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Research

How some tropical trees benefit from being struck by lightning: evidence for *Dipteryx oleifera* and other large-statured trees

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Summary

- Lightning strikes kill hundreds of millions of trees annually, but their role in shaping tree life history and diversity is largely unknown.
- Here, we use data from a unique lightning location system to show that some individual trees counterintuitively benefit from being struck by lightning.
- Lightning killed 56% of 93 directly struck trees and caused an average of 41% crown dieback among the survivors. However, among these struck trees, 10 direct strikes caused negligible damage to *Dipteryx oleifera* trees while killing 78% of their lianas and 2.1 Mg of competitor tree biomass. Nine trees of other long-lived taxa survived lightning with similar benefits. On average, a *D. oleifera* tree > 60 cm in diameter is struck by lightning at least five times during its lifetime, conferring these benefits repeatedly. We estimate that the ability to survive lightning increases lifetime fecundity 14-fold, largely because of reduced competition from lianas and neighboring trees. Moreover, the unusual heights and wide crowns of *D. oleifera* increase the probability of a direct strike by 49–68% relative to trees of the same diameter with average allometries.
- These patterns suggest that lightning plays an underappreciated role in tree competition, life history strategies, and species coexistence.

Introduction

Lightning is a powerful and generally understudied agent of tree death. Other agents of tree mortality, such as drought and fire, shape patterns of forest biodiversity, niche differentiation, and diversification due to their differential effects on individual trees and tree species (Simon *et al.*, 2009; Bartlett *et al.*, 2016; Esquivel-Muelbert *et al.*, 2019). Lightning also has differential effects among different tree species (Richards *et al.*, 2022), but research into lightning-struck trees has focused on its negative effects. Consequently, the potential for positive effects of lightning on trees is largely unexplored, and little is known about the capacity for lightning strikes themselves (i.e. not lightning-caused fire) to influence tree life history and patterns of biodiversity. Here, we quantify the positive ecological effects of direct lightning strikes to individual tropical trees of certain species and the fitness consequences of lightning survival (McInerny & Etienne, 2012).

Lightning strikes are key agents of forest disturbance. In tropical forests, a typical lightning strike directly attaches to a large canopy tree, and the electrical current subsequently moves through air gaps, branches, or lianas (woody vines) to secondarily damage neighboring trees (Yanoviak *et al.*, 2017; Gora *et al.*, 2023). Tropical trees damaged by lightning exhibit progressive crown dieback that often results in mortality over a period of months (Yanoviak *et al.*, 2020); by contrast, trunk damage and fires commonly associated with lightning in temperate forests are exceedingly rare in tropical forests (Gora *et al.*, 2021). In the mature lowland forest of central Panama – to our knowledge, the only forest globally with systematically located and field-surveyed lightning strikes – a single lightning strike, on average, damages 23.6 trees, kills 5.3 of these damaged trees, causes 7.36 Mg of woody biomass turnover, and kills 7.1 lianas (Gora *et al.*, 2021). Lightning appears to cause similar damage patterns across tropical forests (Sherman *et al.*, 2000; Gora & Yanoviak, 2020).

How could an individual tree benefit from being struck by lightning? Lightning strikes secondarily damage trees and lianas close to the directly struck tree (Gora *et al.*, 2020b), which presumably compete with the directly struck tree for light and belowground resources. Lianas substantially reduce tree growth (van der Heijden *et al.*, 2015; Reis *et al.*, 2020), survival (Visser *et al.*, 2018), and reproduction (García León *et al.*, 2018), and neighboring trees have similar effects (Uriarte *et al.*, 2004; Rüger *et al.*, 2009, 2011a,b). If a directly struck tree survives lightning with minimal damage while neighboring trees and infesting lianas are killed, competitive release should impart net benefits in terms of health, survival, and fecundity.

Regardless of potential benefits, the ability to survive lightning could be fundamental to some life history strategies. Lightning nonrandomly strikes the tallest trees with the largest crowns (Gora *et al.*, 2020b) and is a major driver of mortality for the largest trees in tropical forests, causing 40–50% of mortality for trees > 60 cm in trunk diameter in central Panama (Yanoviak *et al.*, 2020; Gora *et al.*, 2020a). Because large trees have higher fecundity and disproportionately contribute to population growth rates (Visser *et al.*, 2016; Bruijning *et al.*, 2017; Qiu *et al.*, 2021), large-statured species could experience strong selective pressure from lightning. Indeed, tropical tree species that experience more frequent lightning strikes tend to be more tolerant to lightning (Richards *et al.*, 2022). If certain species consistently survive lightning, this survival ability could substantially increase their average longevity and fecundity. Furthermore, lightning survival could contribute to the diversification of tree architecture, with tree species that are not tolerant to lightning selected for small crowns, while lightning-tolerant species are released from such pressure and possibly even experience the opposite selection if the benefits of being struck are high.

Here we combine many types of data (Supporting Information Table S1) to test the hypothesis that individual trees of certain species benefit from being struck by lightning. Using a unique lightning tracking system, we located 94 lightning strikes to 93 different trees in a mature tropical forest (as described in Yanoviak *et al.*, 2020; Gora *et al.*, 2021), and we present the first long-term evaluation of these trees using field- and drone-based observations. We quantified the survivorship, crown and trunk condition, liana colonization, and neighboring tree mortality among these directly struck trees over 2–6 years post-strike, and we compare these trends among species, focusing on a large-statured, lightning-tolerant tropical tree species, *Dipteryx oleifera* (Richards *et al.*, 2022). We further evaluated whether the expected benefits of lightning survival for *D. oleifera* were observable as population-wide patterns of healthier tree condition, lower liana infestations, higher mortality of neighboring competitors, and reduced light competition when compared to community-wide trends. We performed parallel analyses of all long-lived, large-statured taxa that survived lightning to demonstrate that patterns consistent with these benefits are observable among many individuals across several species rather than being exclusive to *D. oleifera*. We used population modeling to quantify the fitness benefits of lightning survival for *D. oleifera*, and we explored the influence of tree allometry on these benefits. These data provide the first evidence that some trees counterintuitively benefit from being struck by lightning (Fig. 1).

Materials and Methods

Study site

All data were collected in seasonally moist tropical forest within the Barro Colorado Nature Monument in central Panama (9.210°N, 79.745°W). Average rainfall at this site is 2650 mm yr^{-1} and there is a 4-month dry season from late December to April. Lightning strikes are concentrated during the wet season with an average lightning frequency of 12.7 cloud-to-ground strikes $\text{km}^{-2}\ \text{yr}^{-1}$ (Yanoviak *et al.*, 2020).

Resurveys of directly struck trees

We located 94 lightning strikes using a lightning location system and field surveys from 2014 to 2019. The lightning location system located 70 lightning strikes using a combination of cameras recording lightning strikes as they entered the forest canopy and field change meters measuring electromagnetic pulses emitted by each strike (Yanoviak *et al.*, 2017). An additional 24 lightning strikes were identified outside of the focal monitoring area using field diagnostics developed during this project. Specifically, we identified lightning-damaged trees as those exhibiting leaf necrosis among the branches nearest to the directly struck tree, or its lightning-damaged neighbors (referred to as ‘flashover’ damage). See references Yanoviak *et al.* (2017), Gora & Yanoviak (2020), and Gora *et al.* (2021) for detailed descriptions of the sensors and field methods.

