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Lightning is a major cause of large tree mortality in a lowland neotropical forest

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Summary

- The mortality rates of large trees are critical to determining carbon stocks in tropical forests, but the mechanisms of tropical tree mortality remain poorly understood. Lightning strikes thousands of tropical trees every day, but is commonly assumed to be a minor agent of tree mortality in most tropical forests.
- We use the first systematic quantification of lightning-caused mortality to show that lightning is a major cause of death for the largest trees in an old-growth lowland forest in Panama. A novel lightning strike location system together with field surveys of strike sites revealed that, on average, each strike directly kills 3.5 trees (> 10 cm diameter) and damages 11.4 more.
- Given lightning frequency data from the Earth Networks Total Lightning Network and historical total tree mortality rates for this site, we conclude that lightning accounts for 40.5% of the mortality of large trees (> 60 cm diameter) in the short term and probably contributes to an additional 9.0% of large tree deaths over the long term.
- Any changes in cloud-to-ground lightning frequency due to climatic change will alter tree mortality rates; projected 25–50% increases in lightning frequency would increase large tree mortality rates in this forest by 9–18%. The results of this study indicate that lightning plays a critical and previously underestimated role in tropical forest dynamics and carbon cycling.

Introduction

Tree mortality is a key component of carbon cycling and can shape local biodiversity, yet the relative contributions of different mechanisms to tree mortality remain unknown for most tropical forests (McDowell *et al.*, 2018). Among-site variation in tree mortality determines variation in above-ground biomass in tropical forests (Johnson *et al.*, 2016), with large tree mortality in particular having disproportionately large effects on carbon storage (da Costa *et al.*, 2010; Lutz *et al.*, 2018; Meakem *et al.*, 2018). Quantifying these patterns is increasingly important because climatic change is expected to alter tree mortality rates (Breshears *et al.*, 2005; van Mantgem *et al.*, 2009) with profound consequences for forest physiognomy and ecosystem function (Dale *et al.*, 2001; Phillips *et al.*, 2009; McDowell *et al.*, 2011). Historically, agents such as windthrow and drought were considered the primary causes of tree mortality in most broadleaf tropical forests (Phillips *et al.*, 2010; Bennett *et al.*, 2015; Negrón-Juárez *et al.*, 2017), but supporting data are limited (McDowell *et al.*, 2018). Here, we show that a neglected phenomenon – lightning – is the single most important cause of large tree mortality in an old-growth lowland tropical forest of central Panama. This site experiences lightning frequency comparable to many lowland tropical forests worldwide (Cecil *et al.*, 2014), and thus the results serve as a first estimate of the role of lightning in tropical forest dynamics at the global scale.

Lightning frequency is highest in the tropics (Cecil *et al.*, 2014), where it strikes thousands of trees each day. Lightning is a major agent of disturbance in mangrove forests, where lightning gaps represent up to 15.0% of total forest area at any given time (e.g. Smith *et al.*, 1994; Sherman *et al.*, 2000; Amir & Duke, 2019). However, the relative importance of lightning to mangrove tree mortality rates has never been quantified, and mangroves are spatially limited (0.7% of tropical forest area; Giri *et al.*, 2011). By contrast, the contribution of lightning to tree mortality in terrestrial tropical forests (99.3% of all tropical forest area) has never been accurately quantified, and is generally assumed to be minor (Magnusson *et al.*, 1996). This is largely because detecting and accurately attributing individual tree mortality to lightning is difficult (Komarek, 1964; Yanoviak *et al.*, 2017). Trees directly killed by lightning in terrestrial tropical forests typically die standing, often snap within months of death and generally have no obvious lightning scars (Furtado, 1935; Anderson, 1964; Brünig, 1964; Komarek, 1964; Magnusson

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et al., 1996; Tutin *et al.*, 1996; Yanoviak *et al.*, 2017). Lightning also indirectly kills trees by facilitating lethal infestations by insects and fungi (Taylor, 1974; Carey *et al.*, 1994; Fernando *et al.*, 2010), or weakening trees that are eventually uprooted (Taylor, 1974; Chao *et al.*, 2009). Most tree censuses are conducted at 5–10 yr intervals, and decomposition proceeds rapidly in tropical climates, meaning that most dead trees are encountered more than 1 yr after their deaths. Consequently, lightning-killed trees often are indistinguishable from trees that die standing due to drought, disease and other causes, or those snapped by storms (Putz & Milton, 1996; Gale & Barfod, 1999; Chao *et al.*, 2009). The few previous publications reporting lightning-caused mortality of trees in tropical terrestrial and swamp forests have focused exclusively on direct mortality, and are mostly case reports that provide no basis for quantifying the overall importance of lightning to tree mortality (Furtado, 1935; Anderson, 1964; Magnusson *et al.*, 1996; Tutin *et al.*, 1996).

