Hurricanes and phytophagous insects: Disturbance effects on the abundance of an invasive insect[1]

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ABSTRACT

Hurricanes are known to affect plants and animals and their interactions. Usually, hurricanes defoliate trees and reduce the abundance and density of arthropods. The parasitic arthropod *Holopothrips tabebuia* was first reported in Puerto Rico in 2006. By 2007, it had established populations on two hosts: *Tabebuia aurea* and *Tabebuia heterophylla*. In September 2017, Hurricane María defoliated both hosts. This study aimed to determine the effects of a powerful hurricane on the abundance of this parasite and its relationship with its hosts. Although Hurricane María caused greater defoliation in *T. aurea* than in *T. heterophylla,* the post-hurricane abundances and densities of the parasite were much lower in both hosts. A negative correlation between the damage to the host caused by the hurricane and the infestation by the parasite was found. Evidence supports that hurricanes indeed have a negative effect on the dynamics of *H. tabebuia* and its relationship with its hosts.

Key words: Bignoniaceae, *Holopothrips tabebuia*, parasitism, plant-animal interactions, Thysanoptera

RESUMEN

Huracanes e insectos fitófagos: Efectos de los disturbios en la abundancia de un insecto invasivo

Se sabe que los huracanes afectan a plantas y animales y sus interacciones. Por lo general, los huracanes defolian los árboles y reducen la abundancia y densidad de los artrópodos. El artrópodo parásito *Holopothrips tabebuia* se informó por primera vez en Puerto Rico en 2006. Para 2007, se habían establecido poblaciones en dos huéspedes: *Tabebuia aurea* y *Tabebuia heterophylla*. En septiembre de 2017 el huracán María defolió ambos hospederos. Este estudio tuvo como objetivo determinar los efectos de un poderoso huracán sobre la abundancia de este parásito invasor y su relación

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con su huésped. Aunque el huracán María provocó mayor defoliación en *T. aurea* que en *T. heterophylla*, la abundancia y densidad del parásito después del huracán fueron mucho más bajas en ambos hospederos. Se encontró una correlación negativa entre el daño al huésped causado por el huracán y la infestación por el parásito. La evidencia respalda que los huracanes efectivamente tienen un efecto negativo en la dinámica de *H. tabebuia* y su relación con el huésped.

Palabras clave: Bignoniaceae, *Holopothrips tabebuia*, parasitismo, interacción planta-animal, Thysanoptera

INTRODUCTION

The disturbance generated by hurricanes affects plants, animals and their interactions. Plant damage, for instance, ranges from defoliation to loss of branches and death (Brokaw and Grear, 1991; Brokaw and Walker, 1991; Francis, 2000; Walker, 1991; Whigham et al., 1991). In 1989, Hurricane Hugo caused various tree species in Puerto Rico's El Yunque forest to lose more than 75 percent of their leaves (Walker, 1991), representing a significant accumulation of biomass in the forest (Whigham et al., 1991). Furthermore, canopy structure of the forest was altered (Brokaw and Grear, 1991), changing habitat availability for other organisms, such as animals.

Changes in animal abundance after a hurricane are associated with a shift of niches in the ecosystem. Litterfall species, such as the forest frog, *Eleutherodactylus coqui* Thomas, increased four-fold (Woolbright, 1991). The increase in litterfall, however, represents a change in the canopy habitats for other animals. Abundances of stick insects (*Lamponius portoricensi* Rehn and *Agamemnon iphimedeia* Moxey), a common invertebrate in the canopy, were reduced after Hurricane Hugo hit El Yunque (Willig and Camillo, 1991; Willig et al., 2011).

Species interactions such as predatory-prey and plant-animal are also affected by hurricanes (Khaliq et al., 2014; Spiller and Agrawal, 2003; Spiller and Schoener, 2007; Willig and Camillo, 1991). Predation can be reduced if the predator abundance is reduced (Spiller and Schoener, 2007; Woolbright, 1991). As for the prey, it has been reported that predation pressure increases after hurricanes (Willig and Camillo, 1991). A change in the diet of predators after hurricanes has been documented (Waide, 1991). After Hurricane Hugo, stomach content in birds in El Yunque showed a shift in the arthropods consumed (Waide, 1991).

