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Invasive rodent responses to experimental and natural hurricanes with implications for global climate change

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ARTICLE

Special Feature: Tropical Forest Responses to Repeated Large-Scale Experimental Hurricane Effects

Invasive rodent responses to experimental and natural hurricanes with implications for global climate change

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Abstract

Hurricanes cause dramatic changes to forests by opening the canopy and depositing debris onto the forest floor. How invasive rodent populations respond to hurricanes is not well understood, but shifts in rodent abundance and foraging may result from scarce fruit and seed resources that follow hurricanes. We conducted studies in a wet tropical forest in Puerto Rico to better understand how experimental (canopy trimming experiment) and natural (Hurricane Maria) hurricane effects alter populations of invasive rodents (*Rattus rattus* [rats] and *Mus musculus* [mice]) and their foraging behaviors. To monitor rodent populations, we used tracking tunnels (inked and baited cards inside tunnels enabling identification of animal visitors' footprints) within experimental hurricane plots (arborist trimmed in 2014) and reference plots (closed canopy forest). To assess shifts in rodent foraging, we compared seed removal of two tree species (*Guarea guidonia* and *Prestoea acuminata*) between vertebrate-excluded and free-access treatments in the same experimental and reference plots, and did so 3 months before and 9 months after Hurricane Maria (2017). Trail cameras were used to identify animals responsible for seed removal. Rat incidences generated from tracking tunnel surveys indicated that rat populations were not significantly affected by experimental or natural hurricanes. Before Hurricane Maria there were no mice in the forest interior, yet mice were present in forest plots closest to the road after the hurricane, and their forest invasion coincided with increased grass cover resulting from open forest canopy. Seed removal of *Guarea* and *Prestoea* across all plots was rat dominated (75%–100% rat-removed) and was significantly less after than before Hurricane Maria. However, following Hurricane Maria, the experimental hurricane treatment plots of 2014 had 3.6 times greater seed removal by invasive rats than did the reference plots, which may have resulted from rats selecting post-hurricane forest patches with greater understory cover for foraging. Invasive rodents are resistant to hurricane disturbance in this forest. Predictions of increased hurricane frequency from expected climate change should result in forest with more frequent periods of grassy understories and mouse presence, as well as with heightened rat foraging for fruit and seed in preexisting areas of disturbance.

KEYWORDS
canopy disturbance, cyclone, foraging shift, frugivory, granivory, grass understory, Luquillo Experimental Forest, *Mus musculus*, Puerto Rico, *Rattus rattus*, rodent abundances, seed predation, Special Feature: Tropical Forest Responses to Repeated Large-Scale Experimental Hurricane Effects

INTRODUCTION

Hurricanes greatly alter ecosystems and often the species that occupy them (see special journal issues: Middleton & Smith, 2009; Shiels & González, 2014; Turton, 2008; Walker et al., 1991; this issue). Our understanding of how hurricanes affect vertebrate wildlife mostly has been through studies focused on birds (Freeman et al., 2008; Wiley & Wunderle, 1993) or primates (Behie & Pavelka, 2005; Schaffner et al., 2012; Tsuji & Takatsuki, 2008). Because hurricane impacts to forests include stripping leaves and branches, as well as flowers, fruits, and seeds upon which a suite of animals rely, hurricanes most often negatively affect vertebrate wildlife abundances, and especially frugivores (Gannon & Willig, 1994; McConkey et al., 2004; Pavelka et al., 2007; Waide, 1991; Wunderle et al., 1992; Wunderle, 2017). For example, populations of howler monkeys (*Alouatta pigra*) decreased by 88% following a major hurricane (i.e., Categories 3–5 on Saffir-Simpson scale) in Belize (Pavelka et al., 2007), and the brown lemur (*Eulemur fulvus fulvus*) population on Mayotte Island decreased by 50% following a hurricane (Tarnaud & Simmens, 2002). Additionally, bird species declined by 10.2% immediately after Hurricane Maria in Puerto Rico and frugivorous species were most negatively impacted as several species decreased by 70%–80% (Wunderle, 2017). Despite the negative effects of hurricanes on many vertebrate species, hurricanes can benefit some species (e.g., Greater Antillean long-tongued bat [*Monophyllus redmani*]: Gannon & Willig, 1994; roe deer [*Capreolus capreolus*]: Widmer et al., 2004) or not significantly change species abundances (Jamaican tody [*Todus todus*]: Wunderle et al., 1992; mountain coqui frog [*Eleutherodactylus portoricensis*]: Lopez-Hernández & Puente-Rolón, 2021). Hurricanes may benefit wildlife by the creation of new habitats (Brown et al., 2011; Saïd & Servanty, 2005; Woolbright, 1991), or through reductions in abundances of competitors or predators (Gannon & Willig, 1994).

Invasive rodents, particularly *Rattus* spp. and *Mus musculus* (house mice), inhabit most islands and continents worldwide (Atkinson, 1985; Towns, 2009). Omnivorous diets and the ability to live successfully in anthropogenic and natural environments have enabled these species to occupy a wide range of ecosystems and play important roles in food webs (Shiels, Pitt, et al., 2014; Towns, 2009). The damage caused by these species is widespread, including $20 billion per year in the United States alone, affecting agriculture, human health and safety, and natural resources (Pimentel et al., 2000). On islands, these invasive rodents are responsible for some of the greatest numbers of plant and animal extinctions (St Clair, 2011; Towns et al., 2006).

How rodents respond to hurricanes has not been well studied, especially in natural settings such as forests. In urban settings following hurricanes, invasive rodents can become hyperabundant and may help drive local outbreaks of zoonotic disease (Peterson et al., 2020; Rael et al., 2016). In natural settings of a dry forest and a coastal wildlife preserve, Shiels et al. (2020) reported an increase in invasive house mice and no change in invasive black rat (*R. rattus*) incidences (presence and activity) following Hurricanes Irma and Maria passing over the US Virgin Islands in the Caribbean. Similarly, when Cyclone Heta passed over the South Pacific island nation of Niue, black rat abundance in forest and scrub did not change relative to before the storm (Powlesland et al., 2006). In the southern United States, Pries et al. (2009) reported that beach mice (*Peromyscus polionotus*) decreased in abundance simultaneously with the loss of their dune habitat from Hurricane Ivan. In a Mexican dry forest, hurricanes reduced rodent species diversity and the dominant rodent's (*Liomys pictus*) population abundance, which possibly resulted in declines in seed dispersal (Tapia-Palacios et al., 2018). Aside from these four studies, little is known about rodent responses to hurricanes in natural settings.

