

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



Melissa E. Kemp*, Elizabeth A. Hadly

Department of Biology, Stanford University, Stanford, CA 94305-5020, USA

ARTICLE INFO

Article history:

Received 24 January 2015

Available online 13 January 2016

Keywords:

Lizards
Caribbean
Paleoecology
Vertebrate paleontology

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.

© 2015 University of Washington. Published by Elsevier Inc. All rights reserved.

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.

* Corresponding author at: Department of Organismic and Evolutionary Biology, Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA.
E-mail address: mkemp@fas.harvard.edu (M.E. Kemp).

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 sparverius*) 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

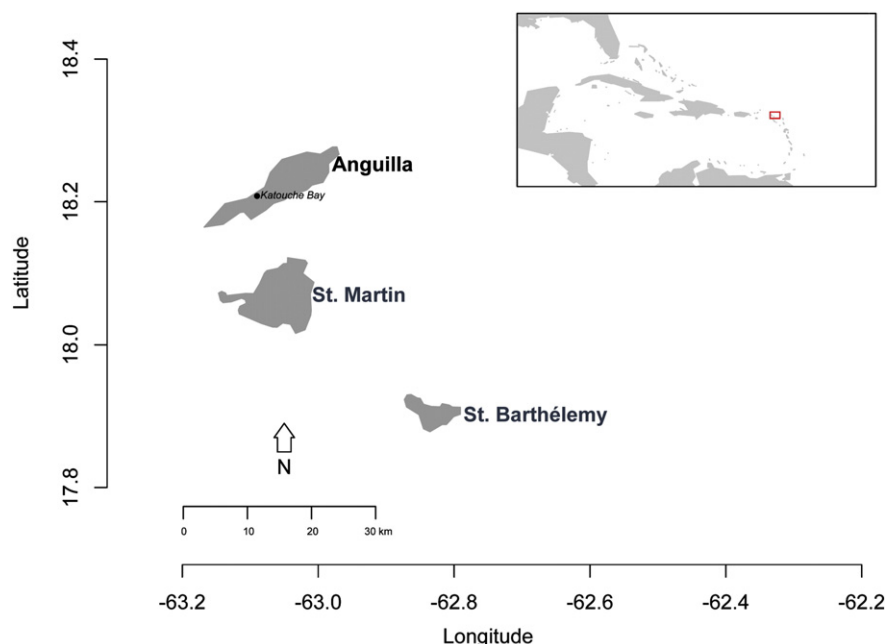


Figure 1. Map of Anguilla and surrounding islands.

