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Aaron B. Shiels

USDA, APHIS, Wildlife Services, Aaron.B.Shiels@aphis.usda.gov

Gabriela E. Ramirez de Arellano

University of Puerto Rico - Mayaguez

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**Cover Photograph:** A Black Rat (*Rattus rattus*) consuming seeds of the native tree *Guarea guidonia* in the Caribbean National Forest, PR, USA. Image captured at night using a trail camera. © Aaron B. Shiels and Gabriela E. Ramírez de Arellano.

## **Invasive Rats (*Rattus* sp.), but not always Mice (*Mus musculus*), are Ubiquitous at All Elevations and Habitats within the Caribbean National Forest, Puerto Rico**

Aaron B. Shiels<sup>1,\*</sup> and Gabriela E. Ramírez de Arellano<sup>2</sup>

**Abstract** - Invasive rodents, particularly rats (*Rattus* spp.), occupy >80% of the world's islands and are among the greatest threats to native biodiversity and agriculture on islands. At the time of their introduction in the 1500s, there was at least 1 native rat species in Puerto Rico. Today there are no native rodents remaining in Puerto Rico, but *R. norvegicus* (Norway Rat) may be found in urban settings, and *R. rattus* (Black Rat) are the most common rat across the island including within natural areas, and invasive *Mus musculus* (House Mouse) may also be found in urban and non-urban habitats. The Caribbean National Forest (CNF; locally El Yunque) in northeastern Puerto Rico has some native and endangered species vulnerable to rat predation. The objective of our study was to determine the presence and distribution of invasive rodents (rats and mice) across elevations and habitats within the CNF. We used 104 tracking tunnels, which are baited ink cards placed in tunnels so that foot prints of animal visitors could be identified, to determine presence of invasive rodent species. We placed 3 tracking tunnels at each 50-m elevation-gain ( $n = 66$  total tunnels), on the edge of forest habitat from sea level to 1070 m at El Yunque peak along the main road (Highway 191) through the CNF. We established additional tracking tunnels ( $n = 38$ ) in the major habitats in the CNF, including treefall and hurricane gaps, landslides, stream edges, and continuous forest. House Mice had not been previously reported in the CNF, and were found only at the forest edge along Highway 191 at elevations of 50–150 m and 300–1070 m, whereas rats (*Rattus* sp.) were found at all elevations and in all habitat types sampled. Logistic regressions revealed that mice and rat presence each increases with elevation (mice:  $P = 0.0352$ , rat:  $P = 0.0019$ ), though total rodent presence did not. Knowledge of the habitat types and elevations that these invasive rodents occupy can inform management strategies for rodent control and native species protection.

### **Introduction**

Rodents (*Rattus* spp. and *Mus musculus* L. [House Mouse]) have been introduced to many ecosystems worldwide and are among the most widespread and problematic invasive animals affecting islands (Angel et al. 2009, Shiels et al. 2014, Towns et al. 2006). Through mostly unintentional introductions by humans, these rodents occupy >80% of the islands worldwide (Atkinson 1985, Towns 2009). In addition to having negative impacts on agricultural resources, invasive rodents are a threat to many native species on islands. Invasive House Mice are known to

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<sup>1</sup>USDA, National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521, USA. <sup>2</sup>University of Puerto Rico at Mayagüez, Biology Department, Mayagüez, PR 00681, USA. \*Corresponding author - aaron.b.shiels@aphis.usda.gov.

damage and depredate plants and insects, whereas invasive rats *R. rattus* L. (Black Rat), and *R. norvegicus* Berkenhout (Norway Rat) are known to consume seabirds, forest birds, snails, arthropods, and a variety of plants including large-seeded species (Shiels and Drake 2011, Shiels et al. 2013, Towns et al. 2006). Due to their high fecundity, lack of effective predators, and generalist diets, invasive rodent populations rapidly expand on islands, and few habitats and ecosystems in urban and natural areas are free of at least 1 of these rodent species (Drake and Hunt 2009, Shiels 2010).

