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Higher tree diversity is linked to higher tree mortality

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Examining the relationship between tree diversity and ecosystem functioning has been a recent focus of forest ecology. Particular emphasis has been given to the impact of tree diversity on productivity and to its potential to mitigate negative global change effects; however, little attention has been paid to tree mortality. This is critical because both tree mortality and productivity underpin forest ecosystem dynamics and therefore forest carbon sequestration. Neglecting tree mortality leaves a large part of the picture undocumented. Here we show that increasingly diverse forest stands have increasingly high mortality probabilities. We found that the most species-rich stands in temperate biomes had mortality probabilities more than sevenfold higher than monospecific stands (∼0.6% year^{-1} in monospecific stands to 4.0% year^{-1} in the most species-rich stands) while in boreal stands increases were less pronounced but still significant (∼1.1% year^{-1} in monospecific stands to 1.8% year^{-1} in the most species-rich stands). Tree species richness was the third-most-important predictor of mortality in our models in temperate forests and the fifth-most-important predictor in boreal forests. Our results highlight that while the promotion of tree diversity undoubtedly has many positive effects on ecosystem functioning and the services that trees provide to humanity, it remains important to consider all aspects of forest dynamics in order to properly predict the implications of maintaining and promoting tree diversity.

diversity effects | biodiversity and ecosystem functioning | tree survival | competition | tree mortality

Tree mortality is a key ecosystem process in forests. It drives shifts in species compositions and stand densities (1–3) and plays an essential role in the coexistence of diverse communities (4). Tree mortality is natural and unavoidable, but it is being exacerbated by global environmental change, thereby leading to ecosystem collapses in some regions (5) and potentially pushing other systems past tipping points into novel states (2). Along with productivity (i.e., gain in live biomass of a stand each year), tree mortality also governs aboveground carbon storage and carbon inputs into soils in forest ecosystems. Neglecting to examine relationships between tree diversity and tree mortality may be one reason that while diversity–productivity relationships are largely documented to be positive in forest communities (6–8), support for a direct positive effect of tree diversity on live total aboveground biomass remains equivocal or muted in comparison to diversity–productivity relationships (9, 10). Given the recent interest in afforestation and reforestation as one method to offset fossil fuel emissions of CO_2 (11) and the increasing interest in the potential for the promotion of tree diversity in improving forest productivity (12, 13), we require better knowledge of the relationship between tree diversity and tree mortality. Without it, we risk a flawed understanding of how tree diversity affects overall forest carbon sequestration and how its promotion and maintenance may act as a potential avenue for mitigating global environmental change.

The reasons that trees die are varied, and the relative importance of drivers depends on the context of local competitive neighborhoods and site potential (14, 15). Following stand establishment, competition for shared limiting resources is a major driver of tree mortality in forests recovering from disturbance (15, 16) later being replaced by biotic and abiotic agents (14). This competition for limiting resources is typically asymmetrical, with the largest trees acquiring the most resources (17). Because of this competition, the relative size of an individual tree compared to the average within a stand is an important predictor of tree mortality (15). In diverse stands, the magnitude of competition-based mortality may be reduced because intraspecific competition is generally assumed to be stronger than interspecific competition because individuals of the same species occupy the same niche (18). As species diversity within a stand increases, however, the likelihood of two individuals being of the same species or competing for the same niche space decreases to a minimum before increasing again with even higher levels of diversity. For example, having contrasting levels of shade tolerance (8, 19) and crown structures (20) is important in driving diversity–productivity relationships. In turn, higher diversity can

Significance

Despite a significant amount of recent research describing how tree species diversity improves forest productivity, few studies examine how tree diversity affects tree mortality, which is a key ecosystem function that drives succession, composition, and competition. Using a plot network from across Canada and the United States, here we show that plots with higher tree diversity also experience higher tree mortality. This effect becomes even more prominent when tree diversity effects are modeled holistically; in particular, more-diverse plots have higher stem densities, translating into higher mortality probabilities. We call for the use of integrated model frameworks when examining the response of forest ecosystem functions to diversity, thus ensuring proper accounting of direct and indirect effects.

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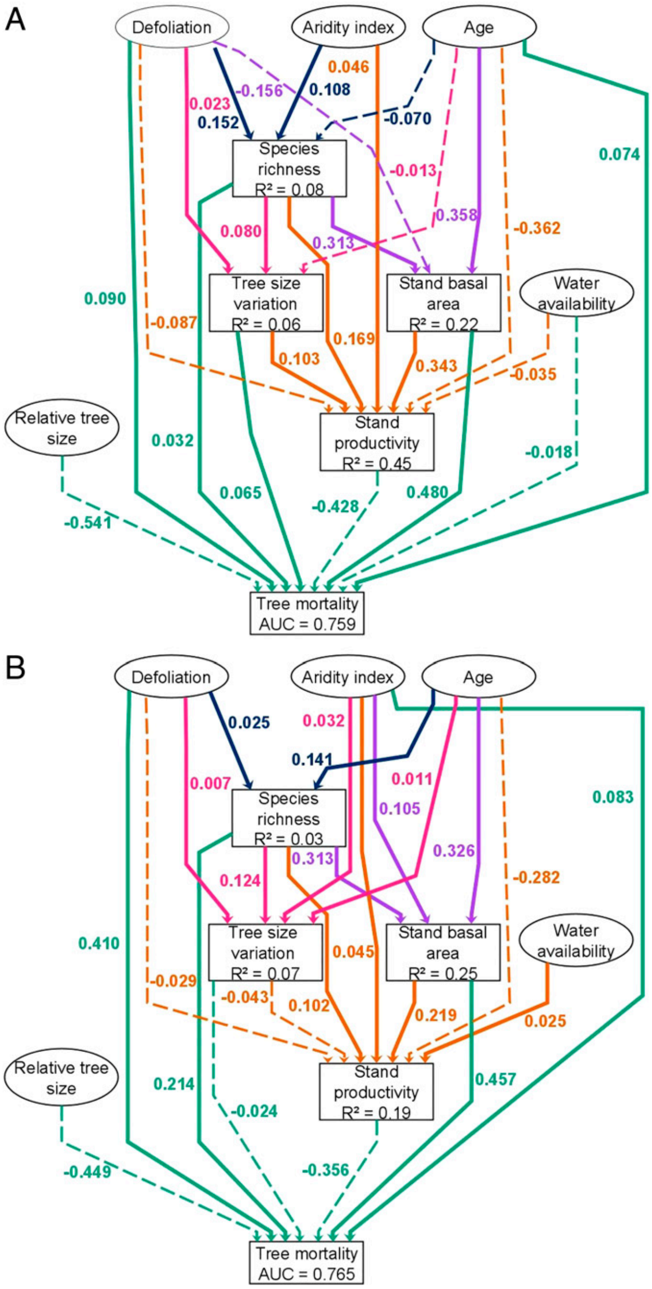

