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Early Holocene turnover, followed by stability, in a Caribbean lizard assemblage

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ABSTRACT

Understanding how communities are impacted by environmental perturbations is integral for addressing the ongoing biodiversity crisis that impacts ecosystems worldwide. The fossil record serves as a window into ancient interactions and the responses of communities to past perturbations. Here, we re-examine paleontological data from Katouche Bay, Anguilla, a Holocene site in the Lesser Antilles. We reveal that the site was more diverse than previously indicated, with long-term, continuous records of three genera of extant lizards (*Anolis*, *Ameiva*, and *Thecadactylus*), and the early Holocene presence of *Leiocephalus*, a large ground-dwelling lizard that has since been completely extirpated from the Lesser Antilles. The disappearance of *Leiocephalus* from Katouche Bay resulted in high turnover, decreased evenness, and decreased species richness—a trend that continues to the present day. Our body size reconstructions for the most abundant genus, *Anolis*, are consistent with the presence of only one species, *Anolis* cf. *gingivinus*, at Katouche Bay throughout the Holocene, contrary to previously published studies. Additionally, we find no evidence of dwarfism in *A.* cf. *gingivinus*, which contrasts with a global study of contemporary insular lizards. Our data reveal that the impacts of diversity loss on lizard communities are long lasting and irreversible over millennia.

Introduction

The loss of taxonomic diversity from within a community is not without consequences. Not only can it change how an ecosystem functions, but it can also affect the community's structure: it can lead to extinction cascades, novel species interactions, and dominance of prey species and competitors (Paine, 1966; Cox and Elmqvist, 2000; Säterberg et al., 2013). Quantifying changes in community structure that result from extinction and extirpation events informs how communities might respond to pending diversity loss, and immense perspective can be obtained through studying past turnover events. The structural changes that occurred around and after the Pleistocene–Holocene transition are a prime example of how we can learn about community change from the past. Extinction and extirpation events of the late Pleistocene and Holocene are the most accurate corollary for ongoing and future extinctions, because humans were then, as they are today, inextricably linked to climatic and biodiversity change worldwide (Koch and Barnosky, 2006).

As humans and climate change continue to put pressure on ecosystems, evidence is mounting that immediate action should be taken to counteract their detrimental and synergistic effects, most notably biodiversity loss and cascading impacts on ecosystems worldwide. Work is underway to predict how major taxonomic groups will fare in this uncertain future through the use of fossils. The fossil record reveals that vertebrate species responses to past environmental change were not synonymous; in mammals, for example, the loss of many large-bodied species at the terminal Pleistocene led to a rise in small mammal populations and the replacement of congeneric species (Blois et al., 2010; Dirzo et al., 2014). The resulting communities are completely different from what they were during the Pleistocene. In contrast, non-avian reptile and amphibian communities remained relatively stable throughout the Quaternary (Fay, 1988; Holman, 1991; but see Bell et al., 2010), although some geographic contexts, such as insular systems, may tell a different story. The Caribbean, for example, saw range contraction in a number of reptiles during the Quaternary (Pregill and Olson, 1981), and changes in traits such as body size (Pregill, 1986).

Here, we seek to elucidate how a Caribbean lizard assemblage changed from the earliest Holocene to the present by focusing on community structure and taxonomic diversity. We center our study on the previously excavated site of Katouche Bay, Anguilla (Roughgarden, 1995). The primary goals of our study are to (1) place the Katouche Bay site into a broader chronology of Quaternary paleontological sites in the Caribbean and elsewhere; (2) describe the taxonomic diversity of the site throughout the Quaternary; and (3) determine how the loss of taxonomic diversity impacted community structure.

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Biogeography and background of Anguilla and the Katouche Bay site

Anguilla (Fig. 1), a small island in the northern Lesser Antilles, plays an important role in Caribbean paleontology and biogeography; its proximity to the Greater Antilles renders it integral to understanding the dispersal of taxa between the Greater Antilles and the Lesser Antilles. Anguilla is part of a larger island bank that includes St. Martin and St. Barthélemy; these islands were connected during the lower sea level stands of the Pleistocene and the present land above sea level represents only 6% of the bank's actual area (McFarlane et al., 1998). The calcareous substrate of Anguilla preserves a rich fossil record that neighboring volcanic islands do not harbor. Fossils suggest that the biota underwent a significant reduction in diversity during the Quaternary. Anguilla's most noted fossil species is the blunt-toothed giant hutia *Amblyrhiza inundata*, a large rodent that went extinct at least 50 ka (McFarlane et al., 1998), but the pre-Columbian lizard fauna remains understudied, despite its significance to understanding biogeographic and macroevolutionary trends in the Caribbean island system as a whole.

The *Anolis* lizard fauna of Anguilla proves particularly challenging when attempting to characterize diversification in the Lesser Antillean clades of this genus. *Anolis* is a widely distributed, speciose genus of Neotropical lizards, with over 150 species found in the Caribbean alone; 23 of these species are endemic to the Lesser Antilles (Losos, 2009). *Anolis pogus*, a lizard now restricted to the relatively humid island of St. Martin, once had a larger range that included Anguilla and St. Barthélemy. Despite intensive sampling efforts and the existence of suitable environments on Anguilla around Katouche Bay and Mango Garden, the species has not been sighted since two specimens purportedly from Anguilla but with unknown provenances were collected in the early 20th-century (Lazell, 1972).