Puerto Rico currently has 3 invasive rodent species: Black Rats, Norway Rats, and House Mice. At the time of non-native rodent introductions in the 1500s, there was at least 1 native rat species in Puerto Rico: *Heteropsomys insulans* Anthony (Insular Cave Rat or Spiny Rat). Turvey et al. (2007) and others hypothesize that extinctions of a native shrew and the native Spiny Rat were driven by predation and/or competition with introduced Black Rats in Puerto Rico, rather than massive-scale deforestation for sugarcane (not commencing until the late 1700s) or the introduction of *Herpestes javanicus* (É. Geoffroy Saint-Hilaire) (Small Indian Mongoose), which did not occur until 1877. In addition to the Spiny Rat, there were at least 2 much larger native rodent species in Puerto Rico: *Elasmodontomys obliquus* Anthony (Plate-toothed Giant Hutia), which has been estimated to have had a mean body weight of 13.7 kg (McFarlane 1999), and a newly described large arboreal species (*Tainotherium valei*; Turvey et al. 2006). *Isolobodon portoricensis* J.A. Allen (Puerto Rican Hutia) was another rodent species that has been described in the prehistoric fauna, and this rodent was introduced to Puerto Rico, presumably as a food source, from nearby Hispanola by pre-Columbian Amerindians (Turvey et al. 2007). All of these native or non-European rodent species are extinct. However, the presence of native rodents in Puerto Rico may have been beneficial to the contemporary native flora and fauna, as theory predicts that islands that lacked native rodents have native biota that are more likely to suffer herbivory and predation from introduced rodents than are biota on islands with native rodents (Drake and Hunt 2009).

Black Rats are currently documented as the most widespread invasive rodent species in Puerto Rico, as they occupy urban, suburban, and natural areas (De León 1964, Miranda-Castro et al. 2000, Weinbren et al. 1970). In the Caribbean National Forest (CNF) in northeastern Puerto Rico, Black Rats previously have been the only rodent species documented, and this rodent is a threat to many native species including the endangered *Amazona vittata* Boddaert (Puerto Rican Parrot; Engeman et al. 2006, Snyder et al. 1987, Zwank and Layton 1989). Norway Rats are generally restricted to urban areas and possibly agricultural settings in Puerto Rico (De León 1964, Miranda-Castro et al. 2000), whereas House Mice distributions are not well known in Puerto Rico but have been documented in and around suburban areas (Tamsitt and Fox 1970).

The CNF is often described as a patchwork of forest habitats that reflect different types of disturbances (e.g., treefalls, hurricanes, landslides, flooding, drought) in varying states of recovery (Brokaw et al. 2012, Shiels and Walker 2013). In addition to gaining a better understanding of how invasive rodents are distributed

along the elevational gradient in the CNF, there is additional interest in discovering rodent establishment and activity within the many habitat types in the CNF. Prior to our study, Black Rats, which are the most common rodent species in island forests (Shiels et al. 2014), were documented in the CNF within continuous forest at ~300–600 m elevation (Engeman et al. 2006, Weinbren et al. 1970). Rodents are often in areas of relatively high plant cover presumably to limit their exposure to predators (Arthur et al. 2005, Cox et al. 2000, King et al. 1996); therefore, older gaps with established vegetation ground-cover rather than young (e.g., <1 year) gaps may be favored by these rodents. King et al. (1996) found that House Mouse abundance was greater in densely vegetated areas, such as disturbed sites along roads or plantations, than in the more open understory of the forest interior. Additionally, Shiels et al. (2017) determined that House Mice are often found in disturbed habitats with grass present, and Black Rats are more generalist in their habitat occupancy but are most commonly found in habitats with trees.

The objective of our study was to determine the presence and distribution of invasive rodents (rats and mice) across elevations and habitats within the CNF. Specifically, we sought to determine (1) whether rats or mice occur in each of the main disturbed forest habitats (i.e., treefalls, landslides, stream edges, hurricane areas) and undisturbed forest habitats (i.e., continuous forest) within the CNF, and whether some habitats have greater rodent presence and activity than others, and (2) which rodents occur along the 1–1075-m elevation gradient that passes through the Northern Ecological Corridor (NEC) and the CNF along Highway 191, and if there are predictable patterns of rodent presence and activity matched with elevation. Knowledge of the habitat types and elevations that these invasive rodents occupy can inform management strategies for rodent control and native species protection.

