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Reassessing the Status of a Data-Deficient Insular Population of a Critically Endangered Species

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Abstract—**The conservation status of more than 160,000 species has been assessed following IUCN guidelines, with greater than 13% considered data deficient. Maintaining an accurate understanding of native populations is challenging, especially for species with geographically large or discontinuous insular ranges. Here we assessed a data deficient population of a critically endangered reptile within the Caribbean biodiversity hotspot. We surveyed the island of Antigua for three weeks to assess whether the native *Iguana delicatissima* remains present. Morphological data from 98 observed and 29 captured iguanas showed no sign of pure remaining *I. delicatissima*; whilst 19 individuals had some morphological features of *I. delicatissima*. Sequence data and discriminant analyses of 17 microsatellite loci assigned all captured iguanas to *I. iguana*, although the presence of two *I. delicatissima* alleles are indicative of an old introgressed population. The only present mtDNA haplotype matched to the non-native iguana population on Grand-Terre, Guadeloupe. This provides genetic evidence of hurricane-mediated translocation as proposed happened in the aftermath of two 1995 hurricanes when debris-rafts with iguanas landed on Anguilla, Barbuda, and Antigua. The rapid decline of *I. delicatissima* places urgency on finding and conserving any surviving remnant populations, which we show are likely absent from Antigua, though we cannot rule out the presence of a few individuals.**

Within the ongoing sixth mass extinction wave (Ceballos et al. 2020), conservationists are rushing to assess species' extinction risks and conservation needs, summarized in the Red List of the International Union for the Conservation of Nature (IUCN 2024). Whilst over 160,000 species have already been assessed, a relatively large percentage is categorized as data deficient (Cazalis et al. 2023), which means that insufficient knowledge and data are available. Besides species, populations or areas within a species' distribution range can also lack (certain) data, especially when distribution ranges are geographically large or discontinuous, such as species occurring on islands.

The Caribbean region is one of the global biodiversity hotspots (Myers et al. 2000), however, >15% of IUCN-assessed species are threatened with extinction (IUCN 2024). Considering reptiles, a highly diverse group within the region that are often endemic to a single geographic bank, 38% of currently assessed species are threatened with extinction (IUCN 2024). Whilst species can occur on multiple banks, even species endemic to a single bank often occur on more than a single island/islet (Uetz et al. 2024). Maintaining an accurate understanding of native populations across this insular region can therefore be problematic and logistically challenging (R.S. Thorpe, personal communication). This is however essential as Caribbean reptiles are especially affected through high human impact that further elevates their extinction risk (Jesse et al. 2024). Ongoing introductions of non-native species, many of which are non-native reptiles (Thorpe 2022), furthermore homogenize herpetofauna assemblages and can cause declines of native populations and eventual extinctions that negatively impact functional trait diversity (Capinha et al. 2020; Kemp 2023).

The Lesser Antillean Iguana, *Iguana delicatissima* Laurenti, 1768 (Iguanidae), is an endemic, long-lived reptile of the Lesser Antilles, occurring between Anguilla and Martinique (except for Saba and Montserrat). Since European arrival, *I. delicatissima* populations have been subject to numerous threats, resulting in drastic range-wide declines and numerous local extirpations. Consequently, following red list guidelines, the species has been uplisted from Vulnerable to Endangered (Breuil et al. 2010), and Critically Endangered (Van den Burg et al. 2018a). Threats include the introduction of non-native mammals (e.g., small Indian mongoose and domestic cats), habitat destruction, and

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road mortality by human traffic (Breuil 2002; Knapp et al. 2014, 2016). However, nowadays the main threat comes from non-native iguanas which hybridize with and outcompete *I. delicatissima* (Day et al. 2000; Vuillaume et al. 2015; Van den Burg et al. 2018b; Pounder et al. 2020).

A first understanding of the severe conservation status of *Iguana delicatissima* populations became apparent during the early 1990s. Initial assessments indicated that several island populations had already gone extinct (Barbuda, St. Kitts, and Nevis), while others were facing a similar threat (Antigua and Îles de Les Saintes) (Day 1991, 1993; Breuil 1993, et al. 1994; Reichling 1995). Subsequent work has focused largely on the populations across the French West Indies as well as those populations that were not under immediate threat of extinction (Anguilla, St. Eustatius, and Dominica) (Day et al. 2000; Reichling 2000; Breuil 2002).

