Tropical tree species differ in damage and mortality from lightning

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Abstract

Lightning is an important agent of mortality for large tropical trees with implications for tree demography and forest carbon budgets. We evaluated interspecific differences in susceptibility to lightning damage using a unique dataset of systematically located lightning strikes in central Panama. We measured differences in mortality among trees damaged by lightning and related those to damage frequency and tree functional traits. Eighteen of 30 focal species had lightning mortality rates that deviated from null expectations. Several species showed little damage and 3 species had no mortality from lightning, whereas palms were especially likely to die from strikes. Species that were most likely to be struck also showed the highest survival. Interspecific differences in tree tolerance to lightning suggest that lightning-caused mortality shapes compositional dynamics over time and space. Shifts in lightning frequency due to climatic change are likely to alter species composition and carbon cycling in tropical forests.

Introduction

Interspecific differences in tree mortality can shape the effects of global change on forests[1,2]. More frequent and intense stressors in recent years have increased tree mortality rates, decreasing carbon storage and shifting tree species composition in some tropical forests[3]. The structure of future forests depends on how these changes affect individual species[4,5]. For example, more severe droughts are already increasing the abundance of drought-resistant taxa across Amazonia[3]. In the only tropical forest where it has been systematically quantified, lightning causes 40% of mortality among the largest trees, and thereby has important implications for tree demography and forest carbon storage[6,7]. Yet, there is little information regarding interspecific differences in the effects of lightning on trees. Given that lightning strikes tropical forests 35-67 million times annually[8] and strike frequency appears to be increasing[9], quantifying interspecific differences in lightning-tree interactions is critical to understanding how lightning influences the structure of tropical forests today and in the future.

There is a long history of speculation that tree species differ in both exposure to and damage from lightning strikes[10–12]; however, few data exist. In wet tropical forests, a single lightning strike typically kills or damages dozens of trees as the electrical current diffuses through the canopy[6,13–15]. Lightning generally strikes the tallest trees with the most expansive crowns in a patch of forest and travels through the crowns of neighboring trees[6,7]. As a consequence, many understory and midstory trees are protected against direct lightning damage by their relatively small stature. Other factors, like tree architecture and liana loads, appear to similarly protect some trees by shaping the path of electrical current through the canopy[7,16–18]. These factors can explain a given tree's likelihood of exposure to lightning. However, they do not explain why some trees die from lightning while others are minimally damaged (i.e., tolerance) or quickly recover (i.e., resilience)[12,16,19]. Interspecific differences in lightning exposure, tolerance, and resilience likely influence tree demography and forest dynamics as lightning frequency changes over space[8] and time[9].

Traits that would convey tolerance or resilience to lightning are not well understood. Models suggest that higher electrical resistivity should increase damage, all else being equal[18], and wood with lower water content and less vascular area typically has higher resistivity[16,20]. Thus, variation in vascular traits (e.g., vessel size, vessel density, wood density) among species could consistently affect the outcome of a lightning strike via differences in electrical resistance in the cambium[21]. Likewise, the tendency to resprout following disturbances like fire facilitates tree recovery and varies interspecifically[22]. Thus, it is likely that anatomical and physiological differences among tree species also underlie interspecific differences in the probability of death, damage, and recovery following a lightning strike.

The principal goal of this study was to determine whether tree species in a lowland tropical forest exhibit evidence of lightning tolerance and resilience. We hypothesized that the probability of exposure to and damage from lightning differs among species and that these differences are linked to functional traits. We predicted that some species consistently exhibit lower overall mortality and less physical damage when exposed to lightning (i.e., tolerance), and that some species consistently recover from a lightning strike, even when the damage is severe (i.e., resilience). We also expected that tree species with higher rates of exposure exhibit greater tolerance or resilience. Finally, we tested whether tree wood and leaf functional traits are associated with lightning tolerance, with the goal of providing a predictive framework for evaluation of a broader range of species.

