## ORIGINAL ARTICLE



# Ant communities respond to a large-scale disturbance along an elevational gradient in Puerto Rico, U.S.A.

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### **Abstract**

Large scale disturbances are known to significantly alter aspects of both species diversity and ecosystem function. In the Caribbean, hurricane events are a significant form of disturbance, the effects of which have been shown to alter food web function, especially in the terrestrial environment. Although hurricanes have been studied from a variety of their effects on ecosystems, there is little research on how these storms affect species along elevational gradients. Within terrestrial habitats, ants form the basis of many food webs, being both numerically dominant and functioning in a variety of roles within the food web. On September 20th, 2017 Hurricane Maria, a category 4 storm, crossed over the island of Puerto Rico, causing significant damage to both human and natural systems. We collected data on ant abundance and composition from 150 samples of leaf litter along a 700 m elevational gradient during June the year of and after the storm event. Ant abundance increased by 400% after the storm with many common ant species seeming to benefit, especially at lower elevations. There were subtle changes in ant richness, with declines generally after the storm, but yet again this response was dependent on elevation. This is one of the first studies to consider how terrestrial insect communities are affected by large hurricane events across elevations, and our results are in contrast to past work showing declines in ant abundance after such storms.

Abstract in Spanish is available with online material.

## KEYWORDS

ant, disturbance, elevation, Maria, Puerto Rico

## | INTRODUCTION

Natural disturbances such as forest fires, floods, mud slides, hurricanes, tsunamis, earthquakes, excessive wind, and heat waves play an important role in ecosystem dynamics (Seidl et al., 2011). All types of disturbances can have a strong influence on the structure, composition, and function of the habitats that they interact with (Seidl et al., 2011). Many of these disturbances are beneficial to ecosystem processes and may pave the way for the evolution of species diversity (Pausas & Keeley, 2019). However, natural disturbances can also damage ecosystems and lead to rapid species loss

(Florec et al., 2020). It has been predicted that the frequency and intensity of disturbances, such as hurricanes, will change as a result of climate change (Lugo, 2000).

Hurricanes are storm systems that develop from low pressure and warm temperatures in tropical and subtropical waters (Heron et al., 2008). Hurricanes are a complex type of disturbance that is accompanied by wind and rain, which themselves represent two other natural disturbance types (Lugo, 2000). As such, hurricanes influence ecosystems, often determining the structure and function of the community of plants and animals that are exposed to them (Gardner et al., 2005). Hurricanes create environmental stressors that have

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Biotropica. 2024;00:1-10. wileyonlinelibrary.com/journal/btp caused shifts in species abundance (Savage et al., 2018), shifts in population fluctuations, plant damage, mortality, litter inputs, animal niche dynamics, and changes in ecosystem processes (Ackerman et al., 1991). Hurricanes can have direct and indirect as well as visible and invisible effects on many organisms (Wiley & Wunderle, 1993). For example, direct, visible effects of a hurricane on a forest ecosystem are snapped branches, defoliation, and uprooted trees (Lugo, 2008). An indirect effect would be contracting foliage, causing variability in light and nutrient availability throughout the forest (Lugo, 2008). All of these effects likely interact to produce specific responses to a storm in a specific place at a specific time.

Ants (Order Hymenoptera, Family Formicidae) are one of the most important groups of insects, especially in the tropics (Folgarait, 1998; Wilson & Holldobler, 2005), and are a key component of the terrestrial food web, and their responses to abiotic, biotic, and functional changes suggests that they are a useful indicator group of environmental changes (Tiede et al., 2017). In general, various abiotic factors are thought to influence ant diversity, including the high environmental variation at different elevations (Pérez-Toledo et al., 2022). With regard to hurricanes, however, the data examining the response of ant communities are lacking. In one study conducted on the Bahamian islands before and after Hurricane Floyd (ca. 1999), considerable declines in overall ant abundance and changes in the composition of species occurred post-hurricane (Morrison, 2002). Besides abundance, hurricanes can also negatively affect ant assemblages via environmental effects (Philpott et al., 2010), including by directly influencing ant-plant mutualism via traits associated with ant activities (Piovia-Scott, 2011). In addition, areas with a greater degree of flooding can be less vegetated and thus affect ant presence (Morrison, 2002). After a hurricane in Nicaragua, Cecropia spp. trees were greatly reduced and arboreal ant species like Azteca spp. that associated with these trees likely declined as a result (Philpott et al., 2010). Additionally, below ground macrofauna, such as ants, are vulnerable to inundation because they lack the ability to escape floods and typically decrease in abundance as a result (Coyle et al., 2017). Wind disturbance from hurricanes can also result in increased debris such as leaf litter and wood material on the forest floor (Coyle et al., 2017). Additionally, hurricane winds can produce changes in species composition (Van Bloem et al., 2005). Forests, along with the community of organisms that live there (including ants, Hoenle et al., 2022), can take decades to recover, and recovery trajectories are not always predictable (Brokaw et al., 2012).

