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Research

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Lightning Damage Facilitates Beetle Colonization of Tropical Trees

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Abstract

Lightning is a common agent of disturbance in many forest ecosystems. Lightning-damaged trees are a potentially important resource for beetles, but most evidence for this association is limited to temperate pine forests. Here, we evaluated the relationship between lightning damage and beetle colonization of tropical trees. We recorded the number of beetle holes on the trunks of trees from 10 strike sites (n = 173 lightning-damaged trees) and 10 matching control sites (n = 137 control trees) in Panama. The trunks of lightning-struck trees had 370% more beetle holes than control trees. The abundance of beetle holes increased with increasing total crown dieback among both control and lightning-damaged trees, and with larger tree diameter among lightning-struck trees. Beetle holes also were more abundant in trunk sections of lightning-damaged trees located directly below a damaged section of the crown. The results of this study suggest that lightning damage facilitates beetle colonization in tropical forest trees and provide a basis for investigations of the effects of lightning-caused disturbance on beetle population dynamics and assemblage structure.

Key words: abundance, Coleoptera, disturbance, Panama, tropical forest

The temporal and spatial distribution of disturbance affects community structure and ecosystem processes (Pickett et al. 1989). Lightning strikes are important agents of natural disturbance in many forest environments (Yanoviak et al. 2015), and the damaging effects of lightning on trees are especially well-documented in temperate forests (Komarek 1964, Taylor 1974). Lightning strikes in temperate forests affect animal communities by igniting fires or providing habitat and food resources for many vertebrate and invertebrate species (e.g., Baker 1973), especially bark beetles and wood-boring beetles (Coulson et al. 1983, Outcalt 2008). However, the effects of lightning damage on animal population and community dynamics in other forests is unknown.

Lightning is an important source of tree damage and death in tropical forests (Anderson 1964), and is a major cause of mortality specifically for the largest trees (>60 cm diameter) in central Panama (Yanoviak et al. 2020). Observations from Asian, Central American, and Amazonian forests indicate that lightning strikes typically damage groups of trees, including individuals up to 45 m from the directly-struck tree (Magnusson et al. 1996; Yanoviak et al. 2017, 2020). Within these disturbances, the severity of lightning damage generally decreases with distance from the strike point, and most lightning-killed trees are clustered near the center of the disturbed area (Anderson 1964). Although many trees near the perimeter of tropical lightning strike sites survive, their crowns often have extensive damage, which facilitates infestation by insects and pathogens (Anderson 1964, Komarek 1964, Anderson and Anderson 1968, Coulson et al. 1983). Whereas beetle colonization of lightning-struck pine trees initially tends to be concentrated near damaged bark sections (Anderson and Anderson 1968), similarly conspicuous external damage is rare in tropical trees (Yanoviak et al. 2017). Thus, the distribution of electrical damage within a tree (whether systemic or localized to certain sectors of the trunk) and its relationship to beetle colonization is unknown.

Observations during surveys of lightning strike sites in Panama (Yanoviak et al. 2017, 2020) suggested that lightning-damaged trees are important resources for wood-boring and bark beetles in tropical forests. However, to date, most evidence of associations between lightning damage and the abundance or distribution of beetles is from temperate coniferous forests of the southeastern and western United States (e.g., Johnson 1966; Anderson and Anderson 1968; Coulson et al. 1983, 1986, 1999; Lovelady et al. 1991). In these forests, wounds to pine trees caused by lightning are attacked by large numbers of bark beetles and result in greater beetle production relative to other types of damage (Johnson 1966, Hodges and Pickard 1971). There is some evidence that pine tree defenses are compromised by lightning damage (i.e., reduced resin flow rate; Anderson and Anderson 1968, Hodges and Pickard 1971); regardless of the mechanism, beetle infestations of lightning-caused wounds commonly kill the host tree (e.g., Chapman 1923, Komarek 1964, Baker 1973, Taylor 1974, Outcalt 2008). In contrast, knowledge of lightning-beetle associations in the tropics is limited to anecdotal observations (e.g., Sharples 1933) and one study of beetle damage to mangrove seedlings in presumed lightning-caused gaps (Sousa et al. 2003).