Black rats and house mice are two rodent species that occupy the Luquillo Experimental Forest (LEF) of northeastern Puerto Rico (Shiels & Ramírez de Arellano, 2018; Zimmerman et al., 2021). There are no extant native rodents in Puerto Rico, and the ecological roles of the three or more native rodent species that were in Puerto Rico's prehistoric fauna are largely unknown (Turvey et al., 2007). Whereas house mice are restricted to roadsides and do not occupy the forest interior, black rats are the most abundant rodent in the LEF and occupy all habitats, including those across the range of common disturbances in the forest (i.e., landslides, treefall gaps, hurricane plots, riparian zones, and mature forest; Shiels & Ramírez de Arellano, 2018). Black rats are important frugivores and seed predators in the canopy and on the ground in the LEF (Shiels & Ramírez de Arellano, 2019; Weinbren et al., 1970; Willig & Gannon, 1996), and are threats to many native birds including the endangered Puerto Rican parrot (*Amazona vittata*) (Engeman et al., 2006; Zwank & Layton, 1989).

In this study, we sought to better understand how the incidence of invasive rodents and their foraging behaviors (fruit and seed removal) are affected by hurricanes. We sampled within the canopy trimming experiment (CTE) treatment and reference plots prior to and following Hurricane Maria. The CTE is a long-term hurricane experiment in the LEF that was designed in early 2000 with replicate treatment and control (reference) plots to determine (1) the mechanistic factors driving forest responses to major hurricanes (Shiels et al., 2015; Shiels & González, 2014), and (2) the repeated effects of hurricane damage to this tropical forest, as hurricane frequency is predicted to increase in this region as a result of global climate change (Emanuel, 2013). The most recent canopy trimming treatments of the CTE occurred in 2014. Unexpectedly, in 2017, Hurricane Maria passed over the LEF and the CTE. These events set up an opportunity to compare forest plots that experienced just one hurricane versus others that experienced two hurricanes (one natural and one simulated) within three years. We asked the following questions:

1. How do rodent incidence (determined via tracking tunnels) and seed removal differ before and after a major hurricane, and in canopy-trimmed plots versus reference plots?
2. What are the types of rodents and other vertebrates that remove seeds from the forest floor prior to and following hurricane disturbance, and do certain vertebrates more readily remove certain types of seeds over others prior to and following disturbance?

MATERIALS AND METHODS

Study site

Our study was conducted in the CTE plots, which are at 300–425 m elevation in El Verde Field Station (EVFS; 18°20′ N, 65°49′ W) section of the LEF in northeastern Puerto Rico. The LEF is a 19,650-ha tropical evergreen forest where temperature and precipitation are only mildly seasonal. Mean monthly temperature at EVFS is 25°C, and mean annual precipitation is 346 cm (Brokaw et al., 2012). Disturbances in this forest, such as landslides, hurricanes, treefalls, and floods, result in modified habitats that affect resource heterogeneity and redistribution of animal populations (Reagan & Waide, 1996; Shiels & Ramírez de Arellano, 2019). The most common trees at the site are *Dacryodes excelsa* (Burseraceae), *Prestoea acuminata* var. *montana* (syn. *Prestoea montana*; Arecaceae), *Sloanea berteroana* (Elaeocarpaceae), and *Manilkara bidentata* (Sapotaceae; Shiels et al., 2010), and average canopy height is 18.1 ± 0.3 m (Shiels & González, 2014).

The CTE was designed with three replicates (Blocks A, B, and C), each containing four 30 × 30 m plots (Figure 1) to represent the original four treatment combinations (a factorial design, with and without canopy trimming and with or without debris addition) that were established by 2004 (Shiels et al., 2015; Shiels & González, 2014). The four treatments were as follows: (1) trim + debris, (2) trim + no debris, (3) no trim + debris, and (4) no trim + no debris (control or reference treatment). In 2014, there was a second iteration of the CTE where only the trim + debris treatment was reapplied. To complete this treatment, the same methods were used as in 2004, which were that all non-palm trees ≥15 cm dbh within the 30 × 30 m plot had branches that were less than 10 cm diameter removed; non-palm trees 10–15 cm dbh were trimmed at 3 m height; palm trees ≥3 m had all leaves removed and the apical meristem preserved (Richardson et al., 2010; Shiels et al., 2010; Shiels & González, 2014). The area trimmed included the vertical projection of the 30 × 30 m plot; the 20 × 20 m core area of each plot was used for data collection and measurement. By 2014, both canopy openness and the major attributes of vegetation treated during the 2004 CTE factorial experiment had recovered to pretreatment levels (see Hogan et al., 2022). Therefore, for our rodent study (executed in 2017–2018), we considered the reference plots to be those that had not been disturbed for 13 years or more (i.e., trim + no debris, no trim + debris, and no trim + no debris; $n = 9$ plots) and the treatment plots ($n = 3$) were the trim + debris (herein referred to as the treatment or trimmed canopy plots).

Prior to our study, three major hurricanes passed over the LEF in the last 30 years. Our study's pre-hurricane measurements for rodents occurred 2–3 months prior to Hurricane Maria passing over the LEF on 20 September 2017, and our post-hurricane sampling occurred 9 months after this hurricane.

Measurements of canopy openness and grass cover

To better describe the environmental conditions of the 12 plots used in our study, we measured the openness of