Results

Lightning tolerance among species

The likelihood of mortality from lightning differed among species, as did the severity of damage from strikes, indicating that some species can tolerate lightning exposure relatively well. Across species, the probability of dying from lightning damage decreased with distance from the directly struck tree and with larger DBH (Extended Data Fig. 1; Tables S1 & S2). Directly-struck trees were two orders of magnitude more likely to die than secondarily damaged trees, and only canopy or emergent trees were directly struck by lightning.

Observed mortality rates in 18 of 30 species deviated significantly from model predictions based on tree DBH and distance from the struck tree (Fig. 1; Extended Data Fig. 2; Table S3). Species that were more likely to die than predicted also had higher average crown dieback (Extended Data Fig. 3; $R^2 = 0.64$, $F_{1,25} = 51.3$, $p = 7.0 \times 10^{-8}$). Lightning-struck palms (*Astrocaryum standleyanum*, *Oenocarpus mapora*, and *Socratea exorrhiza*) were especially likely to die. Lightning-associated mortality greatly exceeded the rate expected without lightning (Fig. 1), with four exceptions: *Dipteryx oleifera* (n = 13), *Hura crepitans* (n = 12), and *Pouteria reticulata* (n = 8) exhibited no mortality following lightning strikes, and only one of 27 *Gustavia superba* died from lightning damage. Removing palms from the model had little effect on the results (Table S5, Fig. S1).

Lightning resilience among species

Only one species, *Trichilia tuberculata* (n = 18), showed a propensity to recover crown foliage following lightning damage (Fig. 2). Across species, average crown dieback increased by 8.2% per year for up to 450 days following a lightning strike, indicating that most of the species we studied are not resilient to lightning. Initial damage was the most important predictor of the damage rate of change (ROC) over time ($\chi^2 = 18.07$, $p = 2.1 \times 10^{-5}$). Specifically, individuals with < 25% crown dieback in the initial census tended to recover or not change, whereas individuals with higher initial damage tended to decline or die (Extended Data Fig. 4). ROC was not related to tree DBH after accounting for initial damage ($\chi^2 = 0.03$, $p = 0.87$).

Resprouting from the trunk, distinct from crown recovery, was most common in heavily damaged trees. The frequency of resprouting increased with amount of crown dieback ($\chi^2 = 178.85$, $p = 2.2 \times 10^{-16}$) and declined with increasing tree size (DBH; $\chi^2 = 5.10$, $p = 0.02$). Distance from the struck tree and interactions did not contribute to the best model. Resprouting was not universal among species; *Virola nobilis* (n = 7) showed no evidence of resprouting regardless of damage (Extended Data Fig. 5).

Lightning damage frequency associated with tolerance

Species that are frequently damaged by lightning[7] were less likely to die from that damage (Fig. 3A and Extended Data Fig. 6A; $R^2 = 0.29$, $F_{1,24} = 10.02$, $p = 0.004$). However, this relationship is driven by infrequently damaged palms and is not significant if they are removed ($R^2 = 0.10$, $F_{1,21} = 2.28$, $p = 0.15$). Nonetheless, of the three species with the highest probability of damage, *D. oleifera* and *H. crepitans* showed no mortality, as noted above, and *Ceiba pentandra* (n = 7) lost one sapling-sized individual; these species survived all direct lightning strikes (10, 2, and 1 direct strikes per species, respectively). Excluding DBH from the models did not alter the relationship between damage frequency and mortality, indicating that mortality differences among species extend beyond size-related differences (Fig. 3B and Extended Data Fig. 6B; $R^2 = 0.33$, $F_{1,24} = 11.94$, $p = 0.002$; excluding palms: $R^2 = 0.09$, $F_{1,18} = 1.76$, $p = 0.20$).