Fig. 1. Structural model of the relationship between species richness and individual tree mortality in (*A*) boreal and (*B*) temperate forest plots. Colors represent each submodel, solid lines represent positive relationships, and dashed lines represent negative relationships. Numbers beside the pathways indicate the effect size of the relationship. All coefficients are standardized and are thus directly comparable. Only significant pathways are presented. The coefficient of variation (R^2) is calculated including only the pathways shown (i.e., the random effects are omitted). Coefficient estimates and their associated confidence limits, as well as the R^2 when including the random effects, are presented in *SI Appendix*, Table S5. AUC, area under the curve.

promote higher stand densities (21), which necessarily means increased pressure on site resources and therefore higher average tree mortality (15). In stands where all growing space is utilized and productivities are high, this higher density can lead to more intense competition and thus higher tree mortality. Whether higher tree species diversity can reduce tree mortality by reducing intraspecific competition or whether higher competitive pressures from higher productivities in more-diverse stands lead to an overall increase in tree mortality remains uncertain.

Climate and site conditions can also affect relationships between biodiversity and ecosystem functions such as productivity (6, 22). In harsher environments, competition between neighboring individuals is thought to be weaker than facilitation (23), leading to more positive biodiversity–ecosystem functioning relationships (6, 22) and potentially lower mortality. However, in more-favorable environments, tree diversity may cause an increase in competitive intensities through an increase in productivity, leading to higher tree mortality. As with many ecosystem functions in forests, tree mortality is strongly controlled by stand developmental stage (15). Recent studies have suggested that structural complexity (i.e., stands with a high variation in individual stem and canopy size) drives positive diversity–productivity relationships in natural forests (24). Higher structural complexity may also reduce individual mortality probabilities because vertical stratification among trees reduces direct competition with other factors being equal. Finally, biotic agents are a leading cause of catastrophic losses in individual trees and forest dieback (14, 25). Many biotic agents, including bark beetles, defoliators, and fungi, are species-specific and thus may alter tree species diversity by causing mortality in only one species within a stand. Controlling for these important drivers of tree mortality and their possible downstream effects on mortality through their effects on tree species diversity is essential to understanding the overall mechanisms driving any diversity–mortality relationships.

Here we sought to examine the relationship between tree diversity and tree mortality in forest communities. To account for both the direct effect of tree diversity on individual tree mortality and the indirect effect of tree diversity on tree mortality through tree diversity's effects on other mediating variables (e.g., higher diversity may increase stand densities, which in turn lead to higher mortality probabilities), we used piecewise structural equation models. These models have the advantage of allowing us to test diversity effects in a more holistic way while also modeling tree diversity effects at the level of organization at which they operate: density, size variation, and productivity at the stand level and their effects on mortality probabilities at the stem level. We examined individual-level tree mortality data from 29,172 plots of forest inventory data representing more than 1.6 million individual trees from across Canada and the United States. Of these plots, 3,426 were considered boreal and 25,746 were considered temperate using the World Wildlife Fund biome classification (26). Plots were taken from governmental and industrial permanent sample plot networks, measured between 1956 and 2019, and had to have a minimum of 3 censuses of the same location with reliable repeated measurements of all individual trees within the plot through time. A more detailed description of the plot characteristics is presented in *Materials and Methods*.

Results

Overall, we found good agreement between our models and data (Fig. 1). Tree species richness (i.e., the number of unique species in a plot) was directly positively associated with tree mortality probability in both biomes (Fig. 2). However, the magnitude of association was smaller in boreal biomes than in temperate biomes (Fig. 1). Tree species richness was related to higher mortality probability in both biomes when both direct and indirect effects were considered (Fig. 2). Indirect effects were the effects of tree species richness on mortality probabilities mediated by tree species richness on tree-size variation, stand basal area, and productivity. In temperate forests, there was a more than sevenfold increase in mortality probabilities

