New Phytologist

Lianas increase lightning-caused disturbance severity in a tropical forest

Evan M. Gora[1,2], Stefan A. Schnitzer[2,3], Phillip M. Bitzer[4], Jeffrey C. Burchfield[5], Cesar Gutierrez[2] and Stephen P. Yanoviak[2,6]

[1]Cary Institute of Ecosystem Studies, Millbrook, New York, NY 12545, USA; [2]Smithsonian Tropical Research Institute, Balboa, Panamá; [3]Department of Biological Sciences, Marquette University, Milwaukee, WI 53233, USA; [4]Department of Atmospheric and Earth Science, The University of Alabama in Huntsville, Huntsville, AL 35899, USA; [5]Earth System Science Center, The University of Alabama in Huntsville, Huntsville, AL 35899, USA; [6]Department of Biology, University of Louisville, Louisville, KY 40208, USA

Author for correspondence:
Evan M. Gora
Email: gorae@caryinstitute.org

Received: *29 November 2022*
Accepted: *14 February 2023*

New Phytologist (2023) **238:** 1865–1875
doi: 10.1111/nph.18856

Key words: biomass mortality, forest turnover, global change, Panama, tree death, trees.

Summary

- Lightning is an important agent of plant mortality and disturbance in forests. Lightning-caused disturbance is highly variable in terms of its area of effect and disturbance severity (i.e. tree damage and death), but we do not know how this variation is influenced by forest structure and plant composition.
- We used a novel lightning detection system to quantify how lianas influenced the severity and spatial extent (i.e. area) of lightning disturbance using 78 lightning strikes in central Panama.
- The local density of lianas (measured as liana basal area) was positively associated with the number of trees killed and damaged by lightning, and patterns of plant damage indicated that this occurred because lianas facilitated more electrical connections from large to small trees. Liana presence, however, did not increase the area of the disturbance. Thus, lianas increased the severity of lightning disturbance by facilitating damage to additional trees without influencing the footprint of the disturbance.
- These findings indicate that lianas spread electricity to damage and kill understory trees that otherwise would survive a strike. As liana abundance increases in tropical forests, their negative effects on tree survival with respect to the severity of lightning-related tree damage and death are likely to increase.

Introduction

Global change is increasing the tree mortality rates and weakening the capacity of tropical forests to uptake and store atmospheric carbon (Brienen *et al.*, 2015; Qie *et al.*, 2017; Bauman *et al.*, 2022). Multiple agents are hypothesized to contribute to increasing tree mortality rates, including drought, fire, lianas, and lightning (McDowell *et al.*, 2018; Yanoviak *et al.*, 2020). In tropical forests, lightning strikes are important but typically underappreciated agents of disturbance, despite these forests experiencing 35–67 million lightning strikes each year (Gora *et al.*, 2020) and some evidence that lightning frequency is increasing (Harel & Price, 2020). An average lightning strike in central Panama – the only forest with systematically monitored lightning strikes – kills 5.3 trees and damages an additional 18.3 trees, resulting in 7.4 Mg of biomass mortality per strike (Gora *et al.*, 2021). At the landscape level in this Panamanian forest, lightning causes 16.1% of woody biomass mortality and 40–50% of deaths for trees > 60 cm in diameter (Yanoviak *et al.*, 2020; Gora *et al.*, 2021). The ecological effects of individual lightning strikes are highly variable, with the few strikes described across tropical forests ranging from 1 to 116 trees damaged and 0–65 trees killed per strike (Anderson, 1964; Magnusson *et al.*, 1996; Sousa *et al.*, 2003; Gora & Yanoviak, 2020). However, we know little about the potential mechanisms underlying this variation, and whether stand density, tree species characteristics, and the presence of lianas can help explain this variation (Yanoviak, 2013; Richards *et al.*, 2022). Quantifying how these factors influence the ecological effects of lightning is key to understanding how lightning shapes forest dynamics, both across forest types and into the future.

The pathway of electric current transfer among trees likely influences the number of trees killed and the spatial extent of lightning-caused disturbance (hereafter *lightning disturbance*). Observations of lightning damage in tropical forests indicate that the electric current from a strike is distributed among multiple trees aboveground through two separate mechanisms. First, electricity can bridge air gaps between neighboring trees via ‘flashover’ (Furtado, 1935; Anderson, 1964), which occurs when electric current spreads from tree-to-tree via an airborne channel (Uman, 2008; Yanoviak *et al.*, 2017). Flashover occurs only at very high electric fields (*c.* 500 kV m^{-1} of flashover; Uman, 2008) and when vegetation is in close proximity (typically < 1 m; Yanoviak *et al.*, 2017), thus providing a barrier or limit to the spread of lightning damage. Second, electricity can transfer between trees via direct connections provided by physical contact between the branches or trunks of neighboring trees (Supporting Information Fig. S1). Accordingly, a greater number of physical connections could facilitate the flow of electricity to increase lightning disturbance severity and spatial extent.

Lianas increase the structural complexity of a forest patch, connecting trees together and potentially affecting the distribution of damage caused by a lightning strike. Lianas provide physical connections among trees and can reduce the distance between tree crowns that would otherwise be separated due to crown shyness (Putz *et al.*, 1984; Adams *et al.*, 2019). Thus, physical contact and flashover from lianas presumably increase the number of trees that can be electrocuted by a given strike, relative to flashover among trees alone (Fig. 1b). Furthermore, lianas are particularly likely to carry electric current because of their high electrical conductivity (Yanoviak, 2013; Gora *et al.*, 2017). The contribution of lianas to patterns of electric current transfer and their influence on lightning disturbance characteristics, however, remain unknown.

We quantified lightning disturbance characteristics in association with lianas and with inferred patterns of electric current transfer in a lowland Panamanian forest. Specifically, we combined a unique dataset of systematically located lightning strikes (patterns of plant damage and death among these strikes were previously published in Yanoviak *et al.*, 2020 and Gora *et al.*, 2021) with visual observations of plant damage patterns and forest plot data describing co-located tree and liana communities. We hypothesized that lianas influence the severity and area (spatial extent) of lightning disturbance in forests. We predicted that both liana basal area and liana-associated electrical connections are positively associated with the: number of trees damaged per strike; number of trees killed per strike; percent of damaged trees that die; per strike biomass turnover; and physical area across which trees were damaged by lightning. Finally, we determined whether liana basal area was associated with higher frequency of electrical connections via liana physical contact and flashover.

