

1 FATES OF TREES DAMAGED BY LOGGING IN AMAZONIAN BOLIVIA

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Abstract

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Estimation of carbon losses from trees felled and incidentally-killed during selective logging of tropical forests is relatively straightforward and well-documented, but less is known about the fates of collaterally-damaged trees that initially survive. Tree response to logging damage is an important and overlooked ecological processes potentially affecting 2-5% of all extant tropical trees. Here we report on the fates of damaged trees over the first 8-years after logging in a transitional Amazonian forest in Eastern Bolivia. Mortality rates of damaged trees peaked in the first year after logging, and then slowly declined to background rates by the end of the study, indicating that if a damaged tree survives 8 years, it then runs approximately the same annual mortality risk as an undamaged tree. Of all types of logging damage, crown damage reduced growth rates the most while inclined trees suffered the highest mortality rates. Neither wood density nor tree size conferred tolerance to damage, though species with bark exudates were less tolerant of damage. Surprisingly, damaged trees survived droughts better than undamaged trees, perhaps due to their proximity to felling gaps and concomitant reduced above- and below-ground competition or due to their reduced leaf areas and associated reductions in water stress. While this study only tests one interaction between an aspect of climate change and logging, we found a positive signal for forest resilience. This response should be considered amongst others in models of managed forests in climate change scenarios.

Keywords: Logging, Silviculture, Tropical Forest, Trees, Damage, Mortality, Growth, Drought

Introduction

Selective logging affected 20% or more of tropical forests in 2000-2005 (Asner *et al.*, 2009). With 400 million hectares officially designated as timber production areas (about 24% of all extant tropical forests; Blaser *et al.*, 2011), plus a large but unknown amount logged less-formally, logged forests occupy a greater area in some regions than do unlogged forests (Edwards *et al.*, 2014). Logging has a multitude of effects on forests in addition to the felling of trees and removal of merchantable logs. Among these effects is the collateral damage to trees in selectively logged stands where 7 – 41% of stems are unintentionally killed, 9 – 21% are damaged but at least initially survive (Jonkers, 1987; Uhl and Vieira, 1989; Pinard and Putz, 1996; Bertault and Sist, 1997; Werger, 2011), and often >50% of stems fall into one of those two categories (e.g. Nicholson, 1958). Rough calculations using these estimates indicate that 2 – 5% of all extant tropical trees may suffer, or will suffer, some sort of commercial logging damage. The fates of damaged trees that initially survive will affect the global carbon cycle, biodiversity retention, and other important forest functions.

While several studies on selective logging in tropical forests report the incidence of collateral damage and the proportions of trees immediately killed (e.g., Johns *et al.*, 1996; Jackson *et al.*, 2002; Picard *et al.*, 2012), data on the long-term fates of damaged trees are less available (but see Sist and Nguyen-Thé, 2002; Mazzei *et al.*, 2010; Werger, 2011). Such data are needed to understand delayed effects of logging on forest structure, function, and composition, as well as to inform silvicultural decisions and predict future yields. At the same time, because the proportions of trees that suffer initially non-fatal damage are modest and overall mortality tree mortality rates tend to be low, voluminous data are required to quantify the relationship between them. To address this gap, we report on the growth and mortality rates of damaged trees over the

first 8 years after selective logging of a tropical moist lowland forest on the southern rim of the Amazon Basin in Bolivia.

Damaged trees may suffer elevated mortality rates for years or decades after logging, survive but grow slowly, develop heartrots and stem hollows, or largely recover. In the absence of long-term data, most stand projection models assume that overall tree mortality rates are elevated for the first 5-10 years after logging and then decline back to pre-logging rates (e.g., Pinard and Cropper, 2000). In contrast, selective logging in Uganda (14 - 21 m³/ha) was followed by elevated mortality rates that persisted for at least 18 years (Kasenene and Murphy, 1991). Similarly, without the benefit of data on logging damage, Hawthorne *et al.* (2012) reported that mortality rates of trees near felling gaps and skid trails in Ghana returned to background rates only after 22 years, whereas areas within logged stands but away from skid trails or gaps did so after only 15 years. In a Brazilian forest subjected to reduced-impact logging (RIL; average logging intensity of 21 m³/ha), mortality rates of damaged trees were higher than undamaged trees during the year after logging, but were then lower for the next 2-5 years (Table 2 in Mazzei *et al.*, 2010).

Damaged trees are expected to grow slowly and suffer elevated risks of mortality for a number of reasons. Most prominently, damaged stems, branches, and roots are susceptible to infection by pathogens and wood-rotting organisms that, if not successfully compartmentalized, may kill the trees outright or render them prone to breakage (Shigo, 1984). To the extent that the capacities of trees to compartmentalize decay and close bark wounds increase with wood density and production of resin or latex (Romero and Bolker, 2008; but see Romero *et al.*, 2009), the likelihood of post-damage mortality should decrease with those traits. On the other hand, it is not clear whether the traits associated with high wound closure rates (e.g., thick bark and latex

production) vary inversely with the ability to compartmentalize xylem decay (e.g., high wood density). Specifically, Romero and Bolker (2008) provide evidence for this tradeoff in a detailed study but with a low sample size, whereas Poorter *et al.* (2013) found no relationship between wood density and bark thickness in species from the same forest. If such a tradeoff exists, an increase in one trait may not confer greater overall tolerance due to the concomitant decrease in another.

In regards to the effects of mechanical damage on subsequent growth rates, large reductions are expected from crown loss due to reduced photosynthetic surface area coupled with the physiological costs of branch replacement (Rutishauser *et al.*, 2011). Similarly, root damage reduces tree access to water and nutrients while it can compromise structural integrity. These initially non-lethal injuries are also expected to render trees more vulnerable to wind storms, droughts, pathogens, and herbivores (Franklin *et al.*, 1987). While damaged trees are likely to suffer due to the reasons mentioned above, they may also recover quickly due to their likely proximity to the above and below-ground gaps opened by logging (Herault *et al.*, 2010).

To inform predictions about future yields, forest structure, and composition, we take physiological and functional ecological perspectives and ask how different types and severity of logging damage affect tree mortality and growth over time, if some functional traits confer tolerance to that damage, and how damage interacts with drought to affect tree mortality. We predicted that: (1) mortality rates of damaged trees increase initially but then decline to rates similar to those of undamaged trees; (2) trees with snapped stems that resprouted new crowns suffer high mortality rates both initially due to physiological and structural stress and over the longer term due to the effects of pathogens; (3) root damage is more strongly associated with increased mortality rates than crown damage, whereas (4) crown damage is more associated with

decreased growth rates than root damage. Additionally, to test the effect of plant functional traits expected to be related to damage tolerance we predicted that: (5) post-damage survival increases with tree size because larger trees have more stored reserves from which to draw; (6) trees with high wood density suffer lower mortality rates after damage due to their ability to compartmentalize decay and due to their biomechanical resistance to breakage; and, trees with (7) thick bark and (8) latex are more likely to survive than those with thin bark and without latex, given the same damage and all other things being equal, since thick bark and latex are associated with the ability to close wounds quickly (Romero and Bolker, 2008). If there are tradeoffs between wound closure and compartmentalization traits, then we would not expect wood density, bark thickness, or latex production to be associated with damage tolerance. Thus, lack of support for hypotheses (6), (7), and (8) might suggest the existence of this tradeoff. Finally, to test the interaction between tree damage and drought, we have two hypotheses: (9) damaged trees suffer greater increases in mortality during droughts than undamaged trees, and (10) trees with root damage suffer more from drought than those with crown damage due to root-damaged-trees' already-compromised hydraulic capacity.

Methods

This study was conducted in permanent plots of the Long-Term Silvicultural Research Program (LTSRP) that are maintained by the Instituto Boliviano de Investigacion Forestal within the forestry concession of Agroindustria Forestal La Chonta, 30 km east of Ascención de Guarayos, Bolivia (15°47'S, 62°55'W; hereafter, La Chonta). This semi-deciduous forest receives an average of 1580 mm of precipitation annually with 4 months (May-September) that each receive <100 mm (Peña-Claros *et al.*, 2012). The soils of La Chonta are largely nutrient-rich inceptisols (Quintero, in prep). The concession's terrain is undulating with some granitic

outcrops (i.e., inselbergs), none of which occur in the permanent sample plots. In terms of both climate and tree species composition, the vegetation is transitional between wet Amazonian forests to the north and dry Chiquitano forests to the south (Toledo *et al.*, 2011); it falls within WWF's Global 200 Southwestern Amazonian Moist Forest region and is on the edge of the Amazon Basin. Approximately 30% of the 169 tree species that grow to be >10 cm DBH (stem diameter at 1.4 m or above buttresses) are deciduous (Peña-Claros *et al.*, 2012). Another noteworthy feature of La Chonta is the abundance of lianas. In unlogged forest, 73% of trees >10 cm DBH reportedly carry at least one liana >2 cm DBH, infested trees carry 9.3 lianas on average, and 35% of tree crown areas are liana covered (Alvira *et al.*, 2004).

The LTSRP plots were established in 2000-2001 to investigate the effects of different intensities of logging and silvicultural treatments. The permanent plots include three blocks of four 27 ha treatments: control (no logging); normal logging; logging with light silviculture; and, logging with intensive silviculture. Trees were sampled before logging using a nested design: all trees >40 cm DBH (stem diameter at 1.3 m or above buttresses) were located and measured, with all trees >20 cm DBH measured in half the plot and all trees >10 cm DBH in 4 1-ha subplots within each treatment (i.e., 36 ha of logged forests for trees >10 cm DBH). Plots were subjected to reduced-impact logging (RIL) in 2001-2002, 3-7 months after plot establishment, and then remeasured after 1, 2, 4, 6, and 8 years (Table S 1). The crown illumination index (Dawkins and Field, 1978) as modified by Clark and Clark (1992) was recorded for each tree upon remeasurement. Per RIL guidelines, lianas in trees to be felled were cut approximately 6 months prior to logging. Additional silvicultural treatments were applied in some plots after logging (see Peña-Claros *et al.*, 2008 for more details).

During the first post-logging census, types and severities of logging damage were recorded. Damage to roots (3 severity classes: no root damage, superficial root damage [light damage to buttress or surface roots with diameter > 5 cm, e.g., scraped by skidder], or major root breakage), bark (3 severity classes: none, small <20 x 20 cm, or large > 20 x 20 cm), and crowns [6 severity classes: 0%, 1-25%, 26-50%, 51-75%, 76-99%, and 100% of the crown lost; see Mostacedo *et al.* (2006) for more detailed descriptions of the methods] as well as stem inclination (4 severity classes: bole straight, leaning, split and leaning, or uprooted) were recorded. We removed uprooted trees from the analysis because we assumed them to be dead, and this analysis focuses on damaged but living trees. We also removed all trees (damaged or not) that died before the first post-logging census conducted 150 - 269 days after the harvest because we are interested in the fates of damaged trees that survived logging (for immediate collateral damage and further contextual information see Jackson *et al.*, 2002; Mostacedo *et al.*, 2006; Peña-Claros *et al.*, 2008). We excluded all new recruits and trees in the 4 ha that burned in 2004.

To account for the increasingly dry conditions of our study site over the 2000-2010 period, as indicated by increases in the Maximum Climatological Water Deficit (MCWD; Shenkin, 2014), we included MCWD as a term in the model whenever we also included time-since-logging to account for this potentially confounding factor (MCWD versus time-since-logging; Pearson correlation = -0.59; Figure 6). The Climatological Water Deficit (CWD) is calculated as the difference between daily precipitation and estimated evapotranspiration (ET). MCWD is calculated as the most negative CWD experienced during a particular interval (Malhi *et al.*, 2009). Precipitation data are from a weather station in Guarayos, Bolivia, 50 km to the northwest of the study site, and ET is estimated to be 100 mm/mo.

To simplify some analyses we classified trees into 4 damage severity groups: no damage, minor damage (small bark damage, superficial root damage, 1 – 50% crown damage, a leaning stem, or a combination thereof), other major damage (large bark damage, root breakage, 51 – 99% crown loss, leaning and split stem, or a combination thereof), or resprouted (100% crown loss; see Table 1).