Functional traits associated with tolerance

Of the six traits we tested (leaf area, specific leaf area, leaf % nitrogen, maximum height, wood density, and vessel lumen area) those with the greatest explanatory power with respect to the tree mortality residuals were wood density, vessel lumen area, and leaf % nitrogen (Table 1; $R^2 = 0.53$, $F_{3,29} = 13.00$, $p = 2.5\text{x}10^{-5}$). Species that had the highest probabilities of dying from lightning damage had less dense wood, lower leaf N, and smaller vessels, while those with the opposite traits displayed greater lightning tolerance. These multivariate relationships were significant despite non-significant univariate relationships between mortality residuals and vessel size and leaf N, and a strong positive correlation between vessel size and wood density (Fig.4).

Discussion

Here we provide robust empirical evidence that lightning strikes affect different tropical tree species differently, placing lightning among mortality agents that can shape forest composition[1,2,23]. These results suggest that species most commonly struck by lightning have developed some lightning tolerance, whereas recovery following a strike plays a relatively minor role and depends largely upon the severity of initial damage from the strike. These interspecific differences in survival and their relationships with functional traits suggest that lightning influences patterns of forest turnover and community dynamics with consequences for how forests respond to global change.

Interspecific differences in lightning mortality suggest that lightning influences tree community assembly and coexistence. In the short term, differences in lightning survival will determine which trees persist in the forest, particularly in the canopy, and thereby influence tree species composition. In the long term, lightning likely influences population-level fecundity and tree fitness by killing large trees[6,7] that contribute disproportionately to per-capita population growth rates[24,25]. Moreover, the negative relationship between the likelihood of lightning damage and the probability of survival suggests a trade-off between lightning survival and exposure (Fig. 3A). Ultimately, further research is needed to fully evaluate the benefits, costs, and underlying mechanisms of lightning survival.

Lightning frequency already varies considerably among forests globally[8] and is projected to increase in some regions[9]. This spatial and temporal variation should produce corresponding compositional changes based on species tolerance to lightning. Future increases in lightning frequency will favor trees that tolerate lightning while negatively affecting canopy species that are less tolerant, particularly those that do not recover well. As more trees die, particularly large trees, carbon stocks will be substantially reduced[4,5]. Yet, the results of this study suggest a compensatory mechanism by which forests avoid decreases, or perhaps even experience increases, in carbon storage as the proportion of heavy-wooded, lightning-tolerant trees increases. Species able to recover following lightning should also persist under higher lightning regimes even if they have limited tolerance to lightning (Fig. 2). The capacity of forests to shift compositionally in response to changing lightning regimes, and geographic variation in that capacity, will be a key factor in determining the effect of climate change on tropical tree communities and the tropical forest carbon sink.

Although smaller trees in mature forests commonly avoid lightning damage via protection from their larger neighbors[6], small stature does not impart immunity from lightning damage. Trees in the understory were more likely to die if damaged by lightning than their canopy counterparts, and this was true both across and within species. The particular sensitivity of palms to lightning, attributable to damage to the single apical meristem that precludes recovery[22,26,27], was offset by the relatively few palms damaged compared to their abundance on BCI. By contrast, other small-statured species (e.g., *Gustavia superba*) appear to be relatively tolerant of lightning damage. Some species common to the understories of mature forests form the canopy in some secondary forests. As more forest area globally shifts to young, short-statured forests[4], the differences in lightning tolerance among secondary forest species will become increasingly important in informing forest composition.

The correlations between functional traits and probability of mortality reported here provide a foundation for future mechanistic work. The results suggest that trees with higher wood density, but relatively larger vessels and higher leaf nitrogen, are more likely to survive lightning strikes. Low wood density occurs in fast-growing, short-lived trees[28]; thus, these results are consistent with other observations that pioneer species are more susceptible to this growth-independent hazard[29]. Wood density and vessel area are negatively correlated because total vessel area trades off with structural support, so the species showing the highest tolerance to lightning would have relatively large vessels (and higher hydraulic conductance) for a given wood density, a combination that enables more efficient transport in taller trees[21]. Lower leaf nitrogen is an indicator of shade tolerance[30], and lightning-sensitive understory species likely drive this pattern.