Materials and Methods

Study site and lightning location system

We conducted this study in the seasonally moist tropical forest on Barro Colorado Island (BCI) in central Panama (9.210°N, 79.745°W) from 2015 to 2020. This site has an average annual temperature of 26°C, mean annual rainfall of 2650 mm, and a 4-month dry season (< 100 mm monthly rainfall from January–April; temperature and rainfall data from 2000 to 2017; Paton, 2017). Croat (1978) and Leigh (1999) provide detailed descriptions of this forest and its biota.

We located lightning strikes using a combination of cameras and electric field change meters across a progressively increasing study area (from 2.25 km^2 to 15 km^2; Yanoviak *et al.*, 2017; Gora *et al.*, 2021). We surveyed lightning strikes recorded on multiple cameras from 2015 to 2019. In 2018 and 2019, we detected additional lightning strikes using waveform data from four electric field change meters, which measured electrical pulses emitted from lightning strikes (Yanoviak *et al.*, 2017). The camera system coverage varied over time from *c.* 2.25 to 10 km^2, whereas the field change meters located strikes across 15 km^2. This study used 78 lightning strikes located in areas with relevant information about lianas and electric current transfer, including 64 strikes located with the monitoring system and an additional 14 lightning strikes located using field-based diagnostics of lightning damage (Yanoviak *et al.*, 2017).

Lightning strike field surveys

We monitored 1921 trees that exhibited conspicuous lightning damage among the 78 lightning strikes. We identified lightning damage to trees based on previous observations of verified lightning damage in this and other tropical forests (Furtado, 1935; Anderson, 1964; Yanoviak *et al.*, 2017; Gora & Yanoviak, 2020).

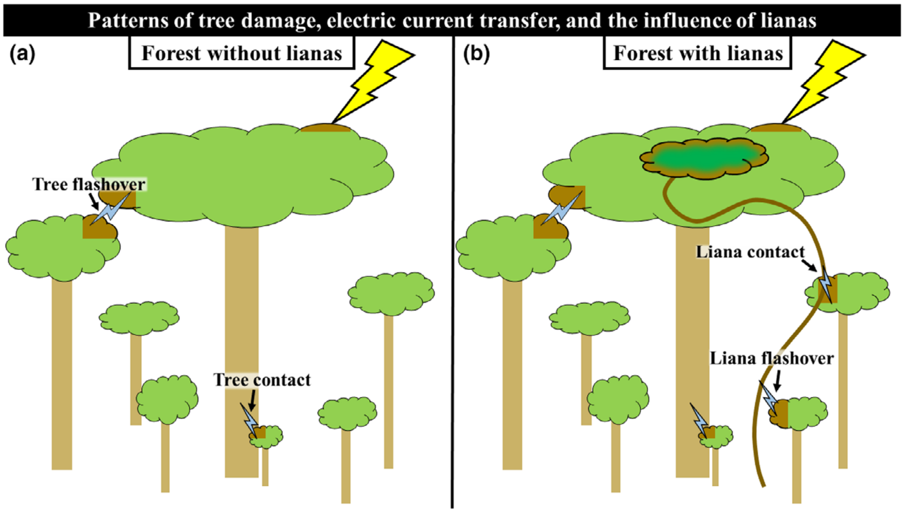

Fig. 1 Lianas facilitate electric current transfer among trees. Graphical representation of patterns of tree damage and inferred pathways of electric current transfer. The influence of lianas on patterns of tree damage is depicted by the contrast between a hypothetical forest stand without lianas (a) to a stand with lianas (b). Electric current transfer among plants is depicted as blue lightning bolts labeled with the pathway they represent.

The condition of each affected tree was first evaluated within 4 months of the lightning strike, and subsequently up to four times within 23 months of poststrike.

For trees in 65 lightning strikes, we identified the source of the electric current (hereafter *electric current source*) based on diagnostic spatial patterns of leaf necrosis presumably associated with electric current transfer (Yanoviak *et al*., 2017). Secondarily damaged trees (i.e. trees that were not directly struck) exhibited patches of short-term leaf necrosis at the location where electric current apparently entered their tissues from a neighboring tree or liana (Figs 1, S1). We identified the electric current source of the lightning damaged tree within 4 months of the lightning strike by identifying adjacent lightning-damaged trees or lianas with concurrent necrosis. This short time frame reduced the potential for patterns of apparent electric current transfer to be obscured by plant death and decomposition. We used these surveys to determine whether the electric current source for each tree was physical contact with a liana (hereafter *liana physical contact*), physical contact with a tree (hereafter *tree physical contact*), flashover from a nearby liana (hereafter *liana flashover*), or flashover from a nearby tree (hereafter *tree flashover*). We assigned a source of lightning damage to 1434 of the 1681 damaged trees among the 65 strikes; no electric current source was assigned if the damage patterns were ambiguous.

We quantified the severity and area of 78 lightning disturbances based on visual surveys of lightning-damaged trees from the ground (all metrics of disturbance were based on trees ≥ 1 cm DBH and did not include lianas). For each strike, we mapped the location of each damaged tree using a laser rangefinder and compass (1921 total trees). We recorded the status of each tree (living or dead) and measured its diameter at breast height (DBH). For trees that were damaged but not killed by the strike, we estimated percent crown dieback as the proportion of crown volume that recently died (Stolte *et al*., 2002). We estimated the biomass of each tree using an allometric equation based on tree DBH, wood density, and local environmental variability (i.e. temperature variability, precipitation variability, and drought intensity; Chave *et al*., 2014). Wood density was based on taxon-specific measurements (Condit *et al*., 2019) for the 802 trees with species-level information, and site-specific average wood density (0.54 g cm^{-3}) for the 1119 trees lacking species identifications (Muller-Landau, 2004). We estimated the disturbed area associated with each strike as a convex hull bounded by the rooting points of all lightning-damaged trees (Gora *et al*., 2021). This metric of disturbed area is directly comparable with plot-based assessments of forest dynamics, and it is not meant to represent canopy gap area. We also measured the number of trees damaged, the number of trees killed, and the proportion of damaged trees that died. We used this information to estimate total biomass turnover as the biomass of each dead tree plus the proportion of crown biomass lost from each surviving tree (i.e. crown dieback). We assumed tree crowns contain 19.3% of total tree biomass based on field measurements of tropical trees in the biomass and allometry database for woody plants (Falster *et al*., 2015; Gora *et al*., 2019). Data for the 11 strikes in 2019–2020 were from 1 to 4 months of poststrike because pandemic-related restrictions prevented further visits, whereas data for the other 66 strikes were from 10 to 23 months of poststrike (Fig. S2). We confirmed that the results did not meaningfully change with the removal of the 11 strikes monitored for < 5 months (Tables S1).