Regardless of latitude, disturbances such as lightning influence the structure of forest insect and decomposer communities via the production of dead wood (Stokland et al. 2012, Ulyshen 2016). Clusters of dead trees created by lightning strikes (whether directly or via secondary beetle infestation) constitute major contributions to the resource pool for saproxylic insects (Grove 2002, Jacobs et al. 2007). The amount and diversity of dead wood, and its spatial and temporal distribution are important determinants of the structure of saproxylic beetle assemblages in particular (e.g., Schiegg 2000, Gossner et al. 2013, Seibold et al. 2016). Thus, it is likely that the frequency and distribution of lightning-caused disturbance plays a key role in beetle population dynamics and the maintenance of beetle diversity in tropical forests.

The main goal of this study was to determine whether beetle colonization of tree trunks is associated with lightning damage in a lowland forest of Panama. We hypothesized that trees damaged by lightning are attractive to wood-boring and bark beetles. Specifically, we predicted that trees killed or damaged by lightning have higher quantities of beetle damage, measured as abundance of beetle holes in their trunks, compared with trees in patches of forest lacking recent lightning damage. Secondarily, given the assumption that electric current travels directly down the trunk through the vascular tissue, we predicted that beetle damage is biased toward sections of tree trunks directly beneath lightning-damaged portions of the crown.

Materials and Methods

Study Site

Field work was conducted on Barro Colorado Island (BCI) in central Panama. BCI is a seasonally moist lowland forest that receives ca. 2,500 mm average annual precipitation and an average of 12.7 cloud-to-ground lightning flashes km^{-2} yr^{-1}, concentrated in the wet season between May and December (Leigh et al. 1996, Yanoviak et al. 2020).

Location of Lightning-Damaged Trees

This project focused on recent lightning strikes located in the BCI forest using a camera-based monitoring system (Yanoviak et al. 2017). Briefly, this system uses video surveillance cameras to locate lightning strike sites via triangulation. Strike sites were surveyed for up to 14 mo post-strike between May 2018 and July 2019. Each survey focused on identification and measurement of the directly struck tree and all neighboring trees damaged by the strike (Yanoviak et al. 2017). Lightning damage was visible as crown dieback (i.e., branches that recently defoliated), and we recorded lightning damage severity as the percent of a tree crown that exhibited dieback. Explosive damage or fires caused by lightning were never observed in this study. We matched each strike site with a control site that lacked recent history of lightning damage. Control sites were centered around a focal tree of the same species and approximately the same trunk diameter as the focal tree in the corresponding strike site. We selected control sites such that their diameter distribution was similar to that of a corresponding strike site (Supp Fig. 1 [online only]).

Beetle Damage Surveys

We surveyed beetle damage in trees of 10 strike sites and 10 corresponding control sites during June and July of 2019. We only surveyed trees >10 cm in diameter at breast height (DBH), as in a similar study (Crook et al. 2004). For each tree, we also recorded the distance from the central tree, percent crown dieback (the percent of the crown that had recently defoliated), and tree size (DBH). We surveyed between 6 and 39 trees (average = 16) at each site. Similar to the method used by Anderson and Anderson (1968), we divided the trunk into eight 45° sections based on the cardinal directions (N, NE, E, etc.). Following the methods of Fierke et al. (2005), we counted all holes >0.5 mm in diameter in the trunk between 0.8 m and 1.8 m above the ground (Supp Fig. 2 [online only]). We used metal forceps to clear mosses or lichens that obscured holes in the bark (Crook et al. 2004). To test whether beetle holes were more abundant in trunk sections that likely conducted electric current, we also recorded the presence of lightning damage in the crown section directly overhead of each trunk section by projecting the eight trunk sections vertically (Fig. 1; Furtado 1935, Magnusson et al. 1996, Yanoviak et al. 2017).