In 2021, we revisited each lightning strike site to survey the condition of the directly struck tree. This included nine directly struck *D. oleifera* (Benth.) trees, one of which was struck twice (2016 and 2019) and 84 trees of other species (Table S2). All analyses exclude the second lightning strike to the twice-struck *D. oleifera* individual, except for calculations of neighboring tree mortality and biomass loss. Trees were recorded as dead if no living leaf or wood tissues were observed. For surviving trees, we recorded six metrics of tree condition and liana infestation. Using visual assessments of tree crowns from the ground, we recorded crown dieback as the percent of existing crown volume that recently died (in 5% increments), and crown loss as crown volume missing from historical damage, scored on an ordinal scale: < 5% of idealized crown volume missing, 5–25% missing, 25–50% missing, 50–75% missing, and 75–100% of the crown missing (adapted from Arellano *et al.*, 2018). We documented all trunk damage, defined as heart rot or other wounds penetrating the bark and extending > 0.5 m in length. We recorded crown illumination as an ordinal index of potential light interception: 1 = crown exposed to neither overhead nor lateral light; 2 = < 10% of crown exposed to vertical light with some lateral light exposure; 3 = 10–90% of crown exposed to vertical light; 4 = > 90% of the crown exposed to vertical light, but limited lateral light exposure; and 5 = crown fully exposed to vertical and lateral light (Arellano *et al.*, 2021). Lastly, we recorded liana infestation as the percent of a crown infested with lianas on an ordinal scale (0%, < 25%, 25–50%, 50–75%, or > 75%), and as counts of lianas infesting the tree. Each liana stem with roots was counted independently, regardless of connections to other rooted stems. We restricted these observations to directly struck trees to limit potential confounding factors related to uncertain within-strike electric current and damage distributions. Specifically, the distribution of electric current among neighbors of directly struck trees is unknowable with current technology and therefore must be inferred from visible damage, which could be

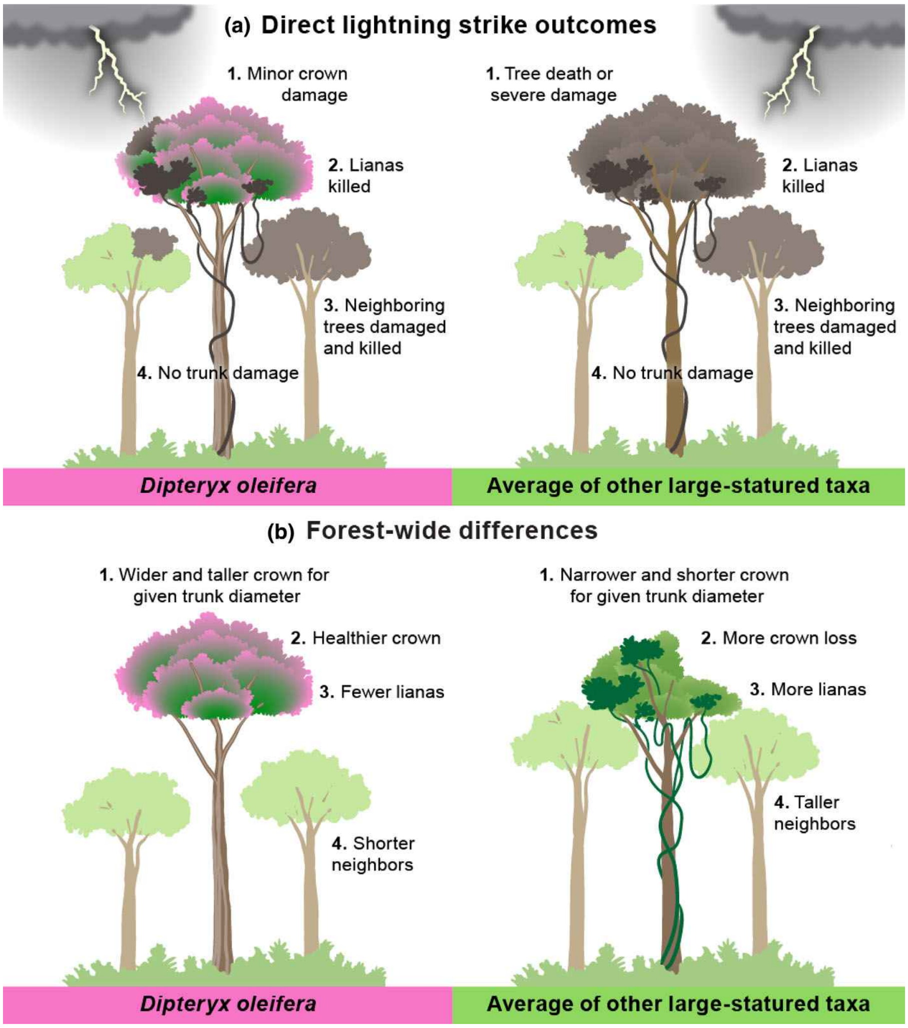

Fig. 1 *Dipteryx oleifera* trees differ from other large-statured taxa in their responses to lightning strikes and their population-level condition, allometry, and liana infestations. Panel (a) compares the effects of lightning on *D. oleifera* and associated flora with the average effects of lightning on all other large-statured trees. Panel (b) depicts forest-wide differences in allometry, crown condition, liana infestation, and competitor stature between the general population of *D. oleifera* relative to other large-statured taxa.

confounded by lightning tolerance at the edges of a lightning-caused disturbance.

Identifying tree taxa that are potentially lightning-tolerant

In addition to *D. oleifera*, we also identified long-lived, large-statured taxa that presumably survive lightning on a regular basis, hereafter referred to as 'potentially lightning-tolerant' trees. The goal of this effort was to test whether other individual trees also benefit from surviving direct lightning strikes in a manner similar to *D. oleifera*. We prioritized a low false positive rate, and thus consider our classification of *potentially lightning-tolerant taxa* to be conservative. We evaluated taxa with directly struck trees and classified those taxa as potentially lightning-tolerant if they met two criteria: (1) trees survived all observed direct lightning strikes; and (2) they exhibited low historic mortality rates as large individuals > 60 cm in diameter, defined as less than half of the community-wide mortality rate for these large trees ($< 0.9\%\ \mathrm{yr}^{-1}$; Yanoviak *et al.*, 2020). We used large tree survivorship as a criterion to reduce the likelihood of a false positive assignment of lightning tolerance, especially given that the sample sizes of directly struck trees were very small for most species (1–2 trees per species). Large trees are frequently struck and damaged by lightning (cumulative direct and secondary lightning damage occurs in 1.986% of trees > 60 cm diameter at breast height (DBH) yr^{-1}; Gora *et al.*, 2020b), and therefore trees with low mortality rates as large individuals can be presumed to have a high probability of surviving lightning strikes. We note that the mortality rates of large trees of other directly struck species were much higher than those of taxa identified as potentially lightning-tolerant (Fig. S1).

The directly struck tree taxa were classified as potentially lightning tolerant as follows. In total, 11 tree species exhibited no mortality in response to direct lightning strikes. Four of these species exhibited mortality rates $> 0.9\%\ \mathrm{yr}^{-1}$ as large trees, and we thus excluded them from classification as potentially lightning-tolerant taxa (*Aspidosperma cruentum* = 1.45% yr^{-1}; *Jacaranda copaia* = 2.55% yr^{-1}; *Handroanthus guayacan* = 1.24% yr^{-1}; *Platypodium elegans* = 2.40% yr^{-1}). The remaining seven tree species had mortality rates $< 0.9\%\ \mathrm{yr}^{-1}$ and were classified as potentially lightning-tolerant taxa: *D. oleifera*, *Cavanillesia platanifolia*, *Hura crepitans*, *Ceiba pentandra*, *Chrysophyllum cainito*, *Terminalia oblonga*, and *Vatairea erythrocarpa*. These seven potentially tolerant species included 18 individuals that survived 19 direct lightning strikes (Table S2). In addition to *D. oleifera*, we had sufficient data to estimate the number of lightning strikes that three of these taxa experience during their residence time as trees > 60 cm in diameter (see Supporting Information for details). Specifically, these data indicate that the average *C. pentandra* is directly struck at least 8.1 times during its lifetime, the average *C. platanifolia* is directly struck at least 1.5 times, and the average *H. crepitans* is directly struck at least 1.8 times. We infer that these taxa must be surviving some lightning strikes, and using the methods described below, we evaluate whether the complete pool of potentially lightning-tolerant taxa experience similar low costs, high benefits, and population-wide characteristics consistent with *D. oleifera*.