Bark data were provided by Poorter *et al.* (2013), who measured bark thickness in this study area using small squares of bark (c. 5 cm x 5 cm) removed from trees at 50 cm above the soil surface; they measured stem diameters at 50 cm and 130 cm. We regressed bark thickness on DBH for each species and used these relationships to estimate each tree's bark thickness. Poorter *et al.* (2013) also classified tree species based on whether or not they produced exudates (i.e., latex or resins). Trees of species for which we did not have data were excluded from analyses involving bark thickness and exudates.

To evaluate whether there is a tradeoff between damage containment (xylem-based) and damage closure (phloem-based) strategies, we abbreviate Chave *et al.*'s (2009) criteria for identifying an economic spectrum of tradeoffs. First we examine whether xylem- and phloem-based traits previously found to be associated with damage tolerance co-vary. Second, we evaluate whether those traits are associated with damage tolerance (i.e., whether they are “functional”). If bark thickness, wood density, or exudate production are associated with tolerance, and if there are correlations (positive or negative) between traits among species, we interpret this as evidence for the existence of a tradeoff between xylem- and phloem-based defenses. Chave *et al.* (2009) point out that plants are likely to maximize fitness by making allocation decisions across a spectrum of traits comprising all tissues. Thus, testing these three

wood-based traits should not be construed as a predictive model for damage tolerance, but rather as an investigation of the specific tradeoff between some xylem- and phloem-based traits.

Data Analysis

Two types of responses to damage were considered: growth and mortality. Growth models were fit using maximum likelihood methods as linear mixed models on repeated measures of trees over time and their associated growth rates. Growth rates were quantified as $(DBH_{t2} - DBH_{t1}) / (time_2 - time_1)$ for each census interval. When the effect of damage types were included as fixed effects, orthogonal polynomial categorical coding was used because damage classes were ordinal or ratios.

Throughout this paper we use the term “survival model” to mean a model in which positive coefficients have a positive relationship with survival rates, whereas “mortality model” indicates a negative relationship between coefficients and survival rates. Two types of generalized linear mixed survival and mortality models were employed. The first fit survival and mortality events to repeatedly-measured individuals during each census period up to 8 years after logging, and included individual and treatments across blocks as random effects (4 treatments across 3 blocks yielded 12 random effect levels). The second type of mortality model employed the same framework, but fit total mortality after 8 years (i.e. no repeated measures) to simplify interpretation of model results. A complementary log-log link function transformed the binary survival probability to an infinite continuous scale. All predictors (both categorical and continuous) were scaled such that they centered on 0 to improve interpretability of interactions and had a standard deviation of 1 to improve interpretability of the predictor’s relative strength of influence on the predicted variable compared to the other predictors (Schielezeth, 2010). Analyses were performed using the lme4 package (Bates *et al.*, 2011) in the R statistical environment (R Core Team, 2012).

Model results are plotted as $e^{\text{coefficient value}}$, which for generalized linear mixed models with complementary log-log links such as we are using, corresponds to hazard ratios (Heisey *et al.*, 2014). A hazard ratio represents the ratio of the probability of survival or mortality of the group corresponding to the model coefficient to the probability of survival or mortality of the control group with the lowest level of that coefficient. For example, the stem inclination predictor has a value of ~ 1.6 in Figure 2a. Thus, trees with “split and leaning” stems (see Table 1) are 1.6 times more likely to die after 8 years than trees with upright stems.

Our survival and mortality analyses have at least two advantages over classical survival analysis given the available data. First, our data are strongly interval censored (i.e., the exact date of tree death is not known; we only know that a tree died between two census dates), which complicates classical survival analyses. Second, our analyses involve both group- and individual-level variation (or “frailty” in the survival analysis literature). Both of these can be handled in survival analyses, but adding each one restricts the scope of procedures that can be used.

Results

Of the 25,734 surveyed trees >10 cm DBH that survived logging, 2.5% suffered minor damage, 1.6% major damage, and the stems of 1.4% snapped and resprouted (Table 2). Resprouted trees suffered the highest cumulative mortality over the 8-year post-logging monitoring period, followed by those with other major damage, and finally those with minor damage (Figure 1a). Annual mortality rates for all damage groups were highest in the first post-logging census, declined sharply in the next census, and then declined slowly thereafter (except for the minor damage group which remained more-or-less constant) until the final census in year 8 when the mortality rates approach those of undamaged trees (Figure 1b). Mortality rates of trees with minor and major damage rose in 2006-2007, 6 years after logging, during which

period an El Niño drought occurred (Lewis *et al.*, 2011; Shenkin, 2014). Mean mortality rates of undamaged trees fall within the 95% confidence interval of rates for trees with minor damage by the fourth year after logging, while mortality rates in the other groups remained higher than for undamaged trees until year 8.

Root damage, bark damage, crown damage, and especially stem inclination were all associated with substantial increases in tree mortality (Figure 2a). Compared with undamaged trees, snapped and resprouted trees were almost 2.5 times as likely to die, and trees with other major damage 2 times as likely to die within 8 years after logging. Other than during the first post-logging census interval (i.e., 150 - 269 days post-logging) when they were 3-times more likely to die (Figure 1b), trees with just minor damage did not suffer significantly-elevated risks of mortality (Figure 2b). Models that included DBH did not detect elevated mortality rates of trees with minor damage when considering the entire 8-year post-logging interval (Figure 2b). In contrast, models that did not include DBH found elevated mortality of trees with minor damage, indicating an interaction between DBH and the minor damage group. More to the point, this interaction implies that the minor damage group contained a disproportionate number of small trees, and thus when the elevated mortality rates of small-DBH trees were accounted for, the additional mortality risk associated with having received minor damage was lower.

Growth rates of trees with major (-0.05 cm/year; 95% CI 0.12 to -0.02) and minor (-0.06 cm/year; 95% CI 0.13 to 0.00) damage were slower than undamaged trees, but these effects were only marginally significant (Figure 3b). Trees that suffered crown damage showed the most notable reductions in growth rates, with snapped trees (100% crown loss) growing 0.33 cm less in diameter per year than not-snapped trees (Figure 3a and Figure S 2). Recorded root damage was associated with reductions in growth up to 0.15 cm / year, though there was substantial

variation in this relationship (Figure 3a and Figure S 3). Just as the size of bark damage failed to affect mortality rates, neither did it affect growth rates substantially (Figure 3a and Figure S 4). Although stem inclination was associated with increased post-logging mortality rates, it apparently did not affect growth (Figure 3a and Figure S 5).

To elucidate how tree size relates to responses to mechanical damage, we examined the interactions between DBH and various types and classes of damage. While larger DBH trees (including damaged and undamaged trees) suffered lower mortality rates than smaller DBH trees (Figure 2a), likelihood ratio tests show that the interactions do not differ from zero (Table 3). Still, of all the interactions tested, tree size most noticeably modified the effects of bark damage, though in the direction opposite the expected (i.e., smaller trees seemed to tolerate more bark damage; Figure 4). Tree size also did not affect mortality responses to damage between damage groups except in the case of resprouted trees, for which smaller trees tolerated crown loss better than larger trees (Figure 4b). This marginally-significant result suggests that mortality rates increased more for larger than for smaller trees that snapped and resprouted, after accounting for overall effects of DBH on mortality rates.

Contrary to our expectations, higher wood density only marginally reduced mortality of damaged trees compared to non-damaged trees (wood density : damaged term, estimate = -0.45, SE = 0.034, $p < 0.19$; Figure S 6). Likelihood ratio tests are equivocal because, while addition of the wood density: damage interaction did not improve the model, further addition of the wood density direct effect did (Table S 2). We interpret this to mean that while high wood density is related to lower mortality rates for trees overall, high wood density is not important in protecting trees against logging damage-induced mortality. AIC tests with all permutations of these terms (not shown) result in all models being within 2.3 AIC units of each other (the simplest model

containing just DBH and a binary damage variable (yes/no), and excluding wood density terms, is slightly more parsimonious by 1.9 AIC points).

While trees with thicker bark experienced higher mortality overall after accounting for DBH, thicker bark had almost no effect on reducing mortality from damage (Figure S 7). These results remained largely the same when we restricted the analysis to trees that either experienced no damage or damage to the bark (e.g., trees that had damaged crowns but not bark were removed; Figure S 8).

In contrast to the wood-density and bark-thickness results, the capacity to produce latex was related to post-logging survival of damaged trees, but not in the expected direction. Considering just non-damaged trees, exudate-producing species actually survived better overall. In contrast, mortality rates of exudate-producing trees increased much more as a result of damage over the 8-year post-logging interval than those of trees that do not produce exudates (Figure S 9).

Our evaluation of potential tradeoffs between damage tolerance strategies found that, in contrast to wood density and bark thickness, latex production showed an appreciable effect on the survival of damaged trees. Of the three two-way correlations among these three traits, only bark thickness and wood density of tree species were correlated, with thicker-barked trees having less-dense wood (correlation coefficient = -0.29, Pearson $P = 0.0483$, $n = 46$ species; means of bark thickness and wood density did not differ across species that produce exudates versus those that do not, two-sample t -test, $t = 0.29$, $df = 42.3$, p -value = 0.78 for estimated bark thickness at 130 cm DBH and $t = -0.58$, $df = 38.1$, p -value = 0.57 for wood density).

Drought, time since logging, and whether a tree was damaged or not had the largest influence on mortality rates in models that considered other factors but reduced damage to a

binary response variable (damaged/not damaged; Figure 5). Compared to damaged trees, mortality rates of undamaged trees increased more during droughts. The nested model without the damaged:MCWD term is better than that without the damaged:time since logging term. Regardless, the full model with both interactions explains the data better than either of the nested models (Table 4). While mortality rates did not decline linearly with time since logging (Figure 1b), the drought model does not consider the first pre-logging observation, and thus does not have to fit the non-linear mortality peak in the first post-logging census. Hence, the assumption of a linear relationship between mortality rates and time since logging is supported. We conclude that both time since logging and interval dryness affect the mortality rates of damaged trees.

Looking further into the interaction of drought with damage type, we found that trees with root damage suffered greater declines in survival due to drought than did those with crown damage (Figure S 11). During drier periods, root damage reduced tree survival, and neither crown damage, bark damage, nor inclination had significant effects.

We found little difference in tree response to damage across the 3 silvicultural treatments. Mortality of damaged trees over the 8-year interval did not vary across treatments when damage was coded as a binary response variable (damaged/not damaged; not shown). When we disaggregate the damage types across the treatments, most interactions are not significantly different across treatments. There are one significant and two marginally-significant interactions all involving the Improved treatment: trees with bark damage were better off in the Improved treatment ($p < 0.007$), and trees with root and crown damage were marginally worse off ($p < 0.087$ and $p < 0.057$ respectively; Figure S 10).

Discussion

This study was carried in a forest logged with recommended RIL practices and then subjected to various silvicultural treatments. The area disturbed by logging and damage to the residual stand in this forest were lower than reported in other studies, but total collateral tree damage was in line with other studies due to higher impacts of skid trails (Jackson *et al.*, 2002).

Mortality rates of damaged trees were initially high after logging but then nearly converged on those of undamaged trees within 8 years at which time they were only 1–2% higher than background rates; for trees with only minor damage, convergence took only 3 years (Figure 1b). These results suggest that if a damaged tree manages to survive for 8 years after logging, it is likely to have a lifespan similar to an undamaged tree, though longer-term data are needed to confirm this conclusion. Our findings are in line with those of Sist and Nguyen-Thé (2002), who found that mortality rates more than doubled for damaged trees for 2 years post-logging, and those of Ruslandi *et al.* (pers comm; 2012) who found that mortality rates of damaged trees remained slightly elevated 6 years post-logging in the same forest.

Snapped and resprouted trees seem to have largely recovered after 8 years. Those that managed to survive to the last census interval of the study had mortality rates indistinguishable from trees with other major damage during that last interval. This result refutes the hypothesis that mortality of resprouts will remain high due to pathogen infection.

Trees snapped by logging may have an advantage over trees similarly damaged by natural disturbance. After 8 years, 57% of the 372 trees whose crowns snapped and resprouted in our study were still alive, whereas Putz and Brokaw (1989) found that only 30% of 88 snapped and resprouted trees in an unlogged forest in Panama were still alive after 7 – 11 years. Greater levels of overall disturbance and other treatments such as liana-cutting and silvicultural

treatments may play roles in the observed differences, though many other differences exist between these two forests.