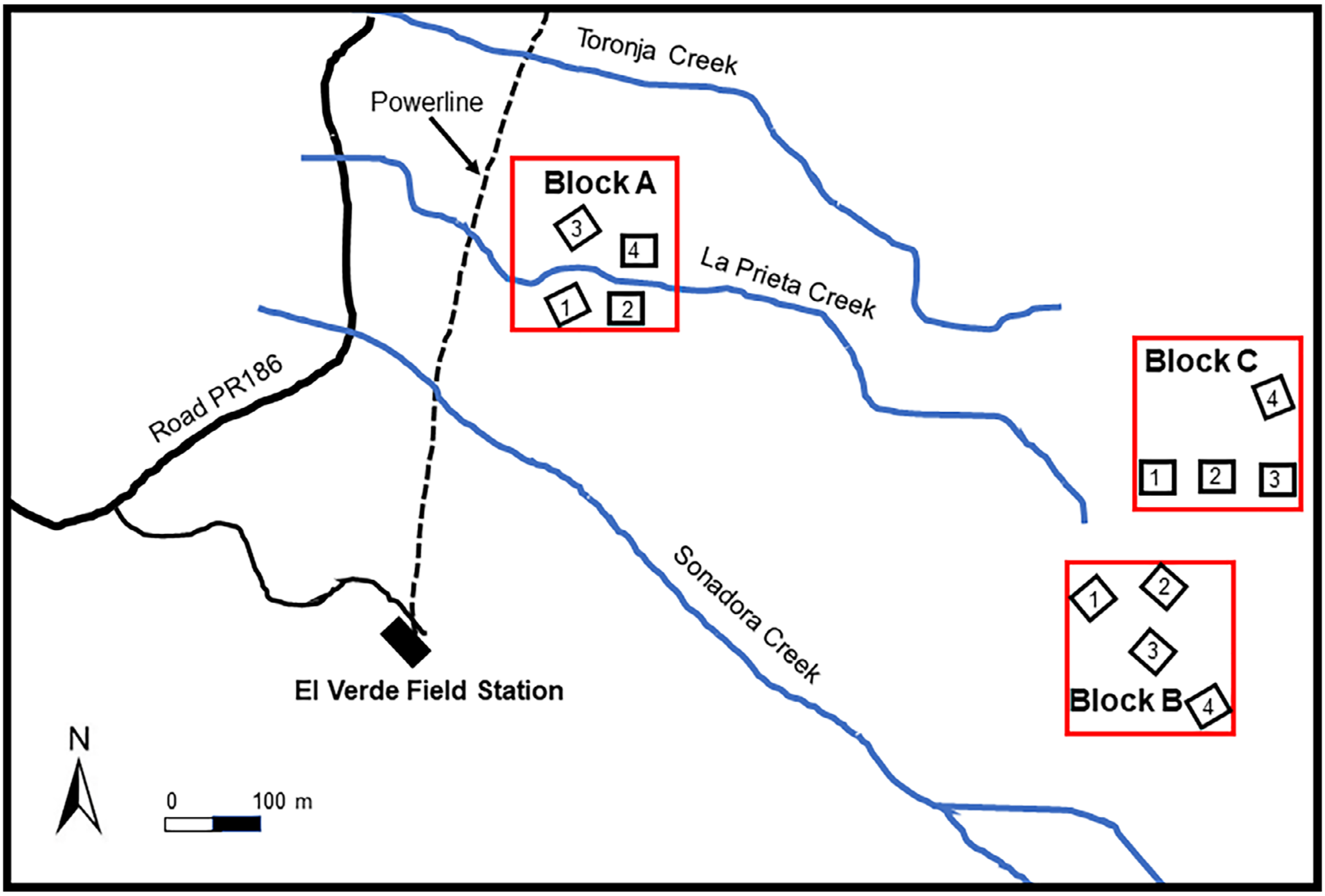

FIGURE 1 Map of the El Verde section of the Luquillo Experimental Forest, Puerto Rico, showing the 12 numbered plots (1–4, divided into three blocks) used in this study. Plots A3, B2, and C2 are the trimmed canopy plots whereas the remaining plots are the reference plots. Each plot was separated by at least 30 m distance.

the canopy and the grass coverage before and after the hurricane. Both canopy openness and grass cover are variables known to influence rodent behavior (Cox et al., 2000; Shiels, Pitt, et al., 2014; Shiels et al., 2017). Canopy openness was determined 9 months before and 9 months after Hurricane Maria by taking hemispherical pictures using a digital camera (Nikon 4500, Nikon Inc, Tokyo, Japan) with a fish-eye lens (Nikon FC-E8) positioned at 1 m height above ground using a tripod, at five locations (i.e., the four corners and the center) in each 20 × 20 m measurement area of the plot. The photos were taken on the following dates: 7–16 December 2016 (pre-hurricane), and 1–3 July 2018 (post-hurricane). Each picture was analyzed for percent canopy openness using Gap Light Analyzer software (version 2; Simon Fraser University, Cary Institute of Ecosystem Studies), setting thresholds at 82 for all 2016 pictures and 152 for all 2018 pictures; the higher threshold was needed in 2018 to prevent the greater light levels from obscuring the remaining vegetation. Percent canopy openness was based on the average of the five pictures per plot. Grass cover (percent ground coverage <1 m height) was visually estimated to the nearest 1% in September or early October of each year since the onset of the experiment within five permanent 1 × 3.5 m subplots within each of the 12 plots (see Shiels et al., 2010). We obtained an annual average of the five subplots per plot to use in our analysis ($n = 3$ for canopy-trimmed plots; $n = 9$ for reference plots) for 2012–2019.

Tracking tunnels

To assess rodent incidence, which is a reflection of abundance and activity, we used tracking tunnels in each plot. Tracking tunnels are inked and baited cards placed in tunnels enabling foot prints of vertebrate visitors to be identified to genus (Madden et al., 2019; Shiels & Ramírez de Arellano, 2018, 2019). In each of the 12 CTE plots, two tracking tunnels that were 60 cm long with 10 × 10-cm openings were randomly placed approximately 10 m apart from each other; one tunnel was placed on the ground, and the other tunnel was secured by plastic straps on a branch or liana in the lower canopy at an average height of 135 cm (SE = 5 cm). Whereas house mice are frequently active on the ground and to heights of about 1 m above ground (Shiels, 2010), black rats are known to be both arboreal and ground active (Madden et al., 2019; Shiels, 2010; Towns, 2009). Paper cards placed in each tracking tunnel had bait in the middle, which was surrounded by ink. The bait was a 2 × 2-cm coconut chunk placed on top of Skippy peanut butter. Coconut and peanut butter are highly attractive to *Rattus* spp. and house mice (Shiels, 2010; Shiels et al., 2017; Shiels & Ramírez de Arellano, 2018). All tracking tunnels, cards, and ink were purchased from Pest Control Research LP (www.traps.co.nz). Tracking tunnels were deployed for a total of 48 h prior to (4 June 2017) and following (9 June 2018) Hurricane Maria. Previous studies in the LEF and the US Virgin Islands show that rats and mice visit tracking tunnels within 24 h (Shiels et al., 2020; Shiels & Ramírez de Arellano, 2018, 2019), and although we checked them for tracks at 24 and 48 h, we used 48 h in our analysis. Because of the close distance between the two tracking tunnels in each plot, the presence of foot tracks of rodents in either tunnel (on the ground or in the lower canopy) was used as indication of presence in the plot and was subsequently used in the statistical analysis (i.e., $n = 12$ plots per year). Although the nightly distances traveled by rodents in the LEF are unknown, rodents could have moved between plots during our study. However, the distances between adjacent plots (at least 30 m) were probably large enough to prevent frequent nightly movements as black rats in Hawaiian forest moved a maximum of 31 m linear distance in a night, and house mice moved a maximum of 21 m linear distance in a night (Shiels, 2010). After our 2018 sampling was completed and we learned of the invasion of house mice into some plots in Block A, we resampled the four plots in Block A using tracking tunnels set for 48 h (checked for tracks at 24 and 48 h) in December 2021 to determine whether house mice were still present in the forest interior closest to the road 4 years after Hurricane Maria.