Relative abundance of lizard taxa at Katouche Bay

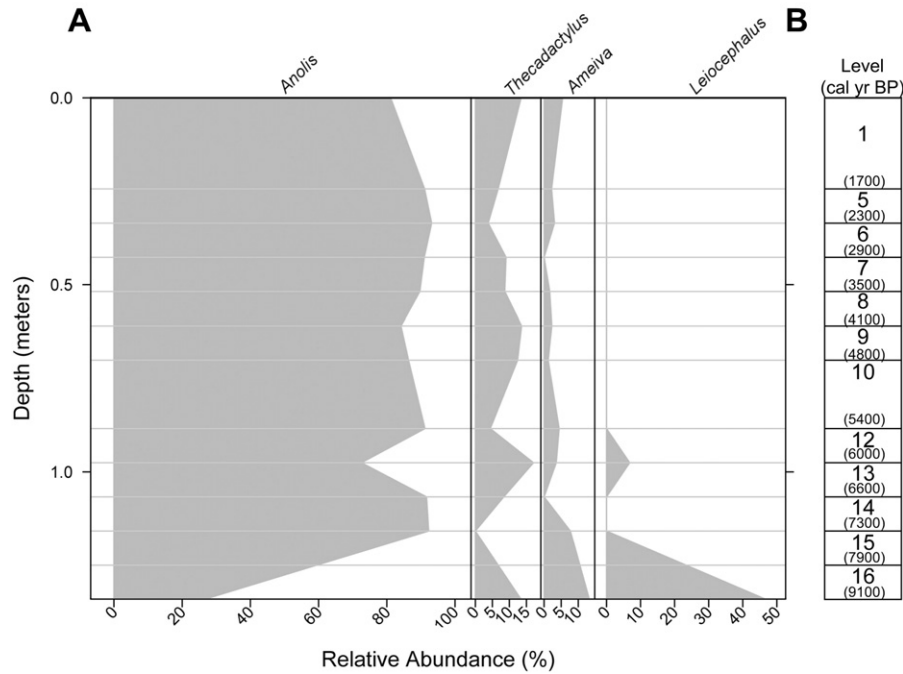


Figure 2. Relative abundance of lizard taxa at Katouche Bay. A shows the rarefied relative abundance of lizard taxa at Katouche Bay, B is a schematic of the stratigraphic levels, with ages in cal yr BP.

USNM numbers 236362–236369), and following previously published studies on the Quaternary herpetofauna of the Caribbean (Etheridge, 1964; Pregill, 1981). We used modern geographic distributions of genera to guide the selection of comparative material used in our taxonomic identifications. We attempted to make species-level designations, but due to the fragmented nature of the fossils, only genus-level designations were possible in most cases.

We determined the minimum number of individuals (MNI) and the number of identified specimens (NISP) for each taxonomic group. MNI was calculated as the minimum number of complete dentaries of a specific side (either right or left) found per level. Because the number of fossil specimens was not evenly distributed throughout the deposit, ascertaining relative abundance from NISP or MNI counts alone is somewhat biased, although NISP is a less biased estimator of abundance (Grayson, 1973). One additional challenge was that we relied on previously collected material from Katouche Bay and thus did not conduct the excavation ourselves. However, notes from the 1985 excavation were readily available and were thorough. Specimens from levels 2, 3, 4, and 11 were either removed prior to our receipt of the collection, or grouped and stored with contiguous levels in such a way that we could not reassign materials to their original, specific levels. We accounted for discrepancies in sample size through rarefaction. For each level, we standardized our data to reflect the smallest sample size (n = 12, level 14) by randomly sampling 12 species from a population representing the actual proportions of taxa within each particular level. This subsampling procedure was repeated 1000 times to determine the rarefied relative abundance of each taxon. These rarefied data were also used to determine species richness, evenness, and turnover in the community through time, calculated using the R package *vegan* (Oksanen et al., 2015). The R package *analogue* (Simpson, 2007; Simpson and Oksanen, 2013) was used to create a pollen diagram of relative abundance for the lizard taxa at Katouche Bay. All statistical analyses were conducted in R (R Core Team, 2014).

Due to the highly fragmented nature of skeletal material from all other taxa besides *Anolis*, we were only able to reconstruct body size for material of *Anolis*, and only at levels in which full dentaries were

preserved. For material of *Anolis*, we reconstructed snout-vent length (SVL), a commonly used body-size metric in squamates, in order to corroborate species identifications. Previously, body-size reconstructions were used to detect species richness and sexual dimorphism in ancient populations of *Anolis* (Etheridge, 1964; Lazell, 1972). An equation to estimate SVL was developed from specimens of *A. pogus* and *A. gingivinus* using a linear regression of specimen tooth row to SVL. The longest linear distance of the tooth row of fossil material was measured on complete dentaries and used in this equation; the equations can be found in Table 1 and the dental row measurements of fossil material can be found in Supplementary Table 1.

We used a number of statistical tests to evaluate the body sizes of fossil *Anolis* lizards with the intention to surmise the number of species present, and whether they underwent changes in body size over time. The Hartigan's dip test of unimodality was used to detect whether data from *Anolis* were unimodal, indicating the presence of a single species, or not, which would lead us to conclude that either multiple species of *Anolis* were present or that the one species present was sexually dimorphic. An analysis of variance (ANOVA) was used to detect differences in body size through time.

Results

Geologic age determination

We obtained two new radiocarbon dates for the Katouche Bay site, each from a single charcoal sample at level 10 (Table 2). The two dates, 4958–5090 cal yr BP and 5047–5203 cal yr BP, are concordant and consistent with the Katouche Bay fossil site being Holocene in age. The two models we constructed did not differ significantly (Kolmogorov–

Table 1 Snout-vent length reconstruction equation.