Although ants occur in a variety of habitats across the world, mountains often offer unique habitat for the study of responses to environmental change because of their altitude and temperature variations that are dissimilar to sea level (McCain & Grytnes, 2010). Mountains also provide an elevational gradient that offers historical insight, important components to climate change response, and testing ground for scientific theory (Longino & Colwell, 2011). Ants are one of the most dominant taxa in the leaf litter layer of forest in Puerto Rico (Reagan & Waide, 1996) and can be found at various elevations across the island (Smith, 1936). Studies show that plants associated with ant mutualism decrease at higher elevations (Plowman et al., 2017),

with species richness and functional diversity of ants also decreasing (Reymond et al., 2013). In Mexico, the structure of leaf-litter ant communities along an elevational gradient can be attributed to temperature (Pérez-Toledo et al., 2020). Studying a dominant tropical species, such as ants, along an elevational gradient may provide essential data for monitoring biotic response to climate change (Longino & Colwell, 2011). At present, the interactive effects of hurricanes and elevational effects for ants has not been fully explored.

The main island of Puerto Rico is subjected to intense natural disturbances including hurricanes (Reagan & Waide, 1996). Puerto Rico has endured several large hurricanes over the past five decades including Hugo (1989, Category 4), Georges (1998, Category 3) and Maria (2017, Category 4). Hurricane Maria made landfall as a category 4 hurricane (Cortés, 2018) with sustained winds of 209–251 kmh<sup>-1</sup> causing catastrophic damage (Taylor et al., 2010). Research indicates that hurricane occurrences are most active in La Niña years (Jagger & Elsner, 2006). Hurricane Maria occurred during a La Niña event (Murakami et al., 2018) and experienced the strongest winds since 1928 at 250 kmh<sup>-1</sup> (Hosannah et al., 2021) even though the La Niña event was not considered the primary cause of the hurricane (Murakami et al., 2018).

Comparable data on the biota before a natural disturbance, such as a hurricane, are rare (Spiller et al., 1998). This deficiency is often related to the unpredictability of such large disturbance events and the lack of opportune collections before the event rather than after. Few studies have been able to examine the effects of large-scale disturbances like hurricanes on tropical ant communities given the unpredictable nature of these disturbances. The effects of a disturbance such as a hurricane on leaf litter invertebrates at the population, community, and ecosystem level have been reported elsewhere; however, there are few studies on the effects of a hurricane on tropical ants across these scales (Reagan & Waide, 1996).

This study examined ant distribution in the Luquillo mountains of Puerto Rico before and after Hurricane Maria that passed over the center of the island on September 20, 2017. Specifically, we had two aims. First, we examined how ant abundance and community composition changed across a 700m elevation transect. Second, we compared data collected before and after the storm. Based on environmental factors, such as temperature, we hypothesized that ant diversity and abundance would decrease with increasing elevation (e.g., Bruhl et al., 1999; Burwell & Nakamura, 2011; Fisher, 1996; Guerrero & Sarmiento, 2010; Reymond et al., 2013). We also hypothesized that Hurricane Maria would have a generally negative effect on ants due to forces like flooding and disruption of vegetation, as well as potential alterations in the abiotic environment. Interactions between effects due to hurricane Maria and elevations have the potential to produce unexpected outcomes on the ant community.

