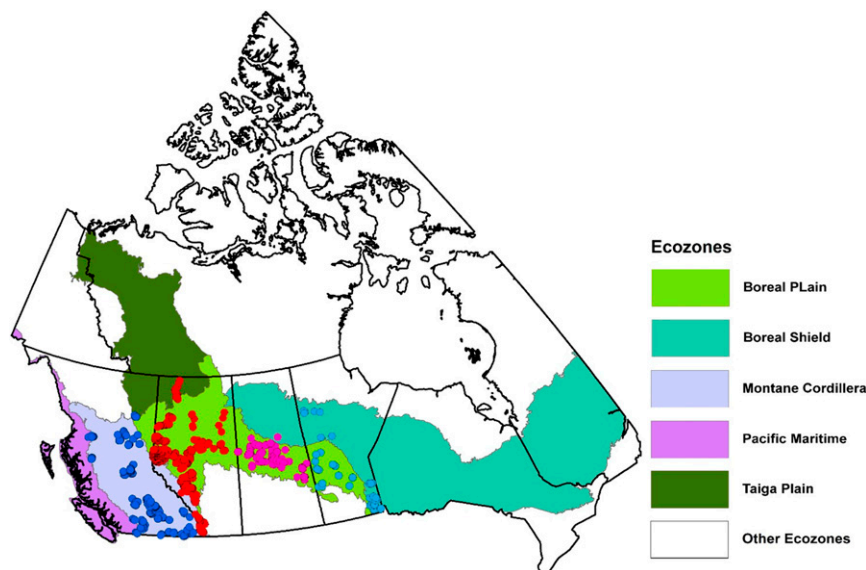
Fig. 1. Locations of 1,680 permanent sample plots (PSPs) in western Canada. Each dot stands for one PSP. Four colors (dark blue, red, pink, and light blue) were used to show the distribution of PSPs in each of four provinces: British Columbia (777), Alberta (563), Saskatchewan (290), and Manitoba (50). The background colors represent Canada's ecozones.

plain and the Montane Cordillera ecozones but not in the boreal shield or the taiga (*SI Appendix*, Fig. S3).

Compared with the growth rates, recruitment rates showed a similar but weaker trend of decrease over time (Fig. 2*E* and *SI Appendix*, Fig. S4). There was a significant decrease in recruitment rate for all of the plots combined (Fig. 2*E*; $P < 0.0001$, GNMM), and recruitment decreased most rapidly in younger forests (50–80 y old; $P < 0.0001$), followed by mature forests (80–120 y old; $P = 0.0038$), with no significant change detected in old-growth forests (≥ 120 y old; $P = 0.507$). Among the nine tree species studied, recruitment significantly decreased in five species ($P < 0.001$), whereas recruitment of balsam fir slightly increased ($P = 0.0167$) but did not change in jack pine (*Pinus banksiana*), white birch (*Birch papyrifera*), and balsam poplar (*Populus balsamifera*) (Fig. 2*F*). A significant decrease ($P < 0.001$) in recruitment was found in British Columbia and Manitoba but not in Alberta and Saskatchewan (*SI Appendix*, Fig. S4). For ecozones, only Montane Cordillera showed a significant decrease in mortality. The decrease in recruitment rates was more consistent at different elevations and tree size classes.

To explore possible drivers of the changes of tree demographic rates, we examined correlations between the three demographic rates, climatic variables, and tree competition. Most climatic variables in the four provinces showed significant changes in the last five decades, although considerable interannual variations exist (*SI Appendix*, Table S2). MWMT increased in all of the provinces ($P < 0.0004$, LMM) except British Columbia ($P = 0.1426$). MCMT appeared to increase significantly in the four provinces ($P < 0.0001$). MAP declined in British Columbia and Alberta ($P < 0.0001$) but increased in Saskatchewan and Manitoba ($P < 0.0007$).