The lack of correspondence between growth (Figure 3b) and mortality rates (Figure 2b) of trees with minor damage, major damage, and resprouts is puzzling. While resprouted trees suffered both high mortality and low growth rates, trees with other major damage suffered increased mortality but not much diminution in growth. In contrast, trees with minor damage suffered only small increases in mortality but reductions in growth rates that were not detectably different from the effects of major damage. This pattern might be understood if the weaker trees with major damage are more likely to die, and those that do survive are more likely to thrive. If trees with minor damage are not very likely to die, then even trees that were disadvantaged prior to receiving damage may persist but grow even more slowly. Other explanations might include correlations between damage intensity and increased resource availability due to proximity to logging gaps.

Trees with slight crown damage grew faster than undamaged trees as evidenced by a negative crown damage² term in Figure 3a, and hence a downward-facing parabolic shape in the growth response to crown damage. Inspection of the prediction lines in Figure S 2 corroborates this result, as 1-25% crown damage corresponds to increased growth rates compared to the 0% damage class, and declines thereafter. This is likely attributable to slightly-damaged trees being nearby logging gaps and hence able to benefit from competitive release. Trees with heavier damage are also likely to be nearby gaps, but will be too damaged to take advantage of the freed-up resources.

Root and crown damage both slightly increased mortality, whereas crown damage substantially decreased growth rates compared to root damage, especially when it was severe. Given the

correlated nature of damage data (e.g., an inclined tree is likely to have suffered root damage), disentangling the individual effects of each type of damage remains a challenge. When we remove all other damage factors except root and crown damage, root damage is a stronger predictor of mortality than crown damage (coefficients of 0.39 and 0.32 for root and crown damage, respectively, both $p < 0.001$), whereas crown damage has a stronger influence on growth than root damage [coefficients of -0.090 ($p < 0.05$) and -0.104 ($p < 0.001$) for root and crown damage, respectively]. Our findings only partially support our hypotheses that root damage is of more consequence for tree mortality whereas the effects of crown damage are mostly on growth rates: crown damage was consistently more important in terms of growth, whereas the effects of root and crown damage on mortality were similar.

DBH had an unexpectedly-small influence on the mortality rates of damaged trees. While it is possible that our sample sizes were too small to detect an effect in a model with 7 – 9 terms, the model term related to the role of tree size in damage tolerance (DBH : damaged) is still small and insignificant when simplifying the model to 3 terms: damaged/not-damaged (estimate = 0.29, $P < 0.001$), DBH (estimate = -0.11, $P < 0.01$), and their interaction (estimate = 0.016, $P = 0.65$). If DBH does influence damage-induced mortality, the effect is noisy and difficult to discern (Figure 2b).

Contrary to our expectation, the mortality rates of damaged trees did not decrease with increasing wood density. The mean response did reflect our expectation that trees with higher wood densities experienced lower mortality rates overall, but wood density did not significantly affect damage tolerance (Figure S 6). Adding wood density to the survival models did not improve them in terms of AIC, but neither did it degrade them (Table S 2). Thus, while wood

density seems to have some marginal explanatory power for mortality of damaged trees, it is apparently not a strong factor.

Could logging damage tend to be more severe than damage from natural disturbances, and hence favor trees that are efficient at constraining xylem-decay versus closing off wounds? If that is the case, we would expect to see a positive signal from the wood-density analysis, but such a signal was lacking. This remains an intriguing question for future research.

While bark thickness does protect trees from fire in this forest (Shenkin, 2014), it does not seem to protect them from mechanical damage. Poorter *et al.* (2013) reported a negative relationship between bark thickness and wood density in a dry Bolivian forest, and an insignificant but negative relationship in the same forest as this study. In contrast, we find a significantly negative relationship between wood density and bark thickness. Thus, while these traits may be traded off with each other, neither seem to have direct effects on damage tolerance and are therefore not likely to play a role in damage tolerance strategies.

The surprising and relatively strong result that exudate-producing tree species were more vulnerable to damage than non-exudate-producing species is difficult to explain. It may be that an economy of damage tolerance is at work here, and that while species with exudate production are more able to close wounds quickly, they may be less able to constrain xylem decay (Romero and Bolker, 2008). Exudate-producing species had similar bark thickness and wood densities as non-exudate-producing, and the relationship between wood density and bark thickness is not different between species with and without exudates.

While mechanical strength has long been considered an important property of wood in tradeoffs (Baas *et al.*, 2004), Chave *et al.* (2009) expanded the consideration of resilience to disturbance to include defensive properties of wood as quantified by wood secondary compounds

in addition to mechanical strength and elasticity. We expected but failed to find support for the role of wood density and bark thickness in tradeoffs of damage tolerance strategies. Exudates do seem to play a role, but they are traded off with neither investment in wood density nor in bark thickness.

We found that under drought conditions, mortality rates of damaged trees increased less than those of undamaged trees. This result bears further investigation, but one possible explanation is that damaged trees are likely to be near logging gaps and skid trails where they receive more light and suffer less below-ground competition for water, which allows them to weather droughts better than trees in intact areas. Another explanation is that crown damage reduces leaf area, thereby reducing water demands that cannot be satisfied during droughts. While counterintuitive, these results are supported by other studies that have found that drought can, in some cases, benefit surviving trees (Anderegg *et al.*, 2015), and that thinned stands may weather drought better than non-thinned ones (McDowell and Allen, 2015). Thus, if greater resource availability outweighs damage incurred, then slightly damaged trees near gaps may understandably perform better than undamaged interior trees during drought.

Drought and damage may interact via a number of pathways. For example: root damage may reduce water potentials beyond what drought would otherwise cause, thereby precipitating cavitation or at least leaf wilt. Similarly, crown damage may reduce non-structural carbohydrate storage prior to drought, thereby making trees vulnerable to drought-induced mortality (Doughty *et al.*, 2015), or it might increase survival by reducing leaf area and therefore transpirational water demand. Hence, while we hypothesized that root damage would affect tree survival during droughts more than crown damage, various outcomes could reasonably be expected. Our

analysis indicates that trees with root damage fared worse than those with crown damage during droughts (Figure S 11).

Drought conditions were correlated with time since logging in this study (Figure 6). Given that our drought models used total mortality and not repeated measures over time, the model results remain valid.

Conclusion

Overall, tree growth and survival varied with the types and severities of logging damage. While the functional and ontogenetic traits we tested had only minor effects on the fates of damaged trees for reasons we do not yet understand, the overall patterns of mortality rates amongst damage groups were clear. Further research into the unexpected response of damaged trees to drought could prove fruitful, as could investigation of the apparent lack of influence of functional traits on damage tolerance. It remains important to determine the proportions of damaged trees that end up with stem hollows and other defects that render them unsuitable for timber and prone to breakage.

Our results largely corroborate current the current modeling practice of maintaining elevated mortality rates of damaged trees for 5 – 10 years after logging before returning to background rates. We find no evidence that logging intensity affects how individual trees respond to damage. Still, there is a paucity of information about the variation of these effects across space and other factors.

Rough calculations using tropical timber production areas and rates of collateral tree damage (see Introduction) indicate that many tropical trees have or will suffer damage due to logging animals, wind, fire, or other causes. A better understanding of the factors that affect tree damage during logging, the fates of those damaged trees, and implications for forest dynamics

would help to link these mechanisms to global-level processes. Larger analyses that incorporate more sites would be a first step towards this end.

Acknowledgements

We thank the Instituto Boliviano de Investigacion Forestal (<http://www.ibifbolivia.org.bo>), and in particular Nataly Ascarruz, Bonifacio Mostacedo, and Marisol Toledo, without whose perseverance over the years this work, and the work of many others, would not be possible. We would also thank the many field assistants who made this study possible, Lourens Poorter for graciously sharing his bark thickness and exudate data, Carlos Pinto for his work and data on fire in the study area, Wendell Cropper for his guidance with stand modeling, Ervan Rutishauser, Anand Roopsind, and Ruslandi for helpful comments, José Miguel Ponciano for helping with models involving varying census interval lengths, and two anonymous reviewers for their comments that improved the manuscript. This work was supported in part by the WWF Kathryn S. Fuller Science for Nature Fund.

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 602

603 Tables

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605 Table 1. Types and severities of recorded logging damage to trees and the simplified classes

606 used in this analysis. Damage class is based on the highest class for which the tree would

607 qualify. Thus, if a tree suffered only small bark damage but also had 70% crown loss, we

608 assigned it to the Major Damage class.

<i>Assigned Damage Severity Class</i>	No Damage	Minor Damage	Major Damage	Resprout
<i>Damage Type</i>				
Root	None	Superficial	Breakage	
Bark	None	Small	Large	
Stem	Straight	Leaning	Split & Leaning	
Crown	0%	1-50%	51-99%	100% (snapped)

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Table 2. Number of trees damaged during logging per damage category (sm = small) in the LTSRP plots in a semi-deciduous moist forest in Bolivia. Trees found dead in the first post-logging census are not included.

		<i>Root Damage</i>			none			superficial			breakage		
		<i>Bark Damage</i>	none	sm	large	none	sm	large	none	sm	large		
<i>Stem Inclination</i>	<i>Crown Damage</i>												
Straight	0%	21161	125	57	0	45	44	0	1	8			
	1 - 25%	0	76	9	0	4	2	0	0	0			
	26 - 50%	0	59	20	0	4	2	0	0	1			
	51 - 75%	0	23	34	0	0	2	0	1	0			
	76 - 99%	0	21	65	0	2	5	0	0	1			
	100%	0	47	255	0	2	5	0	0	1			
Leaning	0%	0	6	5	0	12	5	0	3	5			
	1 - 25%	0	2	6	0	1	2	0	0	0			
	26 - 50%	0	7	1	0	0	3	0	0	1			
	51 - 75%	0	4	2	0	0	1	0	0	0			
	76 - 99%	0	1	5	0	0	0	0	0	0			
	100%	0	1	3	0	0	1	0	0	1			
Toppled	0%	0	1	5	0	0	0	0	0	11			
	1 - 25%	0	0	0	0	0	1	0	0	1			
	26 - 50%	0	0	0	0	0	0	0	0	1			
	51 - 75%	0	0	0	0	0	0	0	0	0			
	76 - 99%	0	0	2	0	0	0	0	0	2			
	100%	0	0	10	0	0	1	0	0	8			

Table 3. Likelihood ratio tests for interactive terms in the mortality model of Figure 4. The model tested was $P(\text{mortality 8 years after logging}) \sim \text{DBH} * (\text{bark damage size} + \text{root damage severity} + \text{crown damage severity} + \text{stem inclination})$. The likelihood ratio test was performed

620 by dropping each interaction term below from the model, fitting that simplified model, and
 621 comparing it with the more complicated model.

	ΔAIC	LRT	Pr(> Chisq)
DBH : bark damage size	0	1.98116	0.1593
DBH : root damage severity	0	1.91388	0.1665
DBH : crown damage severity	2	0.06166	0.8039
DBH : stem inclination	1	1.07693	0.2994

622

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624 Table 4. AIC of survival model with all terms (Figure 5 and model 1), the full model with the
625 damaged : MCWD interaction removed (model 2), and the full model with the damaged :
626 t_since_logging term removed (model 3). cp represents canopy position.

	dAIC	df
dbh + pc * mcwd_adj + damaged * mcwd_adj + damaged * t_since_logging	0.0	11
dbh + pc * mcwd_adj + damaged * t_since_logging	3.2	10
dbh + pc * mcwd_adj + damaged * mcwd_adj	1675.2	9

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Figure Legends

Figure 1. (a) Tree survivorship as a function of time since logging and damage severity. (b) Mortality rate as a function of time since logging and damage severity. Mortality rate at 0 years after logging was set to the mortality rate of the control plots during the first census interval. Ribbons indicate 95% Pearson-Klopper confidence intervals in both figures.