Here, we quantify the role of lightning as an agent of tree mortality in the old-growth lowland tropical forest of Barro Colorado Island (BCI), Panama. We determined the locations of 32 lightning strikes using a camera-based lightning monitoring system, and repeatedly censused those locations to quantify associated tree damage and mortality (Yanoviak *et al.*, 2017). This enabled us to provide the first complete quantification of the role of lightning in tree mortality in any forest. We surveyed each strike site repeatedly over 11–25 months to quantify the average numbers of trees killed and damaged per strike (*c.* 1 ha of forest per strike; see the Materials and Methods section). We combined these averages with remotely sensed cloud-to-ground lightning frequency data for 2013–2018 (Liu & Heckman, 2012) and local measurements of lightning frequency to calculate the expected numbers of trees killed by lightning per area per year. We further compared these estimates with historical total tree mortality rates in a 50 ha forest dynamics plot (Hubbell & Foster, 1983) at the study site over 1985–2015 to estimate the relative contribution of lightning to total tree mortality.

Materials and Methods

Study site

Field work was conducted on BCI in central Panama (9.152°N, 79.846°W). BCI is a 15 km^2 island of seasonally moist lowland tropical forest in the Gatun Lake portion of the Panama Canal. It receives *c.* 2600 mm of rain annually with a distinct dry season (January–April, < 100 mm monthly precipitation) and an average annual temperature of 27°C (Leigh *et al.*, 1996). Data collection was concentrated in the relatively old-growth forest in and around the 50 ha forest dynamics plot (Hubbell & Foster, 1983).

Lightning location and damage surveys

We established a camera-based system to accurately determine the location of lightning strikes in the BCI forest. Briefly, three to five video cameras, either mounted on towers extending above the forest canopy or at nearby mainland sites, provided recordings of storm events over BCI during the wet seasons of 2015, 2016 and 2017. The system operated only during the wet season (May–December), when the vast majority of storms occur. Cameras were positioned such that *c.* 65% of the BCI forest was in the field of view of at least one camera, and 15% of BCI was simultaneously in the field of view of at least two cameras. The area of highest camera coverage was centered around a 50 ha forest dynamics plot (described below) to facilitate comparisons with long-term forest dynamics trends. The contact point of any flash recorded on two cameras subsequently could be estimated within 30 m of its actual location via triangulation. This system is described in detail elsewhere (Yanoviak *et al.*, 2017).

After each storm, we isolated candidate lightning flashes from the video recordings using an algorithm that searched for individual video frames with greater brightness than the preceding portion of the video. Using the known locations and orientations of all cameras, we calculated the position of each lightning strike that was recorded on multiple cameras. We successfully located every strike recorded on at least two cameras (n = 18 strikes), usually within days of the event, providing the first unbiased sample of lightning strike locations in any forest.

Detailed observations from these strikes provided a reliable set of criteria for the identification of lightning damage for this forest (Yanoviak *et al.*, 2017). Using these criteria, we identified and monitored eight additional lightning strikes recorded on a single camera and six strikes outside of the camera recording area. We recognized the possibility that our field-located strikes could be biased toward strikes that are relatively more severe and therefore easy to find (Mäkelä *et al.*, 2009). We thus tested for differences between field-located (n = 14) and camera-located (n = 18) strikes in the numbers of trees killed or damaged in each size class. The numbers of trees killed or damaged in field-located strikes were similar to or less than the numbers in camera-located strike sites (Supporting Information Methods S1; Table S1), so we used all strikes for subsequent analyses.

A given strike site was defined as the focal struck canopy tree and the zone of damage surrounding that tree, which typically involved multiple individuals in an asymmetrical pattern extending up to 45 m from the focal tree (Fig. S1). Identification of the focal struck tree was never ambiguous > 2 months following a strike. Each strike site analyzed here was surveyed repeatedly for 11–25 months, depending on the strike date (surveys are ongoing). Surveys typically were conducted at 1–6, 11–13, and 24 months after a strike. During the initial survey, we examined every tree > 10 cm diameter at breast height (i.e. 1.3 m above the ground or immediately above the buttresses; hereafter DBH) within 30 m of the central struck tree for lightning damage and, when necessary, expanded this survey distance until no additional damaged trees were encountered. We recorded tree size (DBH), crown dieback (%) and alive/dead status for all lightning-damaged trees at each site in the initial survey (Yanoviak *et al.*, 2017). Subsequent surveys evaluated crown dieback (%) and alive/dead status of trees previously identified as damaged or possibly damaged (when unclear).

During each survey, one of the authors (EMG) and one or more field assistants walked 8–12 radial transects originating at the focal tree, with each transect > 50 m long. The 14 strike sites located within the BCI 50 ha forest dynamics plot (Hubbell & Foster, 1983) were mapped using spatially explicit data from the most recent plot census (2015), and all trees > 10 cm DBH within 45 m of the focal tree were surveyed for lightning damage (n = 3353 trees). Collectively, our investigation of 32 lightning strikes resulted in > 30 ha of surveys and the examination of *c.* 8000 trees > 10 cm DBH for damage. Damaged trees within each strike site were assigned to size classes based on DBH, with small defined as 10–30 cm DBH, medium as 30–60 cm and large as > 60 cm (Lutz *et al.*, 2018). We estimated 95% confidence intervals for the number of trees damaged per strike within each size class by bootstrapping the number of trees damaged per strike over the number of lightning strikes surveyed (32 strikes). Trees that were mechanically killed or damaged by lightning-struck neighboring trees as they fell or fragmented (Brünig, 1964) were not included among those considered to have been killed or damaged by lightning.

