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RESEARCH ARTICLE

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A mechanistic and empirically supported lightning risk model for forest trees

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Abstract

1. Tree death due to lightning influences tropical forest carbon cycling and tree community dynamics. However, the distribution of lightning damage among trees in forests remains poorly understood.
2. We developed models to predict direct and secondary lightning damage to trees based on tree size, crown exposure and local forest structure. We parameterized these models using data on the locations of lightning strikes and censuses of tree damage in strike zones, combined with drone-based maps of tree crowns and censuses of all trees within a 50-ha forest dynamics plot on Barro Colorado Island, Panama.
3. The likelihood of a direct strike to a tree increased with larger exposed crown area and higher relative canopy position (emergent > canopy >>> subcanopy), whereas the likelihood of secondary lightning damage increased with tree diameter and proximity to neighbouring trees. The predicted frequency of lightning damage in this mature forest was greater for tree species with larger average diameters.
4. These patterns suggest that lightning influences forest structure and the global carbon budget by non-randomly damaging large trees. Moreover, these models provide a framework for investigating the ecological and evolutionary consequences of lightning disturbance in tropical forests.
5. *Synthesis*. Our findings indicate that the distribution of lightning damage is stochastic at large spatial grain and relatively deterministic at smaller spatial grain (<15 m). Lightning is more likely to directly strike taller trees with large crowns and secondarily damage large neighbouring trees that are closest to the directly struck tree. The results provide a framework for understanding how lightning can affect forest structure, forest dynamics and carbon cycling. The resulting lightning risk model will facilitate informed investigations into the effects of lightning in tropical forests.

KEYWORDS

carbon cycling, disturbance, forest dynamics, Panama, tree mortality

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1 | INTRODUCTION

Tropical forests are disproportionately important to the global carbon budget (Feldpausch et al., 2012; Pan et al., 2011) and their carbon stocks are strongly influenced by the patterns of tree mortality (Johnson et al., 2016; Meakem et al., 2017). Lightning is a major agent of large tree mortality in many tropical forests (Anderson, 1964; Brünig, 1964; Sherman, Fahey, & Battles, 2000; Yanoviak et al., 2020) and thus likely is an important determinant of tropical forest structure (Galbraith et al., 2013; Johnson et al., 2016). However, information regarding the distribution of lightning damage within forests is largely limited to anecdotes, unstructured counts of lightning-damaged trees and post hoc studies of gap dynamics in mangroves (Anderson, 1964; Amir, 2012; Furtado, 1935; Magnusson, Lima, & Lima, 1996; Sherman et al., 2000; reviewed by Komarek, 1964; Yanoviak et al., 2015). This knowledge gap is problematic because it limits our understanding of the dynamics of tropical forests and impedes predictions of how these ecosystems will respond to potential increases or decreases in lightning frequency (Finney et al., 2018; Romps, Seeley, Vollaro, & Molinari, 2014; Williams, 2005). Addressing this knowledge gap requires a mechanistic understanding of lightning disturbance in tropical forests.

Lightning-caused tree damage results from cloud-to-ground (CG) lightning flashes. Each CG flash is produced by the union of two or more relatively low-voltage electrical channels (leaders) that develop in advance of the flash. Descending leaders originate in storm clouds and approach the ground in a series of bifurcating segments, ultimately generating an inverted dendritic structure spanning many square kilometres and with many potential contact areas on the ground (Figure S1; Rakov & Uman, 2003). Simultaneously, short (typically <10 m) ascending leaders extend vertically from electrically grounded objects within each potential contact area (Rakov & Uman, 2003, p. 110; Uman, 2008, p. 11). The return stroke—the powerful electrical discharge perceived as a lightning strike by humans—occurs when a descending leader unites with an ascending leader (hereafter *attachment*). Lightning attachment typically is limited to a single tree (hereafter the *directly struck tree*) even in dense forest; however, the electric current distributed from a single attachment point commonly damages or kills additional trees up to 45 m from the directly struck tree (hereafter *secondary lightning damage*; Anderson, 1964; Furtado, 1935; Magnusson et al., 1996). Secondary lightning damage apparently occurs infrequently in temperate forests (Murray, 1958; Taylor, 1974), potentially because of the higher electrical resistivity of temperate trees (Gora, Bitzer, Burchfield, Schnitzer, & Yanoviak, 2017), but is characteristic of lightning damage in tropical forests (Anderson, 1964; Furtado, 1935; Magnusson et al., 1996; Yanoviak, Gora, Burchfield, Bitzer, & Detto, 2017).

The physical pattern of CG strike development provides the foundation for understanding factors affecting the predictability of a strike location. Although lightning frequency varies geographically, an individual lightning strike is unpredictable at large spatial extents because the atmospheric processes influencing its path are not well understood. However, the predictability of a CG lightning strike location (i.e. the attachment point) increases at smaller spatial grains (e.g. within a hectare) based on the characteristics of electrically grounded objects (Uman, 2008). Specifically, tall objects with larger surface area have higher strike probabilities than nearby shorter and smaller objects (Uman, 2008). Thus, all else equal, the probability of a direct lightning strike to any given tree should increase with greater crown area and height relative to nearby trees (Figure 1).