Quantifying how specific disturbances, like lightning, differentially affect species is essential for refining ecosystem models and making predictions about future forest structure and composition[4,5]. We have only a rudimentary understanding of how lightning kills trees, or whether it causes damage that is unobservable using visual field surveys, which is crucial information that underlies mechanisms of tolerance. Likewise, we suspect that structural differences among trees affect their probability of experiencing secondary damage from lightning. More data are needed to rigorously evaluate this possibility. Finally, interspecific differences in survival following lightning exposure suggest that lightning-created forest gaps have different successional trajectories from other types of disturbance. Additional long-term data are needed to evaluate this possibility. Ultimately, a complete understanding of the ecological effects of lightning will require an experimental approach, even if only practical at small scales. Given the importance of lightning as a source of tree mortality, especially for large trees, our scant knowledge of its basic ecological effects remains a critical gap in our study of forest dynamics.

Materials and Methods

We used data from 97 lightning strikes documented in the Barro Colorado Nature Monument, Panama, during the wet seasons of 2015-2020. We used a camera-based monitoring system, supplemented with data from 3-4 field change meters in 2018-2019, to locate 70 strikes[31]. An additional 27 strike sites were located post hoc using reliable field diagnostics[15]. We confirmed that sites located using field diagnostics were comparable to those located with the monitoring system (Table S6-S7, Fig. S2). We recorded all trees visibly damaged by lightning in each site. We cannot determine whether other trees were exposed to lightning but showed no damage. For each damaged tree, we measured diameter at breast height (DBH), distance from the directly struck tree, estimated crown dieback (percent of crown volume that died), and the presence of resprouts. We subsequently revisited most strike sites to track changes in these variables over time. Trees were considered to have died from lightning if they showed visible lightning damage in the first census and died at some point during the census period. Because the proximate cause of death is sometimes difficult to distinguish, we did not differentiate between trees that died from exposure to electrical current and trees that died from indirect effects of a strike (e.g., falling trees). The dataset includes 2,284 trees greater than 1 cm DBH that were noticeably damaged by lightning. Of these, 865 trees were identified to species, representing 137 taxa across 45 families. The 30 most common species were represented by 8 or more individuals.

Lightning tolerance among species

We performed all analyses in R version 4.2.0[32] and all figures were produced using the R package 'ggplot2'[33]. To predict the probability of mortality, for each tree, we constructed a generalized linear mixed model with binomial errors using the R package 'glmmTMB'[34]. We included distance from the struck tree, DBH, and their interaction as fixed factors; prior work showed that these factors are important in predicting the distribution of lightning damage[6,7]. We also added a binary term for directly struck vs. secondary damage (hereafter, "strike status") and a random intercept term for strike site. DBH was log-transformed to meet model assumptions. We used likelihood ratio tests using the R package 'lmtest'[35] to compare the fit of competing models excluding predictors. We compared predicted to observed values within bins for each continuous predictor to evaluate model fit.

We analyzed residuals of the 30 most common species to evaluate interspecific differences in expected survival. We used this approach rather than including a species term in the model for three reasons: 1) we lacked the data to fit species-specific mortality curves; 2) the identified individuals were a biased subset of our data, primarily representing larger-statured species; and 3) identified trees were non-randomly distributed among strike sites. To evaluate whether mortality rates differed from expectations by species, we bootstrapped model residuals over the number of individuals within each species with 1000 iterations. We also tested whether each species' observed mortality differed from predicted using pairwise tests based on the z-distribution. We used linear regression weighted by the number of occurrences for each species in the mortality data to determine whether mean crown dieback for a species predicted its residual in the mortality model. We also tested this relationship with palms removed from the dataset because of their different physiology. We used Cook's distance to test for undue influence of any species on the regression results.