Local lightning frequency

We determined the cloud-to-ground (CG) flash rate density for BCI using 6 yr of continuous data from the Earth Networks Total Lightning Network (ENTLN; Liu & Heckman, 2012). The major advantage of this network is that it specifically identifies CG flashes, which are the focus of this study. Due to uncertainties in classification as in-cloud (IC) or CG, and changes in detection efficiency over time, we conservatively retained only the ENTLN-classified CG flashes with peak current > 10 kA (Rudlosky, 2015). Estimates of CG frequency from these data represent a lower bound because the network misses an unknown proportion of CG flashes. The ENTLN data show that CG flash frequency on BCI is relatively moderate for Panama, and substantially lower than forested areas to the north, east and south of the study site (Fig. S2). Consequently, our estimates of CG flash frequency, and our estimates of lightning-caused tree mortality, are conservative at both local and regional scales. The ENTLN data show that the 0.05 degree latitude × 0.06 degree longitude region including BCI received 12.7 CG lightning flashes (fl) $km^{-2}\,yr^{-1}$ (95% confidence interval (CI): 10.9–14.5 CG fl $km^{-2}\,yr^{-1}$) from 2013 to 2018, and thus we estimate that BCI receives *c.* 190 CG strikes per year. We estimated the 95% CI by bootstrapping the daily CG flash rate density over the 2191 d of ENTLN data.

The camera system was operational during 83% of the total wet season days from 2015 to 2017 and recorded 14 CG contact points in the 50 ha plot. Correcting for the duration of the study period, and assuming that lightning does not occur in the dry season and is evenly distributed across the wet season, this corresponds to a local frequency of 11.2 CG fl $km^{-2}\,yr^{-1}$. However, this is an underestimate because some lightning strikes were probably missed during *c.* 10% of the observational period due to equipment malfunctions.

Historical tree mortality

We used 30 yr of forest dynamics data from the 50 ha plot on BCI to estimate total tree mortality rates from 1985 to 2015 (Hubbell & Foster, 1983). Each tree within the 50 ha plot was mapped, identified to species, measured in diameter, and recorded as dead or alive every 5 yr from 1985 to 2015. For each census interval, we divided these data into three size classes based on the sizes of trees at the initial census: 10–30, 30–60 and > 60 cm DBH. We calculated the instantaneous mortality rate (m) of trees for each size class and census interval as

$$m = \frac{\log_e N_0 - \log_e S_t}{t} \qquad \text{Eqn 1}$$

where N_0 is the number of living trees at the beginning of the census interval, t is the duration of the census interval and S_t is the number of those trees that survived until time t (Table S2; Kohyama *et al.*, 2018). For each size class, we calculated the average mortality rate across census intervals to obtain a single historical mortality rate for 1985–2015.

For the largest size class (> 60 cm DBH), we estimated tree residence time—the average remaining lifespan of trees over 60 cm DBH—as the inverse of the average instantaneous mortality rate ($1/m$). We compared residence times for these trees under current mortality rates (which include the effects of lightning), and under reduced mortality rates following exclusion of the estimated contributions of lightning to tree deaths, as detailed below.

Lightning-caused mortality

We combined the ENTLN measurement of CG lightning frequency with the field surveys of lightning-caused mortality and plot-based measurements of tree mortality to estimate lightning-caused instantaneous mortality rates (m_L; Datasets S1–S3). We calculated the probability of a tree being damaged by lightning (p_L) as the product of the number of trees damaged per lightning strike and the average number of ground strikes per area per year (12.7 CG fl $km^{-2}\,yr^{-1}$) divided by the density of trees per unit area. We estimated the first-year mortality rate of lightning-damaged trees (q; trees yr^{-1}) as the proportion of lightning-damaged trees that were dead at the time of the 11–13 month census (average census time = 1.01 yr). Combining these values, we estimated the nonlightning background mortality rate (m_b; i.e. all nonlightning sources of tree mortality) for each size class:

$$m_b = \frac{(m - p_L * q)}{(1 - p_L)} \qquad \text{Eqn 2}$$

where m is total mortality as estimated with Eqn 1, p_L is the probability that a tree is damaged by lightning and q is the probability that a lightning-damaged tree dies within 1 yr (see Methods S1 for derivation). We calculated the short-term lightning-caused mortality rate, m_L, as background mortality, m_b, subtracted from total mortality, m. Calculations were performed separately for each size class (e.g. p_L for trees > 60 cm DBH differed from p_L for trees 30–60 cm DBH). To calculate 95% CIs for the lightning-caused mortality rates, we propagated uncertainty in our estimates of the number of trees damaged per strike and the number of ground strikes per year by using the high and low CIs for these calculations. Trees that were mechanically killed or damaged by lightning-struck neighboring trees as they fell or fragmented were not included among those considered to have been killed or damaged by lightning (unless they were also directly affected by lightning), and thus this approach underestimates lightning-caused mortality.