Little is known about the Antiguan *Iguana delicatissima* population for which skeletal remains have been excavated from at least two Amerindian archaeological sites: Indian Creek and Mill Reef (Jones 1985; Wing 1989). The population appears to have been assessed by iguana experts only twice. Lazell (1973) reported having searched the entire Antiguan bank, and observed *I. delicatissima* only at Gaynor's Ghaut on Antigua, where he found 12 animals. Later, Mark Day refers to his assessment in the early 1990s as *I. delicatissima* likely being nearly extinct (Breuil et al. 1994; Reichling 1995), even though no published data or analyses on his fieldwork is to be found. Later, Censky and Kaiser (1999) and Breuil (2002) indicated the Antiguan population remained present, without commenting on its further status. Thereafter, Daltry (2007) reported *I. delicatissima* was likely extirpated, referencing a personal comment, no data supported this status, though subsequent publications have reported the Antiguan population to be extinct (e.g., Breuil et al. 2010; Knapp et al. 2014). Here we reassess the status of this data deficient population for which no photographic confirmation could be found of animals in the wild post-1973, but for which video footage was obtained for a purported *I. delicatissima* individual present at the Wadadli Animal Nature Park in 2015. This provided some hope that pure *I. delicatissima* might still be present on Antigua.

MATERIALS AND METHODS

Prior to our fieldwork, we collated data on iguana sightings from Antigua reported between 2015 and 2021, through the Facebook and iNaturalist platforms. These records informed our fieldwork planning during November, 2023, when we spent three weeks surveying Antigua for iguana presence. We particularly focused on parts of Gaynor's Ghaut, given Lazell's (1973) mention of the only colony in that area, where we performed several diurnal and nocturnal surveys. We note that Lazell (1973) did not specify the exact location where he sighted the native animals. Additionally, we visited areas across the island, prioritizing areas with known iguana presence, where we performed both diurnal and nocturnal surveys to optimize capture potential. We surveyed randomly (no transects) for more than 100 search hours.

When iguanas did not flee, we captured these either by hand or noose. We then collected a 0.3 ml blood sample from the caudal artery for subsequent analyses to assess the species status, and took photographs from the lateral, dorsal, and ventral sides of the head, the lateral and ventral sides of the body, as well as the femoral pores and the 4th toe. We additionally measured snout-vent length and tail length to the nearest mm. All iguanas were released at their capture locality. We used morphological characters identified by Lazell (1973) and Breuil (2013) to assess any presence of *Iguana delicatissima* among the photographed and captured iguanas, which would have an absence of bands on the tail, no nuchal spines, no subtympanic plate, but with keeled ventral scales, and seven to eight gular spines.

Blood samples were utilized to assess the species status of each iguana and geographic origin for non-native iguanas and their haplotypes and alleles (e.g., Van den Burg et al. 2023). We implemented Sanger sequencing of the mitochondrial NADH dehydrogenase subunit 4 (ND4) and the nuclear MutL homolog 3 (MLH3) genes following laboratory protocols explained in Malone et al. (2017) and Van den Burg et al. (2018b). Gel-electrophoresis confirmed PCR fragments were forward and reversed-sequenced. We subsequently assessed chromatograms in Geneious Prime v.2024.0.5 (Kearse et al. 2012). Quality-checked ND4 and MLH3 haplotypes were thereafter compared to published GenBank records and unpublished sequences. Additionally, we analysed 17 microsatellites that were designed for *I. delicatissima* and have subsequently been used across the *Iguana iguana* (Linnaeus, 1758) species complex (Valette et al. 2013; Van den Burg et al. 2021a). Generated microsatellite allele data were compared to native samples from the IguanaBase microsatellite database (Van den Burg et al. 2021b). We used discriminant analyses of principal components (DAPC) to estimate species assignment using two datasets, one including both *I. delicatissima* and the *I. iguana* species complex, and the second restricted to the species complex.

