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Original Research Article

Vegetation associations and relative abundance of rodents on St. Eustatius, Caribbean Netherlands

Hannah Madden ^{a,b,*}, Tinde Van Anandel ^c, Jeremy Miller ^c, Michael Stech ^c, Kevin Verdel ^d, Eline Eggermont ^d^a Caribbean Netherlands Science Institute (CNSI), P.O. Box 65, St. Eustatius, Caribbean, the Netherlands^b NIOZ Royal Netherlands Institute for Sea Research, and Utrecht University, P.O. Box 59, 1790 AB Den Burg, Texel, the Netherlands^c Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, the Netherlands^d University of Utrecht, Heidelberglaan 8, De Uithof, 3584 CS Utrecht, the Netherlands

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ABSTRACT

Since the introduction of non-native rodents to the Caribbean region, these invaders have successfully occupied many, if not most, islands where they pose tremendous threats to native biodiversity and ecosystems. The objective of our study was to conduct a preliminary assessment of the relative abundance of invasive alien rodents in different vegetation types on the small Caribbean island of St. Eustatius, which has no native rodent species. We used tracking tunnels (baited ink cards placed in tunnels to identify the prints of animals lured to the card) to determine the presence of rodent species. We collected data in 25 × 25 m ($n = 13$) and 5 × 5 m ($n = 130$) plots to determine whether elevation, number of tree species, canopy cover or other microhabitat components were correlated with rodent relative abundance. Invasive rodents are present in varying relative abundances in rural areas on St. Eustatius. House mice (*Mus musculus*) were not recorded inside the terrestrial protected areas, whereas black rats (*Rattus rattus*) were detected in all elevations and all but one vegetation type sampled. We determined significant correlations between some of the habitat characteristics, especially elevation, canopy height, leaf litter cover and number of tree species, which showed significant collinearity with 27 of 45 pairwise comparisons. There was a significant correlation between rodent relative abundance and the number of tree species, but not between elevation, number of living trees, number of shrubs, rainfall, canopy cover, canopy height, leaf litter cover, leaf litter depth, or slope. There was a significant difference within vegetation types for the frequency of traps containing rat versus mouse tracks. Our study was impacted by two major hurricanes in September 2017.

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1. Introduction

The introduction of non-native rodents has profound impacts on indigenous flora, fauna and ecosystems in tropical regions such as the Caribbean (e.g., Harper and Bunbury, 2015; Hilton and Cuthbert, 2010; Kairo, 2003). Rodent species that

* Corresponding author.

E-mail addresses: Hannah.madden@cnsi.nl (H. Madden), Tinde.vanandel@naturalis.nl (T. Van Anandel), Jeremy.miller@naturalis.nl (J. Miller), Michael.stech@naturalis.nl (M. Stech), Kgm.verdel@gmail.com (K. Verdel), e.d.c.eggermont@gmail.com (E. Eggermont).

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have invaded the region are the black rat (*Rattus rattus* Linnaeus, 1758), house mouse (*Mus musculus* Linnaeus, 1758), Norway or brown rat (*Rattus norvegicus* Berkenhout, 1769), and red-rumped agouti (*Dasyprocta leporina* Linnaeus, 1758; Taylor, 2010). Rats and house mice are among the most widespread invasive alien species occupying >80% of island groups worldwide (Atkinson, 1985). Many, if not most, Caribbean islands have been colonised by one or more species of non-native rodents (Borroto-Páez and Woods, 2012). These were first likely introduced in the 17th century and thereafter invaded the region (Abdelkrim et al., 2005). Native biota on islands have often evolved in the absence of mammalian predators, and compared with organisms found on the mainland, island species generally comprise fewer populations and/or have smaller total population sizes (Reaser et al., 2007). These characteristics, coupled with isolation and endemism, make island ecosystems especially sensitive to disturbance, whereby species are more vulnerable to extinction at rates that often exceed those of continental species. Thanks in part to their generalist diets (Shiels et al., 2013), non-native rodents are able to thrive in these insular ecosystems (Courchamp et al., 2003).