Statistical Analysis

We used a generalized linear mixed-effects model with Poisson errors to determine how the abundance of beetle holes varied with tree characteristics and location (R package *lme4*; Bates et al. 2014). We included disturbance status (control or strike), tree size, percent crown dieback, distance from the central tree, and the pairwise interactions between disturbance status and the three continuous predictors as fixed effects. A unique identifier for each pair of sites was included as a random effect. We logit-transformed crown dieback and z-transformed both tree DBH and distance from the central tree to meet model assumptions and facilitate model convergence. We

Fig. 1. A lightning strike site viewed from above (A) and from the ground (B). Most of the trees near the center of the site are dead, and crown damage (% dieback) decreases conspicuously from the center to the perimeter.

used Pearson correlation to test for collinearity among continuous predictors in the model.

We also used a generalized linear mixed-effects model with Poisson errors to test whether the number of beetle holes was greater in trunk sections directly below damaged portions of the crown, while accounting for variation among trees and the total amount of damage they experienced. The model only included lightning-struck trees with both damaged and undamaged sections of their crowns (*n* = 76 trees); total crown dieback and the status of the above crown section (damaged or undamaged) were fixed effects, and unique tree identity was a random effect. We compared models based on AIC and report changes in AIC values with inclusion of each fixed effect. We confirmed that the size (DBH) of struck and control trees fit the same probability distribution using a two-sample Kolmogorov–Smirnov test (package *stats*). All analyses were conducted in the R statistical environment (version 3.5.2; R Core Team 2018).

Results

We surveyed 173 trees at the 10 strike sites and 137 trees at the 10 control sites. Trees in lightning strike sites had ca. 370% more beetle holes (mean ± SE: 140.45 ± 6.58) than trees in the corresponding control sites (30.00 ± 2.31; intercept ΔAIC = −1607.8; Figs. 2–4; Supp Table 1 [online only]). The number of beetle holes in lightning-struck trees increased with greater crown dieback and increasing tree size (DBH), but these predictors had relatively weaker positive associations with beetle hole counts in control sites (dieback: interaction ΔAIC = −2.2; DBH: interaction ΔAIC = −76.0; Figs. 2 and 3; Supp Table 1 [online only]). In contrast, the number of beetle holes per trunk decreased with distance from the central tree at control sites, but was relatively unchanged with distance at strike sites (interaction ΔAIC = −43.6; Fig. 4). Multicollinearity was not problematic; distance was weakly correlated with tree size ($r = 0.14$, $P = 0.012$) and crown dieback ($r = -0.23$, $P < 0.001$), but dieback was not correlated with tree size ($P = 0.34$). The average number of beetle holes also differed among sites (ΔAIC = −1176.2).

The distribution of tree DBH was similar between control and struck trees ($D = 0.09$, $P = 0.52$; Supp Fig. 1 [online only]), but the focal trees in control sites tended to be larger than most of the surrounding trees (Supp Fig. 3 [online only]). We reanalyzed only the control data with a general linear model (Supp Fig. 3 [online only]) to determine whether those large trees caused the decline in beetle hole abundance with increasing distance in control sites (Fig. 4). Excluding the focal trees from the analysis eliminated the significant relationship (ΔAIC = 1.5).

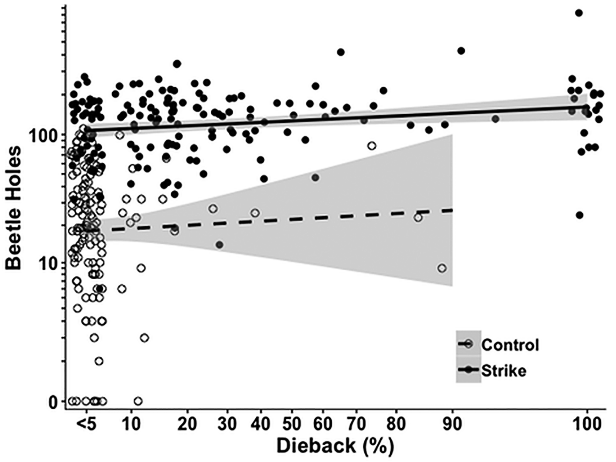

Fig. 2. The abundance of beetle holes per tree in lightning strike sites versus control sites as a function of percent dieback. Shading illustrates the 95% confidence interval.