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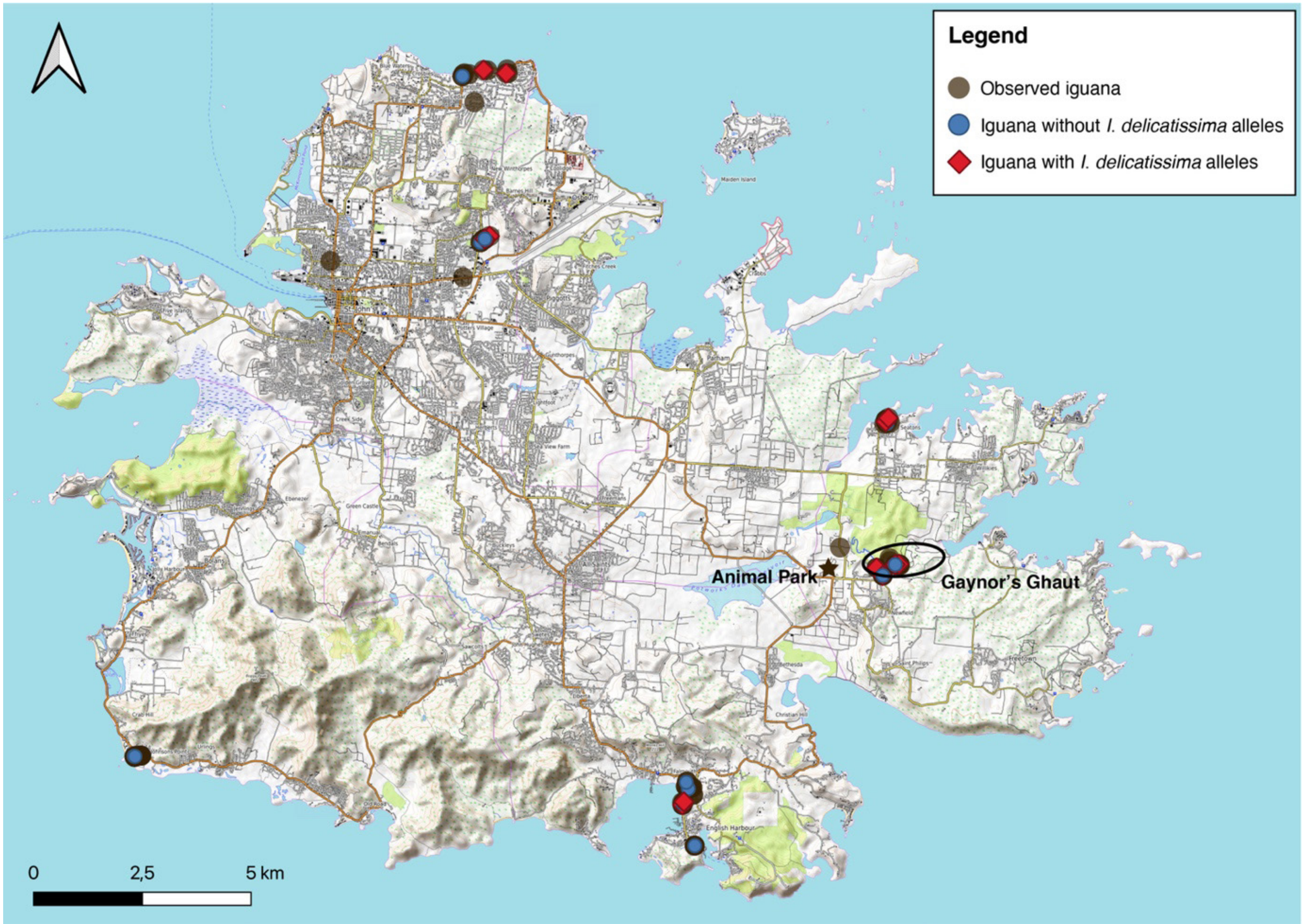

FIG. 1. Distribution map of iguanas on Antigua, showing locations of observed iguanas and localities of genetically assessed animals. Star shows the location of the Animal Nature Park, and encircled area indicates Gaynor's Ghaut.

RESULTS

We observed 98 iguanas on Antigua, of which we hand- or noose-captured 29 during November, 2023 (Fig. 1). All captured iguanas were found to have striped tails, nuchal spines, and a subtympanic plate, which are all *Iguana iguana* features. A total of 17 individuals had (slightly) keeled ventral scales, and three of these individuals also had seven or eight gular spines, i.e. *I. delicatissima* features. All non-captured iguanas were identified as pure non-native *I. iguana* except for two individuals: a single captive adult individual currently present in the Wadadli Animal Nature Park, and one wild young juvenile from Gaynor's Ghaut. These two animals had morphological characteristics that matched with introgressed iguanas, with only one single or a few *I. delicatissima* characteristics. The juvenile had longitudinal stripes along the tail, keeled ventral scales posterior to the cloaca, and an absence of bands on the tail (all *I. delicatissima* features) whilst still having a subtympanic plate (an *I. iguana* feature). The captive adult specimen did not have a clearly enlarged subtympanic plate and had seven gular spines (*I. delicatissima* features), but did have a banded tail and nuchal spines (*I. iguana* features).