Figure 2. (a) Relative risks of types of damage resulting from a mixed model of mortality within 8 years after logging of the cohort of trees present pre-logging. The vertical dashed line indicates the value at which there is no change in relative risk from the baseline case. The center dots indicate predicted values, the thick horizontal bands indicate the 50% confidence interval, and the thinner, wider bands indicate the 95% confidence interval. Thus, for example, bark damage size is not a significant predictor, root damage severity is marginally-significant, and crown damage severity is significant. Individual trees and treatments crossed with blocks comprised the random effects (not shown). Damage classes were coded as numeric predictors, scaled to a standard deviation of 1, and centered around 0 (see Methods). A positive estimate indicates that higher values of that predictor correspond to higher mortality rates. Thus, for example, relative risk of mortality declines with increasing DBH, and risk of mortality increases with crown damage severity.

(b) Predicted relative risk of mortality over the 8 year post-logging interval as a function of damage severity class. Data and methods as in Figure 2a.

Figure 3. (a) Orthogonal polynomial coefficients for model of stem diameter growth rates as a function of different types of damage, canopy position, and DBH. Significant values for higher powers of the predictors would indicate a shape corresponding to that polynomial in the predicted variable. For example, crown damage² is significant and negative, indicating that there is a downward-facing parabolic shape in the growth response to crown damage..

(b) Growth rates (DBH increments) modeled as a function of damage groups, canopy position, and DBH. Canopy position is included here because it was found to be an important predictor of growth in previous studies (Shenkin, 2014).

Figure 4. (a) Relative risks of mortality of damaged trees within 8 years of logging as in Figure 2a, with interactions between DBH and damage types. Model as described in Methods with predictors as seen in the figure, and individual and treatment random effects.

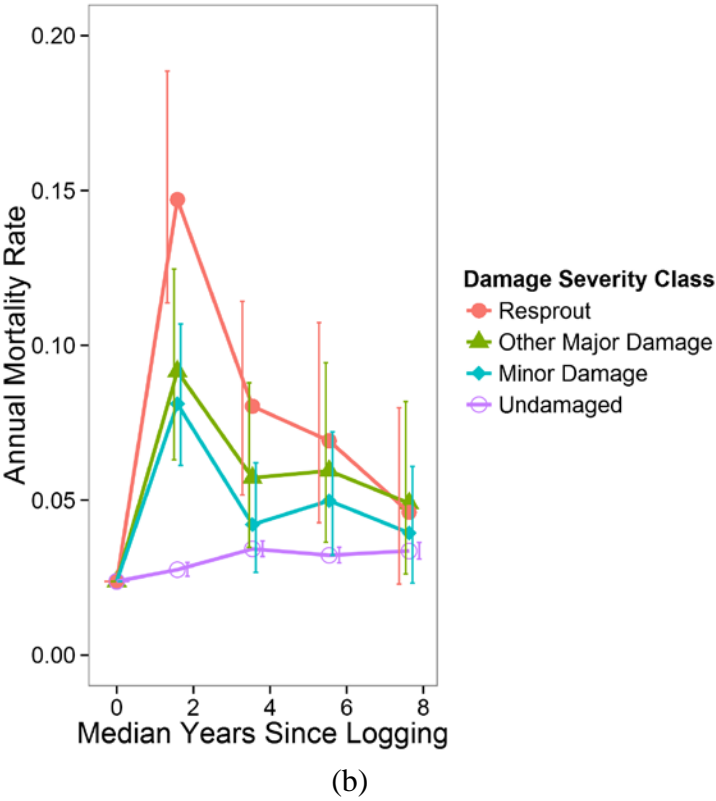
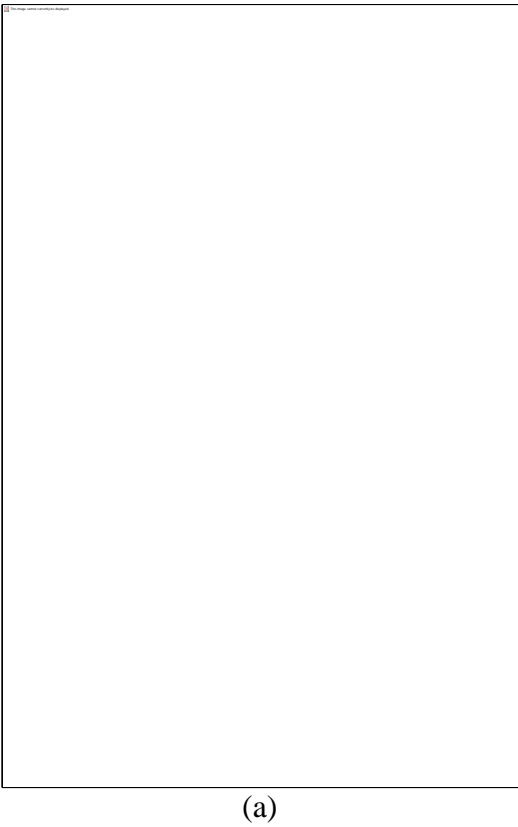
(b) Relative risks of mortality as in Figure 2a, with interactions between DBH and damage groups and DBH.

Figure 5. Repeated-measures survival model including all terms and corrected for variable census lengths. A positive estimate indicates that the term is associated with higher survival rates. This survival model fits survival (coded as 1) and mortality (coded as 0) events of individual trees as repeated measures over each census interval. Random effects include a term for individual trees and a term for treatment crossed with block.

Figure 6. Illustration of the correlation between Maximum Climatological Water Deficit (MCWD) and time since logging. Dots represent observations of trees in this study.

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678 Figures
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683 Figure 1
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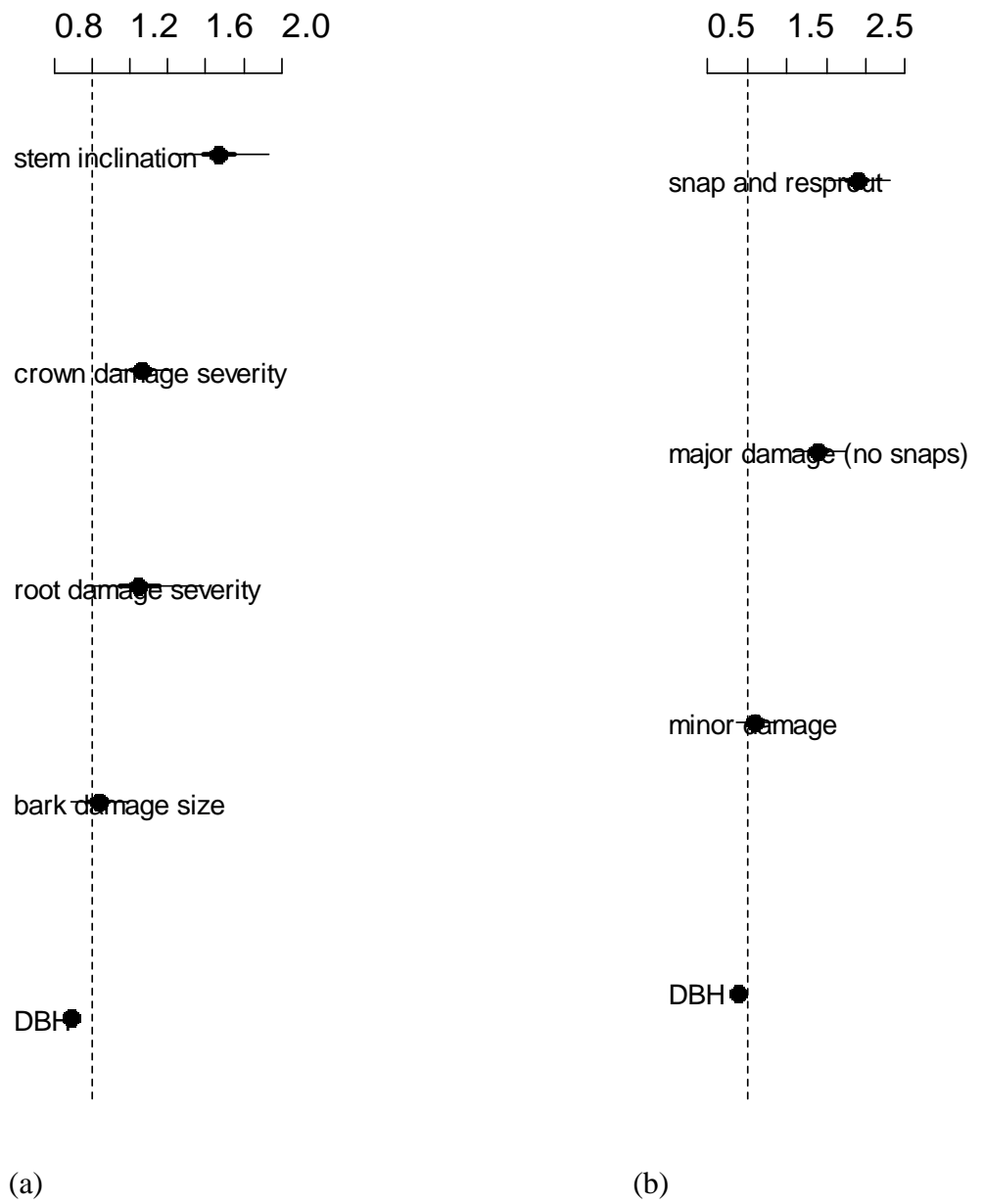
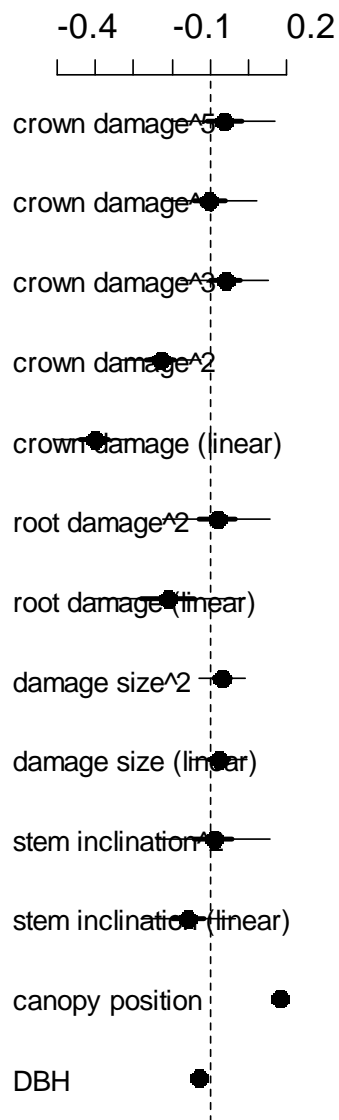
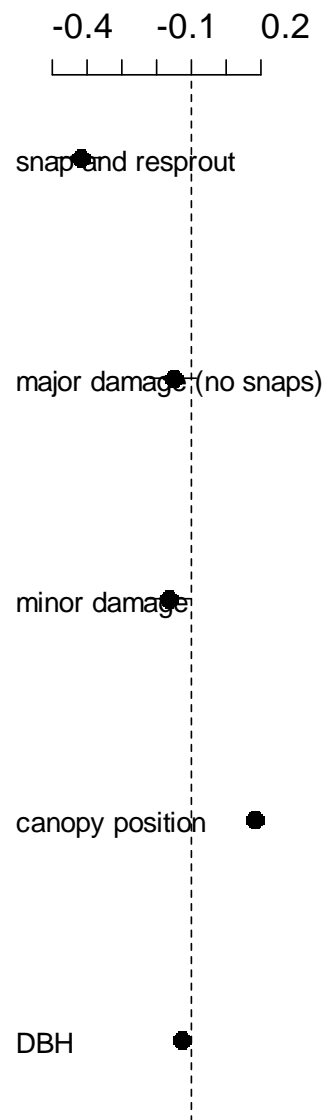