Surveys of control trees for contextualizing tree condition

We surveyed additional trees to produce control groups for contextualizing observed patterns of lightning damage and to evaluate population-level differences between *D. oleifera* trees, or potentially lightning-tolerant trees in general, vs the full community of large-statured trees. First, we surveyed the largest trees (≥ 60 cm) in the co-located 50-ha plot surviving since 1980, excluding individuals that were within 10 m of a larger living tree ($n = 217$; Table S3). We selected these trees as controls because *D. oleifera* and the other potentially lightning-tolerant trees were characterized by high survivorship and their tendency to be the largest tree in a patch of forest (i.e. they were not a random subset of the population). Using this control group reduces the likelihood of identifying spurious effects resulting from differences in tree stature and longevity, rather than the effects of lightning. Because the analyses focus on *D. oleifera* trees and there were relatively few of these large individuals in the 50-ha plot, we also surveyed all *D. oleifera* trees lacking evidence of recent lightning damage across an additional 16 ha of mapped forest plots in mature forest on Barro Colorado Island ($n = 15$ additional *D. oleifera* trees; Meakem *et al*., 2024). Trees were judged to lack recent lightning damage based on the absence of obvious flashover damage among neighboring trees (Yanoviak *et al*., 2017). We surveyed the condition of all control trees in 2021 using the same protocol as the resurveys of directly struck trees.

Together, these data produced three control groups: (1) *D. oleifera controls*, which included only *D. oleifera* trees ($n = 44$); (2) *potentially tolerant controls*, which included all trees of the potentially lightning-tolerant taxa ($n = 94$; 44 *D. oleifera*, 10 *C. platanifolia*, 18 *H. crepitans*, 16 *C. pentandra*, 5 *C. cainito*, and 1 *T. oblonga*); and (3) *heterospecific controls*, including all surveyed trees that were not potentially lightning-tolerant ($n = 147$). We confirmed that differences in tree diameter did not meaningfully influence the results by repeating the analyses using only *D. oleifera* trees or the potentially tolerant control trees within the diameter range of directly struck trees ($n = 21$ *D. oleifera* trees or $n = 71$ potentially lightning-tolerant trees; Notes S1).

Evaluating the costs of being struck by lightning

We compared patterns of survival and damage among *D. oleifera* trees that were directly struck with *D. oleifera* controls, and directly struck trees of all other species. We used Kaplan–Meier curves and a log-rank test to compare survival between directly struck *D. oleifera* trees and other directly struck trees (function *pairwise_survdiff*, package SURVMINER; Kassambara *et al*., 2017). We performed comparisons of initial crown dieback (i.e. 1 yr post-strike), final crown dieback, final trunk damage, and crown loss between directly struck *D. oleifera* trees and each of the other two groups. We compared initial crown dieback between directly struck *D. oleifera* trees and other directly struck trees, estimating initial crown dieback as that observed among trees that were alive during the survey period closest to 1 yr post-strike (average of 1.23 yr post-strike for 9 *D. oleifera* trees vs 1.04 yr for 37 trees of other species). Comparisons of final crown dieback, final crown loss, and final trunk damage only included surviving directly struck trees at the end of the survey period (i.e. 9 *D. oleifera* trees and 21 other trees). We used *t*-tests for unequal variances to compare dieback, a Wilcoxon rank-sum test to analyze crown loss, and Fisher's exact test to contrast crown illumination category and the frequency of trunk damage. We repeated these analyses comparing directly struck, potentially lightning-tolerant trees to potentially lightning-tolerant controls and directly struck trees of all other species.

Competitive release: tree mortality, biomass turnover, and liana reductions

We quantified lightning-caused tree mortality and biomass turnover among trees neighboring directly struck trees. We resurveyed each strike 1–4 times post-strike; 83 strikes in 2015–2018 were last surveyed 10–18 months post-strike, and 10 strikes from 2019 were last surveyed 1–7 months post-strike (fieldwork in 2020 was curtailed because of the COVID-19 pandemic and secondarily damaged trees were never surveyed at one strike location). Trees were considered to be damaged by lightning if they exhibited unambiguous lightning damage in the post-strike surveys, and to be killed by lightning if they exhibited lightning damage and died during the post-strike survey period (Yanoviak *et al*., 2017; Gora & Yanoviak, 2020). Lightning damage is observable as short-term leaf necrosis among branches within *c*. 1 m of the branches or trunk of the directly struck tree or a secondarily damaged tree (Yanoviak *et al*., 2017; Gora & Yanoviak, 2020). Consequently, neighboring trees were defined as lightning-damaged trees with damaged branches within *c*. 1 m of the directly struck tree or a secondarily damaged neighbor. This field-based approach is preferable to approximating the neighborhood based on rooting position because lightning can damage trees with rooting positions as far as 45 m from the directly struck tree, yet those same trees are within 1 m of the directly struck tree in three-dimensional space due to their aboveground growth pattern.

Per-strike tree mortality and biomass turnover were recorded as reported previously (Gora *et al*., 2021), but here included only the neighboring trees (excluding directly struck trees themselves). We estimated biomass turnover using allometric equations for biomass, crown dieback observations, and literature values for the average proportion of tree biomass contributed by branches. Tree biomass was calculated with a diameter-based allometric equation (eqn 7 in Chave *et al*., 2014) using DBH corrected for measurement height (Cushman *et al*., 2014). Crown dieback was defined as the estimated proportion of crown volume that had recently died (Stolte *et al*., 2002). The proportion of tree biomass contained in branches was estimated using a DBH-based allometric equation based on the BAAD database (Falster *et al*., 2015; Gora *et al*., 2021). We used Welch's *t*-test to compare the number of trees killed and neighboring tree biomass turnover between direct strikes to tolerant tree taxa and all other species. We compared per-strike biomass mortality surrounding directly struck *D. oleifera* trees and surrounding all directly struck trees to the mean annual mortality flux (Mg of biomass mortality per year) within 5 m bins of distance from the 20 *D. oleifera* trees > 60 cm in the Barro Colorado Island (BCI) 50-ha plot from 1982 to 2015. We repeated these analyses comparing directly struck, potentially lightning-tolerant trees to the mean mortality flux surrounding all potentially lightning-tolerant trees (12 *C. platanifolia*, 25 *C. pentandra*, 20 *D. oleifera*, 7 *C. cainito*, and 43 *H. crepitans*; Notes S1).

We used data from the initial and final surveys of each directly struck tree to evaluate the influence of lightning on liana infestation. We used paired *t*-tests to compare the number of lianas infesting each surviving directly struck tree between their first survey and their final survey. We repeated these analyses for *D. oleifera* trees directly struck by lightning, other tree species, and potentially lightning-tolerant trees. We compared the reductions in liana infestations to expected liana mortality based on community-wide liana mortality rates in this forest (see Notes S1).