## 2 | METHODS

Samples were conducted in the Luquillo Experimental Forest (LEF), a 11,330ha site located on the eastern side of the main island of

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Puerto Rico, U.S.A. Average annual rainfall is 3460mm (McDowell & Estrada-Pinto, 1988) and monthly temperatures range from 21 to 25°C (Brown, 1983). In both 2017 and 2018 sampling took place between June 14 and July 24, which are within the wet season for the island. The elevation transect we used occurred in a mixed forest, typical of Tabonuco forest (Uriarte et al., 2019), composed of both large hardwoods (e.g., Dacryodes excelsa) and gap specialists like Prestoea montana and Cecropia peltata, across fifteen different elevations. Sample sites were from 300m to 1000m elevation at 50 m elevation increments (n = 15). At each elevation, 10 plots (total 10 m × 10 m) were laid out in a 2 x 5 grid, with no space between adjacent plots. Within each plot, we sampled litter using a 0.5 m<sup>2</sup> PVC frame in either the northwest corner in the upper five plots or northeast corner in the lower five plots. As the goal of the sampling was to collect litter invertebrates, the frame was placed to avoid any large obstructions (e.g., boulders). Thus, we produced 150 samples (15 elevations with 10 plots at each). Individual plots were processed using Winkler sacs, which are a passive means to extract invertebrates by using their own behavior (Besuchet et al., 1987; Sabu & Shiju, 2010). Bulk samples of leaf litter from each plot were first vigorously agitated for 1 min over a 1.25 cm mesh screen to separate invertebrates from large debris. This sifted material was then placed into Winkler sacs that were then hung in place for 48 hrs. At the bottom of the Winkler sac collection bag, we placed a container of 95% ethanol to catch and preserve all invertebrates. Following sorting of invertebrates from debris, ants were then separated into 0.25-dram shell vials for each plot within each elevation. This original sampling design ended in late July 2017, but on September 20th, 2017 Hurricane Maria passed over the island and did considerable damage to the forest (e.g., removal of the of canopy with stem breakage and uprooting of stems, Uriarte et al., 2019). We decided to resample the plots at the same time during the next year (June 2018) to maintain continuity in seasonality. All methods were the same except samples on plots were collected in the opposite corner to minimize any differences due to our removal of litter in 2017. Given the severity of the storm, no sites in the LEF escaped without damage, and thus we did not have access to any control sites to compare to pre-storm samples. The LEF has also seen significant human disturbance in the form of agriculture (i.e., coffee) and logging, however these practices took place before the purchase of the property in the 1930s (Thompson et al., 2002) and no records of these disturbance exist above ~400 m; it is not clear that any of these disturbances took place along the studied transect.

# 3 | STATISTICAL ANALYSES

We analyzed our data to address five ant biodiversity measurements (Gotelli et al., 2011) for the effects of Hurricane Maria across elevations. Abundance-level measurements included the total number of individuals per sample (N) and frequency of occurrence (the number of samples in which a species occurred, in the 10 samples from each elevation). Community-level measures

included species richness per sample (S), total species richness in the 10 samples per elevation, and compositional changes in ant species abundance patterns (therefore producing a measure of community).

To examine changes in our N and S we performed a Repeated Measures multivariate analysis of variance (MANOVA) that considered year (2), elevation (15), and their interaction as independent variables. To meet statistical assumptions, we used a  $\ln_{(n+1)}$ transformation for both S and N on the raw data. To assess potential changes in ant frequency of occurrence, we performed logistic regressions on the nine most common species of ants encountered. These species made up 97% of all individual ants collected across years (i.e., Brachymyrmex sp., Hypoponera opacior, Linepithema iniquum, Nylanderia sp., Pheidole flavens, P. moerens, Solenopsis sp., Strumigenys rogeri, and Wasmannia auropunctata). Because of taxonomic uncertainties three of these species were included only at the genus level (Brachymyrmex sp., Nylanderia sp., Solenopsis sp.). So as to control for comparison-wide error rate across species within the same samples we adjusted the p-values downward (p = .05/9 = .006).

Finally, to assess compositional changes in the nine most common taxa, we first performed a Principal Components Analysis (PCA) to reduce correlated taxa (e.g., Everly & Yee, 2023). We retained PCs with eigenvalues >1.00. Retained PC axes were then analyzed using MANOVA with sampling period (2), elevation (15), and their interaction as independent variables. Standardized canonical coefficients (SCCs) were used to assess the dependent variables most responsible for significant effects (Scheiner, 2001). All analyses were conducted in SAS (SAS, 2016).