### Field-Site Description

This study occurred in the Caribbean National Forest (CNF), also known as El Yunque National Forest (or El Yunque), which includes the Luquillo Experimental Forest, in northeastern Puerto Rico (18°18'N, 65°50'W). The CNF is a 19,650-ha tropical evergreen forest, where mean annual precipitation is 2000–4000 mm, the amount of rainfall increases with elevation, and there is high year-to-year variation and mild seasonality. Mean monthly temperatures vary from 20 °C at 1050 m elevation to 25 °C at 300 m elevation (Brokaw et al. 2012). The elevation of the CNF spans ~150–1075 m. Historically, major hurricanes (i.e., category 3–5 on Saffir-Simpson Scale) have passed over the CNF every 50–60 years on average (Scatena and Larson 1991); yet only 9 years separated the major hurricanes of Hugo (1989) and Georges (1998), and the category 4 Hurricane Maria (2017) occurred just 19 years after the last major hurricane. Hurricanes and other major storms passing over the CNF frequently cause canopy defoliation and branch loss that results in gap formation (Brokaw et al. 2012) and numerous landslides, especially adjacent to roads (Shiels and Walker 2013).

The forest types in the CNF are partially distinguished by elevation. Below ~600 m elevation, Tabonuco Forest is present, occupying ~48% of the CNF and

characterized by the dominant tree *Dacryodes excelsa* Vahl. (Tabonuco), yet other trees that are common include *Prestoea acuminata* (Wiild.) H.E. (Sierra Palm), *Manilkara bidentata* (A. DC.) A. Chev. (Ausubo), and *Sloanea berteriana* Choisy (Motillo). Above the average cloud-condensation level (~600 m), *Cyrilla racemiflora* L. (Palo Colorado; 30% of CNF) replaces Tabonuco in all but the steep slopes and poorly drained soils where Sierra Palm Forest dominates (18% of CNF). Above ~750 m, the Dwarf Forest (4% of CNF) is found, characterized by dense stands of short trees and shrubs (e.g., *Tabebuia rigida* Urb. [Roble de Sierra] and *Ocotea spathulata* Mez. [Nemoca Cimarrona]) that commonly experience wind-driven clouds (Brokaw et al. 2012, Reagan and Waide 1996). Rodent sampling that occurred at sea level was outside the CNF but within the NEC, which is 1202 ha of undeveloped and protected land that includes 10.5 km of coastline; the NEC receives 1500 mm of rainfall per year and is dominated by coastal forest-shrubs and scattered wetlands (Guzmán-Colón and Roloff 2014).

Black Rats have been documented in the CNF in closed-canopy habitat of Tabonuco, Palo Colorado, and Palm forest; however, Norway Rats and House Mice have not been previously documented in the CNF despite rodent trapping (Engeman et al. 2006, Weinbren et al. 1970, Willig and Gannon 1996) and tracking-plate assessment (Engeman et al. 2006) in many of the same areas that we sampled in our study.

## Methods

To determine presence of invasive rodent species at all sampled habitats and elevations, we used tracking tunnels, which are baited ink cards placed in tunnels (60 cm long with 10 cm x 10 cm openings; Fig. 1) so that foot prints of animal visitors can be identified. At each location, we placed a tracking tunnel on the ground and a card inside the tunnel that had an ink reservoir surrounding the bait (Skipppy creamy peanut butter topped with a 2 cm x 2 cm coconut chunk). Tracking tunnels are not accurate in predicting rodent densities because a single rodent could visit multiple nearby tracking tunnels; however, our 20-m minimum spacing between tracking tunnels was an attempt to limit the same individuals visiting multiple tunnels. All tunnels, cards, and ink were purchased from Pest Control Research LP ([www.traps.co.nz](http://www.traps.co.nz)). Although Black Rats have been the only rats ever recorded in the CNF, it is not possible to unequivocally distinguish between rat species' tracks present in tracking tunnels; therefore, rodent tracks were scored as either rat or House Mouse.

