

INTERACTIVE EFFECTS OF TREE SIZE, CROWN EXPOSURE, AND LOGGING ON DROUGHT-INDUCED MORTALITY

Alexander Shenkin^{1,2}, Benjamin Bolker³, Marielos Peña-Claros⁴, Juan Carlos Licona⁵, Nataly Ascarrunz⁵,
Francis E. Putz¹

¹Department of Biology, University of Florida, Gainesville, FL 32611, USA

²Environmental Change Institute, University of Oxford, South Parks Road, Oxford OX1 3QY, UK

³Departments of Mathematics & Statistics and Biology, McMaster University, Hamilton, ON 8S 4K1,
Canada

⁴Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700 AA
Wageningen, The Netherlands

⁵Instituto Boliviano de Investigacion Forestal (IBIF), Casilla 6204, Santa Cruz, Bolivia

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ABSTRACT

Large trees in the tropics are reportedly more vulnerable to droughts than their smaller neighbors. This pattern is of interest due to what it portends for forest structure, timber production, carbon sequestration, and multiple other values given that intensified El Niño Southern Oscillation (ENSO) events are expected to increase the frequency and intensity of droughts in the Amazon region. What remains unclear is what characteristics of large trees

renders them especially vulnerable to drought-induced mortality and how this vulnerability changes with forest degradation. Using a large-scale, long-term silvicultural experiment in a transitional Amazonian forest in Bolivia, we disentangle the effects of stem diameter, tree height, crown exposure, and logging-induced degradation on risks of drought-induced mortality during the 2004/2005 ENSO event. Overall, tree mortality increased in response to drought in both logged and unlogged plots. Tree height was a much stronger predictor of mortality than stem diameter. In unlogged plots, tree height but not crown exposure was positively associated with drought-induced mortality, whereas in logged plots, neither tree height nor crown exposure was associated with drought-induced mortality. Our results suggest that at the scale of a site, hydraulic factors related to tree height, not air humidity, are a cause of elevated drought-induced mortality of large trees in unlogged plots.

INTRODUCTION

The Amazon region is predicted to experience hotter and more frequent droughts as a result of elevated sea surface temperatures that intensify El Niño Southern Oscillation (ENSO) events and affect the intertropical convergence zone [1, 2]. As a result, forests there may face increased tree mortality rates due to water stress [3, 4]. At the level of individual trees, drought-induced mortality is likely to vary with interactions among microenvironmental conditions and tree characteristics. Understanding these interactions and their underlying mechanisms is needed to predict the fates of trees and forests in a changing climate. Here we examine the effects of the 2005 ENSO event on tree mortality in a selectively logged transitional Amazonian forest in Bolivia.

Predicting individual tree responses to drought remains challenging but a number of characteristics reportedly contribute to drought tolerance and avoidance, including narrow vessels, high wood density, and high leaf mass per area as well as various hydraulic properties of leaves and wood. One reported pantropical pattern is that large trees suffer elevated risks of drought-related mortality [5-9, but see 10, 11, 12]. This relationship is of particular concern due to its implications for forest structure, timber production, and carbon sequestration as the climate changes.

The two principal mechanisms proposed for large tree vulnerability to drought focus on the decreased soil water potential that droughts cause. First, as soil water potential decreases, so do plant water potentials. To overcome gravity, tall trees must maintain higher xylem tensions than short trees, and with increased xylem tension comes increased cavitation risk [5, 9]. Xylem cavitation decreases hydraulic conductivity, leading to more negative leaf water potentials, often reduced stomatal conductance, and reduced net photosynthesis. Secondly, given that metabolic maintenance costs increase with tree size, large trees are more likely to suffer carbon deficits than smaller trees if photosynthesis is constrained by cavitation or stomatal closure [4]. Both of these mechanisms result in increased mortality risk either directly as a result of carbon deficits, inability of the leaf's anti-oxidant system to scavenge reactive oxygen species [13], or indirectly via increased susceptibility to pests, pathogens, and other causes of mortality [14]. Despite abundant circumstantial evidence, these proposed mechanisms for large tree vulnerability to drought await explicit tests.

While droughts affect both soil water potentials and air humidity, the former has been the primary factor invoked to explain large tree vulnerability to drought (but see [11]). Increased vapor pressure deficits (VPDs) during droughts due to reduced air humidity and increased air

temperature likely contribute to large trees' vulnerability to drought, and may better explain drought-induced mortality than tree size. Trees with exposed crowns, regardless of their height, require more water for transpirational cooling and experience relatively high VPDs. High VPDs lead to high transpiration rates per unit of carbon fixed. Therefore, when soil water potentials are low, trees with exposed crowns may fix less carbon (in the case of isohydry or facultative deciduousness) and/or suffer xylem cavitation (in the case of anisohydry), and hence be particularly susceptible to drought-induced mortality. For this reason, we hypothesize here that canopy exposure is a better predictor of tree mortality than tree size (i.e., stem diameter (DBH) or height).

FOREST MANAGEMENT AND DROUGHT

Trees in a stand compete for soil water, and consequently, when stands are thinned, remnant trees may access a larger share of that water via expanded root systems and increased soil water availability [15, 16]. Thinning may also increase total available soil water by increasing the total amount of precipitation reaching the forest floor due to a reduction in LAI and hence interception of precipitation [17, 18] and transpiration [19]. Ground water levels may also rise in treefall gaps [19], potentially allowing trees to access ground water that previously relied on soil water, and potentially benefiting neighboring trees via hydraulic lift [20].

Numerous studies in temperate forests have shown that thinning reduces drought stress and increases resistance and resilience to drought across a broad range of forest types [21-27] with a few exceptions [28, 29]. The drought-related benefits conferred by thinning may be limited by soil water storage capacity [15] and may decline over time [23]. For example, tree architecture and physiology may adapt to thinning-induced increases in water availability by decreasing their Huber values (sapwood area:leaf area) and increasing stomatal conductance,

rendering them more vulnerable to future droughts [17]. Emerging understory vegetation may also compete with remnant trees for soil water [15]. To maintain the drought resistance benefit of thinning, repeated treatments are recommended [30, 31]. Finally, the extent to which thinning protects remnant trees from drought may depend on abiotic conditions and vary across gradients such as elevation [21, 22, 32, 33].

Managing temperate forests for resistance and resilience to climate change, typically via influencing the species mix, size distribution, and stand basal area, is a topic of current discussion [34-38]. In comparison, the same discussions about tropical forests are relatively data-deficient and lack direct tests [39]. Caution in extending results from temperate to tropical forests is warranted given their myriad differences and the finding of substantial differences among temperate forests in responses to thinning [23]. The few available studies on drought effects on tropical trees hint that they respond similarly to their temperate counterparts. In particular, Leighton and Wirawan [5] reported that during a major drought in Borneo, large trees benefitted from low-intensity understory fires that killed many small trees, possibly due to reduced competition for water. Similarly, Shenkin, Bolker [40] showed that logging-damaged trees suffered from droughts less than undamaged trees, likely due to their proximity to logging gaps.

Key to understanding how logging affects tropical forest responses to drought is whether it renders large trees more or less vulnerable, and how this response varies with size and crown exposure. For example, reduced belowground competition and increased throughfall in logged plots may confer drought-resistance to trees of all sizes. In contrast, if large trees live especially close to their drought stress limit, logging may confer on them a particularly large advantage. Alternatively, logging may allow small trees to build carbon reserves and therefore benefit more

from logging than large trees. On the other hand, logging may expose small trees to high VPD, thereby increasing their vulnerability to drought. Sparse evidence exists to support differential responses to drought across size and exposure classes: Kolb, Agee [41] and Erickson and Waring [42] found that older, and presumably larger, pines in Arizona fared better during droughts in logged than unlogged plots, and Trouvé, Bontemps [43] found that understory trees suffered more from drought in dense but not in open stands.

To address these questions, we compare the powers of tree size and crown exposure to explain drought-induced mortality, examine how logging changes those relationships and whether logging buffers large trees against drought. In particular, we test our expectation that logging confers drought resistance to large trees in our study system. Finally, we reflect on the implications of these results for future research and our understanding of the futures of undisturbed and managed tropical forests.

MATERIALS AND METHODS

This study was conducted in the Long-Term Silvicultural Research Plots (LTSRPs) of the Instituto Boliviano de Investigación Forestal (IBIF) within the forestry concession held by Agroindustria Forestal La Chonta, 30 km east of Ascención de Guarayos, Bolivia (15°47'S, 62°55'W). This semi-deciduous forest (hereafter "La Chonta") receives an annual average of 1580 mm of precipitation with 4 months (May-September) that each receive <100 mm [44]. The forest contains tree species from both wet Amazonian lowland forests to the north and dry Chiquitano forests to the south and falls within WWF's Global 200 Southwestern Amazonian Moist Forest Region. Located on the southern edge of the Amazon Basin, approximately 30% of the tree species that grow to be >10 cm DBH are deciduous and liana densities are very high

[45]. The soils of La Chonta are a mosaic of what have been described as nutrient-rich sedimentary ultisols [46] and poorer soils derived from the Brazilian Precambrian Shield [47]. The concession's terrain is undulating with some granitic outcrops (i.e., inselbergs), none of which are in the permanent sample plots.

The LTSRPs established in 2000/2001 include three blocks of four 27 ha treatments: control (no logging); normal logging; improved logging; and, improved logging with intensive silvicultural treatments [45]. All logging was selective, planned, and carried out by trained crews according to reduced-impact logging (RIL) guidelines. Pre-felling of lianas in to-be-felled trees was carried out approximately 6 months prior to logging, and lianas were cut from future crop trees in the improved and intensive treatments. Trees overtopping future crop trees of commercial species were girdled in the improved and intensive plots, and the soil was scarified in gaps in the intensive plots to encourage pioneer tree establishment.

Within each plot, all trees >40 cm DBH are censused semi-annually, with trees >20 cm and >10 cm DBH censused in half of the main plot and in 4 1-ha plots, respectively. Censuses often took more than a year to complete due to the size of the experiment and logistical challenges. After the initial pre-logging census in 2000-2001, five more censuses were conducted (2001-2002; 2002-2003; 2004-2005; 2006-2007; 2009). In total, 46,194 individual trees were measured across the entire study, 9854 of which were excluded due to being in a burned area or suffering silviculture-induced mortality. On average, 29,744 individuals trees were encountered during each census, 7713 of which were >40 cm DBH.

Each tree in every census was assigned a crown exposure class with the system of Clark and Clark [48]: 1 (no direct light), 2 (some lateral light), 3 (10-90% overhead light), 4 (>90% overhead light), and 5 (full overhead and later light). During the first census in 2000 – 2001,

tree heights were visually estimated by experienced crews. Heights for the following censuses were predicted with a height allometry model to predict tree heights from DBH for all trees across all census intervals. If a tree was present in the first census, and hence had a height measurement, we maintained its offset from the general allometry such that if a tree was 1m taller than the allometry would predict in the first census, we predicted it would be 1m taller than the mean prediction every subsequent census based on its DBH. Coefficients from models based on height may be very different than from those based on DBH for two reasons: the allometric relationship between height and DBH is non-linear, and because we included the individual offsets in height prediction described above. See Supplementary Information for details.

We used precipitation records from the nearest long-term weather station in Ascención de Guarayos, accessed via the Bolivian National Meteorological and Hydrological Service database (<http://www.senamhi.gob.bo/>). Over the course of the study (2000 – 2011), annual precipitation averaged 1318 mm, with a maximum of 1798 mm in 2007 and a minimum of 994 mm in 2010.

We calculate soil water deficits with the Climatological Water Deficit (CWD) model, a simple bucket model that fills with precipitation and assumes evapotranspiration of 3.33 mm/day [49-51]. We start calculations of CWD on 1 January 1970 and then run them forward day-by-day, adding daily precipitation and subtracting 3.33 mm/day (Figure S 2 and Figure S 3), and capping CWD at a maximum of 0 (saturated soil). For each census interval, the Maximum Climatological Water Deficit (MCWD) is the most negative value of CWD observed (Figure S 2 and Figure S 3). Logging and other factors affect the soil moisture environment experienced by trees; thus, we use MCWD here as a general indicator of climatological drought conditions.

MODEL FORMULATION AND SELECTION

We constructed models that include the direct effects and interactions of variables representing factors pertinent to our questions: drought (MCWD), tree size (DBH, height), crown exposure (crown position; CP), and logging. A subset of models (Model 11, Model 12, Model 21, Model 22) contain just size and not crown exposure predictors. These simpler models address the direct question of whether large trees are more vulnerable to drought than small ones, and leave the question of the roles of size versus exposure for the more complex models.

We distinguish between classes of models based on different metrics of tree size (DBH, height, or both DBH + height) and whether they distinguish between logged and unlogged areas (Table S 1). We tested the effects of logging with two further classes of models: those run on the complete dataset that include a variable (*logged*) indicating whether the tree is in a logged (1) or unlogged (-1) plot; and those run on data from logged and unlogged plots separately. We did not compare across models fit to separate datasets as this would introduce unnecessary complexity; instead, we used these models to reduce complexity and to aid interpretation of differences between logged and unlogged plots.

Our models integrate, instead of separating out, the effects of species in order to reduce complexity, aid interpretation, and promote generality of results. Logging shifts species composition to more acquisitive recruits [52] and drought-tolerant seedlings [53]. Functional composition of recruits and regeneration may or may not have a strong effect on drought-induced mortality of larger trees. Either way, the species-agnostic approach integrates the effect of this compositional shift instead of separating it out.

We rank classes of models with corrected-AIC scores to gain insight into the most important predictors of mortality. For hypothesis testing, we examine predictor direction and significance in the higher ranking models that contain our variables of interest. To avoid data

dredging, we confine our models formulations to those we deem to contain ecologically informative interactions instead of testing a complete set of possible permutations. Because height was derived in part from DBH when direct estimates were not available, we limit our use of models that include both predictors.

STATISTICAL MODELS

Unless otherwise indicated, models were fit using generalized linear mixed models [GLMMs; 54] in the R statistical environment [55] with the lme4 package [56]. When GLMM fits indicated potential convergence issues, we verified parameter estimates by fitting Bayesian models via the R INLA package [57] with the same structure as the GLMM model. GLMM parameter confidence interval estimates were unreliable in these cases and are thus not reported. Instead, we rely on Bayesian 95% credible intervals as determined by the 0.025 and 0.975 quantile values shown in the coefficient plots (SI). To test for a non-linear relationship between mortality and tree size, we examine scaled model residuals [58]. Confidence intervals in prediction plots were determined using Wald estimates, as models typically took hours to converge, and hence bootstrap methods were unavailable. We used bootstrap techniques applied to GLMs fit to data from the driest intervals to test for absolute differences in mortality rates of the largest trees between logged and unlogged plots.

Data were coded such that mortality (coded as 1) and survival (coded as 0) were associated with an individual census interval. Census intervals varied in length, and this variation was accounted for by including offsets in our models (see Supporting Information). We used a binomial error structure with a complementary log-log link function. An “event” consists of one observation of one individual from one census to the next. For example, if an

individual survived through all four census intervals, there are four “survival events” for that tree.

We include random effects in our models to account for block effects (δ_k) and repeated measures (γ_i). To account for block effects, we assign a random variable for all 12 plots since 4 treatments nested within 3 blocks would be too few levels. When models were run on just the data from the unlogged plots, blocks were included as fixed instead of random effects, as there were too few levels to treat them as random effects. To aid interpretation, we present just the structure of the linear predictor βX_{ij} and omit other covariates when listing models.

In all models, independent variables were scaled such that $sd = 1$ and centered on 0 where appropriate to render outputs interpretable [59]. Unless otherwise indicated, trees that died due to felling, collateral logging damage, or silvicultural treatments were removed, as were trees in areas that burned in 2004.