Plant-animal interactions are strongly affected by hurricanes (Schowalter and Ganio, 1999; Spiller and Schoener, 2007). In fact, weather changes affect the status of insect pests in terms of population dynamics, distribution, abundance, intensity and feeding behavior (Khaliq et al., 2014). It has been reported that after a hurricane

herbivory can increase either by a reduction of herbivore predators or by higher susceptibility of new sprouted plant material (Spiller and Agrawal, 2003; Spiller and Schoener, 2007). New shoots in plants, for instance, are more susceptible to herbivory due to higher palatability (e.g., nitrogen concentration, fewer trichomes) (Spiller and Agrawal, 2003).

Phytophagous insects should be more susceptible to hurricanes since damage befalls the insect directly and occurs indirectly through the host. Because plants are greatly affected by the impact of a hurricane, damage to phytophagous insects could be significant (Brokaw and Grear, 1991; Brokaw and Walker, 1991; Walker, 1991; Whigham et al., 1991). However, little information is available on phytophagous insects and their interactions with plants after a hurricane event. Moreover, insect pests are common in places affected by hurricanes such as the tropics (Nair, 2007).

In 2006, a new report of a phytophagous insect was made for Puerto Rico (Cabrera and Segarra, 2008; Cabrera et al., 2008). This invasive insect (*Holopothrips tabebuia* Cabrera and Segarra) feeds on trees of the Bignoniaceae family, creating galls on its foliage (Cabrera and Segarra, 2008; Cabrera et al., 2008). Density data on this invasive insect suggest that this species is spreading and increasing infestation in two host species, *Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S. Moore and *Tabebuia heterophylla* (DC.) Britton (Cabrera et al., 2008). We will analyze the effects of a hurricane disturbance on the phytophagous species. Using *Holopothrips tabebuia* as our model, we aim to determine the effect of an intense hurricane on its abundance pattern and its interaction with two hosts: *Tabebuia aurea* and *Tabebuia heterophylla* in tree populations previously studied.

METHODS

Study Site. —Observations were made in seven locations in Puerto Rico. The sites visited were the municipalities of San Juan, Caguas, Cidra, Salinas, Santa Isabel, Arecibo and Mayagüez. The sites selected are urban sites, since both tree species *Tabebuia aurea* and *Tabebuia heterophylla* (Figures 1-A, 1-B, respectively) are frequently planted as ornamental trees. San Juan and Arecibo are located in the northern part of the island, Salinas and Santa Isabel are in the south, Caguas and Cidra are in the central part of the island, and Mayagüez, in the west. From each site, a total of 25 individuals per tree species were sampled for *Holopothrips tabebuia* (Figure 1-C).

Sampling.—Hurricane María hit the island on 20 September 2017. Two months later, we started sampling *Tabebuia aurea* and *Tabebuia*