The effects of the height and area of grounded objects on lightning strike distributions are well-established in physical theory, but supporting evidence is limited for forest trees. Many studies propose that emergent trees (i.e. trees substantially taller than their neighbours; King & Clark, 2011) are more likely to be struck than shorter nearby trees (Figure 1b; Anderson, 1964; Palik & Pederson, 1996; Plummer, 1912), but support for this pattern is anecdotal or circumstantial (Reynolds, 1940; Tutin, White, & Mackanga-Missandzou, 1996; Yanoviak et al., 2015). Moreover, the effect of differences in height among neighbouring canopy trees may be too small to detect (Bazelyan & Raizer, 2000). If we assume no effect of tree height, then the likelihood that a tree is directly struck by lightning is expected to be proportional to its exposed crown area (i.e. the 2-dimensional crown surface visible from above; Figure 1a; Uman, 2008). However, the role of crown area remains unexplored in this context.

After lightning attaches to one tree, secondary damage to surrounding trees primarily occurs via flashover—the jumping of electric current from one object to another across an air gap (Darveniza, 1992; Furtado, 1935; Yanoviak et al., 2017). Field observations indicate that lightning jumps from the directly struck tree

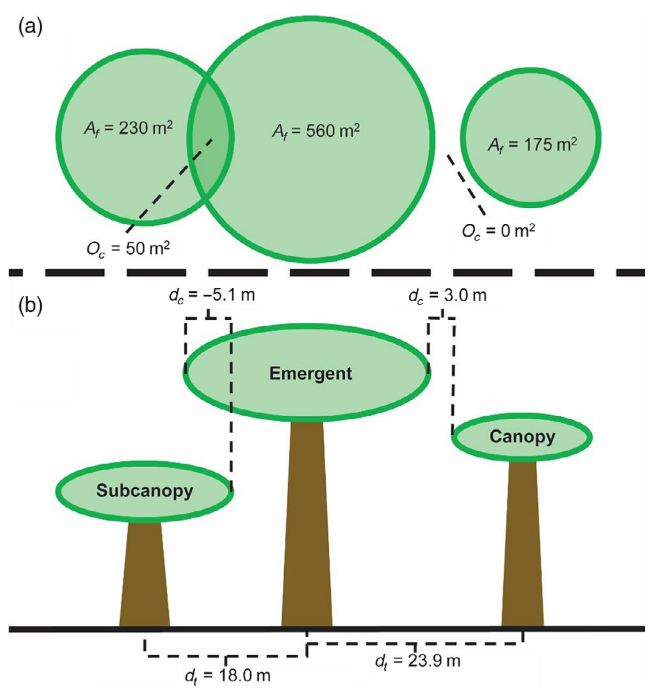

FIGURE 1 Hypothetical crowns of canopy trees viewed from above (Panel a) and in profile (Panel b) depicting key variables used in the models: exposed crown area as A_f, idealized crown overlap as O_c, idealized inter-crown distance as d_c, trunk distance as d_t and canopy position (subcanopy, canopy, emergent) [Colour figure can be viewed at wileyonlinelibrary.com]

to the nearest branch of a neighbouring tree, regardless of ground-level distance to that neighbour (Anderson, 1964; Furtado, 1935; Yanoviak et al., 2017). This is consistent with the principles of electromagnetism; the electrical resistance of air is *c*. 13 orders of magnitude greater than that of tree tissues (Defandorf, 1955), thus the most important factor determining whether a tree experiences flashover presumably is the proximity of its branches to the directly struck tree. Although less common, secondary damage also occurs when the branches of neighbouring trees are in direct contact or are connected by lianas (Yanoviak et al., 2017). Consequently, factors that increase proximity to neighbouring crowns, such as large crown area or the presence of neighbouring trees with expansive crowns, should increase the likelihood of secondary lightning damage (Anderson, 1964).

Here we propose and empirically test a mathematical framework for predicting the frequency of lightning damage to trees. We hypothesize that the likelihood of lightning-caused tree damage is a function of tree size (i.e. height and crown area) and inter-crown distance. We predict that the probability a tree is directly struck by lightning increases with exposed crown area and canopy position (i.e. relative height within the local forest; emergent > canopy > subcanopy). We also predict that the likelihood of secondary damage increases with shorter inter-crown distance and that this relationship changes with tree size (i.e. larger trees are more likely to experience secondary damage). We combine the empirical models of direct and secondary lightning damage to produce a lightning risk model that is testable in any forest. To generate hypotheses about the broader ecological effects of lightning, we use this risk model to predict the frequency of lightning damage for *c*. 20,000 trees in a lowland tropical forest and explore the ecological implications.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in the 50-ha forest dynamics plot (Condit, 1995) in the seasonally moist lowland tropical forest on Barro Colorado Island (BCI) in central Panama (9.210°N, 79.745°W). The mean annual temperature is 26°C and mean annual rainfall is *c*. 2,650 mm (2000–2017), concentrated during a long wet season (mid-May to December; Paton, 2017). The wet season is characterized by frequent thunderstorms, and the forest experiences 12.7 CG lightning strikes/km^2 annually (Liu & Heckman, 2012; Rudlosky, 2015; Yanoviak et al., 2020). Croat (1978) and Leigh Jr. (1999) provide additional details about the study site.

