

1 Hurricane-induced population decrease in a Critically Endangered long-lived reptile

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16 ABSTRACT

17 Catastrophic events, like hurricanes, bring lethal conditions that can have population-altering
18 effects. The threatened Caribbean dry forest occurs in a region known for its high-intensity
19 hurricane seasons and high species endemism, highlighting the necessity to better understand
20 hurricane impacts as fragmentation and clearing of natural habitat continues. However, such studies
21 remain rare, and for reptiles are mostly restricted to *Anolis*. Here we used single-season occupancy
22 modeling to infer the impact of the intense 2017 Atlantic hurricane season on the critically
23 endangered Lesser Antillean Iguana, *Iguana delicatissima*. We surveyed 30 transects across eight
24 habitats on St. Eustatius during 2017-2019, which resulted in 344 individual surveys and 98 iguana
25 observations. Analyses of abundance and site occupancy indicated both measures for 2018 and
26 2019 were strongly reduced compared to the pre-hurricane 2017 state. Iguanas at higher elevations
27 were affected more profoundly, likely due to higher wind speeds, tree damage and extensive
28 defoliation. Overall, our results indicate a decrease in population estimates (23.3-26.5%) and
29 abundance (22-23.8%) for 2018 and 2019, and a 75% reduction in the number of opportunistic
30 sightings of tagged iguanas between 2017-2018. As only small and isolated *I. delicatissima*
31 populations remain, our study further demonstrates their vulnerability to stochastic events.
32 Considering the frequency and intensity of hurricanes are projected to increase, our results stress the

33 urgent need for population-increasing conservation actions in order to secure the long-term survival
34 of *I. delicatissima* throughout its range.

35 **Keywords**

36 Abundance, Caribbean, Detection probability, Disturbance event, Habitat, Hurricane, *Iguana*
37 *delicatissima*, Monitoring, Site occupancy, St. Eustatius

38

39 **Introduction**

40 Hurricanes bring lethal conditions to populations in their path. These events can either directly
41 affect natural populations, through e.g., mortality (Reagan 1991; Wiley and Wunderle 1993; Spiller
42 et al. 1998; Behie and Pavelka 2005; Morcilo et al. 2020; Marroquin-Paramo et al. 2021), or
43 indirectly e.g., when food presence and abundance is impacted (Cely 1991). Selective mortality
44 sweeps have been shown to drive both evolution (Donihue et al. 2018) and community diversity
45 (Johnson and Winker 2010; Meléndez-Vazquez et al. 2019). Additionally, catastrophic winds can
46 aid dispersal of species (e.g., Censky et al. 1998). Although studies on the effects of hurricanes are
47 rising given their projected increase (Webster et al. 2005), such studies are dependent on pre-
48 hurricane data and hurricane trajectory, and are thus lacking for many species.

49 From a conservation perspective, the population-diminishing threat of hurricanes is
50 especially of concern for closed island populations, which often represent restricted-range and
51 endemic species. As natural habitat disappears and fragmentation continues to worsen (Jacobson et
52 al. 2019; Powers and Jetz 2019), understanding how stochastic events affect remaining populations
53 is crucial. In a rare long-term study on an endangered Bahamian woodpecker (*Melanerpes*
54 *superciliaris nyeanus*), Akresh et al. (2020) demonstrate that the population experienced significant
55 declines as a result of various hurricanes but was able to recover after several years, however
56 increased future hurricane frequency could prevent this. Contrarily, a study on a small, 350-
57 individual, population of *Cyclura nubila* revealed that the passing of Hurricane Ivan (2004) had no
58 effect on its size (Beovides-Casas and Mancina 2006), demonstrating the resilience of large rock
59 iguanas to catastrophic events. Overall, studies concerning the effect of hurricanes on reptile species

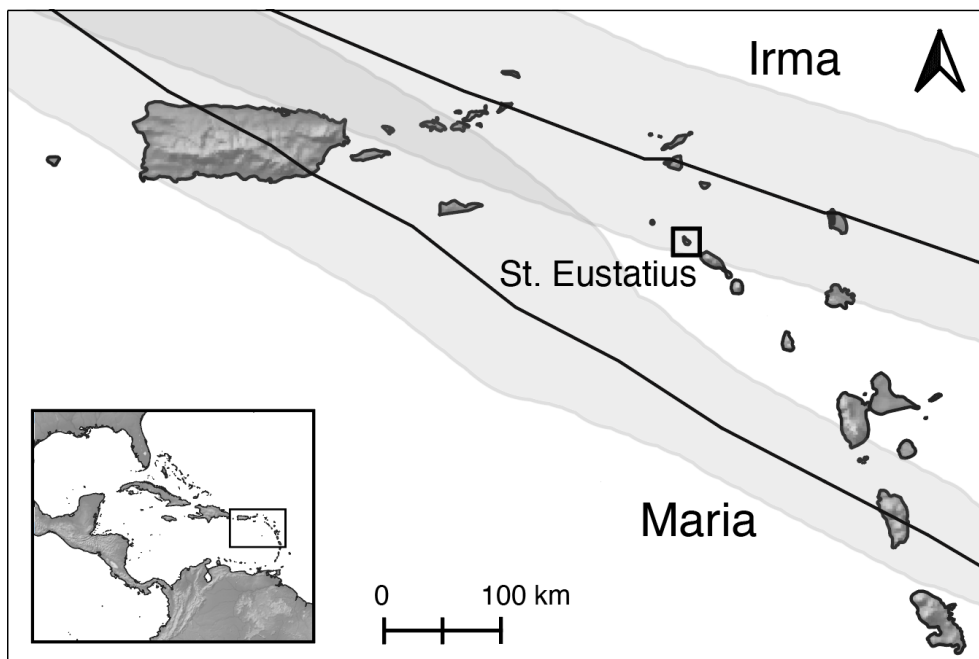
60 have mainly focused on small-size species (e.g., *Anolis*: Spiller et al. 1998; Schoener et al. 2001;
61 Losos et al. 2003; Donihue et al. 2018, 2020; Dufour et al. 2019; Rabe et al. 2020). Insular iguanas
62 are highly endangered ecological keystone species, and generally are the largest native remaining
63 terrestrial species (IUCN 2020). As Caribbean hurricane frequency is projected to increase (Bender
64 et al. 2010), understanding the impacts of hurricanes on iguana populations is important and is
65 frequently highlighted but rarely quantified (Alberts 2004; Fogarty et al. 2004; Powell 2004;
66 Pasachnik et al. 2012; but see Hayes et al. 2004, 2016; Beovides-Casas and Mancina 2006).

67 Among Caribbean Iguanids, the conservation status of the Lesser Antillean iguana (*Iguana*
68 *delicatissima*) has experienced the most rapid deterioration (van den Burg et al. 2018a). Its pre-
69 Colombian range has to date decreased by >80%, predominantly due to hybridization with *Iguana*
70 *iguana* lineages (Vuillaume et al. 2015; Pounder et al. 2020), a process that was recently initiated
71 on the last remaining ≥ 2 km² islands where *I. delicatissima* occurs (van den Burg et al. 2018b,
72 2020; B. Angin pers. comm.). Left uncontrolled, the genetic loss of these populations will lead to a
73 >99% decrease in their native range (van den Burg et al. 2018a). Critically, the five remaining
74 populations that are free of nonnative iguanas occur on <2 km² islets with low estimated population
75 sizes (only Petite Terre >1,000 individuals; Angin 2017; Pounder et al. 2020). Beyond the spread of
76 *I. iguana* (Knapp et al. 2020), other threats come from habitat destruction, pets and free-roaming
77 livestock, as well as other anthropogenic causes (e.g., vehicle-caused mortality) (Debrot et al. 2013;
78 Knapp et al. 2014, 2016; van den Burg et al. 2018c). Although hurricanes are cited as a potential
79 threat to population survival (e.g., Fogarty et al. 2004), only two studies have addressed this topic.
80 Namely, Knapp and Valeria (2008) provide some insight through an observational account of nest
81 site degeneration and iguana mortality caused by Hurricane Dean (2007) on Dominica. Focusing on
82 Petite Terre (Guadeloupe), a second study provides insight into a likely decrease in population size
83 due to Hurricane Hugo (1995; Lorvelec et al. 2004). However, since the monitoring methodology
84 has been questioned (Breuil and Ib  n  , 2008; B Angin pers. comm.), no conclusions can be drawn.
85 This study also predated new analytical tools and updates (e.g., Fiske and Chandler 2011).