Equation	Slope (m)	Intercept (b)	R ²
SVL = e ^{0.72 * (ln(tooth row length)) + 2.4}	0.72	2.4	0.87

Table 2
New ^{14}C dates for Katouche Bay, Anguilla.

Sample number	Material	Level	$\delta^{13}\text{C}$	Fraction modern	D^{14}C	^{14}C age	2- σ age range (cal yr BP)
CAMS# 160603	Charcoal	10	−25	0.5746 ± .0023	−425.4 ± 2.3	4450 ± 35	4958–5090
CAMS# 160604	Charcoal	10	−25	0.5699 ± .0022	−430.1 ± 2.2	4515 ± 35	5047–5203

Smirnov Test, $D = 0.0714$, p -value = 1; Supplementary Figs. 1 and 2), so we used Model One to describe the timing of faunal changes at Katouche Bay. Our estimates suggest that the fossil accumulation at Katouche Bay began around 9700 cal yr BP and extended, without known unconformities, until the present (Table 3).

Taxonomic identifications

We identified 773 lizard specimens and attributed these materials to four lizard genera: *Anolis*, *Ameiva*, *Leiocephalus*, and *Thecadactylus*. The materials are all dentaries, maxillae, and premaxillae. The criteria used for each attribution are given below.

A. cf. gingivinus

Anolis is distinguished from other taxa by the following characteristics: tricuspid posterior teeth with a wide central cusp flanked by reduced lateral cusps; teeth that become unicuspid anteriorly; and maxillae with a triangular facial process. There are two species of *Anolis* endemic to the Anguillan bank: *A. gingivinus* and *A. pogus*. It is notoriously difficult to identify *Anolis* to the species-level from dentaries and maxillae alone and body size has been used to differentiate fossil remains of co-occurring species in the Lesser Antilles (Etheridge, 1964; Pregill, 1981). Body-size reconstructions of fossil material are consistent with a single, sexually monomorphic species of anole *A. gingivinus* (Hartigan's dip test of unimodality, $p = 1$). Both *A. gingivinus* and *A. pogus* have distinct mean body sizes, despite some overlap in body size range: *A. gingivinus* ranges in size from 41 mm–72 mm, whereas *A. pogus* is 36 mm–50 mm. The median body size (61 mm) of the Katouche Bay specimens is within the range of present-day body sizes for *A. gingivinus* but is significantly larger than any known *A. pogus* specimen (Wilcoxon signed-rank test, $p < 0.0001$).

Body size of *A. cf. gingivinus* shows high variability throughout the unit, going from a median of 52 mm (mean = 52 mm) at 7900 yr to a median of 63 mm (mean = 60 mm) in the most recent depositional level (ANOVA; Fig. 3). We find no evidence of dwarfism in *A. cf. gingivinus* during the Holocene. On the contrary, it appears that *A. cf. gingivinus* becomes larger throughout the Holocene ($p < 0.001$). We attribute this significant variation to a few stratigraphic levels as pairwise comparisons of all stratigraphic levels reveal that the majority of

Table 3
Depth ages based on age-depth model produced from calibrated radiocarbon dates of Katouche Bay, Anguilla.

Time (cal yr BP)	Depth (m)	Level
0	0	0
1658	−0.24	1
2279	−0.34	5
2901	−0.43	6
3522	−0.52	7
4144	−0.61	8
4766	−0.70	9
5387	−0.79	10
6009	−0.88	12
6630	−0.98	13
7252	−1.07	14
7874	−1.16	15
9117	−1.34	16
9738	−1.43	17

specimens at the Katouche Bay site are not different from one another (Tukey HSD, Table 4).

Ameiva sp.

The following osteological characters allowed us to identify this taxon as *Ameiva* sp.: maxillae with high facial process lacking dermal ornamentation; large bicuspid posterior teeth; and small, unicuspid anterior teeth. Currently, there are two species of *Ameiva* inhabiting the Anguilla bank: the widespread *Ameiva plei* which can be found on Anguilla, St. Martin, and St. Barthélemy; and *Ameiva corax*, a species restricted to Little Scrub Island, which is off the coast of Anguilla.