### 4 | RESULTS

We collected a total of 26 species of ants across the pre- and post-hurricane sampling events, with 24 before and 18 after the disturbance (Table 1). We collected >400% more ants in the same plots after (total N=3635) compared to before the hurricane (total N=873). The MANOVA for N and S produced significant effects of year ( $F_{2,269} = 40.76$ , p < .001), elevation ( $F_{28,540} = 5.90$ , p < .001), and their interaction ( $F_{28,540}$ =2.78, p<.001). In all cases, N had larger SCCs, indicating it contributed more to differences compared to S. For N, there was a general decline in N as elevation increased, and specifically there were significantly more ants in samples from 350 and 450 m after the hurricane compared to before (Figure 1). Total richness per elevation did seem to generally vary between years (lower richness in 2018 vs. 2017) and decreased from low to high elevation (Figure 2a). For mean S per plot, we also found a general decline of richness across elevations and richness was higher in 2017  $(1.57\pm0.04)$  than 2018  $(1.38\pm0.05)$ . Even though the interaction was significant, we were unable to detect significant differences between plots at the same elevation between years (Figure 2b).

Based on logistic regressions, no species displayed a significant elevation by year interaction, nor difference between years.

TABLE 1 Ant species present (X) versus absent (–) across an elevational gradient during the summers before (2017) and after (2018) Hurricane Maria, in the Luquillo Experimental Forest, Puerto Rico.

Species	2017	2018
Anochetus mayri	Х	Х
Brachymyrmex sp.	X	Χ
Cardiocondyla minutior	Χ	-
Cyphomyrmex minutus	X	Х
Eurhopalothrix gravis	Χ	-
Hypoponera opacior	X	Χ
Linepithema iniquum	X	Х
Monomorium floricola	Χ	-
Monomorium pharaonis	-	Х
Myrmelachista sp.	Χ	-
Nylanderia sp.	Χ	Х
Nylanderia microps	Χ	X
Odontomachus ruginodis	X	Х
Pheidole flavens	Χ	X
Pheidole moerens	X	Х
Pseudoponera stigma	Χ	-
Rogeria foreli	Χ	-
Solenopsis sp.	Χ	X
Strumigenys eggersi	Χ	Х
Strumigenys gundlachi	X	X
Strumigenys margaritae	Χ	-
Strumigenys rogeri	Χ	Х
Tapinoma litorale	Χ	-
Temnothorax isabellae	Χ	Х
Wasmannia auropunctata	Χ	Х
Zatania cisipa	-	Χ

However, six of the nine species did display significant differences across elevation (*Brachymyrmex* sp. ( $\chi^2$  = 10.68, df = 1, p = .011), *P. flavens* ( $\chi^2$  = 4.39, df = 1, p = .036), *P. moerens* ( $\chi^2$  = 8.33, df = 1, p = .039), *Solenopsis* sp. ( $\chi^2$  = 23.73, df = 1, p < .001), *S. rogeri* ( $\chi^2$  = 20.50, df = 1, p < .001), and *W. auropunctata* ( $\chi^2$  = 54.88, df = 1, p < .001)). In all cases, abundance of these species were higher at lower elevations (Figure 3).

The PCA reduced the nine taxa down to 4 PCs which combined explained 60% of the variation among groups. Besides significant effects of time ( $F_{4,267}=3.04$ , p<.001) and elevation ( $F_{56,1080}=3.04$ , p<.001), we also identified a significant time by elevation interaction ( $F_{56,1080}=2.56$ , p<.001). Based on SCCs the PC axes one (SCC=1.08), two (0.61), and four (0.70) were largest (PC 3=-0.02) and thus most explained the interaction. The first PC contained three species (Brachymyrmex sp., S. rogeri, W. auropunctata), PC2 contained two (P. moerens, Solenopsis sp.), and PC 4 contained two (Nylanderia sp., P. flavens). In all cases, lower elevations (i.e., 340, 400, or both) saw a significant increase in abundance in 2018 over 2017 (Figure 4).

