Neighbourhood canopy cover alleviates increased tree mortality after exceptionally dry summers at a climatic range limit

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Abstract

Populations situated at range margins are often at their environmental niche limit. The stress gradient hypothesis posits that facilitation effects should be more common in such conditions, but few studies have examined the joint effects of biotic interactions and climatic factors on vital rates at species range limits. We used eight years of annual unmanned aerial vehicle surveys to assess the sensitivity of tree mortality to summer moisture deficits across a landscape near the climatic moisture limit of forest cover in the Northern Great Plains. Trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*), which were near the edge of their climatic niches, both experienced higher mortality in years following exceptionally dry summers. Mortality increases for these species were especially pronounced in open areas, as well as for tall trees and those on upper-slope positions. Individuals surrounded by neighbours appeared to better withstand high summer moisture deficits, possibly because microclimatic buffering reduced water loss. A third species, lodgepole pine (*Pinus contorta* var. *latifolia*), was resistant to summer moisture deficits and seemed to benefit somewhat from reduced competition at mid-slope positions. We conclude that facilitation from neighbourhood-scale canopy cover may help alleviate effects of climate-related environmental change at species' range limits.

Key words

Climate change, climate moisture index, drought, forest, neighbourhood interactions, *Picea glauca*, *Pinus contorta*, *Populus tremuloides*, stress gradient hypothesis, topographic position, unmanned aerial vehicles

Introduction

The geographic range of a species is normally defined by the area over which environmental conditions, together with biotic interactions such as competition and predation, enable a non-negative average rate of per-capita population growth (Holt et al. 2022). Populations at range margins are often at the limit of their environmental niche, and are thus vulnerable to changes in the environment that push them outside of the range of conditions under which they can persist. Climate change is a particularly acute threat in this regard, as it can lead to increases in mortality at the warm and dry edges of species' ranges, possibly triggering population declines or extinctions. This can in turn result in a retraction of species' range limits, reductions in local species diversity, changes in community composition, and losses of ecosystem functions and services (Thomas et al. 2006, Sheldon et al. 2011, Grimm et al. 2013).

Ecological responses at species' range limits depend on the sensitivity of demographic rates to environmental factors that will be affected by climate change. Climate-dependencies in growth, survival, or fecundity at range limits have been reported across many taxa (Sexton et al. 2009). The extent to which climate responses are shaped by local biotic interactions has not been well explored, however. Competitors and natural enemies create additional pressures on survival and reproduction that can exacerbate the effects of adverse environmental conditions. Conversely, the stress gradient hypothesis posits that facilitation is more common in harsh environments and may alleviate negative environmental effects on fitness (Bertness and Callaway 1994). Few studies to date have examined the joint effects of biotic interactions and climatic factors on demography at species range limits (Matías and Jump 2012, Stanton-Geddes et al. 2012). Variation in the climate-sensitivity of vital rates within a population – which may result from local biotic interactions or other factors – is important to understanding the potential for population declines or extinctions in these marginal environments.

In this study, we investigate the mortality responses of three co-occurring tree species to exceptionally high summer moisture deficits at a dry range limit. Individual variation in mortality during abnormally dry conditions can arise through biotic and abiotic factors that influence either water availability or demand. For example, moisture sensitivity can depend on the number and size of neighbours in the local area around a given tree. Trees that are surrounded by many tall neighbours experience greater competition for water (as well as light and nutrients) and may thus be more sensitive to drought (Bradford et al. 2022). On the other hand, transpiration by neighbours may help create microclimates with lower vapour pressure deficits, thereby reducing water loss. Moisture sensitivity can also vary with tree size, as trees that are tall require greater soil water potentials to transport water to their crowns, and those with large crowns have higher transpiration rates (Bennett et al. 2015). Such trees may have deeper root systems though for accessing soil water that is unavailable to smaller individuals. Topographic variation across a landscape can lead to greater moisture sensitivity in areas where rapid drainage reduces water availability, such as upper slopes, ridges, and hilltops. However, moisture sensitivity may be higher in valleys where individuals tend to be poorly acclimated to dry conditions (Zuleta et al. 2017). The importance of each of these factors is likely to vary between species. Drought-sensitive species and those near the limit of their climatic niche are expected to experience the greatest increases in mortality under dry conditions. Species that are more drought tolerant may show weaker mortality responses, or even reduced mortality if a drought alleviates competitive effects from their heterospecific neighbours (Cavin et al. 2013).