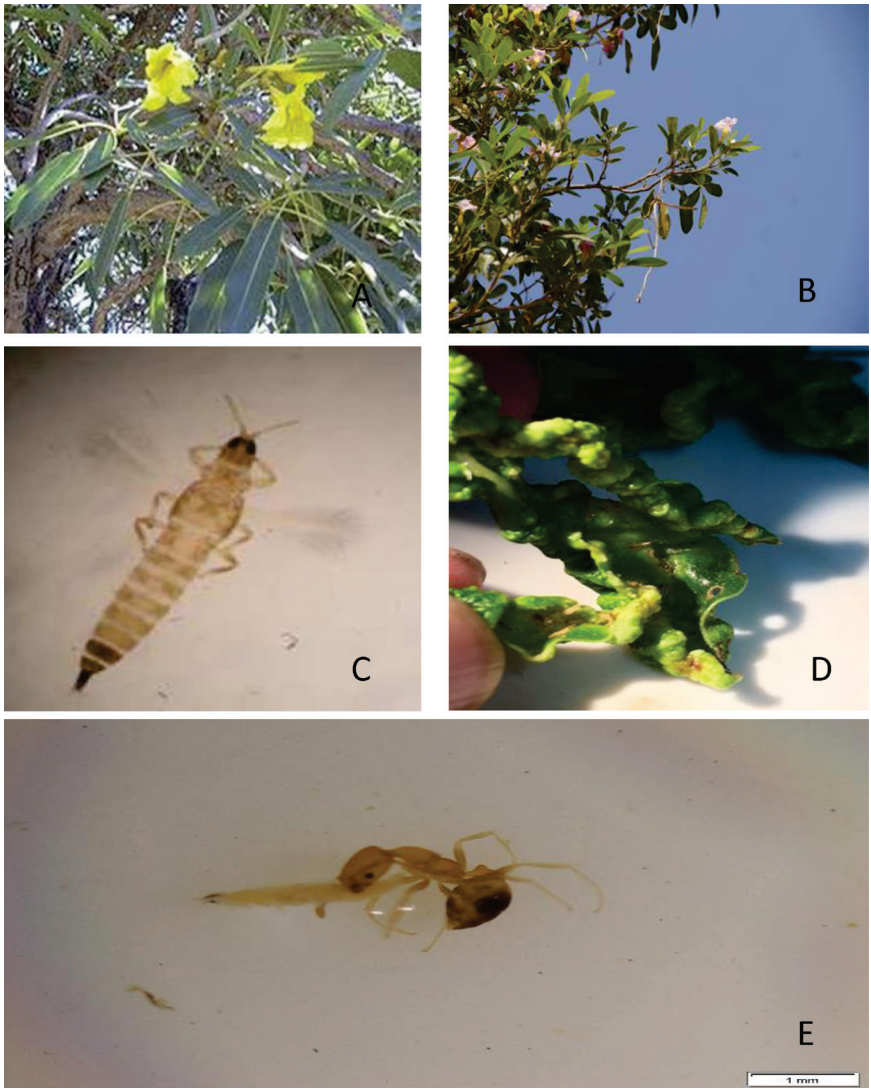

FIGURE 1. A. *Tabebuia aurea,* B. *Tabebuia heterophylla,* C. Adult of *Holophothrips tabebuia,* D. Damaged leaves caused by *Holophothrips tabebuia,* E. Predation of a nymph of *Holophothrips tabebuia* by *Trichomyrmex destructor*.

heterophylla. To determine the disturbance effect on *Holopothrips tabebuia*, we assessed each tree for the percentage of damage caused by the hurricane, infestation (%) of the parasite *H. tabebuia* (Figure 1-D), the abundance of this parasite, and presence of its predators. In sum, 175 trees of each *Tabebuia* species were sampled.

To determine the percentage of damage caused by the disturbance, we observed the trees and estimated the damage to the oval canopy (Gilman and Watson, 1993). This visual determination ranged from 0 percent, where no damage was observed, to 100 percent where the tree had lost all its leaves and branches. After the visual estimation of the damage, we determined if the tree was infested by *Holopothrips tabebuia*. The percentage of infestation was categorized as follows: 1) 0 percent infested, 2) less than 25 percent infested, 3) between 26 and 50 percent, 4) between 51 and 75 percent, and 5) more than 75 percent of infestation. The percentage, estimated visually, was based on the number of leaves with at least one gall present. Also, the percentage of infested trees was determined for each site. The damage to the leaves by *H. tabebuia* is characteristic (Figure 1-D), therefore, the percentage of infestation was easily determined for each tree sampled.

After both visual estimations were concluded, 46 leaves were randomly collected to determine the abundance and densities of the invasive insect and its possible predators. The abundance of nymphs and adults of *H. tabebuia* was analyzed after the collected leaves were observed in the laboratory to determine the number of individuals present in the damaged leaves. A stereoscope (Nikon SMZ 800)[5] was used to determine the number of adults and nymphs of *H. tabebuia* and to identify the parasites and predators present in the leaves.

Statistical analysis.—Data was analyzed with a Mann-Whitney *U*-test to determine significant differences in measured variables between *Tabebuia* species. A Spearman correlation was made between damage caused by the disturbance and the abundance of the stages of *Holopothrips tabebuia*, as well as the percentage of infestation of *Tabebuia heterophylla*. All tests were done using the software InfoStat (v. 2017) (Di Rienzo et al., 2017).