Leiocephalus sp.

Leiocephalus is represented at Katouche Bay by highly fragmented dentaries. The dentition of *Leiocephalus* is distinguished from the dentition of other lizards by the flared, fan-shaped tricuspid teeth that lizards in this genus and in the genus *Leiolemus* possess (Pregill, 1981). The teeth of *Leiocephalus* are further distinguished from those of *Leiolemus* by a central cusp that is clearly delimited from the lateral cusps flanking each tooth. The *Leiocephalus* material from Anguilla was previously referred to as *Leiocephalus cf. cuneus*, a species described by Etheridge from fossil material on Barbuda (1964), an island 146 km from Anguilla that sits on a separate island bank. Due to the fragmented nature of the remains, it is impossible to say whether the Anguillan samples represent *L. cf. cuneus* or another species.

Thecadactylus sp.

Thecadactylus sp. is represented at Katouche Bay by highly fragmented dentaries. The teeth of *Thecadactylus* are distinguished

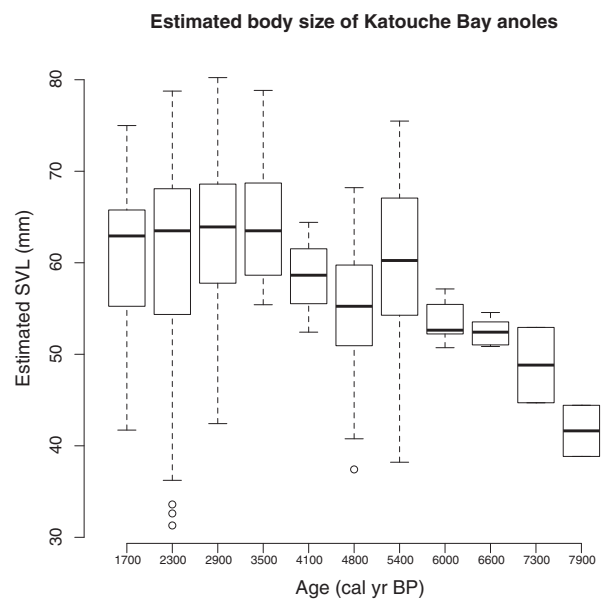


Figure 3. Body size of *Anolis gingivinus* through time at Katouche Bay.

Table 4

Tukey HSD test results for Katouche Bay anole body sizes. Highlighted pairwise comparisons were statistically significant ($p < 0.05$).

Stratigraphic level	1	5	6	7	8	9	10	12	13	14
5	1.00									
6	0.97	0.87								
7	0.85	0.71	1.00							
8	1.00	1.00	1.00	0.99						
9	0.74	0.22	0.02	0.02	1.00					
10	1.00	1.00	0.82	0.62	1.00	0.76				
12	0.86	0.62	0.24	0.15	1.00	1.00	0.88			
13	0.82	0.62	0.29	0.18	1.00	1.00	0.85	1.00		
14	0.83	0.73	0.50	0.37	0.98	1.00	0.85	1.00	1.00	
15	0.16	0.10	0.04	0.02	0.60	0.65	0.18	0.84	0.93	1.00

from other large genera of geckos in the Caribbean (e.g. *Tarentola* and *Aristelliger*) by being thinner, straighter, and less pointed than teeth in these other two genera (Etheridge, 1964; Pregill, 1981). Throughout the Lesser Antilles, *Thecadactylus* is represented by the widespread species *Thecadactylus rapicauda*, although another species, *Thecadactylus oskrobapreinorum* was recently described based on morphological differences, but no genetic data or osteological characters have been described for this new species (Koehler and Vesely, 2011). *T. oskrobapreinorum* is restricted to St. Martin on the Anguillan bank.