## 5 | DISCUSSION

Our study documented 26 ant species across elevations (including some to genus, likely containing several species) across the 2 years of sampling. This likely captured most species in the LEF. For instance, Osorio-Pérez et al. (2007) found only 14 species in the LEF using a combination of Berlese funnels, baits, and arboreal traps, whereas a report by Lavigne (1970) notes 30 species. Work by Torres and Snelling (1997) lists 71 species, except this is from a survey across the entire main island of Puerto Rico and includes other affiliated islands. Thus, our sampling appeared to capture the faunal diversity of litter associated ants in the LEF. The generally lower ant diversity from mainland systems can be explained by the depauperate nature of islands, as well as the frequency of disturbance the LEF experiences (Reagan & Waide, 1996).

This is the first study we are aware of to consider the effect of a large disturbance on ant communities across an elevational gradient. Specifically, we examined how ant abundance and community composition changed in Puerto Rico after Hurricane Maria and across elevations. Our first aim hypothesized that ant diversity would decline with increasing altitude, based on environmental factors such as temperature (Nowrouzi et al., 2016). We found that after Hurricane Maria there were significantly more ants at lower elevations, specifically at 350 and 450m. However, there was no significant elevation by year interaction for any species, but six of nine species displayed significant differences in frequency of occurrence across elevation, with fewer ant species present as we sampled up the mountain. This result is consistent with other studies investigating ants and elevation (e.g., Bruhl et al., 1999; Burwell & Nakamura, 2011; Fisher, 1996; Reymond et al., 2013).

For our second aim we hypothesized that Hurricane Maria negatively affected ants likely due to alteration of the abiotic environment. In general, the most common ant species appeared to benefit from this wide scale disturbance with higher numbers present afterwards, but we did not detect an expansion or contraction in areas where ants occurred. Thus, our data suggest that the storm may have benefited species in the short term by allowing for more or larger colonies, but didn't allow them to expand spatially. We do note that control sites (i.e., locations not affected by the storm) did not exist for inclusion in this study, and therefore we cannot say for sure that the changes we observed were due only to the hurricane. Given that the sampling took place along the same transect and at the same time of year, our results speak to the high likelihood of the profound effect of Hurricane Maria on the LEF. However, we only sampled approximately 10 months after the storm (12 months after our initial sampling), and thus it is possible that other long-term effects could have occurred. For instance, for large flooding events (likely those experienced after a large hurricane) the duration of flooding is important, and at longer time scales (e.g., 5 years) responses of the ant communities may be tied to vegetation structure that itself takes many years to recover (Philpott et al., 2010).

Ecological disturbance is an important factor for ant community dynamics (Andersen, 2018). The effects of disturbance on

FIGURE 1 Differences in mean (± 1 SE) ant abundance per elevation from 300-1000 m between 2017 (prehurricane, open symbols) and 2018 (posthurricane, gray symbols).

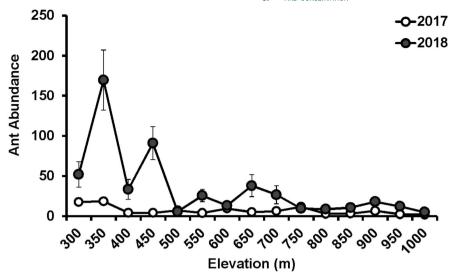
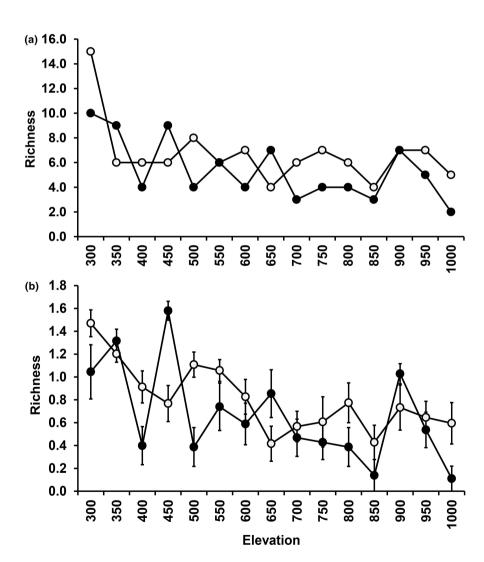