Seed removal trials

Trials were conducted to determine whether rats had removed native seeds from the forest floor. Two common tree species, muskwood (*Guarea guidonia*, Meliaceae) and sierra palm (*P. acuminata*, Arecaceae), were chosen based on their fruit and seed availability during the trial period (June–July 2017 and 2018). Plant species are hereafter referred to by genus. When the first set of seed removal trials occurred in 2017, there were four species (*Guarea* and *Prestoea* plus two others) tested in the CTE plots and additional plots of disturbed habitats (e.g., treefall gap, powerline gap, and riparian plots) and undisturbed forest (Shiels & Ramírez de Arellano, 2019). However, after Hurricane Maria, we were unsuccessful at locating ripe fruits and seeds (hereafter referred to as seed) of the four target species, so we narrowed our seed removal trials to just two species. Freshly fallen *Guarea* seeds were collected in 2017 and 2018 from the forest floor near EVFS. While freshly fallen *Prestoea* seeds in 2017 also were collected from the forest floor near EVFS, the lack of available fresh *Prestoea* seed in 2018 required us to search further outside of EVFS vicinity and collect ripe seed from one tree as well as below two other trees. Seeds of both species were stored in a refrigerator in 2017 to slow their decomposition until used in the trials (Shiels & Ramírez de Arellano, 2019), yet 2018 seeds were used within 24 h of collection, so no refrigeration occurred. Prior to placing the seeds in field plots, conspecific seeds were mixed and then chosen randomly to appear in each station (Caged vs. Open) of the 12 CTE plots (Figure 1). The two treatments per plot were spaced 10 m apart and randomly assigned as either: (1) Caged treatment, where the seeds were enclosed within a metal-mesh (1-cm aperture) cage (30 × 30 × 30 cm; lacking a floor) to exclude all rodents and other frugivorous vertebrates from accessing them, or (2) Open treatment, where seeds were placed on the forest floor without any caging, allowing all animals to freely access them. Because seed size differed between the two species (*Guarea*: 4.3 ± 0.2 g, *Prestoea*: 12.4 ± 0.5 g), the number of seeds placed in each station was six for *Guarea* and three for *Prestoea*. At each of the 12 Open treatment replicates, Reconyx HyperFire trail cameras (models HC500 and HC600) were positioned no more than 50 cm from the seeds, secured to a tree at 30–50 cm aboveground, and adjusted to face the seeds to monitor the organisms responsible for seed contact (see below) and removal. The cameras were set to take from 2 to 5 pictures 1 s apart every time they were triggered by motion. The number of seeds removed from each station was monitored on 1, 3, and 7 days after being set. If any seeds were missing on these days, then the Secure Digital card was replaced with a blank one and the pictures were observed for the following: date, time, animal pictured, contact with seed (including contact with any part of the animal's body, as well as consumption or removal), and removal of seed. At the end of each trial, and to ensure independence among trials, every treatment station (Open and Caged) was moved at least 3 m to another random location in the plot. Trial dates in 2017 were as follows:

Guarea 11–18 June and *Prestoea* 17–24 July. Trial dates in 2018 were as follows: *Guarea* 30 June–7 July and *Prestoea* 17–24 June.

Statistical analysis

To evaluate treatment effects on canopy openness, we used a repeated measures ANOVA, and compared the effects of trimming treatment (trimmed canopy [$n = 3$] vs. reference [$n = 9$]), hurricane treatment (before Hurricane Maria [2016] vs. after Hurricane Maria [2018]), and their interaction (trimming × hurricane). Prior to this analysis, we transformed the canopy openness response variable using arcsin square-root and checked treatment combinations to meet assumptions of homoscedasticity and normality.

To evaluate differences in rat incidence (i.e., presence of rat tracks inside tracking tunnels after 2 days of observation) between trimming treatment and hurricane treatment (2017 vs. 2018), we used a binomial generalized linear mixed-effects model that included the interactions of these treatment factors in one model. To account for repeated measurement in 2017 and 2018, we used the $(1|X)$ notation to specify plot as a random effect by using the command glmer in R package lme4. For this analysis, and to ensure that we were not overestimating rat tracking by counting both a tracking tunnel on the ground and in the lower canopy of the same plot, rat tracking tunnel observations from tunnels in the lower canopy were combined with those on the ground. A separate logistic regression (binomial generalized linear mixed-effects model) was used to determine whether rat tracking was more frequent in the lower canopy versus on the ground (i.e., habitat treatment) during 2017–2018. Importantly, sample sizes are low in our study (i.e., $n = 3$ for trimmed canopy and $n = 9$ for reference plots), and commonly recommended minimum "rules of thumb" range from 10 to 20 events for each covariate in a logistic regression (Stoltzfus, 2011). Although we were restricted by plots already established for the CTE and the unpredictable timing of a major hurricane, our findings should be interpreted with the knowledge that these low sample sizes constrain statistical power for detecting differences related to treatments.

To assess evidence of differences in seed removal between Caged and Open treatments, we included both species ($n = 48$ per Caged and Open per treatment) in generalized linear model with binomial errors; once we determined that the Open treatments were indeed receiving frequent seed removal and Caged treatments were not ($z = 2.289$, $SE = 0.615$, $p = 0.0221$; only 2 of 216 seeds disappeared from Caged treatments during all trials), we excluded the Caged treatment in all subsequent analyses. Therefore, to determine the variables influencing the total numbers of seeds removed by Day 7 (Open treatment only), we used a generalized linear mixed-effects model (with Poisson errors) that included canopy treatment, hurricane treatment, seed treatment (*Guarea* vs. *Prestoea*), and the interactions of these treatment variables in a single model. To account for repeated measurement (2017 and 2018), we used the $(1|X)$ notation to specify plot as a random effect by using the command glmer in R package lme4. The same cautions stated for our logistic regression analyses regarding our low sample sizes and likelihood of low statistical power apply to the seed removal analysis. All statistical analyses were conducted in R version 4.2.0, and significant differences were based on $p \leq 0.05$.

RESULTS

Measurements of canopy openness and grass cover

In our 2016 sampling, which was 2 years after the CTE canopy trimming occurred and 1 year prior to Hurricane Maria, the canopy openness for the trimming treatments was within 0.5% of each other (trimmed canopy [mean ± SE]: 5.40 ± 0.75%, reference: 4.90 ± 0.25%). Hurricane Maria caused a significant hurricane treatment effect ($F_{1,10} = 807.65$, $p < 0.001$) for canopy openness (measured in 2018, 9 months after the storm) as both trimmed canopy ($n = 3$) and reference plots ($n = 9$) increased three to four times relative to the 2016 pre-hurricane state (2018 trimmed canopy: 16.77 ± 0.64%, 2018 reference: 18.15 ± 0.79%). There was no significant trimming treatment effect ($F_{1,10} = 0.04$, $p = 0.855$) and no trimming treatment × hurricane treatment interaction ($F_{1,10} = 3.13$, $p = 0.107$) despite post-hurricane canopy openness tending to be approximately 1.5% greater in the reference plots relative to the trimmed canopy plots.