INTERPRETING COEFFICIENTS

Coefficients of the linear predictor $\eta = \beta X_{ij}$ in GLMMs with complementary log-log links, when exponentiated, can be interpreted as hazard ratios (HRs). Specifically, $HR = 1 - \exp(\text{coefficient})$. If $\exp(\text{coefficient}) = 1$, then that characteristic has no influence on HRs. In our case, a hazard ratio is the increase in annual probability of mortality compared to the control or mean group due to a unit increase in a characteristic. Thus, if the expected mortality rate of a tree with $DBH = \text{mean}(DBH_{ij})$ is 2% and the DBH coefficient is -0.7, then $HR = 1 - \exp(DBH) = 0.5$. Hence a unit increase in DBH corresponds to a 50% decrease in expected annual mortality relative to the mean expected annual mortality rate of 2%, resulting in an expected 1% annual mortality rate. As another example, if an HR of 1.05 is reported, this indicates that a unit increase of that variable raises a base mortality rate of 2% by 5%, to an

expected 2.1%. A potential source of confusion when reporting HRs is that, when reported as percentages, they might erroneously be interpreted as additive terms to the base mortality rate; in fact, they should be interpreted as multiplicative. For example, if an HR of 1.05 (5%) is reported the resulting mortality rate due to a unit increase of the variable is not $2\% + 5\% = 7\%$, but rather $2\% \times 105\% = 2.1\%$.

Because our predictors are scaled, the unit of change corresponds to one standard deviation of that characteristic in our observed data. The logged plot dummy variable, *logged*, was coded with contrasts -1 (unlogged) and 1 (logged). Therefore, HRs including the *logged* variable should be doubled.

RESULTS

2005 ENSO IN LA CHONTA

La Chonta experienced a severe drought in 2004/2005 (Figure S 2). CWD typically reaches zero during the wet season, but failed to do so in those years. MCWD reached its lowest point of -635 mm H₂O since 1970 in the 2004 dry season, surpassed only by the 2010 dry season that is not addressed here (Figure S 3).

MODEL COMPARISON

Our interest in the effects of logging and drought led us to examine whether the inclusion of those factors improved the models. Models that included interactions between MCWD and height, and MCWD and crown exposure, had similar AIC scores to those without them, which indicates that these interactions lend enough explanatory power to warrant their inclusion (Table S 4). Height-based models were not more parsimonious when logging was included, though all

height-based models were similar enough to warrant examination of the factors of interest in this study.

The models we tested grouped principally according to whether they included height or DBH. Height-based models were better predictors of mortality than DBH-based models in general ($\Delta\text{AICc}_{\text{Model 15} - \text{Model 5}} = -260$, Table S 4), and all height-based models fell within a relatively small range of ΔAICc ($\Delta\text{AICc}_{\text{Model 8} - \text{Model 24}} = -6.2$), while DBH-based models varied substantially ($\Delta\text{AICc}_{\text{Model 15} - \text{Model 12}} = -24.5$). As such, we focus our discussion on height-based models, though we note results from DBH-based models where appropriate.

Lagged MCWD predictors were weak and thus discarded. Scaled residuals did not indicate a non-linear response of mortality to tree size (Figure S 15), so we maintained a linear modeling framework. An expanded explication of model results can be found in Supporting Information.

ROLES OF TREE SIZE AND CROWN EXPOSURE IN OVERALL MORTALITY

We first present non drought-related factors that influence tree mortality, and then address factors affecting drought-induced mortality below. Height and DBH were strongly associated with overall reductions in mortality risk. Crown exposure was, unexpectedly, associated with increased mortality risk in height-based models (Figure S 12), and strong decreases in mortality risk in DBH-based models (Figure 3, Figure S 9a).

DOES LOGGING AFFECT THE ROLES OF TREE SIZE AND CROWN EXPOSURE IN TREE MORTALITY?

The two modes of inference employed here conflict: height-based models were not improved by adding logging interactions, but the 3-way interaction $h:\text{logged}:\text{MCWD}$ was

positive and significant, indicating that the role of height in drought-induced mortality was significantly different between logging treatments. Furthermore, consistent shifts in the roles of size and crown exposure in drought-induced mortality were observed when fitting models to separate logged and unlogged datasets (see below). Finally, a number of terms that include the logging predictor were significant in our models (e.g. Figure 3). Predictions indicate that, while the coefficients of the interactive terms are not large, they exert important influences on tree mortality (Figure 1, Figure 2, Figure S 11b, Figure S 14). We therefore conclude that logging does affect the roles of size and crown exposure in drought-induced mortality.

ROLES OF TREE SIZE AND CROWN EXPOSURE IN DROUGHT-INDUCED MORTALITY

Overall, mortality rates increased during drier intervals (Figure S 5) as expected, which is confirmed by the negative coefficients for the MCWD term in all our models (Figure 3, Figure S 9, Figure S 10, Table S 7).

Across all plots (Figure 1a) and within logging treatments (Figure 1b, c), tree height was associated with greater shifts in mortality risk during droughts than was crown exposure. Tree height was associated with increased drought-induced mortality risk in unlogged plots, but not so in logged plots (Figure 1a, b, Figure S 12a, Figure 3c, d). This difference was confirmed by the positive and significant 3-way interaction between height, logging, and MCWD ($h:logged:MCWD = 1.047$ in Model 29, Figure 3a, Figure S 9a, Table S 7). The result is that, in unlogged plots, mortality increased more quickly as a result of drought in taller trees than in shorter trees (Figure 1c).

In the case of DBH-based models, DBH was associated with reductions in drought-induced mortality (i.e. drought tolerance) in logged plots, and was not associated with a directional effect in unlogged plots (Figure S 9e, f).

The effect of crown exposure on drought-induced mortality was consistent between logged and unlogged plots, and varied primarily as a result of whether tree height was included in the model or not. Crown exposure was not an important predictor of drought-induced mortality in height-based models, and was associated with an increased risk of drought-induced mortality in DBH models.

RELATIVE IMPORTANCE OF TREE SIZE AND CROWN EXPOSURE IN DROUGHT-INDUCED MORTALITY

Estimating predictor importance by comparing models, we found that models that included crown exposure's influence on drought-induced mortality fit the data slightly better than those including height (Table S 4). Specifically, Model 7 ($h + CP \cdot MCWD$) had a lower AICc score ($\Delta AICc = 0.59$) than Model 6 ($CP + h \cdot MCWD$). Conversely, tree height's mean influence on drought-induced mortality was stronger than that of crown exposure in the unlogged plots (Figure 3a; Model 20 in Table S 7, $h:MCWD = -0.077$, $CP:MCWD = -0.010$). Neither factor played a strong role in predicting drought-induced mortality in logged plots (Figure 3c).

Predictions show that the difference in mortality between height classes changes more than that between crown exposure classes across the range of MCWD we observed when examining effects both controlling (Figure 1a) and not controlling (Figure 1b,c) for each other. Figure S 12 further shows that in unlogged plots, when controlling for other effects, the difference in mortality between height classes changes more as a function of drought than the difference in mortality between crown exposure classes.

The weight of evidence when comparing the roles tree height and crown exposure leads us to conclude that tree height is a more important determinant of drought-induced mortality than crown exposure, especially in unlogged plots.

In DBH-based models, DBH was slightly more important than crown exposure in logged plots, but acted in a direction opposite from expectation (i.e., drought-induced mortality decreased with tree size; Figure S 9e, f). Neither predictor was a significant predictor of drought-induced mortality in unlogged plots, so we do not evaluate relative importance in that case.

THE EFFECT OF LOGGING ON DROUGHT-INDUCED MORTALITY OF LARGE TREES

Removing the crown exposure predictor height-based models allows for a direct test of the effect of tree height across logging treatments, regardless of the effect that logging may have on crown exposure. These models show that mortality rates of a 35 m-tall tree in a logged plot had a 1.1% chance of dying during a drought year with -619 mm H₂O MCWD, whereas the same tree in an unlogged plot had a 1.6% chance. Due to the rarity of large-tree mortality events, non-parametric bootstrap tests found that these differences were not significant.

DISCUSSION

The influences of tree height, stem diameter, and crown exposure on drought-induced mortality are complex and vary according to other covariates and logging. In general, tree height the strongest correlate with drought-induced mortality, increasing the risk of drought-induced mortality in unlogged plots. Stem diameter had the opposite effect, tending to decrease the risk of drought-induced mortality when it had an influence. Crown exposure seemed to render trees vulnerable to risk during droughts, but when height was added to models, this effect was reduced; the correlation between crown exposure and tree height (Pearson $r = 0.57$) may partially explain this reduction.

Our results suggest that hydraulic factors associated with tree height, such as decreased hydraulic conductance, greater embolism risk, or decreased leaf water potentials are more likely causal factors of the observed pattern of large-tree vulnerability to drought than local VPD variation or other dimensions of tree size. The hypothesis that crown exposure plays a larger role than tree size in drought-induced mortality was not supported by our data. While crown exposure was more likely to be associated with increased drought risk than stem diameter across conditions and models, tree height seems to be a more important predictor, particularly in unlogged areas.

The magnitude of the interactions between tree height, diameter, crown exposure, and MCWD often ranged from 20 – 35% of the magnitude of the direct effects. This constitutes an important indicator of how trees and forests respond to drought, and could have important implications for future forest structure.

While previous studies associated increased stem diameter with increased drought risk [5-8, but see 10, 11], our results indicate that tree height, not stem diameter, is the likely cause of this pattern. Indeed, diameter is actually more likely to confer drought tolerance than predispose trees to drought risk. We show here how studies that do not control for crown exposure or tree height could come to the conclusion that stem diameter is positively associated drought-induced mortality. Crown exposure and tree height, which both tend to increase with stem diameter, predispose trees to drought-induced mortality more strongly than diameter buffers them. This means that when these covariates are not included, models may find stem diameter positively associated with drought-induced mortality.

DOES LOGGING INCREASE DROUGHT RESISTANCE IN THIS TROPICAL FOREST?

While we found that the relationship between tree size and drought risk differed as a function of logging, we did not find that trees across all size classes were better off in logged plots during droughts. This finding is in contrast to studies in temperate forests showing that thinning may assist trees of all sizes to resist drought. Studies across gradients of environments and forest types in the tropics are needed to determine if the drought-tolerance conferred by logging in temperate forests is truly absent in tropical forests.

DOES LOGGING PROTECT LARGE TREES FROM DROUGHT?

Taller trees suffer larger increases in drought-induced mortality than shorter trees in unlogged plots. This pattern is diminished or absent in logged plots. Predictions indicate that this trend, in droughts deeper than measured here, may lead to elevated rates of drought-induced mortality of large trees in unlogged plots when compared to logged plots. Nonetheless, because large trees are relatively rare, and mortality of those trees even more so, we did not find a significant difference in the mortality rates of large trees between logged and unlogged plots during the deepest drought examined in this study. Thus, further study, examining deeper droughts or larger sample sizes, are necessary to bring clarity to this question.

Increased tree height and crown exposure did not leave trees vulnerable to drought in logged plots, which contradicts our hypothesis. Indeed, the relationship between crown exposure and drought response differed little between logged and unlogged plots. We expected that rapid exposure of many trees to high VPDs and insolation due to logging would render them vulnerable to drought-induced mortality. Increased soil water availability in logged plots may counteract these potentially damaging conditions given that the trees most likely to suffer post-logging shocks are on the edges of logging gaps where they benefit from increased soil water availability.

Tests of relationships between tree size dimensions, neighborhood metrics such as canopy position, and drought-induced mortality across rainfall and disturbance gradients in the tropics are needed to elucidate the determinants of drought vulnerability. Key questions for future research include: how does thinning via selective logging affect stand-level resistance and resilience to drought across tropical forests? How do edaphic factors alter the interactive roles of tree structural and functional characteristics in determining drought vulnerability? And, how do different logging intensities and silvicultural treatments interact with tree characteristics to affect drought vulnerability?

WHY DO TREES GROW TALL?

One finding from this study that contradicted our expectations about overall (not drought-induced) mortality stood out: crown exposure was associated with higher mortality rates when controlling for tree height, especially in unlogged plots (crown pos = 1.087 in Figure 3d; Figure S 12b). The assumed primary function for trees growing tall is to out-compete neighbors in a contest for the limiting resource of light. We would therefore expect crown exposure to be associated with lower mortality rates when controlling for tree height, and tree height to be associated with higher mortality rates when controlling for crown exposure. Instead, our results suggest the opposite: that at least in terms of mortality, advantage lies in a tree growing tall, and that crown exposure is a negative consequence of this growth in this regard rather than its purpose.

While unexpected, this result should be seen in its proper context. That is, mortality is just one facet of fitness, and growth, reproduction, viability, and other fitness-related traits may have different relationships with height and exposure. Furthermore, unbalanced species compositions across treatments and collinearity between height and crown exposure may

underlie this pattern. Nonetheless, the assumption that gaining an exposed crown is the ultimate goal of growing tall could serve as an interesting topic for further research.

IMPLICATIONS FOR FUTURE FORESTS

Phillips, van der Heijden [60] suggest that large tree vulnerability to drought may place an upper limit on tropical tree sizes in the future. Our findings corroborate this conclusion in undisturbed forests to a certain degree, but not so in disturbed areas.

Much of our knowledge about how tropical forests respond to drought is derived from studies in plots specifically chosen for their lack of disturbance. Since at least half of extant tropical forests are managed or disturbed [61], it is equally important to understand the response of these “degraded” forests.

Our results support the view that tall trees are particularly vulnerable to drought in undisturbed forests. However, after a certain proportion of large trees die due to drought, and if logging approximates that process of drought-culling of large trees, then the remnant large trees may no longer be particularly vulnerable. In fact, their size, and stem diameter in particular, may serve to buffer them against future droughts.

If our finding that, in logged forests, drought-induced mortality does not depend on tree height holds across the tropics, then instead of a limit on tree size as previously suggested, we may see an initial reduction in the density of large trees in drought-stressed but unlogged areas, which could then level off to lower densities in a more drought-affected world.

Recent studies [e.g. 3] suggest that forests will experience ever increasing drought-induced mortality rates as a result of contemporary changes including a changing climate and anthropogenic disturbance. What these studies often fail to consider is how vulnerability to drought may change as forests degrade. Here we find that the reduced competition that logging

affords during droughts seems to counteract the size signal in drought-induced mortality found in unlogged areas. Thus, while pristine forests are likely to feel the full brunt of droughts in the near term, they may change to a different, degraded, steady state of lower basal area that might weather the future changes bearing down on them [62]. These lower density forests may be more able to persist as climate change progresses.

IMPLICATIONS FOR POLICY AND RESEARCH

Our results indicate the importance of distinguishing between undisturbed and selectively logged forests when making projections regarding how forests will respond to climate change-induced changes. Specifically, projections of future carbon and timber stocks should take into account that in terms of mortality, large trees may suffer disproportionately in closed canopy forests, but such a size signal may reduce or disappear as stands thin due to drought induced mortality or selective logging.

Stand thinning has been suggested as a potential protective measure to pre-adapt temperate forests to climate change-related increases in drought frequency and intensity. This study does not support such a treatment for conferring tolerance across all stem size classes. Thinning in order to protect large trees, however, remains an open question. Further studies of deeper droughts in tropical forests are necessary to answer this question. Population modelling studies are necessary to project the implications of altered mortality regimes into the future. These questions are especially pertinent in regions where droughts are expected to increase in depth and frequency.