2.2 | Forest structure data

We modelled the probability of lightning damage (direct strike or secondary damage, separate models) as a function of tree size, canopy position, location relative to neighbouring trees and species identity for trees in the 50-ha forest dynamics plot on BCI. Data on tree DBH (trunk diameter at 1.3 m height or above buttresses), location (to 0.1 m) and species identity for all trees >10 cm DBH (20,829 trees of 218 species) were obtained from the 2015 census of the plot (Condit et al., 2019). We used orthomosaics constructed from drone overflights in October 2014 (Park et al., 2019) to identify trees with parts of their crowns visible from above, and to measure exposed crown area of each tree (the area of each tree crown visible from directly above). Hereafter, trees with any portion of their crown visible from above are referred to as *exposed trees*. We manually delineated individual crowns with exposed crown area greater than 50 m^2 in the orthomosaic (1945 crowns), and then linked delineated crowns to tagged trees in the field (Graves, Caughlin, Asner, & Bohlman, 2018). During the field work linking trees to crowns, we scored the canopy position of each exposed tree as emergent, canopy or subcanopy, based on the amount of direct or lateral light received by each tree (King, 1996; King, Wright, & Connell, 2006). Subcanopy trees were those with 10%–90% of their crowns exposed to sunlight from directly above, meaning each had some of its crown in direct light but was shorter than at least one neighbouring tree having an overlapping crown. We measured the height of exposed trees by subtracting the ground elevation (obtained from LiDAR) from the canopy surface elevation estimated from the drone-acquired images using photogrammetry. Additional details are given in Supporting Information: Methods.

We used drone and field-based measurements of tree characteristics to evaluate the probability of direct strikes, but we only had this information for exposed trees. Consequently, we used allometric equations to estimate crown area and crown radius for every tree in the plot to assess the distribution of secondary lightning damage. We used species-specific allometric equations, when available, to calculate expected tree height and crown area for each individual tree (139 of the 218 species), and community-wide allometries for other species (Martínez Cano, Muller-Landau, Wright, Bohlman, & Pacala, 2019). We calculated expected geometric mean crown radius for each tree from the expected crown area ($r_c = \sqrt{\frac{A_c}{\pi}}$, where r_c is the expected crown radius and A_c is crown area) assuming that tree crowns were elliptical on a horizontal plane.

2.3 | Lightning damage surveys

We recorded lightning-caused tree damage resulting from 19 lightning strikes in the 50-ha plot from 2015 to 2018. These strikes were located using a camera-based lightning monitoring system (Yanoviak et al., 2017). Any gaps in our monitoring period were short in duration and applied consistently across the 50-ha plot. Thus, these data are an unbiased sample of lightning strike damage and likely represent a complete sample of lightning strikes in the 50-ha plot during the study period. We visited each strike site within 1 month of the strike, identified the directly struck tree and surveyed every tree >10 cm diameter within 45 m of the directly struck tree for characteristic lightning damage (i.e. directionally biased dieback from flashover; Yanoviak et al., 2017). Because lightning damage often was subtle in the short term, we resurveyed these strike sites for damaged trees at regular intervals. For this study, secondary lightning damage was based on surveys from *c*. 1 year post-strike (11–14 months). We did not include secondary damage for two of the direct strikes because the secondarily damaged trees extended beyond the plot edge. We surveyed a total of 3,728 trees, of which 19 were directly struck and 276 were secondarily damaged by lightning.

2.4 | Modelling direct lightning strikes

For all exposed trees, we modelled the probability of a direct lightning strike as a function of exposed crown area and canopy position (emergent, canopy, subcanopy). We first fit a model in which the probability of a direct strike is proportional to exposed crown area, with no effect of canopy position,

$$P_{Di} = a\,A_i, \tag{1}$$

where P_{Di} is the probability that a tree i is struck directly, A_i is the tree's exposed crown area (m^2) and a is a fitted parameter for the probability of a direct strike per m^2 of exposed crown area. We compared this crown area-only model to a null model in which the probability of a direct strike was equal for all trees with exposed crown areas >50 m^2.

Given that canopy position likely also influences the probability of a direct lightning strike (Palik & Pederson, 1996; Plummer, 1912; Yanoviak et al., 2015), we then fit a more complex model in which the coefficient of crown area (a in Equation 1) differed for emergent (N = 162), canopy (N = 1,034) and subcanopy trees (N = 749). To fit this model, we maximized the log likelihood,

$$\mathcal{L}_D = \sum \left[S_i \log\left(a_{c_i} A_i\right) + N_i \log\left(1 - a_{c_i} A_i\right)\right], \tag{2}$$

where $\mathcal{L}_D$ is the total log-likelihood of the model; i represents an individual tree; S_i is the number of times the tree was struck directly by lightning (always 0 or 1 in this study); N_i was the number of times the tree was not struck (out of 19 lightning strikes); a_{c_i} is the optimized coefficient of crown area for the ith tree with canopy position of emergent, canopy or subcanopy; and other variables are the same as in Equation 1. All models were fit using the function *optim* in R version 3.5.2 (R Core Team, 2018). We compared the models using AIC (ΔAIC > 2 was considered significant) and we calculated profile likelihood confidence intervals using the function *mle2* (package BBMLE; Bolker, 2017). We confirmed that the maximized parameter estimates matched the analytical expectation that the probability of a strike equals the number of strikes per ha of crown area per strike. To assess whether lightning always struck the tallest tree locally, we compared the absolute height and, to account for topography, separately compared the maximum altitude between the directly struck trees and all exposed trees within 45 m of their location at the ground level.