For genetics, we successfully generated ND4 haplotypes from 28 individuals that all had the same published ND4 haplotype, as previously identified for non-native iguanas from Iles de Les Saintes and Grand-Terre, Guadeloupe Archipelago (Martin et al. 2015; Breuil et al. 2019; KJ561226, MN590154–58). Equally, all generated MLH3 haplotypes (n = 29) were identical to a published haplotype known from the *Iguana iguana* clade IIb *sensu* Stephen et al. (2013) (Van den Burg et al. 2023; OQ556119). For the 17 microsatellites, none of the 29 individuals had missing data. The DAPC assignments for all 29 individuals were identical to *I. i. iguana*, and clustered around this group within

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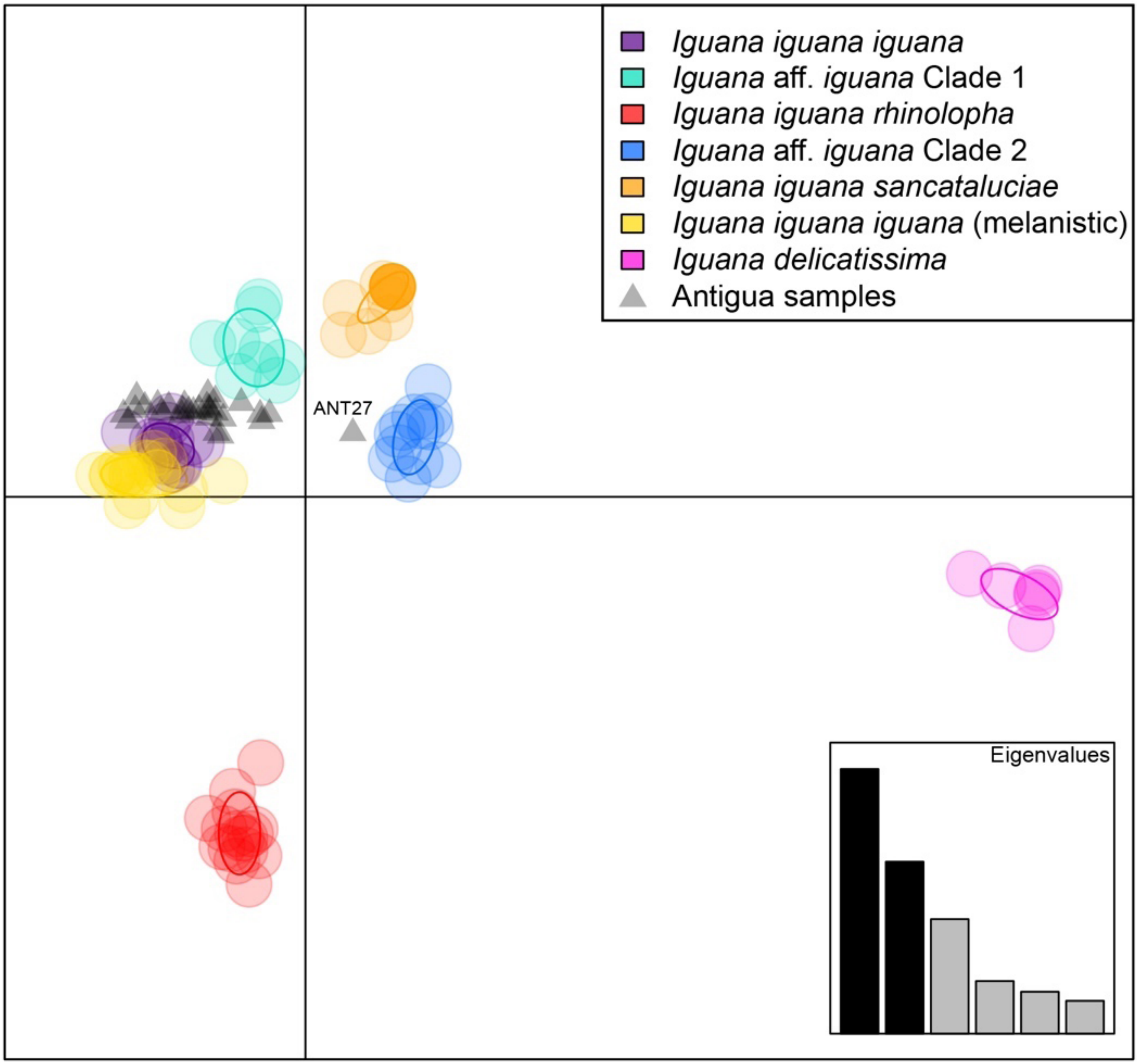