Prior to the 2014 CTE treatment, there was little grass cover (<0.5%) in trimmed canopy plots and reference plots. Following the 2014 CTE treatments, the canopy-trimmed plots steadily increased to >20% cover just before Hurricane Maria, whereas the reference plots remained at <0.5% cover (Figure 2). After Hurricane Maria, and when grass cover was measured 21 days after the storm, grass cover in trimmed canopy plots declined by about 5% and then steadily rose to reach >35% cover by 2019. In the reference plots, the post-hurricane response of grass cover quickly increased after the 2017 sampling, reaching 15% by 2018 and 20% by 2019 (Figure 2).

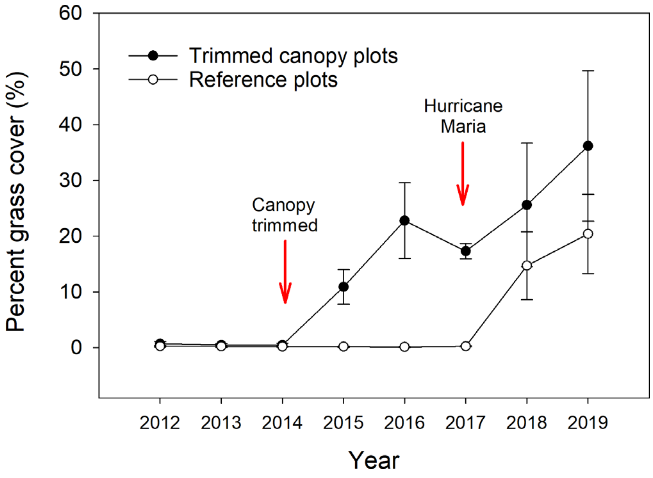

FIGURE 2 Mean ± SE percent grass cover in trimmed canopy plots ($n = 3$) and reference plots ($n = 9$) before and after the 2014 canopy trimming experiment and the 2017 Hurricane Maria. Grass was measured 21 days after Hurricane Maria passed over during the 2017 sampling.

Tracking tunnels

Tracking tunnels revealed that rats were present on the ground and in the lower canopy in both trimming treatments (i.e., trimmed canopy and reference) prior to and after Hurricane Maria. Although rats were the only rodent detected in 2017, there were two plots with house mice present in 2018 (Figure 3). Both plots with house mice were in reference plots that were closest to the road (170–220 m distance). Our sampling in December 2021, which was 4 years after Hurricane Maria, revealed that house mice were still present in these two forest plots. In the 2017–2018 sampling, there was no significant difference in rat tracking (percent incidence) between the trimming treatments ($z = 0.38$, $\mathrm{SE} = 1.46$, $p = 0.702$). Similarly, there were no significant differences between hurricane treatments ($z = 0.98$, $\mathrm{SE} = 1.04$, $p = 0.325$) nor the interaction between trimming treatments and hurricane treatments ($z = 0.51$, $\mathrm{SE} = 2.02$, $p = 0.611$), indicating that the major hurricane did not alter rat incidence at this site. In both 2017 and 2018, two of the three canopy-trimmed plots had rat tracking.

When a separate model was run to determine whether the rat incidence differed between the ground versus lower canopy, and before versus after Hurricane Maria, there were no significant differences. That is, rat incidences were not significantly different for habitat treatment (ground vs. canopy; $z = 0.57$, $\mathrm{SE} = 0.60$, $p = 0.109$), hurricane treatment ($z = 0.84$, $\mathrm{SE} = 2.02$, $p = 0.415$), or their interaction ($z = 1.72$, $\mathrm{SE} = 1.25$, $p = 0.086$). In 2017, 9 of 12 tunnels in the lower canopy contained rat tracks and 7 of 12 tunnels on the ground contained rat tracks. In 2018, 5 of 12 tunnels in the lower canopy had rat tracks and 7 of 12 tunnels on the ground had rat tracks.

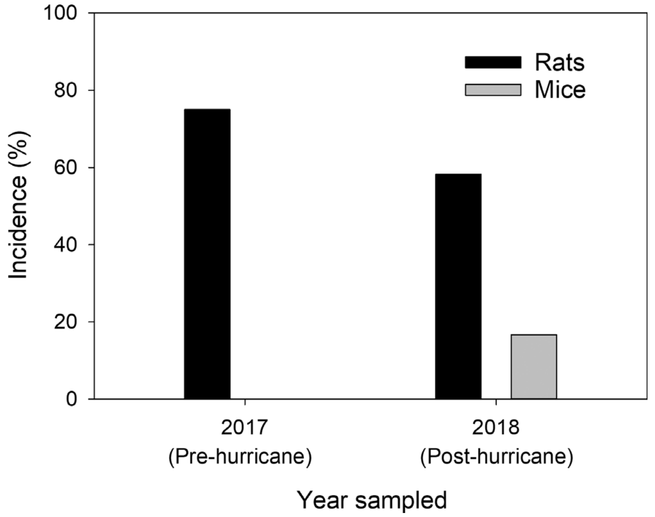

FIGURE 3 Incidence (%) of black rats (*Rattus rattus*) and house mice (*Mus musculus*) determined using tracking tunnels placed in the Luquillo Experimental Forest, Puerto Rico, prior to and after Hurricane Maria. There were 12 plots sampled, with two tracking tunnels in each plot placed on either the ground or in the lower canopy. Incidence was calculated as the number of plots with tunnels tracked by each species out of the total number of plots with tunnels ($n = 12$).

Seed removal trials

Numbers of vertebrate accessible seeds removed from the forest floor in each 7-day trial were 4–14, with up to 19.4% removed for *Guarea* and 13.9% removed for *Prestoea*. Our model outputs had two statistically significant individual variables (seed treatment and hurricane treatment) and one interaction (trimming treatment × hurricane treatment) that influenced the numbers of seeds removed by vertebrates at 7 days. There was a significant seed treatment effect, where *Guarea* had greater seed removal than did *Prestoea* for both years of study ($z = 2.20$, $\mathrm{SE} = 1.05$, $p = 0.028$). When seed removal for 7 days for both tree species was combined, there was a significant hurricane treatment effect, where more seeds were removed prior to the hurricane (in 2017) than after the hurricane (in 2018) ($z = 2.20$, $\mathrm{SE} = 1.05$, $p = 0.028$). In fact, there were about three times as many seeds removed by vertebrates prior to the hurricane as after the hurricane (Figure 4). Additionally, there was a significant trimming treatment × hurricane treatment interaction ($z = 2.20$, $\mathrm{SE} = 1.23$, $p = 0.028$) that was driven by an average of 3.6 times greater numbers of vertebrate removed seeds