As well as being limited by food availability (French et al., 1974; Gilbert and Krebs, 1981; Petryszyn, 1982), rodent densities are known to vary with local vegetation structure. This suggests that available food resources are strongly associated with microhabitats, which in turn can be used to determine rodent relative abundance (Price and Waser, 1984). However, accurately assessing the density of small mammal populations in a variety of habitats is labor-intensive and costly (Engeman and Whisson, 2006), thus necessitating the use of relative abundance measures (Caughley, 1977; Pollock et al., 1990). In addition to being cheaper and quicker to measure, relative abundance indices can often provide useful information (Caughley, 1977; Blackwell et al., 2002). The techniques most commonly employed to determine relative indices of rodent abundance are snap trapping and footprint tracking (Innes, 1990; Innes et al., 1995; Brown et al., 1996). In addition to the advantages mentioned above, these types of indexing techniques significantly reduce the risk of coming into contact with zoonotic diseases such as hantavirus or leptospirosis (Whisson et al., 2005), although they are not without risk. Rodents favor areas with relatively high plant cover, which is thought to reduce their risk of predation (King et al., 1996; Cox et al., 2000; Shiels and Ramírez de Arellano, 2018). House mice may be more prevalent in disturbed, densely vegetated habitats with grass present, whereas black rats are often found in habitats with trees, but can occupy a wide range of habitats (Shiels et al., 2017).

House mice are one of the most widespread invasive alien mammals on islands, yet conservation actions on invasive rodents have primarily focused on rats (Howald et al., 2007; Angel et al., 2009; Duron et al., 2017). On islands in the Southern Ocean, mice have been documented feeding on at least 15 species of endemic, native and introduced flora species, as well as several invertebrate fauna species. On Gough Island two seabird species experienced high breeding failure as a result of mice, which were observed attacking and killing chicks up to 300 times their mass (Wanless et al., 2007). Wanless et al. (2007) argue that the impacts of mice are likely to be most detrimental on islands where they are the only introduced mammal, since in the absence of larger introduced mammalian competitors high densities of mice can trigger predatory behavior. The impacts of rat predation on native species vary widely and depend on factors such as the physical environment, food availability, the behavior and population density of rats, and the presence of other predators or competitors (Angel et al., 2009). On Lord Howe Island, five species of indigenous forest birds became extinct within five years following the introduction of black rats (Townes et al., 2006). Similarly, on Midway Island, two species of land birds disappeared within 18 months. On Big South Cape Island in New Zealand, numerous endemic and native bat and bird species went extinct following the introduction of invasive black rats (Townes et al., 2006). Where both rodents coexist, rats are considered strong competitors of mice, negatively impacting their abundance and even excluding them entirely when food supplies are limited (Choquenot and Ruscoe, 2000; Courchamp et al., 2000; Ruscoe, 2001; Caut et al., 2007). Studies in New Zealand forests have demonstrated that where populations of mice and ship rats coexist, mice are scarcer than rats (King et al., 1996). However, mice populations can spike dramatically following measures to control rats (Innes et al., 1995; Murphy et al., 1999; Caut et al., 2007; Witmer et al., 2007a,b).

St. Eustatius is a special municipality of The Netherlands situated in the northern Lesser Antilles with a human population of around 3900 (CBS 2013). No research on rodent presence and distribution had previously been conducted on St. Eustatius, and one of the objectives of our study was to determine the relative abundance of rodents in different vegetation types and at varying elevations. Two Important Bird Areas (IBA) are designated for St. Eustatius. The Quill IBA (AN008) provides a habitat for a number of restricted-range, forest-dependent species, and Boven IBA (AN007) provides nesting habitat for a regionally important breeding population of red-billed tropicbirds (*Phaethon aethereus*, Linnaeus, 1758, hereafter tropicbirds) (Collier and Brown, 2008; Geelhoed et al., 2013). This preliminary assessment forms part of a larger rodent control pilot project targeting two key biodiversity areas on St. Eustatius, namely the lower outer slope of the Quill volcano and Pilot Hill. The former falls within the aforementioned IBA (AN008) and the latter is a coastal habitat that supports nesting tropicbirds, where previous studies have documented predation of eggs by invasive rats (Chan, 2013; Madden, 2015).

Two native rodent species have been documented from archeological sites on the St. Christopher Bank. The oryzomyine rice rat (*Pennatomys nivalis*, Turvey et al., 2010) is thought to have been extirpated by European settlers in the early 20th century (Brace et al., 2015). The red-rumped agouti no longer exists on St. Eustatius, but a subspecies (*Dasyprocta leporina noblei*) is described as present on St. Kitts (Borroto-Páez and Woods, 2012). Today, the black rat and house mouse are recorded as present on St. Eustatius (Van Buurt and Debrot, 2012), whereas the brown rat (*Rattus norvegicus*) is not (Borroto-Páez and Woods, 2012). Besides bats, no other native mammals are listed as being present on St. Eustatius (Pedersen et al., 2018). The presence of rats in rural areas can have significant negative impacts not only on native birds, but also on crabs, reptiles and insects, as well as indigenous flora (Shiels et al., 2013; Samaniego-Herrera, 2014). Elucidating the detrimental effects of rodents on native species, particularly in the aforementioned conservation hotspots, is a crucial step towards developing an

effective control/eradication management plan. The aim of this study was to conduct a preliminary assessment of rodent densities in different vegetation types, which will be repeated throughout the duration of the project to assess temporal fluctuations in rodent populations and to determine whether these are affected by rainfall, microhabitat, or other factors.