Here, we use eight years of annual unmanned aerial vehicle (UAV) surveys to evaluate how the mortality rates of three northern tree species varied with climatic moisture availability during a period in which summer moisture reached at least a 40-year minimum. Our study area is situated in an elevated forest-grassland landscape within the Northern Great Plains that is at the climatic moisture limit of one species (white spruce, *Picea glauca*), and approaching that of a second (trembling aspen, *Populus tremuloides*). Our objectives were to evaluate how the sensitivity of individual-level tree mortality to climatic aridity varies with (a) species, (b) neighbourhood canopy cover, (c) height, and (d) topographic position, under conditions that presage the increases in summer moisture deficit expected later this century. We predicted that individuals with the greatest increases in mortality risk following one or more dry summers will be those that are (a) near the edge of their species' climatic moisture niche, (b) in gaps or along forest edges, (c) tall, and (d) situated on upper slopes.

Methods

Study area. We collected tree mortality data in Cypress Hills Interprovincial Park, a 35 000 ha protected area that straddles the southern Alberta-Saskatchewan border in western Canada (49º 40' N, 110º 15' W; 1100-1400 m a.s.l.). The park is situated within the Northern Great Plains, a cold semi-arid ecoregion where extended summer water deficits prevent the establishment of widespread forest cover. Locally, the park encompasses a 400-m plateau where somewhat cooler temperatures (2 °C mean annual temperature) and greater precipitation (550 mm mean annual precipitation) than the surrounding region support a mix of fescue prairie grassland and spruce, pine, and aspen forests. We quantified climatic water deficit for this area by the difference between monthly precipitation (P) and potential evapotranspiration (PET) (Climate Moisture Index, CMI = P – PET). The area has experienced a drying trend over the past decade, with the five-year average of CMI over the summer months (Jun-Sep) decreasing to -26 mm, the lowest value in at least 40 years (Fig. 1). For context, mean summer CMI was -21 mm during a major drought from 1999-2001 (Sauchyn et al. 2003). Summer CMI values are expected to decrease further by the middle and end of the 21st century, likely pushing this area outside of the climate envelope that would support extensive forest cover.

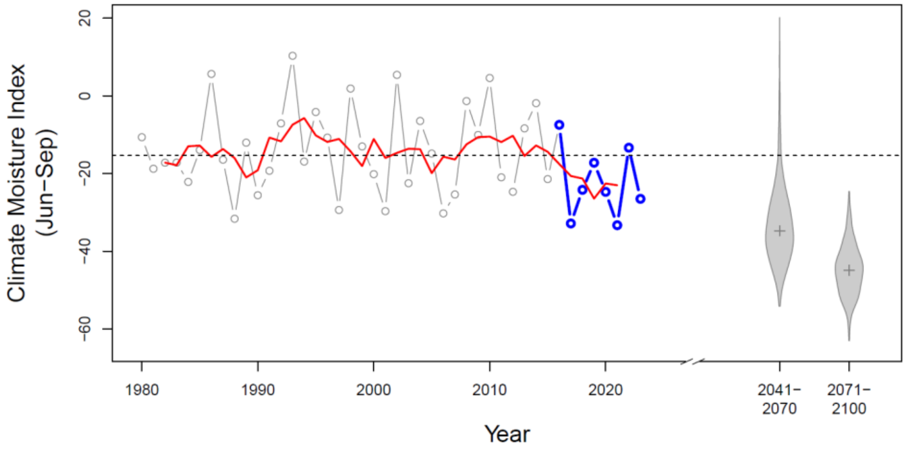

Fig. 1. Past and projected future range of Jun-Sep Climate Moisture Index (P – PET) values for Cypress Hills Interprovincial Park. Blue points and lines show the period covered by annual tree mortality surveys in this study. The red line shows a five-year running mean. The dashed horizontal line shows the average over the 44-year time series. Conditions are expected to become considerably drier in the coming decades, as shown by violin plots of the distribution of future summer CMI projections. CMI projections are based on 100 weather simulations from each of five Earth System Models in the CMIP6 model intercomparison project (ACESS-ESM1-5, CanESM5, GFDL-ESM4, MRI-ESM2-0, UKESM1-0-LL), under a SSP2 emissions scenario.