We placed 3 tracking tunnels at each 50-m elevation-gain ( $n = 66$  total tunnels; Fig. 2), confirming elevation using a Garmin GPS calibrated at sea level, beginning in coastal forest at sea level (1 m elevation) within NEC at the west end of Balneario La Monserrate (Playa Luquillo), and then in forest along the main road (Highway 191) entering and traveling through the CNF to El Yunque peak (1075 m). We refer to this gradient as the Highway 191 elevation gradient. Our final sampling point had the 3 tunnels span 1050–1070 m to ensure sampling was as close to the peak as possible while still under forest cover. At each 50-m elevation point, we spaced the 3 tunnels ~20 m linear distance from the next closest tunnel; the tunnel spacing was based on average maximum nightly linear movements of mice and rats measured in

Figure 1. Picture of a tracking tunnel (rectangular black tube) with an inked tracking card baited with peanut butter and ready to be inserted into the tunnel.



Hawaiian forest (Shiels 2010). Rodent activity at a site was measured as the number of tunnels (up to 3) for which there were rodent tracks present. We set tracking tunnels ~3–5 m from the road edge along this 0–1070 m elevation gradient on 31 July 2017, and recovered them 1 day later.

We established additional tracking tunnels ( $n = 26$ ) in Tabonuco Forest (300–485 m elevation) near El Verde Field Station (Fig. 2) on 4 June 2017 and checked their tracking after 1 day and 2 days. We placed these tunnels at different locations to determine invasive rodent presence in the major habitats in the CNF, including a treefall gap ( $n = 1$ ), landslides ( $n = 3$ ), 1.5-year-old hurricane gaps ( $n = 3$ ), 12-year-old hurricane gaps ( $n = 3$ ), stream edges ( $n = 7$ ), closed-canopy forest near a road ( $n = 3$ ), and closed-canopy interior forest ( $n = 6$ ). We also sampled the Palo Colorado Forest in closed-canopy forest (540–570 m elevation) by placing 12 tracking tunnels in Puerto Rican Parrot habitat (Fig. 2) on 10 June 2017 and recovering them after 1 day; 6 tunnels were placed on each side of the Espíritu Santo River and were not closer than 50 m to the river. Each tunnel was ~20–30 m distance to the next closest tunnel in Palo Colorado Forest and ~20–50 m to the next closest tunnel in Tabonuco Forest. The treefall gap was <2 years old and ~66 m<sup>2</sup> (6 m x 11 m), and the landslides were each <1 year old



Figure 2. Map of northeastern Puerto Rico, with Caribbean National Forest (El Yunque National Forest) identified in green. Each blue triangle is a 50-m elevation increment and represents 3 tracking tunnels along the elevation gradient. The red triangle is El Verde Field Station, and the tracking tunnels that were placed in each habitat are clustered in that part of the forest (the Tabonuco Forest type). T = treefall gap ( $n = 1$ ), L = landslide ( $n = 3$ ), Y = 1.5-yr-old hurricane gap ( $n = 3$ ), O = 15-yr-old hurricane gap ( $n = 3$ ), S = stream edge ( $n = 7$ ), R = continuous forest near road ( $n = 3$ ), F = continuous forest interior ( $n = 6$ ); the single P represents a cluster of tracking tunnels ( $n = 12$ ) within the Palo Colorado Forest type, near Puerto Rican Parrot habitat. Map provided by the US Forest Service and modified; elevations and site locations estimated.

and ~98–400 m<sup>2</sup> (7 m x 14 m, 13 m x 15 m, and 20 m x 20 m), which is within the typical size range for landslides in the CNF (Shiels and Walker 2013). The hurricane gaps of both ages were created for a long-term study, called the Canopy Trimming Experiment (CTE), to examine mechanistic factors that influence forest responses to hurricane disturbance (Shiels and González 2014); the gaps were 900 m<sup>2</sup> (30 m x 30 m) and the prevalence of increased light relative to the closed canopy forest was maintained for about 1.5 years following gap creation (Shiels and González 2014, Shiels et al. 2010). Of the 7 tracking tunnels placed at the stream edge, 4 were along the Prieta Stream and 3 were along the Quebrada Sonodora River; occasionally the tunnels were <1 m to the water's edge, but typically we situated them 1–1.5 m away. The stream edges were noticeable light gaps relative to closed-canopy forest plots. The plots near road and within closed-canopy forest were 15–50 m from the road, and were within 75 m of a landslide site. The closed interior forest plots were chosen based on a known land-use history of no significant disturbance for nearly 30 years (since Hurricane Hugo). Our study was completed ~1.5 months prior to Hurricane Maria passing over the CNF on 20 September 2017.