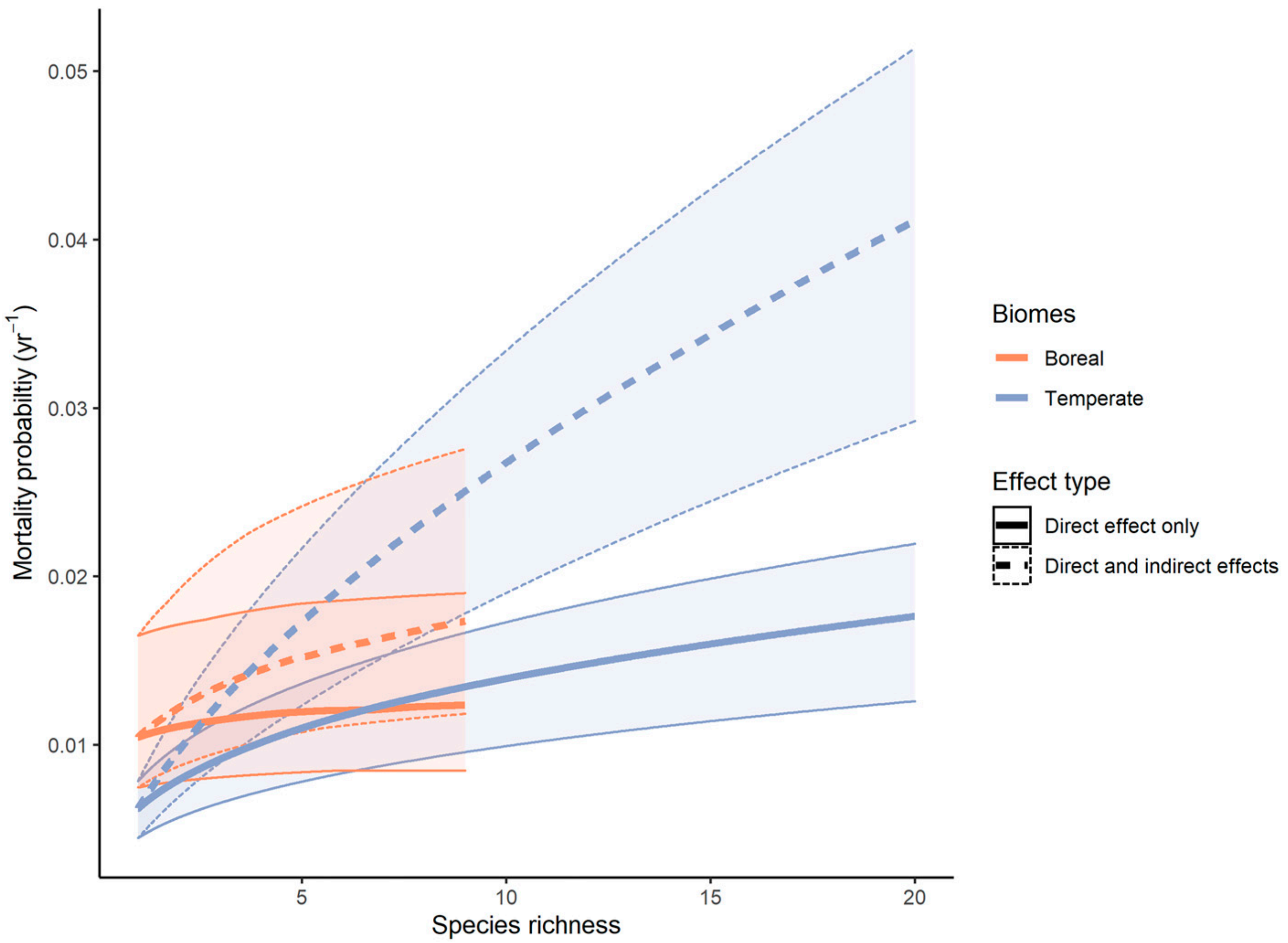

Fig. 2. Response of annualized tree mortality to tree diversity. Lines represent estimates of annual tree mortality probability from piecewise structural equation models, fitted by biome, while holding all other predictors at their mean. Solid lines represent the direct effect of tree species richness and dotted lines represent the combination of direct and indirect effects of tree species richness on tree mortality probability. Bands represent 95% confidence interval estimated through bootstrapping.

between monospecific plots and the most species-rich plots, from 0.6% y^{-1} to 4.0% y^{-1}, while in boreal forests the increase was less pronounced: from 1.1% y^{-1} in monospecific plots to 1.8% y^{-1} in the most species-rich plots (Fig. 2). Tree species richness was the third-most-important predictor when considering both direct and indirect effects in temperate forests and the fifth most important in boreal forests (Fig. 3). Notably, the direct effect of tree species richness on tree mortality probability was relatively less important (only the fourth-most-important predictor in temperate forests and the seventh-most-important in boreal forests). The response of tree mortality to tree diversity was consistent when using abundance-weighted diversity indices, when adjusting these indices for differences between plots in stem densities and plot area, and when scaling diversity within biomes and ecoregions (see *Materials and Methods*). The response was also consistent when we replaced the stand basal area with the stand-density index (SDI; see *Materials and Methods*), which is a more common measure of stand-level competition (21). This finding provides further evidence that the indirect effect of tree diversity on tree mortality through stand basal area is likely due to higher productivities causing higher competitive intensity for access to site resources (e.g., light, nutrients, or water).

Relative tree size was the most important predictor of tree mortality in both boreal and temperate forests when considering direct and indirect effects (Fig. 3). Stand age had a significant but weak direct relationship with tree mortality in boreal forests and no detectable relationship with tree mortality in temperate forests (Figs. 1 and 3). However, the indirect effect of stand aging was highly important in both biomes (Fig. 3). When considering only direct effects, stand basal area was the most (temperate) or second-most (boreal)-important predictor; however, it was the fourth-most-important predictor when including indirect effects for both biomes. Stand productivity was the third-most-important predictor of tree mortality in both biomes, respectively; when plots had higher productivity, they experienced less mortality on average, even after controlling for effects of age, density, and diversity (Figs. 1 and 3). Across both biomes, the expected positive diversity–productivity relationship was present, which led to an indirect negative effect of tree diversity on tree mortality. Both defoliation due to biotic agents and reduced water availability increased tree mortality probability in boreal biomes, while only defoliation was significant in temperate biomes (Fig. 1), although these factors were relatively unimportant compared to other predictors (Fig. 3). Finally, increasing tree-size variation was associated with higher mortality probabilities in boreal forests and lower mortality probabilities in temperate forests, on average; however, these effects were unimportant compared to other predictors (Figs. 1 and 3).