We found that competition was strongly correlated with tree mortality rates over the last five decades (Fig. 3 *A* and *D*). We performed separate analyses for stand age groups, provinces, ecozones, elevations, and tree size classes. About 80% of these analyses showed significantly positive relationships between tree mortality and competition when using stand basal area as the competition index (Fig. 3*A*). Similar results were obtained using the other two common competition indexes, SDI and BAL (Fig. 3 *A* and *D*). This finding was also supported by the separate analyses for different stand age groups (*SI Appendix*, Fig. S5) and for small

plots (<0.1 ha in plot size; 1,111 plots) and large plots (≥ 0.1 ha in plot size; 569 plots) (*SI Appendix*, Fig. S6). The result remained the same if stand age was included in the models as an additional explanatory variable (*SI Appendix*, Fig. S7) or the Markov transition models were used to account for temporal correlation in demographic rates (*SI Appendix*, Fig. S8). The significant correlation between mortality rate and competition found in our study is in accord with those from other long-term inventory-based mortality studies in temperate forests (8, 20, 22) and boreal forests (12, 23), but is discordant with recent studies that argued competition was not correlated with changes in mortality rate in temperate forests (6) and boreal forests (11). In these later studies, the increased mortality was attributed to the effect of drought. However, mortality in these later studies was modeled only as a function of climate variables with no explicit consideration of the effect of competition. Further, these studies used much smaller datasets (76 plots in ref. 6 and 96 plots in ref. 11).

Still, in addition to competition, we also found that climate change had a significant but weaker effect on the increased mortality rates over the last five decades (Fig. 3 *A* and *D*). Among the mortality analyses for the entire study zone, stand age groups, provinces, ecozones, elevations, and tree size classes, nearly 80% of the analyzed groups showed significantly positive correlations between summer temperature (MWMT) and tree mortality. Increased summer temperature may lead to higher respiration costs, higher heat stress (e.g., drought), higher risk of cavitation (24–26), and thus higher tree mortality rates. This result was similar to those of previous studies (6, 11, 14, 26) that showed positive correlations between mortality rates and air temperature. However, it is noteworthy to mention that these previous studies used mean annual temperature (MAT), not MWMT, in their analyses. In our study region, MAT is closely related to MCMT, not MWMT (*SI Appendix*, Fig. S9). Because of the large difference between the summer and winter temperatures in high latitudes, we found it preferable to use MWMT and MCMT, not MAT, for modeling the effect of climate change on forest dynamics (27, 28). Winter temperature (MCMT) showed negative correlations with tree mortality, suggesting tree mortality decreases in warmer winters.