Drone measurements of crown damage and relative height

We used digital surface models to measure *D. oleifera* canopy damage and evaluate the degree to which *D. oleifera* crowns were more emergent relative to other emergent trees. Emergent categorically defines trees with crowns that are fully exposed to lateral light (i.e. crown illumination level 5; Arellano *et al*., 2021) and is also used here quantitatively to refer to the height that an emergent tree crown extends above the surrounding canopy surface. Digital surface models were produced at 1 m resolution using photogrammetric point clouds based on RGB images from drone flights of BCI in 2015, 2018, and 2020. Point clouds were aligned to airborne lidar data for this study site from 2009, thus enabling alignment with the lidar-based digital elevation model and calculation of canopy heights (see Cushman *et al*., 2022 for detailed photogrammetry methods). We manually delineated tree crowns in drone images to measure changes in crown height and crown area for directly struck *D. oleifera* ($n = 9$) from 2015 to 2018 or 2018 to 2020, depending on which interval included the lightning strike. On average, the pre-strike drone flights were conducted 1.44 yr before the strike (SD = 0.67 yr), and the post-strike flights were 1.06 yr after the strike (SD = 0.60 yr). We compared pre-to-post strike crown height and area using a paired *t*-test. We also measured average crown height and surrounding crown height (crown height in the area within 10 m of the focal tree crown boundary) of every emergent tree in the *D. oleifera* control and heterospecific control datasets from the BCI 50 ha plot ($n = 44$). We used a linear model to compare surrounding crown height between *D. oleifera* trees ($n = 15$) and all other emergent trees ($n = 38$), including focal tree height, focal tree type (*D. oleifera* or other), and their interactions as predictors. This dataset excluded two trees that appeared to be dead or dying, neither of which were *D. oleifera* trees. We repeated this analysis including only trees taller than the shortest *D. oleifera* (i.e. dropping control trees shorter than the shortest *D. oleifera*) and including only trees from the 50-ha plot to confirm that absolute tree height and recent strike status had limited influence on these results.

Differences in tree condition and liana infestations among the broader tree community

We evaluated how the general population of *D. oleifera* trees differed from the broader community of large-statured trees. To evaluate whether there are consistent differences between the general populations of *D. oleifera* trees and other tree taxa, we compared crown dieback (*t*-test), crown loss (Wilcoxon rank-sum test), trunk damage (Fisher's exact test), liana infestations (Wilcoxon rank-sum test), and crown illumination (Fisher's exact test) between *D. oleifera* controls and heterospecific controls. We repeated these analyses comparing potentially lightning-tolerant controls and heterospecific controls. We also used field surveys of liana infestation among 1509 trees with exposed crowns in the BCI 50-ha plot (Gora *et al*., 2020b) to evaluate whether *D. oleifera* trees tended to have lower liana infestations than other common canopy species ($n = 34$ species with at least 15 exposed individuals in the 50-ha plot). We used ANOVA to test for differences in average liana infestation among these exposed trees.

Estimating the lifetime benefits of lightning survival

We calculated mortality rates of large (> 60 cm DBH) *D. oleifera* trees using 2537 tree-years of data for 132 trees in 128 ha of mapped plots at our field site (Wright *et al*., 2018; Condit *et al*., 2019). We calculated the mortality rate for these trees, accounting for variable census intervals (Kubo *et al*., 2000), and estimated their expected residence time in this size class as one divided by the mortality rate. We estimated the number of lightning strikes experienced during the residence time of these large trees as the product of the mean expected direct strike frequency for these trees (Gora *et al*., 2020b) and their longevity after reaching 60 cm DBH, propagating uncertainty in longevity (i.e. the 95% CI). This estimate assumes that the direct strike probabilities of *D. oleifera* trees in the 50-ha plot are representative of the distribution of *D. oleifera* direct strike probabilities after they reach > 60 cm in DBH.

We calculated expected cumulative liana mortality and cumulative competitor biomass killed as the product of the expected number of strikes and mean values from the directly struck *D. oleifera*. Thus, expected cumulative liana mortality was the product of the observed mean reduction in liana infestation among potentially lightning-tolerant trees that were directly struck (3.1 lianas) and the expected number of strikes. Similarly, we estimated cumulative competitor biomass killed as the product of per-strike competitor biomass loss and expected direct strikes. We calculated 95% CIs on the cumulative effects by numerically propagating variation in the estimated numbers of direct lightning strikes per *D. oleifera* tree and the observed competitor biomass killed or liana reduction per direct strike to potentially lightning-tolerant trees.

Survival analysis of historic tree neighborhoods

We used mixed-effects Cox proportional hazards models to test whether historic mortality surrounding *D. oleifera* trees was higher than that around other large, surviving canopy trees. Using data from the co-located BCI 50-ha plot, we tested whether trees rooting within 10 m of living *D. oleifera* trees had a higher mortality risk than trees within 10 m of living trees of other species (see Methods S1 for details). The proportional Cox models included time until death or right-censored survival as the response, and fixed effects for log-transformed DBH, log-transformed distance from the focal canopy tree, neighborhood type (*D. oleifera* vs all other trees), and their interactions (R package COXME; Therneau & Therneau, 2015). We included the focal canopy tree as a random effect. We tested the contribution of fixed effects to model fit based on Akaike information criterion (AIC) values, retaining terms that decreased model AIC.

Estimating the contributions of lightning survival to *D. oleifera* longevity and fecundity

We estimated the cumulative benefits of lightning survival only for *D. oleifera* because we had the best available demographic and lightning response data for this tree species. To do this, we fit demographic models to field data and then ran simulations of *D. oleifera* lifetimes using those models. We compared *D. oleifera* longevity and seed production under three scenarios: (1) *observed demographics* using observed mortality, fecundity, and growth; (2) *no indirect benefits* using observed mortality, fecundity, and growth with added competition and liana infestations assuming that they were not reduced by lightning; and (3) *no benefits* = we added competition and liana infestations in the same manner as scenario 2, and we assumed that these *D. oleifera* trees died from direct lightning strikes at the average rate for non-*D. oleifera* trees in this forest. We estimated the total benefits of lightning survival for *D. oleifera* trees by comparing the observed demographics and no benefits scenarios, and we estimated the contribution of indirect benefits (i.e. decreased competition and liana infestations) to fecundity and longevity by comparing the observed demographics and no indirect benefits scenarios. This approach is detailed in Methods S1 (Tables S4–S6).

Comparisons of tree allometry

We evaluated the species-level associations between the estimated probability of being directly struck and tree crown area, tree height, and tree DBH using field measurements and detailed allometry data for this forest (Martínez Cano *et al.*, 2019). We calculated the average direct strike probability and average DBH for species with at least 15 trees with exposed crowns in the BCI 50-ha plot (i.e. $> 50\ \mathrm{m}^2$ of crown area visible from above) because they could conceivably be directly struck by lightning. The direct strike probability was calculated using an empirically validated mechanistic model of direct strike probability based on crown area and crown exposure (understory, canopy, or emergent; Gora *et al.*, 2020b). We then estimated the expected height and crown area for each of these trees assuming they exhibited the community-wide tree allometry for trees in this forest. To estimate how their architecture differed from the community average, we divided their observed height and crown area by their respective allometric expectations. We visualized the associations between these variables with scatterplots to explore how the size, structure, and allometry of *D. oleifera* contributed to their high strike probability.

We used the 28 *D. oleifera* in this dataset to estimate the contributions of *D. oleifera* allometry to their expected strike probabilities. To assess the influence of crown area, we recalculated their expected direct strike probability using the community-wide allometric crown area for their diameter. We also estimated the contributions of their extreme height allometry to their expected strike probability by assuming all 18 emergent *D. oleifera* individuals instead had canopy-level exposure (i.e. crown illumination index of 4 instead of 5). We then compared the probability of being directly struck by lightning under these two hypothetical scenarios to the expected probability of a direct strike to these *D. oleifera* trees using their actual allometries and canopy exposures.

Results

The minor costs and major benefits of direct lightning strikes to *D. oleifera* trees

The observed costs of being directly struck by lightning were negligible for *D. oleifera* trees (Table S2; Figs 1, 2, S2–S4; Video S1). This species survived all 10 direct strikes to 9 individuals (Figs 2, S2) with only minor visible injuries. Damage was so minimal that peak crown dieback of directly struck *D. oleifera* (mean ± SD: 7.8 ± 5.1%) did not differ significantly from dieback among the general population of conspecifics (i.e. *D. oleifera* controls; mean ± SD: 7.4 ± 12.2%; *t*-test: $t < 0.1$, df = 38.0, $P = 0.980$; Fig. 2). Repeat digital surface models from drone photogrammetry confirmed that these directly struck trees did not decrease in crown height or crown area during the 2- to 3-yr interval encompassing the strike date (height: $t = 0.6$, df = 8, $P = 0.547$; area: $t = 0.5$, df = 8, $P = 0.657$; Fig. S3).