Figure 2

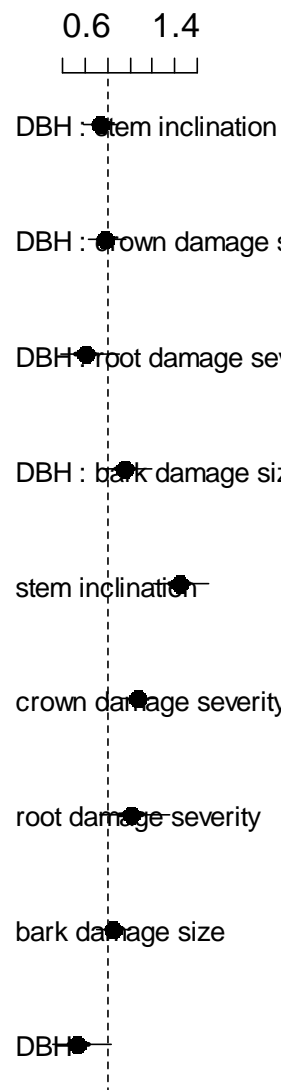


(a)

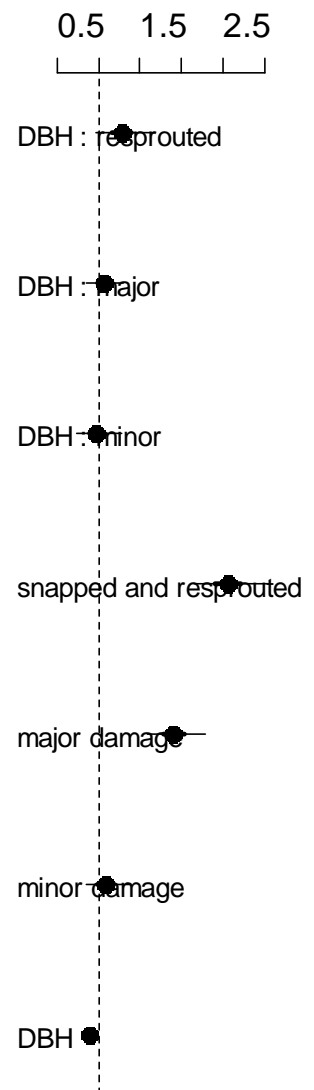


(b)

Figure 3



(a)



(b)

Figure 4

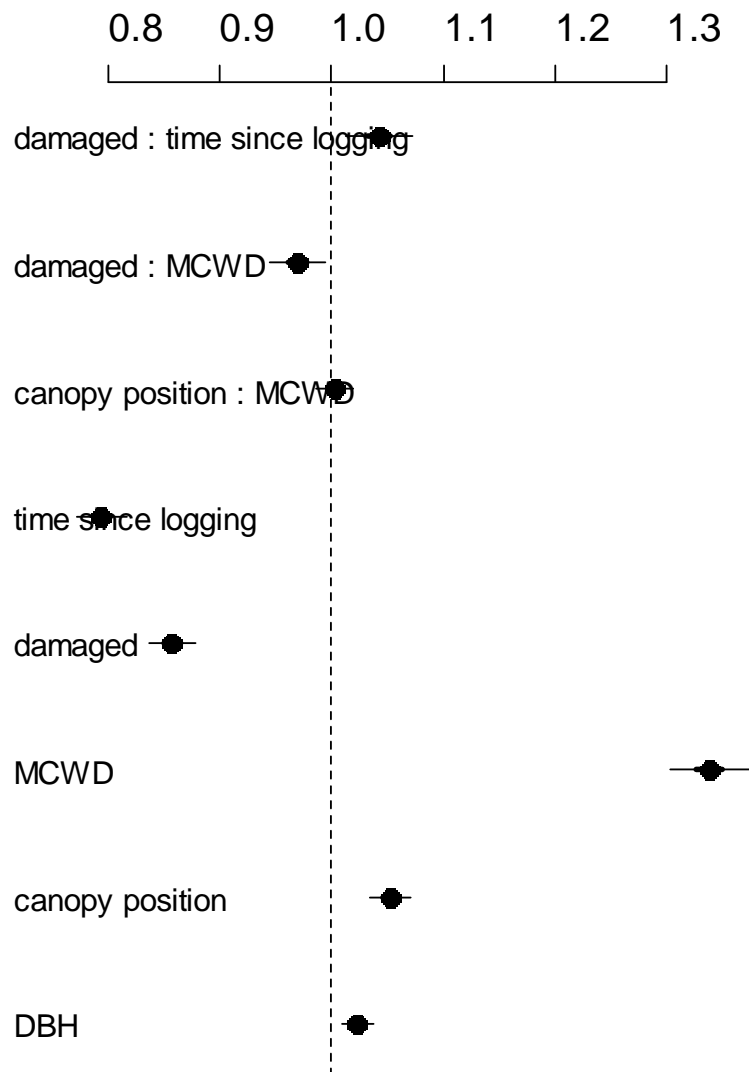


Figure 5

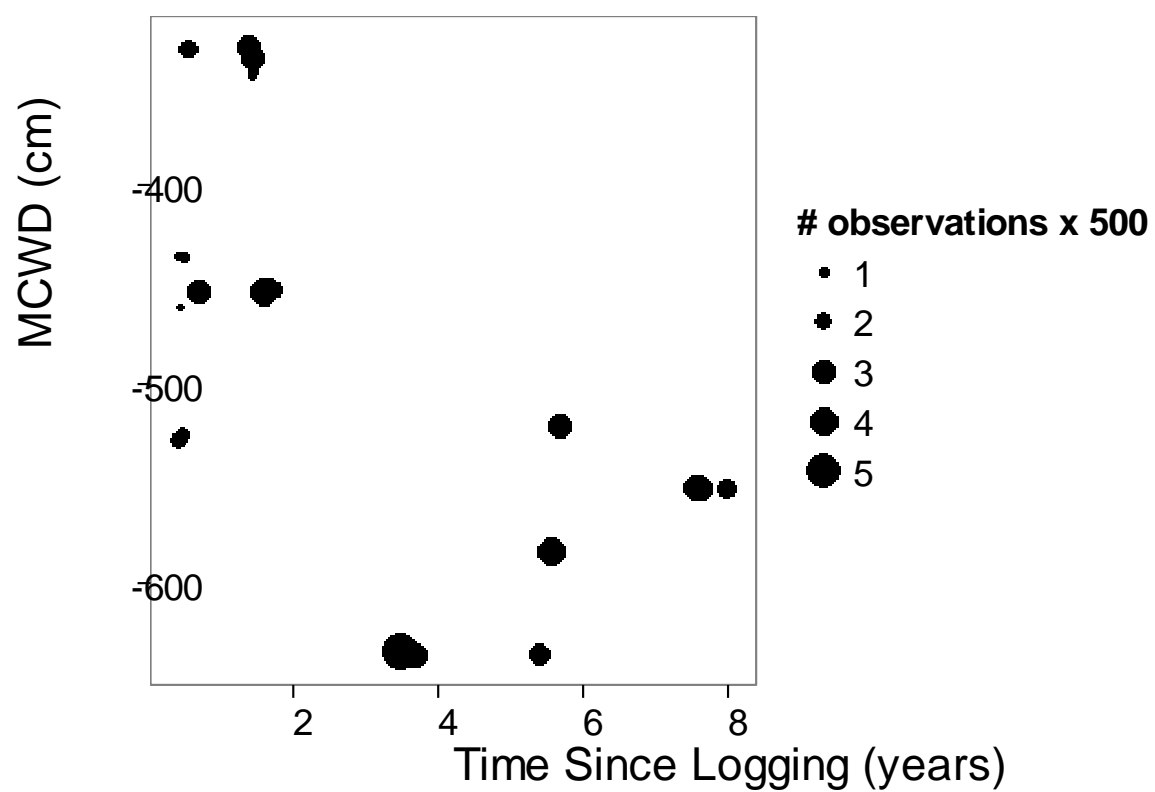


Figure 6

700 Supplementary Information

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702 Supplementary Tables

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704 Table S 1. Logging and census dates.

Block	Census 1	Logging	Census 2	Census 3	Census 4	Census 5	Census 6
1	Feb – May 2001	Sep – Nov 2001	Apr – May 2002	Apr – May 2003	Apr 2005	Apr 2007	Apr 2009
2	Oct – Nov 2000	Feb – Jul 2001	Sep – Oct 2001	Oct – Nov 2002	Oct 2004	Sep – Oct 2006	Apr – May 2009
3	Nov 2001 – Jan 2002	Jan – Jul 2002	Nov – Dec 2002	Nov 2003	Nov 2005	Nov 2007	Oct – Nov 2009

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708 Table S 2. Likelihood ratio test for the model fit in Figure S 6 with the direct effect of wood
709 density (WD, model 2) and its interaction with the damaged category (dam, model 3) removed.

710

	Df	AIC	BIC	logLik	deviance	Chisq	Chi Df	Pr(>Chisq)
no_wd_glmer	5	22601.0	22641.0	- 11295.5	22591.0			
wd_int_glmer	7	22603.2	22659.3	- 11294.6	22589.2	1.7	2	0.4178
survmle.damage.tot_mort.grp.wd.glmer	7	22603.2	22659.3	- 11294.6	22589.2	0.0	0	1

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Supplementary Figure Legends

Figure S 1. As in Figure 1b, but with trees separated according to DBH class (labeled to the right of each subplot) and without an estimate of pre-logging mortality rates. Resprouted trees were removed in the >60 cm class as there were only 2 individuals in that class, both of which died by the 2nd census.

Figure S 2. Observed (violin plots) and predicted (lines) annual growth rates of trees per DBH class. The width of violin plots reflect the probability density of observations at that y-value, translating the discrete points to a continuous estimate using kernel density estimation. Widths of these violin shapes relate to the number of trees observed with that growth rate for that combination of crown damage and DBH class. All individual shapes have the same total area. Predictions based on the following model: $\frac{DBH_2 - DBH_1}{t_2 - t_1} \sim N(DBH + \text{canopy_position} + \text{crown_damage} + \text{root_damage} + \text{damage_depth} + \text{bark_damage_size} + \text{tree_leaning}, \sigma^2)$, including individuals, and treatment crossed with block as random effects. Plot truncated at -0.5 and 2 cm/year. There were no trees >50 cm DBH with crown damage classes 4 or 5. Observations are not balanced with respect to canopy position of trees, and predictions are balanced means of canopy positions crossed with diameters with random effects removed. Observations of crown damage classes include trees with other damage (e.g., observations of growth rates of trees with 0% crown damage include leaning trees and trees with root and bark damage), whereas the prediction lines are for trees with no other damage.

Figure S 3. As in Figure S 2 but for root damage classes

737

738 Figure S 4. As in Figure S 2 but for bark damage size classes

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740 Figure S 5. As in Figure S 2 but for stem inclination classes

741

742 Figure S 6. Relative risks of mortality of damaged trees during the 8 year post-logging interval

743 as in Figure 2a, including wood density and its interaction with tree damage as a binary variable.

744 Model as described in Methods with predictors as seen in the figure, and individual and

745 treatment random effects.

746

747 Figure S 7. Relative risks of mortality of damaged trees during the 8 year post-logging interval

748 as in Figure 2a, including bark thickness and its interaction with tree damage as a binary

749 variable. Model as described in Methods with predictors as seen in the figure, and individual and

750 treatment random effects.

751

752 Figure S 8. Relative risks of mortality of damaged trees during the 8 year post-logging interval

753 as in Figure 2a, including bark thickness and its interaction with bark damage. Trees that were

754 damaged but that did not experience damaged to the bark were removed from this analysis.

755 Model as described in Methods with predictors as seen in the figure, and individual and

756 treatment random effects.

757

758 Figure S 9. Relative risks of mortality of damaged trees during the 8 year post-logging interval

759 as in Figure 2a, including whether a tree species produces bark exudates (latex or resins), and its

interaction with bark damage. Species for which we did not have exudate data were removed from this analysis. Model as described in Methods with predictors as seen in the figure, and individual and treatment random effects.

Figure S 10. Relative risks of mortality of damaged trees during the 8 year post-logging interval including the effects of logging treatments (described in Methods) and their interactions with tree damage types. Model is as in Figure 2a, but using a GLM because treatment is modeled as a fixed effect, and hence Block is also a fixed effect since there are too few blocks (3) to use it as a random effect, and hence there are no random effects. Interactions with treatments only shows Improved and Intensive treatment effects, as a differential effect from that of the Normal RIL logging treatment.

Figure S 11. Repeated-measures, relative risk survival model including all terms and corrected for variable census lengths, as in Figure 5. A positive estimate indicates that the term is associated with higher survival rates.