Plot data for lianas and trees

For 22 lightning strikes that occurred in the BCI 50-ha plot, we used recent censuses of lianas and trees to quantify local forest structure. We also collected current transfer data for nine of the 22 strikes. In 2007 and 2017, all rooted liana stems were located, identified, and mapped to the nearest 0.1 m (Schnitzer *et al*., 2012). We used the 2007 liana data because 15 of the 22 strikes occurred before the 2017 liana census was completed (Schnitzer *et al*., 2021); however, we confirmed that plot-wide spatial variation in liana basal area was strongly correlated between 2007 and 2017 ($r = 0.84$; Methods S1; Dutilleul *et al*., 1993). We summed the basal area of all lianas rooted within 15 m of the directly struck tree to estimate local liana density for each strike. We used basal area because it is likely a better estimate of total liana biomass, and presumably liana-based connections, than size-independent measures of liana density. We used 15 m as the threshold because, on average, 82.6% of lightning-damaged trees were within 15 m of the directly struck tree. We confirmed that the strong influence of liana basal area on per-strike tree damage and death was consistent using smaller (10 m) and larger (20 m) distance thresholds. We used the 2015 tree census data to determine whether tree density (trees ha^{-1}) and basal area (Condit *et al*., 2019) influenced the effects of lianas on lightning strike characteristics.

Statistical analyses

We evaluated how the severity and area of lightning disturbance varied with aspects of local forest structure for 22 lightning strikes in the co-located 50-ha forest plot (569 lightning-damaged trees; Table S1). We used a generalized linear model with gamma errors to explain variation in disturbed area, and generalized linear models with Poisson errors and a log-link function for counts of damaged and dead trees. To confirm that lianas increased lightning disturbance severity via their effects on small trees, we repeated the analyses of damaged trees with separate models for small (1–10 cm in DBH), medium (10–50 cm), and large (> 50 cm) trees. We used Gaussian linear models to explain variation in biomass turnover, mean DBH of lightning-damaged trees, the diameter of the directly struck tree, and the percent of damaged trees that died (R Core Team, 2019). As predictors, these models included liana basal area, tree basal area, and tree density based on plot data for lianas and trees within 15 m of the directly struck tree. We log-transformed biomass turnover to meet model assumptions, and we confirmed that the predictors did not exhibit collinearity (Pearson $R < 0.20$ and VIF < 3). We assessed the significance of each term using partial F-tests for Gaussian models and likelihood ratio tests for Poisson and Gamma models. We reran these models using liana basal area from 2017 to confirm that the results were consistent regardless of the liana census.

We used similar models to determine how patterns of electric current transfer influenced lightning disturbance severity and disturbance area ($n = 65$ strikes; Table S1). These models included the proportion of electrical connections via physical contact with lianas (*liana physical contact*), physical contact with trees (*tree physical contact*), and the proportion of noncontact electrical connections via lianas (*liana flashover*) as predictors (Fig. 1). We did not include a term for flashover among trees in the models because it is perfectly collinear with the other predictors. Specifically, the proportion of tree flashover is implicit in these models because it equals 1 minus the sum of the other three terms. The proportions of trees with each type of connection were estimated from the total number of trees with known electric current sources on a per strike basis (retaining 85.3% of 1681 possible trees). We included the same response variables, used the same model error structures, and applied the same approach to model selection as described for the analyses of local forest structure.

Using the nine strikes with both forest plot and electric current transfer data (329 lightning-damaged trees; Table S1), we used beta regression to determine whether lianas contributed more to electric current transfer where lianas were more abundant (function *betareg* in package BETAREG; Zeileis *et al.*, 2016). We included local liana basal area (i.e. basal area within 15 m of the directly struck tree) as the predictor in two models with either liana physical contact or liana flashover as the response variable. We used Wald tests to assess significance and examined residuals to confirm appropriate model fit.

We performed all analyses in the *R* statistical environment. We interpret patterns based on the magnitude of their effects, but we also refer to results with *P*-values 0.05–0.10 as marginally nonsignificant.

Results

Among all strikes with local forest structure data ($n = 22$), lightning disturbance was more severe where liana basal area was higher (Fig. 2). The number of trees damaged and killed per strike increased with increasing liana basal area within 15 m of the directly struck tree (Fig. 2a,d). More small trees (< 10 cm DBH) were damaged in forest patches with higher liana basal area, whereas larger trees (> 10 cm) exhibited no associations with forest structure, indicating that lianas primarily transferred electricity to many small trees (Tables 1, S3; Fig. S3). Local liana basal area was not associated with biomass turnover, damaged tree mortality, or total disturbed area (Table 1; Figs 2g,j, S4). The positive relationship between lianas and disturbance severity was not confounded by correlations with local tree density or basal area. Local tree density exhibited weak negative associations with the number of trees damaged and killed, and no association with damaged tree mortality or biomass turnover (Fig. 2c,f,i,l). Local tree basal area was also not associated with any disturbance metric (Table 1; Figs 2b,e,h,k, S4). Using liana basal area from 2017 instead of 2007 produced similar results; the only differences were that significant associations between tree density and the numbers of trees damaged and killed became nonsignificant (Fig. S5).

Liana-associated electrical connections were strongly positively associated with tree mortality and damage. There were strong positive relationships between the percentage of liana physical contact (Fig. 1) and the number of damaged trees per strike, the number of trees that died per strike, and the percentage of the damaged trees that died (Fig. 3a,d,g). Liana flashover and tree physical contact also had positive relationships with the number of damaged trees and the number of trees that died from the lightning event; however, these relationships were weaker than liana physical contact (Fig. 3b,c,e,f). There was no association between the percentage of damaged trees that died and either liana flashover or tree physical contact (Fig. 3h,i). Woody biomass turnover was not associated with any metric of electric current transfer, indicating the effects of physical contact and liana connections on mortality did not translate into detectably greater biomass loss (Fig. 3j,k,l). The lack of a biomass turnover response could be explained, in part, by the smaller average diameter of the additional damaged trees (Table 2). The number of small trees (< 10 cm DBH) damaged per strike increased with higher rates of liana physical contact, liana flashover, and tree physical contact. By contrast, damaged trees 10–50 cm DBH only increased with higher rates of liana physical contact, and damaged trees > 50 cm DBH did not change with any metric of electric current transfer (Table S3; Fig. S6). The diameter of the directly struck tree was not associated with any aspect of electric current transfer ($F_{3,61} = 0.37$, $P = 0.776$), indicating that the smaller average DBH of damaged trees was not related to an overall decrease local forest height. Variation in per strike disturbed area was not associated with any aspect of current transfer (Table 2; Fig. S7).