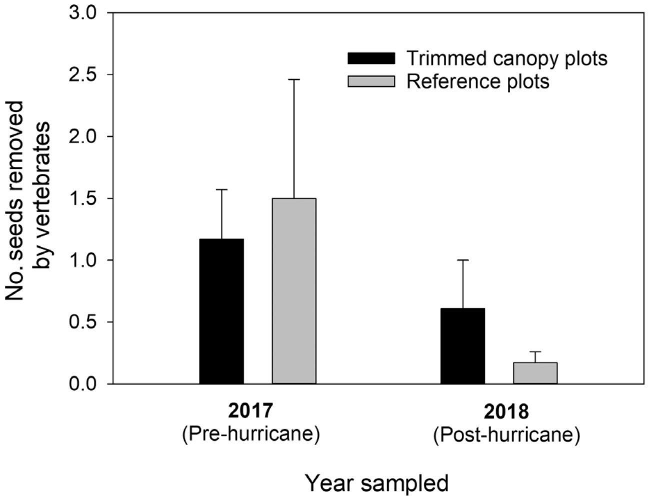

FIGURE 4 Mean ± SE number of seeds (*Guarea guidonia* and *Prestoea acuminata* combined) removed by vertebrates in trimmed canopy plots ($n = 3$) and reference plots ($n = 9$) before and after Hurricane Maria.

from the trimmed canopy plots (0.61 seeds removed) than the reference plot (0.17 seeds removed) following Hurricane Maria (Figure 4). Prior to Hurricane Maria, the trimmed canopy plots had similar numbers of seeds removed as the reference plots (Figure 4). The main effect of the trimming treatment was not statistically significant ($z = 0.62$, $\mathrm{SE} = 0.94$, $p = 0.536$). Despite *Guarea* having twice as many seeds (14 seeds vs. 7 seeds) taken by vertebrates in 2017 (pre-Hurricane Maria) as in 2018 (post-Hurricane Maria), and there was a similar tendency to remove more *Prestoea* seeds from the trimmed canopy plots than from the reference plots, no significant difference characterized seed removal between species or years (seed treatment × hurricane treatment: $z = 1.86$, $\mathrm{SE} = 1.61$, $p = 0.063$). Finally, the three-way interaction (seed treatment × trimming treatment × hurricane treatment) was not significant ($z = 1.91$, $\mathrm{SE} = 1.77$, $p = 0.076$). It is unlikely that our use of numbers of seeds removed has biased our conclusions about the relative attractiveness of each species to vertebrates because all experimentally offered seeds at a station (i.e., either six for *Guarea* or three for *Prestoea*) were rarely removed from a station. In fact, there were just two occurrences with *Guarea*, and none with *Prestoea*, where all seeds at a station were removed.

Based on the monitoring cameras, the number of days it took for seeds to be removed by vertebrates differed between species and between year. Seed removal tended to take longer after the hurricane (2018) than before the hurricane (2017). *Prestoea* seeds were always removed during the first 1–3 days after placement in the plots, as it took 1.5 ± 0.5 (mean ± SE) days until seeds were removed in 2017, and 1.3 ± 0.3 days in 2018. For *Guarea*, six of the seven seeds removed in 2017 were removed in 1 day, averaging 2.6 (±0.7) days, whereas in 2018 *Guarea* seeds were either removed at 3 or 5 days after being placed in the plots, averaging 4.7 (±0.3) days.

All seed removals by vertebrates were captured by trail cameras except for the disappearance of two seeds of *Guarea* in 2017 and 1 seed of *Prestoea* in 2018. The number of pictures with vertebrates removing seeds was $n = 10$ for *Guarea* 2017, $n = 7$ for *Guarea* 2018, $n = 4$ for *Prestoea* 2017, and $n = 4$ for *Prestoea* 2018. The main species removing seeds was the black rat, accounting for $\geq 75\%$ of all seed removal regardless of species and year. Birds were the only other animal that removed placed seeds during our study; ruddy quail doves (*Geotrygon montana*) removed some of the seeds of each species (two seeds of *Guarea* in 2017, one seed of *Prestoea* in 2018), and a pearly eyed thrasher (*Margarops fuscatus*) removed a *Guarea* seed in 2018. Additional vertebrates that were pictured passing by the seeds or sniffing them included a feral cat (*Felis catus*) in 2017 and several mongooses (*Herpestes auropunctatus*) in 2017 and in 2018.

DISCUSSION

The dramatic opening of the forest canopy by major hurricanes drives most of the abiotic and biotic changes in the LEF (Shiels, González, et al., 2014; Shiels et al., 2015; Zimmerman et al., 1996), and canopy openness appears to be a key factor for the changes in invasive rodent species. Canopy openness increases light in the forest understory, benefitting increased growth and recruitment of understory plants including grasses (Shiels et al., 2010) and such an expansive understory that follows major hurricanes like Hurricane Maria facilitates invasive house mouse establishment in the forest interior. The dominant black rats also shift foraging behavior as a result of these storms; patches of disturbed forest are more frequented locations for fruit and seed foraging. Whereas some wildlife species are quite sensitive to hurricane effects, even in forests adapted to major disturbances like those reported in the LEF (e.g., walking sticks [*Lamponius portoricensis*]: Zimmerman et al., 1996; Puerto Rican parrot: Beissinger et al., 2008; Engeman et al., 2006), invasive rodents appear resistant to the ecosystem changes resulting from these large storms.

Resistance of rodents and forest wildlife

Invasive black rats dominate the rodent community before and after hurricanes, and their relative presence (indicated by tracking tunnels) did not change significantly following hurricanes. Unlike urban areas where very high invasive rodent populations can be observed in the months following major hurricanes (Peterson et al., 2020; Rael et al., 2016), the incidence of rodents in the LEF did not change after experimental or natural hurricanes, including the 9 months after Hurricane Maria. Nonetheless, low sample sizes preclude our ability to make stronger conclusions about the changes in rodent populations and behaviors, as we were restricted by the incorporation of plots that were already established for the CTE and the unpredictable timing of a major hurricane. Changes in the relative presence of sympatric rodent species 9 months after major hurricanes were documented in a coastal ecosystem on St. Croix where the house mouse population increased and the black rat population remained constant (Shiels et al., 2020). Additional evidence of invasive rodent resistance has been reported after a major hurricane in the South Pacific, where both black rat and Pacific rat (*Rattus exulans*) population estimates in forest and scrub were unchanged 8 months after the hurricane (Powlesland et al., 2006). The level of resistance and resilience demonstrated by these invasive rodent species may be unsurprising given their successful establishment in a wide variety of ecosystems, ranging from commensal to natural settings far away from humans (Shiels, Pitt, et al., 2014; Towns, 2009). Tracking tunnels and monitoring of seed removal trials revealed the presence of black rats on the ground and lower canopy in patches of the LEF with different levels of hurricane disturbance. These persistent populations of invasive rodents can threaten native flora and fauna, especially after hurricanes cause additional stress to native species.