Most of the present forest in the study area originated from large fires in the 1880s (Strauss 2001). The dominant tree species are lodgepole pine (*Pinus contorta* var. *latifolia*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*), with balsam poplar (*Populus balsamifera*) occasionally present. Lodgepole pine is a drought-tolerant pioneer species that occurs throughout the Rocky Mountain and Pacific coast regions. Trembling aspen is a shade-intolerant species that occurs across the boreal forest and mountainous areas of the western United States. White spruce is a shade-tolerant boreal species that occurs in very few areas with a drier climate than our study area. Based on Little's (1971) range maps, 21%, 6% and 1% of the respective distributions of lodgepole pine, trembling aspen, and white spruce have a lower summer CMI than our study area (Fig. 2). Within the Cypress Hills, lodgepole pine is restricted to the plateau's upper slopes, trembling aspen is most often found at middle slopes, and white spruce is dominant in lower slopes and valleys.

UAV surveys and data processing. We assessed individual-level mortality of canopy trees in 49 sites distributed across the elevational range of the study area, with balanced representation of the three tree species. Each summer from 2016-2023 we flew an unmanned aerial vehicle (DJI Phantom 3 Standard, Phantom 4 Standard, or Matrice 200 Series v2) at these sites 40-70 m above the canopy. The UAVs repeatedly traversed a rectangular area averaging 3 ha in size (range 2.2 - 3.9 ha) while taking downward-facing digital photographs that had at least 90% front and side

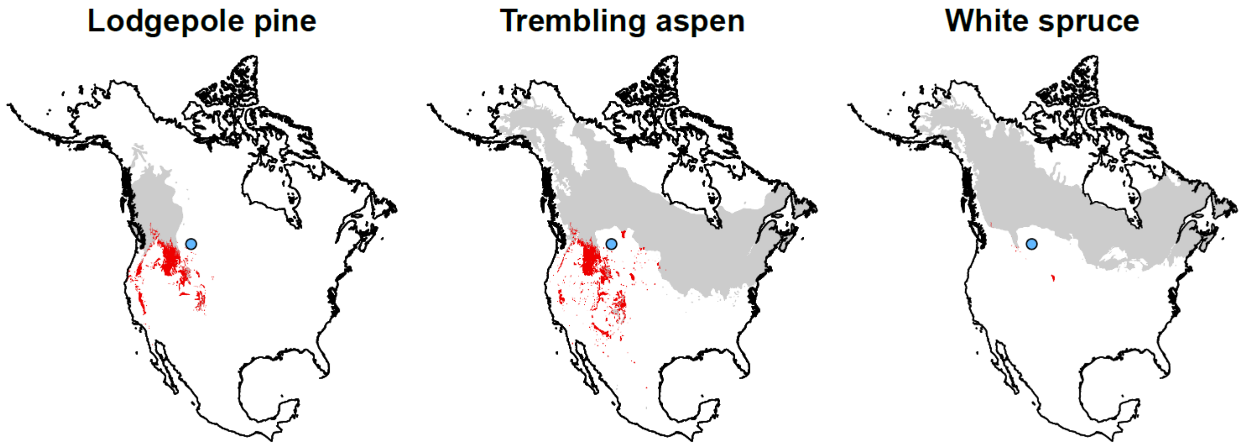

Fig. 2. Range maps for lodgepole pine trembling aspen, and white spruce. Areas in grey and red have wetter and drier summers, respectively, than the study area (blue circle) based on their Jun-Sep Climate Moisture Index.

overlap. We then used photogrammetric software (Agisoft Metashape) to reconstruct a 5-cm resolution orthomosaic, digital terrain model (DTM), and digital surface model (DSM) for each site in each year. The difference in elevation between the DSM and DTM produced a raster layer of the height of the canopy surface above the ground (canopy height model, CHM). We subsequently co-registered the annual orthomosaic and CHM layers for each site across years.