We compared lightning-caused mortality to the probability that a random tree of the same species would have died during the same time period. We constructed mortality curves using data from the BCI 50 ha plot[36] collected in six 5-year census periods (1985-2015) for all species in our dataset. The curves include any deaths caused by lightning before our monitoring began in 2015. We used those curves to calculate the probability that each tree damaged by lightning in our dataset would have died given its DBH and the length of time we monitored it. These historic mortality probabilities were then compared with observed lightning mortality rates to ascertain whether deaths attributed to lightning were distinct from background rates.

Lightning resilience among species

We also tested for interspecific differences in the fate of trees that survive initial lightning damage. This analysis included trees that were censused more than once, excluding trees that were dead in the first census. Because initial census dates were later for some strikes, we confined the date of the first census to be between 30 and 105 days after the strike. The final census was also constrained to be separated from the first census by 250-450 days. We calculated a rate of change (ROC) for each tree by taking the difference in crown dieback between the last census interval and the first census interval and dividing that by the number of days between the two censuses. We bootstrapped the ROC 1000 times over the number of trees within each species to calculate confidence intervals.

We used the ROC values to assess recovery or decline by species, where positive ROC values indicate decline over time and negative values indicate recovery. First, we tested whether DBH and the level of dieback observed in the first census (hereafter, initial damage) influenced ROC with a linear mixed model. We included days between censuses as a covariate and strike site as a random intercept. Second, for species with 10 or more individuals, we used a permutation test to determine whether mean ROC values for each species deviated from those expected by chance. To generate the null expectations for each species, we randomly selected ROC values for each individual of that species from the observed ROC values for the same value of initial damage among all species. We repeated this process for 10,000 permutations to generate the null distribution and then compared these values to the observed mean.

As a second measure of recovery, we considered whether trees differed in resprouting following damage. We recorded resprouts as present or absent, and used a generalized linear mixed model with binomial errors to test whether resprouting depended on the maximum level of crown dieback and tree DBH. We included strike site as a random intercept. We bootstrapped model residuals 1000 times within each species to generate species-specific confidence intervals to compare with model predictions.

Lightning damage frequency associated with tolerance

We used the species-level expected lightning damage frequencies that were previously calculated for all trees over 10 cm DBH with 25 or more individuals in the BCI 50 ha plot[7] and compared these to the species residuals from the mortality model. We used linear regression to test for a relationship between predicted damage and mortality residuals, including species with at least 8 individuals from the mortality model. Because DBH was included as a predictor in both the damage and mortality models, and tree size varies interspecifically, we separated the total species effect by running each model excluding DBH and comparing the residuals by species from the two models. Residuals for both models were bootstrapped as described for the mortality model above. Both linear regressions were weighted by species occurrence in the lightning mortality dataset. We also conducted the same analysis without palms because they differ biologically from other trees (i.e., monocots vs. dicots) and we used Cook's distance to test for undue influence of outliers. This comparison is based on the structure and composition of the BCI 50 ha plot captured in the 2015 census[36].

Functional traits associated with tolerance

We tested whether species mortality probabilities from lightning were associated with functional traits. We selected commonly measured traits, including leaf area, specific leaf area (SLA), leaf nitrogen content (N_{mass}), and maximum plant height that capture various elements of growth strategy[28]. We also include two wood characteristics, wood density and vessel lumen area, that we expected to relate to the electrical conductivity of wood[21,37,38]. The majority of these data were collected on BCI [21,28] and accessed from the TRY database[39]. Leaf area and vessel area were log-transformed to meet model assumptions. Using residuals from the lightning mortality model, we constructed weighted linear regressions for 33 species with ≥ 5 individuals represented in our dataset that had species mean values available for all traits. The regression was weighted by the sample size for each species, and we scaled and centered all predictor variables. We used stepwise selection based on AIC values to identify the most parsimonious model, and a variance inflation factor cutoff of 5 to test for highly correlated variables. None of the variables was excluded due to correlation.