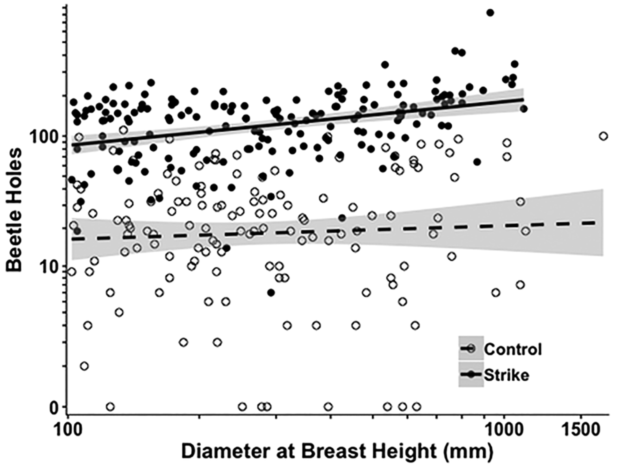

Fig. 3. The abundance of beetle holes per tree in lightning strike sites versus control sites as a function of tree size (DBH). Shading illustrates the 95% confidence interval.

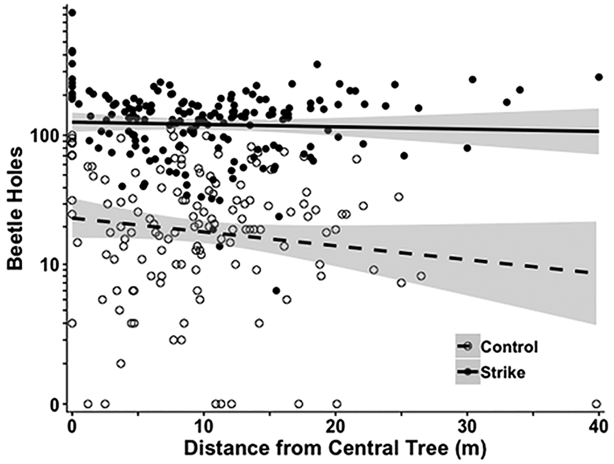

Fig. 4. The abundance of beetle holes per tree in lightning strike sites versus control sites as a function of distance from the central tree (m) in each site. Shading illustrates the 95% confidence interval.

Finally, more beetle holes occurred in trunk sections directly below lightning damaged (mean ± SE: 18.34 ± 0.55) versus undamaged (16.39 ± 0.42) sections of tree crowns (ΔAIC = −53.7; Supp Table 2 [online only]). The total amount of dieback in a crown did not meaningfully influence this pattern (ΔAIC = −1.5).

Although we do not know which taxa created the holes observed in this study, adult wood-boring beetles occasionally were seen on focal tree trunks (Supp Fig. 2 [online only]). Flight intercept traps (8-funnel Lindgren traps with 95% ethanol as a killing agent) placed in selected control and strike sites for a separate, ongoing study were dominated by Curculionidae: Scolytinae (51.7% of total catch) and Platypodinae (14.2%) in strike sites. In contrast, Ptilodactylidae (21.9%) and Curculionidae: Curculioninae (12.5%) were relatively most abundant in trap collections from control sites.

Discussion

Here we show that lightning-damaged tropical forest trees have more beetle damage than similar trees with no known recent history of lightning damage. We further show that the number of beetle holes found on trees within lightning strike sites increases with tree size and the severity of lightning damage. Collectively, these outcomes suggest that lightning-damaged trees are a key resource for beetles in this tropical forest, as observed in temperate forests (e.g., Coulson et al. 1983). The consistently high beetle hole counts, even among trees with minimal lightning damage, also suggest that either all types of lightning damage are attractive to beetles, or that lightning damage facilitates collateral (i.e., contagious) beetle damage. However, fully evaluating these possibilities, and the possibilities of host specificity or interspecific differences (among trees and beetles), will require collecting more information than was feasible in this short-term study.