From this imagery, we manually identified 49 891 points representing the approximate centre of each tree crown that was visible in the orthomosaics and alive in 2016. We manually classified these crowns to species and as alive or dead in each subsequent year based on the presence of green foliage and whether they remained standing. We combined balsam poplar and trembling aspen because poplar is only 5% as abundant as aspen in the study area, and crowns of these species could not be easily distinguished in our imagery. For sites containing aspen or poplar, we used supplemental UAV imagery collected during leaf-off conditions to help identify individual trees and their species. To assess classification success we matched a subset of the crowns to 1495 trees within a set of permanent plots that we re-censused biennially from 2016 to 2021. Species identity was correct for 94% of the ground-truth trees. Across all observation years, live/dead status was correct for 98% of live trees and 90% of dead trees.

We measured tree height for each marked crown from the maximum CHM value within a 0.5 m radius of the crown's centre in a given year. Tree heights derived from UAV photogrammetry have elsewhere been shown to be accurate to 0.5 m (Jurjević et al. 2020). We assigned the median height from the years in which a tree was alive as its estimated height. We calculated local neighbourhood canopy cover for each tree as the proportion of CHM cells within a 15 m radius of the crown's centre that had heights greater than 2 m. Local canopy cover was calculated annually for each canopy tree. There were 23 cases where site imagery for a particular year was missing, and another 16 sites for which the CHM in the year 2020 was of poor quality. For these cases (11% of all observations) we used a Bayesian data imputation procedure to estimate a distribution for each missing local canopy cover value from the values observed in the previous and subsequent year (canopy cover around a given tree did not tend to change much from year to year). This imputation approach allowed us to propagate uncertainty in the missing canopy cover values into parameter estimation during model fitting.

In addition to tree height and local canopy cover, we calculated a measure of topographic position for each site and water deficit for each year. We used the Canadian Digital Elevation

Model (Natural Resources Canada 2013) to extract elevation values within a 1 km radius of each site, then calculated the Topographic Position Index (TPI) as the difference between the site's elevation and the mean surrounding elevation. Positive TPI values represent upper-slope or hilltop locations, whereas negative TPI values represent lower-slopes or valleys. We obtained annual summer (Jun-Sep) CMI values by using BioSim software (Régnière et al. 2017) to extract data from four nearby weather stations, adjust for differences in elevation, estimate potential evapotranspiration (Hogg 1997), and calculate a distance-weighted average for the study area.

Statistical models. We fit Bayesian generalized mixed models to assess how annual mortality rates for the three tree species varied with tree height, local canopy cover, TPI, and summer CMI. Our response variable represented whether a tree that was alive in one year was dead (=1) or alive (=0) the following year. The variables tree height and TPI were constant over time, but local canopy cover and summer CMI changed annually. Our model used local canopy cover from the previous year (or its imputed value) to predict whether a tree died. We accounted for potential lagged responses to moisture deficits by using a weighted average of CMI values from the three previous summers, with weights for each year estimated during model fitting for each species. All predictor variables were standardized to have zero mean and unit variance. We included all two-way interactions between predictor variables, as well as random intercept terms to capture overall variation among sites and species-specific variation among years.

Individual tree death followed a Bernoulli distribution where the probability of mortality was modelled as a logistic function of a linear combination of the standardized predictor variables, interactions, site effect, and year effect. There were 583 trees whose year of death was uncertain because of missing site imagery in a particular year. We marginalized the log-likelihood terms for these observations across the two possible years of death to account for this observation uncertainty (i.e., the probability of mortality over two years was calculated as a weighted average of the probability of dying in year 1, and the probability of surviving year 1 then dying in year 2). We used $N(0,0.5)$ regularizing priors for all regression coefficients, $N(-4.5,0.5)$ priors for model intercepts (representing about 1-2% mortality per year for an average tree), Dir(1.5, 0.9, 0.6) priors for CMI weights (representing mean prior weights of 0.5, 0.3, and 0.2 for the 1st, 2nd, and 3rd preceding year, respectively), and $N(0,1)$ priors for standard deviations of random effects and imputed canopy cover values. Models were fit using Markov chain Monte Carlo (MCMC) sampling with the brms 2.20 package in R 4.4.2 (Bürkner 2017).

Results

We observed 5901 tree deaths over seven years, which represented an average annual mortality rate of 1.0% for lodgepole pine, 3.0% for trembling aspen, and 1.7% for white spruce (Table 1). Annual mortality in individual sites ranged from 0.0 - 9.4% per year. Annual species-specific mortality rates ranged from a low of 0.6% to a high of 4.2%.