FIG. 2. Discriminant analysis of principal components scatterplot representing 17 microsatellite loci from reference IguanaBase individuals (coloured circles) and 29 individuals from Antigua (grey triangles).

the plotted morphospace (Fig. 2). Visual comparison of generated allele sizes to native samples in IguanaBase indicated that for two markers an allele unique to *I. delicatissima* was present; IgdL13 (allele 246, 10 matches across nine iguanas) and IgdL25 (allele 186, 4 matches across four iguanas) (Van den Burg et al. 2021a, 2021b). ANT27 was homozygous for allele 246 of IgdL13 (Fig. 2). No individual had an *I. delicatissima* allele for both loci. Additionally, for all but two other markers we retrieved alleles present in *I. i. rhinolopha*, *I. i. iguana*, *I.* aff. *i.* clade II, *I.* aff. *i.* clade I, *I. i. insularis*, and the melanistic *I. i. iguana* populations of Saba and Montserrat (Van den Burg et al. 2021a). Both IgdL19 and IgdL20 had alleles that fall outside the known *I. i. rhinolopha* allele size range (Van den Burg et al. 2021b). Geographically, iguanas with and without *I. delicatissima* alleles were present at all locations, except for the southwest of Antigua (Fig. 1).

DISCUSSION

The ongoing global decline in species and population sizes (e.g., Butchart et al. 2010; Pereira et al.

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2010) illustrate the importance of understanding population status across distribution ranges of endangered and threatened species, especially when those are discontinuous. Here, we assessed the status of a presumed extinct population of the critically endangered *Iguana delicatissima* that lacked a formal assessment. Our three-week field effort and resulting morphological and genetic results from across the island indicate the absence of an *I. delicatissima* population on Antigua, although we found evidence of introgressed individuals.

Non-native iguanas are known to spread among Lesser Antillean islands through different pathways. These include those with an anthropogenic origin, such as transfer and release of pets, transfer on cargo ships, and transfer with aid-release materials (Van den Burg et al. 2020; Debrot et al. 2022). Censky et al. (1998) reported on natural dispersal between islands when non-native iguanas were observed on floating debris shortly after Hurricanes Luis and Marilyn passed in 1995. Whilst Censky et al. (1998) reported non-native iguanas arriving on both Anguilla and Barbuda, Day and Hodge (1998) and later Lindsay and Mussington (2009) reported that, equally on Antigua, large numbers of non-native iguanas arrived in 1995 by means of sea transport on floating debris. Censky et al. (1998) deducted that the origin of those arriving iguanas was the Guadeloupe Archipelago, given the tracks of both hurricanes combined with the average direction of oceanic currents in the region; however, no study subsequently provided data supporting this claim. Our mtDNA data provide some support for this inter-regional transfer, since all 28 Antigua specimens for which we generated ND4 sequences had a haplotype that has been reported from the Guadeloupe Archipelago (Martin et al. 2015; Breuil et al. 2019). This haplotype falls within the *Iguana iguana* clade IIb *sensu* Stephen et al. (2013), from South America, although it has not yet been reported from a native locality.