FIGURE 2 Total richness (A) and mean richness ( $\pm$  1 SE ) (B) per elevation from 300-1000 m between 2017 (prehurricane, open symbols) and 2018 (posthurricane, solid symbols).



ant communities are typically indirect, including, but not limited to, competition, resource availability, microclimate, and habitat structure (Andersen, 2018). Ant communities respond to the same disturbance in different ways based on functional composition and biogeographical history (Andersen, 2018). Often, tropical ant

species have narrow elevational ranges (Nowrouzi et al., 2016). This is due to a substantial climate change with elevation and limited thermal tolerance (Nowrouzi et al., 2016). A narrow elevational range coupled with disturbance can likely cause a shift in the species abundance across the elevational gradient (Andersen, 2018).

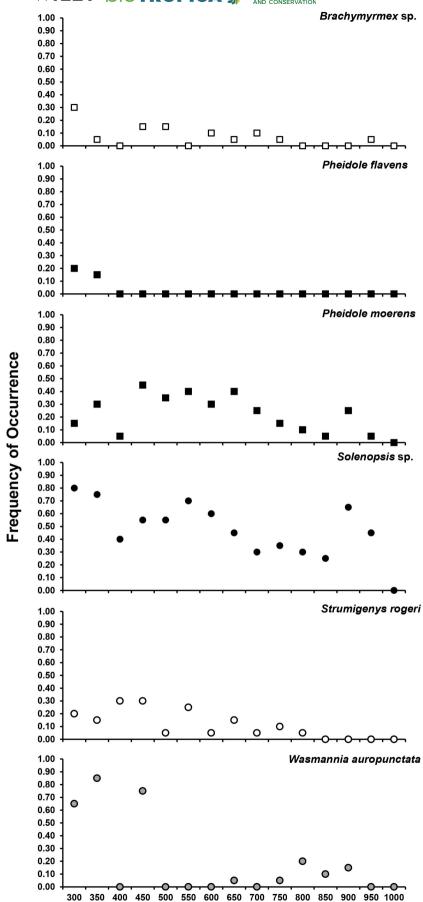


FIGURE 3 Variation in ant species across elevations based on the results of significant logistic regressions. Each panel represents changes in ant frequency of occurrence (presence/absence) from 300 - 1000 m.

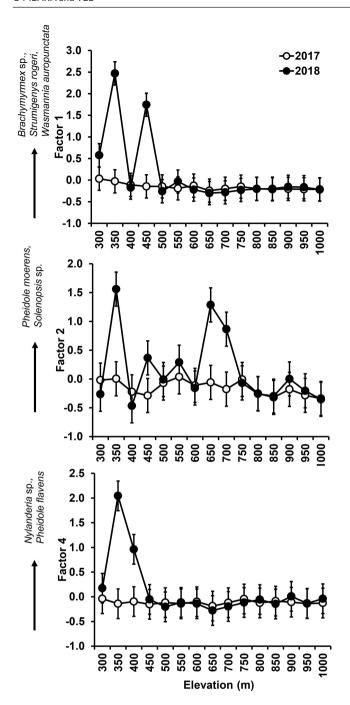


FIGURE 4 Plots of PC factors (LS means  $\pm$  SE) axes based on PCA analysis from 300-1000 m between 2017 (pre-hurricane, open symbols) and 2018 (post-hurricane, solid symbols). Plots are of factor scores from PC1, PC2, and PC4, which made the greatest contributions to significant differences among elevations between years.

Our data generally conform to this idea after Hurricane Maria, with dramatically more ants captured after this large disturbance event at certain elevations, but no wide-scale changes in frequency of occurrence.