86 Within the northern Lesser Antilles, St. Eustatius supports one of the last remaining *I.*
87 *delicatissima* populations. This population suffered a major decline during the 1990s, in part due to
88 consumptional demand on neighboring St. Maarten (Debrot et al. 2013), and is currently threatened
89 by ongoing hybridization with *I. iguana* (van den Burg et al. 2018b). Despite the occasional arrival
90 of stowaway iguanas, continuous monitoring has only resulted in 15 (Debrot et al. in review.)
91 identified nonnative (pure or hybrid) animals, thus hybridization is believed to be minimal
92 (unpublished data). The most recent estimates put the population size at below 500 individuals
93 (Debrot et al. 2013), which has presumably since decreased due to ongoing anthropogenic threats
94 (van den Burg et al. 2018c). Additionally to threats common for the species (see above), the
95 population on St. Eustatius faces death by entrapment in abandoned cisterns, invasive rats, and the
96 spread of the nonnative invasive Mexican creeper or Corallita (*Antigonon leptopus*) (Fogarty et al.
97 2004; Debrot et al. 2013; van den Burg et al. 2018c). Although St. Eustatius fell within the
98 trajectory of major 2017-season hurricanes (Fig. 1), an impact assessment for *I. delicatissima*
99 population is lacking.

100 The 2017 Atlantic hurricane season was categorized as hyperactive, with an accumulated
101 cyclone energy score within the top ten since registration started (Schultz et al. 2018). Of the six
102 2017 hurricane-force systems, two closely passed St. Eustatius. On 6 September, the center of
103 Hurricane Irma passed at ~54 km, and on 19 September, Hurricane Maria passed at roughly 110 km
104 distance (Fig. 1; NOAA 2020). The goal of our study was to utilize iguana-survey data collected
105 during 2017–2019 in order to assess the impact of the 2017 hurricane season on the St. Eustatius *I.*
106 *delicatissima* population. To that end, we used island-wide transect survey data to estimate
107 abundance, detection probability, and site occupancy per habitat type and year. Changes in
108 occupancy, defined as the probability of a site being occupied (MacKenzie et al. 2002), provide a
109 robust proxy for population declines, particularly for sparsely populated and cryptic species (Dénes
110 et al. 2015; Beaudrot et al. 2016). We hypothesized that if population estimates were stable over
111 this 3-year period, this would suggest that iguanas are resilient to catastrophic weather events.

112 However, if population estimates varied, this would suggest that external factors (directly and/or
113 indirectly) impacted iguana survival.



114
115 **Fig. 1** Best trajectory paths and regions with hurricane force winds ($\geq 64kt$) for Hurricane Maria and Irma in
116 the northern Greater Caribbean region. Data from the National Hurricane Center.

117

118 **Materials & Methods**

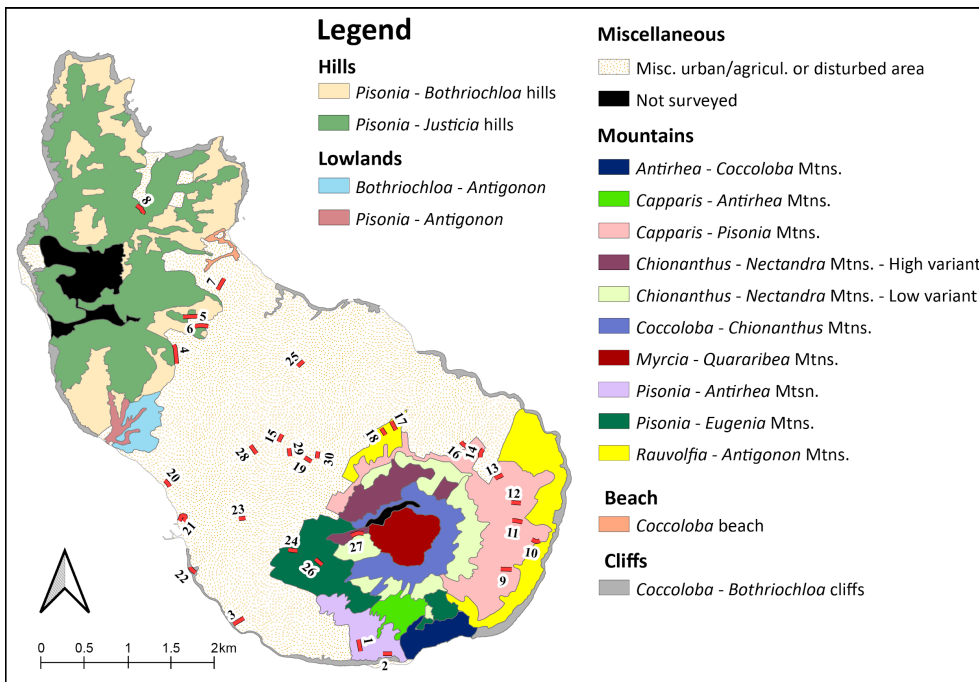
119 *Study area*

120 This study took place on St. Eustatius (17.49°N, -62.98°W), a small (21 km²) Leeward island within
121 the northern Lesser Antilles (Fig. 1), with a human population of approximately 3,100 (Statistics
122 Netherlands 2020). Habitat falls within the Caribbean dry forest and local climate is defined as
123 Tropical Humid (Trewartha and Horn 1980), with over 90% of the island having a tropical savanna
124 climate (<400 m) (De Freitas et al. 2012). Annual temperature fluctuates around 25–33 °C, with
125 average annual rainfall around 1000 mm while the highest elevations receive <2,000 mm (Rojer
126 1997; van Andel et al. 2016). Geographically, the island consists of two mountainous areas that
127 originate from volcanic activity and uplift on the northern and southern end. These areas are
128 separated by a lower elevational plain where most anthropogenic activity occurs. Historic island-
129 wide agricultural practices have downgraded the habitat quality which has partially recovered due

130 to a significant decrease in such practices and conservation efforts, though habitats are affected still
131 by grazers, erosion and invasive species (van Andel et al. 2016).

132
133 *Transects*

134 Between 2017–2019, we conducted repeated count transect surveys to estimate site
135 occupancy, detection probability and abundance of the *I. delicatissima* population (Royle and
136 Nichols 2003). For this, we placed a total of 30 transects over the island, each 100 m in length, and
137 visually surveyed up to 25 m on both sides (Fig. 2). Surveys were performed by minimally one
138 observer with iguana-fieldwork experience, during hours of general iguana activity (Pasachnik et al.
139 2002), and were limited to non-rainy days given ectotherm activity. We recorded the date, survey
140 duration (min.), elevation (m), number of observers, and observed number of iguanas. Due to
141 limited capacity to conduct surveys, transects were surveyed a maximum of six times per year.
142 Transects included 47% of present habitat types representing 78.3% of the island’s surface. Several
143 habitat types were not surveyed due to access restrictions (e.g., *Bothriochloa - Antigonon*) or
144 physical safety (e.g., *Antirhea - Coccoloba* mountains). Furthermore, the northern area was
145 surveyed less often than other habitats due to logistics and access difficulty of the area, and given an
146 oil transshipment company occupies 10–15% of the island’s surface area. Following De Freitas et al.
147 (2012) nomenclature, surveys were performed in eight habitat types (see Fig. 2, Table 1): *Pisonia -*
148 *Antirhea* mountains; miscellaneous urban/agricultural or disturbed land; *Pisonia - Justicia* hills;
149 *Capparis - Pisonia* mountains; *Rauvolfia - Antigonon* mountains; *Coccoloba - Bothriochloa* cliffs;
150 *Pisonia - Eugenia* mountains; *Chionanthus - Nectandra* mountains.