Following Hurricane Maria, mice invaded the forest interior by colonizing the grassy understory. Although we cannot say definitively that the grassy forest understory that is common after hurricanes (Shiels et al., 2010; Walker et al., 1996) caused house mice to colonize these habitats, it is well known that house mice prefer grassy habitat and are frequently the more dominant rodent species relative to black rats in grasslands (Moseley et al., 2022; Shiels et al., 2017). When dry forest and adjacent grassland habitats were compared in Hawaii, house mice outnumbered black rats (220:1) in grassland, whereas black rats dominated (5:1) in forest (Shiels et al., 2017). Across the LEF and prior to major hurricanes, house mice are generally confined to grassy roadsides (Shiels & Ramírez de Arellano, 2018), and grass is typically absent or <0.5% cover in the forest interior (Shiels et al., 2010, this study). Additionally, Madden et al. (2019) reported that house mice were not found in protected areas of little disturbance on St. Eustatius during their sampling just prior to, and during the first 5 months after, Hurricane Maria. House mouse abundance tended to increase along the LEF roadsides after Hurricane Maria (A. B. Shiels, unpublished data), and significantly increased in a coastal ecosystem at nearby St. Croix (Shiels et al., 2020). Similar to house mice, the grass-seed-consuming black-faced grassquit (*Melanospiza bicolor*) invaded the interior forest of the LEF after Hurricanes Hugo, Georges, and Maria (Wunderle, 1995; J. M. Wunderle, unpublished data). After persisting for 2 years in the grassy forest interior that followed Hurricane Hugo, the black-faced grassquits declined in the forest interior and resumed their occupancy of roadsides and in gaps (J. M. Wunderle, unpublished data). Isolated gaps with grassy understories like those that we measured in 2017 and that were produced by the CTE do not facilitate house mouse establishment because they are surrounded by closed forest that lacks grass. It was not until Hurricane Maria (or a previous hurricane when rodent responses were not measured in the LEF) that the interior of the forest had an abundance of grass cover that connected to the grassy roadside habitat where house mice reside; this continuous grassy habitat likely served as a corridor for house mice to expand from the roadsides into the closed canopy forest. The CTE plots (A1 and A2, Figure 1) that were closest to the road (Highway 186) were indeed those that had house mice established in 2018, and these two CTE plots were 170 and 220 m from the road. At the time of the tracking tunnel sampling in 2018, the mean grass cover was approximately 10%–25%. Our sampling in December 2021 of the four CTE plots closest to the road (Block A) revealed house mice were still present in A1 and A2 4 years after the hurricane and when grass cover had decreased to an average of 14% in these two plots. How long the house mouse population will persist in the forest interior is unknown, but we expect that it will retreat with the shift back to little grass cover, like that experienced prior to a hurricane, and the return interval to pre-hurricane grass cover previously documented in the CTE plots was approximately 5 years (Shiels et al., 2010). Another possibility is that house mice will not retreat with the closure of the forest canopy and reduction in grass cover, but they will remain established in the forest interior and possibly invade further into the forest after the next hurricane. Nevertheless, with forecasts of increased hurricane frequency (Emanuel, 2013), forests like the LEF may experience greater periods of both grass and house mice persistence along roadsides and forest interiors.

Forest alterations from major hurricanes have benefitted some vertebrate wildlife beyond the invasive rodents. Understory bird species increased in southern US hardwood forests following Hurricane Katrina because of favorable understory habitat created with enhanced resources (e.g., *Rubus* sp. fruit and cover) following the opening of the forest canopy (Brown et al., 2011). Roe deer foraging and habitat use increased in forest patches of dense grass and other early successional plant species that established in areas of severe damage resulting from Hurricane Lothar in France (Saïd & Servanty, 2005; Widmer et al., 2004). Pérez-Rivera (1991) observed a major shift in the Antillean euphonia (*Euphonia musica*) diet and foraging behavior 1–4 months after Hurricane Hugo. After the hurricane, this canopy mistletoe specialist foraged in the mid-story and understory where some fruit was present and was also gleaning leaves for insects and eating arthropods out of bromeliads. Whereas house mice in our study appeared to benefit from the favorable vegetative understory resulting from Hurricane Maria, black rats appeared to shift their plant-foraging activity after Hurricane Maria to patches of previously disturbed forest that had greater understory plant density and cover than areas surrounding the previously disturbed patches (Hogan et al., 2022; Shiels et al., 2010). Similar to black rats shifting to preexisting gaps for fruit and seed foraging following Hurricane Maria, many bird species in the LEF responded similarly after Hurricane Hugo passed over in 1989. Specifically, Wunderle (1995) reported that preexisting forest gaps, which had high fruit production during the months following Hurricane Hugo, were hotspots for bird densities and observations.

Consumption dynamics

Seed removal from the forest floor occurred nearly exclusively by black rats, as 75%–100% of the trail camera evidence confirmed black rats removed placed seeds of *Guarea* and *Prestoea*. The only other species contacting experimental seeds were ruddy quail doves and pearly eyed thrashers. Despite having documented house mouse presence using tracking tunnels in two of our plots, mice were never photographed visiting or passing by the *Guarea* and *Prestoea* seeds. House mice generally consume smaller seeds (e.g., grasses and herbs; Shiels et al., 2013) than those that we used, and this is another reason why black rats are often greater threats than are mice to many native tree species (Auld et al., 2010; Shiels, Pitt, et al., 2014). Following Hurricane Maria, *Guarea* and *Prestoea* seed removal by black rats greatly declined but was on average 3.6 times greater in the trimmed canopy plots than in reference plots. A likely explanation for this pattern is that black rats more frequently utilized the patches of forest with denser understory vegetation for foraging. Black rats favor areas of dense vegetation cover more than open habitat (Cox et al., 2000; Shiels, Pitt, et al., 2014), and it may be more difficult for predators to detect and catch rats in dense ground cover. Common predators of black rats in the LEF include the cryptic and native Puerto Rican boa (*Epicrates inornatus*) (Reagan, 1984), and invasive mongoose and feral cat (Engeman et al., 2006; Reagan & Waide, 1996). Both mongoose and cat were photographed in the vicinity of the placed *Guarea* and *Prestoea* seeds. In Australia, Bennett (1990) found that black rats were more common in disturbed and fragmented forest than in continuous forest stands. Additionally, vegetation cover was identified as an important component for differences in black rat presence in the LEF (Shiels & Ramírez de Arellano, 2019), and *Guarea* seeds were removed significantly more frequently by black rats in disturbed areas of forest and stream gaps than in continuous forest. Similarly, disturbed areas of early successional vegetation were LEF habitats where the greatest bird nest predation occurred following Hurricane Hugo, and the ground and understory nest predation reported was presumably due to black rats (Latta et al., 1995). Frequent black rat activity and foraging on the ground and lower canopy may affect plant recruitment and bird egg survival, and especially so in previously established gaps when a major hurricane passes over the forest. Furthermore, after major hurricanes, the closed forest areas that were not gaps prior to the hurricane may be safe sites for seeds and eggs to escape black rat predation.