FIGURES

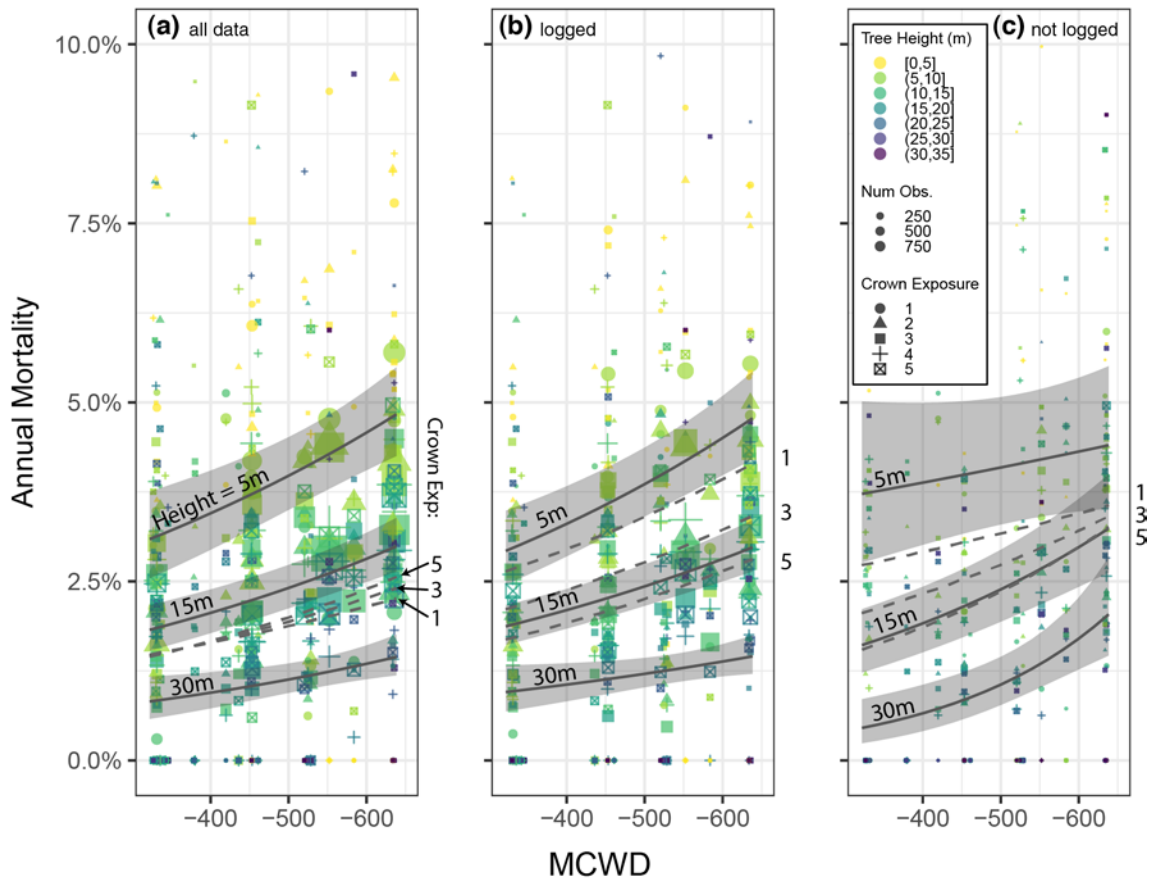


Figure 1. Mortality rates as a function of MCWD, tree height, and crown exposure in observed data (points) and modelled predictions (lines and 95% mean confidence intervals). Panels show (a) the effects of height averaged across crown positions 1 - 5, and crown position averaged across heights 5 - 35m, across all data (full height model, Model 5), (b) the effects of height (Model 22) and crown position (Model 23) in logged plots, and (c) in unlogged plots. The height and crown exposure effects in panels (b) and (c) are not controlled for each other, as reflected in the respective model formulae. Conditions go from wet to dry along the x-axis from left to right. Crown position 1 is in the shaded understory, while crown position 5 is fully illuminated.

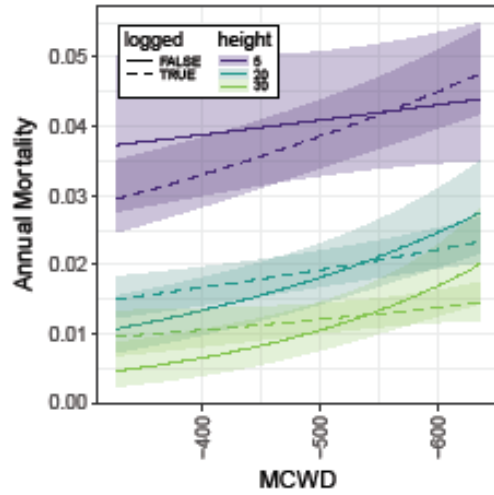
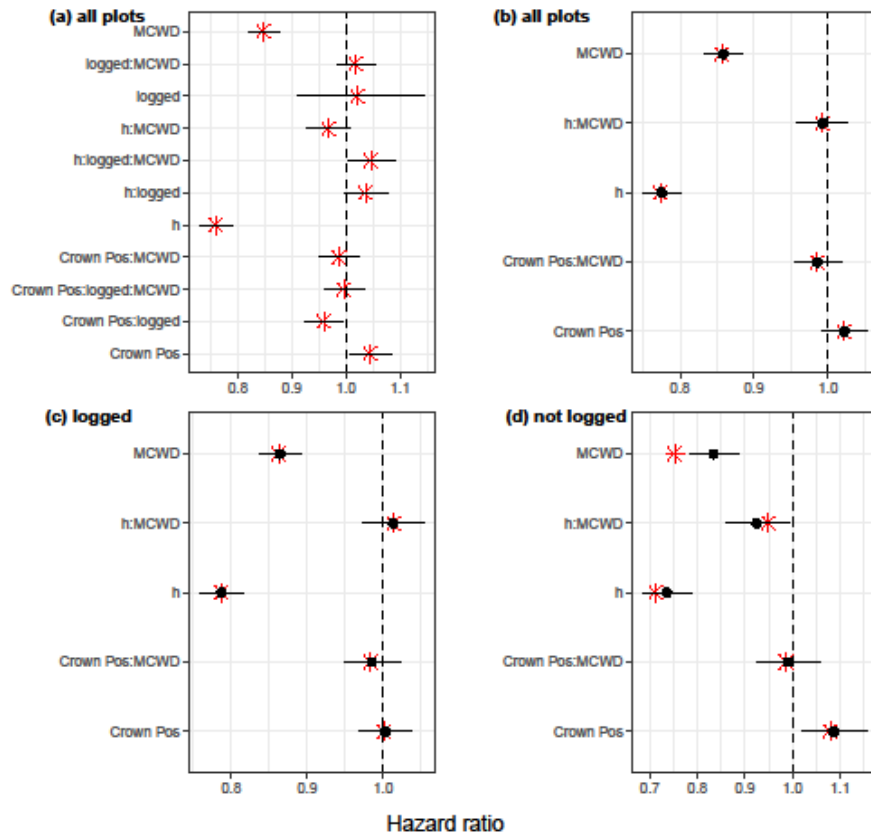


Figure 2. Annual mortality rates and 95% mean Wald confidence intervals for tree heights not corrected for crown exposure (Model 22).



490

491 Figure 3. Hazard ratios (exponentiated coefficients) derived from selected height-based models:

492 (a) full height logging model (Model 29), (b) full height model (Model 5), and the same full

493 height model parameterized with (c) logged (Model 19) and (d) unlogged (Model 20) data.

494 Black points are the 0.5 quantiles and horizontal bars are the 95% credible intervals from a

495 Bayesian INLA algorithm, and red stars are the mean parameter estimates of the corresponding

496 GLMM fit. Intercept and random effects are removed for readability.

497

498

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COMPETING INTERESTS

We have no competing interests.

AUTHORS’ CONTRIBUTIONS

MP, AS, JL, FP and NA carried out the field work and participated in data analysis, FP and MP participated in the design of the experiment; AS and BB carried out the statistical analysis; AS and FP drafted the manuscript; FP, AS, and MP conceived of the study. All authors and gave final approval for publication.

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SUPPORTING INFORMATION

TREE HEIGHT ALLOMETRY MODEL

We built a height allometry model to predict tree heights from DBH for all trees across all census intervals. The linear mixed model is specified as

$$\log(h_{i1}) = b + a \log(DBH_{i1}) + \gamma_s S_i + \delta_b B_i + \varepsilon_{i1}$$

where h_{i1} is the measured tree height i during the first census, DBH_{i1} is its measured stem diameter, S_i is a vector of the species of the individuals, B_i the tree's treatment block, γ_s and δ_b the random variables associated with the corresponding vectors, and the error term is $\varepsilon_{i1} \sim N(0, \sigma^2)$. We assigned the height estimated from this allometry ($h_{allom,ij}$) to each tree in each census that lacked height estimates. For each tree i whose height was measured during the first census, we added its residual (ε_{i1}) to the estimate, since trees tall for their DBH in census 1 are also likely to be tall for their DBH in later censuses, and vice versa, and because the model with residuals added fit the data better than the model without (Table S 3). Hence,

$$h_{allom,ij} = \begin{cases} h_{allom,ij} + \varepsilon_{i1}, & \text{if } h_{i1} \text{ exists} \\ h_{allom,ij}, & \text{otherwise} \end{cases}$$

When our models included DBH and not h_{allom} , the assumption is that DBH is a better proxy for height than crown exposure, insofar as we are testing whether height or crown exposure is the principal cause of drought vulnerability. To test this assumption, we fit two models (Equations 2 and 3) with scaled and centered predictors, the second of which contains the DBH allometric fit, and compared the magnitudes of the coefficients of those predictors.

$$h_{i1} = b + a DBH_{i1} + c CP_{i1} + \delta_b B_i + \varepsilon_{i1} \quad (1)$$

$$h_{i1} = b + a (0.631 * DBH_{i1}^{0.5517}) + c CP_{i1} + \delta_b B_i + \varepsilon_{i1} \quad (2)$$

HEIGHT ALLOMETRY RESULTS

The height allometry model explained 66% of the variation in $\log(h)$ ($R^2_{GLMM(c)}$), with 52% explained by the fixed effect alone (DBH; $R^2_{GLMM(m)}$; [63]). The model with fit parameters was:

$$h = 0.63 DBH^{0.552}$$

Comparing the strength of the DBH and crown exposure predictors for tree height, we found that DBH was a stronger predictor of height than crown exposure, the former having a coefficient twice the magnitude of the latter (Table S 2). The height allometry predictor (a in Equation 3) was an even stronger predictor of tree height. These results indicate the DBH is a better proxy for tree height than crown exposure, and that by comparing DBH versus crown exposure predictors in our models, we are able to test the height versus crown exposure hypothesis.

Visual estimation of tree height has been shown to outperform laser hypsometers in the one case we are aware of it having been tested [64]. That the models here that include tree height predict mortality better than those that include stem diameter lends further credence to the validity of the height estimates.

INTERPRETING INTERACTIONS

Understanding the effects of tree size and crown position on drought vulnerability requires interpretation of interactive models terms. Because our models estimate effects on mortality rates, positive coefficients indicate that increases in that predictor result in increases in mortality risk whereas decreases indicate decreased mortality risk. For negative coefficients, the

inverse is true. A negative DBH coefficient would indicate that increases in DBH are associated with decreased mortality rates. MCWD becomes more negative under drier conditions. Therefore, a negative MCWD coefficient would indicate that decreases in MCWD (drier conditions) are associated with increased mortality rates: $\downarrow \text{MCWD} \times \downarrow \text{coefficient} = \uparrow \text{mortality}$.

An interactive term represents the product of two predictors (Figure S 1e-f), and fits a new coefficient to that new predictor. By interacting DBH with MCWD, for example, we can examine how DBH changes how MCWD affects mortality rates. If DBH and MCWD coefficients have the directions posited above and the “DBH:MCWD” term is positive, then we can infer that increases in DBH reduce the effect of MCWD, as the MCWD coefficient is always negative. Thus, we would conclude that larger trees are less sensitive to MCWD either via a reduced vulnerability to drought, a reduced benefit from wet conditions, or both. If “DBH:MCWD” is negative, then increases in DBH reinforce the negative MCWD effect, indicating that larger trees are more vulnerable to drought or benefit more from wet conditions. Figure S 1 provides a graphical description of this concept.

To determine whether crown exposure or DBH was associated with increased mortality during droughts, we fit models that included either the crown position:MCWD interaction or the DBH:MCWD interaction. We compare the fit of these models to the data using corrected-AIC. If trees with either exposed crowns or large diameter trunks experienced especially elevated mortality rates during dry census intervals, we would expect to see negative interaction terms between crown position and MCWD, or DBH and MCWD, respectively.

DETAILED DISCUSSION OF MODEL RESULTS

MODELS THAT IGNORE LOGGING

Height-based models

When height instead of DBH was included in models that did not distinguish logged vs unlogged plots, neither height nor crown exposure were strong predictors of drought-induced mortality (i.e. h:MCWD and CP:MCWD were small; Figure 3b, Table S 7). Instead, height was strongly and negatively associated with overall (not drought-induced) mortality risk. The direct effect of crown exposure switched from being strongly associated with increased survival probabilities in DBH-based models (Table S 7) to being associated with slight increases in mortality risk in height-based models.

The model including the CP:MCWD interaction (Model 7) was slightly better than the one including the h:MCWD interaction (Model 6; $\Delta \text{AIC}_{7-6} = -0.59$), and the magnitude of the CP:MCWD predictor was slightly larger than the h:MCWD predictor (Table S 7, Figure 3b).

Thus, while crown exposure is a slightly stronger predictor of drought-included mortality than tree height, neither factor is a strong predictor when tree height is included in the model.

DBH-based models

Across all plots, when including only DBH as the size predictor, mortality rates of large trees were less sensitive to drought than those of smaller trees (DBH:MCWD > 0; Table S 7, Figure S 9). In other words, mortality rates of small trees increase more as a result of drought than large trees. According to the full DBH model (Table S 7), in wet conditions, annual mortality rates of large and small trees are predicted to be nearly identical, with rates between 1% for fully exposed trees and 2% for fully shaded trees (Figure S 13a, Figure S 14). As conditions become drier, however, mortality rates of small trees (10cm DBH) increase rapidly to

3-4%. Large trees suffer little due to drought if they are shaded, but they suffer more if exposed (Figure S 13a, Figure S 14). Annual mortality rates range from 1.0 – 1.3% for 150 cm DBH trees in crown exposure classes 3 – 5 in wet conditions, but increase to 1.7% during droughts; this represents an absolute increase of 0.4 – 0.7%, compared with an increase of 2.4 – 2.8% for 10 cm trees. These results hold even when crown position is removed from our models and only DBH or height are tested (Table S 7).

Increased crown exposure is associated with increased vulnerability to drought – the opposite effect of tree size ($CP:MCWD < 0$; Table S 7,). In other words, mortality rates of exposed trees rose more as a result of drying conditions than those of shaded trees (Figure S 13b). Mortality rates of 10 cm trees rose 2.4% (absolutely, not as HR) across the wettest to driest conditions when in canopy position 1 (no direct light), compared with a 2.8% rise when in canopy position 5 (exposed from above and laterally). In contrast, mortality rates of 150 cm trees rose only 0.4% when in canopy position 3 and by 0.6% when in canopy position 5.

LOGGING MODELS

Across the suite of tested models, a consistent pattern emerged of how logging shifts the roles of tree size and crown exposure in determining drought-induced mortality. Tree size, both in terms of DBH and height, was less of a disadvantage during droughts in logged plots compared to unlogged plots (Figure 3, Figure S 9). DBH shifted from conferring drought tolerance in logged plots to being a non-factor in unlogged plots. Height shifted from being a non-factor in logged plots to magnifying drought-vulnerability in unlogged plots. The effect of crown exposure on drought-induced mortality was consistent between logged and unlogged plots, and varied primarily as a result of whether tree height was included in the model or not. Crown exposure was associated with increased risk of drought-induced mortality in DBH models, and was not an important predictor of drought-induced mortality in height models. The most parsimonious height-based logging model (Model 28) contains a negative interaction between logging and crown exposure, indicating that tree mortality was largely insensitive to variation in crown exposure in logged plots, whereas tree mortality increased with increasing crown exposure mortality in unlogged plots. We examine these patterns in more detail below.