2.5 | Modelling secondary lightning damage

For all *neighbouring trees* to a directly struck tree (i.e. all trees >10 cm DBH with rooting points located within 45 m of the trunk of the directly struck tree), we fit models for the probability of secondary lightning damage as a function of tree size and position relative to the directly struck tree. We used 45 m as the threshold for this neighbourhood based on the furthest observed distance of secondary damage (43 m). In total, these models included 234 damaged trees and 3,940 undamaged trees distributed among 17 strikes (excluding directly struck trees and two strikes within 45 m of the plot boundary). No trees were damaged by multiple strikes despite 355 trees appearing in two strike zones. Because the source of lightning damage was known based on the timing of each strike, we were able to unambiguously assign lightning-damaged trees that appeared in two strike zones (N = 39) to a specific strike.

Secondary lightning damage typically occurs between the closest branches of adjacent trees (Yanoviak et al., 2017), and thus would ideally be modelled as the shortest distance between the focal struck tree and the crown of the tree that may or may not have secondary damage. Lacking such data, we instead evaluated the following three proxies for the distance between or overlap between the two trees: (a) the distance between tree rooting points (i.e. trunk locations at ground level); (b) the estimated distance between the edges of tree crowns (idealized inter-crown distance) and (c) the estimated area of overlap between crowns (idealized crown area overlap; Figure 1). We expected the effects of all three proxies to depend on tree size, and thus each model also included tree DBH and its interaction with the relevant proxy. DBH was weakly correlated with idealized inter-crown distance ($r = -0.12$, $p < 0.001$) and idealized crown area overlap ($r = 0.18$, $p < 0.001$), but it exhibited no relationship with trunk distance ($r = 0.01$, $p = 0.605$). We fit logistic models for the probability of secondary lightning damage with fixed effects for tree size, the distance proxy and their interaction, and a random effect for strike site, using the function *glmer* in the LME4 package in R (R Core Team, 2019). To facilitate model convergence, we normalized DBH in all models (*scale* function in R). We determined the best fit model for each proxy by testing each fixed effect using nested model reduction based on AIC values. We also used AIC to compare models based on each proxy. We confirmed that the predicted probabilities matched the observed proportions of secondary damage in the field.

Idealized inter-crown distance and crown overlap were based on the assumptions that each tree crown was circular when viewed from above, centred around its trunk and had the mean crown area expected given its DBH and species identity (Martínez Cano et al., 2019). We estimated the idealized inter-crown distance as the distance between the trunk locations less the sum of the two crown radii (Figure 1b). We estimated the area of crown overlap between neighbouring tree crowns along a horizontal plane (hereafter *idealized crown area overlap*; Figure 1a). We modelled each proxy separately because they exhibited multicollinearity. Idealized inter-crown distance was strongly correlated with trunk distance ($r = 0.94$, $p < 0.001$) and idealized crown area overlap was correlated with idealized inter-crown distance ($r = -0.44$, $p < 0.001$) and trunk distance ($r = -0.38$, $p < 0.001$).

2.6 | Integrated lightning risk model

We combined the best supported models for the probability of a direct strike and the likelihood of secondary damage to produce a lightning risk model for forest trees on BCI. We calculated the probability of a direct lightning strike for all exposed trees using the best fit model for a direct strike, and multiplied that value by the number of annual strikes at the study site (6.35 strikes; Yanoviak et al., 2020) to obtain the predicted annual number of strikes for each exposed tree. We then estimated the predicted annual frequency of secondary damage for each tree as the sum of the frequency of secondary damage from all exposed trees within 45 m (Supporting Information: Methods). Finally, we constructed the total lightning risk model for forest trees by adding the predicted frequency of direct lightning damage to the predicted frequency of secondary damage for each focal tree (see Equation 3).

2.7 | Ecological implications of the lightning risk model

We used the lightning risk model to calculate the predicted frequency of lightning damage for all focal trees above 10 cm DBH in the 50-ha plot (focal trees being each of 20,829 trees >10 cm DBH). We assumed that only exposed trees with crown areas above 50 m^2 could be directly struck by lightning, and only trees within 45 m of a directly struck tree could experience secondary lightning damage (Yanoviak et al., 2020). To retain all data while ensuring that each tree was surrounded by exposed trees distributed over equivalent areas, we mirrored exposed trees that were within 45 m of the plot edge on the outside of the plot. This approach assumed that local forest structure was representative of surrounding forest; we observed no consistent differences in forest structure between the edge and the centre of the plot. To evaluate the model, we tested whether the lightning risk model predicted real variation in tree damage rates associated with differences in tree DBH. Specifically, we scaled the number of strikes in the lightning risk model to the total number of strikes observed in this study ($N = 19$) and compared the predicted probability of lightning damage to the real proportions of lightning-damaged trees binned within 10 quantiles of DBH ($N = 20{,}829$).

To generate hypotheses about the ecological effects of lightning, we examined how predicted lightning damage frequency was related to focal tree characteristics and neighbourhood forest structure using Pearson correlations. Specifically, we tested how predicted lightning damage frequency ($N = 20{,}829$ trees) was correlated with focal tree DBH, basal area of neighbouring trees, stem density of neighbouring trees, and maximum and average values of exposed neighbouring trees' DBH, height and allometric crown area. Neighbouring trees were defined as those within 45 m of the focal tree. We used tree DBH from the 2015 census of the 50-ha plot and exposed tree height as estimated from the orthomosaics. We log-transformed the predicted damage frequency, average exposed neighbour DBH and average exposed neighbour crown area to meet the assumptions of Pearson correlation. We expected average predicted lightning strike frequency to differ among species because of interspecific differences in tree size. To assess this pattern, we calculated average predicted lightning damage frequency and average DBH for all 111 tree species with at least 25 individuals (19,876 trees total).