We estimated total lightning-caused mortality (trees directly killed plus eventual deaths) under the assumption that 10% of the lightning-damaged trees still surviving at 11–13 months will die prematurely as a result of their injuries (Methods S1). Specifically, we added 10% of the remaining damaged trees from each individual strike to the first-year count of dead trees before recalculating the mortality rate of lightning-damaged trees (q). We then used the same procedure described above to estimate the long-term rate of lightning-caused mortality. We estimated the proportion of total tree mortality caused by lightning as m_L/m (Fig. 1).

To estimate the changes in tree mortality associated with predictions of increased lightning frequency, we calculated the additional mortality expected to occur with 25% and 50% increases in lightning frequency (Price & Rind, 1994; Williams, 2005). Specifically,

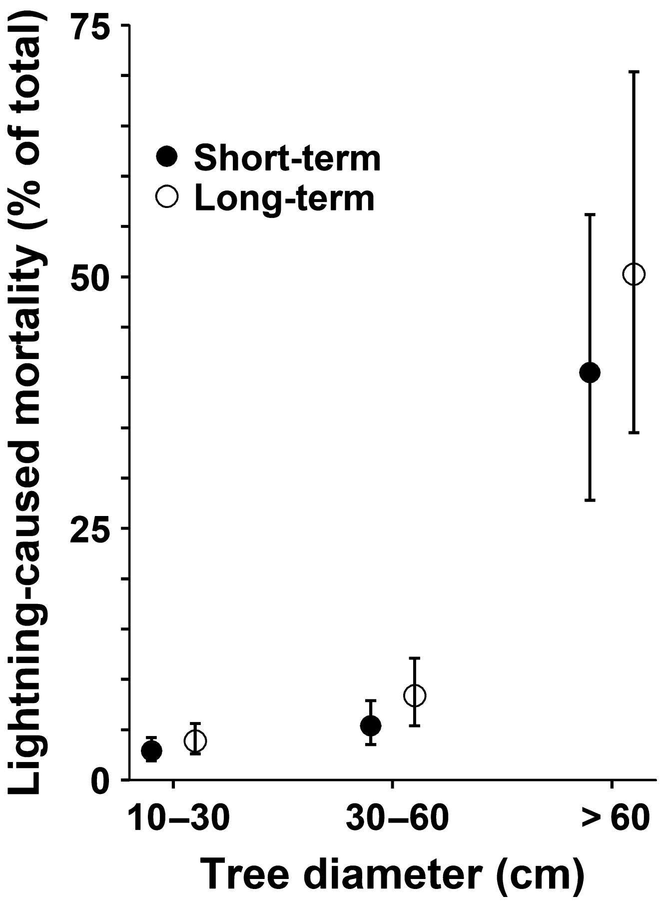

Fig. 1 The current (closed circles) and estimated (open circles) contribution of lightning to total tree mortality by tree size class. Current mortality is based on tree deaths recorded up to 13 months following a strike; estimated mortality includes current mortality plus expected premature mortality of 10% of damaged trees occurring > 1 yr following a strike. Bars are 95% confidence intervals.

we calculated the total tree mortality rate under increased lightning regimes by multiplying the lightning-caused mortality rate, m_L, by 1.25 or 1.5 for 25% or 50% increases in lightning frequency, respectively, and adding these values to the historical mortality rate (all sources of mortality combined). We divided this estimate by historical mortality to estimate the increase in mortality resulting from increased lightning frequency. We assumed that historical mortality (regardless of source) and the number of trees killed per strike remained the same.

Spatial patterns of lightning damage

We analyzed the spatial distribution of tree damage and death caused by lightning using the 14 strikes recorded in the 50 ha plot on BCI (Datasets S1, S4). We used logistic regression to estimate the likelihood that a tree was killed or damaged as a function of its size class (a categorical variable with three classes, as described above) and distance from the focal struck tree (a continuous variable spanning 0–45 m; see Methods S1). We included the strike site as a random effect. We tested the significance of each fixed effect (size class and distance) and their interaction using nested model reduction with Akaike's information criterion (AIC) values and P-values from likelihood ratio tests (Methods S1). When the interaction was significant, we split the data into subsets and repeated these analyses with pairwise comparisons among size classes. For each size class, we converted fitted log odds to probabilities and plotted the estimated probability that individual trees were damaged or killed as a function of distance within 45 m of the central tree (Figs S3–S5).

All analyses and calculations were performed in the R statistical environment (R Core Team, 2019). We used the *lme4* package for all mixed-effect models (Methods S1).