Among the strikes with both local liana and electric current transfer data ($n = 9$), lianas facilitated a higher percent of physical connections where liana basal area was higher ($\chi^2 = 3.88$, $P = 0.049$; Fig. S8) and exhibited a nonsignificant positive trend with liana flashover ($\chi^2 = 2.37$, $P = 0.124$; Fig. S8). Both patterns were weak due to small sample size.

Patterns of electric current transfer varied substantially among lightning strikes (Fig. 4). Among damaged trees assigned a source of electric current, 70.4% had tree flashover connections, 10.7% had liana flashover connections, 8.6% had liana physical contact connections, 5.8% had tree physical contact connections, and 4.5% were directly struck by lightning. Within a strike, the total contributions of lianas ranged from 0 to 87.5% of electric connections, 0 to 50% for liana physical contact, and 0 to 45.5% for liana flashover (Fig. 4).

Discussion

Our findings show that lianas increase the severity of lightning disturbance in forests, with variable effects depending on tree stature (i.e. understory vs canopy). Lianas appear to increase lightning disturbance severity by providing electrical connections to additional understory trees within the footprint of the disturbed area. Our field observations indicated that these smaller trees

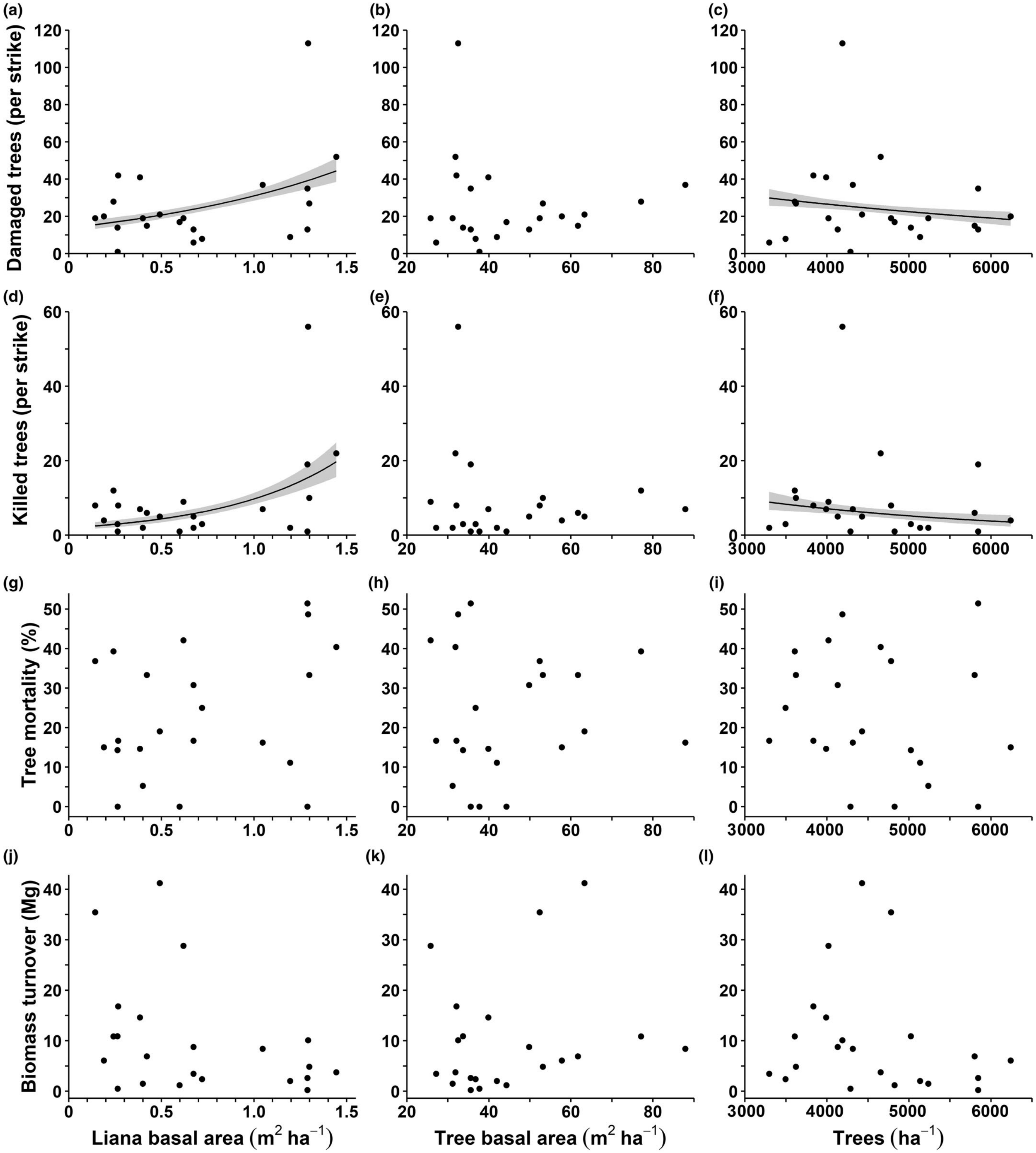

Fig. 2 Lightning damages and kills more trees where liana basal area is greater. Modeled relationships between four aspects of per strike lightning disturbance severity and each of liana basal area, tree basal area, and tree density within 15 m of the directly struck tree ($n = 22$ strikes for each plot). Tree mortality (%) is the percent of damaged trees that died. Significant relationships are represented by fitted curves (solid black lines) and shaded bands represent 95% confidence intervals calculated by holding the other predictors constant at their mean. Panels (a–f) include results of generalized linear models with Poisson errors and a log-link function. The relationships depicted in panels (g–l) were not statistically significant.

Table 1 Results of linear models explaining variation in lightning disturbance characteristics as a function of local forest structure.