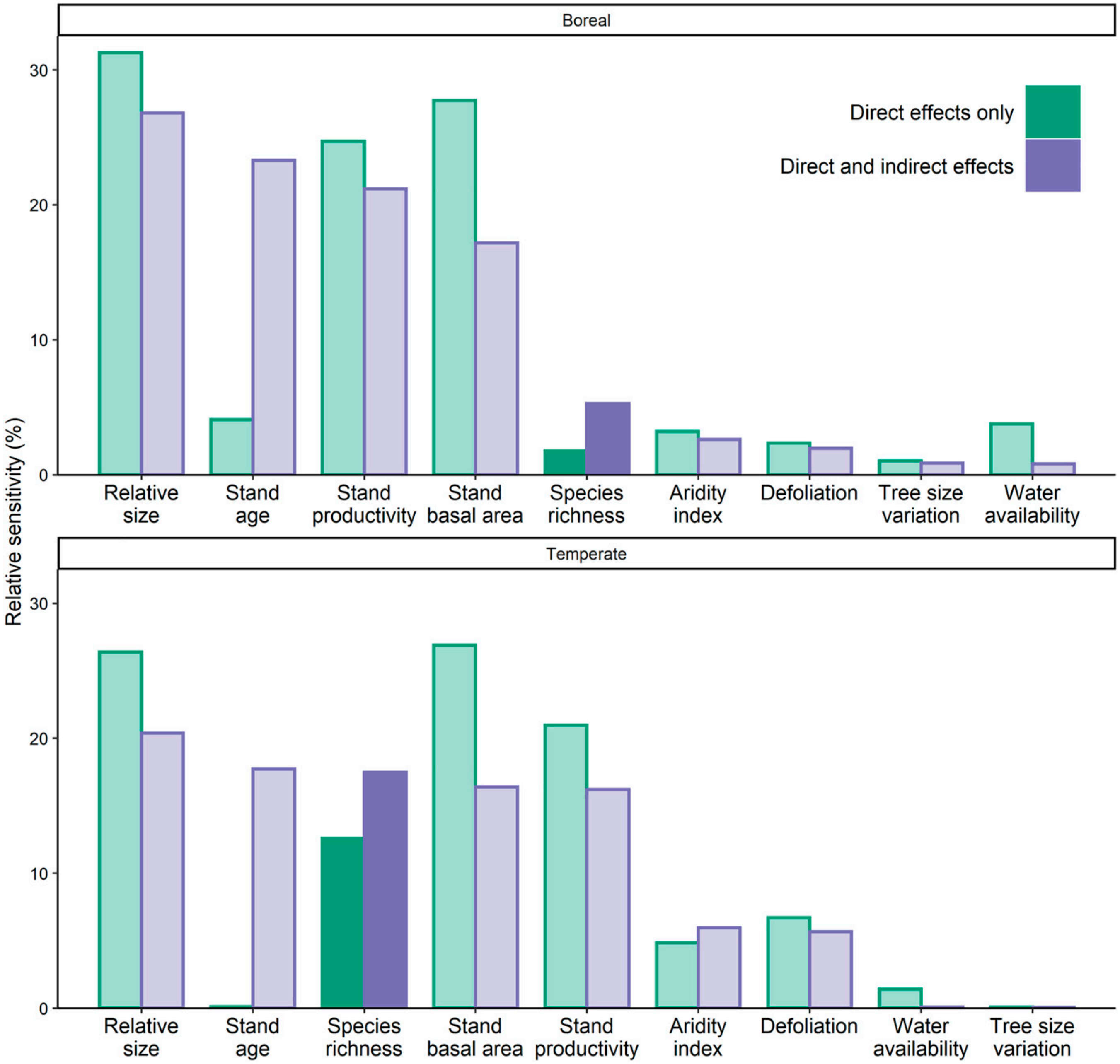

Fig. 3. Relative sensitivity of annualized tree mortality to all predictors by biome. Relative sensitivity was estimated as the ratio of the SD of mortality estimated by each predictor across its range to the sum of the effects of all predictors. Bars represent the relative sensitivity of each predictor and are ordered in decreasing sensitivity of tree mortality to direct plus indirect effects of each predictor. The effect of species richness is highlighted for ease of interpretation with all other predictors represented with opaque bars.

Discussion

We found that across a large permanent sample plot network, diverse stands had higher tree mortality probabilities than less-diverse stands through both direct and indirect pathways. The difference in the magnitude of response of tree mortality to the direct effect of species richness in temperate versus boreal biomes provides further evidence that stands with higher tree diversity in more-favorable climates might experience more-competitive dominance by a few species (6) and therefore experience higher tree mortality probabilities as less-competitive individuals die off after establishment. It is important to note that our tree mortality probabilities are calculated at the stem level, allowing us to account for species-specific mortality probabilities. This means that the underlying mechanism driving the diversity effect is not due to selection effects, when more-diverse stands have the potential to contain species with higher mortality probabilities than less-diverse stands, but instead from complementary effects arising from the modification of individual interactions in more-diverse stands. Further, we removed all plots from our analysis that had any evidence of management activities, or silvicultural interventions, meaning that the direct relationship between tree diversity and tree mortality is not likely to be related to stand improvement undertaken by forest managers.