Results

Lightning is the single most important agent of large tree mortality in this tropical forest; it directly causes 40.5% of deaths of trees > 60 cm in diameter (hereafter 'large trees'), and 4.5% of deaths of all trees > 10 cm in diameter (Fig. 1). Trees were considered to be directly killed by lightning if they were visibly damaged by the strike (Yanoviak *et al.*, 2017), had no signs of wind damage and died standing within 13 months (at a rate in excess of background mortality, see the Materials and Methods section). Each strike killed an average of 3.5 trees within 13 months (range: 0–12, Figs 2, S6), including 0.94 large trees (range 0–4). ENTLN lightning frequency data indicate that BCI receives an average of 12.7 CG fl km^{-2} yr^{-1}, leading us to estimate that lightning kills 11.4 large trees and 38.4 total trees km^{-2} yr^{-1}. This compares with total mortality averaging 28.1 large trees and 850.5 total trees km^{-2} yr^{-1} for this site. Additionally, lightning-caused mortality disproportionately impacts the very largest trees: trees > 100 cm in diameter account for only 16% of all large tree mortality, but represent 35% of lightning-caused large tree mortality.

Because tree death often occurs slowly and lightning initiates various processes that can kill damaged trees over time spans greater than 1 yr, we expect the total contribution of lightning to tree mortality to be higher over the long term (Taylor, 1974; Fernando *et al.*, 2010). Indeed, some trees with substantial progressive partial crown damage (i.e. dieback) due to lightning died a few months after the 11–13 month window used to estimate direct mortality (Figs 2, S6). Each strike damaged an average of 11.4 additional trees (range: 2–32; Tables S1, S2), including 2.13 large trees. This damage was often severe: 14% of damaged trees had > 50% crown dieback and another 18% had 25–50% crown dieback. Trees with this amount of crown damage have more than double the mortality rates of trees with intact crowns within 6 yr (Arellano *et al.*, 2019), suggesting that many other trees will die prematurely as a result of their injuries. If 10% of damaged trees ultimately die prematurely due to lightning (Methods S1), then lightning causes a total of 50.3% of large tree mortality and 6.1% of total tree mortality (Fig. 1).

Observations of local lightning frequency corroborated the ENTLN-based estimates of tree mortality rates. Local lightning frequency was 11.2 CG fl $km^{-2} yr^{-1}$ based on camera-recorded flashes from 2015 to 2017 (see the Materials and Methods section). Using this local estimate of lightning frequency in place of the ENTLN-based estimate reduced the estimated contribution of lightning to 36% (CI: 29–43%) of large tree mortality in the short term (4.0% of total tree mortality), and 44% (CI: 35–54%) of large tree mortality in the longer term. Because the ENTLN data cover a longer time span and lightning frequency varies among years, we consider the ENTLN-based frequencies to be a better basis for estimating the long-term mean strike rate and associated contributions to tree mortality.

Large trees were killed and damaged by lightning at higher rates than small trees (Fig. 3). Spatially explicit analyses of the 14 strikes that occurred within the mapped 50 ha plot showed that this was true at every distance from the focal struck tree (Figs S1, S3–S5). The differences in damage with tree size and distance probably reflect 'flashover' among trees that form the local closed canopy. Flashover occurs when electric current jumps across air gaps between branches of adjacent canopy trees, resulting in dieback of affected branches (Furtado, 1935; Murray, 1958; Taylor, 1974; Yanoviak *et al.*, 2017). Because the crowns of large trees extend over a larger area and volume, lightning damages larger trees across a relatively large area, whereas smaller trees are damaged less frequently and typically nearer the focal tree (Figs 3, S3–S6). The percentage of damaged trees that died within 13 months was similar for small (10–30 cm), mid-size (30–60 cm) and large trees (25%, 18% and 31%, respectively).

Lightning frequency is expected to change with climate change, and any change in lightning frequency will affect tree mortality rates. Current models suggest that future storms will be substantially larger and more electrically active (Williams, 2005; Romps *et al.*, 2014; but see Finney *et al.*, 2018). CG lightning frequency in the continental United States is projected to increase 25–50% by 2100, corresponding to a 2–4°C increase in average atmospheric temperature (Romps *et al.*, 2014). If similar increases occur in the tropics (Finney *et al.*, 2018) and the number of trees killed per lightning strike remains constant, then annual mortality rates for the largest trees in this forest will increase by 9–18%, with concomitant increases in the total contribution of lightning to tree mortality (.Fig. 4).

Such an increase in lightning-caused tree mortality would substantially alter forest structure, reducing the abundance of large trees and thus reducing forest carbon pools. Current (1985–2015) residence times of large trees are 55 yr (CI: 50–61 yr). Hypothetical removal of all lightning-associated mortality, all else equal, would increase residence times to 93 yr (CI: 77–126 yr). Thus, lightning currently reduces large tree residence times by 40%. The 18.0% increase in lightning-associated mortality