Response variable	Test of significance	Fixed effect	Test statistic	*P*-value	Coefficients (SE)
Trees damaged by lightning	χ^2-test	**Liana basal area**	**67.44**	**< 0.001**	**0.807 (0.098)**
		Tree basal area	0.01	0.930	< 0.001 (0.003)
		Tree density	**10.00**	**0.002**	**−0.0002 (< 0.001)**
		Intercept	–	–	3.397 (0.277)
Trees killed by lightning	χ^2-test	**Liana basal area**	**74.67**	**< 0.001**	**1.590 (0.191)**
		Tree basal area	1.97	0.161	0.007 (0.005)
		Tree density	**10.25**	**0.001**	**−0.0003 (< 0.0001)**
		Intercept	–	–	2.437 (0.522)
Proportion of trees dead	*F* test	Liana basal area	1.92	0.183	0.113 (0.081)
		Tree basal area	0.21	0.654	< 0.001 (0.002)
		Tree density	0.60	0.450	< 0.001 (< 0.001)
		Intercept	–	–	0.257 (0.221)
Woody biomass turnover (Mg)	*F* test	Liana basal area	0.37	0.550	−0.144 (0.235)
		Tree basal area	0.01	0.940	< 0.001 (0.006)
		Tree density	0.83	0.376	< 0.001 (< 0.001)
		Intercept	–	–	1.133 (0.651)
Mean DBH (mm) of damaged trees	*F* test	**Liana basal area**	**13.55**	**0.002**	**−234.533 (63.706)**
		Tree basal area	0.46	0.507	−1.148 (1.696)
		Tree density	0.03	0.870	−0.005 (0.033)
		Intercept	–	–	580.763 (173.488)
Disturbed area (ha)	χ^2-test	Liana basal area	0.37	0.550	−143.570 (235.362)
		Tree basal area	0.01	0.940	0.479 (6.267)
		Tree density	0.83	0.376	−0.110 (0.121)
		Intercept	–	–	1133.325 (640.952)

Fixed effects were tested individually using partial-*F* tests (linear models) or χ^2-tests (generalized linear models). Significant predictors are highlighted in bold. Numerator and denominator degrees of freedom were 1 and 18, respectively, for all test statistics. Woody biomass turnover was log-transformed.

were damaged and killed more frequently in sites with high liana basal area and liana-associated electrical connections (Fig. 1). These patterns show that lianas and lightning, two understudied phenomena that are sensitive to global change, interact to amplify their contributions to increased forest turnover.

The positive effects of lianas on per strike lightning severity does not indicate that lianas cause more damage to all individual trees. Indeed, the ability of lianas to conduct electric current, as captured in this study, is consistent with prior work suggesting that lianas could protect some trees by diverting electric current to their neighbors (Yanoviak, 2013; Gora *et al*., 2017). Additional work at the scale of individual trees is needed to determine how lianas influence the distribution of electricity and damage among trees within a lightning disturbance.

The interaction between lianas and lightning has implications for the geographical distribution of lightning disturbance severity. Liana density is higher in seasonal tropical forests (Schnitzer, 2005; Van Der Heijden & Phillips, 2008; DeWalt *et al*., 2015) and in young tropical forests (Dewalt *et al*., 2000; Letcher & Chazdon, 2009; Barry *et al*., 2015). Accordingly, the average severity of lightning disturbance, in terms of the number of trees damaged and killed, is likely higher in younger and more strongly seasonal forests (Schnitzer, 2005; Parolari *et al*., 2020). The contributions of this interaction to spatial patterns of forest

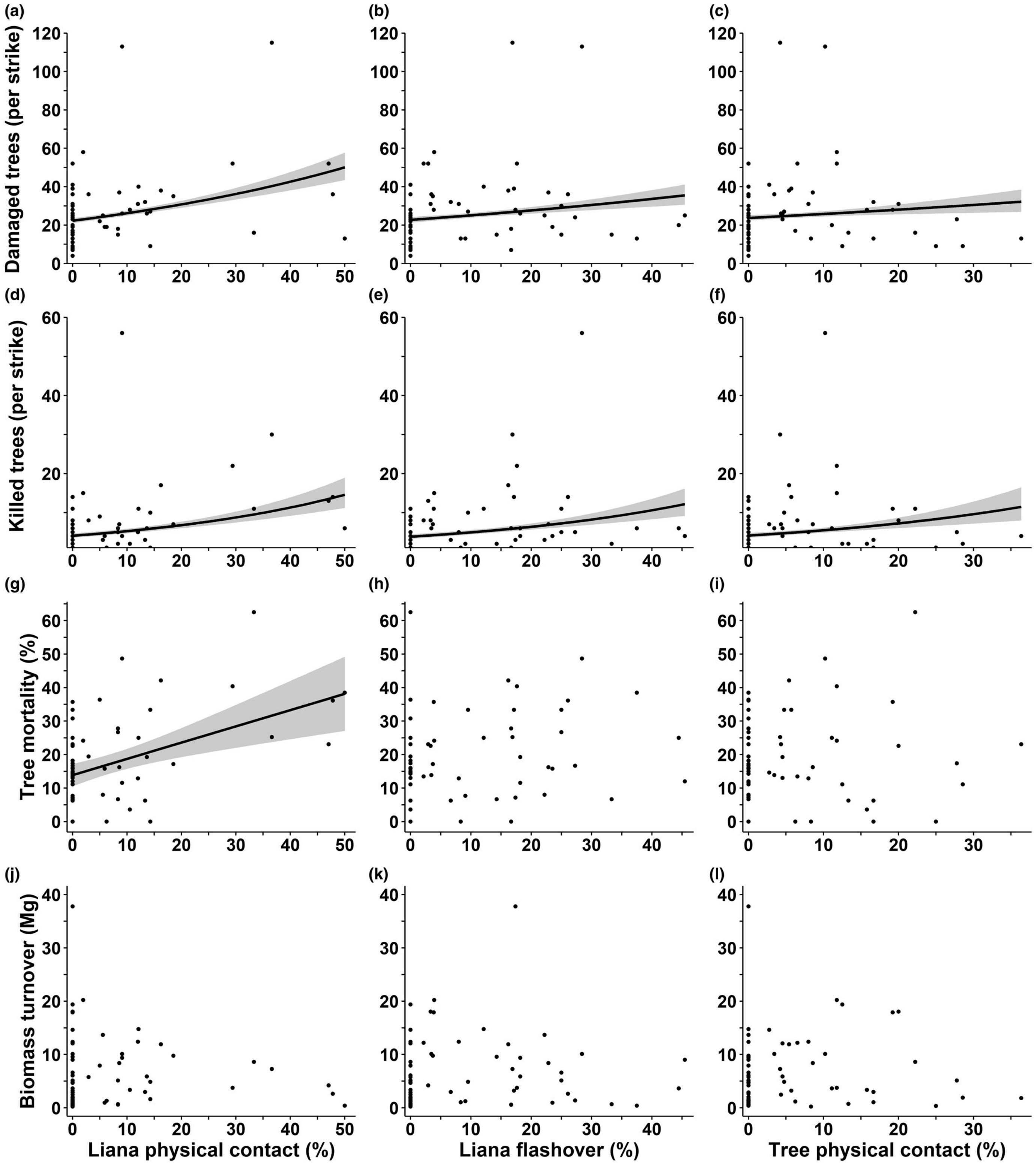

Fig. 3 Patterns of electric current transfer determine lightning disturbance severity. Modeled relationships between four aspects of per strike lightning disturbance severity and three pathways of electric current transfer: liana physical contact, liana flashover, and tree physical contact ($n = 65$ strikes for each plot; Table 1). The predictors are the percent of trees that experienced the respective mode of current transfer among all trees with recorded current sources within a strike. Tree mortality (%) is the percent of damaged trees that died. Significant relationships are represented by fitted curves (solid black lines) and shaded bands represent 95% confidence intervals calculated by holding the other predictors constant at their mean. Panels (a–f) include results of generalized linear models with Poisson errors and a log-link function. Panels (g–l) include results of Gaussian linear models.