2. Materials and methods

2.1. Study areas

St. Eustatius (21 km²) (17° 28' – 17° 32' N, 62° 59'–63° W) comprises two volcanic areas separated by lowlands (Van Andel et al., 2016). Boven (289 m) to the north consists of five extinct volcanic centers, whereas the Quill (600 m) to the south is a dormant stratovolcano (Axelrod, 2017; Roobol and Smith, 2004; Van Andel et al., 2016). The Quill (~220 ha) and Boven (~320 ha) are terrestrial protected areas (TPA) that are actively managed by St. Eustatius National Parks Foundation (Collier and Brown, 2008). The aforementioned IBAs overlap with the TPAs. Both areas are covered in secondary dry forest (Van Andel et al., 2016). Fieldwork was conducted in 13 of the 15 different vegetation types as classified by De Freitas et al. (2012; Fig. 1), which were further examined by Van Andel et al. (2016), and by the other authors in 2017–2019. Vegetation type M6 (*Capparis-Antirhea* mountains) was inaccessible, whereas M8 (*Antirhea-Coccoloba* mountains) was accessible but its steep topography prevented us from effectively conducting fieldwork. Our study did not include any assessment of rodent populations in urban areas.

Vegetation on St. Eustatius varies from evergreen forest inside the Quill crater to abandoned agricultural pastures. The former is home to tall fig trees (*Ficus nymphaeifolia* Mill.) and silk cotton trees (*Ceiba pentandra* (L.) Gaertn.), whereas the latter are plagued by the invasive corallita vine (*Antigonon leptopus* Hook. & Arn.), with just a few scattered trees (Van Andel et al., 2016). In addition to invasive rodents, a number of introduced ruminants inhabit the dry forest habitats of the Quill and Boven, as well as non-forested areas of the island. The density of free-roaming goats inside the protected areas is estimated to be 109/km² (Debrot et al., 2013). Such livestock densities cause soil degradation, loss of organic matter, reduced water retention and erosion. The steep terrain and cliffs of St. Eustatius are more vulnerable to erosion and harbor higher densities of rare species due to micro-habitat availability (Debrot et al., 2013). This is likely to have an additional impact on native flora within the vegetation types sampled, however it was not possible to quantify this in our study. Annual average precipitation is 986 mm (De Freitas et al., 2012), and vegetation at higher elevations receives more rainfall than elsewhere on the island (De Freitas et al., 2012). In the absence of natural water sources the availability of fresh water decreases during the dry season

