Title: Reassessing a Holocene extinction: multiple lines of evidence do not support the historical presence and recent extirpation of a protected anole on the island of Anguilla

Michael L. Yuan[1], Rayna C. Bell[1], Edward A. Myers[1]

[1]Institute for Biodiversity Science and Sustainability, California Academy of Sciences, San Francisco, California, USA

Corresponding author: Michael Yuan (myuan@calacademy.org)

Keywords: Caribbean, *Anolis pogus*, local extinction, historical species ranges, museum collections, archival DNA

Abstract

Accurate assessment of historical species ranges is important for conservation science and management. Inaccurate historical species ranges can lead to incorrect assumptions about local extinctions, population trends, and potential sites for reintroductions. Yet, historical knowledge is often lacking for many species. Here, we examine the case of the bearded anole, *Anolis pogus*, which is long believed to have been recently extirpated from the island of Anguilla. We addressed the evidence for the historical presence and recent local extinction of *A. pogus* on Anguilla using species abundance modeling, fossil and extant morphological data, and archival DNA sequencing from museum specimens. We found that although viable habitat remains on Anguilla, it is highly fragmented. Our data is also not consistent with the prior characterization of two size classes of anoles in Anguilla's fossil deposits as evidence for the two species (*A. gingivinus* and *A. pogus*) that occur sympatrically on neighboring St. Martin. Instead, our data indicate that fossil deposits on Anguilla likely correspond to males and females of the larger anole species, *A. gingivinus*, and is not consistent with the presence of *A. pogus* in the fossil record. Finally, we sequenced the only two known museum specimens of *A. pogus* from Anguilla and demonstrate that these specimens correspond to *A. schwartzi* and were likely missorted (and subsequently misidentified) when a collection from Anguilla and St. Eustatius was originally deposited at the Museum of Comparative Zoology. Together, our results show that there is no evidence for the historical presence, and thus no evidence for the local extinction, of *A. pogus* on Anguilla. These data are vital for the appropriate management of this species of conservation concern. Furthermore, our study provides a case study for the critical assessment of historical species ranges and narratives of extinction.

Introduction

Conservation biology is often complicated by a lack of historical baseline knowledge (Bonebrake *et al.*, 2010; McClenachan, Ferretti & Baum, 2012; Böhm *et al.*, 2013). A prevalent issue is the lack of definitive records on a species' historical range, and by inference, where they have since been extirpated (Carlton, 1996; Wingard, Bernhardt & Wachnicka, 2017; Claude *et al.*, 2019). Anthropogenic activity has been responsible for myriad extinctions throughout the Holocene (Diamond *et al.*, 1997; Ceballos *et al.*, 2015); yet, the specific extinction narratives of several taxa are uncertain or controversial. For example, little is known of the historical distributions of declining turtles throughout Thailand (Claude *et al.*, 2019); the existence of and subsequent Holocene extinction of some *Ara* macaws throughout the Caribbean has been questioned (Olson & López, 2008); and molecular evidence suggests that the Barbados racoon was an extirpated introduced species rather than an extinct endemic (Helgen & Wilson, 2003). Accurate assessment of recent local extinctions provides important context for current and future conservation management, and also for our understanding of fundamental questions of biodiversity science.

The Caribbean is a biodiversity hotspot (Smith *et al.*, 2005) and a source of major insights in ecology and evolutionary biology (e.g., Rosen, 1975; Ricklefs & Lovette, 1999; Losos, 2009; Papadopoulou & Knowles, 2015; Pringle *et al.*, 2019). Yet, the long history of anthropogenic interconnectivity between islands and lack of reliable records means that the issue of inaccurate historical ranges and extinction narratives is particularly prevalent in the Caribbean (e.g., Kaiser, 1992, 1997; Helgen *et al.*, 2008; Olson & López, 2008; Camargo, Heyer & de Sá, 2009; Giovas, 2019; Yuan *et al.*, 2022, 2023). This poses a challenge not only for regional conservation management, but also for biodiversity science. On the other hand, the Caribbean also provides a compelling system in which to build case studies for resolving difficult issues of historical range uncertainty, which may be applied broadly to other taxa around the world.