Table 2 Results of linear models explaining variation in lightning disturbance characteristics as a function of electric current transfer.

Response variable	Test of significance	Fixed effect	Test statistic	P-value	Coefficients (SE)
Trees damaged by lightning	χ^2-test	**Liana contact**	**83.78**	**< 0.001**	**1.620 (0.168)**
		Liana flashover	**21.90**	**< 0.001**	**0.980 (0.205)**
		Tree contact	**7.79**	**< 0.001**	**0.838 (0.296)**
		Intercept	–	–	2.964 (0.042)
Trees killed by lightning	χ^2-test	**Liana contact**	**56.24**	**< 0.001**	**2.545 (0.319)**
		Liana flashover	**34.53**	**< 0.001**	**2.539 (0.414)**
		Tree contact	**18.81**	**< 0.001**	**2.807 (0.622)**
		Intercept	–	–	1.008 (0.101)
Proportion of trees dead	F test	**Liana contact**	**14.71**	**< 0.001**	**0.485 (0.127)**
		Liana flashover	*3.06*	*0.085*	*0.229 (0.131)*
		Tree contact	*3.22*	*0.078*	*0.316 (0.176)*
		Intercept	–	–	0.099 (0.023)
Woody biomass turnover (Mg)	F test	Liana contact	< 0.01	0.950	0.084 (1.330)
		Liana flashover	0.20	0.657	0.613 (1.372)
		Tree contact	0.20	0.657	0.828 (1.853)
		Intercept	–	–	1.135 (0.243)
Mean DBH (mm) of damaged trees	F test	**Liana contact**	**9.48**	**0.003**	**−296.56 (96.29)**
		Liana flashover	**9.00**	**0.004**	**−298.22 (99.38)**
		Tree contact	*3.66*	*0.061*	*−256.64 (134.19)*
		Intercept	–	–	352.35 (17.63)
Disturbed area (ha)	χ^2-test	Liana contact	0.74	0.391	−0.002 (0.002)
		Liana flashover	0.10	0.747	0.001 (0.002)
		Tree contact	0.33	0.568	0.002 (0.003)
		Intercept	–	–	0.002 (< 0.001)

Fixed effects were tested individually using partial F-tests (linear models) or χ^2-tests (generalized linear models). Numerator and denominator degrees of freedom were 1 and 61, respectively, for all test statistics. Woody biomass turnover was log-transformed. Significant predictors are highlighted in bold and a marginally significant result is italicized.

biomass dynamics are less certain; we did not detect an effect of lianas on lightning-killed biomass. It is possible that either lianas do not increase biomass loss or that the additional biomass mortality of a few small trees was not detectable with our sample size because biomass mortality is dominated by a few large trees (Meakem *et al.*, 2018; Gora *et al.*, 2021; Piponiot *et al.*, 2022). Further investigation is needed to test these potential patterns because they could be complicated by other factors, such as variation in lightning strike intensity or tree tolerance to lightning (Richards *et al.*, 2022).

Lianas, lightning strikes, and the interactions between them likely contribute to increases in tree mortality (Brienen *et al.*, 2015; Hartmann *et al.*, 2022). Liana stem densities are increasing in many neotropical forests (Schnitzer & Bongers, 2011; Schnitzer *et al.*, 2021), and lightning strike frequencies are increasing in some tropical regions (Harel & Price, 2020). Individually, each of these factors could increase rates of tree mortality (Ingwell *et al.*, 2010; Visser *et al.*, 2018; Yanoviak *et al.*, 2020). However, given that lianas appear to amplify the damaging effects of lightning, it is possible that these factors are interacting to increase tree mortality rates (McDowell *et al.*, 2018). Given that this interaction specifically increases small tree deaths, increases in lianas and lightning could change forest size structure and composition. Studies of tree damage and mortality linked to

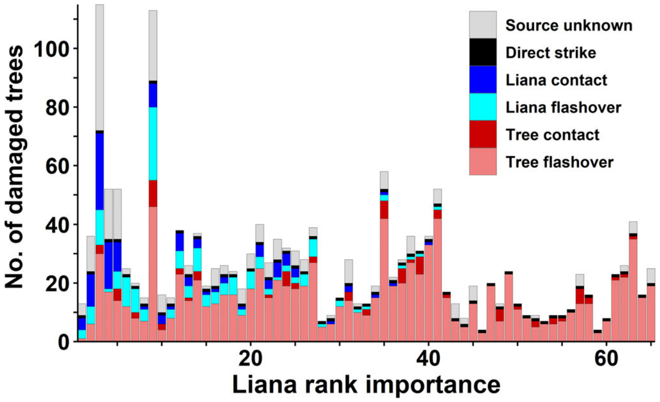

Fig. 4 Stacked bar plots depicting the number of trees within each strike among possible sources of electric current. Each bar represents an individual strike, ordered along the *x*-axis in decreasing proportional contributions of lianas to total current transfer within each strike.

lightning across gradients of lightning frequency and liana density are needed to test this potential effect.

It is also possible that lightning–liana interactions produce a positive feedback loop. Lianas benefit from disturbances because of their ability to proliferate in the high-light environments of forest gaps (Rocha *et al.*, 2020; Schnitzer *et al.*, 2021). The results of this study show that more trees die within a given disturbance footprint when lianas are present, presumably increasing light penetration to the forest floor. If lianas proliferate faster in these more severely disturbed sites, then the lightning disturbances exacerbated by lianas could become hotspots for liana regeneration. Higher liana densities could complete this feedback loop by increasing the severity of future lightning strikes to this site or to adjacent patches of forest. This positive feedback loop could have major implications for the dynamics of liana–tree competition and forest carbon budgets. However, detailed measurements of repeated lightning strikes to the same patch of forest are needed to evaluate this feedback loop and its contributions to increasing liana densities.