We used logistic regression with binomial errors to determine if the ratios of rat, mouse, or total rodent (rat + mouse) presence differed by elevation. We used Fisher's exact tests to determine if rat, mouse, and total rodent presence, after 1 and 2 days following activating the tracking tunnels, differed among habitats; we chose Fisher's exact test over chi-square testing due to expected values of <5 for most factors. Statistical significance was based on  $P < 0.05$ ; all statistical analyses were completed in R version 3.2.3.

## Results

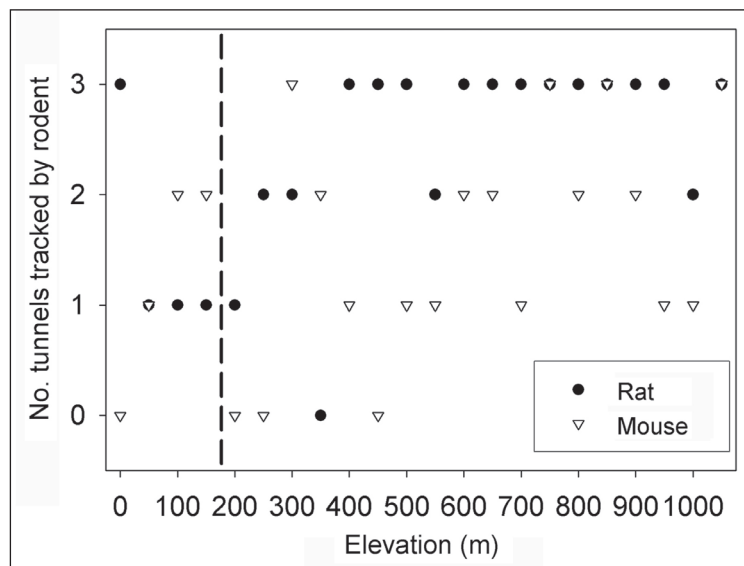
Out of 104 tunnels, 77 (74%) were tracked by rodents, including 70 by rat (67%) and 33 by mouse (32%); 26 tunnels were tracked by both rat and mouse. There were just 2 tunnels (2%) tracked by Mongoose (700 m elevation along Highway 191, and 550 m elevation in Palo Colorado Forest). One tunnel at 1000 m elevation had the tracking card removed from the tunnel and was tracked by a *Felis catus* L. (House Cat). Many tunnels showed evidence of ants and unidentifiable insects (46%), 42% had evidence of *Caracolus caracolla* (L.) snails, 19% had lizard tracks, and 4% had frog (probably *Eleutherodactylus* spp.) tracks. *Caracolus caracolla* snails were commonly residing in the tunnels upon daily checks. Most of the tracking cards had animal tracks, and 64% were tracked by multiple animal species on the same card. Many of the tunnels that had rodent tracking at day 1 had the tracks obscured by day 2 due to portions of the paper-cards eaten by *C. caracolla* snails such that evidence of rodent tracking would have been missed if day 1 tunnel checks had not occurred.

Rats (*Rattus* sp.) were the most common animal visiting tracking tunnels along the Highway 191 elevation gradient. Aside from 350 m along the Highway 191 elevation gradient, at least 1 of the 3 tracking tunnels was tracked by rats at each 50-m elevation interval from sea level to 1070 m (Fig. 3); there were only 15 out of 66 tunnels (23%) that did not have rat tracks (Fig. 3). There was a strong association

between the ratio of rat-tracking and elevation, where rat-tracking frequency significantly increased with elevation ( $P = 0.0019$ ,  $df = 21$ ,  $AIC = 44.034$ ; Fig. 3). House Mouse tracks were found only at the forest edge along Highway 191 at some elevations between 50 m and 150 m and 300 m and 1070 m; 33 out of 66 tunnels (50%) did not have mouse tracks (Fig. 3). The ratio of House Mouse tracking significantly increased with elevation ( $P = 0.0352$ ,  $df = 21$ ,  $AIC = 59.994$ ; Fig. 3). When total rodent (i.e., rat + mouse) tracking was examined along the Highway 191 elevation gradient, there was no significant relationship between rodent tracking and elevation ( $P = 0.0982$ ,  $df = 21$ ).