151

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Fig. 2 Map of St. Eustatius showing transect locations and habitat distribution. Habitat names following De

153

Freitas et al. (2012).

154 **Table 1** Summary of transect surveys conducted on St. Eustatius between 2017–2019. Habitat name

155 following De Freitas et al. (2012). All transects constituted 100 m in length with a surveyed area of 500 m².

Habitat name	Transect nr.	Lat.	Lon.	Start elev. (m)
<i>Pisonia - Antirhea</i> mountains	(1)	17.4672	-62.9681	69
	(2)	17.4659	-62.9643	41
Misc. urban/agricultural or disturbed land	(3)	17.4691	-62.9808	12
	(4)	17.4947	-62.9867	59
	(5)	17.4985	-62.9835	53
	(7)	17.5024	-62.9825	25
	(15)	17.4869	-62.9759	93
	(16)	17.4868	-62.9573	117
	(19)	17.4847	-62.9728	141
	(20)	17.4831	-62.9879	14
	(21)	17.4797	-62.9860	25
	(23)	17.4794	-62.9801	87
	(25)	17.4945	-62.9742	48
	(28)	17.4859	-62.9783	91
	(29)	17.4856	-62.9749	114
(30)	17.4862	-62.9721	123	
<i>Pisonia - Justicia</i> hills	(6)	17.4994	-62.9844	66
	(8)	17.5098	-62.9900	70
<i>Capparis - Pisonia</i> mountains	(9)	17.4742	-62.9518	79
	(10)	17.4774	-62.9499	50
	(11)	17.4790	-62.9508	72
	(12)	17.4806	-62.9510	80
	(13)	17.4837	-62.9527	104
	(14)	17.4862	-62.9547	99
<i>Rauvolfia - Antigonon</i> mountains	(17)	17.4892	-62.9642	104
	(18)	17.4884	-62.9654	117
<i>Coccoloba - Bothriochloa</i> cliffs	(22)	17.4745	-62.9852	12
<i>Pisonia - Eugenia</i> mountains	(24)	17.4764	-62.9748	149
	(26)	17.4754	-62.9726	190

<i>Chionanthus - Nectandra</i> mountains	(27)	17.4780	-62.9670	386
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157 *Opportunistic surveys/sightings*

158 Since 2015, subadult and adult iguanas have been tagged with colored glass beads to
159 facilitate subsequent noninvasive tracking and observations of individuals using unique color
160 combinations (Binns and Burton 2007). To date, 540 unique bead codes have been assigned, and an
161 additional 96 iguanas have been tagged only with PIT tags. This methodology has allowed for
162 opportunistic data collection of the geographic locations of bead-tagged iguanas. We utilized these
163 data as an additional indicator for variation in population size.

164

165 *Data analyses*

166 As our dataset contained a large number of non-detections and small counts of iguanas, we
167 chose an *N*-mixture model approach over distance sampling (Royle 2004). Models were based on
168 four assumptions: (i) the iguana population in each site was closed to colonization and extinction
169 during the sampling period; (ii) iguanas were either detected or not detected during surveys; (iii)
170 iguanas were not falsely detected during surveys; and (iv) iguana detections at each site were
171 independent (Murray and Sandercock 2020). We followed the methods described by Madden et al.
172 (2021). Briefly, we used likelihood-based single-season occupancy models (MacKenzie et al.
173 2017), using the R packages “wiqid” and “unmarked” (MacKenzie et al. 2002; Fiske and Chandler
174 2011), to estimate site occupancy (ψ) in relation to habitat and elevation, while accounting for
175 detectability (p). We modeled detection probability and occupancy probability to estimate iguana
176 abundance (λ), and also tested the influence of independent variables on abundance estimates,
177 including quadratic terms. Resulting models were ranked using Akaike’s Information Criterion,
178 where the detection model with the lowest AICc is best-fitting [AICc; Burnham and Anderson
179 (2002)], while correcting for small sample size. Finally, we tested for overdispersion by assessing
180 the goodness-of-fit of the most parsimonious model in each year (MacKenzie and Bailey 2004)

|

181 with the “mb.gof.test” function in the package “AICcmodavg” using 1,000 simulations, which
182 calculates a Pearson’s chi-square fit statistic from the observed and expected frequencies of
183 detection histories for a given model. All analyses were performed in the R environment v3.5.1 (R
184 Core Team 2019).

185 186 **Results**

187 *Pre-hurricane survey occupancy, detection and abundance estimates*

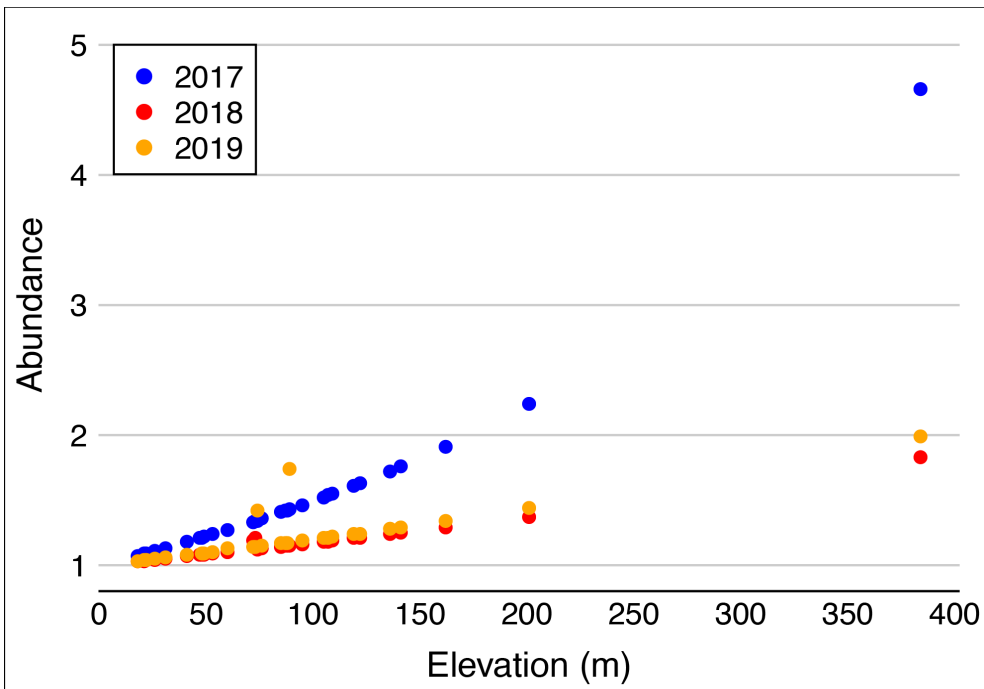
188 We conducted 180 surveys between February and April 2017, prior to hurricanes Irma and Maria,
189 during which we detected 58 individual iguanas. Average transect time was 32 ± 14 minutes. As
190 results for both R packages provided identical patterns we only report “wqid” results here, and
191 “unmarked” results are presented in the Electronic Supplementary Information.