Correlations between precipitation and tree mortality were highly variable across species, age classes, and ecozones. Two drought-related indexes, annual moisture index (AMI) and annual
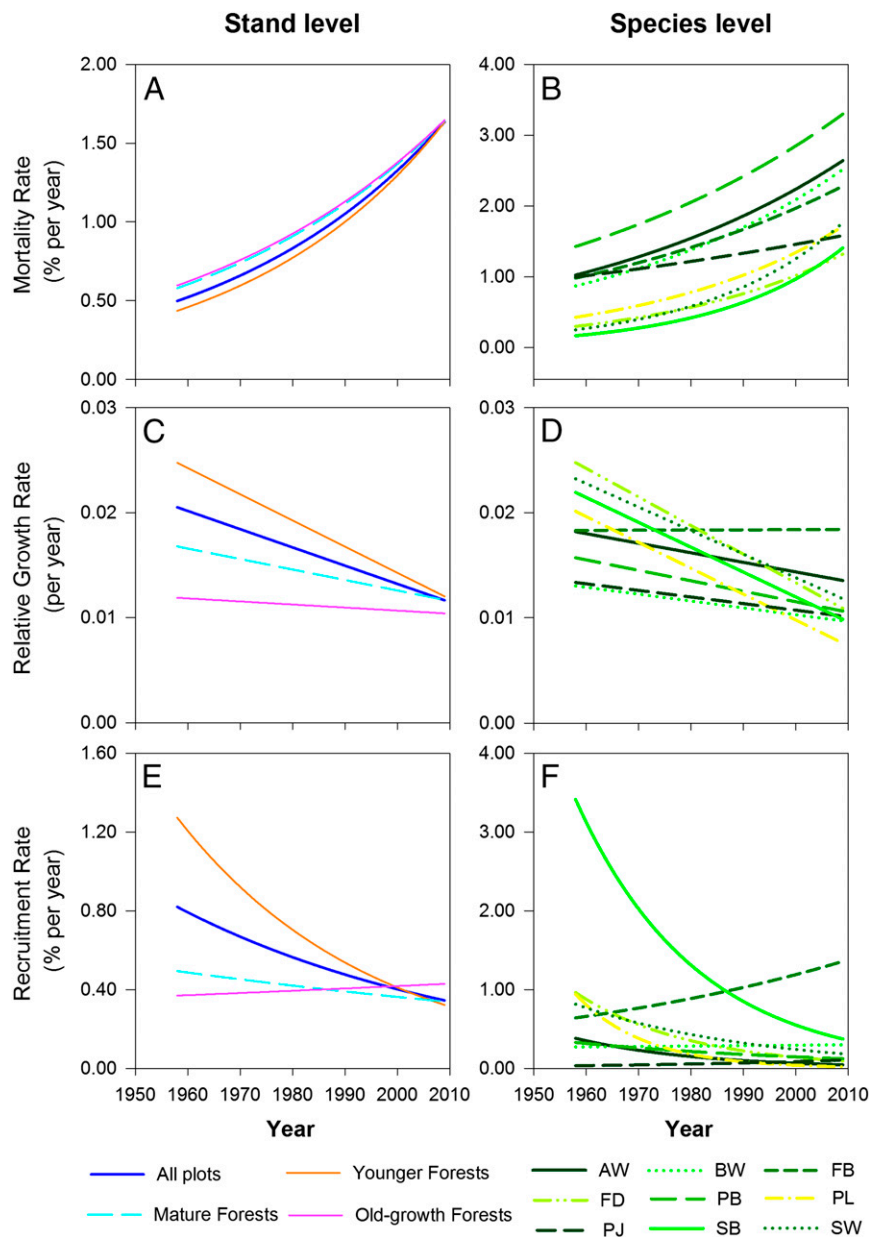
Fig. 2. Modeled trends (1958–2009) of tree mortality (*A* and *B*), growth (*C* and *D*), and recruitment (*E* and *F*) rates at both stand and species levels. A generalized nonlinear mixed model was used for modeling temporal trends of tree mortality and recruitment rates, and a linear mixed model was used for modeling temporal trends of tree growth rates (*Methods*). At the stand level, PSPs were classified into three age groups based on initial stand ages: young forests (50–80 y), mature forests (80–120 y), and old-growth forests (≥120 y). At the species level, modeled trends of nine tree species are shown, including, AW, trembling aspen (*Populus tremuloides*); BW, white birch (*Birch papyrifera*); FB, balsam fir (*Abies balsamea*); FD, Douglas fir (*Pseudotsuga menziesii*); PB, balsam poplar (*Populus balsamifera*); PL, lodgepole pine (*Pinus contorta*); PJ, jack pine (*Pinus banksiana*); SB, black spruce (*Picea mariana*); and SW, white spruce (*Picea glauca*).

mean climate moisture index (CMI), are highly related to MAP (*SI Appendix*, Fig. S9), and they should follow similar trends to those of MAP. Thus, we found no clear evidence about drought-induced tree mortality in western Canada, although drought-induced tree mortality was detected in recent studies in the region based on short-term sampling plots and relatively small datasets (25, 29–31). We argue that how drought affects tree mortality in forests of high latitudes remains an open question and more studies are needed.

For tree growth and recruitment rates, we detected strongly negative relationships with tree competition in over 90% of the analyzed groups (Fig. 3 *B*, *C*, *E*, and *F*). This suggests that competition-induced suppression (e.g., shading and root competition)

was the primary factor limiting tree growth and recruitment over the last five decades (18). In contrast, the three climate variables showed significant correlations with tree growth and recruitment only in over 50% of the analyzed groups. MWMT and MAP had relatively small effects on tree growth (less than 40% of the analyzed groups showed significant correlations), whereas the effect of MCMT on tree growth was mostly negative among the detected significant groups (Fig. 3*B*).