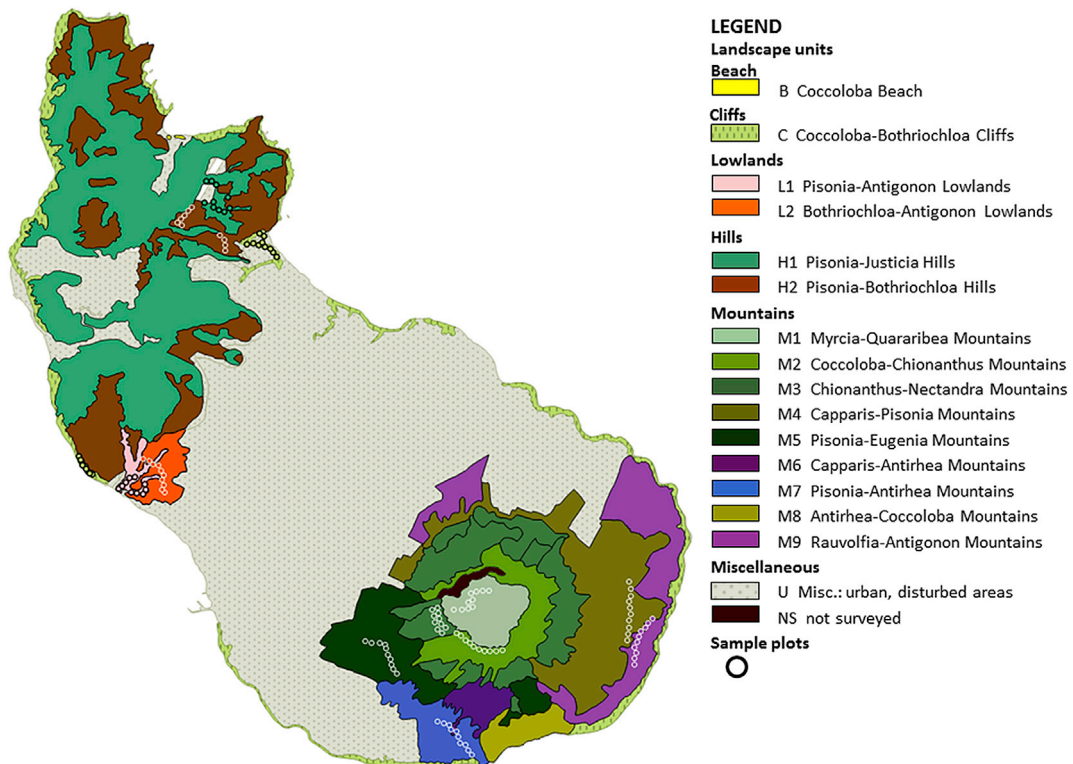


Fig. 1. Landscape ecological vegetation map of St. Eustatius showing locations of tracking tunnels and vegetation plots.

(Madsen and Shine, 1999), however rodents are known to obtain water through the consumption of plant material or rainwater droplets (Shiels et al., 2014) and do not appear to rely on a constant water source (Shiels and de Arellano, 2018). This makes them perfectly adapted to surviving in dry forest and semi-arid environments such as those found on *St. Eustatius*.

2.2. Tracking tunnels

In order to determine the relative abundance of invasive rodent species, data were collected in all accessible vegetation types between July 2017 and February 2018, but not immediately following the passing of Hurricanes Irma and Maria in September 2017. Ten footprint tracking cards were placed in each vegetation type at 50-meter intervals, baited with peanut butter, and tracked over three consecutive nights (Mills et al., 1991; Brown et al., 1996; Brown et al., 1996, 1996; Ogden and Gilbert, 2009). Black Trakka™ (Black Trakka, Warkworth, New Zealand) ink cards were used, followed by homemade cards using masking tape and a mixture of oil and powder paint (Agnew, 2009). Tracking cards were placed on the ground and covered with a cardboard tunnel or construction of natural vegetation. Tunnels were set away from hiking trails or roads (if applicable) in the morning and checked/replaced the following morning. A total of 390 tracking tunnels were placed in 13 vegetation types (30 tunnels per vegetation type over three consecutive nights). The tracks on each tracking plate were examined and the species determined (rat, mouse, crab, lizard, insect, other, or a combination of two or more). Mouse prints were distinguished from rat prints due to their smaller size and the tendency of mice to leave multiple prints on a card. Where we were unsure of the rodent species based on the footprint, we installed a camera trap at the entrance of the tracking tunnel and examined the photos the following day. Tracking rates of plates containing the tracks of a given species are expressed as the frequency of average across three nights. For example, for one tracking tunnel that contained prints on nights 1 and 3 the average was 0.66% (Blackwell et al., 2002).

2.3. Microhabitat

In order to determine whether rodent relative abundance was correlated with one or more microhabitat components, data were collected in a 25 × 25 m plot randomly selected within all ($n = 13$) vegetation types except M6 and M8. In addition, data were collected in a 5 × 5 m plot at each of the tracking tunnel locations ($n = 130$). We combined all data to produce an average from each vegetation type. The microhabitat components were:

1. Elevation: A Garmin Montana 680t GPS device was used to measure elevation.
2. Leaf litter depth: a minimum of five measurements (one in the center and one in each corner) was taken within each plot and averaged to determine leaf litter depth (Cox et al., 2000).
3. Leaf litter cover: the percentage cover of leaf litter was estimated by eye on two separate occasions and averaged (Cox et al., 2000).
4. Number of shrubs: the number of stems standing between 45° and 90° and ≤10 cm in diameter was counted (Van Andel et al., 2016).
5. Number of shrub species: the number of shrub species was counted (Van Andel, 2016).
6. Number of tree species: the number of tree species was counted (Van Andel et al., 2016).
7. Number of trees alive: the number of living trees was counted (Van Andel et al., 2016).
8. Canopy cover: the percentage cover of the canopy was assessed using the same method as for leaf litter cover (Cox et al., 2000).
9. Canopy height: the maximum height of the canopy was measured with a Bushnell Elite™ rangefinder.
10. Slope: slope was measured with a Suunto clinometer in the center of each plot.
11. Local monthly rainfall data were downloaded from <http://www.seawf.com/rainhist.php#monthlyrain>. Total rainfall in the month preceding the placement of each set of tracking tunnels was included in the analysis.