Anolis pogus is a species of conservation concern currently restricted to a single island in the Lesser Antilles: St. Martin (Powell, Henderson & Parmerlee, 2005; Powell *et al.*, 2020). Conservation protections are largely based on the small size of its present range and because the species was thought to have been recently extirpated from the neighboring island of Anguilla (Lazell, 1972; Roughgarden *et al.*, 1989). Like many island systems around the world (Wilmshurst *et al.*, 2014; Graham *et al.*, 2017), the Anguilla Bank Islands (i.e., Anguilla, Saint Martin, Saint Barthélemy, and their satellites) were altered by initial human settlement predating detailed written records (Napolitano *et al.*, 2019). Thus, there is limited information on the historical status of *A. pogus*. Circumstantial evidence for the local extinction of *A. pogus* on Anguilla during the Holocene are based on fossil deposits (Roughgarden *et al.*, 1989; Pregill, Steadman & Watters, 1994; Roughgarden, 1995) and land connectivity across the Anguilla Bank islands during low sea levels (Christman, 1953). However, molecular evidence indicates at least some fossil deposits on Anguilla are singularly *Anolis gingivinus* (Kemp & Hadly, 2016), a widespread species that is extant across the Anguilla Bank Islands. Only two alleged specimens of *A. pogus*, both collected in 1922, have been reported from Anguilla despite extensive surveys. Neither specimen was originally identified as *A. pogus* and both were subsequently re-identified in collection (Lazell, 1972) (S. Kennedy-Gold, personal communication). Some authors have speculated that the species may have also been historically present and subsequently extirpated from the island of St. Barthélemy (Lazell, 1972). However, no fossil or extant records indicate *A. pogus* has any historical presence on Saint Barthélemy (Lazell, 1972). Consequently, the historical presence of *A. pogus* beyond the island of St. Martin remains unclear.

Whether *A. pogus* was extirpated from Anguilla matters not only for conservation assessments and management of the species, but also for our understanding of regional biogeography and the distribution of biodiversity. To address this uncertainty, our study asked three questions. First, do Holocene fossil records reflect a two-species anole community on Anguilla? Second, is there suitable habitat remaining for *A. pogus* on Anguilla and Saint Barthélemy? Third, can we use genetic sequences of historical specimens to confirm the presence of *A. pogus* on Anguilla? We discuss our results clarifying the history of local extinction in *A. pogus* as well as its implications for using integrative datasets to better assess conservation-relevant species histories.

Methods

Assessing fossil evidence of two-species communities

Fossil records of Anguillan anoles come from three archeological sites: Katouche Bay (Roughgarden *et al.*, 1989; Roughgarden, 1995; Kemp & Hadly, 2016), Center Cave, and The Fountain (Pregill *et al.*, 1994). Pregill et al. (1994), argued that the bimodal size distribution of anole fossils found at Center Cave and The Fountain were evidence of a two-species anole community: *A. pogus* and *A. gingivinus*. To confirm this assessment, we compared the size data from Pregill et al. (1994) with both field-collected and museum data from *A. pogus* (43 male; 27 female) and *A. gingivinus* (90 male; 49 female). For comparison, we also measured SVLs from a closely-related species, *A. schwartzi* (78 male; 35 female). Field surveys occurred intermittently between 2020 and 2023. Museum specimens were from the collections of the California Academy of Sciences (San Francisco, CA) and the National Museum of Natural History (Washington, DC). All size data was taken as snout-vent length (SVL).

Abundance modeling on Anguilla and Saint Barthélemy

It has been suggested that deforestation may have contributed to the extinction of *A. pogus* on Anguilla (Pregill *et al.*, 1994). The island of Anguilla was largely deforested for charcoal production during WWI (Howard & Kellogg, 1987) and it has been demonstrated that *A. pogus* is more abundant in closed canopy sites on St. Martin (Jesse *et al.*, 2018; Yuan et al. 2024). However, we lack empirical data on the present-day habitat suitability of Anguilla. We used the random forest model built from abundance surveys on St. Martin (Yuan et al. 2024) to predict abundance-based habitat suitability on the islands of Anguilla and Saint Barthélemy. These models were fit using 100 survey plots ($80m^2$) distributed throughout St. Martin and 1 arc-second resolution environmental rasters. Abundance surveys were visual counts conducted for 40 person minutes and occurred during daylight hours during the 2018–2019 dry season (see Yuan *et al.* 2024). Our abundance model had a root mean squared error of 2.87 individuals when using a 20% of data held for validation and 3.52 individuals using out-of-bag estimation. As predictor variables, we downloaded the same raster layers as the original model, but for Anguilla and St. Barthélemy. Specifically, these were global canopy cover (Hansen *et al.*, 2013), land use (WorldCover2.1; Zanaga *et al.*, 2022), and elevation (SRTM; Farr & Kobrick, 2000) resampled to 1 arc-second resolution. Analyses were performed in R v4.3.2.

Using our abundance model, we compared the level of fragmentation in high quality habitat across islands. We defined high quality habitat as cells with abundance estimates ≥5 based on half of our model's highest estimated abundance on the island of St. Martin. We calculated two fragmentation indices at an island-wide level: aggregation index (He *et al.,* 2000) and edge density. Aggregation index is a ratio determined as the number of adjacent cells divided by the number of possible adjacent cells summed over the landscape with 1 indicating total aggregation. Edge density is a measure of all fragment edges relative to area in meters per hectare. We calculated both fragmentation metrics using *landscapemetrics* in R (Hesselbarth *et al.,* 2019).