At the species level, although different species varied considerably in their responses to competition and climatic variables, the overall results are such that competition affected tree demographic rates more than climate did (Fig. 3 *G–I* and *SI Appendix*, Fig. S10). For tree mortality, four conifer species (two
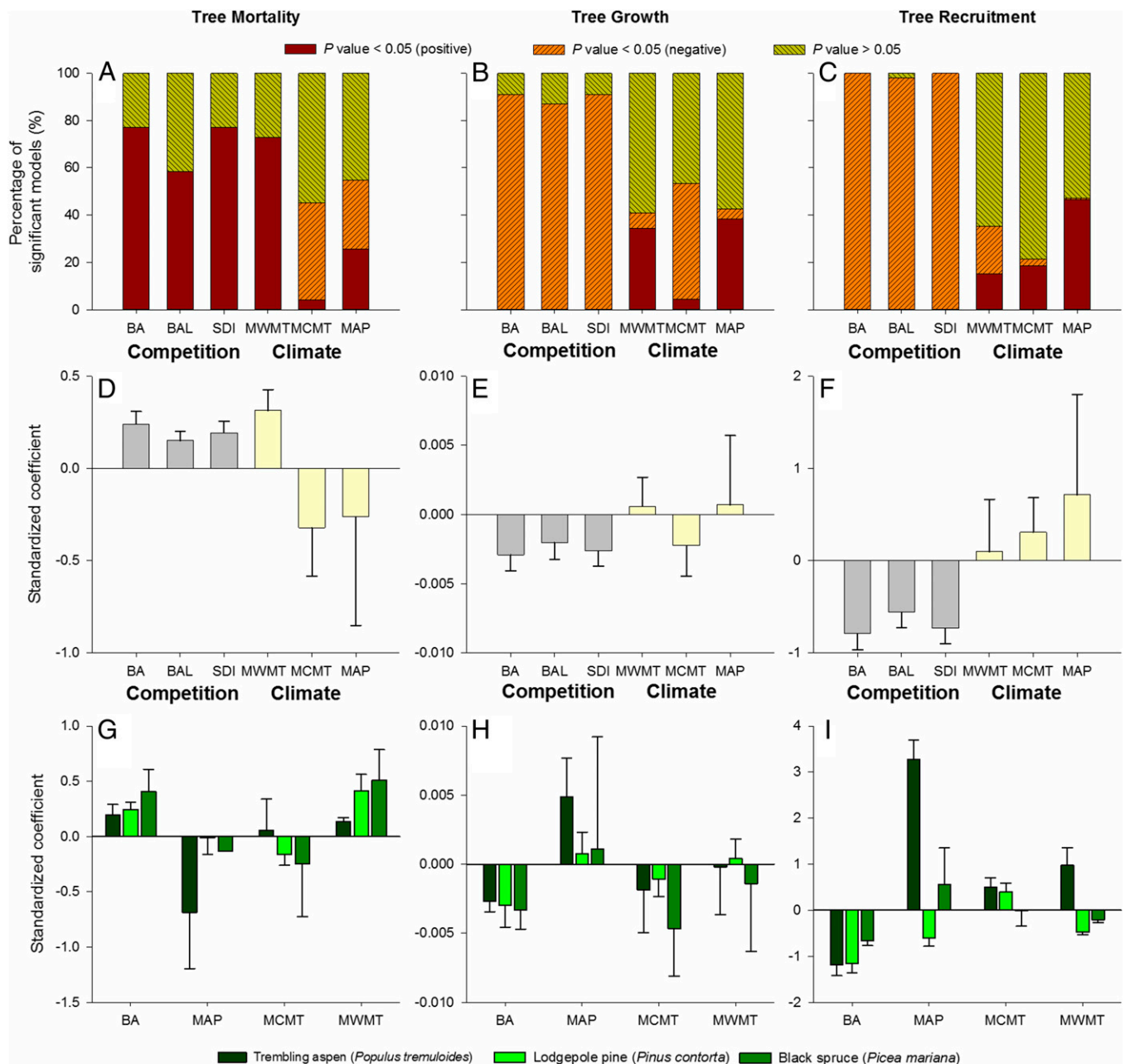
Fig. 3. Summary of the relationships among tree demographic rates, competition, and climate at both stand and species levels. Each bar in the bar plots in *A–C* shows the percentage of the regression models (among all of the models tested) in which each of the variables (on the *x* label) was positively significant, negatively significant, or nonsignificant. We divided the 1,680 PSP data into different groups, including stand age groups, provinces, ecozones, elevations, and tree size. Within each group, the plots were stratified into different classes (e.g., different age classes, different provinces, etc.) and the data of each class were fitted using GNMM for tree mortality and recruitment and LMM for tree growth (*Methods*). Those group classes with <20 plots were excluded from modeling. The competition indexes (BA, stand basal area; BAL, basal area of larger trees; SDI, stand density index) were entered into the models separately, and the three climate variables (MWMT, mean warmest month temperature; MCMT, mean coldest month temperature; MAP, mean annual precipitation) were included in the models simultaneously. Three colors in these bar plots represent three significant levels: significantly positive relationships (dark brown), significantly negative relationships (light brown), and nonsignificant relationships (greenish brown). The box plots in *D–F* show the standardized regression coefficients between demographic rates and competition indexes and climate variables at the stand level. The box plots in *G–I* show the standardized regression coefficients between the demographic rates and the competition indexes and climate variables for three selected tree species (*Methods*). Only the result for the competition index BA is shown as the two other competition indexes had similar results.