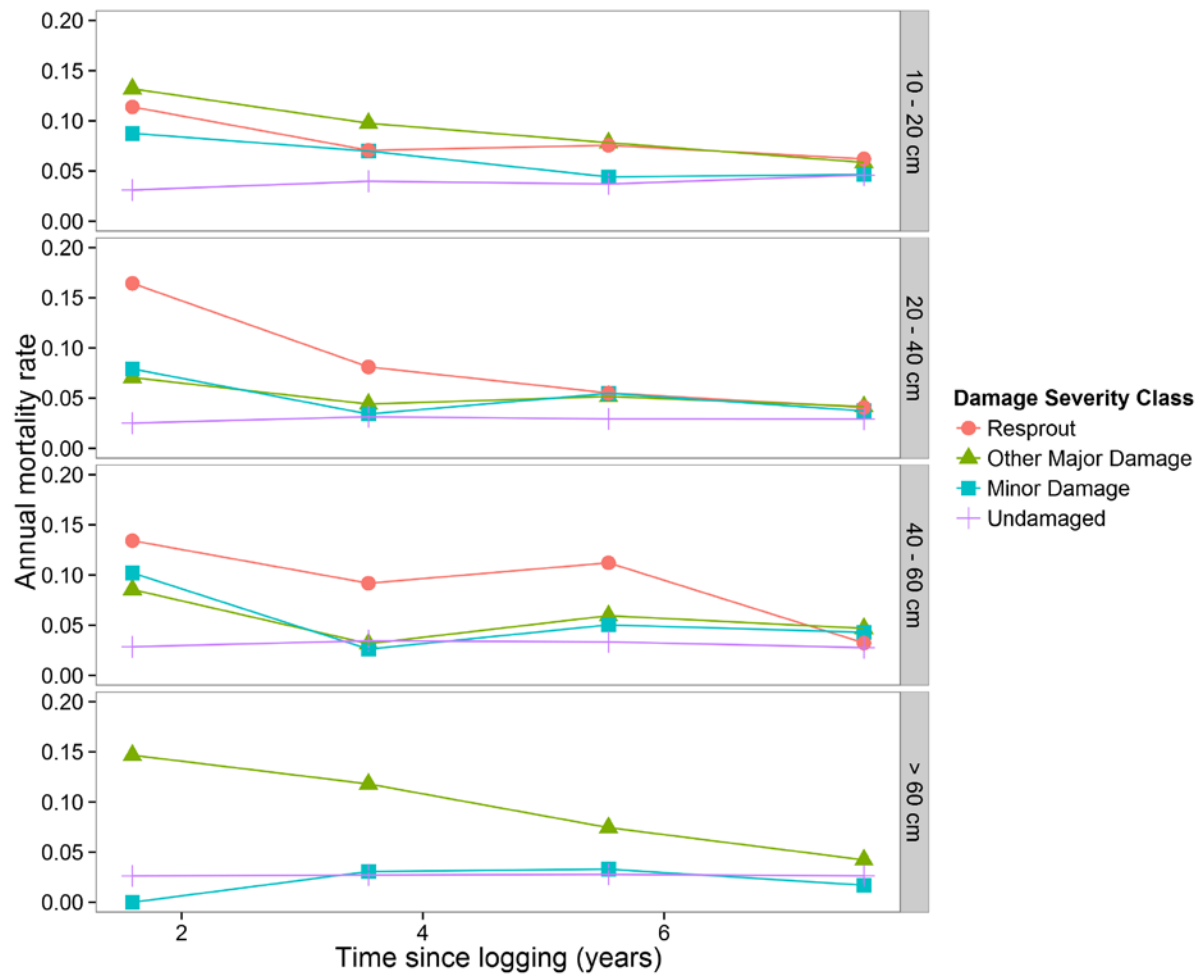


Figure S 1

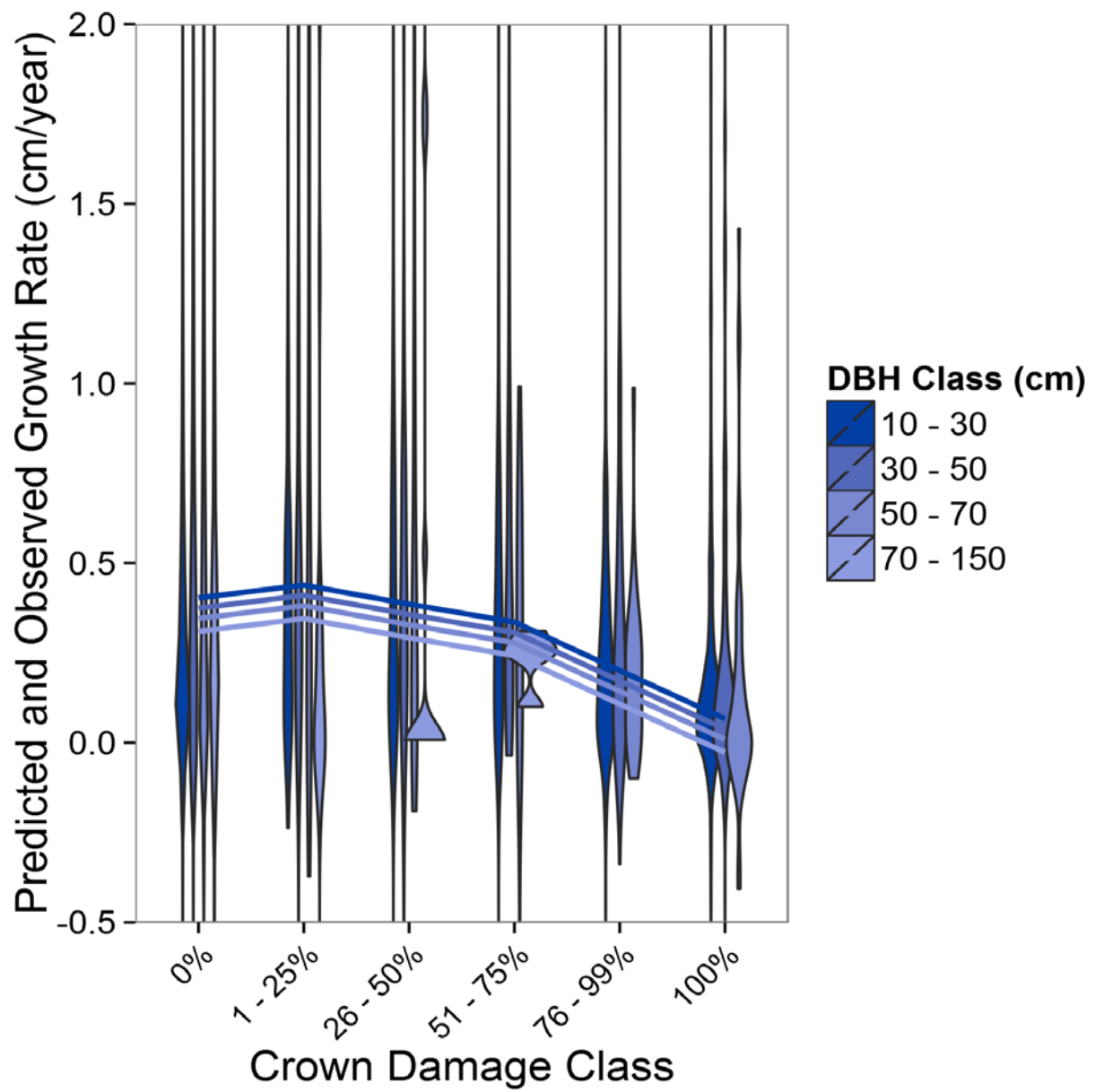
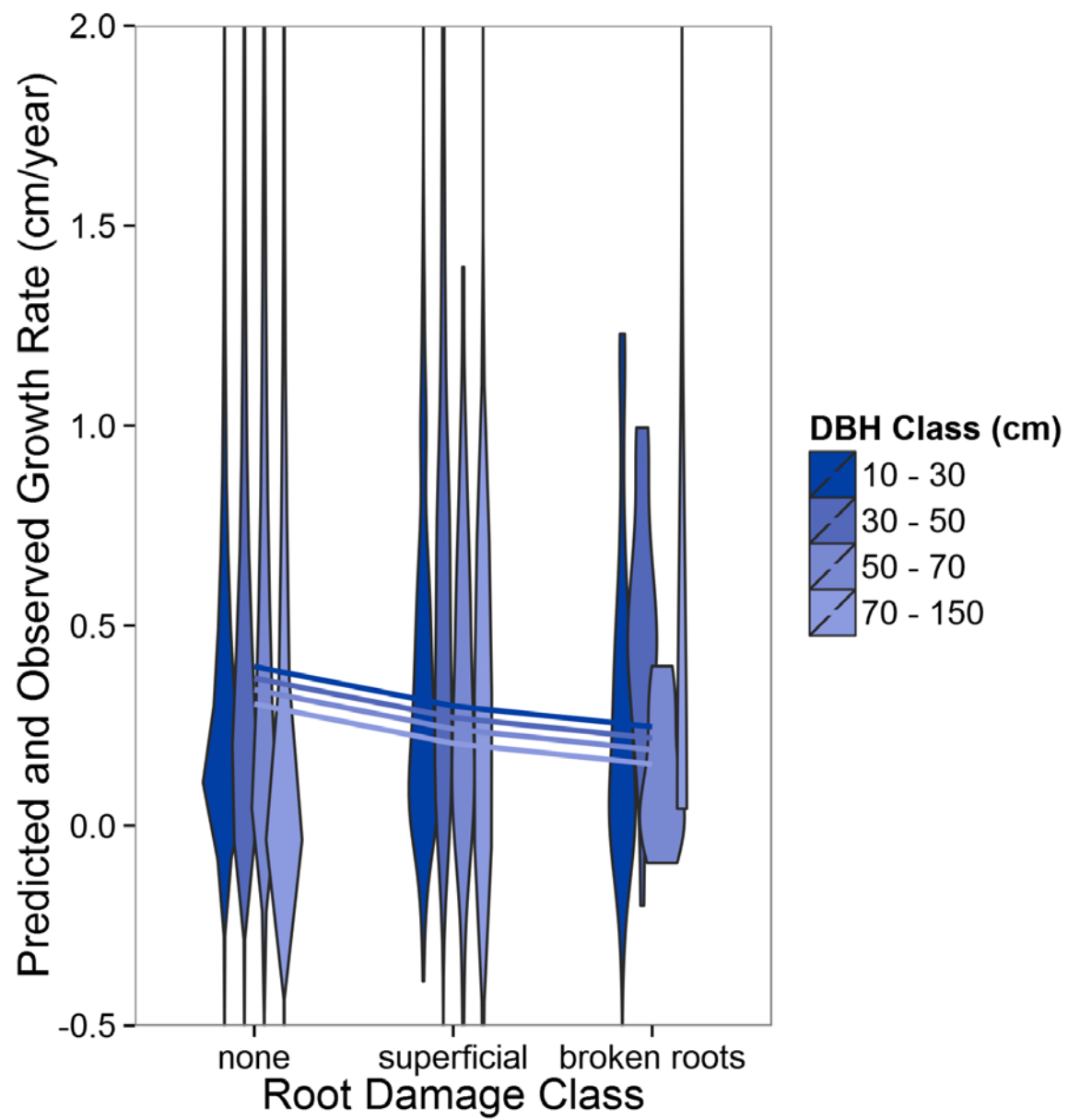