Sequencing historical specimens

Only two *A. pogus* have ever been reported from Anguilla and none from St. Barthélemy. Both specimens were adult males originally collected in 1922 as *A. gingivinus* and subsequently identified as *A. pogus* (Lazell, 1972). We physically examined both specimens, R-16596 and R-16597, from the collections of the Museum of Comparative Zoology (Cambridge, MA) to resolve this discrepancy in their identification. We then performed whole genome sequencing (WGS) on excised liver samples. As the original preservation conditions of these specimens is unknown, we performed a 100°C heat treatment for 20 minutes to break potential cross-links (Hykin, Bi & McGuire, 2015). We then extracted whole genome DNA using the QIAmp DNA Mini kit. We performed WGS using a NEBNext FS Ultra Express Kit. Because the resulting historical DNA was highly fragmented, we shortened enzymatic fragmentation to 5 minutes, but otherwise followed the manufacturer's protocols. Libraries were 150 bp paired end sequenced by Novogene Corporation using an Illumina NovaSeq X.

Our recovered sequences were predominantly mitochondrial (~65% across both specimens). Thus, we opted to map our reads to an *A. pogus* mitochondrial reference genome (Yuan et al. 2024) following QC and adapter trimming. We performed read mapping using BWA-MEM (Li, 2013). We then hard called genotypes by exporting the overall consensus sequence for each specimen. We extracted cytochrome b sequences and used BLAST to confirm species identification. Based on our BLAST results, we selected species for phylogenetic analyses. We generated a maximum-likelihood tree using IQ-TREE 2 (Minh *et al.*, 2020) using both MCZ specimens, 53 *A. pogus* mitogenomes from Yuan et al. (2024), and 35 *A. schwartzi* mitogenomes. Mitogenomes for *A. schwartzi* were assembled *de novo* from WGS data using MITObim (Hahn, Bachmann & Chevreux, 2013) with a cytochrome b sequence as a bait. WGS data for *A. schwartzi* were generated for another study (M.L. Yuan, unpublished data).

Results

Assessing fossil evidence of two-species communities

The estimated SVLs from Center Cave and The Fountain are 55–65 mm and 39–50 mm (Pregill *et al.*, 1994). These ranges overlap with male *A. gingivinus* (median = 56, IQR = 53.6–59.5) and male *A. pogus* (median = 41.2, IQR = 40.3–42.2) (Fig 2A). However, the distribution of estimated fossil SVLs better matched a single species community of male and female (median = 45, IQR = 42.5–46) *A. gingivinus* because the size range of female *A. pogus* (median = 35.9, IQR = 34.5–37.5) was not represented in the fossil deposits. Similarly, fossil size ranges overlapped with male (median = 44.1, IQR = 40.3–46.9) but not female (median = 36.8, IQR = 35.4–38.5) *A. schwartzi* (Fig S1).

Abundance modeling on Anguilla and Saint Barthélemy

When our random forest models (canopy cover + elevation + urbanization) were projected onto Anguilla and Saint Barthélemy, we found that suitable habitat for *A. pogus* persists on both these islands (Fig 1). However, the highest quality habitat was more fragmented on both Anguilla (ED = 3.38 m/ha; AI = 0.77) and Saint Barthélemy (ED = 3.59 m/ha; AI =

0.76) compared to St. Martin (ED = 1.76 m/ha; AI = 0.88). Overall, 18.2% or ~16.7 km2 of Anguilla was inferred to have high quality *A. pogus* habitat. Comparatively, 29.6% or ~7.2 km2 of St. Barthélemy and 36.2% or ~35.1 km2 of St. Martin was high quality habitat. Fossil sites with putative *A. pogus* fossil had low to moderate predicted abundance (Center Cave = 3.67; The Fountain = 5.72), whereas the fossil deposit known to lack *A. pogus* had the highest predicted abundance (Katouche Bay = 7.36).

Sequencing historical specimens

We confirmed that both R-16596 and R-16597 belonged to the *A. wattsi* species group (which includes *A. pogus*) based on keeled midventral scales, which are lacking in the co-distributed *A. bimaculatus* species group including *A. gingivinus* (Lazell, 1972). However, we could not morphologically differentiate between the members of the *A. wattsi* group due to a lack of identifying characteristics in preservation (Lazell, 1972). Our historical DNA sequencing resulted in 102,529,039 reads for R-16596 and 84,411,475 for R-16597. We successfully assembled a mean of 63.5% of the mitochondrial genome at an average depth of 199,620X and 223,521X respectively. We re-identified both R-16596 (best match = PP195496: E = 0.0; 99.8% identity) and R-16597 (best match = PP195494: E = 2.0×10^{-84}; 98.9% identity) as *A. schwartzi* (another member of the *A. wattsi* species group) from St. Eustatius based on extracted cytochrome b sequences. Our maximum-likelihood tree confirms that R-16596 and R-16597 were nested with *A. schwartzi* from St. Eustatius rather than *A. pogus* (Fig 2B).