How might a hurricane affect ants allowing for a substantial increase in numbers of most species? Some species, like *Solenopsis invicta*, are well adapted to withstand excessive rainfall and

flooding by forming rafts (Hooper-Bùi et al., 2020). Although we identified some Solenopsis species in this study, it is unclear if the species identified are resilient in this way. Some species will also relocate to nests at higher elevation during excessive, monsoon type rainfall (Kolay & Annagiri, 2015). Many surface using or epigaeic species forage both in trees and on the ground, and so a likely effect of the hurricane was to concentrate their foraging onto the ground, an effect shown after other disturbances like fire (e.g., Andersen & Yen, 1985). Other abiotic factors such as temperature and humidity have been shown to affect the abundance of Nylanderia sp. and other species (Bentley et al., 2016). However, Nylanderia sp. are invasive in parts of the United States such as Ohio where they have potential to alter the forest floor food web due to their ability to forage in cooler temperatures (Ivanov et al., 2011). Large scale changes in the abiotic environment caused by disturbances like hurricanes could change underlying habitat factors such as shade and cause a shift in distribution of particular ant species. We did note a loss of six species after the hurricane, all of which were rare before the event (~1 individual present in our pre-hurricane samples). Thus, these animals were uncommon regardless of the sampling period, and therefore we cannot attribute the hurricane alone to their absence.

Biotic factors such as vegetation type and leaf coverage have also shown to affect ant communities. Brachymyrmex sp. are a genus that has been shown to be affected by biotic factors like vegetation (Rosson, 2004). Winds from a hurricane are noted to thin forest canopy and transfer leaf biomass and nutrients to the forest floor (Van Bloem et al., 2005). Images of the LEF (Figure 5) show noticeable differences in canopy cover, vegetation growth, and debris from before and after hurricane Maria. The canopy was visibly thinner in 2018 than in 2017 in addition to increase vegetation growth and debris in 2018 (Figure 5). The role of leaf litter in habitats, such as tropical forests, is to provide food, shelter, nutrients, and temperature regulation to organisms that belong to the leaf litter community (Pandey, 2020). Ants belong to the leaf litter community and greatly benefit from all that the leaf litter has to offer. As leaf litter accumulates on the forest floor, depth of litter increases, creating refuge for ants and other arthropods (Kaspari & Yanoviak, 2009). Debris also stimulates litter communities under suitable abiotic conditions (Richardson et al., 2010). Additionally, ant abundance can be seen to increase with litter depth (Kaspari & Yanoviak, 2009). Invertebrate biomass, diversity, and abundance is likely to increase with increased litter deposition (Richardson et al., 2010). We noticed significant litter accumulation after the storm, which was likely a driver for an increase in abundance of many of the species we observed. Disturbance coupled with biotic or abiotic components can influence the species that occupy certain areas, including those in genera sampled here. Strumigenys sp. are influenced mostly by biotic factors and tend to occur in open, disturbed areas (Kitahiro et al., 2014). Pheidole sp. tend to occur in small islands of highly disturbed areas with more abiotic influence. Wasmania auropunctata in the tropical dry forest of Columbia respond favorably to disturbance and can become dominant due



FIGURE 5 Images of the Luquillo Experimental Forest (LEF) before (left, June 2017) and after (right, June 2018) Hurricane Maria. Note the differences in canopy cover, vegetation growth, and debris between the two panels (note that this is not the same patch of forest but taken at similar locations within the forest). Photos by D.A. Yee.

to their ability to monopolize resources (Achury et al., 2020). *W. auropunctata* have also been shown to increase with increased deposition of litter (Richardson et al., 2010). This correlates with the increase of *W. auropunctata* that was observed after Hurricane Maria. These species prefer a disturbed environment, but can also be found in coastal habitats, mid-elevation forests, lower elevations, and dry forests (Sarnat et al., 2015). Thus, species level responses may be tied to their underlying ecological demands.

We found that the abundance of most ant species generally decreased with elevation likely due to a combination of abiotic and biotic factors. The most common ant species appeared to benefit from the wide scale disturbance of Hurricane Maria with higher numbers present afterwards, although these changes occurred mostly at lower elevations. Increased litter on the forest floor likely contributed to the increase in ant abundance after the hurricane. Generally, the species that we found tended to prefer disturbed habitats or respond positively to disturbance, yet the dynamic and unpredictable nature of large disturbances would suggest that more data on the initial and long-term responses of ants to these storms are needed. Given that this work was conducted at a Long Term Ecological Research site, future collections will hopefully fill in knowledge gaps for temporal trends in ant communities.

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#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad. 1vhhmgr1q (O'Meara & Yee, 2023).

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