In contrast with the minor damage to these directly struck *D. oleifera* trees, directly struck trees of other species exhibited high damage and mortality. The majority (64%) of the other 83 directly struck trees died within 2 yr of the strike, as compared to 0 deaths for directly struck *D. oleifera* trees (log-rank survivorship test with DBH correction: $P = 0.004$; Fig. 2). The difference in

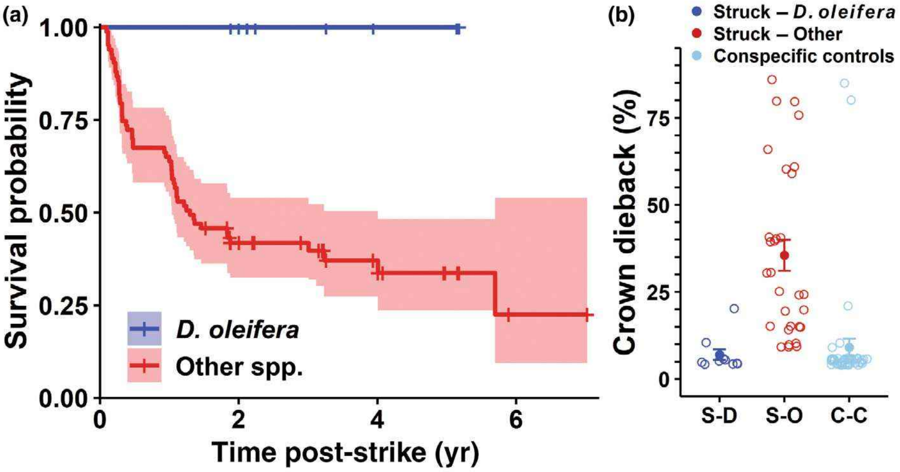

Fig. 2 *Dipteryx oleifera* trees survived direct lightning strikes with minimal damage. *Dipteryx oleifera* trees had 100% survival following 10 direct strikes, whereas 83 directly struck trees of other species showed high mortality (a, Kaplan–Meier survivorship curves for 2014–2021; hash marks represent final surveys of living trees; shading shows 95% confidence intervals). Struck *D. oleifera* showed minimal crown dieback (b) with low levels similar to conspecific controls that were not struck (n = 44), and unlike the high levels of dieback observed among surviving directly struck trees of other species (n = 37). In (b), hollow points represent each tree and filled points with error bars represent group averages with SE. Statistical analyses excluded the second direct lightning strike to one of the *D. oleifera* trees (n = 9).

mortality between *D. oleifera* and other species cannot be explained by differences in mean mortality rates among species (see Notes S1 subsection *Comparisons of observed mortality with alternative survival scenarios*). Among trees surviving after 1-yr post-strike, mean crown dieback was 5.7 times higher for directly struck trees of other species than for *D. oleifera* trees (7.2% vs 41.5% dieback; t-test: t = 6.8, df = 42.6, $P < 0.001$; Fig. 2), and crown loss (i.e. the loss of branches) was three times higher (9.4% vs 26.9% crown loss, respectively; W = 67.5, P = 0.017; Fig. S4).

Lightning caused significant damage and death to trees neighboring the directly struck *D. oleifera* (Video S1). On average, direct lightning strikes to *D. oleifera* killed 9.2 neighboring trees (SD = 17.2) and caused 2.1 Mg (SD = 2.9) of biomass mortality among neighboring trees (neighbors include all lightning-damaged trees; Fig. 3). These deaths were an order of magnitude higher than the 0.95 tree deaths per strike that would be expected over the same time period based on historic mortality rates. Field observations show that lightning-caused damage is concentrated among trees within *c.* 1 m of the directly struck tree in three-dimensional space (Yanoviak *et al.*, 2017; Gora *et al.*, 2023); thus, any comparison with historic mortality based on rooting points underestimates the effects of lightning on neighboring competitors. Nevertheless, among trees rooting within 10 m of *D. oleifera* trees, the biomass killed by lightning (1.03 Mg within 10 m) was 196% greater than average annual biomass mortality, which unavoidably also includes historic lightning damage (Fig. S5). Neither neighboring tree mortality (t-test: t = 0.8, df = 9.1, P = 0.421) nor biomass mortality (t-test: t = 1.0, df = 13.4, P = 0.343) differed between direct strikes to *D. oleifera* and other species; this similarity in neighborhood disturbance severity suggests that the intensity of lightning strikes did not differ between the two groups of trees.

Direct strikes to *D. oleifera* trees also reduced liana loads (Video S1). Liana abundances decreased on all six directly struck *D. oleifera* that were initially infested with lianas (four other struck *D. oleifera* had no lianas before or after the strike). The average number of lianas in a tree decreased 78% from the initial post-strike survey to the final post-strike survey (from 4.1 to 0.9 lianas; paired t-test: t = 2.3, df = 9, P = 0.048; Figs 3, S6). This decrease far exceeds the expected mortality of these lianas over the same time period based on community-wide rates of liana mortality in this forest (0.6 lianas per tree) and contrasted strongly with the concurrent increases in average liana stem densities in this forest (Schnitzer *et al.*, 2021).

We identified comparably negligible costs and substantial benefits when considering the responses of all 18 individuals from the seven long-lived, large-statured tree species that demonstrated the ability to survive lightning (i.e. potentially lightning-tolerant trees). These results are detailed in Notes S1, Figs S1, S2, and S4–S6. Although sample sizes for taxa other than *D. oleifera* were too small to draw conclusions about species-level lightning tolerance, these data show that individual long-lived, large-statured trees generally benefit when they survive direct lightning strikes.

Quantifying the population-wide benefits of lightning survival

Dipteryx oleifera trees repeatedly benefit from being struck by lightning. *Dipteryx oleifera* trees with a diameter > 60 cm DBH have a mortality rate of only 0.357% yr^{-1} (95% CI: 0.144–0.570% based on 132 trees observed for a total of 2537 tree-years). This implies a *D. oleifera* tree reaching 60 cm DBH will live on average another 280 yr (95% CI: 175.5–694.0 yr). Based on their crown area and exposure in the BCI 50-ha plot (Gora *et al.*, 2020b), *D. oleifera* trees > 60 cm DBH are expected