3 | RESULTS

3.1 | Empirical patterns of direct and secondary lightning damage

As predicted, the probability of a direct lightning strike increased with crown area and canopy position (emergent > canopy >>> subcanopy, Table 1; Figure 2; Figure S2). The model including separate coefficients for different canopy positions outperformed the model with only crown area (ΔAIC = 10.4), which in turn outperformed the null model (ΔAIC = 15.8). While many neighbouring trees were taller than the directly struck tree, the average number of taller neighbours was near zero within 10 m of the centrally struck tree (Figure S3). This suggests that the effects of tree height on direct strike probability were greatest at small spatial grains.

TABLE 1 Total crown area, total lightning strikes observed and lightning strike probability per crown area by canopy position, for crowns having exposed crown area greater than 50 m^2 on the BCI 50-ha plot. The per-area direct strike probability is the expected probability of a direct strike per ha of crown area per strike within the 50-ha plot. That is, for any focal tree, the expected probability that the tree is struck (when there is a strike on the 50-ha plot) is equal to its crown area in hectares times this probability

Canopy position	Exposed crowns (N)	Total crown area (ha)	Direct lightning strikes (N)	Per-area direct strike probability (ha^{-1}; with 95% CI)
Subcanopy	749	9.51	0	0.0 (0.0, 0.0071)
Canopy	1,034	14.89	13	0.0459 (0.0253, 0.0756)
Emergent	162	5.90	6	0.0536 (0.0213, 0.1083)

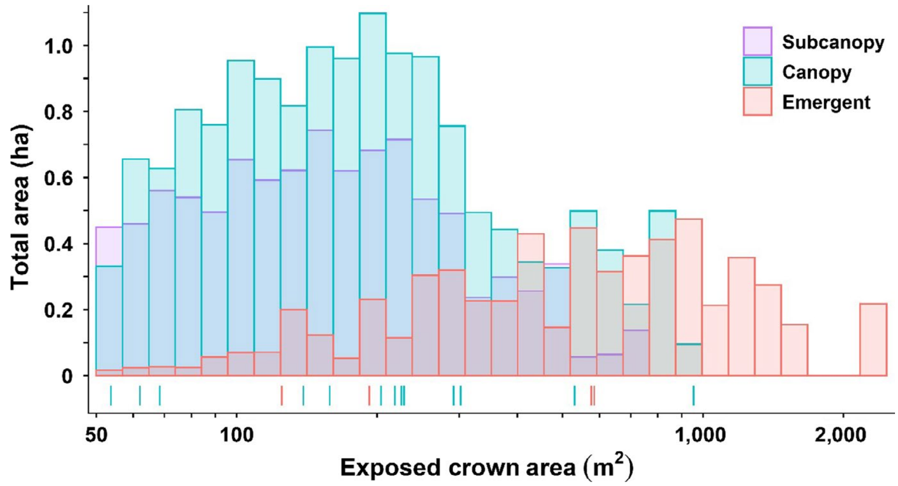

FIGURE 2 Distribution of total exposed crown area across bins of individual trees' exposed crown area for subcanopy, canopy and emergent trees. Vertical lines beneath the histograms indicate the exposed crown areas of the 19 directly struck trees, with colour signifying their canopy position. Data are presented in 30 equal bins on the $\log_{10}$ scale. Only trees with exposed crown area >50 m^2 were included

TABLE 2 Model results for three approaches to estimating the effect of tree proximity on the likelihood of secondary damage. Column ΔAIC represents the change in AIC values with the independent removal of individual fixed effects and model AIC indicates the AIC value of the model with no terms removed. The best supported model is highlighted in bold. The reduced model is only presented when the interaction did not contribute to model fit

Proxy for distance	Model type	Parameter	Coefficient (*SE*)	ΔAIC	Model AIC
Idealized inter-crown distance	**Reduced model**	**Intercept**	**−1.678 (0.229)**	**—**	**1,064.5**
		Inter-crown distance	**−0.203 (0.011)**	**658.5**	
		DBH	**0.440 (0.059)**	**52.1**	
	Full model	Intercept	−1.685 (0.229)	—	1,065.0
		Inter-crown distance	−0.200 (0.011)	658.5	
		DBH	0.482 (0.071)	52.1	
		Inter-crown distance × DBH	−0.008 (0.007)	−0.5	
Trunk distance	Full model	Intercept	0.916 (0.294)	—	1,065.2
		Trunk distance	−0.198 (0.181)	657.8	
		DBH	1.147 (0.181)	141.7	
		Trunk distance × DBH	−0.019 (0.008)	5.6	
Idealized crown overlap	Full model	Intercept	−3.478 (0.197)	—	1,421.2
		Crown overlap	1.080 (0.072)	71.0	
		DBH	0.419 (0.050)	301.8	
		Crown overlap × DBH	−0.171 (0.020)	31.8	

The likelihood of secondary lightning damage decreased with distance from the directly struck tree and increased with tree diameter, as expected (Table 2; Figure 3). These patterns were better described by models based on idealized inter-crown distance or trunk distance than by the model of idealized crown overlap (Table 2; Figure S4). Shorter idealized inter-crown distances increased the likelihood of secondary damage (Figure 3a), and trees with larger DBH and larger crown radii had shorter average inter-crown distances to their neighbours (Figure S5). The best fit model for trunk distance included the interaction between tree DBH and trunk distance. Specifically, the likelihood of secondary damage was relatively higher for large trees at shorter distances but converged with smaller trees at longer distances (Figure 3b). By contrast, the interaction term did not contribute significantly to the idealized inter-crown distance model.