This study provides a robust test of the relationship between lianas and lightning disturbance characteristics. Although it is impossible to directly document electric current transfer with existing technology, the consistent trends among disturbance severity, liana basal area, and inferred contributions to electric current transfer provide strong evidence that lianas amplify lightning disturbance severity by facilitating electric current transfer. This study captured variation among late-secondary and old-growth forests, and further investigations across a broader range of forest types are needed to understand the full effects of forest structure on lightning strike characteristics (e.g. the unexpected relationship in Fig. 2c). Quantifying these and related processes will be key to understanding and predicting lightning disturbance regimes on a changing planet.

Acknowledgements

Oris Acevedo, Melissa Cano, and the staff of the Smithsonian Tropical Research Institute provided for logistical support. Benjamin Adams, Roberta Ethington, Noah Gripshover, Riley Kneale, and Alyssa Stark assisted in the field. Comments from Jane Lucas and Benjamin Adams improved the manuscript. This work was supported by grants from the National Science Foundation (DEB-1354060, DEB-1655346, and DEB-2213246 to SPY; DEB-1354510, DEB-1655554, and DEB- 2213247 to PMB; and DEB- 2213245 and GRF-2015188266 to EMG), the National Geographic Society (9703-15 to EMG), and the Smithsonian Tropical Research Institute (Earl S. Tupper Postdoctoral Fellowship to EMG). National Science Foundation grants DEB-0613666 and IOS-1558093 to SAS supported the liana data collection on the BCI 50-ha plot.

Competing interests

None declared.

Author contributions

EMG conceived study, analyzed the data, and led the writing of the manuscript. EMG, JCB, CG and SPY collected data in the field. PMB and JCB designed and established the lightning location system. SPY coordinated the operation of the lightning location system. SAS designed and managed the collection of all liana census data. EMG, SAS, PMB, JCB, CG and SPY contributed to conceptual development and writing.

ORCID

Phillip M. Bitzer https://orcid.org/0000-0002-6665-9778
Jeffrey C. Burchfield https://orcid.org/0000-0003-2858-053X
Evan M. Gora https://orcid.org/0000-0002-0537-5835
Stefan A. Schnitzer https://orcid.org/0000-0002-2715-9455
Stephen P. Yanoviak https://orcid.org/0000-0001-6425-1413

Data availability

Data are publicly available on the Cary Institute of Ecosystem Studies Figshare (doi: 10.25390/caryinstitute.22184062).

References

Adams BJ, Schnitzer SA, Yanoviak SP. 2019. Connectivity explains local ant community structure in a neotropical forest canopy: a large-scale experimental approach. *Ecology* **100**: e02673.

Anderson JAR. 1964. Observations on climatic damage in peat swamp forest in Sarawak. *Commonwealth Forestry Review* **43**: 145–158.

Barry KE, Schnitzer SA, van Breugel M, Hall JS. 2015. Rapid liana colonization along a secondary forest chronosequence. *Biotropica* **47**: 672–680.

Bauman D, Fortunel C, Delhaye G, Malhi Y, Cernusak LA, Bentley LP, Rifai SW, Aguirre-Gutiérrez J, Menor IO, Phillips OL *et al.* 2022. Tropical tree mortality has increased with rising atmospheric water stress. *Nature* **608**: 528–533.

Brienen RJW, Phillips OL, Feldpausch TR, Gloor E, Baker TR, Lloyd J, Lopez-Gonzalez G, Monteagudo-Mendoza A, Malhi Y, Lewis SL *et al.* 2015. Long-term decline of the Amazon carbon sink. *Nature* **519**: 344–348.

Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman RC *et al.* 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* **20**: 3177–3190.

Condit R, Pérez R, Aguilar S, Lao S, Foster RB, Hubbell SP. 2019. Complete data from the Barro Colorado 50-ha plot: 423617 trees, 35 years. *Dryad*. doi: 10.15146/5xcp-0d46.

Croat TB. 1978. *Flora of Barro Colorado Island*. Redwood City, CA, USA: Stanford University Press.

DeWalt SJ, Schnitzer SA, Alves LF, Bongers F, Burnham RJ, Cai Z, Carson WP, Chave J, Chuyong GB, Costa FRC *et al.* 2015. Ecology of lianas. In: Schnitzer Stefan A, Bongers F, Burnham KD, Putz FE, eds. *Biogeographical patterns of liana abundance and diversity*. Oxford, UK: Wiley-Blackwell.

Dewalt SJ, Schnitzer SA, Denslow JS. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology* **16**: 1–19.

Dutilleul P, Clifford P, Richardson S, Hemon D. 1993. Modifying the *t* test for assessing the correlation between two spatial processes. *Biometrics* **49**: 305–314.

Falster DS, Duursma RA, Baltzer JL, Baraloto C, Battaglia M, Battles JJ, Bond-Lamberty B, van Breugel M, Camac J, Claveau Y. 2015. BAAD: a biomass and allometry database for woody plants. *Ecology* **96**: 1445.

Furtado CX. 1935. Lightning injuries to trees. *Journal of the Malaysian Branch of the Royal Asiatic Society* **13**: 157–162.

Gora EM, Bitzer PM, Burchfield JC, Gutierrez C, Yanoviak SP. 2021. The contributions of lightning to biomass turnover, gap formation and plant mortality in a tropical forest. *Ecology* **102**: e03541.

Gora EM, Bitzer PM, Burchfield JC, Schnitzer SA, Yanoviak SP. 2017. Effects of lightning on trees: a predictive model based on *in situ* electrical resistivity. *Ecology and Evolution* **7**: 8523–8534.

Gora EM, Burchfield JC, Muller-Landau HC, Bitzer PM, Yanoviak SP. 2020. Pantropical geography of lightning-caused disturbance and its implications for tropical forests. *Global Change Biology* **26**: 5017–5026.

Gora EM, Kneale RC, Larjavaara M, Muller-Landau HC. 2019. Dead wood necromass in a moist tropical forest: stocks, fluxes, and spatiotemporal variability. *Ecosystems* **22**: 1189–1205.

Gora EM, Yanoviak SP. 2020. Lightning-caused disturbance in the Peruvian Amazon. *Biotropica* **52**: 813–817.

Harel M, Price C. 2020. Thunderstorm trends over Africa. *Journal of Climate* **33**: 2741–2755.

Hartmann H, Bastos A, Das AJ, Esquivel-Muelbert A, Hammond WM, Martínez-Vilalta J, McDowell NG, Powers JS, Pugh TAM, Ruthrof KX *et al.* 2022. Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. *Annual Review of Plant Biology* **73**: 673–702.

Ingwell LL, Wright SJ, Becklund KK, Hubbell SP, Schnitzer SA. 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology* **98**: 879–887.