Community structure through time

The paleocommunity of Katouche Bay is characterized by one episode of high turnover near the Pleistocene–Holocene transition, from 9000–8000 yr (Fig. 4). This coincides with the declining abundance of *Leiocephalus*, which last occurs at Katouche Bay at 7000 yr (Fig. 2a). Richness loss occurs between 9000–7000 yr, when the community went from four to three taxa, a 25% loss (Fig. 5). The community underwent an

abrupt, drastic, evenness loss at 9000–8000 yr, resulting in a 53% decline (Fig. 6). The decline in evenness signifies a loss in functional stability of the Katouche Bay paleocommunity (Wittebolle et al., 2009), and indeed, it precedes the extinction of *Leiocephalus* at Katouche Bay and the emerging dominance of *Anolis* in the absence of *Leiocephalus*. By 4000 yr specimens of *Anolis* account for nearly 90% of the community (Fig. 2a). While *Thecadactylus* and *Ameiva* do not undergo drastic abundance shifts like *Anolis* does, these two genera persist in low abundance throughout the Holocene and are still found on Anguilla today.

Discussion

Our study of the Katouche Bay site reveals a species turnover event in the Holocene community that would never be revealed by studies employing modern ecological data alone. Following this structural change, the community exhibited stability throughout the Holocene in both species number and relative abundance, unlike other islands in the Lesser Antilles, which saw biodiversity loss in numerous genera (Pregill et al., 1994).

Although a relatively diverse assemblage is preserved, the Katouche Bay deposit does not record the presence of all lizards found on Anguilla (Table 5). This could be due to microhabitat, taphonomic bias, or the manner by which materials were collected during excavation. Geckos like *Sphaerodactylus*, a widespread genus of extremely small lizards are rarely found at all in deposits (Daza et al., 2014), likely due to material loss during the screening of excavated sediment, or differential preservation of material with small-bodied organisms like *Sphaerodactylus* being disfavored. Elsewhere in the Lesser Antilles, the large-bodied lizard *Iguana delicatissima* is confined to archeological deposits (Pregill et al., 1994), and it was a common food source among native peoples (Powell, 2004).

Our results are different from those of Roughgarden and Pacala (1989), because we find no evidence of dwarfism in *Anolis*, and the body size distribution indicates the long-term presence of one *Anolis* species, *A. cf. gingivinus*. Given the limitations of the available osteological characters in identifying specimens to the species level, and evidence of rapid body-size evolution during the Holocene (Pregill, 1986), there are a few alternative interpretations for what our data show. First, our specimens could represent *A. pogus* if *A. pogus* was larger in the past, occupying the body size range of present-day *A. gingivinus*. Alternatively, the material of *Anolis* could represent a species that is not *A. pogus* or *A. gingivinus* that is recently extinct or extirpated from the Anguilla bank.

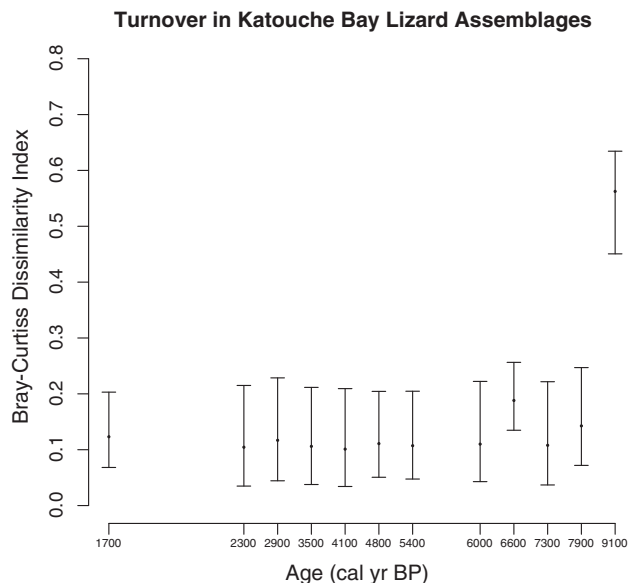


Figure 4. Species turnover through time, as measured by the Bray–Curtis Dissimilarity Index, in the Katouche Bay lizard fauna.