192 Occupancy probability was 100% (range 0–100%), and iguana occupancy and abundance
193 increased with elevation (Figs. 3–4) as well as with survey effort. Occupancy estimates were
194 generally consistent across the habitats sampled (Table 2). Mean detection probability (p) per
195 transect was 0.19 (range 0.14–0.26), which increased to 0.27 when an iguana had been previously
196 detected. The effects of predictor variables ‘survey time’ and ‘week’ on detection and occupancy
197 estimates were negligible ($\Delta AIC_c < 2$). We observed a lack of fit of the null model (without
198 covariates; $\chi^2 = \text{inf}$, $p = 0$, $\hat{c} = \text{inf}$). Estimated mean individual abundance (λ) was $5.91 (\pm \text{SE}$
199 $0.01)$. When habitat and elevation were included as response variables, λ estimates were 1.52 ± 0.65
200 (Fig. 5), which translates to a population estimate across the entire study area (13.5 ha) of 1,364
201 iguanas. Lowest iguana abundance was found in *Coccoloba - Bothriochloa* cliff habitat, and highest
202 in *Chionanthus - Nectandra* mountain habitat.

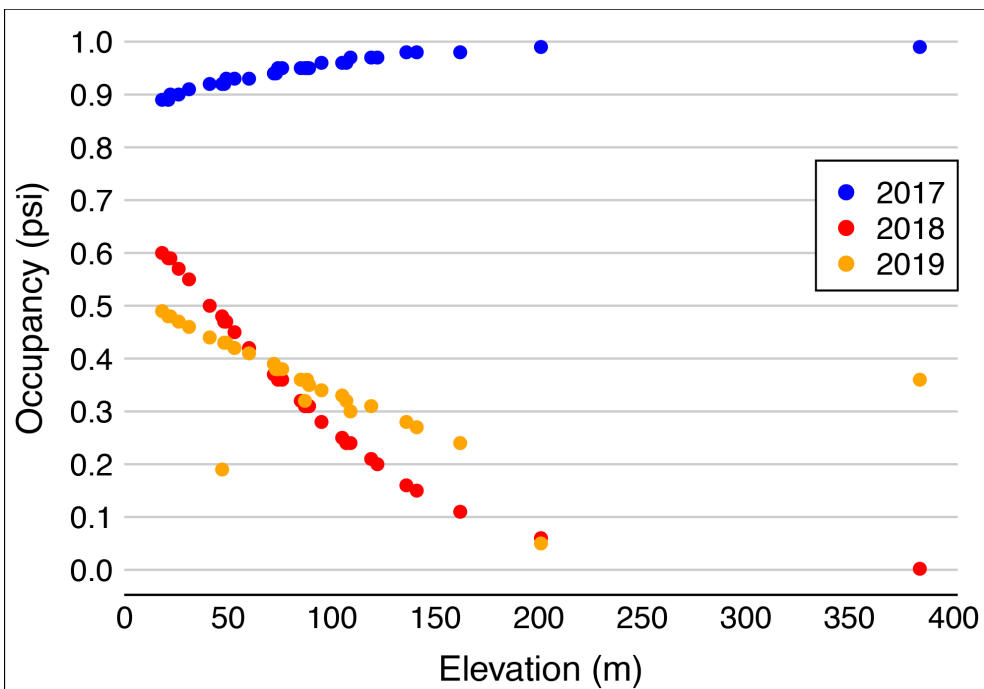
203
204 *Post-hurricane survey occupancy, detection and abundance estimates*

205 Post-2017, we surveyed identical transects between July–December 2018 and March–September
206 2019. Overall, 164 transects were performed during which we detected 13 iguanas in 2018 and 27
207 iguanas in 2019. Average transect time was 19 ± 8 minutes.

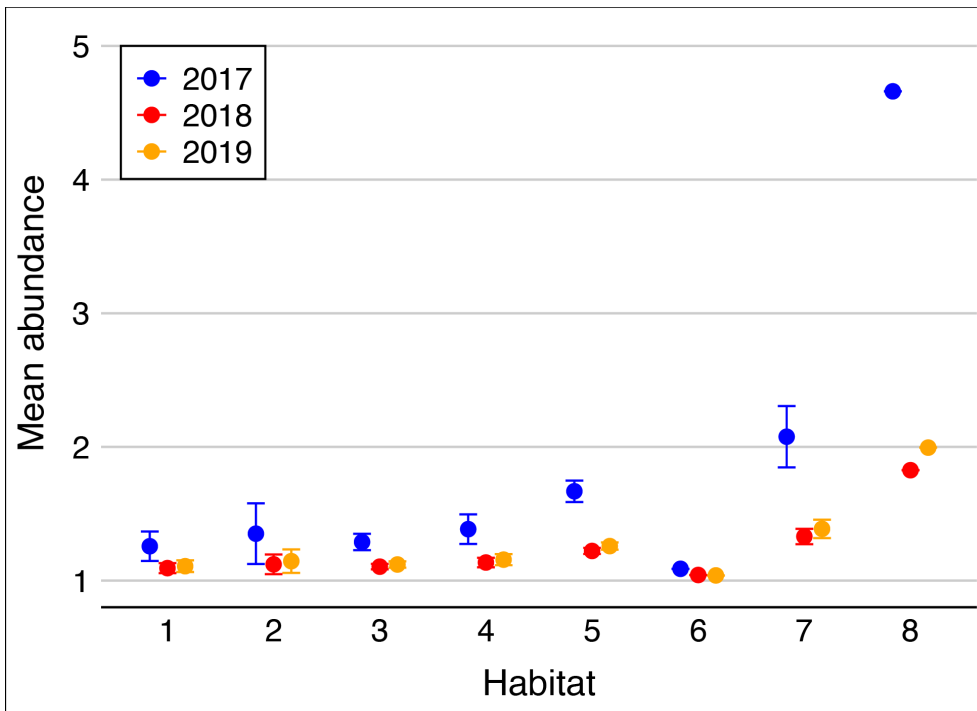
208 Occupancy probability was 32.5% (range 11.8–63.4%) in 2018, and 36.7% (19.2–58.5%) in
209 2019. Iguana occupancy decreased with increasing elevation in 2018 and 2019 (Fig. 3), but
210 increased with survey effort; up to four repeats in 2018 and three in 2019. Occupancy estimates
211 were lower than those from 2017 but generally consistent across habitats (Table 2). p was 0.41
212 (range 0.14–0.74) in 2018, and 0.67 (0.39–0.87) in 2019, decreasing to 0.28 (0.07–0.67; 2018) and
213 0.36 (0.14–0.66; 2019) when an iguana had been previously detected. λ was 5.89 ± 0.02 in both
214 2018 and 2019. Considering habitat and elevation, λ estimates were 1.16 ± 0.15 in 2018 and $1.19 \pm$
215 0.18 in 2019 (Fig. 5), translating to population estimates of 1,046 and 1,003 iguanas, respectively;
216 declines of 23.3% and 26.5% compared to 2017. The covariate ‘survey time’ from the most
217 parsimonious model had a positive effect on detection probability (0.80 ± 0.49) in 2018, however
218 we observed a lack of fit of this model (‘survey time’; $X^2 = \text{inf}$, $p = 0$, $\hat{c} = \text{inf}$). The effect of
219 covariates on detection and occupancy estimates in 2019 were negligible ($\Delta\text{AIC}_c < 2$). There was no
220 evidence for lack of fit in 2019 ($X^2 = 33.86$, $p = 0.66$, $\hat{c} = 0.62$). Habitat abundances were lower in
221 2018 and 2019 compared to 2017, with only abundance range overlap in the *Pisonia - Antirhea*
222 mountain and miscellaneous urban/agricultural or disturbed land habitat types (Fig. 5); compared to
223 2017, average decline in iguana abundance among habitats was 23.8% and 22.0% for 2018 and
224 2019, respectively. Overall, a two-way additive ANOVA indicated no significant difference of
225 iguana abundance among years ($F_{2,14} = 3.49$, $p = 0.059$), and a significant difference between
226 habitats ($F_{7,14} = 3.76$, $p = 0.017$).