Discussion

Our findings did not support the historical presence of *A. pogus* on Anguilla. Our results do not support either the fossil (Pregill *et al.*, 1994) or museum specimen (Lazell, 1972) based evidence previously used to argue for the recent presence and extinction of *A. pogus* on Anguilla. Specifically, we found the bimodal size distribution of fossils described by Pregill *et al.*, (1994) better fits sexual dimorphism in *A. gingivinus* rather than a two anole species community (Fig 2A). Based on evidence from size distributions and ancient DNA sequencing, Kemp & Hadly (2016) also did not find support for two species in Anguillan fossils from a deposit at Katouche Bay. In total, 19 fossil anole dentaries from Center Cave, 13 from The Fountain (Pregill *et al.* 1994), and 302 from Katouche Bay (Kemp & Hadly 2016) have been examined for SVL estimation with no evidence of the presence of *A. pogus*. Paleontological evidence can play an important role in conservation particularly as a tool for assessing historical ranges (Burney & Burney, 2007; Wingard *et al.*, 2017; Claude *et al.*, 2019). Yet, the case of *A. pogus* highlights the importance of interpreting fossil records correctly. As for the two specimens of *A. pogus* collected on Anguilla, our results indicated that they were misidentified. Although we confirmed that they morphologically belong to the *A. wattsi* species group, our genetic evidence indicated that they are *A. schwartzi* rather than *A. pogus*. Specifically, both MCZ R-16596 and R-16597 best matched with *A. schwartzi* from the island of Sint Eustatius (Fig 2B). To rule out the possibility *A. schwartzi* occurred on Anguilla, we compared SVLs from extant populations with Pregill and colleague's (1994) fossil distribution. Although slightly larger than *A. pogus*, female *A. schwartzi* also fall outside the reported fossil body sie range. Furthermore, Lesser Antillean anoles generally do not have natural distributions that cross deep water channels such as between Anguilla and Sint Eustatius (Lazell 1972). Thus, neither St. Barthélemy (Lazell, 1972) nor Anguilla appear to have been recently inhabited by *A. pogus*.

No field notes exist from the original collector of the alleged Anguillan *A. pogus* to definitively explain their misidentification (S. Kennedy-Gold, personal communication). However, circumstantial evidence suggests these specimens were not collected on Anguilla at all, but were missorted specimens that were collected on Sint Eustatius as part of the same expedition. Both specimens were re-identified by Lazell (1972) as *A. pogus* from preserved specimens found in a large series of *A. gingivinus* originally collected by James L. Peters in 1922. The assignment as *A. pogus* was predominantly based on the alleged geography because *wattsi* group anoles are difficult to distinguish in preservation. Although the exact dates are unknown, Peters also visited and collected anoles from the nearby island of Sint Eustatius that same year. In fact, the next specimen in the catalogue sequence, R-16598, begins a series of specimens collected from St. Eustatius that includes several *A. schwartzi*. Therefore, we suggest that the most parsimonious explanation is that MCZ R-16596 and R-16597 were incorrectly sorted into the Anguilla material, which would also explain their initial cataloguing as *A. gingivinus*.

It should be noted that both Center Cave and The Fountain fossil deposits predate European colonization, but not human arrival on Anguilla (Pregill *et al.*, 1994). However, the Katouche Bay deposit does predate human habitation of the island and dates back over 10,000 years before present (Roughgarden, 1995; Kemp & Hadly, 2016). This latter deposit supports the conclusion that *A. pogus* did not occur on the island during the period of human inhabitation. Nevertheless, we cannot draw definitive conclusions about the presence of *A. pogus* on Anguilla prior to the Holocene. The three islands of Anguilla, St. Martin, and St. Barthélemy have been connected as a single landmass during periods of lower sea levels (Christman, 1953) and molecular clock dating of *A. pogus* from St. Martin suggests that extant *A. pogus* last shared a common ancestor in the Pleistocene, 1.80 Ma [1.62-1.98 Ma] (Yuan et al. 2024). Our models also predicted suitable, albeit fragmented, habitat on both islands (Fig 1), although modeling of current conditions would not necessarily be representative throughout the Pleistocene. Thus, it remains possible that the historical distribution of *A. pogus* extended into Anguilla and St. Barthélemy prior to their separation from St. Martin. Nonetheless, we found no evidence that the species persisted on these islands into the Holocene. If *A. pogus* did occur on these islands, their local extinction was more likely caused by environmental pressures associated with changing Pleistocene climate and sea levels. For instance, these Pleistocene environmental fluctuations have been attributed to the extinction of another Anguillan species the blunt-toothed giant hutia, *Amblyrhiza inundata* (Mcfarlane *et al*., 2014). Extinctions of native species following initial human arrival and subsequent European colonization have clearly occurred in the Caribbean (Fitzpatrick & Keegan, 2007; Bochaton *et al.*, 2021) and on islands around the world (Olson, 1989; Steadman, 1995; Martin & Steadman, 1999). However, despite the prevailing narrative, it does not appear that *A. pogus* on Anguilla was one such case.