Here, we focused on beetle damage in trees occurring relatively recently following a lightning strike. However, a succession of saproxylic species will continue to colonize wood for years after a tree dies (Hammond et al. 2001, Stokland et al. 2012), and any given tree can produce multiple generations of multiple beetle species. Given the relatively high frequency of lightning in tropical latitudes (Cecil et al. 2014), and the propensity for these strikes to cause group tree mortality (Anderson 1964, Magnusson et al. 1996, Yanoviak et al. 2020), lightning is a reliable source of dead wood resources for saproxylic taxa. Moreover, because most lightning-killed trees die standing (Anderson 1964, Yanoviak et al. 2017), lightning strikes generate large amounts of dead wood at canopy height, which potentially attracts distinct beetle assemblages (Ulyshen 2012, Li et al. 2017, Seibold et al. 2018). Thus, dead wood produced by lightning strikes likely is an important resource affecting local and regional biodiversity (Grove 2002, Jacobs et al. 2007). Any changes in lightning strike frequency in tropical forests (e.g., due to climatic change; Williams 2005) are likely to have cascading effects on beetle community structure.

The increase in beetle hole abundance with increasing tree size suggests that substrate availability is a major factor influencing beetle colonization (e.g., Lassauce et al. 2011, Seibold et al. 2016). The trunks of lightning-damaged trees potentially act as ecological islands in which beetle species richness would be expected to increase with increases in habitat area (Preston 1962, MacArthur and Wilson 1967). Similarly, the association between beetle hole abundance and the location of crown damage in living trees suggests that lightning current travels vertically through tree vascular tissues, thus (at least initially) creating colonizable habitat only on specific sectors of the trunk, as observed in temperate pine trees (Anderson and Anderson 1968).

The lack of relationship between beetle hole abundance and distance from the central tree in strike sites suggests that even small amounts of damage can promote substantial beetle colonization. Presumably, this is partly driven by contagious beetle infestations spreading from the directly struck trees, as occurs in temperate pine forests (Coulson et al. 1983). Such contagious infestations are likely if lightning damage reduces tropical tree defenses against beetle attack (Anderson and Anderson 1968, Hodges and Pickard 1971). However, evidence for this effect currently is lacking for tropical trees. By contrast, the decline in beetle hole abundance with increasing distance from the focal tree in control sites was an unavoidable consequence of the study design. Specifically, because lightning tends to strike large trees (Gora et al. 2020, Yanoviak et al. 2020) the focal trees in control sites used for comparison often were the largest (thus likely the oldest) in a given patch of forest. Consequently, they had relatively high amounts of beetle damage, and post hoc analysis showed that this difference caused the decline shown in Fig. 4.

The results of this study suggest that lightning damage facilitates beetle colonization of tropical trees. However, fully understanding this phenomenon requires answering at least three non-mutually exclusive questions: is lightning damage more attractive to beetles than other common types of damage in tropical forests (e.g., branch falls, windthrow)?; does lightning damage lead to contagious infestations (i.e., do undamaged trees near strikes have higher rates of beetle colonization than similar conspecifics that are distant from strike sites)?; and does lightning damage compromise tree defenses against beetles or produce unique chemical signatures that are attractive to certain beetle species? Among other variables, answering these questions will require knowing the identities of the colonizing beetle species, their relative abundances, and their distributions in space and time. Investigating these patterns will advance our understanding of factors affecting beetle metacommunity structure and the maintenance of their diversity.

Supplementary Data

Supplementary data are available at Annals of the Entomological Society of America online.

Data Availability

Data from this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.zgmsbcc7z (Parlato 2020).

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