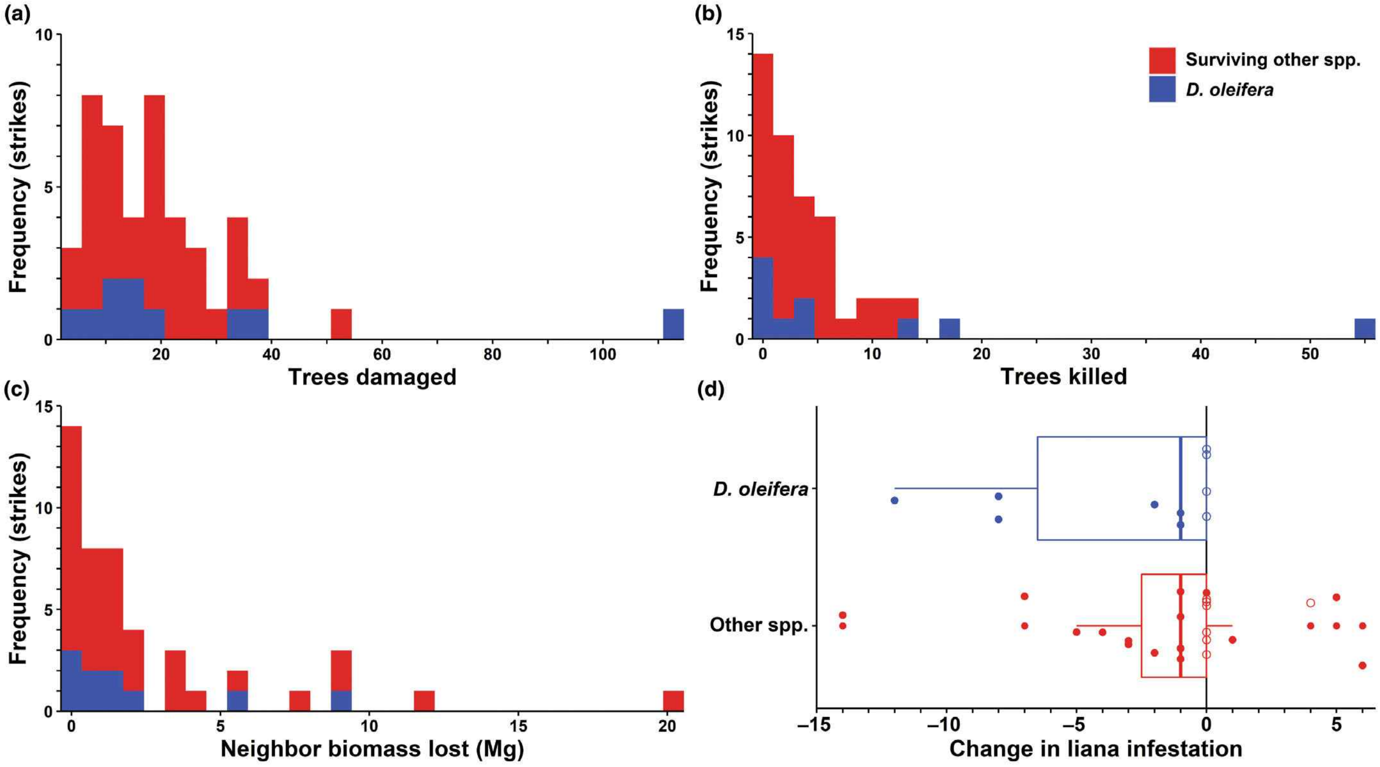

Fig. 3 Effects of direct lightning strikes on neighboring trees and infesting lianas. Lightning strikes damaged (a) and killed (b) many neighbors of the directly struck trees that survived lightning strikes, causing substantial biomass mortality (c). Panels (a–c) are stacked histograms of direct strikes survived by *Dipteryx oleifera* trees and trees of other species. The number of lianas per tree also decreased following direct strikes to all directly struck *D. oleifera* trees with liana infestations (d) and the majority of surviving directly struck trees of other species (see Supporting Information Fig. S6 for patterns over time). Hollow points in (d) represent trees that lacked lianas when they were struck by lightning, whereas filled points had liana infestations.

to be directly struck by lightning every 56.4 yr, or 5.0 times during their residency in this size class (95% CI: 3.1–12.3 strikes per tree; see Notes S1 for other tolerant species). Over that time, lightning strikes to each large *D. oleifera* would be expected to kill an average of 10.4 Mg of neighboring tree biomass (CI: 0.4–29.4 Mg) and 15.4 lianas infesting their crowns (CI: 1–44 lianas).

Historic patterns of mortality within the 50-ha forest plot collocated with our study revealed that trees surrounding large, living *D. oleifera* trees were 48% more likely to die than trees surrounding large, living trees of other species during 1982–2015 (Fig. S7). The strength of this difference decreased with distance from the focal *D. oleifera*, following the expected attenuation of lightning effects with distance from directly struck trees (Yanoviak *et al.*, 2020). This pattern of elevated mortality suggests that lightning meaningfully decreases the long-term survivorship of trees neighboring large *D. oleifera* trees.

The broader population of *D. oleifera* trees at our site exhibited superior condition and canopy position relative to other trees in this forest. Compared to trees that did not exhibit recent lightning damage and were not identified as potentially tolerant to lightning (i.e. heterospecific controls), *D. oleifera* trees that were not struck by lightning during this study (i.e. *D. oleifera* controls) had more intact crowns (13.6% less crown loss for *D. oleifera*; $W = 2137.5$, $P < 0.001$) and similarly minimal crown dieback ($t = 0.4$, df = 62.0, $P = 0.693$) and trunk damage (Fisher's exact test $P = 0.848$; Fig. S8). These patterns match our expectations that the general population of *D. oleifera* trees experienced less historic lightning damage and similarly low levels of recent nonlethal damage when compared to heterospecific controls. *Dipteryx oleifera* controls also had 21.3% lower mean liana cover than heterospecific controls (15.1% vs 36.4%; $W = 2022$, $P < 0.001$). Within the 50-ha plot, mean liana infestations of *D. oleifera* trees were significantly lower than most other common canopy tree species ($F_{33,1475} = 10.3$, $P < 0.001$; Fig. S9; Table S3). Finally, drone imagery revealed that the average canopy surrounding *D. oleifera* crowns was 3.7 m shorter than the canopy surrounding other emergent trees of the same height ($F_{2,50} = 24.8$, $P < 0.001$; Fig. S10), indicating that *D. oleifera* trees experience less competition for light. Beyond *D. oleifera*, the broader group of long-lived, large-statured trees that survived lightning strikes also exhibited healthy crown conditions and notably low liana infestations (Notes S1; Figs S8, S11).

Simulations of *D. oleifera* tree lifespans showed that lightning survival is critical to its longevity and lifetime fecundity (Fig. 4). Compared with a null scenario in which *D. oleifera* trees die from lightning at the same rate as the average for all other taxa and they do not benefit from reduced competition or liana infestations, lightning tolerance enables a 43.9% increase in expected lifespan across all trees > 1 cm DBH (from 37.8 to 54.4 yr) and a 74.0%