3.2 | Lightning risk model for tropical forest trees

The best lightning risk model combined the direct strike model incorporating crown area and canopy position with the secondary damage model based on idealized inter-crown distance and diameter (without the interaction). It took the following form:

$$F_i = S_A \left(a_{c_i} A_i + \sum_j \left[a_{c_j} A_j \frac{e^{-1.678 - 0.203\, d_{i,j} + 0.44\, D_i}}{1 + e^{-1.678 - 0.203\, d_{i,j} + 0.44\, D_i}} \right] \right), \tag{3}$$

where F_i is the predicted frequency at which the focal tree, *i*, experiences lightning damage (hereafter the *predicted lightning damage frequency*; strikes/year); S_A is the number of strikes in the 50-ha plot per year (strikes/year); a_{c_i} and a_{c_j} are the per-area direct strike probability

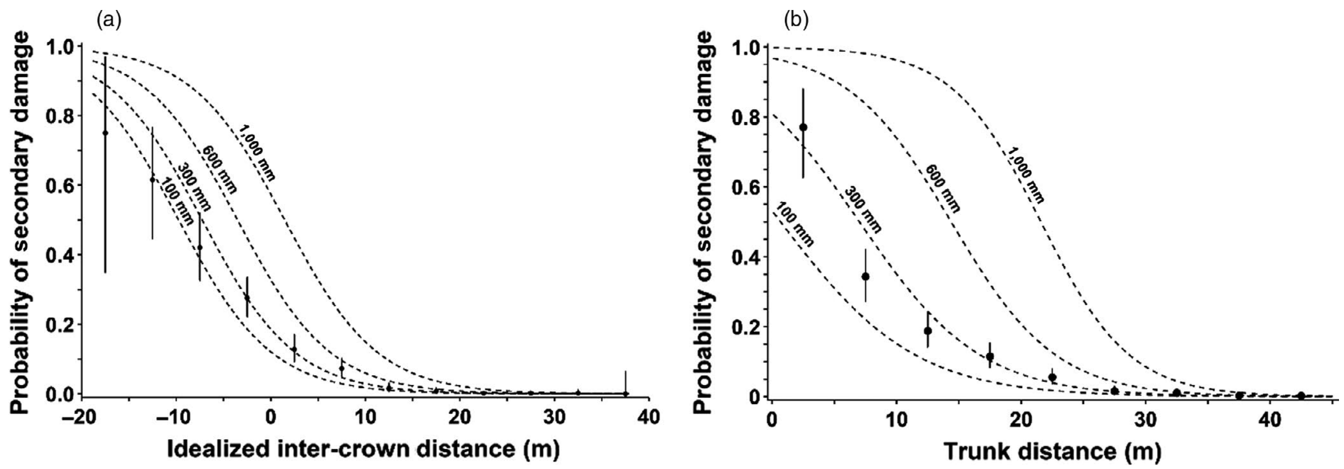

FIGURE 3 The probability of secondary lightning damage to trees as a function of their idealized inter-crown distance (panel a) or their trunk distance relative to the directly struck tree (panel b; N = 20,829). Points represent the proportion of trees damaged within each bin of idealized inter-crown distance or trunk distance (5 m bins) with error bars calculated based on the binomial distribution (Clopper–Pearson method). The lines represent the predicted probabilities from the logistic models holding DBH constant at 100, 300, 600 or 1,000 mm. Negative values of inter-crown distance indicate crown overlap