RESULTS

Tree damage caused by Hurricane María varied among sites. The species *Tabebuia aurea* exhibited greater damage than *Tabebuia heterophylla*; individual trees in Caguas, Cidra and Arecibo had a mean higher than 75 percent of tree damage, while individuals in Salinas showed lower damage (40%) (Figure 2). Most of the municipalities had a mean lower than 45 percent of tree damage, except for San Juan and Caguas, which showed 70 and 90 percent, respectively (Figure 2).

[5]Company or trade names in this publication are used only to provide specific information. Mention of a company or trade name does not constitute an endorsement by the Agricultural Experiment Station of the University of Puerto Rico, nor is this mention a statement of preference over other equipment or materials.

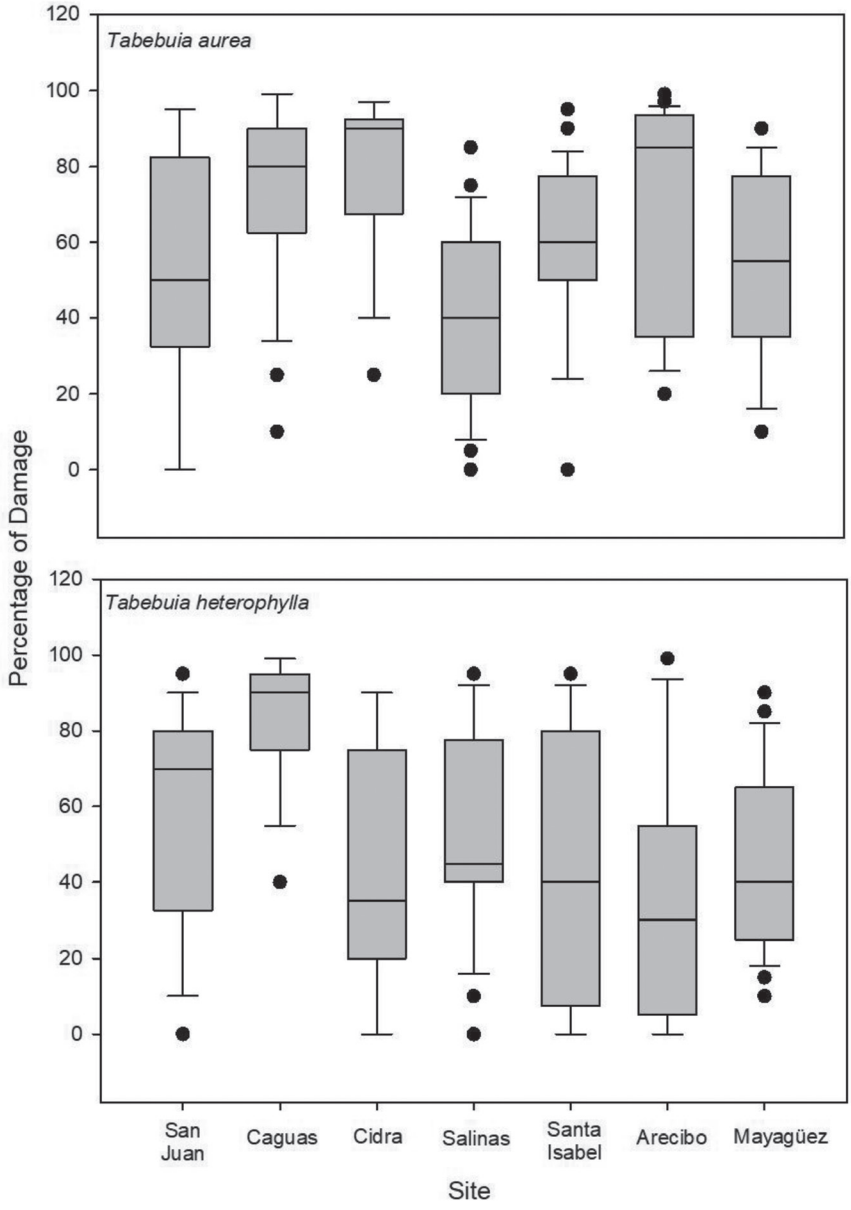

FIGURE 2. Box Plots of percentage of tree damage in two species of *Tabebuia* after Hurricane María (n=25) at seven sites in Puerto Rico. *Tabebuia aurea* (top), *Tabebuia heterophylla* (bottom).