The increased magnitude and importance of the relationship between tree diversity and tree mortality when considering direct and indirect effects combined emphasize the need to approach biodiversity–mortality relationships from a more holistic view: Higher tree diversity results in an increase in stand density and tree-size variation, which are in turn important drivers of tree mortality probabilities. Indeed, the effect of competition on tree mortality probabilities was the strongest effect observed in our analysis: As the relative size of an individual within a stand increased, its mortality probability decreased, which is consistent with asymmetric competition dependent on tree size being a major driver of tree mortality (15, 17). Further, while stand age did not have a direct effect on tree mortality probabilities, it still played an important role as an indirect predictor mediated by stand conditions that change with stand development (e.g., an increase in stand basal area). Approaching the biodiversity–mortality relationships holistically is particularly relevant to boreal forests, where the indirect effect of richness was the strongest relationship between tree richness and tree mortality. In this biome, stands with higher tree diversity had higher stand basal areas and tree-size variation, which amplified tree mortality probabilities (Fig. 1), indicating that tree species richness effects on one aspect of ecosystem functioning can have important downstream consequences.

Similar to many previous studies, we found a positive relationship between diversity and productivity (6–8). In turn, during measurement periods when plots had higher productivity, they experienced lower mortality probabilities, which may reflect niche complementarity between species and reduce the potential for intraspecific competition-driven mortality on more-diverse sites. However, this link is unlikely to be completely causal: High tree growth rates are often correlated with low mortality probabilities over short time periods (27) because trees often experience a decline in growth prior to senescence. Therefore, this decline in mortality with increasing productivity is likely confounded by favorable climate and stand conditions during the census interval. Further, it is important to note that higher productivities over a stand life cycle will necessarily mean higher stand basal areas, which lead to increased pressure on site resources and competition and therefore higher mortality probabilities. Faster-growing trees tend to have shorter longevities (28), and higher average site productivity is correlated to higher stand mortality rates (29) over full stand life cycles. This tendency leads to an interesting pathway wherein tree species diversity may reduce tree mortality over the short term by boosting productivity but increase tree mortality over the long term by increasing stand basal areas above site carrying capacities. It may be that the association between mortality and productivity in stands is reversed: Higher mortality in more-diverse stands may ease pressure on site resources and lead to higher growth for remaining trees that outstrips the basal area lost due to mortality. Further research using both controlled and natural systems into how tree richness improves both short-term stand productivities and long-term stand basal area, while accounting for the increase in competition this implies, is necessary to understand the tradeoffs in this system.

Whether the response of tree mortality to tree diversity will remain static in the face of climate change is unclear. While there is increasing interest in the promotion of tree diversity to offset the negative effects of climate change on stand productivity (12, 13), studies examining this issue are rare (30). If mechanisms for increased tree mortality due to increased tree diversity are related primarily to increases in stand packing and competitive exclusion, then the promotion of tree diversity to maintain or increase productivities may exacerbate these responses. Considering this potential for exacerbated negative effects may be especially important in areas such as the boreal forest, where global environmental change is enhancing productivity but also increasing mortality at even faster rates (31). However, in the case where tree diversity is being promoted or maintained to offset catastrophic events (e.g., pest outbreaks) (32), the benefits of reduced negative effects from these events may outweigh the drawbacks of increasing tree diversity. To properly investigate this possibility, research utilizing an integrated modeling framework targeting stands of varying diversity in regions affected by these drivers is required. Considering these systems holistically and modeling the responses of both productivity and mortality may better reconcile conflicting findings.

Our results emphasize that biodiversity–ecosystem functioning relationships are dependent on many pathways. Fully incorporating these pathways into modeling frameworks is essential to understand the full effect of maintaining or promoting biodiversity on ecosystem functioning and attendant services in forest ecosystems. When modeled holistically, we show that increasing tree diversity will increase tree mortality in temperate and boreal forests. However, this rise in mortality does not cancel the positive effects of tree diversity on short-term productivity or on stand basal area. Indeed, the higher mortality in diverse stands may help drive increases in complementarity through shifts in species abundances. Whether or not the increase in mortality in diverse stands is a driver of diversity–productivity relationships, our results suggest that promoting and maintaining species diversity is still a net positive when management goals are to improve densities and productivities on average.

Materials and Methods

Tree Mortality Data. We compiled data from Canadian provincial governments and the US Forest Inventory and Analysis database. We removed all plots that had any evidence of human intervention (i.e., plots with stumps or trees marked as harvested) to ensure that all recorded mortality was, to the best of our knowledge, natural. Trees were recorded as dead if they either 1) were recorded as dead in the field, or (2) disappeared from subsequent plot remeasurements. Because estimating mortality probabilities is an observation-hungry process (33), we included all plots with at least 3 measurements (i.e., 2 observations of mortality). We considered remeasurements reliable for plots where all trees were tagged and their diameter at breast height and species identity were recorded (*SI Appendix*, Table S1). The first measurement was omitted in all inventories because dead stems were not counted at plot establishment. Our dataset contained 1,655,522 stems contained in 29,172 plots, with a census return interval ranging from 1 to 38 y (mean, 7.4 y; SD, 3.6) and 3 to 9 measurements (mean, 4.4; SD, 1.5). The dataset covered a substantial portion of both countries (*SI Appendix*, Fig. S1) although it was centered on eastern forests, which had more remeasurements and information on stand age.