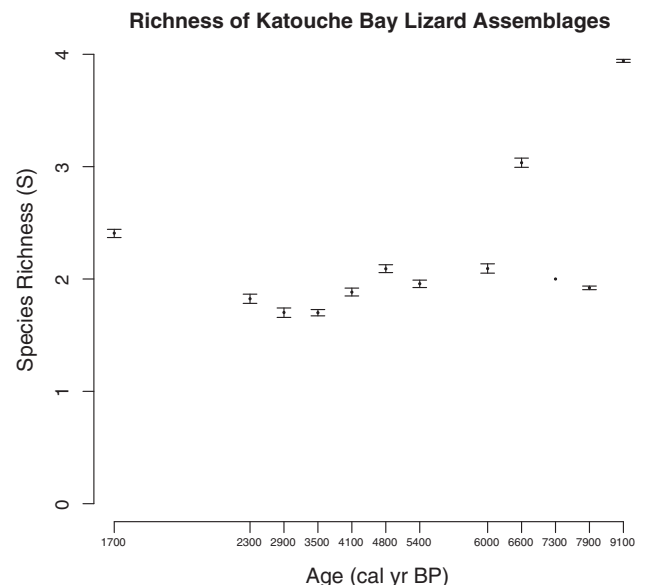


Figure 5. Species richness through time in the Katouche Bay lizard fauna.

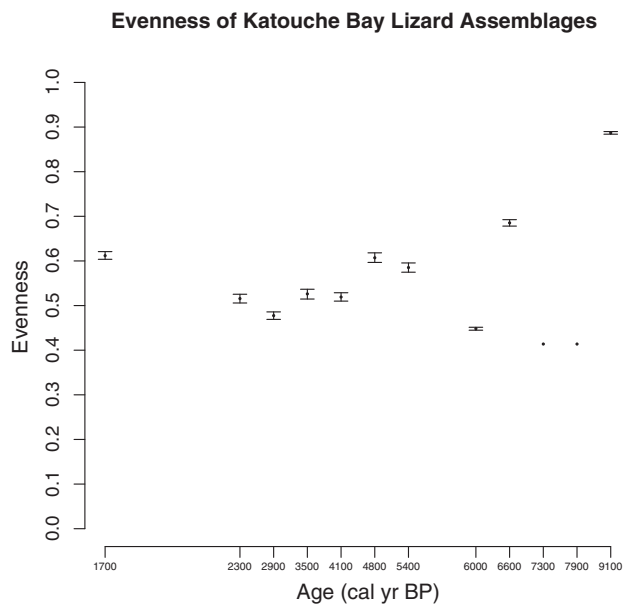


Figure 6. Evenness through time in the Katouche Bay lizard fauna.

Neither of these alternatives is as parsimonious as the conclusion we present here, and both conflict with the most recently available empirical evidence from elsewhere in the Lesser Antilles. If *A. pogus* were present at Katouche Bay and larger in the past, we would expect to see a decrease in body size over time as it approaches its current body size. Body size reconstructions of *Anolis* cf. *ferreus* indicate stability of body size from the Pleistocene onwards (Bochaton et al., 2015), in contrast to the dwarfism predicted by the Holocene dwarfism hypothesis, but consistent with our findings. Given the stability of herpetofaunal communities throughout the Quaternary in North America, the null expectation is that there has been continuity of species through time and space. *A. gingivinus* is the only extant lineage of *Anolis* on Anguilla, it is endemic to the Anguilla bank, and it is widely distributed across the Anguilla bank. It is thus very likely that there has been continuous occupancy of *A. gingivinus* at Katouche Bay for millennia, although additional skeletal material with diagnostic characters would provide further support to our claim. Unfortunately, such materials were not available from the Katouche Bay site. In the absence of such material, we attempted to obtain ancient DNA (aDNA) from the remains of *Anolis* in order to corroborate our designations. Preliminary sequence data from a few specimens that we have processed confirm that fossils we identified as *A. cf. gingivinus* are indeed *A. gingivinus* (Kemp, unpublished data). We would need to sequence aDNA from hundreds of specimens in order to fully conclude that *A. pogus* or another *Anolis* species was not present at Katouche Bay, and given the difficulties associated with obtaining aDNA from tropical localities (Reed et al., 2003), this particular feat may prove impossible.

Table 5
Modern lizard species found on Anguilla.