2.4. Statistical analyses

We transformed percent rodent relative abundance, percent canopy cover, and percent leaf litter cover with an arcsine square root transformation (Sokal and Rohlf, 1995). We performed a *t*-test to compare the frequency of average of rodent (rat versus mouse) tracks in the different vegetation types. We tested the relative abundance of rodents in each vegetation type using the package 'ggpubr' (Kassambara, 2017) in R version 3.5.0 (2018) to determine the association between rodent relative abundance and the microhabitat components (Madsen and Shine, 1999; Cox et al., 2000; Engeman and Whisson, 2006; Christie et al., 2017). We used Fisher's exact tests to determine if rat, mouse, and combined rodent relative abundance, after one and two nights following activation of the tracking tunnels, differed among vegetation types. We conducted pairwise correlations between the microhabitat components. Statistical significance was based on $P < 0.05$.

3. Results

Tracking tunnel data (the percentage of tunnels containing the tracks of a given species, averaged over three nights) revealed rodent relative abundances from 0% to 60% in elevations ranging from sea level to 507 m (Fig. 2). Most of the cards had animal tracks, and 177 (45%) cards contained the tracks of multiple animal species. Of 390 tunnels, 151 (39%) contained rodent tracks, including 128 (33%) by black rat and 23 (6%) by house mouse; 20 tunnels contained both rat and mouse tracks. Seven tunnels in three locations had the tracking card removed. Many tunnels (43%) showed evidence of hermit crabs (*Coenobita clypeatus* J. C. Fabricius, 1787) or burrowing land crabs (*Gecarcinus ruricola* Linnaeus, 1758), lizards (15%) and insects (53%). One card in vegetation type M4 contained a cat print (*Felis catus* Linnaeus, 1758). The high prevalence of terrestrial crabs on St. Eustatius (De Wilde, n.d.), which are also attracted to the lure, may have impacted rodent activity on tracking cards in some of the vegetation types sampled (see also Witmer et al., 2007a,b).

The highest relative abundances of rodent tracks were recorded in vegetation types M3 (55%), M5 (60%), and M7 (60%) at elevations of ~400, ~300 and ~75 m respectively, which fall both inside and outside the Quill National Park. These tunnels contained black rat tracks but no mouse tracks. More rats were detected >100 m, whereas mice were only recorded <100 m. Both house mouse and rat tracks were detected in vegetation types L2 and M9, at elevations of ~10, ~75 and ~55 m respectively. One vegetation type, M4, detected only house mice and no rats. No mouse tracks were detected in the other vegetation types.

There was a significant difference within vegetation types for the frequency of traps containing rat versus mouse tracks ($t = 4.2$, $P = <0.01$). There was no significant difference for the frequency of cards containing rodent tracks; this pattern was observed for tunnels checked after one night ($P = 0.99$; $n = 13$ vegetation types) and 2 nights ($P = 0.99$; $n = 13$) following tracking tunnel activation. Several of the habitat variables were significantly correlated with each other (Table 1). In particular, elevation and canopy height showed significant collinearity with most of the covariates. There was a significant correlation between rodent relative abundance and the number of tree species ($r = 0.59$, $P = 0.03$; Fig. 3), but not between elevation, number of living trees, number of shrubs, rainfall, canopy cover, canopy height, leaf litter cover, leaf litter depth, or slope (Table 2).

4. Conclusions

4.1. Rodent presence and distribution

Thanks to the plasticity of their foraging behavior and their opportunistic characteristics, invasive rodents can persist in a variety of climates and habitats (Galef, 2003). The presence of invasive black rat in all elevations and all but one vegetation type sampled, including the terrestrial protected areas, was confirmed through the use of tracking tunnels. Our results are consistent with previous observations that this species is a generalist with respect to the use of rural areas (Cox et al., 2000; Christie et al., 2017). House mice were detected in three, and both rats and mice were detected in two vegetation types. Rodent relative abundance was significantly correlated with the number of tree species, but not with elevation, canopy cover,