The same as with our mtDNA, the only MLH3 nDNA haplotype found on Antigua is native to iguanas from *Iguana iguana* clade IIb *sensu* Stephen et al. (2013). Although Pounder et al. (2020) did not comment on the origin of non-native ND4 haplotypes generated from iguanas on Anguilla, in some iguanas they found the identical ND4 haplotype as we identified from Antigua (KJ561226, MN590154–58). Genetic data therefore substantiate the proposal by Censky et al. (1998) that non-native iguanas arriving on Anguilla and Antigua in 1995 originated from the Guadeloupe Archipelago. No iguanas from Barbuda have been assessed, although anecdotal accounts from residents suggest that translocation of non-native iguanas from Barbuda to Antigua likely occurred in the early 2000s (K. Lindsay, pers. comm.). Furthermore, the observed absence of any genetic diversity in the Antigua population, especially compared to the non-native population on Anguilla, suggest a natural post-hurricane translocation origin (Censky et al. 1998; Lindsay and Mussington 2009; Pounder et al. 2020), supports a single incursion event to Antigua, or repeated incursions from the same invariable source population (possibly through relocation of Guadeloupe iguanas that arrived on Barbuda). Comparison of genetic diversity to all non-native *Iguana iguana* populations within the Lesser Antilles, e.g., St. Martin, Saba, Guadeloupe, Iles de Les Saintes, and Martinique, shows that the Antigua population is exceptionally uniform (Martin et al. 2015; Vuillaume et al. 2015; Van den Burg et al. 2018b, 2023).

Recent integrative assessments have aided our understanding of native and non-native components within iguanid populations in the Lesser Antilles (e.g., Vuillaume et al. 2015; Van den Burg et al. 2023, 2024). The application of this methodology to the data deficient iguana population on Antigua provides strong support for earlier suggestions that the native *Iguana delicatissima* is locally extirpated (e.g., Daltry et al. 2007). Morphological assessment of observed and captured iguanas, including iguanas from the last known locality (Lazell 1973), showed that only a few *I. delicatissima* characteristics are still present in a small subset of iguanas on Antigua, whilst all others were identified as pure non-native *I. iguana*. We observed only a single individual that lacked *I. iguana* bands on its tail, and one other that lacked a clearly enlarged subtympanic plate and had few gular spines; both were located close to the last confirmed *I. delicatissima* location of Gaynor's Ghaut (Lazell 1973). Only two captured iguanas both had keeled ventral scales and seven to eight gular spines (*I. delicatissima* features), but with all other morphological characteristics identified as *I. iguana*. Similarly, our microsatellite data also indicate a minor contribution of *I. delicatissima* within the sampled Antigua iguana population, with *I. delicatissima* alleles present for only two of 17 analyzed microsatellite loci. Across these two loci, nearly half (45%) of the 29 analyzed iguanas had a single (just one individual was homozygous for one locus) *I. delicatissima* allele, and no iguana had an *I. delicatissima* allele for both loci. Both mtDNA and nDNA haplotypes were monotypic and from *I. iguana*. In combination, our integrative assessment identifies this population as non-native with some evidence of former introgression.

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Iguana delicatissima is native to Antigua, but individuals from the hybridized *I. delicatissima* × *I. iguana* population of Guadeloupe (where hybridization commenced in 1950; Vuillaume et al. 2015) arrived 30 years ago. The *I. delicatissima* characteristics and microsatellite alleles we identified here could therefore either originate from native Antiguan or hybridized Guadeloupian individuals. We note Lazell (1973) already reported that only a few *I. delicatissima* remained present at a single locality on Antigua. As small Indian mongoose, a known predator of hatchlings and juveniles (Van den Burg et al. 2018a), were and remain present on Antigua, *I. delicatissima* population expansion was likely absent prior to the arrival of non-native iguanas in 1995. As morphological characteristics and microsatellite alleles associated with *I. delicatissima* are present in iguanas across Antigua (Fig. 1), we propose that this favors a Guadeloupe origin from the invasion of Guadeloupian-introgressed iguanas. Namely, more recent hybridization between native Antigua *I. delicatissima* and non-native iguanas would arguably have resulted in less geographic spread of *I. delicatissima* characters, as well as in a higher contribution of *I. delicatissima* alleles across the 17 analyzed microsatellites.

While the occurrence of potentially few remaining *Iguana delicatissima* cannot be fully ruled out, our assessment of iguanas across Antigua provides no evidence of a surviving *I. delicatissima* population. We conclude that the population appears functionally extinct, even though there is still a remote possibility of finding and recovering pure animals; efforts should focus on the Gaynor's Ghaut area. We recommend that local stakeholders draw up action steps and agreements for when a pure *I. delicatissima* would be identified, so that its survival chances can be maximized; e.g., allowing rapid translocation to one of the off-shore islands that have been cleared of non-native species (Daltry et al. 2017), or inclusion within a captive breeding program to ensure the genetic signature of this population is not lost.

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