Hurricane María affected plant-animal interaction between *Holopothrips tabebuia* and its hosts. Prior to its impact, approximately 35 percent (S.D. 42.7%) of the island's *Tabebuia aurea* and 59 percent (S.D. 50.2%) of *Tabebuia heterophylla* were infested by *H. tabebuia* (Cabrera et al., 2008). After the hurricane, the percentage of infested trees of both species was lower (5% ± 6.7% for *T. aurea* and 27% ± 21.5% for *T. heterophylla*). Only *T. aurea* trees in three localities (San Juan, Caguas and Cidra) had infestations after María. Nevertheless, more than 40% of trees of *T. heterophylla* in San Juan, Cidra and Arecibo were infested (Table 1). Santa Isabel and Mayagüez had non-infested trees of *T. heterophylla*.

Densities of nymphs and adults of *Holopothrips tabebuia* per leaf were also lower after the hurricane. Nymph densities reported before the hurricane were 0.012 individuals per leaf (ind/leaf) for *T. aurea*, and 1.38 ind/leaf for *T. heterophylla*. After the hurricane, densities of nymphs were lower for both species, with 0.0002 ind/leaf in *T. aurea* and 0.03 ind/leaf in *T. heterophylla.* Adults followed the trend of the nymphs with lower densities reported after the hurricane. Densities of adults before María were 0.02 ind/leaf in *T. aurea* and 0.76 ind/leaf in *T. heterophylla*. After the hurricane, no individual per leaf was reported for *T. aurea,* while 0.06 ind/leaf was reported for *T. heterophylla*.

The population abundance of the phytophagous insect was also affected by the disturbance. After the hurricane, the abundance of *Holopothrips tabebuia* varied between host species, where both stages of the insect, nymphs and adults, were lower in *Tabebuia aurea* than in *Tabebuia heterophylla* (Table 2). Significant differences were observed for both stages ($p<0.0001$). Interestingly, no adult was reported for the host *T. aurea.*

TABLE 1.—*Percentage of infested trees (Tabebuia spp.)* at seven sites in Puerto Rico prior and post Hurricane María (n=25).

	Infested trees (%)			
	Prior to María		Post María	
Locality	*T. aurea*	*T. heterophylla*	*T. aurea*	*T. heterophylla*
Arecibo	12	12	0	44
Caguas	40	100	16	28
Cidra	4	100	4	40
Mayagüez	96	96	0	0
Salinas	0	4	0	24
San Juan	92	100	12	56
Santa Isabel	0	0	0	0

TABLE 2.—*Mean ± Standard Deviation of population variables measured on 46 leaves per tree species of Tabebuia (n=175) at seven localities in Puerto Rico.*

	Abundance Mean ± S.D.		
Abundance	*Tabebuia aurea*	*Tabebuia heterophylla*	*p**
Nymphs of *Holopothrips tabebuia*	0.01 ± 0.151	2.96 ± 9.925	<0.0001
Adults of *Holopothrips tabebuia*	0 ± 0	1.25 ± 4.507	<0.0001
Adults *Trichomyrmex destructor*	1.58 ± 4.485	0.17 ± 0.759	0.002

*Wilcoxon test

Another insect present in the infested leaves was the ant *Trichomyrmex destructor* Jerdon (Figure 1-E) (Sharaf et al., 2016). This ant species was more abundant in *Tabebuia aurea* than in *Tabebuia heterophylla*. The Mann-Whitney *U*-test showed a significant difference in the abundance of *T. destructor* between *T. aurea* and *T. heterophylla* (p=0.002). This ant was also found feeding on nymphs of *Holopothrips tabebuia* (Figure 1-E).

An effort was made to gauge the hurricane effect on this plant-animal interaction. A Spearman correlation was made with *Tabebuia heterophylla* only, because the insect was more abundant on this host. There was a significant (p=0.009) negative correlation between damage to the tree caused by the hurricane and the infestation category (1, 2, 3, 4, 5; See methods). Moreover, the damage to the tree negatively correlated with nymphs and adults of *Holopothrips tabebuia* (Table 3).