Data Availability: The lightning dataset is available in the Dryad repository, https://doi.org/10.5061/dryad.gf1vhhmsp. Data from the Barro Colorado Island 50-ha plot[36] are available in the Dryad repository, https://doi.org/10.15146/5xcp-0d46. Data from the lightning risk model[7,40] are available in the Dryad repository, https://doi.org/10.5061/dryad.c59zw3r48. Data for wood density[37,38] are available in the Dryad repository, https://doi.org/10.5061/dryad.234. Data from the TRY plant database[39] are available from the TRY website, https://www.try-db.org/TryWeb/Home.php.

Code Availability: The R code used for analysis is available in the Dryad repository, https://doi.org/10.5061/dryad.gf1vhhmsp

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Table 1. Multiple linear regression results for trait signal in species residuals from the lightning mortality model. Vessel lumen area was log-transformed and all variables were standardized by scaling.

Parameter	Coefficient	Std. Error	T-value	P-value	Partial R^2
Intercept	-0.05	0.01	-3.37	0.002	
Leaf nitrogen	-0.04	0.01	-2.87	0.007	0.22
Vessel area	-0.06	0.02	-2.97	0.006	0.23
Wood density	-0.11	0.02	-5.44	7.4×10^{-6}	0.51

Figure captions

Fig. 1. Lightning mortality predictions (with 95% CI) by species for common trees (those with n ≥ 8 in the dataset) compared with their historical mortality rates. Residuals indicate difference between model predictions and observed means for each species. Species are ordered by the residual value. Asterisks indicate significant p-values based on a two-sided Z-test as follows: *A. standleyanum* ($p = 1.7x10^{-16}$, n = 9), *O. mapora* ($p = 2.3x10^{-21}$, n = 9), *S. exorrhiza* ($p = 4.6x10^{-101}$, n = 21), *A. membranacea* ($p = 2.5x10^{-4}$, n = 14), *T. arborea* ($p = 7.3x10^{-4}$, n = 13), *F. occidentalis* ($p = 1.6x10^{-5}$, n = 79), *A. blackiana* (p = 0.02, n = 37), *H. triandra* ($p = 3.3x10^{-8}$, n = 28), *D. panamensis* ($p = 1.4x10^{-4}$, n = 8), *P. reticulata* ($p = 3.9x10^{-4}$, n = 8), *H. crepitans* ($p = 4.9x10^{-7}$, n = 12), *G. recondita* (p = 0.002, n = 10), *G. superba* ($p = 5.1x10^{-24}$, n = 37), *D. oleifera* ($p = 1.0x10^{-7}$, n = 13).

Fig. 2. Violin plots of permutation distributions for species mean ROC values (for species with n ≥ 10 individuals in the dataset) overlayed with bootstrapped confidence intervals around the observed mean. Values below zero represent recovery (decreasing crown dieback) and those above zero represent decline (increasing crown dieback). Significant difference of the species mean from the permutation distribution: *T. tuberculata* (p = 0.0002, n = 18); significant difference of the species mean from zero based on bootstrapped distribution*:* *F. occidentalis* (p = 0, n =24), *A. excelsum* (p = 0.001, n = 21), *Q. asterolepis* (p = 0.005, n = 16), T. tuberculata (p = 0, n = 18).

Fig. 3. (A) Mortality model residuals (for species with n ≥ 8 individuals in the dataset) compared with mean damage frequencies projected by the lightning risk model[7] by species. Mortality sample size indicates confidence of the estimate. The color gradient depicts the mean crown dieback among members of the species that were damaged. (B) Residuals from damage and mortality models (for species represented by n ≥ 8 individuals) with DBH removed from both models to capture the full species effect including size differences. See Extended Data Fig. 6 for similar plots showing all species names.

Fig. 4. Top row: Linear regression between species means of mortality model residuals and (A) wood density ($R^2 = 0.38$), (B) vessel lumen area ($R^2 = 0.03$), and (C) Leaf N ($R^2 = 0.10$). Bottom row: Pearson correlations with points color-coded by mortality model residuals for (D) wood density and leaf N (r = 0.15), (E) vessel area and leaf N (r = -0.23), and (F) wood density and vessel area (r = -0.60). Shading indicates standard error of the mean.

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