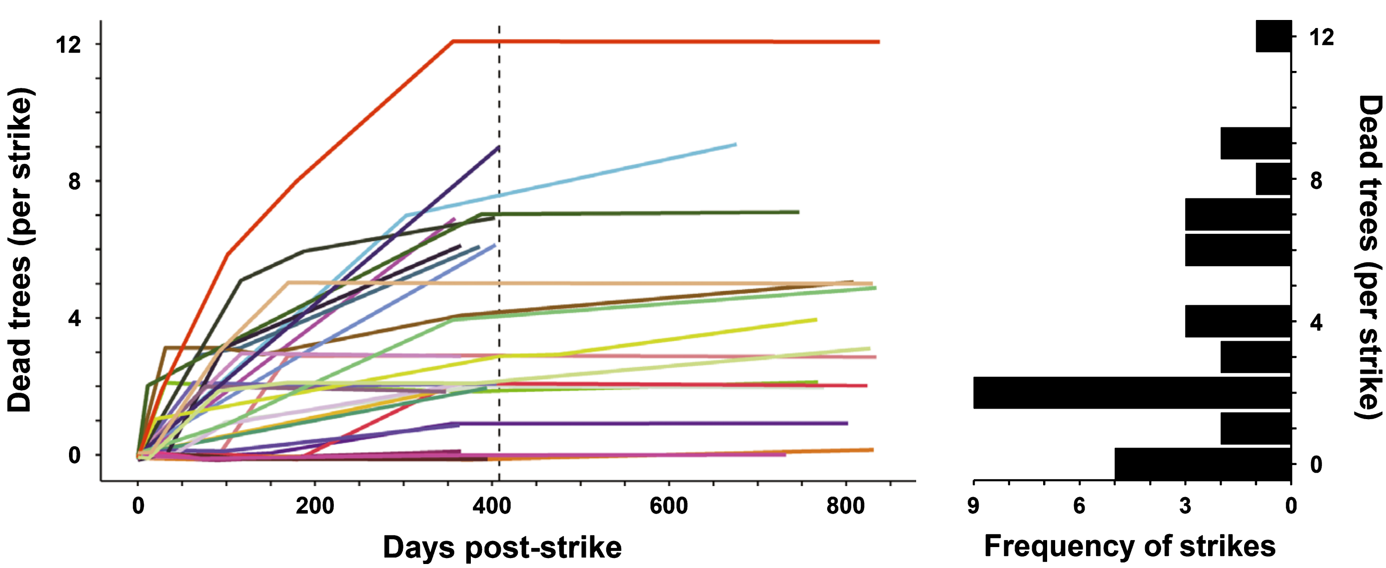

Fig. 2 The observed number of trees killed by lightning at each strike site over time. Each colored line represents an individual lightning strike. The vertical dashed line separates strikes monitored for < 13 months to date (17 strikes) from strikes monitored for > 13 months (15 strikes). Lines are jittered so that each strike is visible. The histogram shows the number of strike sites with a given number of dead trees by 13 months following a strike. Dead tree counts include only those resulting from lightning, and exclude trees that were killed by neighboring tree or branch falls.

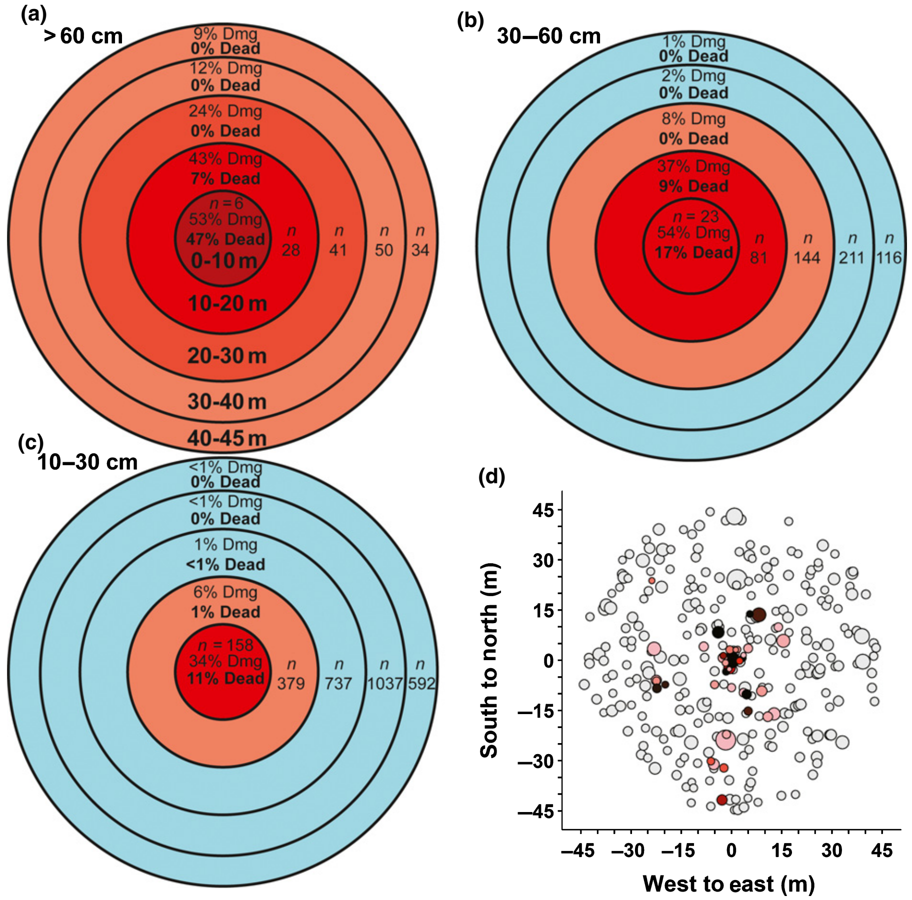

Fig. 3 The proportion of trees killed (Dead) or damaged (Dmg) by lightning at different distances from the focal tree, by size class (a–c). Trees are divided into five bins by distance from the focal tree (0–10, 10–20, 20–30, 30–40 and 40–45 m), and bin colors depict a range from more (red) to fewer (blue) trees affected. *n* = the total number of trees in each bin. (d) A spatially extensive lightning strike. Each point represents an individual tree, with point size proportional to tree size (DBH). Black points in (d) indicate dead trees, red points indicate damaged trees (lighter shades = less damage) and gray points represent unaffected trees.

projected by this study would reduce residence times to 47 yr and disproportionately reduce the abundance of large trees.