Shiels and Ramírez de Arellano (2019) determined that *Guarea* was a much more desired seed for black rats than was *Prestoea*, as three times as many seeds were removed of *Guarea* (31% of placed seeds) than *Prestoea* (9% of placed seeds) prior to Hurricane Maria; however, their seed trials lasted 3 days longer than ours and included more disturbed and undisturbed replicate plots, including treefalls and stream gaps. Similarly, approximately twice as many *Guarea* seeds were removed as *Prestoea* seeds during our study within the CTE plots. The duration for seed removal to occur was longer for *Guarea* than for *Prestoea*, especially after Hurricane Maria. Following Hurricane Maria, *Guarea* seed removal occurred at 3–5 days after beginning trials, whereas seed removal typically occurred at 1 day for *Guarea* before the hurricane and at 1 day for *Prestoea* during pre- or post-Hurricane Maria trials. The smaller seeds of *Guarea* relative to *Prestoea*, and the thicker debris layer generated by the hurricane, may have made black rat ground-foraging for *Guarea* seeds more time-consuming following the hurricane. The low availability of seeds following the hurricane may also have played a role in the equally low seed removal (10%–14%) for *Guarea* and *Prestoea*. There was a noticeable lack of seeds in the LEF during our post-hurricane trials in 2018; only a few species of understory plants had some seeds and it took wide geographic searching for us to obtain enough seeds to complete our trials. In fact, the paucity of available seeds in the LEF after Hurricane Maria was the reason that we were unable to experimentally present more species in our study, as we had originally aimed to replicate trials with all four species used in Shiels and Ramírez de Arellano (2019). Low seed availability following hurricanes, and possibly associated shifts in black rat diet, may have contributed to findings of lower seed attractiveness following hurricanes relative to previous captive feeding trials (Weinbren et al., 1970) and field trials (Shiels & Ramírez de Arellano, 2019) involving black rats in the LEF.

Shifts in foraging behaviors are common in wildlife species following major hurricanes (Pérez-Rivera, 1991; Wiley & Wunderle, 1993). In addition to the spatial shifts in foraging already described for black rats (this study) and birds (e.g., Wunderle, 1995), many species adjust their diet to include more abundant food resources that follow hurricanes. For example, when studying howler monkeys, Behie and Pavelka (2005) reported a switch from fruit and flower consumption to a completely folivorous diet in the weeks after a hurricane; leaf recovery occurs more rapidly following hurricanes than does plant reproductive structures such as flowers, fruits, or seeds. Schaffner et al. (2012) observed that leaves also replaced fruit as the primary food source of spider monkeys (*Ateles geoffroyi yucatenensis*) after hurricanes in the Yucatan. Similarly, Tsuji and Takatsuki (2008) reported that Japanese macaques (*Macaca fuscata*) experienced a dietary shift from eating fruit in the trees and some seeds on the ground before the hurricane to only eating on the ground and only a unique seed type after the hurricane. Although we did not assess the diets of black rats or house mice, previous studies in the LEF and elsewhere demonstrate that both rodent species are omnivores and will opportunistically consume available food items. Black rats in the LEF have been recorded consuming litter and arboreal invertebrates, dead wood, snails, and some plant parts, including fruits and seeds (Willig & Gannon, 1996). Weinbren et al. (1970) conducted caged no-choice feeding trials with fruits of 11 tree species in the LEF by offering them to four individual black rats. They found that rats ate portions of all offered fruit, but some species were eaten more than others. Black rats generally have fruit and seed dominate their diets (reviewed in Shiels, Pitt, et al., 2014), whereas house mice consume relatively high amounts of insects and small arthropods as well as seeds (Shiels et al., 2013; St Clair, 2011). For example, over half of the house mice diet has been reported as lepidopteran larvae (Shiels et al., 2013), and house mice consume only small seeds (Shiels et al., 2013) that were smaller than those we studied and that black rats removed from the forest floor. Given their omnivorous diet and impact on food webs, abundant black rats or house mice have the potential to alter forest ecosystems through their foraging. Black rats are clear threats to native vertebrates and plants via predation of seeds (Shiels, Pitt, et al., 2014), whereas house mice are potential threats to small native arthropods and plants via predation of insect pollinators (Liang et al., 2022; Shiels et al., 2013). Given documented outbreaks of Lepidoptera larvae after hurricanes (e.g., Torres, 1992), mice may reduce post-hurricane caterpillar herbivory of fresh leaves. Also, outbreaks of detritivores (e.g., Coleoptera, potential mouse food) after hurricanes may attract mice into the forest. Further investigation is required to determine whether rodent diets shift following hurricanes and the consequences of those shifts for prey populations and ecosystem services like pollination.

Conclusions and predictions

Prior to and following hurricanes, invasive black rats are an abundant and important part of island forests. Similar to responses of many bird species to hurricanes (Wunderle, 1995), black rats shift their foraging behaviors after hurricanes, when food items are scarce, to capitalize on patches of previously disturbed forest for fruit and seed foraging. We expect that with increased hurricane frequencies, invasive black rats will continue to maintain their prevalence and abundance in the LEF and other similar ecosystems. As shifts in diet are common responses of wildlife to hurricanes (Behie & Pavelka, 2005; Tsuji & Takatsuki, 2008; Wiley & Wunderle, 1993), we expect that black rats may shift from favored fruit and seed to include more invertebrates and nonreproductive vegetative material after these large storms, but this is a hypothesis that needs to be tested. House mice are absent from the forest interior prior to hurricanes, but they expand into the forest, coinciding with elevated grass cover, after major hurricanes. While house mice generally eat more insects and small arthropods than do black rats, and their direct threats to native trees and vertebrates are minimal relative to black rats (Shiels et al., 2013; Shiels, Pitt, et al., 2014), increased hurricane frequency should result in ephemeral periods of more frequent house mouse establishment in the forest interior. More periods when house mice occur in the forest interior following hurricanes are likely to temporarily affect the forest food web, with effects extending to predators such as the red-tailed hawk (*Buteo jamaicensis*) and

Puerto Rican boa that may be attracted to mouse prey and understory foraging opportunities that result from the open canopy. Additionally and perhaps the largest consequences of house mouse prevalence in the forest after hurricanes are the potential negative effects on some insect groups that house mice frequently consume (e.g., Lepidoptera; Shiels et al., 2013; St Clair, 2011) and the potential for house mice to reduce insect pollination of some plant species (Liang et al., 2022). Although invasive rodents have been established in the LEF for many decades (Weinbren et al., 1970), their effects on forest food webs during periods of increased hurricane frequency are likely to be novel and deserve additional study.

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CONFLICT OF INTEREST

Authors herein state that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Shiels et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.r7sqv9sfz.

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