pines and two spruces) showed strong relationships with stand basal area, with other species having relatively weak relationships (a little less than 40% of the analyzed groups showed significant correlations). In contrast, the contributions of climatic variables to tree mortality varied widely among species (*SI Appendix,* Fig. S10). For tree growth and recruitment, all nine tree species

showed significant correlations with stand-level competition, whereas the effects of climate change on tree growth were weak for most tree species (*SI Appendix,* Fig. S10).

High latitudes such as western Canada are expected to experience some of the greatest increases in absolute temperature due to global warming (13). Much evidence has shown prevailing changes

in ecosystems in the region, caused by climate change (32–34). Thus, if impacted, evidence on the impact of climate change in high latitudes should tell us, with a high certainty, much about the consequence and the magnitude of global warming. Our study showed that forest dynamics changed markedly over the last five decades in western Canada. Competition was apparently the main force driving the change, followed by the effect of climate. Competition showed strong effects on all three demographic rates, whereas regional climate change was equally important in affecting tree mortality, but its effects on tree growth and recruitment were limited. Evidently, it is critically important to include endogenous forces such as competition in assessing and predicting forest changes under the current and future climates.

Tree competition is an overarching mechanism driving the establishment, dynamics, and succession of forests (15–18, 35, 36). Competition theory is also the foundation on which forest growth and yield modeling and silvicultural practice are based (18, 37–39). The finding that competition overwhelmed the change in tree vital rates in our study can be explained by tree competition for limiting resources, particularly for light and crown space and also possibly for water and other nutrients through root competition as stands developed over time. This is supported by the observation that stand density (expressed by basal area) for young and mature stands increased over time but changed little for old-growth stands (*SI Appendix*, Fig. S11). As a result, growth and recruitment rates accordingly increased over time for young and mature stands but showed little change for old-growth stands (Fig. 2 *C* and *E*). If the effect of climate change were important, we would expect growth and recruitment rates for old growth also to increase over time. However, this was not observed. In contrast, mortality rates in young, mature, and old-growth stands all showed a similar trend of increase consistent with the effect of climate (Fig. 2*A*). These observations explain why competition and climate both were important in affecting mortality rates but not growth and recruitment rates.

The implications of our findings are profound for three reasons. First, they suggest that competition, as a major endogenous process, plays a key role in driving the dynamics of forests. However, this situation could quickly change as the global temperature continues to rise, particularly in the region of high latitudes (13, 32, 34). Because both competition and climate increased tree mortality, our study suggests that the future tree mortality rates will likely increase due to the combined effects of competition and climate. For tree growth and recruitment, our study showed competition negatively affected tree growth and recruitment but no effects of climate change at the stand level were detected although studies from satellite data (40) showed that global warming facilitated plant growth. However, the positive effect of increasing temperature and lengthening of the growing season could be offset by increasing respiration (5). One of the consequences of these contrasting effects is that the future dynamics of forests will become much less predictable. Second, they suggest that the growth and yield models developed from competition theory remain an important and useful management tool for projecting biomass growth, timber production, and forest change (37–39). To cope with climate change, however, the future growth and yield models need to necessarily incorporate the dimension of climate. Third, it is not too late to make proactive policies to facilitate the mitigation of climate change for sustainable management of forest ecosystems. For making management planning or policy decision, it is important to keep in mind that competition and climate change are not independent but interlocked processes that together affect species distribution (41) and demographic performance (19). It is certain that competition for resources will become more severe as the availability of resources (e.g., soil and water) becomes more variable and less predictable as the climate continues to change (25). To deal with

these uncertainties, adaptive management will be a key strategy for sustaining the future of forests (42).