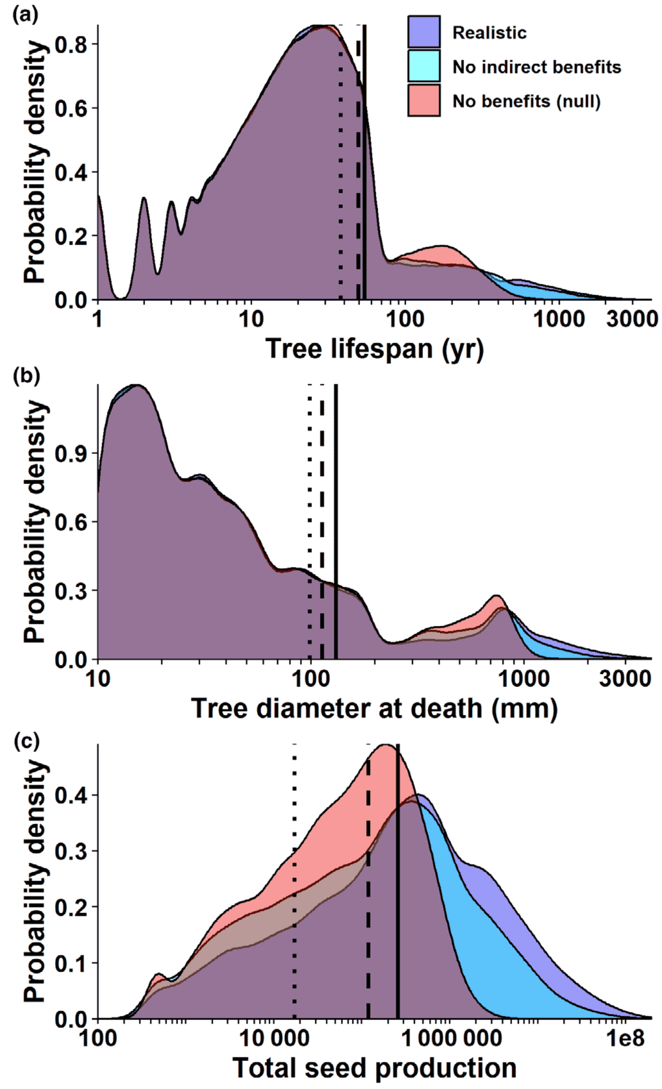

Fig. 4 The lifespan, size, and seed production of simulated *Dipteryx oleifera* trees under three different scenarios. The density plots depict how the ability to survive lightning (no indirect benefits relative to no benefits) combined with the benefits of reduced liana infestation and tree competition (realistic vs no indirect benefits) to increase tree lifespan (a), diameter at time of death (b), and lifetime seed production (c). Each density plot represents the distribution of lifespan, maximum diameter, and fecundity for all 100 000 trees simulated in each of these three scenarios. The vertical lines indicate the population mean values of each response variable for the realistic (solid line), no indirect benefits (dashed line), and no benefits (dotted line) scenarios. The areas where the density plots do not overlap capture how the scenarios differentially influence longevity, maximum diameter, and seed production. Lightning survival influences tree survival, and thereby maximum size, for a small number of trees, but because those trees produce most of the seeds in the population, this result is a large increase in seed production. Note that the *x*-axes are log-scaled, and probability densities are for log-transformed *x* values.

increase in expected lifespan among trees that reached 60 cm DBH (from 259.2 to 451.2 yr; Fig. 4a). Because seed production increases with tree size and lightning primarily kills large trees, lightning tolerance has an even more dramatic influence on lifetime fecundity, which is 14.1 times higher than the null scenario (Fig. 4c). The effects of lightning on reducing competition from neighboring trees and lianas contribute 31.4% of the increases in longevity and 60.4% of the increases in seed production.

The size and architecture of *D. oleifera* increase its probability of being struck by lightning relative to other canopy trees because lightning nonrandomly strikes taller trees with large crown areas. *Dipteryx oleifera* trees tend to have large trunk diameters (Fig. 5a), and they are exceptionally tall and have unusually large crown areas relative to other trees of the same trunk diameter (Fig. 5b). The modelled strike probabilities for the 28 *D. oleifera* trees with exposed crowns (i.e. visible from above) in the 50-ha plot were 149% higher than would be expected if their crown areas followed the community-wide allometry with diameter and 168% higher than if they had the community-wide allometry for both crown area and height. Their extreme allometry explains why the expected direct strike rate to *D. oleifera* trees was more than double that of all other canopy species with similar average trunk diameters (Fig. 5a).

Discussion

Lightning is widely believed to have negative effects on trees. Yet here we provide strong empirical evidence that individuals of at least one lightning-tolerant species benefit from being struck by lightning without experiencing meaningful damage. Moreover, we show that the ability to survive lightning can greatly increase lifetime fecundity and that tree architecture affects expected lightning strike rates with potential feedback effects on tree architecture. Limited sampling of other long-lived, large-statured trees captured similar trends, suggesting that long-lived, large-statured trees generally benefit when they survive lightning strikes, rather than being specific to a single species. These counterintuitive results change our understanding of lightning as an agent of disturbance, with implications for the understanding of tree competition, selection on tree architecture and life history, and tree species niche differentiation.

Lightning shapes the competitive neighborhoods around *D. oleifera*. Prior research showed interspecific variation in lightning tolerance (Richards *et al*., 2022) and even minor interspecific differences in survival can influence patterns of community assembly (Rüger *et al*., 2018), indicating that lightning broadly influences patterns of community assembly. However, our findings are unusual because they show how the fecundity and survivorship of an *individual tree* can increase after it is struck by lightning (Fig. 4). Specifically, the damage and death of neighboring trees and infesting lianas as a result of a lightning strike appears to cause a partial competitive release for the surviving struck trees. Indeed, the low liana infestations of *D. oleifera* trees and the unusually short canopy surrounding their crowns support a population-wide advantage in competition for light. Lightning-tolerant trees could also derive an advantage in belowground competition from the death of nearby competitors or through the fertilization of soil as lightning-killed neighbors decompose. Moreover, lightning will kill additional neighbors and lianas

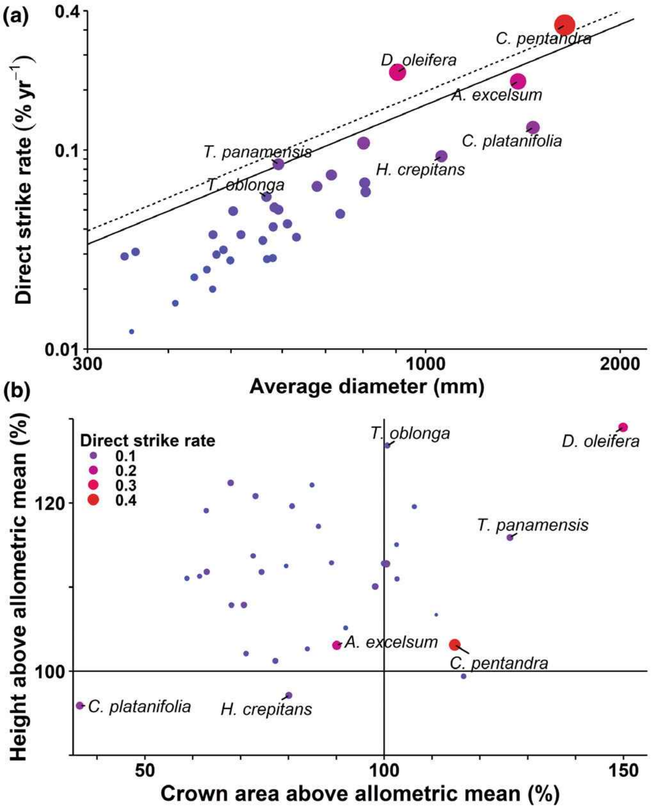

Fig. 5 *Dipteryx oleifera* exhibits unusual allometry that is associated with a higher risk of being directly struck by lightning. Among trees with exposed crowns, the modeled likelihood of being directly struck by lightning (% of trees affected per year) increased with average diameter across species (a). Relative tree height (canopy or emergent) is a strong predictor of the direct strike rate (Gora *et al*., 2020b), and lines represent the expected direct strike rate of canopy (solid line) or emergent (dashed line) trees with community-wide expected mean crown area for a given diameter. *Dipteryx oleifera* trees have larger crown areas and are taller than expected for trees of their diameter (b). Height and crown area relative to the allometric mean are calculated for each individual tree as the observed height and crown area of trees in the BCI 50-ha plot, divided by the community-wide mean expected height and crown area, respectively, for trees of the same diameter in this forest. Points in both panels are species averages with red shading and larger size indicating higher direct strike rates. Solid lines in (b) represent allometric mean height and crown area. Direct strike rates are predictions for real canopy trees in the BCI 50-ha plot based on an empirically validated model, with mean values presented for species with at least 15 canopy trees (i.e. trees with exposed crowns, data from Gora *et al*., 2020b).

when lightning-tolerant trees survive direct strikes to neighboring trees, expanding the cumulative benefits of lightning beyond those quantified in this study. As lightning frequency increases in many regions (Romps, 2019; Harel & Price, 2020), competitive landscapes will change, favoring lightning-tolerant taxa like *D. oleifera*.

The ability to survive lightning strikes could be key to the life history strategy of some tree species. Fundamentally, trees with large exposed crowns inherently have high lightning strike probabilities, and therefore they could not exhibit long residence times in the canopy without the ability to survive lightning. Moreover, the results of this study show that these long-lived, large-statured taxa tend to exhibit benefits of being struck by lightning and, for at least one of these species, a large majority of lifetime fecundity depends on the ability to survive lightning (Fig. 4). For tree species with low recruitment, shade intolerance, and large stature (i.e. a subset of 'long-lived pioneers' like the lightning-tolerant *D. oleifera* and comparable *C. pentandra*; Rüger *et al.*, 2018), the ability to survive lightning may be fundamental to their life history strategies and could facilitate their coexistence with both 'fast' and 'slow' species (Jops & O'Dwyer, 2023). These taxa tend to perform poorly as small trees (e.g. high mortality and low abundance), but they exhibit high survivorship as large trees and are disproportionately well represented in the canopy. This suggests a trade-off between strategies and/or traits that produce high survivorship in the understory vs the canopy.