Aside from some of the areas along the Highway 191 elevation gradient, no House Mice prints were detected from any of the additional habitats sampled. Each of the 8 sampled habitats (treefall, landslide, 1.5-yr hurricane plot, 12-yr hurricane plot, stream edge, closed-canopy forest near roads, closed-canopy Tabonuco forest interior, and closed-canopy Palo Colorado forest interior) had at least 1 tracking tunnel with rat tracks (33–100% of tunnels in each habitat), indicating that rats are present in each habitat type in the CNF (Table 1). Rat tracking did not differ by habitat ( $P > 0.05$ ; Table 1). When the 8 habitats were compared, there was no significant difference among habitats for frequency of rat tracking; this pattern was observed for tunnels checked after 1 day ( $P = 0.9704$ ;  $n = 8$  habitats) and 2 days ( $P = 0.7532$ ;  $n = 7$  habitats because Palo Colorado was not sampled a second day) following tracking tunnel activation (Table 1). When all gaps (i.e., treefall, landslide, hurricane plots, stream edge;  $n = 17$ ) were pooled and compared to closed-canopy forest ( $n = 9$ , or  $n = 21$  if Palo Colorado included), there were no significant differences in rat-tracking frequency, regardless of whether Palo Colorado habitat was included or excluded ( $P > 0.9999$  for each).

Figure 3. Number of tracking tunnels (out of 3 per 50-m elevation increment) with *Rattus* sp. (rat) or *Mus musculus* (House Mouse) tracks, indicating their presence, across the elevation gradient from sea level (1 m) to El Yunque peak (1070 m), PR. All sampling points to the right of the dashed line are within the Caribbean National Forest (CNF), and the sampling points to the left of the dashed line are in forest patches outside the CNF but within the Northern Ecological Corridor.



## Discussion

Previous studies in the CNF determined that invasive Black Rats are common within closed-canopy forest at ~300–600 m elevation, but no other rodent species were found in these habitats (Engeman et al. 2006, Weinbren et al. 1970). Our tracking tunnel findings not only support the establishment of invasive rats (*Rattus* sp.) in the CNF, but also indicate that they occupy and are active at all elevations (1–1070 m) and all main habitats (disturbed and undisturbed) in the CNF. In addition to confirming the establishment of rats across the CNF, our study is the first that we know of that has observed House Mice in the CNF. These mice appear to be restricted to the forest edges near the main road through the CNF (Highway 191), as they were not found in any of the forest habitats sampled beyond Highway 191. Furthermore, we discovered that the presence of rats as well as that of House Mice at the forest edges along Highway 191 each increased with elevation, though the presence of all rodents combined did not. In addition to providing record of the presence of invasive rodents in the CNF, information from our study can be used to develop strategies to manage invasive rodents in the CNF (e.g., we have now identified areas where invasive rodent species can be found, trapped, and controlled), which may be important for native species protection, conservation, and human health.

Based on all previous rat trapping and related evidence in the CNF (F. Cano, USDA Forest Service, CNF, PR, pers. comm.; Engeman et al. 2006; Snyder et al. 1987; Weinbren et al. 1970; Willig and Gannon 1996; Zwank and Layton 1989), it appears that the Black Rat is the only rat species in this forest; Norway Rats are not present. However, distinguishing Black Rat tracks from Norway Rat tracks was not possible by use of our tracking-tunnel methodology, so we were not able to confirm that Black Rats are the only rat species in the CNF. Black Rats are commonly the most abundant invasive rat in island forests, especially in the tropics (Shiels et al. 2014). In related sampling in the same gap and non-gap forest habitats used in our study, 56 pictures of rats visiting native seeds were taken by trail cameras over a

Table 1. Results of tracking tunnels that were set in 7 habitats within Tabonuco Forest ( $n = 26$ ; 300–485 m elevation), near El Verde Field Station, and additional tunnels ( $n = 12$ ) set in the closed canopy interior of Palo Colorado Forest, in Puerto Rican Parrot habitat. Tracking tunnels were checked after 1 day and 2 days in Tabonuco Forest, and after 1 day in Palo Colorado Forest. See Figure 1 for locations of habitats sampled with tracking tunnels.