The lack of clarity for species historical native ranges is a common problem in the Caribbean (Helgen *et al.*, 2008; Olson & López, 2008; Camargo *et al.*, 2009; Giovas, 2019; Yuan *et al.*, 2022, 2023). Other Caribbean taxa whose historical extinctions are controversial include *Ara* macaws (Olson & López, 2008) and *Iguana* lizards (Martin *et al.*, 2015; Breuil *et al.*, 2018). Incomplete or incorrect information on a species' historical distribution can have important consequences for biodiversity science and conservation management (Carlton, 1996; Wingard *et al.*, 2017). For example, conservation efforts have been inadvertently extended toward introduced species such as racoons on Guadeloupe (Pons *et al.*, 1999; Helgen *et al.*, 2008). A lack of empirical data has long posed an issue for conservation questions regarding *A.*

pogus beyond the Anguilla question addressed by our study. The species has historically been considered an obligate of upland forest (Lazell, 1972). However, evidence now shows that the species is actually widespread throughout St. Martin across all habitats (Powell *et al.*, 2005; Jesse *et al.*, 2018; Yuan et al. 2024). The species was also originally thought to be declining despite lack of demographic data (Powell *et al.*, 2020). Again, recent evidence has shown strong census numbers for the species (Jesse *et al.*, 2018) and genomic evidence indicates recent demographic expansion (Yuan et al. 2024). Therefore, it does not appear that anthropogenic activity has meaningfully threatened *A. pogus* with demographic decline or extinction. Taken together, work on *A. pogus* demonstrates the importance of multiple lines of empirical evidence for the accurate assessment of a species conservation status. Controversy regarding the conservation status and historical distributions of Caribbean species is likely to continue given the region's complicated anthropogenic and biogeographic history (Kaiser, 1997; Olson & López, 2008; Giovas, 2019; Napolitano *et al.*, 2019; Nägele *et al.*, 2020) combined with a lack of data for many species (Böhm *et al.*, 2013). Substantial further work is required to build a better conservation and biodiversity science framework for regions like the Caribbean with high uncertainty for historical baselines. Our study provides a case study for integrative assessment of historical species ranges and local extinctions relevant for biodiversity science and conservation.

Acknowledgements

We thank the Nature Foundation Sint Maarten for their research support. Permits for fieldwork were provided by the Nature Foundation Sint Maarten and Direction de L'Environnement de l'Aménagement et du Logement (DEAL) de Saint-Barthélemy et de Saint-Martin. For help in the field, we thank Catherine Jung, Jeffrey Frederick, Lauren Esposito, and the staff of the Nature Foundation Sint Maarten. For help in the lab, we thank Haley Arbon, Athena Lam, and Grace Kim. Fieldwork protocols were approved by the California Academy of Sciences' institutional animal care and use committee. We thank the Museum of Comparative Zoology (Harvard University) for lending us specimens collected from Anguilla and approving destructive sampling for genetic analyses. We thank Stevie Kennedy-Gold for discussion of the provenance of *A. pogus* specimens from Anguilla. For access to specimens we thank Lauren Scheinberg (California Academy of Sciences) and Esther Langan and Addison Wynn (the National Museum of Natural History). We performed molecular work at the Center for Comparative Genomics (California Academy of Sciences). This study was partially supported by an Evolutionary, Ecological, and Conservation Genomics Research Award (award number: AGA24EECG010) to MLY and by the California Academy of Sciences' Islands 2030 initiative.

Author Contributions

MLY conceived of the study and analyzed the data. MLY, RCB, EAM collected the data and designed the methodology. MLY and RCB funded and supervised the study. MLY wrote the manuscript. All authors edited the manuscript and approved of its publication.

Data Availability

Raw sequence data have been accessioned in SRA (PRJNA1268565). All other data are accessioned in Dryad (doi: 10.5061/dryad.44j0zpcs5).

References

Bochaton, C., Paradis, E., Bailon, S., Grouard, S., Ineich, I., Lenoble, A., Lorvelec, O., Tresset, A. & Boivin, N. (2021). Large-scale reptile extinctions following European colonization of the Guadeloupe Islands. *Sci. Adv.* **7**, eabg2111.

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., et al. (2013). The conservation status of the world's reptiles. *Biol. Conserv.* **157**, 372–385.

Bonebrake, T.C., Christensen, J., Boggs, C.L. & Ehrlich, P.R. (2010). Population decline assessment, historical baselines, and conservation. *Conserv. Lett.* **3**, 371–378.

Breuil, M., Vuillaume, B., Schikorski, D., Krauss, U., Morton, M.N., Haynes, P., Daltry, J.C., Corry, E., Gaymes, G., Gaymes, J., Bech, N., Jelic, M. & Grandjean, F. (2018). A story of nasal horns: A new species of *Iguana Laurenti*, 1768 (Squamata, Iguanidae) in Saint Lucia, St Vincent & the Grenadines, and Grenada (Southern Lesser Antilles) and its implications for the taxonomy of the genus *Iguana*. *bioRxiv* 466128.

Burney, D.A. & Burney, L.P. (2007). Paleoecology and "inter-situ" restoration on Kaua'i, Hawai'i. *Front. Ecol. Environ.* **5**, 483–490.