Although a large, global body of literature on climate change and forest dynamics has been developed during the last five decades (3, 6, 9, 11–14), much of this literature provides insights on how trees respond to climate change without sufficient consideration of competition and other factors (43). Our study showed that accurately quantifying the relative contributions of both endogenous and exogenous forces simultaneously to tree demography is crucial not only for increasing our understanding of the underlying causes of the changes in forest dynamics, but also for adequately predicting the impacts of changing climates on forest dynamics.

Methods

Dataset. This study was conducted in fire-originated natural forests in four provinces of western Canada (49°0′–59°43′N, 95°18′–127°54′W), British Columbia, Alberta, Saskatchewan, and Manitoba (Fig. 1). The study region contains 5 of Canada's 11 major forest ecozones. A total of 1,680 permanent sample plots (PSPs) were used in our study (Fig. 1 and *SI Appendix*, Table S1), following the data-screening criteria used in previous studies (4, 6) and also detailed in *SI Appendix*, *Methods*. The 1,680 PSPs contained 320,878 living trees over the study period. For individual plots, the initial census year ranged from 1958 to 1999, with 85% of them being established before 1980 (*SI Appendix*, Fig. S1). Climate data for the PSPs were derived from the programs ClimateWNA v4.62 and ClimatePP v3.21 (44, 45) (details in *SI Appendix*, *Methods*). We calculated historical monthly, seasonal, and annual climate variables for individual years and periods from 1958 to 2009. The following climatic variables were selected for initial consideration in the current study: MWMT (degrees centigrade), MCMT (degrees centigrade), MAP (millimeters), degree days above 5 °C (DD5), MAT, mean annual summer precipitation (MSP), mean annual CMI, and AMI.

Competition Indexes. To assess the effect of competition on tree growth and mortality, we selected three competition indexes that are widely used to measure competition at the stand level (6, 39, 46–48). By these indexes, competition in this study is used as a general term as in the literature (e.g., refs. 17 and 18), referring to a process by which trees (symmetrically or asymmetrically) suppress one another through the use of the shared limiting resources. The indexes are defined as follows:

i) Stand BA: We used BA as a surrogate for stand crowding of each plot, because it combines both tree size and density (46). Stand crowding determines the average resource availability for trees within a stand. Higher stand crowding indicates fewer resources available per individual. BA is considered one of the best competition indexes in the literature (6).

ii) BAL, defined as the total BA (square meters per hectare) of all trees larger than the target tree in DBH. The BAL has been commonly used to capture one-sided (asymmetric) competition in modeling tree growth and mortality (47). In one-sided competition, larger trees impose competitive advantage over smaller trees whereas smaller trees have little effect on the growth and survival of larger neighbors.

iii) SDI: This index is defined as the degree of crowding within stocked areas (48). It is a measure of the stocking of a stand of trees based on the number of trees per unit area and the diameter at breast height of the tree of average basal area,

$$SDI = N \times \left(\frac{DBH_{mean}}{25.4}\right)^{1.605},$$

where N represents trees per hectare, and DBH_{mean} represents the quadratic mean diameter in centimeters.

Data Analyses. Changes of tree demographic rates (mortality, growth, and recruitment rates) over time were analyzed on the stand, species, and regional levels. To assess how changes varied with stand age, we divided the PSPs into three stand age groups, the plots with the initial stand ages 50–80 y (young forest), 80–120 y (mature forest), and ≥120 y (old-growth forest). Also, we divided the PSPs into different groups based on three DBH classes and three elevation gradients to assess how forest structures and demographic rates changed with tree size and plot elevation. Linear mixed models were used for modeling the temporal trends of tree growth and detecting the relationships between tree growth and possible drivers at the stand and species levels (*SI Appendix*, *Methods*). Mean annual tree growth rates were calculated as relative annual growth in total basal area at both

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the stand and species levels. Absolute annual growth rates in total basal area were also calculated and analyzed. We found very similar results from both relative and absolute growth rates, so we reported only the result of relative growth rates. A normal random effect for plot identity was added to account for differences among study plots. We used GNMMs (6) to assess trends of tree mortality and recruitment across multiple plots in four provinces and four main ecozones (*SI Appendix, Methods*). Mortality and recruitment rates were estimated over the census interval length. All parameters were estimated by maximum-likelihood methods. A normal random effect based on plot identity was added to account for differences among study plots.

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