DISCUSSION

Hurricane María had a negative effect on the dynamics of *Holopothrips tabebuia* and its interaction with the hosts. Due to the strength of the winds generated (preliminary data from the National Hurricane Center indicates wind speeds between 266 to 322 kph), defoliation was common to both hosts (*Tabebuia aurea* and *Tabebuia heterophylla*). Defoliation is a typical response of trees to hurricane winds (Francis, 2000; Walker, 1991). Defoliation percentage for *T. heterophylla*, at least

TABLE 3.—*Spearman correlation between percentage of damage of trees of T. heterophylla* (n=125) after Hurricane María and variables measured.

Measured Variable	Correlation coefficient	*p*
Nymphs of *Holopothrips tabebuia*	- 0.27	0.0002
Adults of *Holopothrips tabebuia*	- 0.25	0.0009
Percentage of infestation	- 0.26	0.001

in San Juan, was similar to previous data (Francis, 2000). With less foliage, the availability of habitat for thrips and other species that feed on foliage diminishes, thus indirectly affecting the population of *Holopothrips tabebuia*.

The density and abundance of arthropods can be directly affected by wind speeds. The density of the onion thrip (*Thrips tabaci*) in New York, for instance, is reduced as wind speeds increase (Smith et al., 2016). Since thrips are very small insects with small wings and weak flying mechanisms (Lewis, 1991; Tipping, 2008), it is likely that intense winds will blow them away. Wind speed likely affected directly the abundance and density of *H. tabebuia* in both hosts, therefore altering their interactions. After the hurricane, the density and abundance of *Holopothrips tabebuia* and the number of infested trees in Puerto Rico decreased in both hosts. We suspect that this reduction is temporary, as recovery of the trees can take more than one year. As suggested by Cabrera et al. (2008), data after the hurricane also demonstrated that *Holopothrips tabebuia* has a preference for *T. heterophylla,* After María, *H. tabebuia* has rarely been observed in *T. aurea.*

This preference of host could be due to an increase in predators present in *T. aurea.* The ant *Trichomyrmex destructor*, which was observed feeding on nymphs, increases to three the number of reported predator species on *H. tabebuia.* These predators are: *Montandoniola moraguezi* Puton, a hemipteran (Dobb and Boyd, 2006), *Androthrips ramachandri* Karny, a thrip (Cabrera and Vélez, 2009), and the new report of *Trichomyrmex destructor*. Under starvation, *T. destructor* prefers protein and carbohydrates as food (Annie and Lee, 2007). Other ant species have been documented feeding on thrips (Kirk, 1984).

Hurricane María had an impact on the population of *Holopothrips tabebuia* and its interaction with the host. As the correlation demonstrated, the greater the hurricane damage to the host *Tabebuia heterophylla*, the less abundance of both nymphs and adults of *H. tabebuia*. Furthermore, the more damage *T. heterophylla* sustained after the hurricane, the less infestation observed, underlining that hurricane disturbance indeed influences the abundance and density of *H. tabebuia* and plant-animal interactions in the herbivore-host systems.

CONCLUSION

Hurricane María affected *Holopothrips tabebuia* dynamics and its hosts as in previously reported data on other arthropods and trees (Francis, 2000; Walker, 1991; Willig and Camillo, 1991; Willig et al., 2011). An effect on the plant-insect interaction is also reported, since a lower infestation percentage was observed after the hurricane. Hur-

ricane winds can affect thrips directly by blowing individuals away from their hosts. Additionally, the population of thrips was indirectly affected because trees lost their foliage. New leaf shoots on trees are known to be more palatable (Spiller and Agrawal, 2003), making it likely that thrips colonize these leaves. However, knowing that intense winds cause high individual mortality of thrips (Lewis, 1991), it is possible that the lower infestation percentages are the result of early infestation stages. We recommend that long-term studies continue to monitor this plant-insect system to determine any long-term effect of the hurricane on the population and interaction of *Holopothrips tabebuia* with its hosts, as recovery of the vegetation might trigger a resurgence of the parasite.

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