Height-based models

Unlike the DBH-based models, including whether or not a plot was logged did not improve height-based models. We found no large differences in AICc between the models with $CP:logged$ interactions (Model 26 – Model 28) and $height:logged$ interactions (Model 25; Table S 4). Models fit to logged (Model 19, Figure 3c) and unlogged (Model 20, Figure 3d) data show that taller trees are more sensitive to droughts than shorter trees in unlogged plots ($h:MCWD < 0$; Figure 3d), but not in logged plots (Figure 3c). The $CP:MCWD$ interaction did not change appreciably in the logged and unlogged models.

While increased crown exposure was associated with lower mortality rates in the DBH models discussed above, it was associated with higher mortality rates in height models run on the unlogged data, and had no bearing on mortality in height models run on the logged data. Tree height was strongly associated with lower mortality rates in all models tested.

DBH-based models

Logging resulted in the expected increase in crown exposure of small trees (Figure S 6). We tested the effects of logging on drought-induced mortality in two ways: with models run on data from logged and unlogged plots separately (Model 9, Model 10), and with models run on the complete dataset and including the logging variable (Model 13-17). For this latter set of models, AICc supported the form with a 3-way interaction between DBH, *logged*, and MCWD, and an interaction between CP and MCWD (Model 15, Figure S 9, Table S 4). Predictions for that model are shown in Figure S 14. This model indicates that large trees fare slightly better in logged vs unlogged plots ($HR_{DBH:logged} = -4.4\%$), and that large trees suffer less from droughts in logged plots than they do in unlogged plots ($HR_{DBH:logged:MCWD} = 7.9\%$; Table S 7). This latter finding is supported by the models run on separate logged/unlogged datasets (Model 9 and 10), where $HR_{DBH:MCWD, logged} = 5.2\%$, and $HR_{DBH:MCWD, unlogged} = 0.8\%$. This 3-way interaction between DBH, MCWD, and logging is strong enough to reverse the direction of the relationship between DBH and drought in logged vs unlogged plots. In logged plots, large trees suffer less than small trees due to drought; in unlogged plots, large trees suffer more. A crossover in mortality rates of large and small tree occurs in the unlogged plots (Figure S 14), but is absent in the logged plots. In contrast to tree size, the role of crown position in drought-induced mortality does not change due to logging, maintaining its association with elevated drought-induced mortality risk across treatments ($HR_{CP:MCWD, logged} = -3.1\%$, $HR_{CP:MCWD, unlogged} = -3.8\%$; Table S 7).

Aside from the effect of tree size on drought response, our models are equivocal as to how logging influences drought-induced mortality across all stems regardless of size. While our separate data models (Model 9 and 10) suggest that all trees in logged plots may be more resistant to drought (Table S 7, $HR_{MCWD, logged} = 13\%$, $HR_{MCWD, unlogged} = 22\%$), models integrating all data do not show a significant logged:MCWD interaction (Table S 7, Figure S 9).

To test the prediction based on previous studies that large trees are more vulnerable to drought than small trees in unlogged tropical forests, we removed canopy position from the unlogged model (Model 11). In this formulation, while the DBH:MCWD interaction changes direction (Figure S 9), bootstrap tests on GLMs do not find significant differences in mortality rates of the largest trees across logging treatments during the drought.

Height + DBH-based models

Shifts in the roles of DBH, h, and CP in drought-induced mortality across logging treatments were consistent between models with all predictors (Model 30, Model 31; Figure S 10b,c) and models with just DBH or h. Crown exposure did not affect drought-induced mortality in these models, consistent with the height-based models, and contradicting the DBH-based models.

In these models, in unlogged plots, tree height was associated with increased risk of drought-induced mortality; neither DBH nor CP had a strong influence. In logged plots, DBH decreased the risk of drought-induced mortality, whereas neither height nor CP had strong influence.

RELATIVE IMPORTANCE OF TREE SIZE VERSUS CROWN EXPOSURE

The roles of DBH, tree height, and crown exposure change magnitude and direction depending on whether plots were logged and with the covariates included in the models. In DBH-based models, crown exposure was the principal negative influence on drought-induced mortality in unlogged plots, whereas DBH and crown exposure had similar effect magnitudes but opposite directions in logged plots (Figure S 9a,e,f). In height-based models, height was a

stronger predictor of drought-induced mortality than crown exposure in unlogged plots, whereas neither height nor crown exposure were associated with drought-induced mortality in logged plots (Figure 3). In models including both height and DBH, height was the strongest predictor of drought-induced mortality in unlogged plots, while DBH and crown exposure had little influence. In logged plots, DBH decreased the risk of drought-induced mortality while height and crown exposure had little influence (Figure S 10b,c).

The ranking of drought-induced mortality predictors above, keeping in mind that height-based models were better predictors of mortality than DBH-based models, leads us to conclude that height is the most important determinant of drought-induced mortality in unlogged plots. In logged plots, DBH was the most important predictor, but acted in a direction opposite than what was expected (i.e., drought-induced mortality decreased with tree size). While crown exposure was important in predicting drought-induced mortality in DBH-based models, its diminution in height-based models indicates that it may serve as a proxy for height.

ACCOUNTING FOR VARIABLE CENSUS LENGTHS IN MODELS

The probability that a tree dies in a year ($\Delta t = 1$) is μ_0 , and its probability of surviving is $1 - \mu_0$. Its probability of surviving a variable interval Δt is $(1 - \mu_0)^{\Delta t}$, and of dying during that interval is

$$\mu = 1 - (1 - \mu_0)^{\Delta t} \quad (\text{S1})$$

If the annual probability of mortality μ_0 is a function of a linear combination of factors x , then the probability of mortality $\mu_0 = f(\beta x)$. In our models, $f(\cdot)$ is the complementary log-log function

$$C(\mu) = \log(-\log(1 - \mu)).$$

To model annual mortality rates, we account for varying census lengths by incorporating an offset term. The inverse complementary log-log function is

$$\mu = C^{-1}(\eta) = 1 - \exp(-\exp(\eta))$$

η is our linear predictor, βX . If μ_0 is the mortality rate over a period $\Delta t = 1$ and $\mu_0 = C^{-1}(\eta)$, then

$$\begin{aligned} C^{-1}(\eta + \log \Delta t) &= 1 - \exp(-\exp(\eta + \log \Delta t)) \\ &= 1 - \exp(-\exp(\eta))^{\Delta t} \\ &= 1 - \exp(-\exp(\eta))^{\Delta t} \\ &= 1 - (1 - \mu_0)^{\Delta t} \end{aligned}$$

This formulation, equivalent to Equation S1, correctly incorporates variable census intervals in our annual mortality models. The general form of our models is thus

$$\mu_{ij} = C^{-1}(\beta X_{ij} + \log \Delta t_{ij} + \gamma_i U_i + \delta_k W_k + \varepsilon_{ij})$$

across i individuals, j censuses, where the error is $\varepsilon \sim N(0, \sigma^2)$. β incorporates the coefficient terms of interest that we estimate. γ_i and δ_k are random variables, $\sim N(0, D)$, across the i individuals and k treatments, respectively.

TABLES

Table S 1. Model formulations fit in this study. Models are named for convenience if they are referenced often in the text. When presenting model formulations, we present just the linear predictor (βX_{ij}) for readability, where ‘+’ indicates an additive model, ‘*’ indicates the combination of main and interactive effects, and ‘.’ indicates the interactive effect only. Normal order of operations governs additive and interactive operators.

	Name	Linear predictor (βX)	Dataset
DBH Models			
Model 1	Full DBH	(DBH + CP) * MCWD	All
Model 2	DBH only	DBH * MCWD + CP	All
Model 3	CP only (DBH)	DBH + CP * MCWD	All
Model 4		DBH + CP + MCWD	All
Height Models			
Model 5	Full height	(h + CP) * MCWD	All
Model 6	Height only	h * MCWD + CP	All
Model 7	CP only (H)	h + CP * MCWD	All
Model 8		h + CP + MCWD	All
Logging Models (DBH)			
Model 9	Full logged	(DBH + CP) * MCWD	Logged plots
Model 10	Full unlogged	(DBH + CP) * MCWD + Block	Unlogged plots
Model 11	DBH-only unlogged	DBH * MCWD + Block	Unlogged plots
Model 12	Simple DBH logging	DBH * logged * MCWD	All
Model 13		(DBH + CP + logged) * MCWD	All
Model 14		DBH * logged * MCWD + CP	All
Model 15		DBH * logged * MCWD + CP * MCWD	All
Model 16		DBH + CP * logged * MCWD	All
Model 17		DBH * MCWD + CP * logged * MCWD	All
Model 18		DBH + CP * MCWD + logged * MCWD + CP * logged	All
Logging Models (Height)			
Model 19		(h + CP) * MCWD	Logged plots
Model 20		(h + CP) * MCWD + Block	Unlogged plots
Model 21		h * MCWD + Block	Unlogged plots
Model 22	Simple height logging	h * logged * MCWD	All
Model 23		CP * logged * MCWD	All
Model 24		(h + CP + logged) * MCWD	All
Model 25		h * logged * MCWD + CP	All
Model 26		h + CP * logged * MCWD	All
Model 27		h * MCWD + CP * logged * MCWD	All
Model 28		h + CP * MCWD + logged * MCWD + CP * logged	All

Model 29	Full height logging	$h * \text{logged} * \text{MCWD} + \text{CP} * \text{logged} * \text{MCWD}$	All
Logging Models (DBH + Height)			
Model 30		$(h + \text{DBH} + \text{CP}) * \text{MCWD}$	Logged plots
Model 31		$(h + \text{DBH} + \text{CP}) * \text{MCWD} + \text{Block}$	Unlogged plots

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Table S 2. Height allometry model fits.

	<i>Dependent variable:</i>		
	log(h) H allom (1)	h DBH vs CP (2)	DBH allom vs CP (3)
log(DBH)	0.552*** (0.545, 0.558)		
DBH (scaled)		2.940*** (2.896, 2.984)	
0.631(DBH)^0.5517 (scaled)			3.272*** (3.229, 3.315)
CP (scaled)		1.516*** (1.472, 1.560)	1.213*** (1.170, 1.256)
Intercept	0.631*** (0.592, 0.670)	12.879*** (12.646, 13.111)	12.883*** (12.654, 13.112)
Observations	33,617	33,617	33,617
Log Likelihood	-1,607.272	-88,698.780	-87,211.820
Akaike Inf. Crit.	3,224.544	177,407.600	174,433.600
Bayesian Inf. Crit.	3,266.658	177,449.700	174,475.700
<i>Note:</i>	* ** *** p p p<0.01		

957 Table S 3. AIC comparison of mortality models with height predictors. h_plus_resid is the
 958 height allometry prediction plus model residuals for individual trees (described in Methods), and
 959 h is the height prediction with no correction from residuals.

Modnames	AICcWt	Cum.Wt	Delta_AICc	K	ModelLik
h_plus_resid * MCWD + CP * MCWD	1.00	1.00	0.00	8.00	1.00
h * MCWD + CP * MCWD	0.00	1.00	215.58	8.00	0.00

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Table S 4. AIC comparisons of models fit to data across all treatments. Models fit on data from logged or control plots are not included here.

Modnames	AICcWt	Cum.Wt	Delta_AICc	K	ModelLik
h + CP + MCWD	0.22	0.22	0.00	6.00	1.00
h + CP * MCWD	0.18	0.40	0.35	7.00	0.84
h * MCWD + CP	0.13	0.53	0.94	7.00	0.63
h + CP * MCWD + logged * MCWD + CP * logged	0.10	0.63	1.54	10.00	0.46
h + CP * logged * MCWD	0.08	0.71	2.06	11.00	0.36
h * MCWD + CP * MCWD	0.07	0.78	2.18	8.00	0.34
h * MCWD	0.06	0.84	2.45	6.00	0.29
h * logged * MCWD + CP * logged * MCWD	0.05	0.89	3.01	14.00	0.22
h * logged * MCWD + CP	0.04	0.93	3.35	11.00	0.19
h * logged * MCWD + CP * MCWD	0.03	0.96	3.80	12.00	0.15
h * logged * MCWD	0.03	0.99	4.24	10.00	0.12
h * MCWD + CP * MCWD + logged * MCWD	0.01	1.00	6.17	10.00	0.05
DBH * logged * MCWD + CP * MCWD	0.00	1.00	260.24	12.00	0.00
DBH * logged * MCWD + CP	0.00	1.00	261.87	11.00	0.00
DBH + CP + MCWD	0.00	1.00	263.00	6.00	0.00
DBH * MCWD + CP * MCWD	0.00	1.00	263.07	8.00	0.00
DBH + CP * MCWD	0.00	1.00	263.60	7.00	0.00
DBH + CP * MCWD + logged * MCWD + CP * logged	0.00	1.00	264.09	10.00	0.00
DBH + CP * logged * MCWD	0.00	1.00	264.42	11.00	0.00
DBH * MCWD + CP	0.00	1.00	264.51	7.00	0.00
DBH * MCWD + CP * MCWD + logged * MCWD	0.00	1.00	267.02	10.00	0.00
DBH * logged * MCWD	0.00	1.00	284.70	10.00	0.00
CP * logged * MCWD	0.00	1.00	285.46	10.00	0.00
DBH * MCWD	0.00	1.00	287.51	6.00	0.00

Table S 5. Observations of crown exposure classes versus stem diameter classes across all censuses except the last. The last census is excluded because we use the DBH and crown exposure classes from the beginning of each census interval in our models.

	1	2	3	4	5
[0,10]	148	100	55	43	3
(10,20]	12719	16966	14323	4696	1813
(20,30]	4713	12966	22416	11492	4627
(30,40]	672	3147	8890	8548	4623
(40,50]	213	1131	5024	8054	6429
(50,60]	46	295	1806	3957	4655
(60,70]	18	90	647	1738	2975
(70,80]	8	37	227	847	2025
(80,90]	0	20	77	377	1413
(90,100]	0	3	32	173	961
(100,110]	0	4	18	70	398
(110,120]	0	0	6	36	513
(120,130]	0	0	1	17	192
(130,140]	0	0	0	8	141
(140,150]	0	2	0	16	240
(150,160]	0	1	0	0	90
(160,170]	0	0	0	2	50
(170,180]	0	0	1	3	64
(180,190]	0	0	0	0	8
(190,200]	0	0	1	10	38

979 Table S 6. Observations of crown exposure classes versus tree height classes (h_{allom}) across all
 980 censuses except the last. The last census is excluded because we use the height and crown
 981 exposure classes from the beginning of each census interval in our models.

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	1	2	3	4	5
[0,5]	1668	1361	921	307	73
(5,10]	11066	16558	16213	5674	1587
(10,15]	4748	12975	23814	15760	6949
(15,20]	1018	3672	11441	14489	12793
(20,25]	31	187	1039	3235	7016
(25,30]	1	9	75	557	2508
(30,35]	0	0	21	66	328
(35,40]	0	0	0	0	36

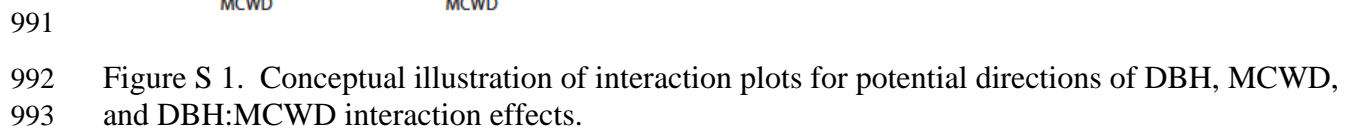
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987 Table S 7. Mean coefficients for all models fit in this study across the entire dataset (i.e. that did
988 not fit separate models to logged and unlogged plots). File available as a separate attachment.