Explanatory Variables. We determined species diversity of the measured stands through species richness, or the sum of the unique number of species present in a plot. Because different forest surveys used different plot sizes, we derived two forms of corrected species richness: one corrected for by plot area (i.e., richness at the mean plot size) and a second version calculated at the mean stem number (30). Because the main effects of richness were statistically comparable and only the effect of richness on basal area per hectare was altered by these adjustments (*SI Appendix*, Fig. S2), we present models using unadjusted richness in the main text. We also examined whether using abundance-weighted diversity indices affected our estimates of the relationship between tree diversity and tree mortality (*SI Appendix*, Fig. S3). Finally, we also examined relative species richness, or the proportion of observed plot richness to the maximum plot richness observed within ecoregions, in an effort to disentangle the effects of diversity from larger-scale biotic and environmental gradients (7) (*SI Appendix*, Fig. S4). Because estimates of the relationship between tree diversity and tree mortality were consistent regardless of adjustment or diversity index chosen, we present unadjusted species richness in the main text.

We used plot spatial locations to derive plot biome, climate, and defoliation information. Biomes were extracted from shapefiles provided by The Nature

Conservancy (34), based on World Wildlife Fund estimates (26), and were then consolidated into two primary groups: temperate and boreal. Plots in tropical biomes were removed from the analysis. We extracted mean annual temperatures and mean annual precipitation from the WorldClim dataset (35) and the aridity index and potential evapotranspiration from CGIAR Consortium for Spatial Information (https://cgiarcsi.community/) (36, 37). Finally, we extracted the standardized precipitation-evapotranspiration index (SPEI) from a global gridded climatology from (https://spei.csic.es/index.html). SPEI is a locally standardized index that estimates water availability through time and has shown an excellent ability to predict drought (38). We included the minimum SPEI experienced by a tree during a census interval as our measure of water availability to reflect short-term drought events. Defoliation events (classified as moderate to severe, or 25% or more defoliation or mortality) were derived from provincial and state aerial surveys and remote sensing platforms. In Canada, data were acquired through the Canadian Forest Service and provincial governments. Defoliation data for the United States were acquired from the US Department of Agriculture Forest Service Detection Surveys program (39). Defoliation events were extracted when only tree species contained within our plots experienced a defoliation event (e.g., outbreaks attributed to *Choristoneura fumiferana* were not noted in *Populus tremuloides* monocultures but were noted in *Picea spp.* and *Abies balsamea* monocultures). Plots that experienced a defoliation event were assigned a value of 1, and those that did not were assigned a value of 0. For mortality models, only stems of the species that was affected by the event were assigned a value of 1.

We used stand age as our measure of stand developmental stage. Methodologies for determining stand age differed by jurisdiction but were typically determined through time since the last known wildfire or the coring of dominant stems just outside of the sample plots. In the case of plots that had their age determined through coring, we averaged the age for each species cored and assigned the plot the oldest species-specific age. We used stand basal area as our measure of competition intensity. We derived the stand basal area for each measurement of each plot by summing the basal area of all live stems and dividing by the plot area in hectares. We also evaluated how a more traditional stand-level competition index, the SDI, affected model outcomes (*SI Appendix*, Fig. S5). Because outcomes were consistent with stand basal area, we present models using stand basal area in the main text. We used the coefficient of variation (SD divided by mean) of the individual basal area within each plot to estimate tree-size variation as our measure of structural complexity. Individual relative tree size was the logarithm of the relative basal area of the individual to the average basal area within a stand at the start of a census period.

The annual productivity of the stand was estimated as the amount of basal area added by the growth of surviving trees plus recruited trees divided by the length of the census interval. Because census intervals varied greatly between and within data providers and plots, we used the productivity of the stand during the census period that mortality was recorded in as a predictor. Distributions of explanatory variables are provided in *SI Appendix*, Fig. S6.

Statistical Analysis. In order to examine the relationship between tree diversity and individual tree mortality probability, we used piecewise structural equation models, which allowed us to account for the repeated-measures nature of our designs through mixed-effects modeling. Pathways presented in *SI Appendix*, Fig. S7 indicated fixed effects in the model, while each submodel included a unique plot identification and the source of the forest inventory to account for nonindependence in the measurements and differences in the survey methodologies, respectively. The full model, as represented in *SI Appendix*, Fig. S7, was tested and then nonsignificant pathways ($\alpha = 0.05$) were removed from the analysis. The models were then refit including only significant pathways (40).

As shown in Fig. 1 and *SI Appendix*, Fig. S7, we used five mixed-effects submodels to present a more holistic view of tree mortality. All models were fit separately for each biome. The first four submodels were fit at the plot level (n= 70,687 observations in the temperate biome and 10,874 in the boreal biome) with Gaussian distributions and identity links. The first submodel estimated stand-level tree species diversity from stand age, climate, and defoliation occurrence as fixed effects and data provider as a random effect. Species richness was transformed by a natural logarithm prior to model fitting. The second submodel estimated stand-level tree size variation (i.e., structural complexity) from stand age, climate, defoliation occurrence, and tree species diversity as fixed effects and plot identity and data provider as random effects. The third submodel estimated logarithmic stand basal area (i.e., density-related competition) from stand age, climate, defoliation occurrence, tree species diversity, and tree-size variation as fixed effects and plot identity and data provider as random effects. The fourth submodel estimated logarithmic annual stand productivity from stand age, climate, defoliation occurrence, water availability, tree species diversity, tree-size variation, and stand basal area as fixed effects and plot identity and data provider as random effects. The fifth and final submodel was fit at the individual stem level to mortality occurrence information (i.e., 0 = live, 1 = dead) and estimated tree mortality probability from stand age, climate, defoliation occurrence, water availability, tree species diversity, tree-size variation, stand basal area, stand productivity, and the logarithm of the relative size of the individual stem as the fixed effects and species identity, plot identity, and data provider as random effects. The fifth submodel, unlike the previous four, was fit using a generalized linear mixed-effects model with a binomial distribution and a logit link function. The logit link function was modified to annualize tree mortality probability to account for differences in census lengths (i.e., some plots revisited every 5 y, some revisited every 10 y, some revisited at random intervals) following Luo and Chen 2013 (41) and Monserud (42):