Camargo, A., Heyer, W.R. & de Sá, R.O. (2009). Phylogeography of the frog *Leptodactylus validus* (Amphibia: Anura): patterns and timing of colonization events in the Lesser Antilles. *Mol. Phylogenet. Evol.* **53**, 571–579.

Carlton, J.T. (1996). Biological invasions and cryptogenic species. *Ecology* **77**, 1653–1655.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Sci. Adv.* **1**, e1400253.

Christman, R.A. (1953). Geology of St. Bartholomew, St. Martin, and Anguilla, Lesser Antilles. *Geol. Soc. Am. Bull.* **64**, 65–96.

Claude, J., Auetrakulvit, P., Naksri, W., Bochaton, C., Zeitoun, V. & Tong, H. (2019). The recent fossil turtle record of the central plain of Thailand reveals local extinctions. *Ann. Paléontol.* **105**, 305–315.

Diamond, J.M., Ashmole, N.P., Purves, P.E., Chaloner, W.G. & Hallam, A. (1997). The present, past and future of human-caused extinctions. *Philos. Trans. R. Soc. Lond. B* **325**, 469–477.

Farr, T.G. & Kobrick, M. (2000). Shuttle radar topography mission produces a wealth of data. *Eos Trans. Am. Geophys. Union* **81**, 583–585.

Fitzpatrick, S.M. & Keegan, W.F. (2007). Human impacts and adaptations in the Caribbean Islands: an historical ecology approach. *Earth Environ. Sci. Trans. R. Soc. Edinb.* **98**, 29–45.

Giovas, C.M. (2019). The beasts at large – perennial questions and new paradigms for Caribbean translocation research. Part I: ethnozoogeography of mammals. *Environ. Archaeol.* **24**, 182–198.

Graham, N.R., Gruner, D.S., Lim, J.Y. & Gillespie, R.G. (2017). Island ecology and evolution: challenges in the Anthropocene. *Environ. Conserv.* **44**, 323–335.

Hahn, C., Bachmann, L. & Chevreux, B. (2013). Reconstructing mitochondrial genomes directly from genomic next-generation sequencing reads—a baiting and iterative mapping approach. *Nucleic Acids Res.* **41**, e129.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O. & Townshend, J.R.G. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* **342**, 850–853.

He, H. S., DeZonia, B. E., & Mladenoff, D. J. (2000). An aggregation index (AI) to quantify spatial patterns of landscapes. *Landsc. Ecol.* 15, 591-601.

Helgen, K.M., Maldonado, J.E., Wilson, D.E. & Buckner, S.D. (2008). Molecular confirmation of the origin and invasive status of West Indian raccoons. *J. Mammal.* **89**, 282–291.

Helgen, K.M. & Wilson, D.E. (2003). Taxonomic status and conservation relevance of the raccoons (*Procyon spp.*) of the West Indies. *J. Zool.* **259**, 69–76.

Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K., Nowosad, J. (2019). landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* 42, 1648-1657.

Howard, R.A. & Kellogg, E.A. (1987). Contributions to a flora of Anguilla and adjacent islets. *J. Arnold Arbor.* **68**, 105–131.

Hykin, S.M., Bi, K. & McGuire, J.A. (2015). Fixing formalin: A method to recover genomic-scale DNA sequence data from formalin-fixed museum specimens using high-throughput sequencing. *PLOS ONE* **10**, e0141579.

Jesse, W.A.M., Behm, J.E., Helmus, M.R. & Ellers, J. (2018). Human land use promotes the abundance and diversity of exotic species on Caribbean islands. *Glob. Change Biol.* **24**, 4784–4796.

Kaiser, H. (1992). The trade-mediated introduction of *Eleutherodactylus martinicensis* (Anura: Leptodactylidae) on St. Barthélémy, French Antilles, and its implications for Lesser Antillean biogeography. *J. Herpetol.* **26**, 264–273.

Kaiser, H. (1997). Origins and introductions of the Caribbean frog, *Eleutherodactylus johnstonei* (Leptodactylidae): management and conservation concerns. *Biodivers. Conserv.* **6**, 1391–1407.

Kemp, M.E. & Hadly, E.A. (2016). Early Holocene turnover, followed by Stability, in a Caribbean lizard assemblage. *Quat. Res.* **85**, 255–261.

Lazell, J.D. (1972). The anoles (Sauria, Iguanidae) of the Lesser Antilles. *Bull. Mus. Comp. Zool.* **143**, 1–115.

Li, H. (2013). Aligning sequence reads, clone sequences and assembly contigs with BWA-MEM. *ArXiv13033997 Q-Bio*.

Losos, J. (2009). *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press.

Martin, J.L., Knapp, C.R., Gerber, G.P., Thorpe, R.S. & Welch, M.E. (2015). Phylogeography of the endangered Lesser Antillean iguana, *Iguana delicatissima*: a recent diaspora in an archipelago known for ancient herpetological endemism. *J. Hered.* **106**, 315–321.