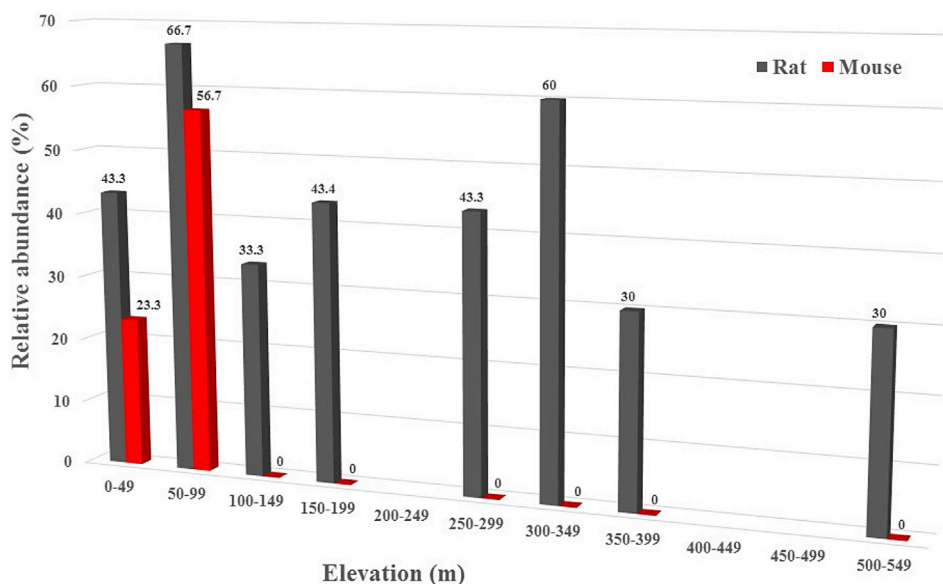


Fig. 2. Relative abundance (%) of black rats (*rattus rattus*) and house mice (*Mus musculus*) in rural areas on St. Eustatius based on tracking tunnel data.

Table 1
Pairwise correlation between habitat variables on St. Eustatius.

| | Elevation | Leaf litter cover | Leaf litter depth | No. shrubs | No. shrub species | No. trees alive | No. tree species | Canopy cover | Canopy height |
|-----------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|---------------|
| Leaf litter cover | 0.61 (0.03) | | | | | | | | |
| Leaf litter depth | 0.77 (< 0.01) | 0.52 (< 0.01) | | | | | | | |
| No. of shrubs | 0.54 (0.06) | 0.47 (0.11) | 0.43 (0.14) | | | | | | |
| No. of shrub species | 0.57 (0.04) | 0.64 (0.02) | 0.37 (0.22) | 0.47 (0.11) | | | | | |
| No. of trees alive | 0.48 (< 0.01) | 0.22 (< 0.01) | 0.21 (< 0.01) | 0.41 (< 0.01) | 0.09 (< 0.01) | | | | |
| No. of tree species | 0.41 (<0.01) | 0.22 (<0.01) | 0.20 (<0.01) | 0.50 (<0.01) | 0.18 (<0.01) | 0.89 (<0.01) | | | |
| Canopy cover | 0.81 (0.01) | 0.77 (0.01) | 0.73 (0.01) | 0.40 (0.18) | 0.39 (0.18) | 0.40 (0.18) | 0.25 (0.42) | | |
| Canopy height | 0.65 (< 0.01) | 0.95 (< 0.01) | 0.52 (< 0.01) | 0.45 (< 0.01) | 0.75 (< 0.01) | 0.17 (< 0.01) | 0.14 (< 0.01) | 0.77 (< 0.01) | |
| Slope | 0.31 (0.30) | -0.23 (0.43) | -0.15 (0.61) | -0.08 (0.78) | -0.04 (0.89) | 0.07 (0.81) | 0.01 (0.99) | -0.18 (0.85) | -0.18 (0.55) |

Significance levels (*P*-values) are given in parentheses. Bold typeface indicates significant correlation.

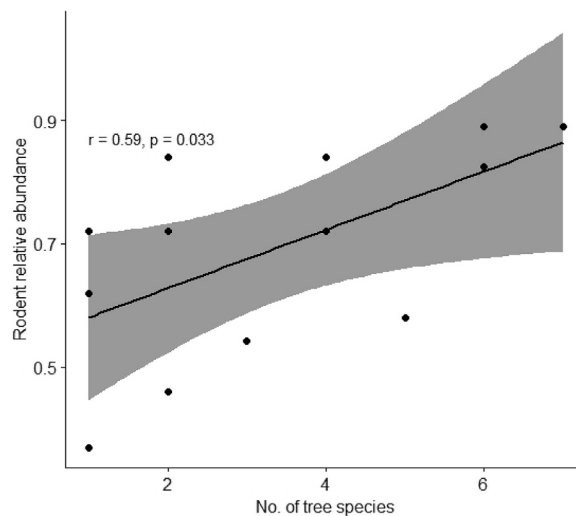


Fig 3. Correlation between rodent relative abundance and the number of tree species on St. Eustatius.

Table 2

Correlation analysis between total rodent (rats + mice) relative abundance and microhabitat components in 13 vegetation types on St. Eustatius. Bold typeface indicates significant correlation.