227
228 **Fig. 3** The effect of elevation on abundance (lambda) estimates of *Iguana delicatissima* based on transect
229 surveys conducted on St. Eustatius in 2017 (pre-hurricane), 2018 and 2019 (post-hurricane).



230
231 **Fig. 4** The effect of elevation on site occupancy estimates of *Iguana delicatissima* based on transect surveys
232 conducted on St. Eustatius in 2017 (pre-hurricane), 2018 and 2019 (post-hurricane).
233



234
235 **Fig. 5** Mean iguana abundance estimates per habitat type for 2017–2019, with standard deviations bars.

236 Habitat following De Freitas et al. (2012): 1 = *Pisonia - Antirhea* mountains; 2 = miscellaneous
237 urban/agricultural or disturbed land; 3 = *Pisonia - Justicia* hills; 4 = *Capparis - Pisonia* mountains; 5 =
238 *Rauvolfia - Antigonon* mountains; 6 = *Coccoloba - Bothriochloa* cliffs; 7 = *Pisonia - Eugenia* mountains; 8 =
239 *Chionanthus - Nectandra* mountains.

240
241 **Table 2** Overview of 2017–2019 site occupancy estimates per habitat of *Iguana delicatissima* on St.
242 Eustatius. Data represents the probability of a site to be occupied (ψ), as well as confidence intervals (CI).
243 Habitat following De Freitas et al. (2012): 1 = *Pisonia - Antirhea* mountains; 2 = miscellaneous
244 urban/agricultural or disturbed land; 3 = *Pisonia - Justicia* hills; 4 = *Capparis - Pisonia* mountains; 5 =
245 *Rauvolfia - Antigonon* mountains; 6 = *Coccoloba - Bothriochloa* cliffs; 7 = *Pisonia - Eugenia* mountains; 8 =
246 *Chionanthus - Nectandra* mountains.

Habitat	2017		2018		2019	
	ψ	CI	ψ	CI	ψ	CI
1	0.98	<0.001–1.00	0.37	0.07–0.81	0.37	0.12–0.71
2	0.98	<0.001–1.00	0.35	0.10–0.73	0.37	0.16–0.63
3	0.99	<0.001–1.00	0.34	0.11–0.66	0.37	0.19–0.59
4	0.99	<0.001–1.00	0.32	0.11–0.64	0.36	0.18–0.61
5	0.99	<0.001–1.00	0.31	0.09–0.66	0.36	0.13–0.67
6	0.99	<0.001–1.00	0.29	0.06–0.72	0.36	0.09–0.76
7	0.99	<0.001–1.00	0.28	0.04–0.78	0.36	0.06–0.83
8	1.00	<0.001–1.00	0.26	0.02–0.84	0.35	0.04–0.88

247 *Bead-tag data*

248 Opportunistic sighting data were collected during 76, 78 and 56 days in 2017, 2018 and
249 2019, respectively. Assessment of the geographic distribution of those data indicates both time and
250 geographic effort was comparably equal for 2017 and 2018, allowing a direct comparison (see
251 Electronic Supplementary Information), though not for 2019. Of the 145 uniquely bead-tagged
252 iguanas observed in 2017, 36 (24.8%) were observed during 2018.

253

254 **Discussion**

255 Our study demonstrates that multiple *I. delicatissima* population parameters decreased following the
256 high-intensity hurricane year of 2017, with a decrease in estimates of population size, abundance,
257 site occupancy, and opportunistic sightings of tagged iguanas. We did not observe a clear
258 boomerang effect, as 2018-2019 parameters were mostly stable. These data are important to
259 consider from a conservation and long-term stability perspective, given the small sizes of remaining
260 populations of this highly endangered species. Overall, we present a rare effect-analysis of
261 hurricane impact on a wild population of a large, long-lived reptile.

262 *Iguana delicatissima* inhabits most vegetation types within its native range, e.g., mangroves,
263 high evergreen forest, dry shrublands, and gardens (for an overview see Henderson and Powell
264 [2009]). On St. Eustatius, earlier studies found that iguana abundance was highest on vegetated
265 slopes/cliffs and on the northwest flank of the dormant volcano where large estates are built within
266 the tall evergreen forest (Fogarty et al. 2004; Debrot et al. 2013). Similarly, we found that iguana
267 abundance was high in habitats on the western slopes of the volcano, though transects were not
268 placed in gardens (Fig. 5). Thus, besides gardens, also the periferic habitats of this residential area
269 are important iguana habitats. Indeed, Knapp and Perez-Heydrich (2012) found that biometric
270 variables did not differ between iguanas living in- and outside of gardens. Furthermore, highest
271 iguana abundance was found in the *Chionanthus* - *Nectandra* mountain habitat (De Freitas et al.
272 2012), at high (386m) elevation on the volcano, however this habitat was covered by a single

273 transect, thus we lack a perspective of variation. Additionally, we found higher iguana abundances
274 in the *Pisonia-Eugenia* mountain habitat, located on the lower/mid (150–200m) south-western
275 slopes of the Quill. This habitat is described as a secondary forest and, according to van Anandel et al.
276 (2016), “has a much lower diversity, density and canopy height than the forest on the wetter slope”.
277 Nevertheless, it is likely suitable and heterogenous habitat for iguanas and supports a variety of tree
278 species including *Bourreria baccata*, *Pisonia subcordata*, *Guettarda scabra* and *Bursera simaruba*
279 (van Anandel et al. 2016) of which several are a known dietary source (Angin and Questel in prep.).

280 In contrast, *Rauvolfia - Antigonon* habitat is described as disturbed, regenerating shrubland
281 with few trees, low floristic diversity and is covered extensively by an invasive vine (van Anandel et
282 al. 2016). Our results show that iguana abundance is surprisingly relatively high in this habitat type.
283 We note that the patch covered by our survey efforts appears of higher quality than the remainder of
284 this habitat type on the south-western side of the island, which is heavily grazed by free-roaming
285 herbivores (van Anandel et al. 2016; Madden 2020). Namely, the included patch has larger trees, is
286 less degraded, and lies adjacent to secondary roads and semi-urban development. Consequently, we
287 believe that our abundance estimates only apply to the covered patch of *Rauvolfia - Antigonon*
288 habitat.

289 Detection probability increased from 2017 to 2019 but was overall low (<0.5) across all
290 years. Nevertheless, detection probability estimates were similar to/higher than those from
291 comparable studies (Bock et al. 2016; Rivera-Milán and Haakonsson 2020). However, when an
292 iguana was previously observed, detection probability was equal across years. We did not test for
293 observer effort, which may account for unequal detection between years and should ideally be
294 consistent (Burton and Rivera-Milán 2014).; for our surveys, average number of observers was
295 constant over the years (between 2–2.4), and surveys were always led by an experienced iguana-
296 fieldwork technician. Vegetation damage (e.g., broken branches) may have resulted in higher
297 detection probability post-hurricane compared to pre-hurricane, though generally iguanas are harder
298 to detect in forested areas than other habitats. We were unable to locate specific published studies

299 on iguanas to support this, but reptile species overall are cryptic and considered difficult to study
300 (e.g., Durso et al. 2011; Sewell et al. 2012).

301 Our study provides evidence that the St. Eustatius *I. delicatissima* population declined
302 during 2017, during which two major catastrophic events hit the island; Hurricanes Maria and Irma.
303 As behavioural data of iguanas during such events are absent, pinpointing the exact cause of decline
304 is more challenging; how did iguanas die, and was that during or after the events? Post-event
305 mortality, in the absence of sustained physical injury, could result from a lower abundance of food.
306 Indeed, the majority of trees were defoliated due to high wind speeds and likely salt spray (Eppinga
307 and Pucko 2018). However, as not all trees were defoliated, and iguanas are known to survive
308 extended periods of drought (van Buurt 2010), we anticipate that post-event mortality due to
309 starvation had a minor contribution to the observed declines. Instead, we hypothesize that hurricane
310 conditions, either led to deadly physical injuries or translocated iguanas into the Caribbean Sea (see
311 Censky et al. 1998). Whether non-deadly on-island translocation is possible is unknown, though as
312 both abundances declined for all habitat and opportunistic sightings declined drastically, this
313 possibility appears unlikely. Although challenging to collect, future data on iguana movement
314 during hurricane events could provide more insight.