Leigh EG Jr. 1999. *Tropical forest ecology: a view from Barro Colorado Island*. Oxford, UK: Oxford University Press.

Letcher SG, Chazdon RL. 2009. Lianas and self-supporting plants during tropical forest succession. *Forest Ecology and Management* **257**: 2150–2156.

Magnusson WE, Lima AP, de Lima O. 1996. Group lightning mortality of trees in a Neotropical forest. *Journal of Tropical Ecology* **12**: 899–903.

McDowell N, Allen CD, Anderson-Teixeira K, Brando P, Brienen R, Chambers J, Christoffersen B, Davies S, Doughty C, Duque A *et al.* 2018. Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytologist* **219**: 851–869.

Meakem V, Tepley AJ, Gonzalez-Akre EB, Herrmann V, Muller-Landau HC, Wright SJ, Hubbell SP, Condit R, Anderson-Teixeira KJ. 2018. Role of tree size in moist tropical forest carbon cycling and water deficit responses. *New Phytologist* **219**: 947–958.

Muller-Landau HC. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* **36**: 20–32.

Parolari AJ, Paul K, Griffing A, Condit R, Perez R, Aguilar S, Schnitzer SA. 2020. Liana abundance and diversity increase with rainfall seasonality along a precipitation gradient in Panama. *Ecography* **43**: 25–33.

Paton S. 2017. *Report of the Physical Monitoring Program of the Smithsonian Tropical Research Institute*. [WWW document] URL http://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado [accessed 1 June 2019].

Piponiot C, Anderson-Teixeira KJ, Davies SJ, Allen D, Bourg NA, Burslem DFRP, Cárdenas D, Chang-Yang CH, Chuyong G, Cordell S *et al.* 2022. Distribution of biomass dynamics in relation to tree size in forests across the world. *New Phytologist* **234**: 1664–1677.

Putz FE, Parker GG, Archibald RM. 1984. Mechanical abrasion and intercrown spacing. *American Midland Naturalist* **112**: 24–28.

Qie L, Lewis SL, Sullivan MJP, Lopez-Gonzalez G, Pickavance GC, Sunderland T, Ashton P, Hubau W, Abu Salim K, Aiba S-I *et al.* 2017. Long-term carbon sink in Borneo's forests halted by drought and vulnerable to edge effects. *Nature Communications* **8**: 1966.

R Core Team. 2019. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Richards JH, Gora EM, Gutierrez C, Burchfield JC, Bitzer PM, Yanoviak SP. 2022. Tropical tree species differ in damage and mortality from lightning. *Nature Plants* **8**: 1007–1013.

Rocha EX, Schietti J, Gerolamo CS, Burnham RJ, Nogueira A. 2020. Higher rates of liana regeneration after canopy fall drives species abundance patterns in central Amazonia. *Journal of Ecology* **108**: 1311–1321.

Schnitzer SA. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *The American Naturalist* **166**: 262–276.

Schnitzer SA, Bongers F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* **14**: 397–406.

Schnitzer SA, DeFilippis DM, Visser M, Estrada-Villegas S, Rivera-Camaña R, Bernal B, Peréz S, Valdéz A, Valdéz S, Aguilar A *et al.* 2021. Local canopy disturbance as an explanation for long-term increases in liana abundance. *Ecology Letters* **24**: 2635–3647.

Schnitzer SA, Mangan SA, Dalling JW, Baldeck CA, Hubbell SP, Ledo A, Muller-Landau H, Tobin MF, Aguilar S, Brassfield D *et al.* 2012. Liana abundance, diversity, and distribution on Barro Colorado Island, Panama. *PLoS ONE* **7**: e52114.

Sousa WP, Quek SP, Mitchell BJ. 2003. Regeneration of Rhizophora mangle in a Caribbean mangrove forest: interacting effects of canopy disturbance and a stem-boring beetle. *Oecologia* **137**: 436–445.

Stolte K, Barbara C, Campbell S, Gillespie A. 2002. *Forest health indicators: forestry inventory and analysis program*. Research Triangle Park, NC, USA: USDA Forest Service, Southern Research Station.

Uman MA. 2008. *The art and science of lightning protection*. Cambridge, UK: Cambridge University Press.

Van Der Heijden GMF, Phillips OL. 2008. What controls liana success in neotropical forests? *Global Ecology and Biogeography* **17**: 372–383.

Visser MD, Muller-Landau HC, Schnitzer SA, de Kroon H, Jongejans E, Wright SJ. 2018. A host–parasite model explains variation in liana infestation among co-occurring tree species. *Journal of Ecology* **106**: 2435–2445.

Yanoviak SP. 2013. Shock value: are lianas natural lightning rods? In: Lowman M, Devy S, Ganesh T, eds. *Treetops at risk: challenges of global forest canopies*. New York, NY, USA: Springer, 147–154.

Yanoviak SP, Gora EM, Bitzer PM, Burchfield JC, Muller-Landau HC, Detto M, Paton S, Hubbell SP. 2020. Lightning is a major cause of large tropical tree mortality in a lowland neotropical forest. *New Phytologist* **225**: 1936–1944.

Yanoviak SP, Gora EM, Burchfield JM, Bitzer PM, Detto M. 2017. Quantification and identification of lightning damage in tropical forests. *Ecology and Evolution* **7**: 5111–5122.

Zeileis A, Cribari-Neto F, Gruen B, Kosmidis I, Simas AB, Rocha AV, Zeileis MA. 2016. Package 'BETAREG'. R Package 3(5). [WWW document] URL https://cran.r-project.org/web/packages/betareg/index.html [accessed 15 July 2021].

Supporting Information

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

Fig. S1 Photographic examples of electric current transfer pathways.

Fig. S2 Distribution of lightning strike surveys over time post-strike.

Fig. S3 Scatterplots of associations between the number of small trees (< 10 cm DBH) or mean tree DBH vs forest structure.

Fig. S4 Scatterplots of the area disturbed by each strike as a function of forest structure.

Fig. S5 Scatterplots comparable to Fig. 2, except using liana census data from 2017.

Fig. S6 Scatterplots of associations between the number of small trees (< 10 cm DBH) or mean tree DBH vs electric current transfer.

Fig. S7 Scatterplots of the area disturbed by each strike as a function of electric current transfer.

Fig. S8 Relationships between liana basal area and patterns of electric current transfer.

Methods S1 Supplemental materials and methods.

Table S1 Distribution of lightning-caused disturbances among analyses.

Table S2 Results for models explaining the effects of electric current transfer on variation in lightning-caused disturbances using a reduced dataset.

Table S3 Results for models explaining variation in lightning-caused disturbance for trees of different sizes.