| Microhabitat component | Pearson correlation coefficient | <i>P</i> -value |
|----------------------------|---------------------------------|-----------------|
| Elevation | 0.22 | 0.48 |
| No. of shrubs | 0.03 | 0.92 |
| Leaf litter depth | -0.09 | 0.76 |
| Leaf litter cover | 0.29 | 0.34 |
| No. of shrub species | 0.22 | 0.48 |
| No. of trees alive | 0.50 | 0.08 |
| No. of tree species | 0.59 | 0.03 |
| Rainfall (mm) | -0.34 | 0.25 |
| Canopy cover | 0.18 | 0.56 |
| Canopy height | 0.16 | 0.60 |
| Slope | 0.13 | 0.67 |

leaf litter cover, or the other microhabitat components. This suggests that the relative abundance of rodents is likely to increase in vegetation types with a higher diversity of trees. Other studies (e.g., Christie et al., 2017; Cox et al., 2000; Shiels et al., 2017) have revealed significant correlations between rodent presence and elevation, temperature, and/or leaf litter cover. Elsewhere, the home range of black rats is estimated to vary in size from 0.1 to 1 ha in all habitat types, depending on food availability and habitat quality (Brown et al., 1996; King, 1990; Bell and Daltry, 2012). The home range of mice is smaller than

that of rats (Howald et al., 2007), therefore placing tracking tunnels at 50-meter intervals significantly limited the risk that the same individual(s) visited multiple tunnels (Brown et al., 1996; Witmer et al., 2007a,b).

Tracking tunnels in vegetation type M4 (*Capparis-Pisonia* mountains) detected mice but not rats. This area of forest on the lower, dry outer slopes of the south side of the Quill is dominated by *Quadrella cynophallophora* (L.) Hutch., *Ficus citrifolia* Mill. and *Citharexylum spinosum* L. and has a lower floristic diversity, density and canopy height than other forest areas on the wetter eastern and northeastern slopes of the Quill (Van Andel et al., 2016). Both mouse and rat tracks were detected in vegetation types L2 (*Bothriochloa-Antigonon* lowlands) and M9 (*Rauvolfia-Antigonon* mountains). L2 is characterized by an abundance of two invasive flora species: corallita (*Antigonon leptopus*) and *Leucaena leucocephala* (Lam.) de Wit (Van Andel et al., 2016). M9 is a heavily grazed, disturbed shrubland, characterized by low floristic diversity, a carpet of corallita, and patches of Acacia trees (*Vachellia* sp.) (Van Andel et al., 2016). In all three areas, signs of mice were found on more tracking plates than rats (Fig. 2) and the microhabitat consisted of shallow leaf litter (<1 cm), low canopy cover (<35%), and low elevation (<80 m). A study by Cox et al. (2000) in New Zealand concluded that *Rattus rattus* occupies forest areas rather than open or scrub habitats, and that their preferred microhabitats comprise a deep leaf litter cover and dense understory with numerous vertical stems. Similarly, a study by Shiels et al. (2017) on Maui revealed that rats overwhelmingly prefer forest habitats over open grasslands. The results of our preliminary assessment are therefore consistent with these observations. Mice, on the other hand, persist in open agricultural and natural habitats where there are few or no competitors (Pocock et al., 2004), which is also consistent with Shiels et al. (2017) and our own data.

4.2. Elevation

Fewer rat tracks were detected at lower elevations, with the exception of vegetation type C (*Coccoloba* – *Bothriochloa* cliffs). This area is characterized by steep cliffs with some areas of rubble and loose soil. The vegetation is dominated by *Coccoloba uvifera* (L.) L. and has a low diversity of shrubs (De Freitas et al., 2012). Tracking tunnels were placed in this vegetation type at low elevation (~28 m) on the northwest coast due to its significance as a nesting site for tropicbirds. The presence of tropicbirds could account for higher rodent relative abundance than may otherwise be found in this vegetation type, since black rats have been documented predated the eggs of this species (Chan, 2013; Madden, 2015; Boeken, 2016). For this reason, and due to the relatively high relative abundance of rats (43.3%), the area was selected as a treatment site within the wider scope of the rodent control project. We recorded 60% rat relative abundance at a relatively low elevation (~51 m) in vegetation type M7 (*Pisonia* – *Antirhea* mountains), which according to De Freitas et al. (2012) is characterized by a low, open shrub layer with a sometimes dense tree layer of up to six meters. This could account for a higher rat relative abundance than might otherwise be expected at this elevation. Tracking cards in all vegetation types sampled within the Quill and Boven National Parks detected black rats at densities of between 30% and 55%. No signs of mice were detected in these areas. The difference for the frequency of traps containing rat versus mouse tracks within vegetation types is to be expected given that some vegetation types only occur at higher elevations.