Discussion

The results of this study reveal an important gap in our understanding of tropical forest dynamics. Historically, studies of canopy tree mortality in terrestrial tropical forests have focused largely on windthrow and drought (Phillips *et al.*, 2010; Bennett *et al.*, 2015; Negrón-Juárez *et al.*, 2017). By contrast, we demonstrate that large trees in an old-growth neotropical forest are most frequently killed after a single traumatic event – a lightning strike. This finding improves our understanding of tree mortality processes and provides a foundation for better representation of tree mortality in models of Earth systems and simulations of forest dynamics.

Lightning is an important agent of disturbance in mangrove ecosystems (e.g. Smith *et al.*, 1994; Sherman *et al.*, 2000; Amir & Duke, 2019), and we expect that it will prove to be a similarly important mechanism of tree mortality at other tropical forest sites (Anderson, 1964; Magnusson *et al.*, 1996). The only other quantitative assessment of lightning-caused mortality in a terrestrial tropical forest found a similar contribution to total tree mortality (Fontes *et al.*, 2018). Specifically, bimonthly assessments of 5808 trees near Manaus in central Amazonia for one year showed that 4.5% of deaths of trees > 10 cm in diameter were due to lightning (Fontes *et al.*, 2018), which was equal to our finding of 4.5% for this size class. Moreover, lightning frequency is high in most tropical forests; 68% of evergreen broadleaf tropical forests experience ≥ 50% of the lightning frequency recorded for BCI (Cecil *et al.*, 2014; Friedl & Sulla-Menashe, 2015). If we assume that the per-strike effects of lightning on BCI are typical of tropical forests globally, then lightning causes more than 25% of large tree mortality in the majority of lowland tropical forests.

Given that lightning is a major cause of large tree mortality, lightning also presumably shapes tropical terrestrial forest dynamics. Spatial variation in lightning frequency probably affects regional variation in biomass turnover rates (Galbraith *et al.*, 2013) and carbon storage (Johnson *et al.*, 2016; Lutz *et al.*, 2018). The ecological relevance of lightning could be high even in tropical forests that have relatively low lightning frequencies, insofar as total mortality rates are also lower. For example, the Guiana Shield has low lightning frequencies (Cecil *et al.*, 2014) and – perhaps not coincidentally – low tree mortality rates (Johnson *et al.*, 2016). These patterns are particularly important given projected changes in lightning frequency. The ecosystem-level consequences of an increase in lightning frequency would be substantial, as large trees (> 60 cm) constitute 49% of the aboveground biomass on BCI (Chave *et al.*, 2003), and shape local plant, animal and microbial communities (Richards, 1998; Wright, 2002; Mangan *et al.*, 2010). Moreover, if the effects of lightning on trees differ interspecifically (e.g. due to their

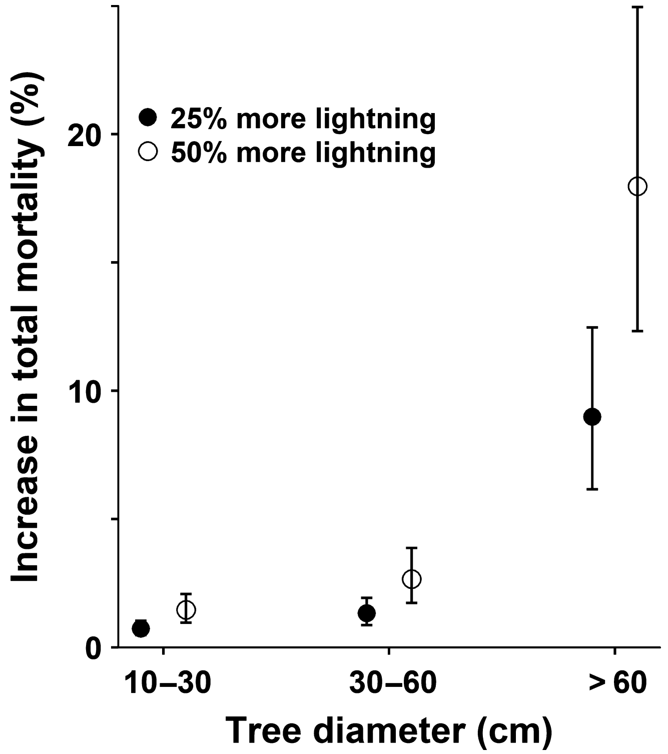

Fig. 4 The projected increase in total tree mortality rates by size class given two scenarios of increased lightning frequency. Increases in cloud-to-ground lightning frequency would lead to increased lightning-caused tree mortality and thus increased total tree mortality. Bars indicate 95% confidence intervals.

electrical properties or susceptibility to colonization by woody vines; Yanoviak, 2013; Gora & Yanoviak, 2015; Gora *et al.*, 2017), any substantial change in lightning frequency could shift the composition of canopy tree communities, with cascading effects on tropical forest ecosystem structure and function.