Martin, P.S. & Steadman, D.W. (1999). Prehistoric extinctions on islands and continents. In *Extinctions in Near Time*: 17–55. MacPhee, R.D.E. (Ed.). Boston, MA: Springer US.

McClenachan, L., Ferretti, F. & Baum, J.K. (2012). From archives to conservation: why historical data are needed to set baselines for marine animals and ecosystems. *Conserv. Lett.* **5**, 349–359.

Mcfarlane, D.A., Lundberg, J. & Maincent, G. (2014). New specimens of *Amblyrhiza inundata* (Rodentia: Caviomorpha) from the Middle Pleistocene of Saint Barthélemy, French West Indies. *Caribb. J. Earth Sci.* **47**, 15-19.

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A. & Lanfear, R. (2020). IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Mol. Biol. Evol.* **37**, 1530–1534.

Nägele, K., Posth, C., Orbegozo, M.I., Armas, Y.C. de, Godoy, S.T.H., Herrera, U.M.G., Nieves-Colón, M.A., Sandoval-Velasco, M., Mylopotamitaki, D., Radzeviciute, R., Laffoon, J., Pestle, W.J., Ramos-Madrigal, J., Lamnidis, T.C., Schaffer, W.C., Carr, R.S., Day, J.S., Antúnez, C.A., Rivero, A.R., Martínez-Fuentes, A.J., Crespo-Torres, E., Roksandic, I., Stone, A.C., Lalueza-Fox, C., Hoogland, M., Roksandic, M., Hofman, C.L., Krause, J. & Schroeder, H. (2020). Genomic insights into the early peopling of the Caribbean. *Science* **369**, 456–460.

Napolitano, M.F., DiNapoli, R.J., Stone, J.H., Levin, M.J., Jew, N.P., Lane, B.G., O'Connor, J.T. & Fitzpatrick, S.M. (2019). Reevaluating human colonization of the Caribbean using chronometric hygiene and Bayesian modeling. *Sci. Adv.* **5**, eaar7806.

Olson, S.L. (1989). Extinction on islands: man as a catastrophe. In *Conservation biology for the next century*: 50–53. Western, D. & Pearl, M.C. (Eds.). Oxford, UK: Oxford University Press.

Olson, S.L. & López, E.J.M. (2008). New evidence of *Ara autochthones* from an archeological site in Puerto Rico: a valid species of West Indian macaw of unknown geographical origin (Aves: Psittacidae). *Caribb. J. Sci.* **44**, 215–223.

Papadopoulou, A. & Knowles, L.L. (2015). Genomic tests of the species-pump hypothesis: Recent island connectivity cycles drive population divergence but not speciation in Caribbean crickets across the Virgin Islands. *Evolution* **69**, 1501–1517.

Pons, J.-M., Volobouev, V., Ducroz, J.-F., Tillier, A. & Reudet, D. (1999). Is the Guadeloupean racoon (*Procyon minor*) really an endemic species? New insights from molecular and chromosomal analyses. *J. Zool. Syst. Evol. Res.* **37**, 101–108.

Powell, R., Dewynter, M., Daltry, J.C. & Mahler, D.L. (2020). *Anolis pogus*. The IUCN Red List of Threatened Species.

Powell, R., Henderson, R.W. & Parmerlee, J.S. (2005). *The reptiles and amphibians of the Dutch Caribbean : St Eustatius, Saba, and St Maarten*.

Pregill, G.K., Steadman, D.W. & Watters, D.R. (1994). Late Quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. *Bull. Carnegie Mus. Nat. Hist.* **30**, 1–51.

Pringle, R.M., Kartzinel, T.R., Palmer, T.M., Thurman, T.J., Fox-Dobbs, K., Xu, C.C.Y., Hutchinson, M.C., Coverdale, T.C., Daskin, J.H., Evangelista, D.A., Gotanda, K.M., A. Man in 't Veld, N., Wegener, J.E., Kolbe, J.J., Schoener, T.W., Spiller, D.A., Losos, J.B. & Barrett, R.D.H. (2019). Predator-induced collapse of niche structure and species coexistence. *Nature* **570**, 58–64.

Ricklefs, R.E. & Lovette, I.J. (1999). The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *J. Anim. Ecol.* **68**, 1142–1160.

Rosen, D.E. (1975). A vicariance model of caribbean biogeography. *Syst. Biol.* **24**, 431–464.

Roughgarden, J. (1995). *Anolis Lizards of the Caribbean: Ecology, Evolution, and Plate Tectonics*. Oxford University Press.

Roughgarden, J., Pacala, S., Otte, D. & Endler, J.A. (1989). Taxson cycle among *Anolis* lizard populations: review of evidence. In *Speciation and its consequences*: 403–432. Sunderland, Massachusetts: Sinauer Associates, Inc.

Smith, M.L., Hedges, S.B., Buck, W., Hemphill, A., Inchaustegui, S., Ivie, M., Martina, D., Maunder, M. & Ortega, J.F. (2005). Caribbean Islands. In *Hotspots Revisited: Earth's*

Biologically Richest and Most Endangered Terrestrial Ecoregions: 112–118. Mittermeier, R.A., Gil, P.R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J. & Da Fonseca, G.A.B. (Eds.). Mexico City: CEMEX.