4.3. Conservation implications

The Quill National Park is a designated IBA due to its importance as a habitat for a number of restricted-range, forest-dependent species, such as bridled quail-dove (*Geotrygon mystacea* Temminck, 1811), purple-throated carib (*Eulampis jugularis* Linnaeus, 1766), scaly-breasted thrasher (*Margarops fuscus* Statius Muller, 1776), and Lesser Antillean bullfinch (*Loxigilla noctis* Linnaeus, 1766) (Collier and Brown, 2008; Geelhoed et al., 2013). Black rat tracks were recorded in differing densities at various elevations within the TPAs, whose presence in the parks can result in detrimental impacts on native biota (Samaniego-Herrera, 2014; Shiels et al., 2013). Examples of successful eradication projects in the region on small, uninhabited islets include Anguilla's Dog Island (Bright et al., 2014) and Redonda (Daltry and Bell, 2018). Many more challenges exist on an inhabited island such as St. Eustatius, whereby stakeholder participation and support play a crucial role (Oppel et al., 2011; Glen et al., 2013). Moreover, unless effective biosecurity regulations are in place and strictly implemented the risk of re-invasion is high. Currently such measures are lacking on St. Eustatius. We note that the failure rate of rat eradication projects in the tropics (16.1%) is significantly higher than outside the tropics (6.3%; Russell and Holmes, 2015).

High numbers of terrestrial crabs (see Witmer et al., 2007a,b) may have inhibited rodent activity on the tracking cards in some vegetation types. Crabs, which are not susceptible to most anticoagulant rodenticides, have been responsible for rodent eradication failure in the tropics due to their consumption of rodenticide bait or interference with bait stations (Campbell et al., 2015; Holmes et al., 2015). Anticoagulant rodenticide can persist in crab tissue for at least 56 days (Primus et al., 2006) and present a secondary exposure pathway for other animals, including humans (Wegmann et al., 2012). 'Essence' compounds such as cinnamon, anise, nutmeg, spearmint, clove, pennyroyal, orange, and lemon could be tested as chemical crab deterrents when implementing rodenticide treatment under the wider scope of this project in the future (Campbell et al., 2015).

4.4. Limitations

In September 2017, category 5 hurricanes Irma and Maria passed to the north and south of St. Eustatius respectively. Whilst urban areas were not severely impacted, hurricane force winds of up to 150 mph caused extensive defoliation of vegetation

across the outer slopes and crater of the Quill, as well as Boven, with 93% of trees showing signs of severe (>75%) defoliation (Eppinga and Pucko, 2018). Rodent populations are thought to decrease significantly immediately following hurricane impact but recover quickly thanks to post-hurricane food supplies (Tapia-Palacios et al., 2017). Our tracking tunnel study took place over seven months. Tracking tunnels were deployed in five vegetation types pre-hurricane and seven post-hurricane. Fieldwork was constrained by hurricane impacts as well as limited staff capacity. Whilst it was desirable to test the influence of two major hurricanes on rodent populations, we were unable to deploy tracking tunnels in rural areas for a period of two months following impact due to inaccessibility. Based on additional tracking tunnel data collected quarterly in 2018 and 2019 (Madden, unpubl. data), however, we are of the opinion that rodent populations recovered and stabilized by the beginning of 2018.

4.5. Discussion

Many studies on the relationship between rodent populations and resource availability are limited in temporal scope and populations may fluctuate based on trophic structure and dynamics, resource limitation, and precipitation (Ernest et al., 2000). Rat dynamics on tropical islands are primarily driven by bottom-up effects with summer high densities associated with seasonal pulses of rainfall, but these vary according to the context-specific characteristics of each island (Ringler et al., 2014). The results of this study provide an initial assessment of invasive rodent presence and distribution in 13 vegetation types on a small, inhabited Caribbean island. Our study demonstrates that rodents are present in all vegetation types and at all elevations sampled on St. Eustatius. Black rats were the most common rodent, present in 12 of the 13 vegetation types sampled and detected in 33% of all tracking tunnels deployed. Mice were present in three vegetation types and detected in 6% of all tunnels deployed. We found a significant correlation between tree diversity and rodent relative abundance. Overall our results concur with other studies that rats favor forest environments, whereas mice typically occupy open habitats at lower elevations (e.g., Cox et al., 2000; Pocock et al., 2004; Shiels et al., 2017; Shiels and de Arellano, 2018). Contrary to studies on other tropical islands (Shiels et al., 2017; Shiels and de Arellano, 2018), rodent relative abundance on St. Eustatius does not appear to be strongly associated with elevation, although this may be due to the island's small size and limited altitudinal range (0–600 m).

Our study did not include any assessment of rodent populations in urban areas, where rats and mice are also present. Fluctuations in relative abundance within the same vegetation types will be measured throughout the duration of the rodent control project in an effort to understand how these may be affected by changes in precipitation, vegetation, and thus availability of food. The results of this preliminary assessment can be used by local government and park management authorities to develop policies and conservation strategies in order to manage invasive rodents in rural areas, which are likely to have detrimental impacts on indigenous biota. Our study highlights the need for research into the effects of invasive rodents on native species (Shiels and Ramírez de Arellano, 2018) on St. Eustatius, both inside and outside the protected areas.

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