990 FIGURES



DESCRIPTIVE FIGURES

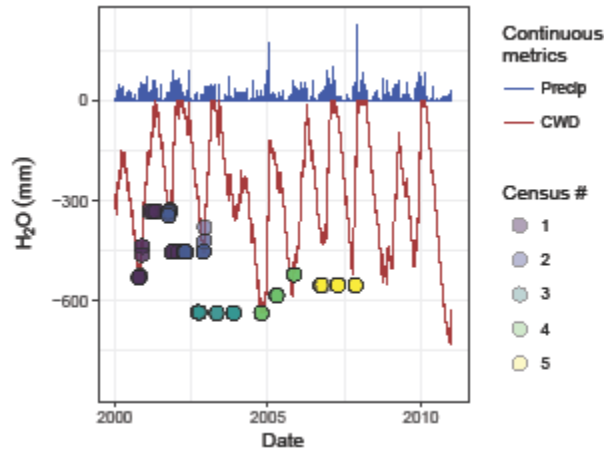


Figure S 2. Precipitation (blue bars), Climatological Water Deficit (CWD, red line), and the MCWD (dots) experienced by trees during the interval between consecutive censuses. Dot color indicates census number.

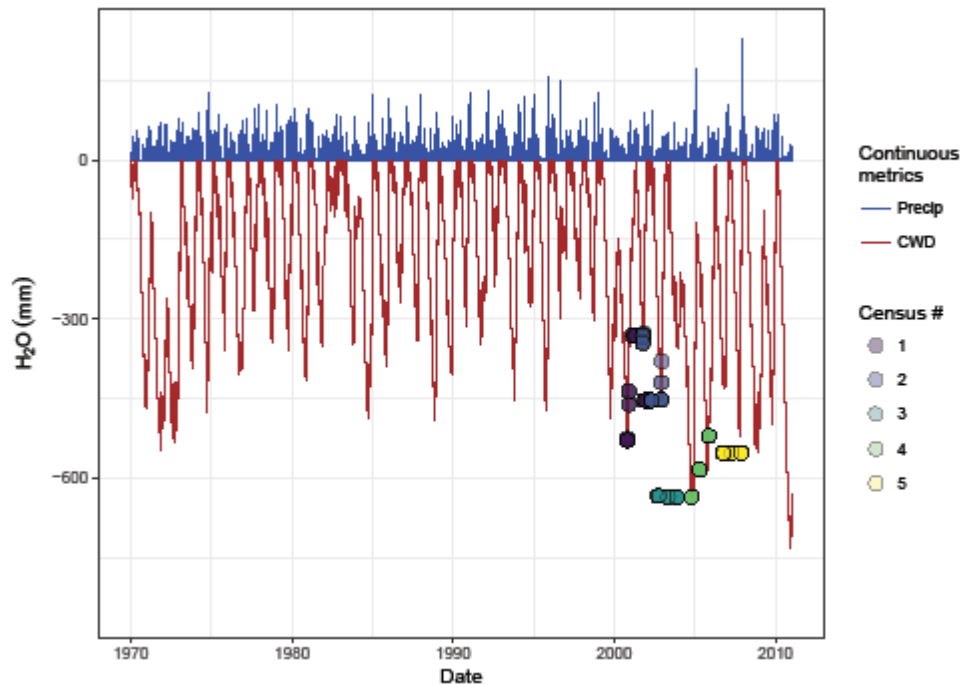
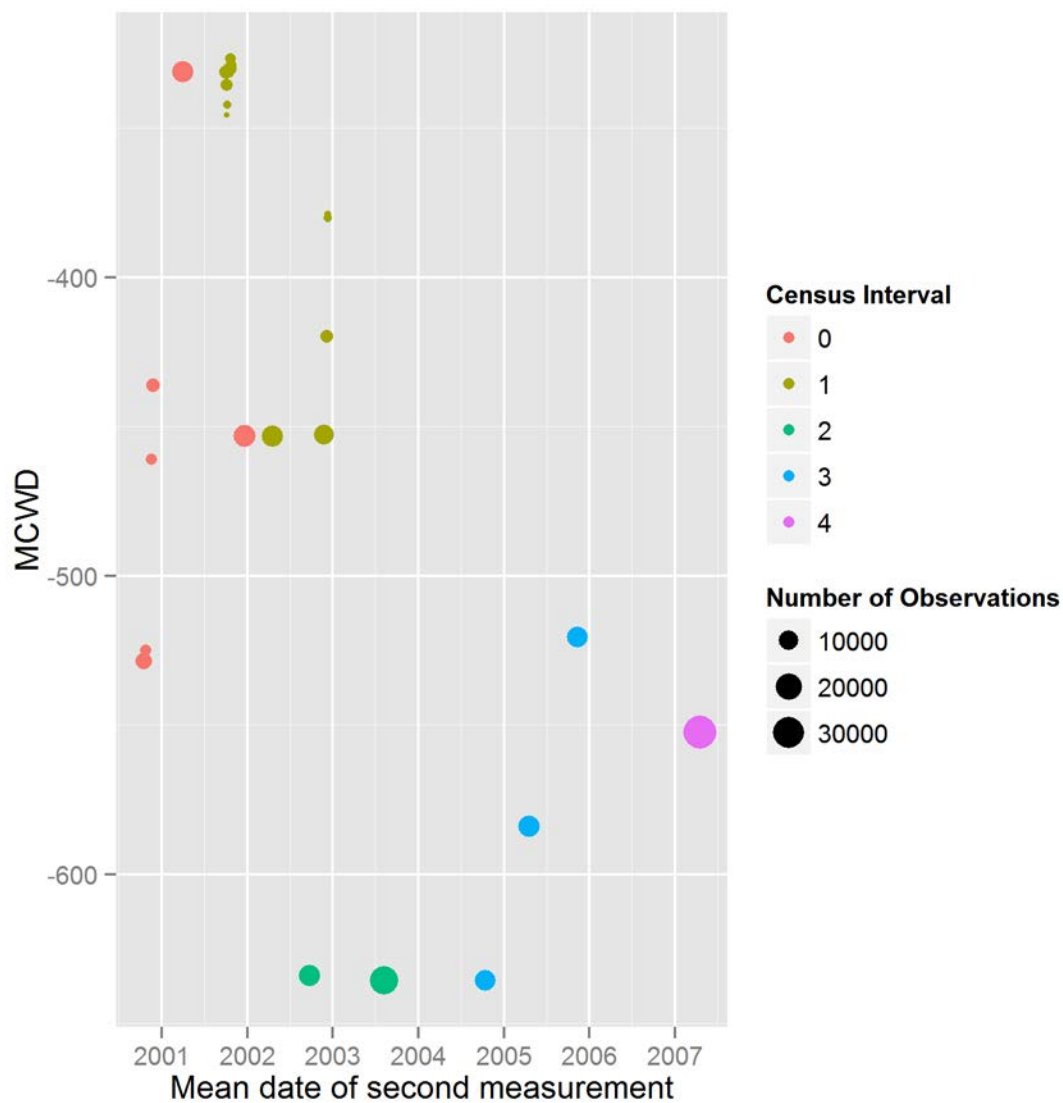


Figure S 3. As in Figure S 2, but with an expanded date range to illustrate the historical context of soil moisture conditions.



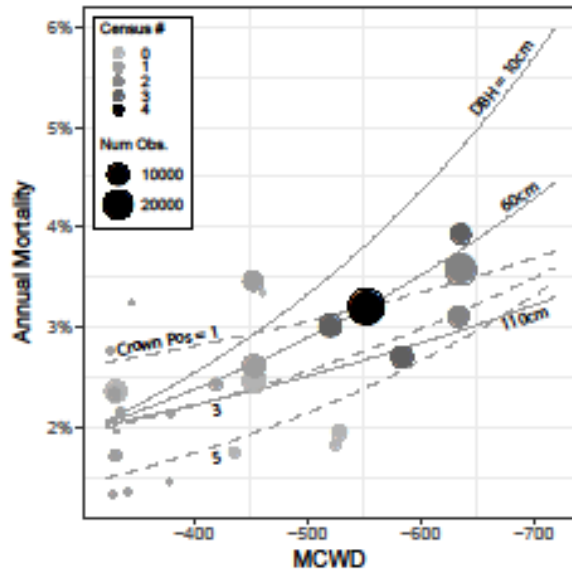
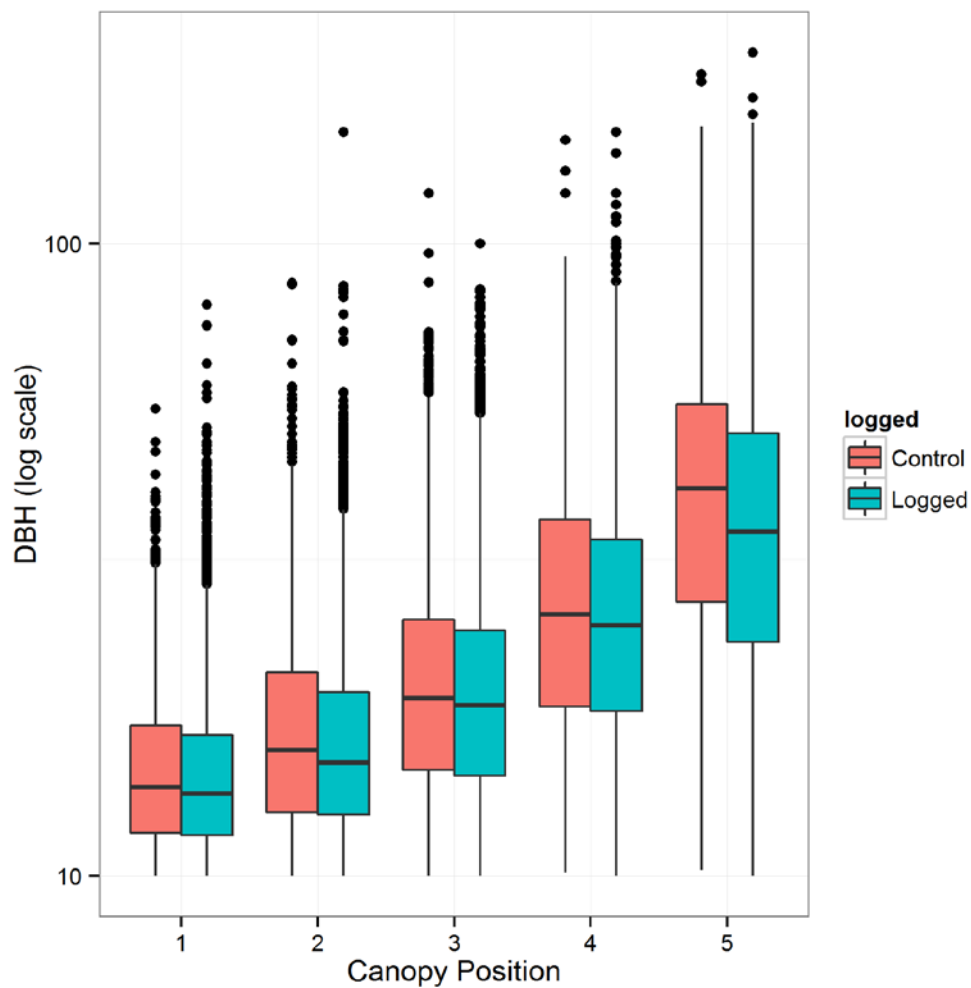


Figure S 5. Mortality rates as a function of MCWD in observed data and modelled predictions. Trees in burned areas or that died as a direct result of forestry operations were removed. Solid lines are mean predictions of the full DBH model (Model 1) for 10, 60, and 110 cm DBH trees averaged across exposure classes; dashed lines are mean predictions for trees with crown exposure classes of 1, 3, and 5 averaged across DBH classes 10 – 200 cm. Conditions go from wet to dry along the x-axis from left to right.

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Figure S 6. Box plot of DBH vs. canopy position (following Clark and Clark [48]: 1 (no direct light), 2 (some lateral light), 3 (10-90% overhead light), 4 (>90% overhead light), and 5 (full overhead and later light)) for all subplots in which trees >10 cm DBH were measured in all post-logging censuses.

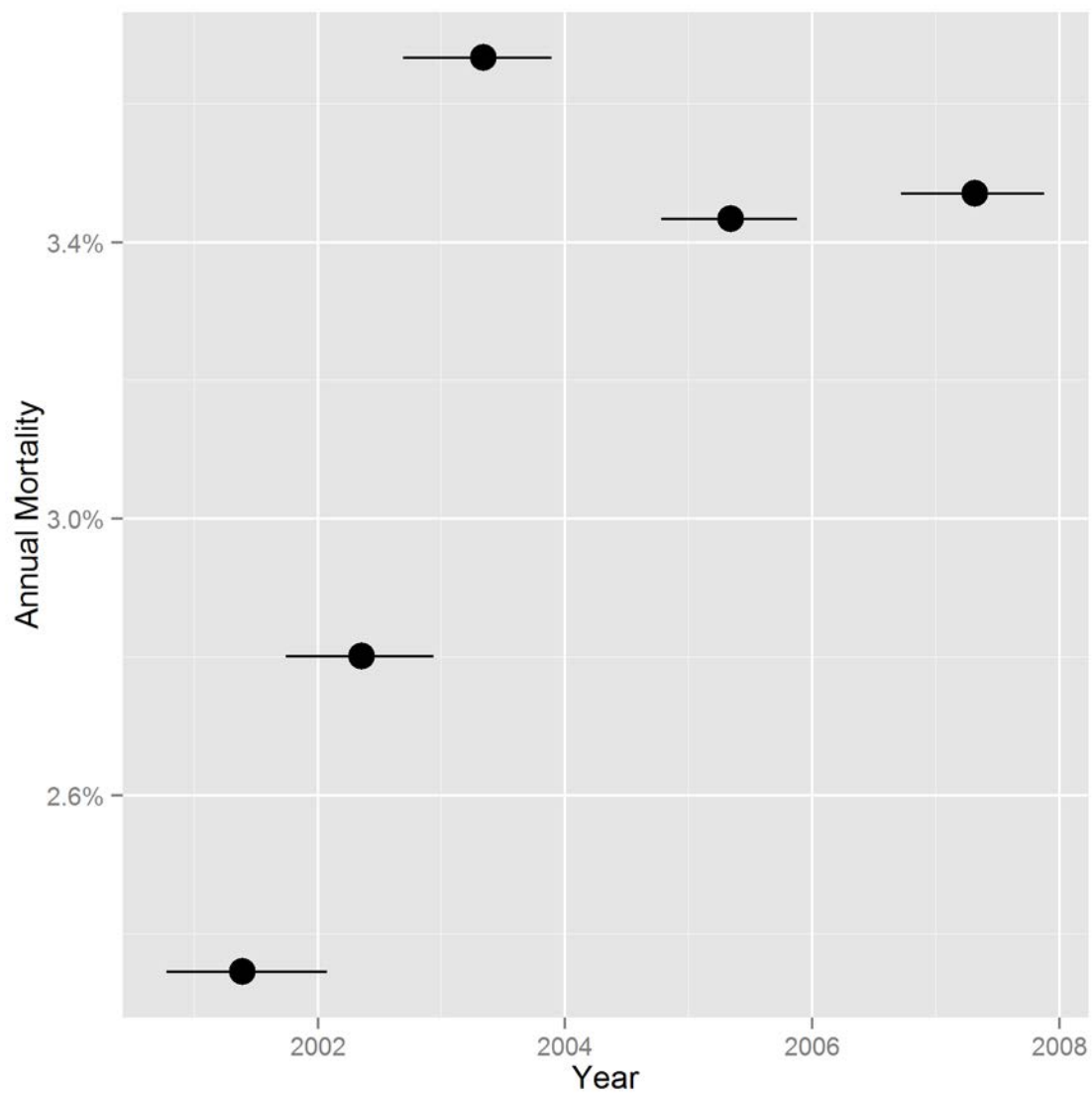


Figure S 7. Large tree mortality rates for each census interval. Tree were removed that died due to logging, silvicultural treatments, and a wildfire. Horizontal lines indicate the time periods over which each census was conducted.