The three species differed in their sensitivity to the previous summers' climate moisture index (Fig. 3). Mortality of lodgepole pine and white spruce was most strongly related to summer CMI over the two most recent summers (mean weights of 0.48, 0.44, and 0.08 for the previous three summers for pine, and weights of 0.50, 0.31, and 0.20 for spruce), but trembling aspen responded most strongly to the summer CMI two and three years earlier (weights of 0.18, 0.46, and 0.36). Model predictions showed that as the weighted summer CMI decreased from -12 to -27 mm (i.e., from typical to unusually dry conditions) overall aspen and spruce mortality were expected to increase from 2.3% (±0.8%) to 4.0% (±1.1%) and from 1.1% (±0.5%) to 1.9% (±0.6%), respectively. Lodgepole pine did not show a clear overall response to drier summers.

Trembling aspen and white spruce that were growing in open neighbourhoods and those that were tall were particularly sensitive to summer CMI (Fig. 4). Following very dry summers (weighted CMI = -27 mm), the mortality rates of aspen and spruce trees with low neighbourhood canopy cover were 3.2 ± 1.5 and 3.2 ± 1.6 times those expected after more typical summers

Table 1. Summary of the number of trees, the number of mortality observations, and the distribution of model covariate values (mean, 5th and 95th percentiles) for each species.

Species	N total	N died	Mortality rate	Topographic Position Index	Local canopy cover	Tree height (m)
Lodgepole pine	18 595	1 174	1.0%	11.2 (-8.7, 26.0)	0.78 (0.55, 0.96)	18.2 (10.1, 23.4)
Trembling aspen	14 990	2 890	3.0%	-7.2 (-35.9, 16.2)	0.72 (0.42, 0.95)	14.4 (7.5, 20.3)
White spruce	16 306	1 836	1.7%	-14.8 (-52.4, 25.4)	0.64 (0.30, 0.91)	16.8 (6.2, 25.9)

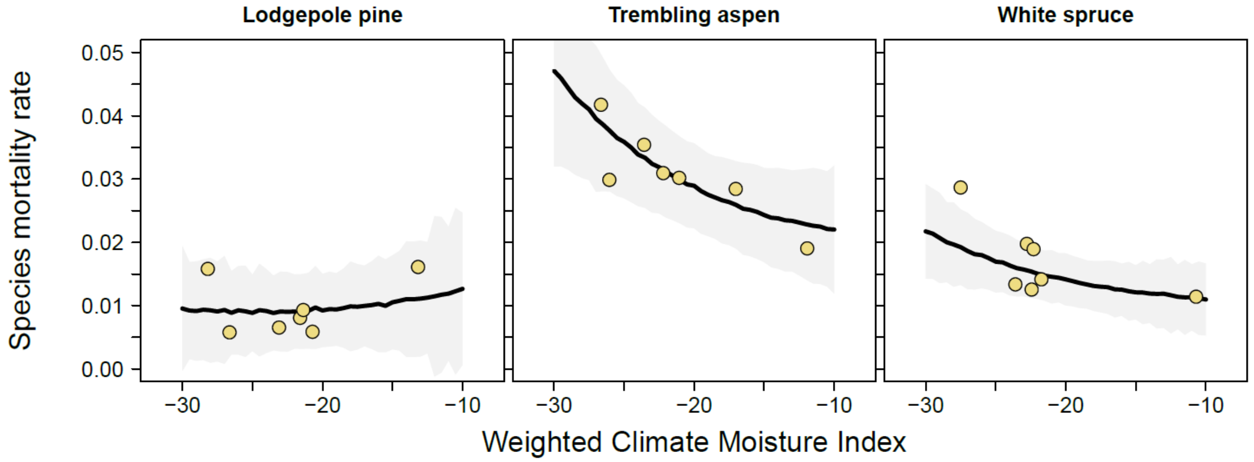

Fig. 3. Relationships between annual species mortality rates and a weighted average of the Jun-Sep Climate Moisture Index over the previous three years. Points represent observed mortality rates for each year. Black lines and grey shaded regions show the posterior mean ± 1 s.d. of model predictions across the observed range of weighted Climate Moisture Index values.