$$p_{ijk} = 1 - (1 - p_{ijk,\,t=1})^{\Delta t}, \tag*{[1]}$$

where p_{ijk} is the mortality probability of an individual stem for the ith tree during the jth census period in the kth plot, Δt is the length of the census period in years, and $p_{ijk,\ t\,=\,1}$ is the annual mortality probability of the ith tree of the jth census period in the kth plot. The logistic regression model used to estimate mortality probability was applied to $p_{ijk,\ t\,=\,1}$ (i.e., annualized mortality). Equations used to develop the models are available in the *SI Appendix*. There was no evidence of spatial autocorrelation among the residuals of the models (*SI Appendix*, Table S2).

We then examined which predictor had the most influence on mortality by comparing estimates of standardized coefficients (i.e., coefficient estimates scaled by the SD of the predictor). This approach is context-dependent insofar as it depends on the range of our observed predictor values. However, it also allowed us to directly examine the relative importance of each predictor within our study and in the context of the permanent sample plot networks that were used. Because our plots represent a wide range of forest conditions and climates, this approach yielded a better representation of the real-world impact of our models that cannot be described by nonstandardized coefficients alone. We also used this approach to estimate the overall importance of each predictor on mortality by examining standardized direct plus indirect effects. All analysis was done in R statistical software, version 4.0.4. Piecewise structural equation models were estimated through the *piecewiseSEM* package (40). Because we had various levels of organization in our data, tests of directed separation were performed manually using the *basisSet* and *dSep* functions in the *piecewiseSEM* package. Model R^2 was estimated using the *rsquared* function in the *piecewiseSEM* package, while the area under the curve was estimated using the *pROC* package. Models were bootstrapped separately 100 times to estimate direct and indirect confidence bands using the *bootMer* function from the *lme4* package (43). Of these iterations, 19 boreal and 26 temperate mortality models failed to converge and were omitted from the confidence interval estimates.

Assessing the Effect of Diversity Indices. To assess whether our choice of diversity indices affected the outcome of our models, we replaced species richness with higher-order Hill numbers in our structural equation models. As the order of Hill numbers increases, more importance is given to species evenness (i.e., equality in species relative abundances in a plot) than to species richness, with the Hill number of order zero equivalent to species richness (44). Overall, the models using higher-order Hill numbers were a good fit to the data, although some were not (*SI Appendix*, Tables S3 and S4). Similar to species richness, higher-order Hill numbers were log-transformed prior to model fitting. Outcomes from models using Hill numbers of order 1 (i.e., the exponent of Shannon's Index or effective species richness) and Hill numbers of order 2 were similar in directionality and magnitude to species richness for all submodels (*SI Appendix*, Fig. S4). Adjusting for differences in plot sizes and stem number had little effect on the directionality of estimates, although stem-adjusted diversity indices had a weaker positive effect on stand basal area than unadjusted or plot area–adjusted diversity indices (*SI Appendix*, Fig. S4).

Given the large variation in tree diversity within biomes and ecoregions, we also examined whether scaling our species richness values within biomes or within ecoregions affected our model estimates. Because we found a consistent response in directionality and a generally consistent response in magnitude (*SI Appendix*, Fig. S5), we report the unadjusted species richness values in the main text.

Assessing the Effect of Competition Indices. While stand basal area is a proxy for stand-level competition, we also examined whether our results were robust to the use of the SDI, which was developed to explicitly measure stand-level competition. Similar to examining the use of different diversity indices, we examined how our models changed when using the SDI in place of stand basal area. Prior to model fitting, the SDI was log-transformed and the models produced similar results to those obtained using basal area (*SI Appendix*, Fig. S6). Because stand basal area can be directly managed for and is a more easily understood and measured predictor, we present stand basal area in the main text.

Data Availability. Anonymized data (all data and codes required to reproduce the findings) have been deposited in Figshare (DOI: 10.6084/m9.figshare.12559001) (45).