The strongly size-dependent effects of lightning (i.e. lightning nonrandomly hits taller trees with larger crown areas) suggest that it acts as a selection pressure on tree architecture. High crown exposure is beneficial because it increases light interception, but *D. oleifera* crowns extended further above their neighbors than other fully exposed emergent trees. Although light interception does not continue to increase with greater height among fully exposed trees, strike probability does continue to increase (Uman, 2008; Gora *et al.*, 2020b). The few other canopy species in our dataset with similarly extreme allometries (*T. oblonga*) or unusually large crowns (*C. pentandra* or *H. crepitans*) also survived all direct lightning strikes (Fig. 5; Table S2). These patterns suggest that lightning could play a role in shaping selection on tree architecture, warranting further investigation.

The mechanisms underlying lightning survival remain unclear, although wood electrical resistance is hypothesized to be important. Trees with lower electrical resistance experience less energetic heating when exposed to electric current, which could reduce tissue damage by lightning and increase survivorship (Gora & Yanoviak, 2015; Gora *et al.*, 2017). Large *D. oleifera* trees have particularly low electrical resistance, which could explain their high survivorship (Gora *et al.*, 2017). Wood electrical resistance depends on multiple anatomical and physiological traits associated with tree vascular tissues (e.g. vessel structure, water content, and ion content), and it is likely that there are multiple pathways to producing low electrical resistance (Gora & Yanoviak, 2015). Interspecific variation in lightning tolerance in our study site is strongly positively correlated with wood density and weakly positively correlated with vessel area and leaf nitrogen (Richards *et al.*, 2022), but these correlations have not been linked to electrical resistance or other mechanisms. Additional work is needed to test the hypothesis that low electrical resistance is a key trait promoting lightning survival, as there are few data on tropical tree electrical properties or lightning tolerance. Other survival mechanisms may also play a role. For example, our field observations suggest that the architecture of certain trees (e.g. *C. pentandra*) diverts electric current away from their trunks and into neighboring trees, thereby protecting a directly struck tree from severe damage. As we have learned from decades of research into fire and drought, unraveling the multiple potential mechanisms underlying lightning survival will likely require intensive physiological and anatomical investigations across many taxa and biomes.

The potential benefits revealed in this study raise the question of why all trees do not have the ability to survive lightning. There are multiple potential explanations. First, the selective value of surviving lightning strikes may be weak where lightning is less frequent (Gora *et al*., 2020a) or for small-statured taxa because they interact less frequently with lightning (Gora *et al*., 2020b). Second, the benefits of traits that enable lightning survival could trade off against costs (e.g. higher construction cost of high wood density, or risky vascular strategies; Richards *et al*., 2022). Third, lightning survival likely requires coordination with additional traits (e.g. tolerance to wind or drought) for the benefits of lightning survival to be realized. For example, large-statured trees are also more vulnerable to wind and water stress (Gora & Esquivel-Muelbert, 2021), suggesting that the total benefits of lightning survival are co-limited by tree tolerance to wind and water stress. Further exploration of these potential costs and trade-offs is needed to understand the role of lightning in shaping tree ecology and evolution.

Although research typically focuses on the negative effects of lightning, there is substantial evidence of lightning tolerance across many species and sites. More than a century of anecdotes suggest that lightning tolerance is found in nearly all forested latitudes and biogeographic realms (Maxwell, 1793; Stone, 1914; Komarek, 1964; Orville, 1968; Taylor, 1977; Tutin *et al*., 1996). Within our own site, the high survivorship of several long-lived, large-statured taxa suggests they must survive lightning strikes, indicating that a meaningful number of taxa could exhibit lightning tolerance in any given forest, consistent with our previous work demonstrating a continuum of lightning tolerance in this forest (27% of 30 species survived lightning more than the community-wide expectation; Richards *et al*., 2022). We know of only two tree species on Earth for which data are sufficient to test for the benefits from lightning (i.e. ≥ 10 direct lightning strikes located without biased detection), and one of these two species exhibits strong benefits (*D. oleifera* benefits whereas 9 of 11 directly struck *Anacardium excelsum* died; Table S2); the likelihood that we identified a unique trait in the first two species sampled is quite low. Overall, there is no evidence that lightning tolerance is rare or that the patterns reported for *D. oleifera* are unusual, and we expect future work to reveal that the ability to survive lightning and benefit from its effects is common among long-lived, large-statured tree taxa.

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Competing interests

None declared.

Author contributions

EMG conceived the study, designed and conducted field data collection, analyzed the data, and led the writing of the manuscript. HCM-L designed and oversaw the drone data and associated tree crown data collections, advised on data analysis, and contributed to conceptual development and manuscript revision. KCC analyzed the drone data and contributed to conceptual development and manuscript revision. SPY managed the lightning location project, collected field data, and contributed to conceptual development and manuscript revision. JHR and PN contributed to conceptual development and manuscript revision. PMB and JCB designed and implemented the lightning location system and contributed to conceptual development and manuscript revision.

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Data availability

Data, code, and Video S1 are publicly available via the Cary Institute FigShare (doi: 10.25390/caryinstitute.24731217).

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Supporting Information

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

Fig. S1 Species-level mean mortality rates for trees > 60 cm in diameter.

Fig. S2 Survival analysis and uncertainty for directly struck trees over 6 yr post-strike.

Fig. S3 Changes in drone-measured crown height and area for directly struck *Dipteryx oleifera* trees.

Fig. S4 Patterns of crown loss and trunk damage for directly struck *Dipteryx oleifera* and potentially lightning-tolerant trees relative to their control groups and other directly struck trees.

Fig. S5 Comparison of biomass mortality among trees neighboring living *Dipteryx oleifera* and potentially lightning-tolerant trees vs those neighboring directly struck trees.

Fig. S6 Patterns of liana infestation among groups of directly struck trees both as before-and-after comparisons and as trends over time.

Fig. S7 Survival analysis shows elevated mortality among neighboring trees of *Dipteryx oleifera* based on trends within the co-located 50 ha forest dynamics plot.

Fig. S8 Comparisons of crown dieback, crown loss, trunk damage, and crown illumination between the general populations of *Dipteryx oleifera* trees and other large-statured taxa.

Fig. S9 Comparison of liana infestation rates between *Dipteryx oleifera* trees and canopy trees of other taxa.

Fig. S10 Analysis of drone-based canopy surface models showing that *Dipteryx oleifera* trees extend further above their surrounding tree canopies than emergent trees of other taxa.

Fig. S11 Comparisons of crown dieback, crown loss, trunk damage, and crown illumination between the general populations of potentially lightning-tolerant trees and other large-statured taxa.

Methods S1 Additional text providing details about methods that are summarized in the main text.

Notes S1 Text describing additional results that support the patterns described in the main text.

Table S1 List of key datasets used in this study and their sources.

Table S2 Species-level summaries of tree responses to direct lightning strikes.

Table S3 Species-level summaries of large, old trees surveyed for comparison to lightning-struck trees and for comparisons of tree condition among these populations.

Table S4 Details of fitted relationships used in simulations of *Dipteryx oleifera* growth, survivorship, and reproduction.

Table S5 Summary of size-dependent patterns of *Dipteryx oleifera* survival.

Table S6 Transition matrix for liana infestation used in simulations of *Dipteryx oleifera*.

Video S1 A *Dipteryx oleifera* tree surviving a lightning strike while its neighboring competitor trees and the lianas in its crown die.