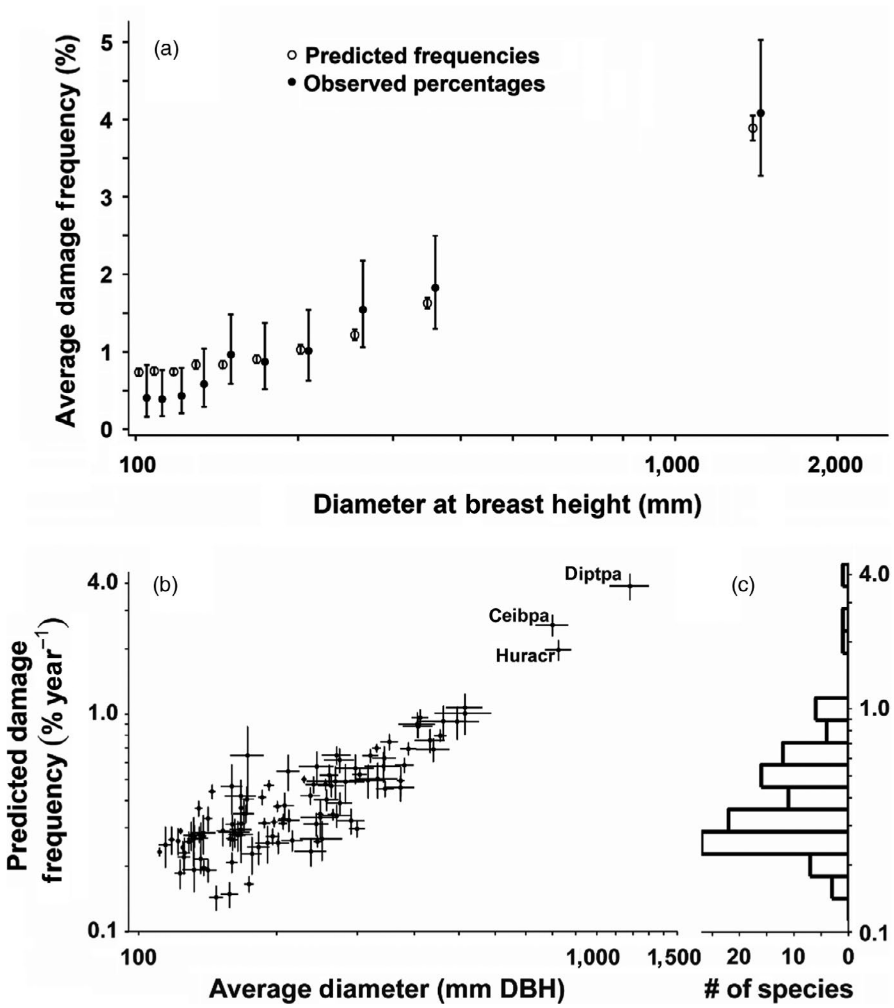

FIGURE 4 Associations of predicted lightning frequency with diameter among individuals and among species. (a) The average predicted frequency of lightning damage (with 95% CI) based on the lightning risk model and the observed percentages of lightning-damaged trees (with 95% CI) by diameter quantile (DBH; N = 20,829 trees). (b) Mean predicted lightning damage frequency (±SE) in relation to mean DBH (±SE) for each tree species with more than 25 individuals >10 cm DBH in the 50-ha plot (means are calculated for trees >10 cm DBH; see Table S1 for details) together with a histogram of species distribution across the range of predicted lightning damage frequency (panel c). The three species with highest predicted lightning damage frequencies are labelled: diptpa = *Dipteryx oleifera* (Fabaceae), ceibpa = *Ceiba pentandra* (Malvaceae) and huracr = *Hura crepitans* (Euphorbiaceae)

given the canopy positions (emergent, canopy or subcanopy) c_i and c_j of the ith and jth trees (Table 1); A_i and A_j are the crown areas of the ith and jth trees; $d_{i,j}$ is the idealized inter-crown distance between the ith and jth trees (m); and D_i is the DBH of the ith tree. The first term in parentheses relates to the direct strike probability, whereas the second term with the summation relates to the secondary damage probability. The lightning risk model performed reasonably well in capturing DBH-related variation in the proportions of trees damaged by lightning (Figure 4a). However, the model tended to overestimate lightning strike frequency for the smallest trees (<15 cm DBH). The trunk distance model of secondary damage performed similar to the idealized inter-crown distance model (Figure S4) and an alternative total lightning risk model based on trunk distance is presented in Supporting Information: Results.

3.3 | Implications of the lightning risk model

Focal tree characteristics were associated with the predicted frequency of lightning damage from the lightning risk model. Larger DBH trees had higher predicted lightning strike frequencies than smaller trees (Figure 4a). For example, the predicted frequency of lightning damage for all trees >10 cm DBH was 0.423% $year^{-1}$ (*SE* = 0.004% $year^{-1}$, whereas the predicted lightning damage frequency for trees >60 cm DBH was 1.986% $year^{-1}$ (*SE* = 0.052% $year^{-1}$). Mean predicted lightning damage frequency differed among tree species in association with average tree size at this point in time (Figure 4b).

Local forest structure was also correlated with predicted lightning damage frequency as calculated from the lightning risk model (Equation 3; Figures S6 and S7). The predicted frequency of lightning damage to any given tree was positively correlated with the increasing average and maximum size of exposed neighbouring trees (Figures S6 and S7). The strength of this relationship was similar whether size was assessed as diameter, height or allometric crown area (range of Pearson *r*: 0.23–0.28). The predicted frequency of lightning damage was also positively correlated with the total basal area of all neighbouring trees (*r* = 0.27). By contrast, local stem density was not correlated with predicted lightning damage frequency (Figures S6 and S7).

4 | DISCUSSION

Given the importance of lightning as a disturbance (Anderson, 1964; Sherman et al., 2000; Yanoviak et al., 2020), uncertainty regarding patterns of lightning-caused damage represents a major limitation to our understanding of forest dynamics and carbon cycling. Here we present an empirical lightning risk model for tropical forest trees that is based on principles of lightning physics. This model provides a foundation for understanding the distribution of lightning damage across landscapes and, because it uses basic tree characteristics, it is readily adaptable to other forests. Empirical patterns of lightning-caused tree damage and the predictions of the model suggest that lightning influences forest structure and carbon cycling at this study site.