The proposition that Katouche Bay, Anguilla, once held a population of *A. pogus* found further support when a fissure in Katouche Canyon containing fossils of *Anolis* was excavated in 1985 (Roughgarden and Pacala, 1989, Fig. 2b). The preservation of fossils in the fissure likely resulted from prey-item accumulation by generations of the American kestrel (*Falco sparvarius*) perching on the cliff. Four key conclusions about the lizard fauna were derived from morphological identifications and conventional radiocarbon dating of a piece of charcoal from the bottom of the unit (Roughgarden, 1995). First, the unit was dated as >10,000 ^{14}C yr BP. Second was the extinction of the curly-tailed lizard *Leiocephalus* from Anguilla, a genus that is now completely extirpated from the Lesser Antilles, although it is still present in the Greater Antilles and the Bahamas. Third was early Holocene dwarfism followed by extirpation of the small-bodied *A. pogus* shortly after island colonization by the larger species of *Anolis*, *Anolis gingivinus*, which is still found on Anguilla today. The fourth and final conclusion was that *A. gingivinus* also underwent dwarfism in the Holocene. The phenomenon of Holocene dwarfism of insular lizards was described previously for a diverse array of globally distributed species (Pregill, 1986). Given its importance in the broader context of anole evolution in the Caribbean and the renewed interest in community change in response to extinction, we chose to restudy the fossil specimens of Katouche Bay and (1) place the Katouche Bay site into a broader chronology of Quaternary paleontological sites in the Caribbean and elsewhere; (2) re-describe the taxonomic diversity of the site; (3) determine how the loss of taxonomic diversity impacted community structure; and (4) reconstruct body sizes for *Anolis* spp. in order to re-evaluate species richness and body size evolution.

Materials and methods

Because the previous radiocarbon date of >10,000 ^{14}C yr BP for Katouche Bay was conventionally done and imprecise, we obtained new AMS dates for the Katouche Bay fossil accumulation. We submitted a sample of charcoal from Level 10 (0.88 m below surface level) for radiocarbon dating at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory (Livermore, California) and received two ^{14}C radiocarbon dates on this material. The ^{14}C radiocarbon dates were then calibrated with Calib 7.0 (Stuiver et al., 2005) using the INTCAL13 curve (Reimer et al., 2013). Because the site exhibits little evidence of bioturbation, we used the new and pre-existing radiocarbon dates to build two age-by-depth models that assume linear deposition until the present. One model includes all available radiocarbon dates for the Katouche Bay site (Model One), whereas the other model only contains the new dates reported in this study (Model Two).

The majority of squamate skeletal elements retrieved from Katouche Bay are highly fragmented mandibles and dentaries. We performed identifications using a comparative collection of specimens (EAH personal collection, Stanford University; the Smithsonian Institution

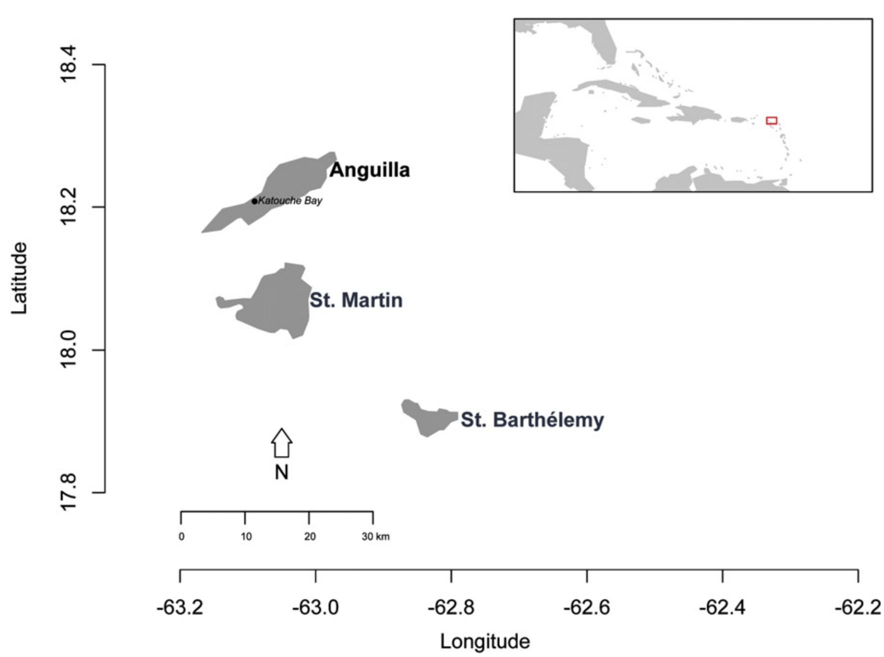

Figure 1. Map of Anguilla and surrounding islands.