315 We found evidence for overdispersion when calculating site occupancy measures for 2017
316 and 2018, which resulted in inflated standard errors (Table 2). However, given the lack of
317 significance of covariates overall (only ‘survey time’ increased detection probability in 2018), we
318 chose to retain AICc model weights than pursue a quasi-likelihood theory (MacKenzie and Bailey
319 2004). We recognize the limitations of our study with regard to the assumptions of occupancy
320 modeling (Murray and Sandercock 2020), however we are confident that we met most if not all of
321 the assumptions. We assumed that iguana detection was independent between sites, given the
322 species’ limited home range (van Wagensveld et al. in prep.), and that the sites surveyed were
323 discrete patches of habitat (except one survey track in the *Chionanthus* - *Nectandra* mountains
324 habitat). Nevertheless, we recognize that there may be more variation in the observed site

325 occupancy data than expected by the models. Considering the already wide confidence intervals,
326 however, we are of the opinion that the models presented offer a realistic representation of the pre-
327 /post-hurricane population data.

328 Despite the small size of St. Eustatius, our results suggest that the 2017 hurricanes affected
329 iguanas disproportionately across the island. Namely, although abundance and occupancy decreased
330 island wide, iguanas at higher elevations suffered stronger declines (Fig. 3–4). This finding is
331 corroborated by data from Eppinga and Pucko (2018) who assessed the impact of both 2017
332 hurricanes on the forests of St. Eustatius and found that a higher percentage of trees was snapped at
333 higher elevations. Eppinga and Pucko (2018) further show that over 90% of all trees were defoliated
334 for >75% and over 75% of trees lost primary branches, suggesting that Irma and Maria heavily
335 affected arboreal species. Indeed, hurricane wind speeds are stronger at higher elevations
336 (Holthuijsen et al. 2012), whereby our findings could be explained by increased mortality through
337 physical injury during hurricane events, as well as subsequently through longer food unavailability
338 (Cely 1991).

339 Understanding the natural movements of study species is important to consider in
340 population assessments (Neilson et al. 2018). Both *Iguana* species are known to remain static
341 throughout most of their life cycle, with movement mainly restricted to the hatchling life stage until
342 settling in breeding populations, and by adult females while traveling to nesting sites (Burghardt
343 and Rand 1985; Bock and McCracken 1988; Knapp et al. 2016). For *I. delicatissima*, the
344 reproductive cycle of populations on arid islands is clearly defined with nesting mainly occurring in
345 June-August (van den Burg et al. 2018a). Reproductive data for the St. Eustatius population remains
346 limited but appears to occur in June-July (pers. obs. by authors), which was considered while
347 planning field surveys. As no large communal nesting sites occur on St. Eustatius (as opposed to
348 Dominica, Knapp et al. 2016), and small isolated nesting sites have been located around the island
349 (Debrot et al. 2013; pers. obs. by authors), we suspect gravid females to undertake little movement
350 and nest within or close to their home range. This is further strengthened by the restricted size and

351 highly fragmented status of the population (Debrot et al. 2013; van den Burg et al. 2018b), with
352 interaction observations being rare (pers. obs. by authors).

353 Despite over half of Iguanidae diversity occurring in the Greater Caribbean region,
354 hurricane impacts on their populations have been rarely addressed. Beovides-Casas and Mancina
355 (2006) performed a total of 60 surveys (12 each during 4 visits) of the *Cyclura nubila* population on
356 Cayo Sijú (Cuba) in 2004, with the final visit post-Hurricane Ivan. Although Ivan passed at ~160
357 km distance with sea level rising by 2.5 meter, their data indicated the population size remained
358 stable. In another study, Hayes et al. (2004) report local extinction of a *Cyclura rileyi* population
359 from a small Bahamian cay following the passing of Hurricane Floyd (1999). However, it is
360 important to note that the authors indicated only three animals were observed by themselves there,
361 with a personal comment from the previous decade about 18 animals. Thus, the subsequent
362 reference of population extirpation following a hurricane event (e.g., Hayes et al. 2016) without
363 mention of these numbers and overall poor knowledge of the population in question appears
364 unjustified. Additionally, Hayes et al. (2004) also report no decrease in adult iguanas from a nearby
365 cay, with a large population. In our study, we found that multiple population parameters decreased
366 after an intense hurricane season; a decrease in I) population size of the studied area (23.3–26.5%)
367 and II) abundance (22–23.8%), as well as III) a 75% reduction in the number of opportunistic
368 sightings of tagged iguanas between 2017–2018. However, as studies remain scarce, equally are
369 generalizations and comparisons. Compared to *I. delicatissima*, *Cyclura* sp. are larger and more
370 robust, mainly non-arboreal iguanas. Although pre-hurricane behavior for *I. delicatissima* is
371 unknown, presumably lighter iguanas that remain arboreal during catastrophic weather events are
372 more vulnerable than heavier, terrestrial iguanas. However, inundation might force *Cyclura* sp. to
373 ascend trees in order to avoid being swept away given their range mostly includes low-elevation
374 islets.

375 To evaluate the impact of catastrophic events on closed populations, consideration of these
376 events' timing compared to a species' reproductive cycle is essential (Schoener et al. 2004). For St.

377 Eustatius, both 2017 hurricanes passed as strong early storms, preceding the main hatching period
378 of the local *I. delicatissima* population while most eggs were incubating and therefore presumably
379 safe in the absence of inundation. Later-seasonal storms are expected to have a more severe impact,
380 as hatchlings are vulnerable to high wind speeds, thus potentially losing most individuals of an
381 entire generation. Indeed, Hayes et al. (2004) compared hatching percentage between subsequent
382 years and reported an extremely small hatchling cohort after the passing of Hurricane Floyd, which
383 hit the Bahamas during the hatching period of *C. rileyi*. No information is available about the
384 percentage of hatched clutches. On St. Eustatius only some nesting occurs on the island's lower
385 elevations with the majority of nest sites found at elevations far higher than sea-level inundation
386 (Debrot et al. 2013). Although data on egg survival and hatching success after inundation is known
387 for some reptilians (Hsu et al. 2021), such data is missing for Iguanids.

388 Effect assessments of the 2017 Atlantic hurricane season are demonstrating its broad impact
389 on ecosystems and their trophic levels; e.g., beach, mangrove and forest ecosystems (Liu et al.
390 2018; Barreto-Orta et al. 2019; Walker et al. 2019; Hall et al. 2020), salt- and freshwater fish
391 communities (Meléndez-Vazquez et al. 2019; Neal et al. 2020), insect species and communities
392 (Cabrera-Asencio and Meléndez-Ackerman 2021), birds (Palmer et al. 2018; Lloyd et al. 2019), and
393 seas slugs (Middlebrooks et al. 2020). For St. Eustatius specifically, our data adds to the
394 understanding of an ecosystem-wide hurricane impact during 2017 which, besides iguanas, affected
395 both forests (Eppinga and Pucko 2018) and the populations of Bridled Quail-dove (Rivera-Milán et
396 al. 2021) and Red-bellied racer (Madden et al. 2021). Importantly, these insights and novel risk
397 assessments are demonstrating the high extinction risk that endemic, island species will face under
398 projected climate change (Manes et al. 2021).