Habitat sampled	Sampled sites and number of tunnels set	No. of rat-tracked tunnels	
		After 1 day	After 2 days
Treefall gap	1	1	1
Landslide	3	1	3
1.5-yr-old hurricane gap	3	2	2
12-yr-old hurricane gap	3	1	2
Stream edge	7	3	4
Closed-canopy forest near road	3	1	3
Closed-canopy interior forest	6	3	3
Closed-canopy interior Palo Colorado forest	12	7	-

2-month period, and all of those rats were identified as Black Rats (A.B. Shiels and G.E. Ramírez de Arellano, unpubl. data). Additionally, recent communications with CNF forest managers have indicated that all rats that have been captured in the CNF, as well as rat carcasses observed along Highway 191, were Black Rats (F. Cano, pers. comm.). Therefore, the rat tracks left in all tracking tunnels in our study are likely to be Black Rats, but an additional study using traps rather than tracking tunnels would be needed to confirm this prediction.

House Mice had not been previously documented in the CNF despite rodent trapping (Engeman et al. 2006, Weinbren et al. 1970, Willig and Gannon 1996) and tracking-plate assessment (Engeman et al. 2006) in some of the same areas that we sampled in our study, including adjacent to Highway 191. However, many live-capture rat traps are not always triggered by mice, and the metal cage traps (e.g., Tomahawk) that are often used for rat trapping have large enough holes that allow House Mice to escape. Alternatively, House Mice may have established in the CNF since the last published rodent sampling occurred, 15 years ago (Engeman et al. 2006). During surveys in Los Tres Picachos State Forest in the central mountains of Puerto Rico (380–1205 m elevation), Miranda-Castro et al. (2000) observed House Mice in just 2 locations near roads at 610 m elevation, whereas Black Rats were abundant across observation sites. It appears that House Mice may be restricted to vegetated areas near main roads in the CNF and Los Tres Picachos. Norway Rats were also documented by Miranda-Castro et al. (2000) at Los Tres Picachos as common below 750 m elevation; however, that report provided no description of how rodent species were determined and no mention of any captures of specimens for examination, without which positive Norway Rat species identification can be challenging. If Norway Rats are indeed present in Los Tres Picachos, their presence may be due to the proximity to active and abandoned agricultural fields (Miranda-Castro et al. 2000).

Elevation can restrict the distributions of many species, and there has been growing interest in studies that assess how future climate change may affect species distributions. Black Rats and House Mice, however, have been documented in most ecosystems in Hawaii from sea level to ~3000 m (Shiels 2010). Although our elevation gradient in the CNF only reached 1070 m at El Yunque peak (1075 m), it is the third highest peak in Puerto Rico, and the 2 higher peaks (Cerro Punta [1338 m] and Tres Picachos [1205 m]; Miranda-Castro et al. 2000) in the central mountains of Puerto Rico also are within the elevation range that Black Rats and House Mice are known to colonize at a similar latitude (Miranda-Castro et al. 2000, Shiels 2010). Our systematic sampling at each 50-m elevation gain therefore indicates that rats (*Rattus* sp.) should be established in all wet forests throughout Puerto Rico, and that rats and House Mice are capable of establishing and surviving at all elevations in Puerto Rico regardless of climate-change predictions (Shiels 2010). There was one elevation interval along Highway 191, at 350 m, that did not have rats tracking any of the 3 tunnels; however, our habitat sampling near El Verde Field Station had both gap and continuous forest plots at 350 m elevation that had rat tracks present. Therefore, we are confident in the conclusion that rats indeed are

present at all elevations in the CNF. Tracking tunnels are not accurate in predicting rodent densities because a single rodent could visit multiple nearby tracking tunnels, even though our 20-m minimum spacing between tracking tunnels, based on previous nightly movement patterns of Black Rats and House Mice in forest (Shiels 2010), was an attempt to limit the same individuals visiting multiple tunnels. A potential explanation for the pattern of increased rat and House Mouse tracking (and therefore rat and mouse activity) with elevation may be that the cooler and wetter conditions at increased elevations (Brokaw et al. 2012) require rodents to be more active and forage greater distances.