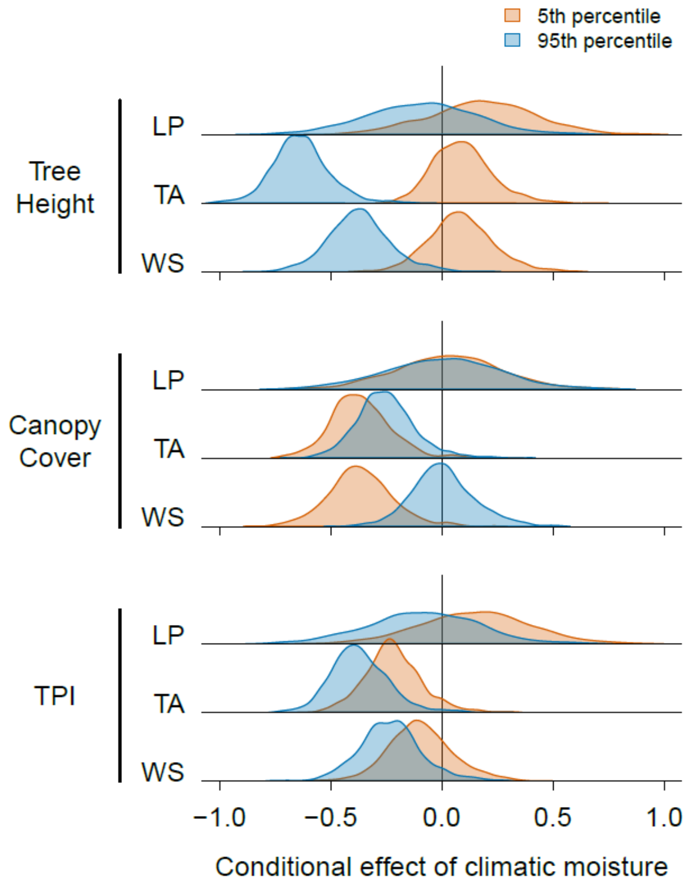

Fig. 4. Posterior distributions of conditional effects of the weighted Jun-Sep Climate Moisture Index on annual tree mortality, evaluated at the 5th and 95th percentiles of tree height, neighbourhood canopy cover, and topographic position index (TPI) for each species (see Appendix S1: Table S1). LP: lodgepole pine; TA: trembling aspen; WS: white spruce.

(CMI = -12 mm), respectively. The same decrease in summer moisture increased the mortality rates of tall aspen and spruce trees by 7.4 ± 3.3 and 3.4 ± 1.7 times, respectively. Local canopy cover did not influence responses to CMI for lodgepole pine, but shorter lodgepole pines seemed to have higher mortality following wetter summers (Fig. 4). All three species exhibited strong interactions between canopy cover and height, with tall trees (but not short ones) experiencing markedly higher mortality in open neighbourhoods (Fig. 5). Shorter trees had higher mortality rates than taller ones in neighbourhoods with greater canopy closure, particularly for aspen and pine.

Both aspen and spruce were somewhat more sensitive to CMI in locations with greater topographic position index values (i.e., on upper slopes), with dry summers leading to mortality rates that were 3.3 ± 1.4 and 2.2 ± 1.1 times those expected after typical summers in these locations (Fig. 4). Mortality rates also varied topographically in several other respects (Fig. 6). Lodgepole pine had higher mortality rates at mid-slopes than on upper slopes, particularly in crowded neighbourhoods (3.4 ± 1.0 times) and following wetter summers (2.6 ± 0.7 times). For spruce in open neighbourhoods, mortality on upper slopes was 1.9 ± 0.6 times that in valleys.