399

400 *Conservation*

401 From a conservation perspective, the status of *I. delicatissima* is at its most benign, with
402 only five populations not directly threatened by on-island hybridization, of which just a single

|

403 island has a >200 population size; Petite Terre (Guadeloupe). Our study further highlights this
404 vulnerability, as local extinction or population declines to unsustainable sizes could be the result of
405 major hurricanes. Especially the extremely small population of Anguilla is vulnerable (Pounder et
406 al. 2020), which currently occurs on a small low-level islet. There, the potential of temporarily
407 holding iguanas to increase hurricane survival should be assessed, given adequate facilities can be
408 utilized. On St. Eustatius, we found no post-hurricane population recovery (or boomerang effect),
409 which could be linked to the small size of the existing population. Therefore, the projected increase
410 in frequency and intensity of catastrophic hurricanes (Bender et al. 2010) is troubling as populations
411 might be unable to recover between subsequent catastrophic events (McCoid 1996; Schriever et al.
412 2009; Selman 2015). However, we note that a short-term boomerang effect was likely absent given
413 the apparent low fecundity on St. Eustatius, possibly due to the population's low genetic diversity
414 (van den Burg et al. 2018b), although a detailed study on fecundity still is absent. Overall, our study
415 strengthens the need for population-increasing measures to be taken.

416 **Acknowledgments**

417 We thank Adam Mitchell, Sarinda Westerhout, Joey Markx, Rupert Redan, and all STENAPA staff
418 and volunteers that helped with data collection. Funding was provided through the Mohamed bin
419 Zayed Species Conservation fund (172517158), International Iguana Foundation, and, the BEST 2.0
420 program.

421

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742 **Electronic Supplementary Material**

743

744 **List of figures and table in this document**

745

746 **Figure S1. The effect of elevation on site occupancy estimates of *Iguana delicatissima* based on**
747 **transect surveys conducted on St. Eustatius in 2017 (pre-hurricane), 2018 and 2019 (post-**
748 **hurricane). Data obtained using R package *unmarked*.**

749

750 **Figure S2. The effect of elevation on abundance estimates of *Iguana delicatissima* based on**
751 **transect surveys conducted on St. Eustatius in 2017 (pre-hurricane), 2018 and 2019 (post-**
752 **hurricane). Data obtained using R package *unmarked*.**

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754 **Figure S3. Iguana density heatmap for opportunistically observed bead-tagged iguanas on St.**
755 **Eustatius, during 2017–2019.**

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757 **Table S1. Overview of 2017–2019 site occupancy estimates per habitat of *Iguana delicatissima***
758 **on St. Eustatius. ψ presents the probability of a site to be occupied, including lower and upper**
759 **confidence intervals (CI). Habitat following De Freitas et al. (2012): 1 = *Pisonia - Antirhea***
760 **mountains; 2 = miscellaneous urban/agricultural or disturbed land; 3 = *Pisonia - Justicia* hills; 4 =**
761 ***Capparis - Pisonia* mountains; 5 = *Rauvolfia - Antigonon* mountains; 6 = *Coccoloba - Bothriochloa***
762 **cliffs; 7 = *Pisonia - Eugenia* mountains; 8 = *Chionanthus - Nectandra* mountains.**

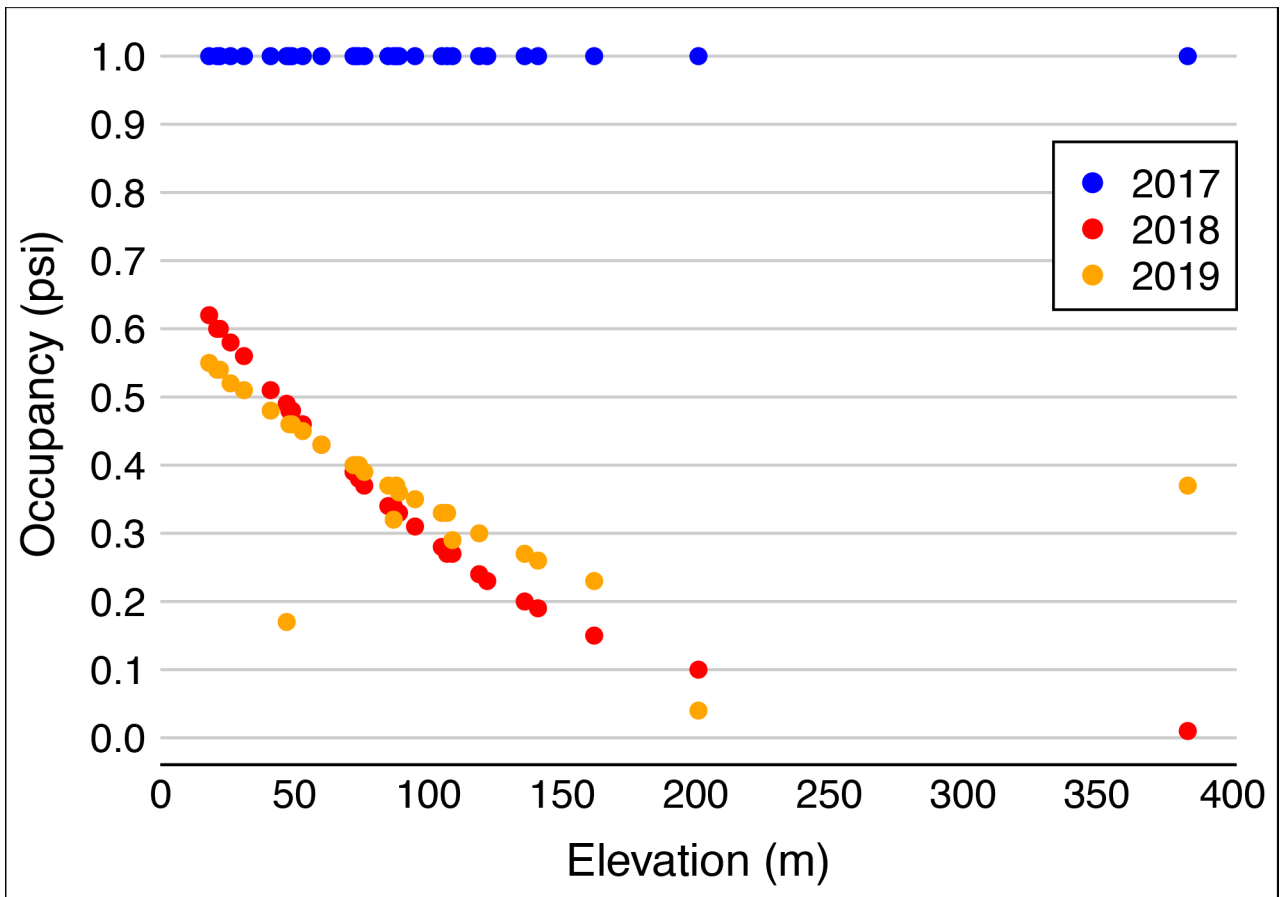
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765 Mean detection probability (p) per transect was 0.01 (inestimable CIs) using “unmarked”.
766 Occupancy probability was 33.1% (11.4–73.8%) in 2018, and 37.5% (19.4–64.0%) in 2019.
767 p was 0.40 (0.12–1.34) in 2018, and 0.47 (0.22–1.02) as estimated using “unmarked”.