Figure S 2

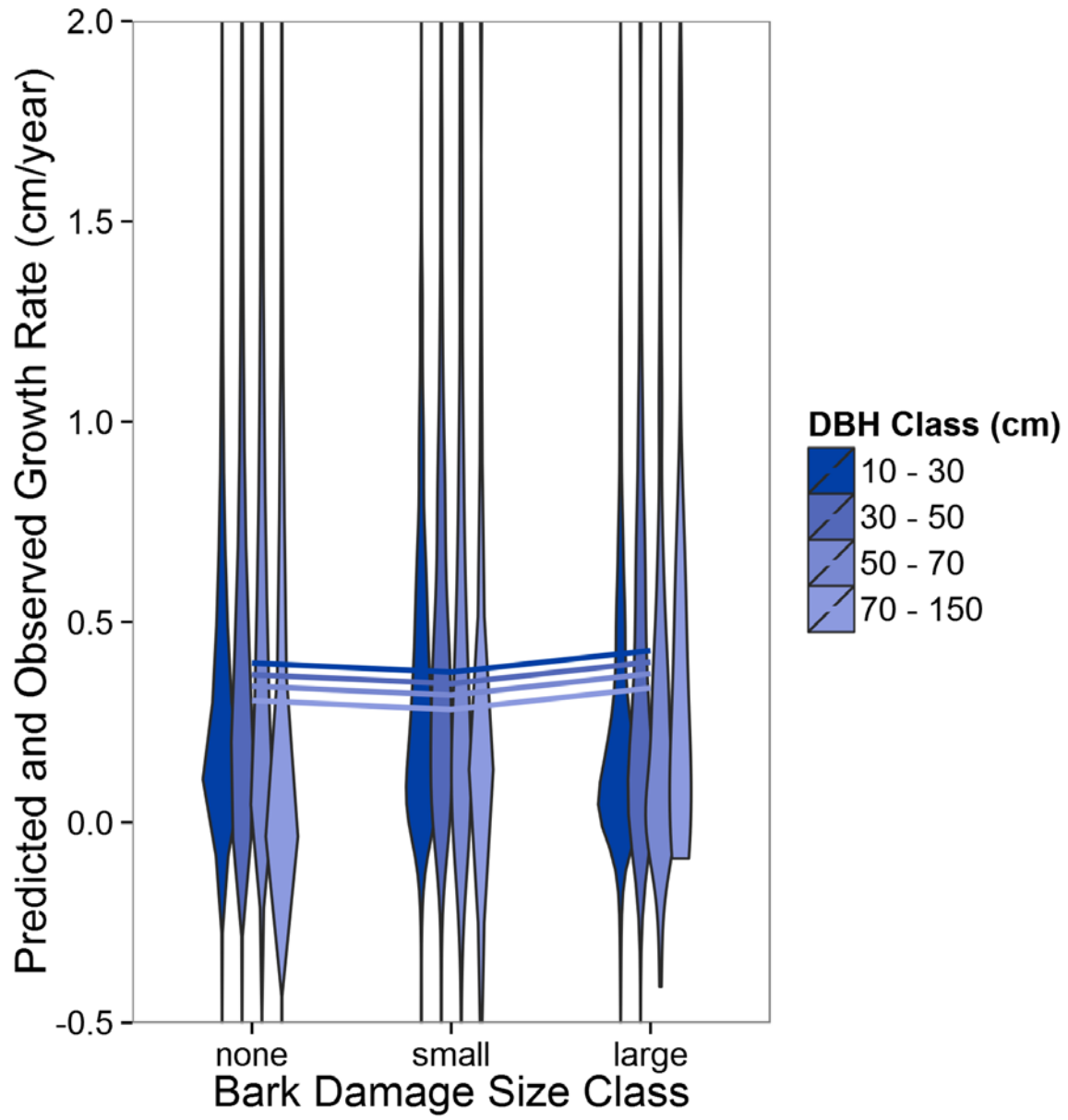
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786 Figure S 3

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789 Figure S 4

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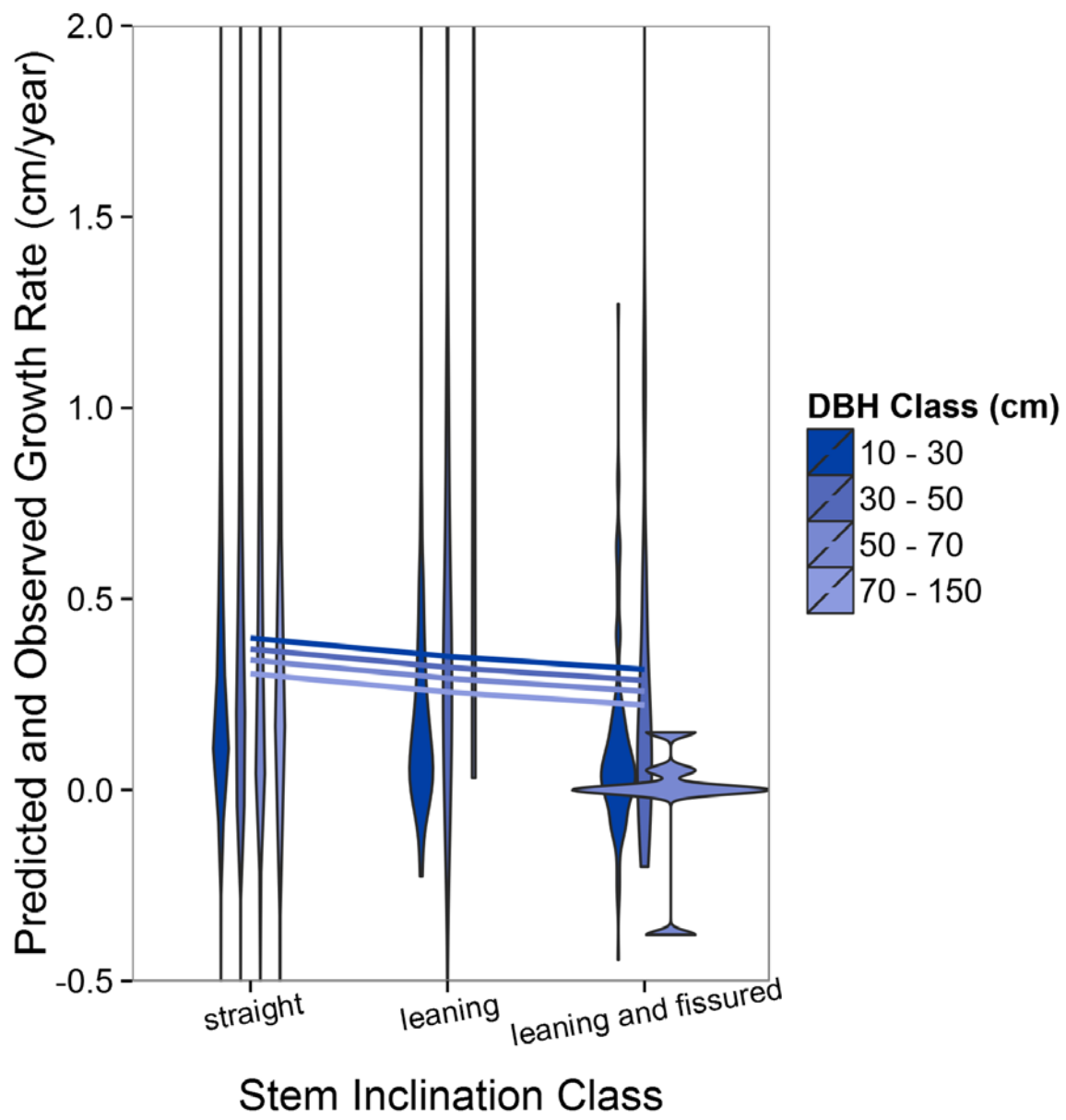
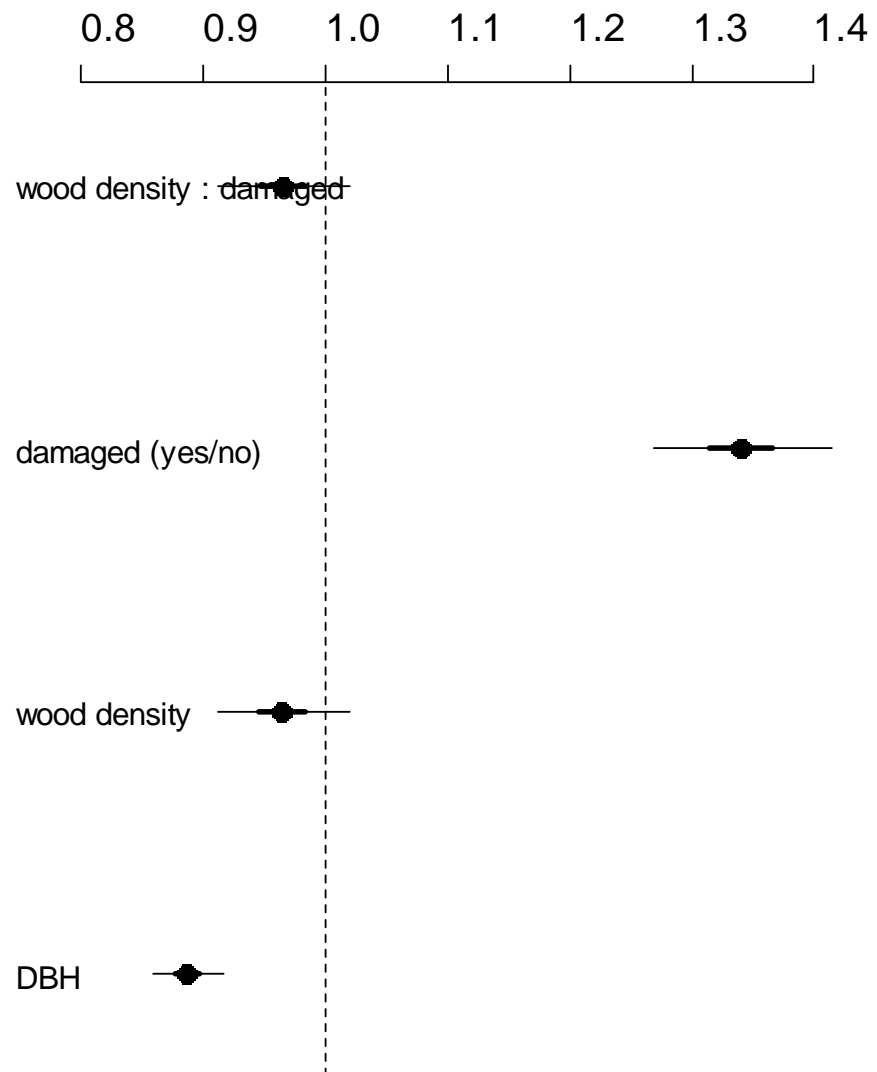