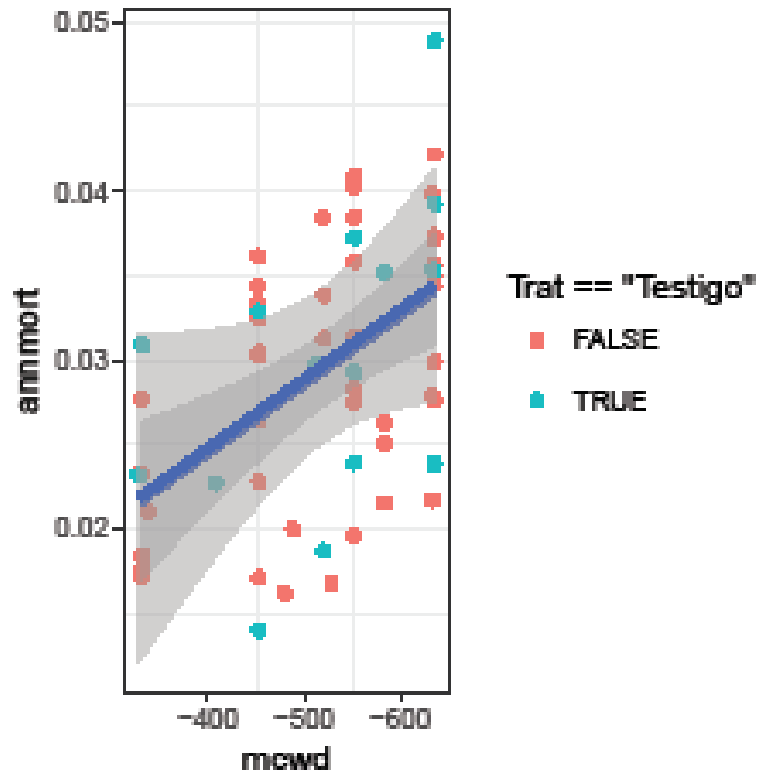


Figure S 8. Annual mortality rates for logged (orange) and unlogged (green) plots. Each point indicates a census in a plot.

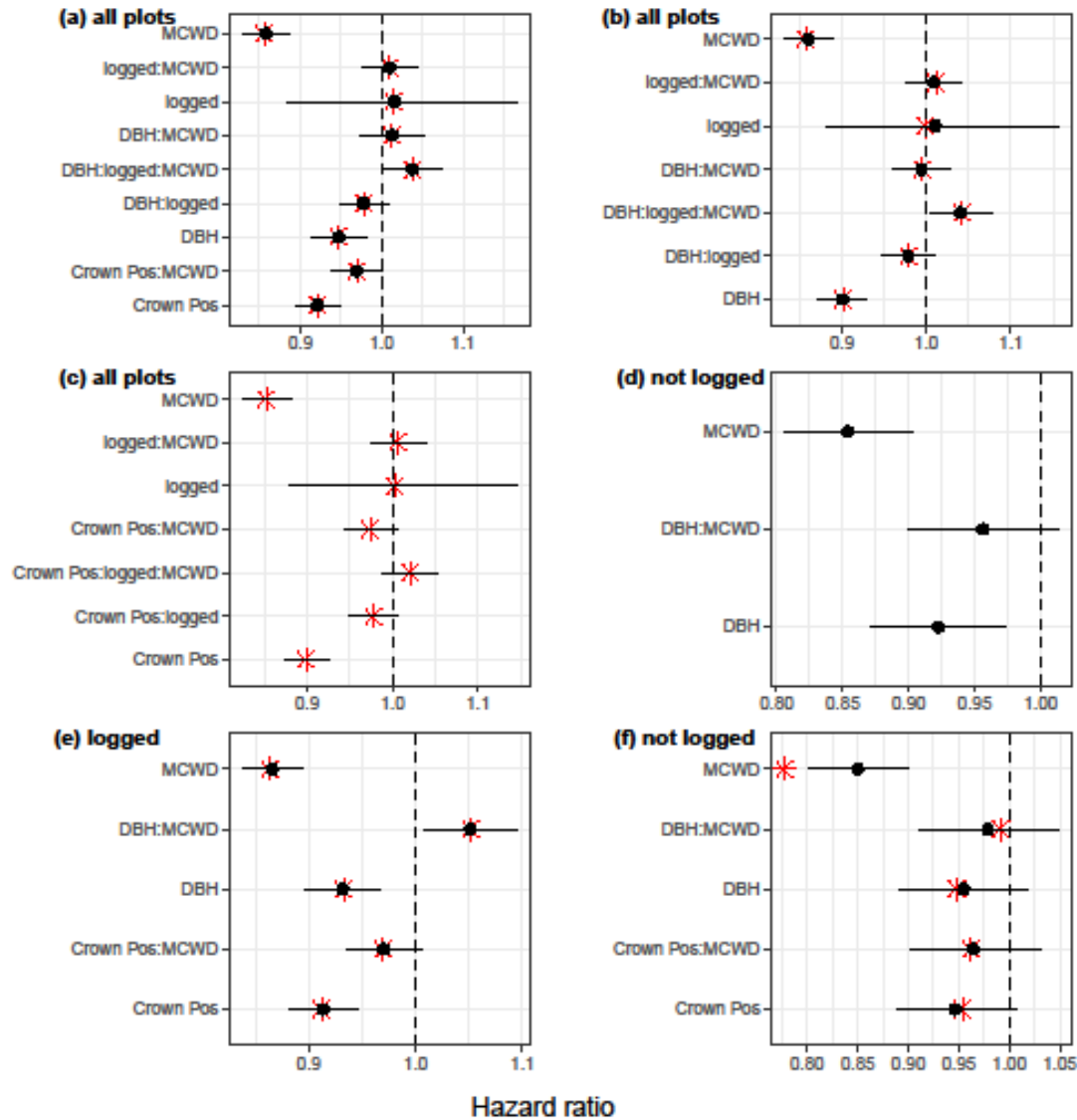
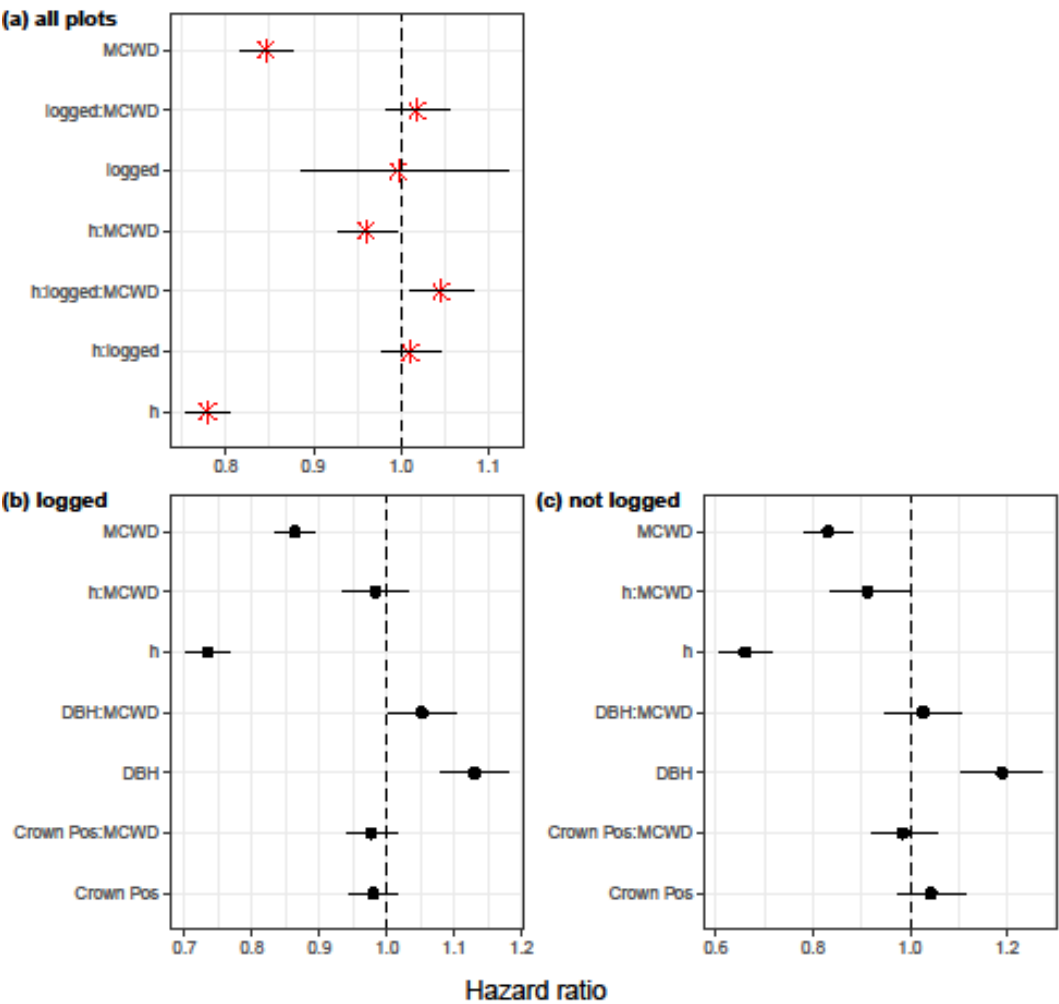


Figure S 9. Hazard ratios (exponentiated coefficients) of selected DBH-based models: (a) The most parsimonious DBH-based model (Model 15, $\text{DBH} * \text{logged} * \text{MCWD} + \text{CP} * \text{MCWD}$), (b) simple DBH logging model (Model 12, $\text{DBH} * \text{logged} * \text{MCWD}$), (c) crown exposure-only model (Model 23, $\text{CP} * \text{logged} * \text{MCWD}$), (d) simple DBH logging model fit with unlogged data only ($\text{DBH} * \text{MCWD}$), and the full DBH model ($\text{DBH} * \text{MCWD} + \text{CP} * \text{MCWD}$) fit in (e) logged and (f) unlogged plots. Black points are the 0.5 quantiles and horizontal bars are the 95% credible intervals fit with a Bayesian INLA algorithm, and red stars are the mean parameter estimates of the corresponding GLMM fit. Intercept and random effects are removed for readability. When black points are missing, the GLMM model converged sufficiently, and the 95% confidence intervals are derived from Wald approximations.

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Figure S 10. Hazard ratios (exponentiated coefficients) of selected height-based models not included in the main text: (a) simple height logging model (Model 22, $h * \text{logged} * \text{MCWD}$), and the model including both height and DBH ($h + \text{DBH} + \text{CP}$) * MCWD fit in (b) logged (Model 30) and (c) unlogged (Model 31) plots. Black points are the 0.5 quantiles and horizontal bars are the 95% credible intervals fit with a Bayesian INLA algorithm, and red stars are the mean parameter estimates of the corresponding GLMM fit. Intercept and random effects are removed for readability. When black points are missing, the GLMM model converged sufficiently, and the 95% confidence intervals are derived from Wald approximations.

PREDICTION PLOTS

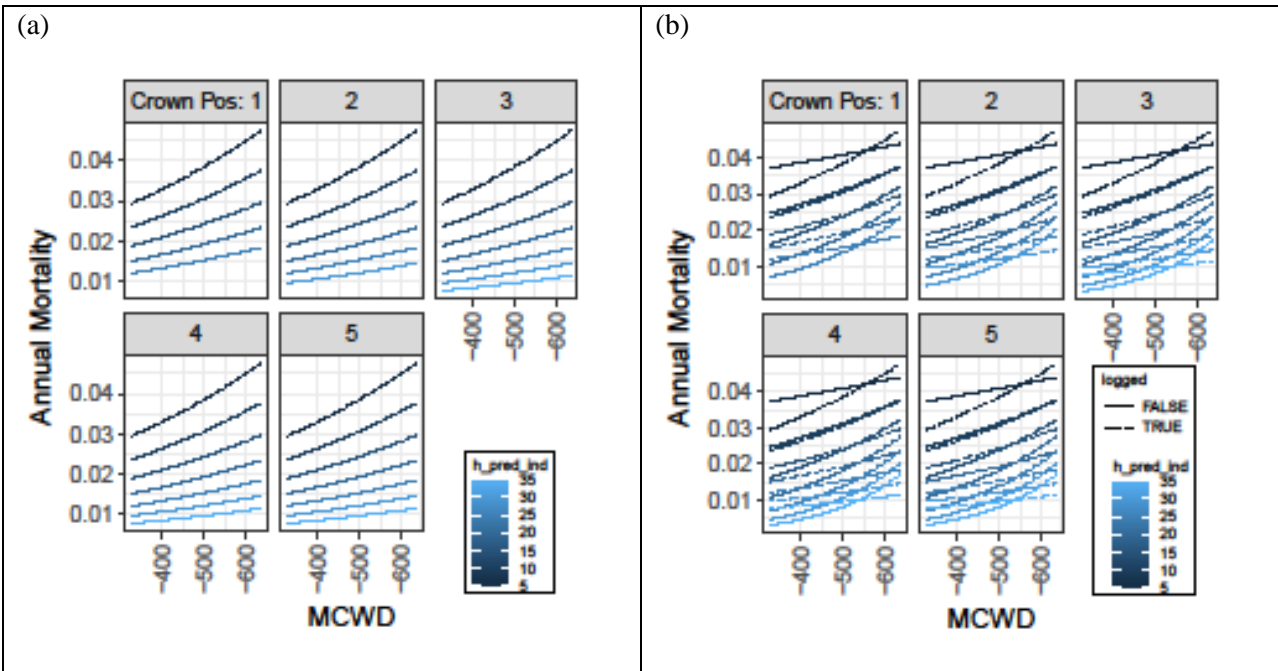
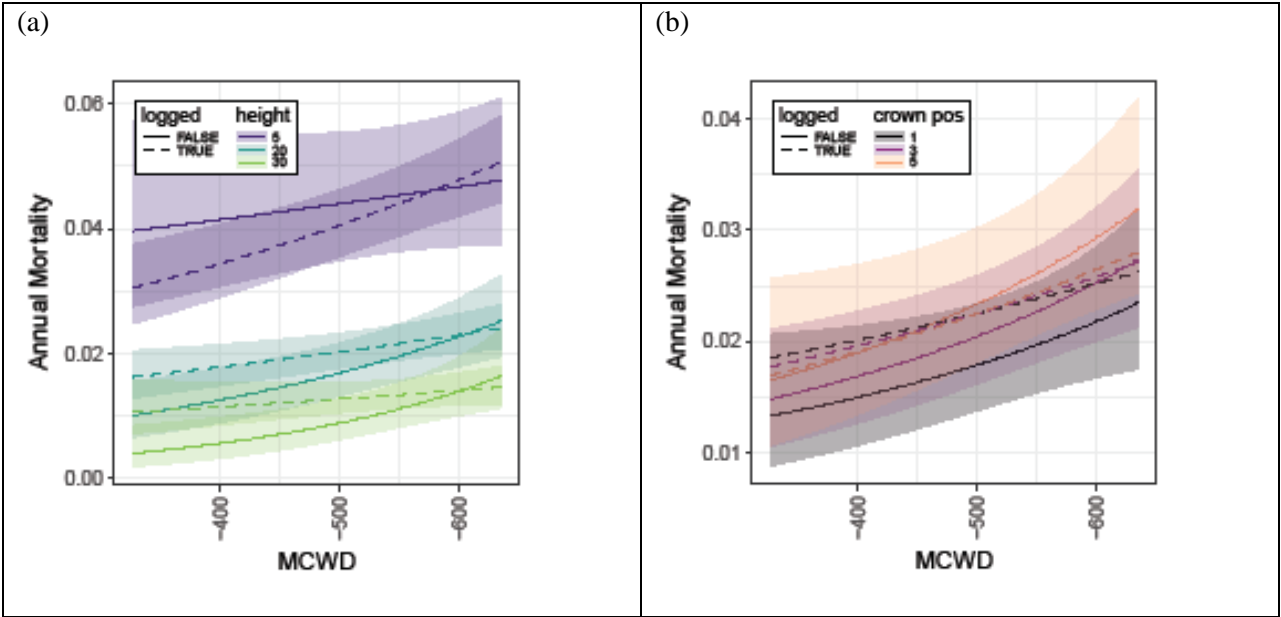


Figure S 11. Predictions of annual tree mortality rates across crown exposure, tree height, and MCWD according to (a) the full height model (Model 5) and (b) preferred logging model (Model 26). Combinations of height and crown exposure for which few data were available were removed from panel (b) (see Table S 6).