Some animals, like *C. caracolla* snails in the CNF, avoid forest gaps (Bloch and Stock 2014), but avoidance or attraction to forest gaps do not appear to be behaviors of rats in the CNF. Our sampling revealed that all major habitats had rats present, and there were no differences in rat-tracking among habitats or gap vs. non-gap areas. Therefore, the type of forest disturbance and stage of plant succession does not appear to significantly influence rat presence. In eastern Australia, Cox et al. (2000) found that Black Rats preferred densely vegetated understories and areas with deep leaf litter. The tracking tunnels that we placed within landslides were on bare soil that lacked leaf litter, as characteristic of young (<1 year old) landslides (Shiels and Walker 2013), yet the tunnels were tracked by rats. The young hurricane plots had a denser understory composed of woody species and grass, whereas the older hurricane plots lacked grass and had a less dense understory, yet rats were found in both habitats. Despite the nearness to a constant water source at the stream-edge sites, tracking tunnels revealed that rats were no more frequent there than in areas far (100s of meters) from streams. Water may not be a limiting resource to rodents in this wet forest, and both rats and House Mice survive well in arid forests (Shiels et al. 2014, 2017). Rats and House Mice typically rely on plants for their water source, either by consuming plant material or pooled water droplets on plant surfaces (Shiels et al. 2014). In Australia, Arthur et al. (2005) conducted experiments in 50 m x 50 m outdoor enclosures and found that House Mouse abundances were greater in areas having reduced exposure to predators resulting from increased habitat cover (grass and downed logs). Dickman (1992) determined that House Mouse abundance roughly correlates with vegetation density in Western Australia, and Shiels et al. (2017) found that Black Rats dominated forest habitat on Maui whereas House Mice dominated the adjacent grassland. Many factors may influence rat and mouse habitat preferences and partitioning, and some of these factors such as dietary niche partitioning and microhabitat use were documented differences between sympatric Black Rats and House Mice in forests in Hawaii (Shiels 2010, Shiels et al. 2013). Additional studies in the CNF would help improve understanding of behaviors of invasive rodent species, and perhaps clarify why House Mice are more restricted in their distribution in the CNF relative to rats.

The low occurrence of Mongoose tracks in our tunnels was similar to other studies that trapped for Mongoose, as Viella (1998) recorded 2 individuals/100 trap days using traps grids in the CNF, which equated to a density estimate of 1.5 individuals/ha in Tabonuco Forest and 2 individuals/ha in Palo Colorado Forest.

Depending on the type of population estimate used, Mongoose were recorded at 0.33–0.97 individuals/ha along Highway 191 at 544–820 m elevation (Palo Colorado Forest), and densities were slightly higher in the Spring than the Fall (Johnson et al. 2016). When Guzmán-Colón and Roloff (2014) sampled for Mongoose along Highway 191 in the CNF and at sea level, they found that Mongooses were much more abundant in the coastal forest of NEC than in the CNF. Feral House Cats were also documented on 1 occasion (1000 m) in our study, and previous trapping in the CNF revealed that House Cats were less common than Mongoose (Engeman et al. 2006). Despite the presence of these rodent predators in the CNF, they do not appear to be substantially suppressing or eliminating invasive rodent populations.

Our documentation of high prevalence of invasive rats in all major habitats and along the entire elevational gradient within the CNF, as well as the presence of mice in some habitats, highlights the need for research that will examine the effects that these non-native rodent species have on native species in the CNF. Although House Mice are much smaller and their negative effects on native biota are generally assumed to be less severe than those of rats (Angel et al. 2009, Shiels et al. 2014, Towns et al. 2006), House Mice frequently damage natural resources and are known to have large and generally unpredictable population spikes (outbreaks) that can result in severe resource loss and damage (Shiels 2010). Rats, especially Black Rats, are the most damaging invasive rodent species for native island biota (Shiels et al. 2014), and they may have substantial negative effects on native plants, invertebrates, and vertebrates on islands like Puerto Rico that once had native rodents.

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