The associations between lightning risk and aspects of tree size potentially explain variation in disturbance regimes and the spatial grain at which lightning is deterministic. Many lightning-damaged trees die from their injuries (Anderson, 1964; Furtado, 1935; Rakov & Uman, 2003), and the higher incidence of lightning damage to large trees explains why lightning is responsible for 40%–50% of large tree mortality on BCI (Yanoviak et al., 2020). Accordingly, it is possible that the positive relationships between the mortality rate of large trees and the exposure of their crowns to light (Arellano, Medina, Tan, Mohamad, & Davies, 2018; Rüger, Huth, Hubbell, & Condit, 2011) or proximity to fragment edges (Laurance, Delamônica, Laurance, Vasconcelos, & Lovejoy, 2000) results at least in part from the greater frequency of lightning damage for these highly exposed trees. The effect of crown exposure is consistent with the expectation that taller trees are more likely to be struck by lightning (Anderson, 1964; Yanoviak et al., 2015), and this association shows that the distribution of lightning damage has a deterministic component, particularly at small spatial grain (<15 m). By contrast, the effect of exposed crown area indicates that stochastic atmospheric processes are important to the likelihood of being directly struck by lightning at larger spatial grains. Collectively, the effects of lightning on large exposed trees suggest that lightning is a major, and generally underexplored, factor shaping the physical structure of tropical broadleaf forests.

The effects of lightning on large trees also suggest that it is important to forest carbon cycling. Large trees contain nearly 50% of above-ground forest biomass (Lutz et al., 2018; Slik et al., 2010) and the higher likelihood of large trees to experience direct and secondary lightning damage and lightning-caused mortality (Yanoviak et al., 2020) suggests that lightning influences the spatial distribution of biomass and carbon within tropical forests. Consequently, the disproportionate effect of lightning on large trees must be considered when upscaling the effects of lightning disturbance or estimating its contributions to forest carbon dynamics. However, the data used in this study were from a single mature tropical forest, and additional studies are needed to characterize lightning-caused disturbance in earlier successional forests.

Multiple factors facilitate the persistence of large trees despite their relatively high probabilities of lightning damage. Given the stochastic distribution of lightning strikes at large scales and their low annual frequency, many trees reside in the canopy for decades before experiencing lightning damage. Many trees also survive the effects of lightning (Yanoviak et al., 2020) and it has long been speculated that the probability of lightning strike survival varies interspecifically (Anderson, 1964; Baker, 1973; Covert, 1924; Maxwell, 1793). If supported, such interspecific differences would indicate that lightning shapes canopy tree composition in addition to forest structure.

The findings presented here provide insight into the ecological importance of lightning; additional studies are needed to understand tree responses to lightning damage. In the long term, the ideal model of lightning-caused tree mortality should integrate the lightning risk model presented here with the previously published model of resistive heating during lightning–tree interactions (Gora et al., 2017). This requires three additional pieces of information: (a) community-wide tree electrical resistivity data, (b) contemporaneous lightning current profiles and (c) quantification of the current distribution within a lightning strike site. Future studies addressing these knowledge gaps will facilitate a fully mechanistic model of lightning disturbance in tropical forests. This model could then be upscaled in combination with lightning climatologies and remote sensing missions, such as space-based LiDAR, to understand how climate-induced changes in lightning frequency will influence forest structure, composition and carbon cycling (Finney et al., 2018; Romps et al., 2014; Williams, 2005). Moreover, this model could facilitate investigations into the ecological and evolutionary importance of lightning, particularly if other major sources of disturbance are quantified.

5 | CONCLUSIONS

The results presented here are particularly robust for three reasons. First, the models in this study are based on established principles of lightning physics (Darveniza, 1992; Uman, 2008). Second, the predictions of these models are supported by empirical patterns and complement descriptions of lightning-caused damage in the Americas and Asia (Anderson, 1964; Brünig, 1964; Furtado, 1935; Magnusson et al., 1996; Yanoviak et al., 2017). Third, the data supporting these patterns are extensive and unique; we present the only existing dataset of recorded lightning strike locations, and they coincide with a rare dataset of drone-mapped tree crowns. Thus, this study provides a solid framework for investigating the role of lightning in ecological and evolutionary processes in tropical forest ecosystems.

Although the lightning damage models presented here are robust, they are simplified and deserve future elaboration and improvement. Our approach assumed that proximity to the directly struck tree determines secondary damage frequency. However, lightning can also flashover from secondarily damaged canopy trees to their smaller neighbours, and incorporating this additional process could improve model fit for small trees. Additionally, although lightning is exceedingly unlikely to pass through an exposed tree crown to strike an unexposed tree (Covert, 1924) and no subcanopy trees were directly struck among 92 strikes located at our study site, lightning might directly strike some unexposed or subcanopy trees (Mäkelä, Karvinen, Porjo, Mäkelä, & Tuomi, 2009). Accurately estimating the frequencies of these rare events will be important to projections of forest turnover based on lightning risk models. The model of direct lightning strikes also was limited in scope. In addition to tree canopy position and exposed crown area (Uman, 2008), topography, soil type and species-specific differences in electrical conductivity are hypothesized to influence the likelihood of direct lightning strikes (Gora & Yanoviak, 2015; Johnson, 1966; Minko, 1975; Stone & Chapman, 1912). These factors could influence lightning strike locations at different spatial grains, but they were not testable in this study due to either insufficient species-level replication or limited variability within the 50-ha plot (topography, soil type). The ongoing systematic location of lightning strikes in the BCI forest (Yanoviak et al., 2017) will build on the mathematical framework presented here to test each of these additional variables in the future.

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AUTHORS' CONTRIBUTIONS

E.M.G. and H.C.M.-L. designed the model and collected the data; J.C.B. and P.M.B. helped design the study; S.P.Y. helped design the study and coordinated the lightning data collection; E.M.G. analysed the data and led the writing of the manuscript. All the authors contributed to writing the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad Digital Repository https://doi.org/10.5061/dryad.c59zw3r48 (Gora et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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