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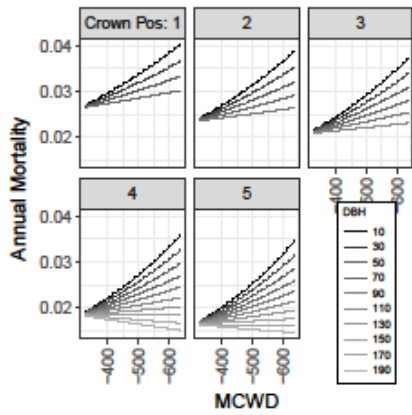
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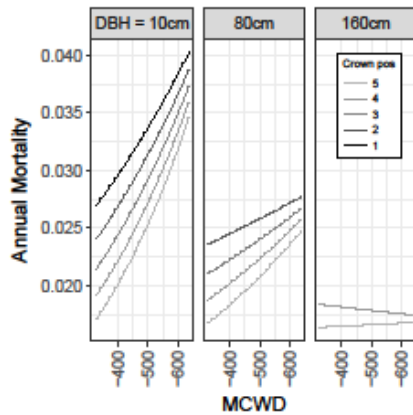
Figure S 12. Annual mortality rates and 95% mean Wald confidence intervals (a) for trees 5, 20, and 30m tall, averaged across crown exposure classes, and (b) for crown exposure classes averaged across trees 5 – 30m tall, as predicted by the most complex height model (Model 29). Confidence intervals removed from logging predictions in panel (b) for readability.

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(a)



(b)



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Figure S 13. Annual mortality rates as predicted by the full DBH model (Model 1, Table S 7) across (a) crown exposure and (b) DBH classes.

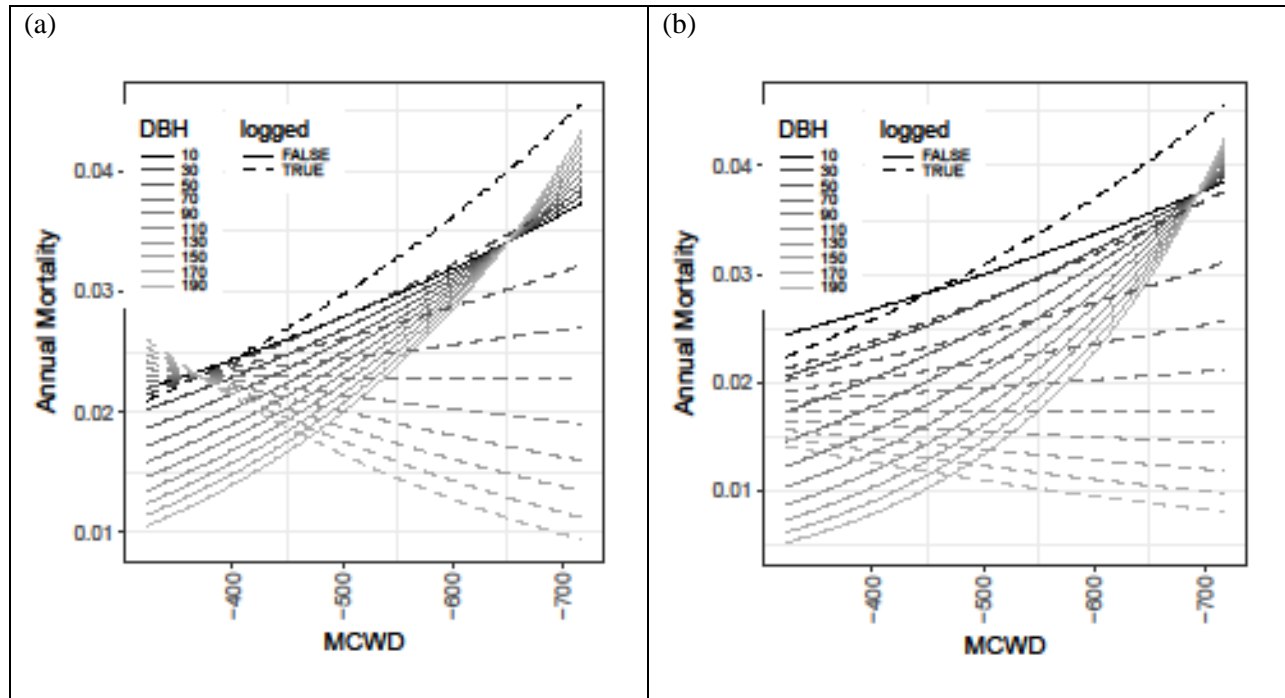
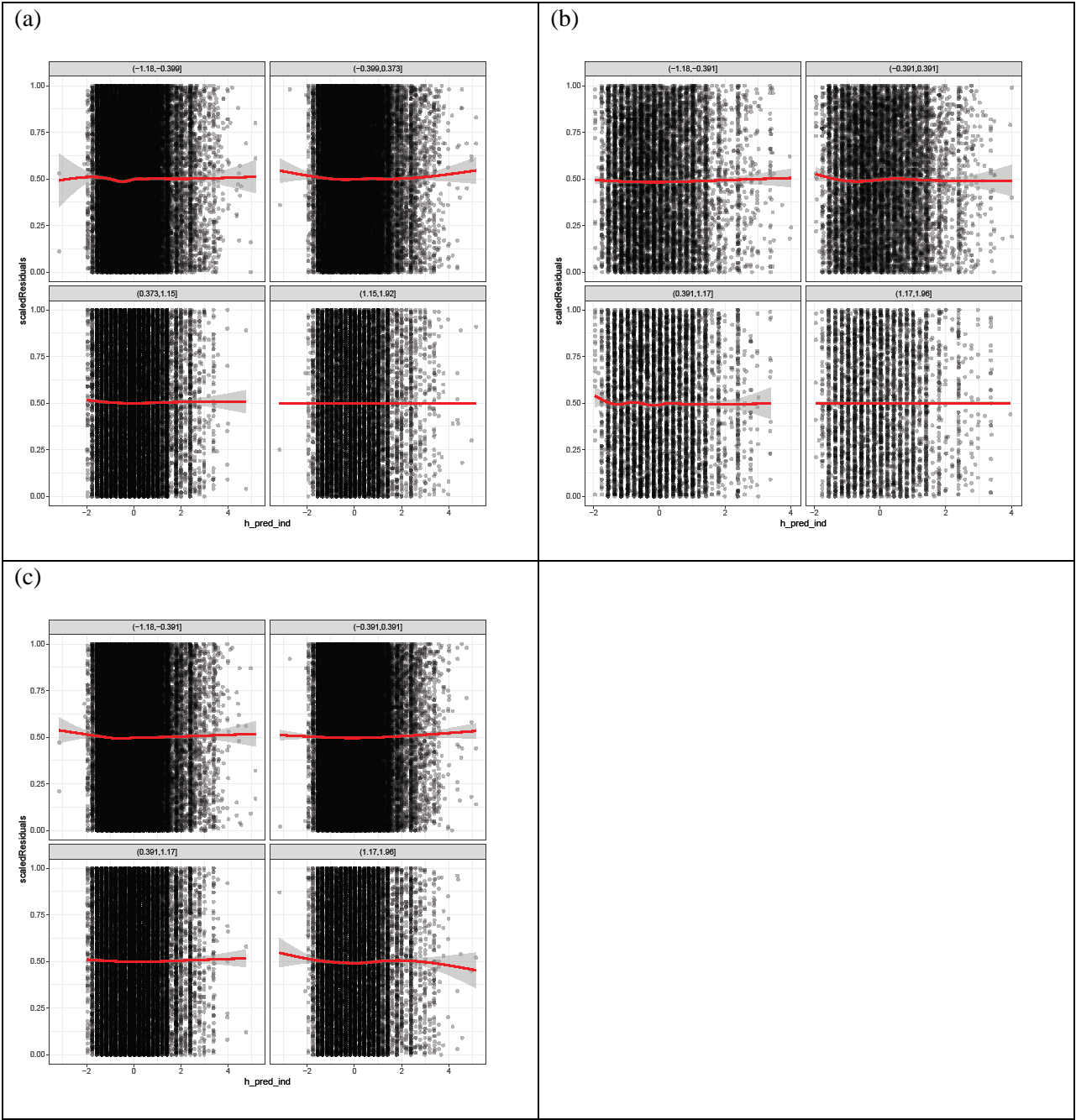


Figure S 14. Annual mortality rates of logged vs unlogged plots across DBH sizes according to (a) the most parsimonious DBH-based logging model (Model 14) and (b) the simple DBH logging model (Model 12). Canopy position had no interactions in this model, so was set to 3 here.

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OTHER FIGURES



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Figure S 15. Scaled residuals of the full height models versus tree height binned across MCWD in (a) logged plots (Model 19), (b) unlogged plots (Model 20), and (c) across all plots (Model 29). Panel titles indicate scaled MCWD range, going from dry conditions in the upper left panels, to wet conditions in the lower right.

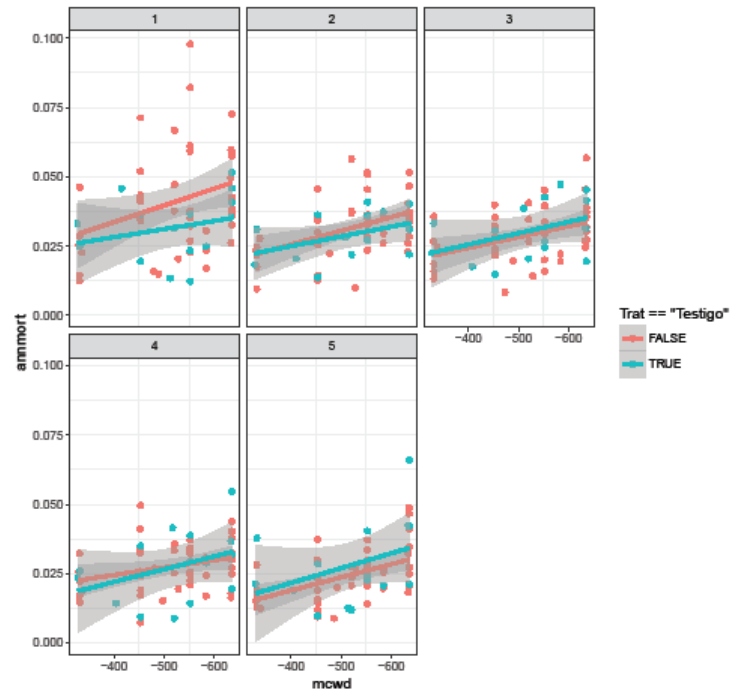
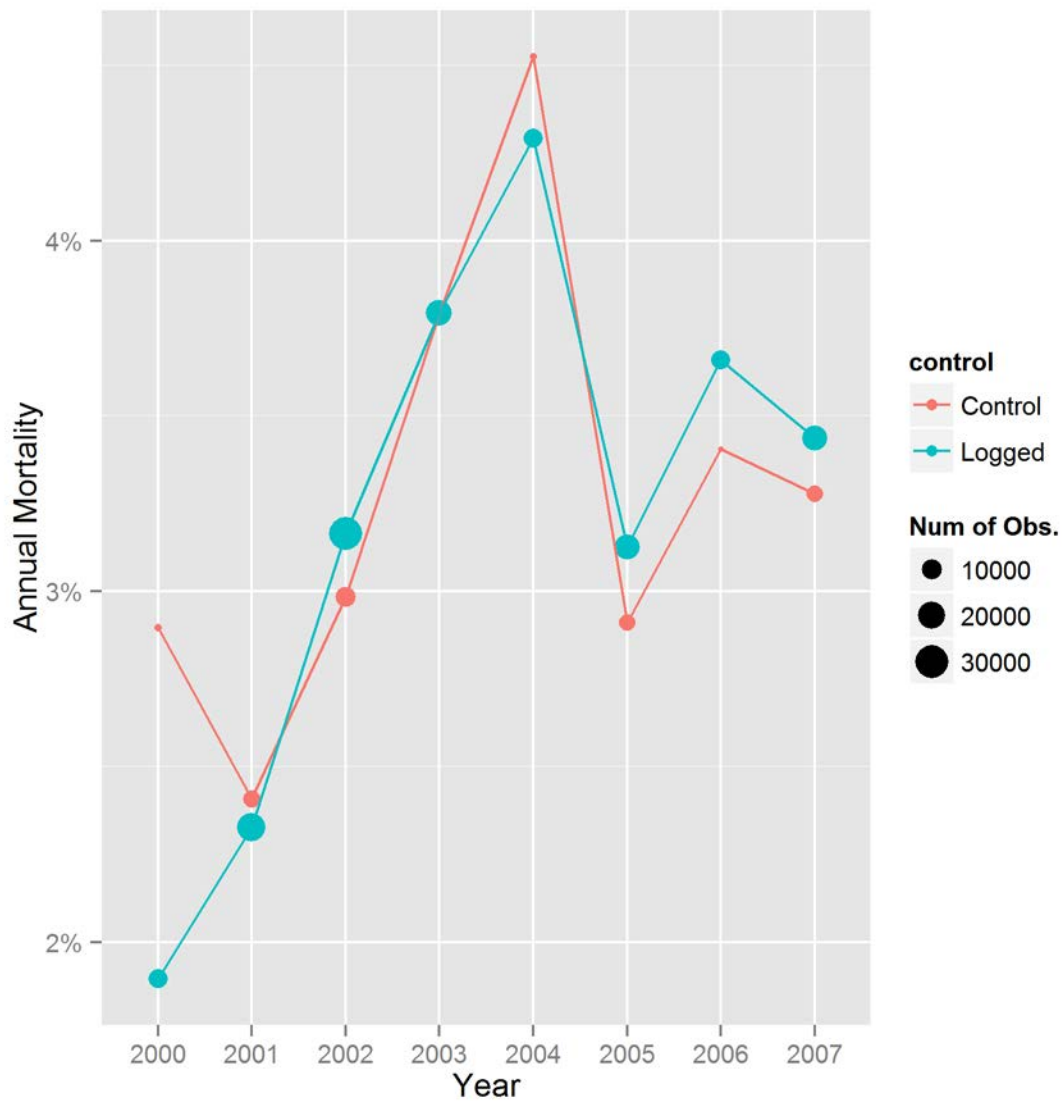


Figure S 16. Annual mortality rates versus MCWD across crown exposure classes for logged (orange) and unlogged (green) plots. Lines are OLS fits.

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Figure S 17. Mortality rates of trees >10 cm DBH versus year of the census. Tree directly killed by logging and silviculture treatments as well as all trees in burned areas were removed. Dot size represents number of survival and mortality events observed.