Caveats and conclusions

Here we show that lightning is an important agent of disturbance in an old-growth lowland tropical forest. The effects of lightning are easily overlooked, even at one of the best-studied tropical forests on the planet. Five of 32 strikes examined on BCI caused no tree deaths in the first year, and in many cases the damage to trees would have gone unnoticed or been misidentified without data from a real-time lightning monitoring system (Yanoviak *et al.*, 2015, 2017). Given the widespread distribution of lightning and the difficulty of identifying its subsequent effects (Magnusson *et al.*, 1996; Mäkelä *et al.*, 2009), we suspect that the ecological role of lightning is underestimated in most tropical forests and in many other terrestrial biomes (Yanoviak *et al.*, 2015). Filling this knowledge gap is necessary for the development of accurate forest dynamics and Earth systems models, and requires the establishment of real-time monitoring systems specifically in regions of high lightning frequency (Cecil *et al.*, 2014).

The estimates generated in this study are conservative in three ways. First, we do not account for associated mortality of nearby trees as lightning-killed trees fragment and fall (Brünig, 1964). Second, ENTLN-based measures of lightning flash frequency represent the lower bound of CG lightning frequency. Moreover, we assume that each CG flash recorded by ENTLN has only a single ground contact point, whereas many lightning strikes (*c.* 25%) have multiple contact points (Stall *et al.*, 2009). Third, the camera system underestimated local lightning frequency because it probably missed lightning strikes during inconsistent periods of observation (see the Materials and Methods section). The estimates provided here do not account for the contributions of infrequent disturbances, such as major droughts or large-scale blowdowns (Negrón-Juárez *et al.*, 2010; Condit *et al.*, 2017), but these infrequent events contribute little to long-term forest turnover (only 1% in the Amazon basin; Espírito-Santo *et al.*, 2010). Consequently, we expect that continued data collection over the long term will reveal that the values presented in this study are underestimates of lightning-caused tree mortality on BCI.

The results of this study highlight how little is known about the ecological effects of lightning in tropical forests. Foundational natural history information about lightning-caused disturbance is limited to mangroves (Smith *et al.*, 1994; Sherman *et al.*, 2000; Amir & Duke, 2019) and four terrestrial forests in south-east Asia and the Americas (Furtado, 1935; Anderson, 1964; Brünig, 1964; Magnusson *et al.*, 1996; Yanoviak *et al.*, 2017). However, these studies provide no empirical information regarding the factors that potentially influence which trees are struck by lightning (e.g. topography, tree structural traits), and which trees are killed by lightning (e.g. tree electrical properties; Gora *et al.*, 2017). Consequently, there is substantial uncertainty regarding how lightning strikes affect forests of different ages, compositions and structures. Likewise, the potential relationship between the magnitude of disturbance and the electrical characteristics of lightning (e.g. polarity, intensity, flash duration) remain unknown. Resolving these problems is essential to understanding the broader ecological effects of lightning strikes in tropical forests.

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Author contributions

SPY conceived the project, co-wrote the manuscript and conducted field work; EMG co-wrote the manuscript, developed the survey protocol, conducted field work and analyzed data; HCM-L co-wrote the manuscript and assisted with data analysis; PMB and JCB designed the monitoring network, analyzed data and conducted field work; MD conducted field work and analyzed data. SP and SPH contributed to the conceptual framework and project logistics. All authors contributed critically to manuscript drafts and gave final approval for publication. SPY and EMG contributed equally to this work.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Explanation of variables used in raw data files S2–S4.

Dataset S2 Raw data used for annual tree mortality rate calculations.

Dataset S3 Raw data for the number of trees killed or damaged by lightning from censuses conducted up to 13 months following a strike.

Dataset S4 Raw data used for spatial analysis of trees killed and damaged by lightning.

Fig. S1 Examples of the spatial patterns of lightning-caused tree damage.

Fig. S2 Variation in the cloud-to-ground flash fraction across Panama.

Fig. S3 Proportions of trees damaged as a function of distance from the central struck tree.

Fig. S4 Proportions of trees killed as a function of distance from the central struck tree.

Fig. S5 Comparisons among size classes of the proportions of trees damaged and killed as a function of distance from the central struck tree.

Fig. S6 Observed number of trees killed by lightning at each strike site over time.

Methods S1 Explanation of supplementary analyses and their outcomes.

Table S1 Comparison of the average number of trees killed and damaged between the camera-located and field-located strikes.

Table S2 Historical tree mortality for each 5 yr census interval from 1985 to 2015 in the 50 ha plot on BCI.