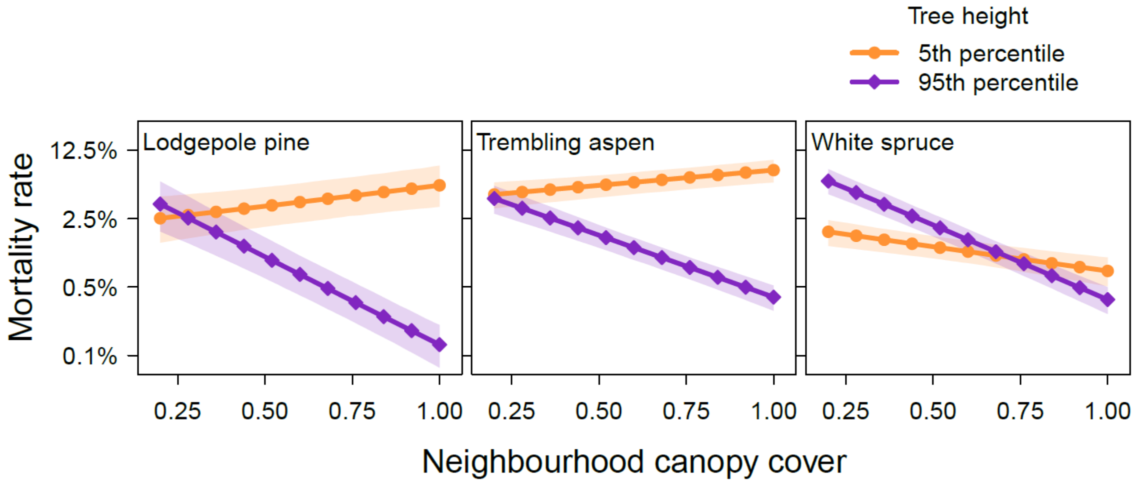

Fig. 5. Effect of neighbourhood canopy cover on the predicted mortality rate of each species, evaluated at the 5th and 95th percentiles of tree height and mean values for the previous year's Jun-Sep Climate Moisture Index and Topographic Position Index. Lines and shaded regions show the posterior mean and 90% credible interval for predicted mortality, respectively.

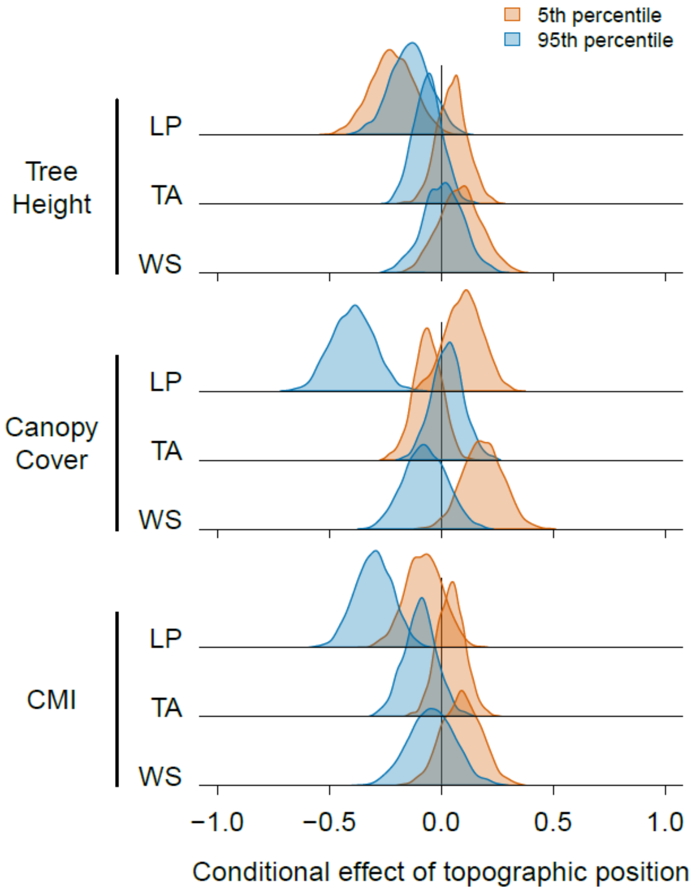

Fig. 6. Posterior distributions of conditional effects of Topographic Position Index on annual tree mortality, evaluated at the 5th and 95th percentiles of tree height, neighbourhood canopy cover, and the weighted Jun-Sep Climate Moisture Index (CMI) for each species (see Appendix S1: Table S1). LP: lodgepole pine; TA: trembling aspen; WS: white spruce.