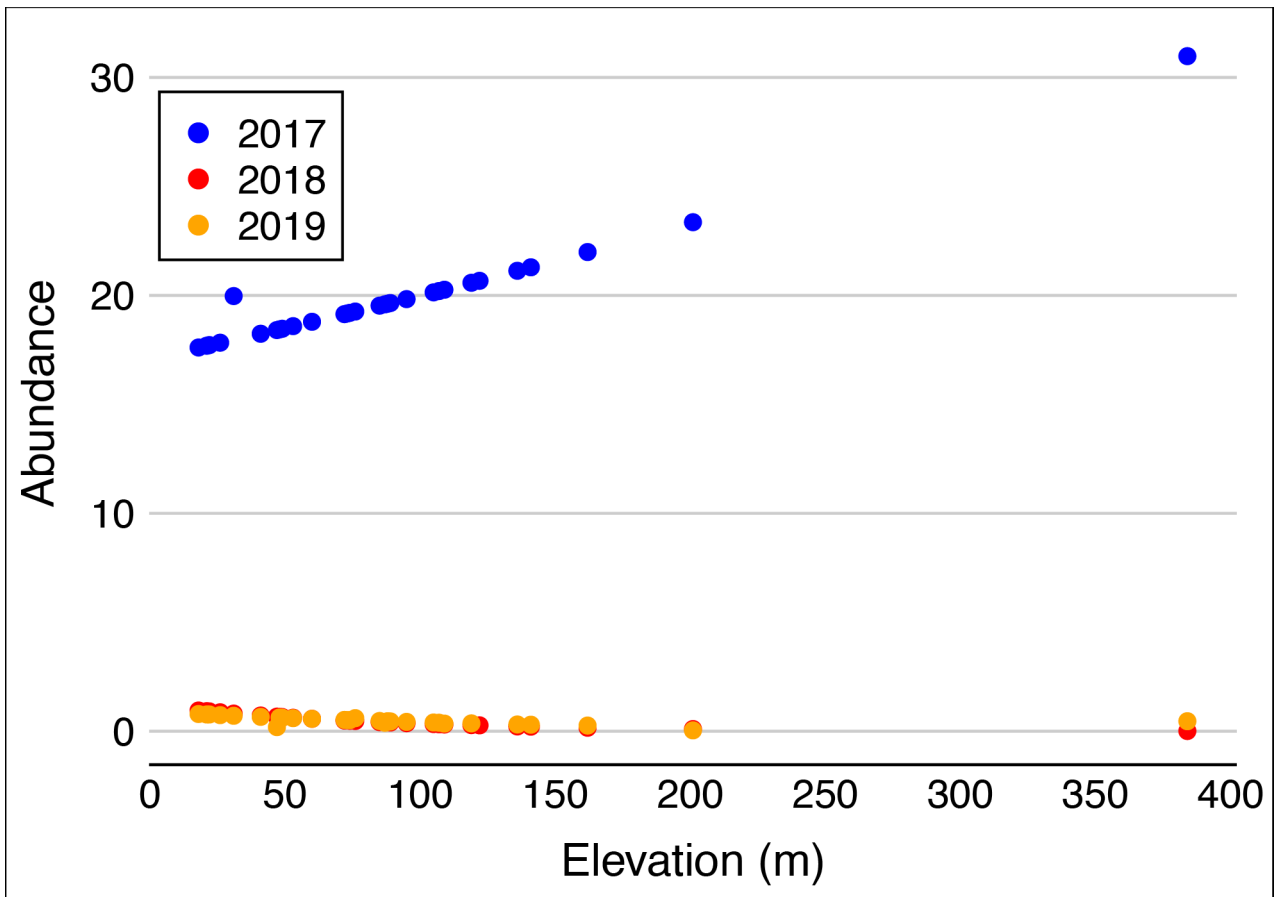
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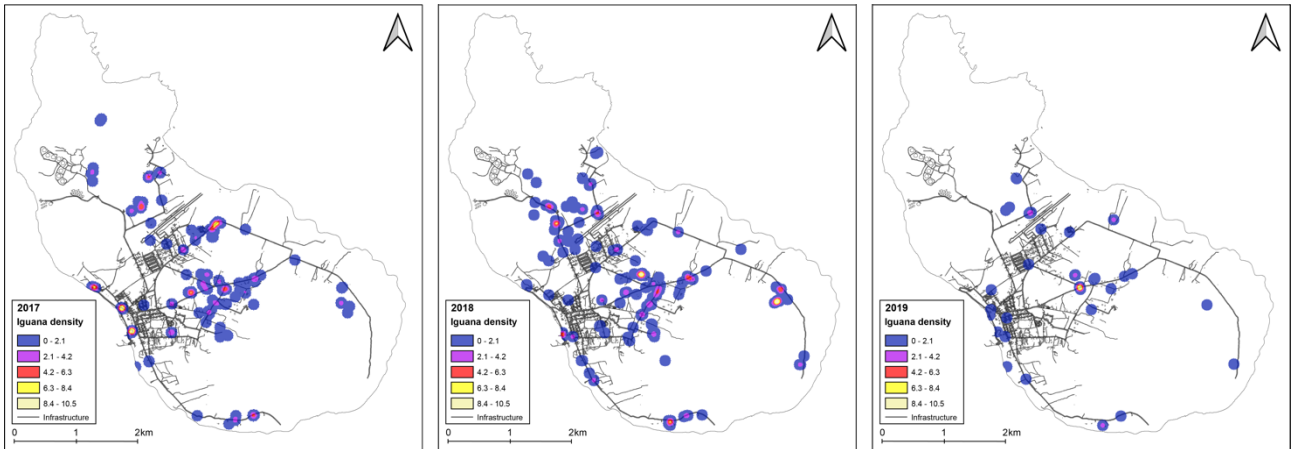
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Figure S1. The effect of elevation on site occupancy estimates of *Iguana delicatissima* based on transect surveys conducted on St. Eustatius in 2017 (pre-hurricane), 2018 and 2019 (post-hurricane). Data obtained using R package *unmarked*.



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Figure S2. The effect of elevation on abundance estimates of *Iguana delicatissima* based on transect surveys conducted on St. Eustatius in 2017 (pre-hurricane), 2018 and 2019 (post-hurricane). Data obtained using R package *unmarked*.



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Figure S3. Iguana density heatmap for opportunistically observed iguanas on St. Eustatius, during 2017–2019. Radius for heatmap analyses was 100m. Total number of iguanas sighted per year; 184 (2017), 208 (2018), 51 (2019).

786 **Table S1. Overview of 2017–2019 site occupancy estimates per habitat of *Iguana delicatissima***
 787 **on St. Eustatius.** ψ presents the probability of a site to be occupied, including lower and upper
 788 confidence intervals (CI). Habitat following De Freitas et al. (2012): 1 = *Pisonia - Antirhea*
 789 mountains; 2 = miscellaneous urban/agricultural or disturbed land; 3 = *Pisonia - Justicia* hills; 4 =
 790 *Capparis - Pisonia* mountains; 5 = *Rauvolfia - Antigonon* mountains; 6 = *Coccoloba - Bothriochloa*
 791 cliffs; 7 = *Pisonia - Eugenia* mountains; 8 = *Chionanthus - Nectandra* mountains.
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Year	Habitat	ψ	low CI	upp CI	Year	Habitat	ψ	low CI	upp CI
2017	1	1.00	<0.001	1.00	2018	5	0.31	0.09	0.77
2017	2	1.00	<0.001	1.00	2018	6	0.30	0.07	0.82
2017	3	1.00	<0.001	1.00	2018	7	0.28	0.05	0.88
2017	4	1.00	<0.001	1.00	2018	8	0.26	0.03	0.94
2017	5	1.00	<0.001	1.00	2019	1	0.36	0.14	0.74
2017	6	1.00	<0.001	1.00	2019	2	0.37	0.17	0.67
2017	7	1.00	<0.001	1.00	2019	3	0.37	0.19	0.64
2017	8	1.00	<0.001	1.00	2019	4	0.38	0.19	0.67
2018	1	0.39	0.08	0.94	2019	5	0.39	0.16	0.75
2018	2	0.37	0.10	0.87	2019	6	0.39	0.13	0.84
2018	3	0.35	0.11	0.80	2019	7	0.40	0.10	0.92
2018	4	0.33	0.11	0.76	2019	8	0.41	0.07	0.97

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