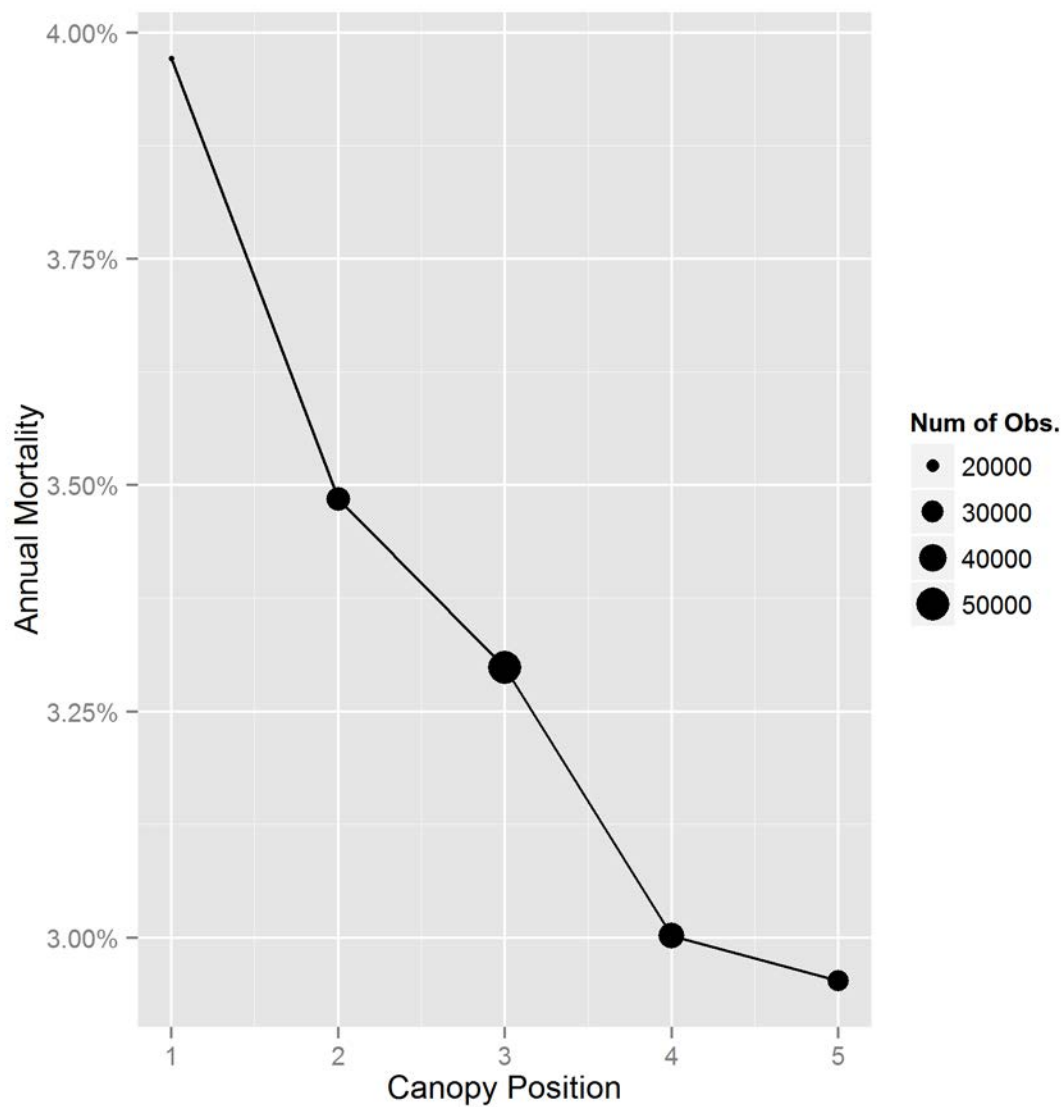


Figure S 18. Adult mortality per crown class (canopy position; Clark and Clark 1992). Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. Dot size represents number of survival and mortality events observed.

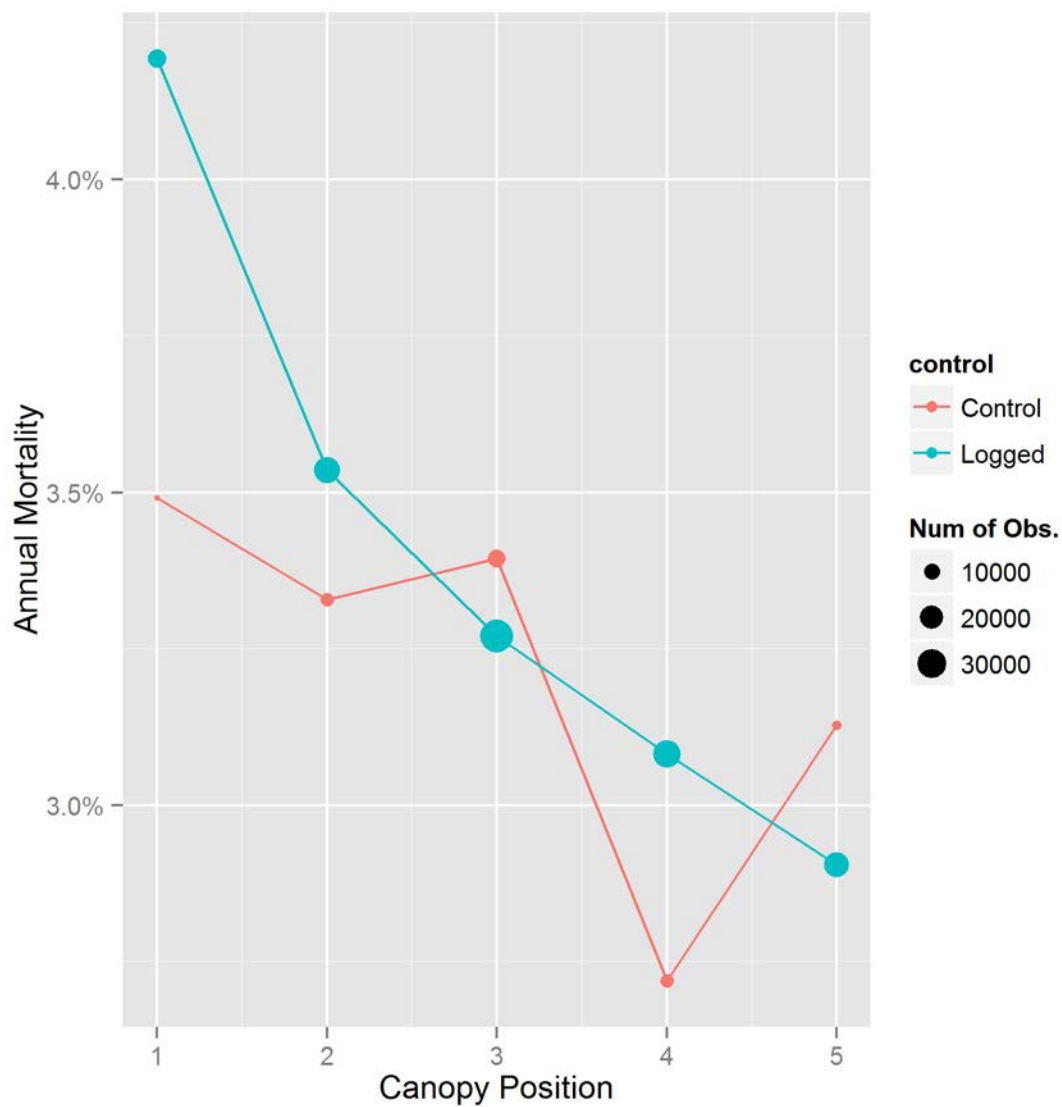


Figure S 19. Adult mortality per crown exposure class for logged and control plots. Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. Dot size represents number of survival and mortality events observed.

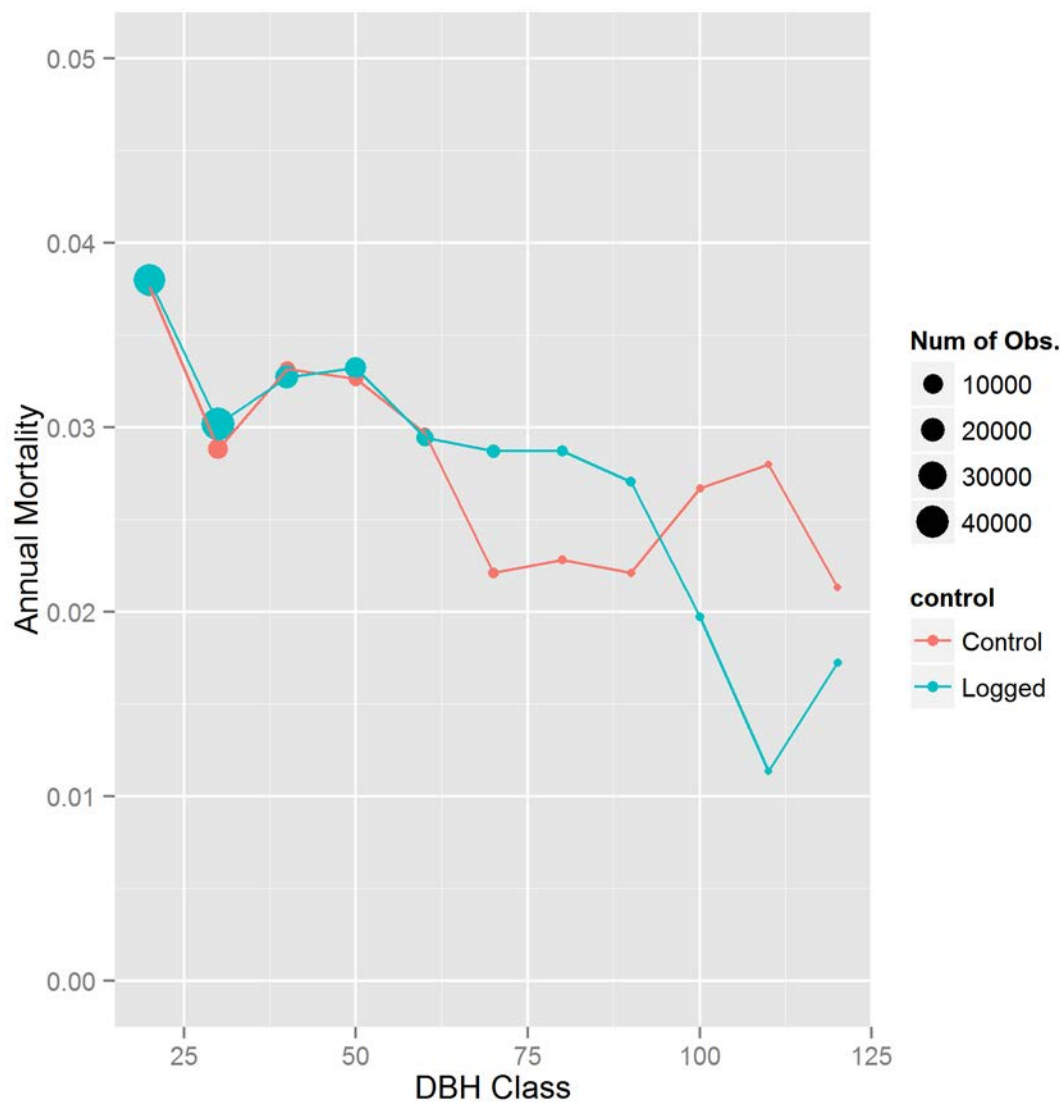


Figure S 20. Adult mortality per DBH class for logged and un-logged plots. Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. Dot size represents number of survival and mortality events observed.

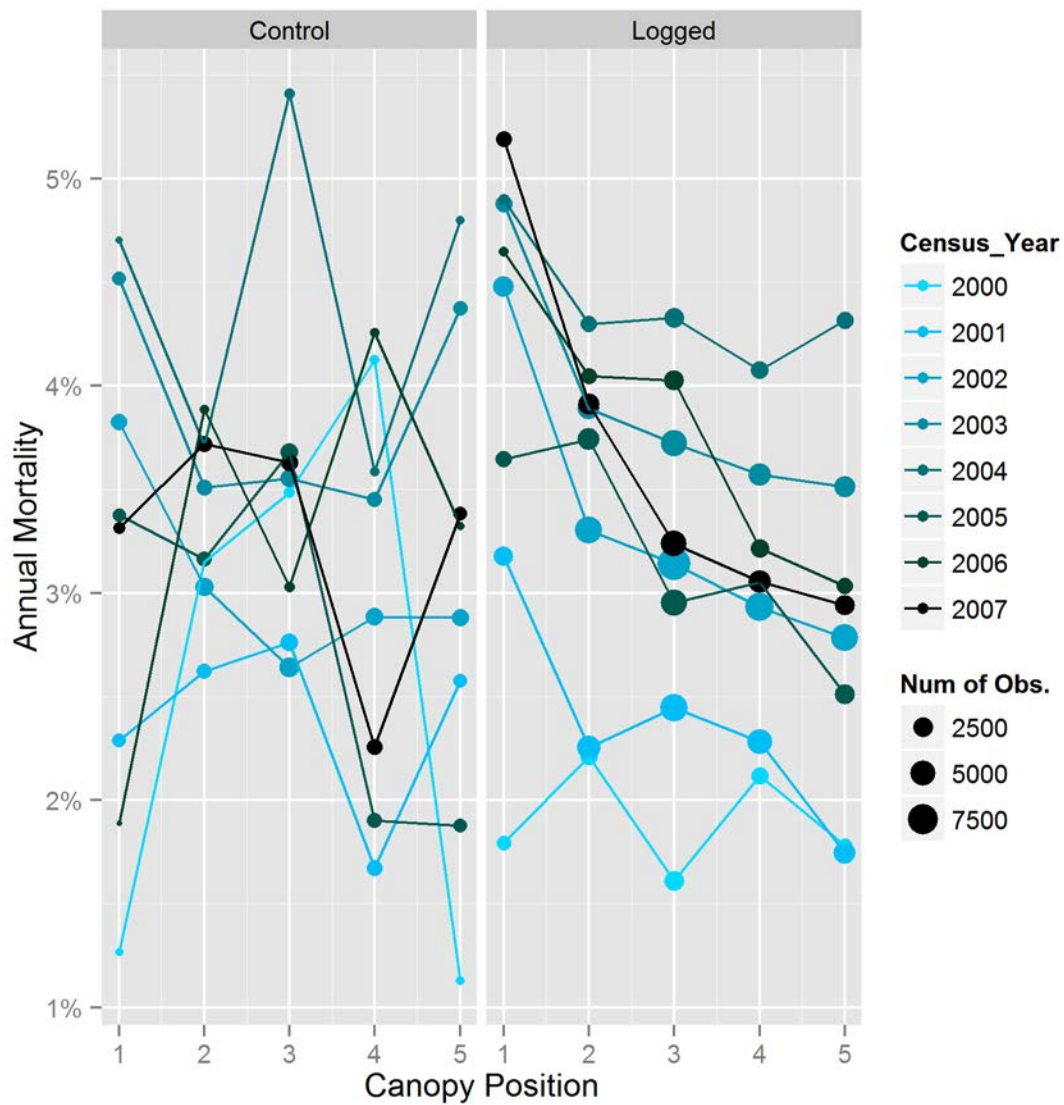


Figure S 21. Adult mortality per crown class for logged and control treatments. Tree deaths due to logging and silviculture as well as all trees in burned areas were removed. Dot size represents number of survival and mortality events observed. Each line represents a different years' census.

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1141
1142 R ENVIRONMENT
1143
1144 R version 3.3.2 (2016-10-31)
1145 Platform: x86_64-w64-mingw32/x64 (64-bit)
1146 Running under: Windows 7 x64 (build 7601) Service Pack 1
1147
1148 locale:
1149 [1] LC_COLLATE=English_United States.1252
1150 [2] LC_CTYPE=English_United States.1252
1151 [3] LC_MONETARY=English_United States.1252
1152 [4] LC_NUMERIC=C
1153 [5] LC_TIME=English_United States.1252
1154
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1157 [8] datasets     methods      base
1158
1159 other attached packages:
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