Discussion

Climate change is expected to produce increasingly unfavourable conditions for populations at the warm and dry edges of their species' range. The rate and extent of population declines in these areas will depend on the local climate-sensitivity of demographic rates and how this is influenced by factors such as biotic interactions, individual size, and topographic exposure. We tested for these sources of variability in tree mortality responses to moisture deficits, which have become increasingly common in precipitation-limited regions of western North America and have had disproportionate impacts at species' range limits (van Mantgem et al. 2009, Anderegg et al. 2019, Liu et al. 2023). We found that annual variation in mortality of trembling aspen and white spruce, two drought-sensitive boreal species near the dry edge of their ranges, was closely related to moisture deficits in previous summers (Fig. 3). Sensitivity to moisture varied considerably among individuals, with tall individuals, those having low canopy cover within their local neighbourhood, and those situated on upper slopes exhibiting the greatest increases in mortality following high summer moisture deficits (Fig. 4).

The positive relationships we found between local canopy cover and aspen and spruce survival following high summer moisture deficits suggests that these species may be benefitting from facilitation. Trees that are surrounded by many neighbours experience greater microclimatic buffering during dry periods (Davis et al. 2019). By contrast, trees that are adjacent to gaps or forest edges encounter higher wind speeds and vapour pressure deficits, which increase water loss when evaporative demand is high. Lower mortality rates in more crowded neighbourhoods could also arise from fine-scale environmental variation or spatially contagious mortality processes; however, such mechanisms do not appear to explain why the positive effects of neighbours were limited to tall individuals, years following high summer moisture deficits, and the two drought-sensitive species. Neighbourhood-scale interactions have been shown to reduce tree mortality from drought and abiotic stress elsewhere (Fajardo and McIntire 2011, Hajek et al. 2022), and positive species interactions are also known to increase drought tolerance at the range limits of other plant species (Afkhami et al. 2014). The overall importance of such mechanisms does not seem to be widely appreciated, however. Although the specific mechanism is necessarily speculative with observational data, a facilitation effect is consistent with the stress gradient hypothesis and suggests that biotic interactions may alleviate the effects of climate-related environmental change for species near the dry edge of their range.

Individual size also had an important effect on climate-sensitivity, with tall aspen and spruce showing the strongest mortality responses to both moisture deficits and low canopy cover. Taller trees are more sensitive to moisture deficits because they require greater soil water potentials to transport water to their crowns and are thus more vulnerable to xylem embolism during drought conditions (Bennett et al. 2015). Taller individuals also tend to have the largest crowns, which increases water loss from transpiration. Because of their greater demands for water, tall trees seemed to benefit the most from the presence of neighbours, with their mortality rates decreasing sharply under greater neighbourhood canopy cover. This size-related variation in climate-sensitivity suggests that frequent summer moisture deficits will likely shift the population structure towards a patchier distribution of smaller-statured individuals over time, leading to reductions in standing biomass and changes in community composition that favour more drought-tolerant species.

Aspen and spruce also experienced a stronger response to summer moisture deficits on upper slopes than in other locations. Drought-related mortality has been found to vary topographically in montane regions as water is redistributed from upper-slopes to nearby valleys (Paz-Kagan et al. 2017). In support of this topographic influence on water availability, we found that spruce in open neighbourhoods exhibited higher mortality on upper slopes than elsewhere. Microclimatic buffering by neighbours may thus be particularly important in more exposed topographic positions, as predicted by the stress gradient hypothesis.

Lodgepole pine, whose range includes drier climates than our study area, did not show elevated mortality in years following high summer moisture deficits. The lack of an overall response for lodgepole pine is unsurprising, as it is one of the most wide-ranging tree species in western North America and is highly tolerant of drought in this part of its range (Montwé et al. 2016). However, we found that lodgepole pine trees at mid-slope positions had greater mortality than on upper slopes when they were surrounded by neighbours and in years that followed relatively wet summers (Fig. 6). Both of these interactions appear to reflect the influence of competition on this shade intolerant species: following dry summers, and in open neighbourhoods, lodgepole pine may have better survival at mid-slope positions (where trembling aspen is more common) because its drought-sensitive heterospecific competitors exert weaker effects upon it. Biotic interactions are thus important to understanding the effects of summer moisture deficits on all three species in our study area.

Over the coming decades, drought and other climate-change factors are expected to have worsening impacts on populations in marginal environments that are pushed beyond their niche limits. Within such populations, positive neighbourhood interactions can have an important role in buffering individuals from adverse environmental conditions. By alleviating increases in mortality, neighbourhood facilitation may contribute to the persistence of populations at the edge of their climatic niche.

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