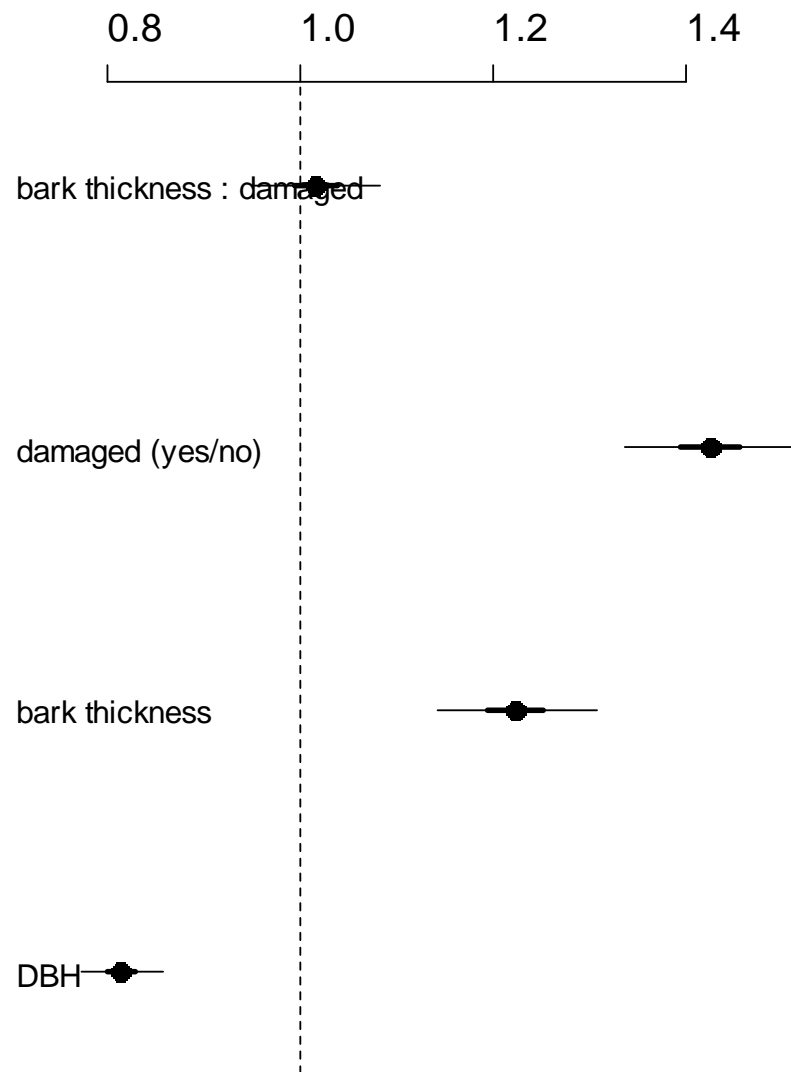
Figure S 5



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795 Figure S 6

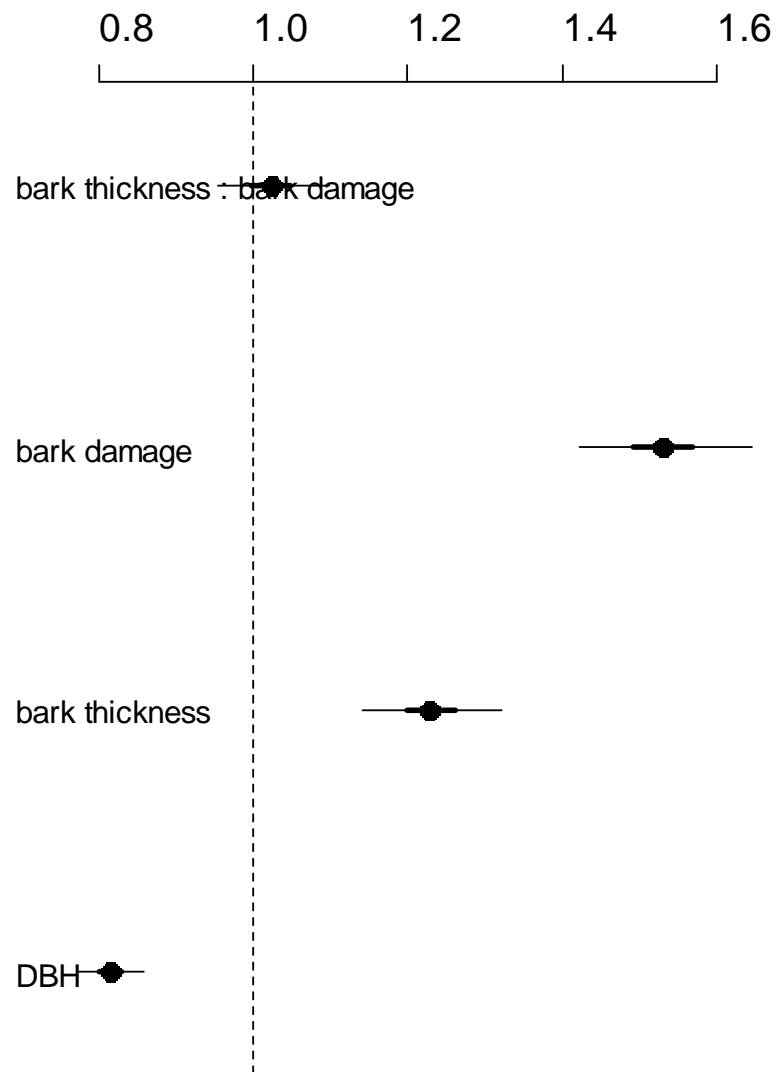
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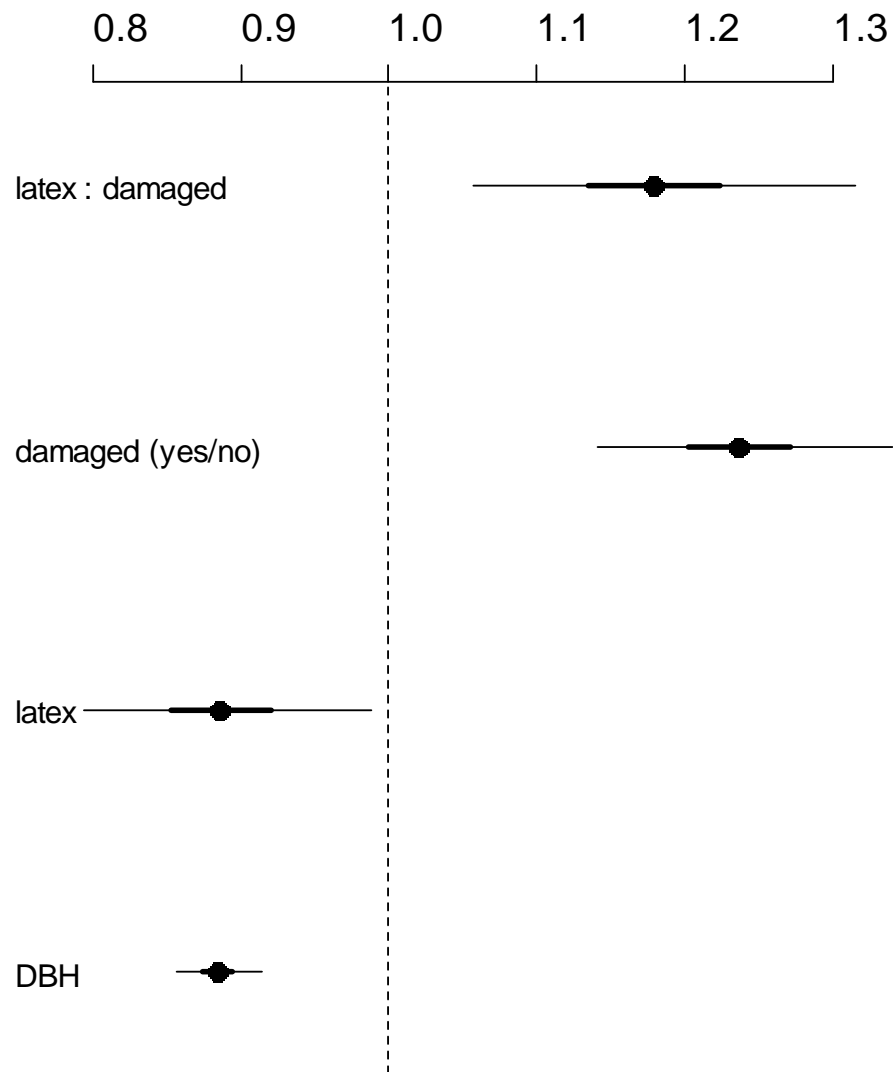
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798 Figure S 7

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 801 Figure S 8
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804 Figure S 9

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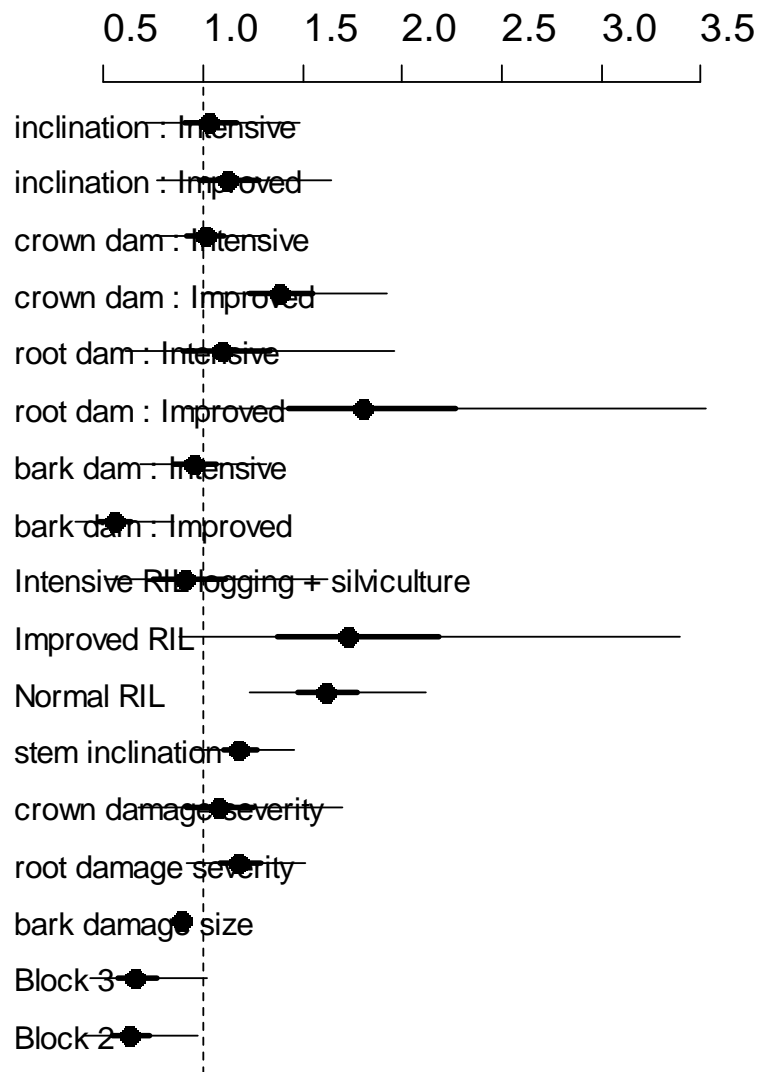


Figure S 10

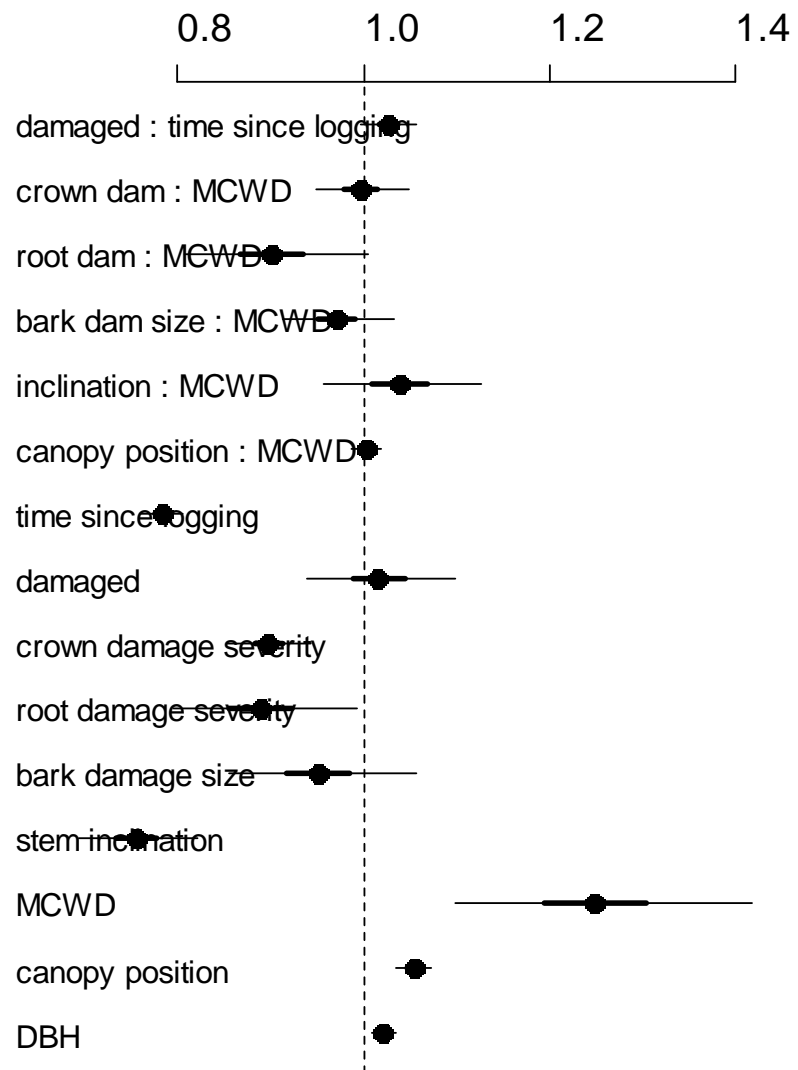


Figure S 11