Steadman, D.W. (1995). Prehistoric extinctions of pacific island birds: biodiversity meets zooarchaeology. *Science* **267**, 1123–1131.

Wilmshurst, J.M., Moar, N.T., Wood, J.R., Bellingham, P.J., Findlater, A.M., Robinson, J.J. & Stone, C. (2014). Use of pollen and ancient DNA as conservation baselines for offshore islands in New Zealand. *Conserv. Biol.* **28**, 202–212.

Wingard, G.L., Bernhardt, C.E. & Wachnicka, A.H. (2017). The role of paleoecology in restoration and resource management—the past as a guide to future decision-making: review and example from the Greater Everglades ecosystem, U.S.A. *Front. Ecol. Evol.* **5**.

Yuan, M.L., Crews, S.C., Esposito, L.A., Allen, L.C. & Bell, R.C. (2023). Confirmed presence of *Sphaerodactylus sputator* on Saba, Caribbean Netherlands. *Herpetol. Notes* **16**, 1–4.

Yuan, M.L., Frederick, J.H., McGuire, J.A., Bell, R.C., Smith, S.R., Fenton, C., Cassius, J., Williams, R., Wang, I.J., Powell, R. & Hedges, S.B. (2022). Endemism, invasion, and overseas dispersal: the phylogeographic history of the Lesser Antillean frog, *Eleutherodactylus johnstonei*. *Biol. Invasions* **24**, 2707–2722.

Yuan, M. L., Merjenburgh, J., van Wagensveld, T. P., Esposito, L. A., Bell, R. C., Myers, E. A. (2024). Competitor decline coincides with demographic expansion and panmixia in *Anolis pogus* on St. Martin. *EcoEvoRxiv.*

Zanaga, D., Van De Kerchove, R., Daems, D., De Keersmaecker, W., Brockmann, C., Kirches, G., Wevers, J., Cartus, O., Santoro, M., Fritz, S., Lesiv, M., Herold, M., Tsendbazar, N.E., Xu, P., Ramoino, F. & Arino, O. (2022). ESA WorldCover 10 m 2021 v200.

Fig 1 Predicted abundances for *A. pogus* on the islands of (A) Anguilla and (B) St. Barthélemy using random forest models (urbanization + canopy cover + elevation) fit to survey data from St. Martin. Sites of deposits containing *Anolis* fossilson Anguilla are shown.

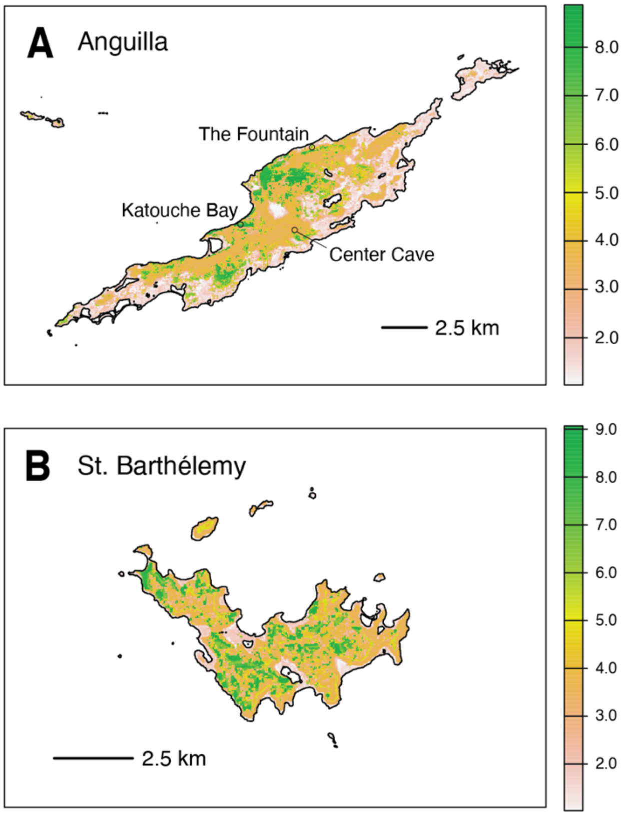

Fig 2 (A) Density plot of *A. gingivinus* and *A. pogus* SVLs collected from specimens and live samples on St. Martin. Males and females are shown separately for each species. Grey blocks represent reported size ranges of *Anolis spp.* fossils from Anguilla reported in Pregill et al. 1994. Female *A. pogus* do not fall within size ranges of Anguillan fossils. (B) Mitochondrial maximum likelihood tree of *A. schwartzi* and *A. pogus* with MCZ samples (R-16596 and R-16597) from Anguilla included. Nodes with bootstrap values above 90 are noted. Note that both MCZ samples, denoted by a star, are nested within *A. schwartzi* from St. Eustatius.