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1. P. Ruiz-Benito *et al.*, Climate- and successional-related changes in functional composition of European forests are strongly driven by tree mortality. *Glob. Change Biol.* **23**, 4162–4176 (2017).
2. A. S. Jump *et al.*, Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Glob. Change Biol.* **23**, 3742–3757 (2017).
3. R. Muscarella *et al.*, Demographic drivers of functional composition dynamics. *Ecology* **98**, 2743–2750 (2017).
4. A. J. Larson *et al.*, Spatial aspects of tree mortality strongly differ between young and old-growth forests. *Ecology* **96**, 2855–2861 (2015).
5. C. D. Allen, D. D. Breshears, N. G. McDowell, On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**, 1–55 (2015).
6. A. Paquette, C. Messier, The effect of biodiversity on tree productivity: From temperate to boreal forests. *Glob. Ecol. Biogeogr.* **20**, 170–180 (2011).
7. J. Liang *et al.*, Positive biodiversity-productivity relationship predominant in global forests. *Science* **354**, aaf8957 (2016).
8. Y. Zhang, H. Y. H. Chen, P. B. Reich, Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. *J. Ecol.* **100**, 742–749 (2012).
9. F. van der Plas, Biodiversity and ecosystem functioning in naturally assembled communities. *Biol. Rev. Camb. Philos. Soc.* **94**, 1220–1245 (2019).
10. E. C. Adair, D. U. Hooper, A. Paquette, B. A. Hungate, Ecosystem context illuminates conflicting roles of plant diversity in carbon storage. *Ecol. Lett.* **21**, 1604–1619 (2018).
11. J.-F. Bastin *et al.*, The global tree restoration potential. *Science* **365**, 76–79 (2019).
12. C. Ammer, Diversity and forest productivity in a changing climate. *New Phytol.* **221**, 50–66 (2019).
13. M. Hisano, E. B. Searle, H. Y. H. Chen, Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biol. Rev. Camb. Philos. Soc.* **93**, 439–456 (2018).
14. A. J. Das, N. L. Stephenson, K. P. Davis, Why do trees die? Characterizing the drivers of background tree mortality. *Ecology* **97**, 2616–2627 (2016).
15. Y. Luo, H. Y. H. Chen, Competition, species interaction and ageing control tree mortality in boreal forests. *J. Ecol.* **99**, 1470–1480 (2011).
16. Y. Luo, H. Y. H. Chen, Climate change-associated tree mortality increases without decreasing water availability. *Ecol. Lett.* **18**, 1207–1215 (2015).
17. N. DeMalach, E. Zaady, J. Weiner, R. Kadmon, Size asymmetry of resource competition and the structure of plant communities. *J. Ecol.* **104**, 899–910 (2016).
18. J. S. Clark, Individuals and the variation needed for high species diversity in forest trees. *Science* **327**, 1129–1132 (2010).
19. E. B. Searle, H. Y. H. Chen, Complementarity effects are strengthened by competition intensity and global environmental change in the central boreal forests of Canada. *Ecol. Lett.* **23**, 79–87 (2020).
20. L. J. Williams, A. Paquette, J. Cavender-Bares, C. Messier, P. B. Reich, Spatial complementarity in tree crowns explains overyielding in species mixtures. *Nat. Ecol. Evol.* **1**, 63 (2017).
21. H. Pretzsch, P. Biber, Tree species mixing can increase maximum stand density. *Can. J. For. Res.* **46**, 1179–1193 (2016).
22. S. Fei *et al.*, Impacts of climate on the biodiversity-productivity relationship in natural forests. *Nat. Commun.* **9**, 5436 (2018).
23. Q. He, M. D. Bertness, A. H. Altieri, Global shifts towards positive species interactions with increasing environmental stress. *Ecol. Lett.* **16**, 695–706 (2013).
24. C. M. Gough, J. W. Atkins, R. T. Fahey, B. S. Hardiman, High rates of primary production in structurally complex forests. *Ecology* **100**, e02864 (2019).
25. W. A. Kurz *et al.*, Mountain pine beetle and forest carbon feedback to climate change. *Nature* **452**, 987–990 (2008).
26. D. M. Olson *et al.*, Terrestrial ecoregions of the world: A new map of life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* **51**, 933–938 (2001).
27. M. Cailleret *et al.*, A synthesis of radial growth patterns preceding tree mortality. *Glob. Change Biol.* **23**, 1675–1690 (2017).
28. E. B. Searle, H. Y. Chen, Temporal declines in tree longevity associated with faster lifetime growth rates in boreal forests. *Environ. Res. Lett.* **13**, 125003 (2018).
29. N. L. Stephenson *et al.*, Causes and implications of the correlation between forest productivity and tree mortality rates. *Ecol. Monogr.* **81**, 527–555 (2011).
30. M. Hisano, H. Y. H. Chen, E. B. Searle, P. B. Reich, Species-rich boreal forests grew more and suffered less mortality than species-poor forests under the environmental change of the past half-century. *Ecol. Lett.* **22**, 999–1008 (2019).
31. H. Y. H. Chen, Y. Luo, P. B. Reich, E. B. Searle, S. R. Biswas, Climate change-associated trends in net biomass change are age dependent in western boreal forests of Canada. *Ecol. Lett.* **19**, 1150–1158 (2016).
32. S. E. Haas *et al.*, Effects of individual, community, and landscape drivers on the dynamics of a wildland forest epidemic. *Ecology* **97**, 649–660 (2016).
33. S. M. McMahon, G. Arellano, S. J. Davies, The importance and challenges of detecting changes in forest mortality rates. *Ecosphere* **10**, e02615 (2019).
34. The Nature Conservancy, Data from "The Nature Conservancy terrestrial ecosystems." Data Basin. https://databasin.org/datasets/9c7bc177c6154d71b0458391f3177053/. Accessed 24 September 2019.
35. S. E. Fick, R. J. Hijmans, WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
36. R. J. Zomer, A. Trabucco, D. A. Bossio, L. V. Verchot, Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agric. Ecosyst. Environ.* **126**, 67–80 (2008).
37. R. J. Zomer *et al.*, *Trees and Water: Smallholder Agroforestry on Irrigated Lands in Northern India* (IWMI, 2007).
38. S. M. Vicente-Serrano, S. Beguería, J. I. López-Moreno, A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *J. Clim.* **23**, 1696–1718 (2010).
39. US Forest Service, Mapping & reporting: Detection surveys. https://www.fs.fed.us/foresthealth/applied-sciences/mapping-reporting/detection-surveys.shtml. Accessed 11 December 2019.
40. J. S. Lefcheck, piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).
41. Y. Luo, H. Y. Chen, Observations from old forests underestimate climate change effects on tree mortality. *Nat. Commun.* **4**, 1655 (2013).
42. R. A. Monserud, Simulation of forest tree mortality. *For. Sci.* **22**, 438–444 (1976).
43. D. Bates, M. Machler, B. M. Bolker, S. C. Walker, Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
44. A. Chao, C.-H. Chiu, L. Jost, Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annu. Rev. Ecol. Evol. Syst.* **45**, 297–324 (2014).
45. E. Searle, Higher tree diversity is linked to higher mortality. Figshare. 10.6084/m9.figshare.12559001.v1. Deposited 27 March 2022.