Species	Endemicity to the Anguilla bank
<i>Ameiva plei</i>	Endemic
<i>Anolis carolinensis</i>	Introduced
<i>Anolis gingivinus</i>	Endemic
<i>Hemidactylus mabouia</i>	Likely introduced
<i>Iguana delicatissima</i>	Native
<i>Iguana iguana</i>	Introduced
<i>Sphaerodactylus parvus</i>	Endemic
<i>Sphaerodactylus sputator</i>	Endemic
<i>Spondylurus powelli</i>	Endemic
<i>Thecadactylus rapicauda</i>	Native

However, several lines of evidence exist that *A. pogus* was on Anguilla in the past, which cannot be ignored. In addition to Anguillan specimens of *A. pogus* collected in the 1920s (Lazell, 1972), an excavation at Center Cave (Pregill et al., 1994) yielded two size classes of anoles, corresponding to *A. pogus* and *A. gingivinus*. Thus, *A. pogus* likely had a restricted range on the Anguilla bank even in prehistoric times.

A restricted range for *A. pogus* has important ramifications for the evolution of body size in its congener *A. gingivinus*, the more widespread Anguilla bank anole. Throughout the Lesser Antilles, co-occurring *Anolis* spp. exhibit character displacement, diverging in body size away from the medium size of species living alone on islands (66 mm; henceforth referred to as solitary lizards; Losos, 1990; Roughgarden, 1995). There are two notable exceptions to this phenomenon: *A. gingivinus* has a medium size (63 mm) despite overlapping with *A. pogus* on St. Martin, and *A. ferreus* is exceptionally large (male SVL = 119 mm) despite being a solitary lizard on Marie-Galante. *A. ferreus* exhibits significant sexual size dimorphism that is in line with the body-size distributions found on islands with two species of *Anolis* lizards (female SVL = 65 mm; Roughgarden, 1995). *A. gingivinus*, on the other hand, may maintain a medium size throughout its range because effectively, it is a solitary lizard due to the restricted range of *A. pogus* on the Anguilla bank, and *A. gingivinus* has functioned as a solitary lizard for much of its evolutionary history.

The only known lizard extinction on Anguilla is that of *Leiocephalus*. *Leiocephalus* was extirpated throughout the Lesser Antilles during the Holocene; in addition to Anguilla, it occurred on at least Barbuda, Antigua, Martinique, and Guadeloupe (Pregill, 1992). Only three species, *L. cuneus*, *Leiocephalus herminieri*, and *Leiocephalus major*, have been described for the Lesser Antilles, but given the high endemism of *Leiocephalus* elsewhere in the Caribbean (Pregill, 1992), and the high endemism of lizards more broadly in the Lesser Antilles, the Anguillan samples probably represent an as yet undescribed species. Further sampling of the fossil record, or genetic identification of the fossil material, is necessary to more fully understand the systematics and distribution of *Leiocephalus* on Anguilla and elsewhere in the Caribbean.

How long *Leiocephalus* persisted on Anguilla is unclear. The last occurrence of it at Katouche Bay predates the earliest human communities on the island (Carder et al., 2007), suggesting that its extinction was caused by non-anthropogenic impacts. However, because *Leiocephalus* fossils are rare at all stratigraphic levels where it occurs, it is impossible to infer the actual last occurrence date with precise certainty. Another excavation on Anguilla yielded materials of *Leiocephalus* material associated with bones of *Rattus*, indicating that the genus persisted well into historic times, although this association could be due to the bioturbation of sediment by land crabs, which is common at Caribbean paleontological and archeological sites. Alcohol-preserved specimens of *L. herminieri* exist for Martinique and Guadeloupe, but the species disappeared shortly after those specimens were collected.

The extinction of *Leiocephalus*, a genus known to prey on other lizards, including anoles (Schoener et al., 1982), may have come as an opportunity for other lizard species to undergo population expansion. Ecological studies reveal that anoles attain higher population densities in the absence of *Leiocephalus* (Schoener et al., 2002) and adapt their perch height in its presence (Losos et al., 2004). The increased relative abundance of *Anolis* starting at 7000 yr could be a signal of ecological release in the fossil record, although it is difficult to say with confidence due to the limited number of stratigraphic levels containing *Leiocephalus*. Yet the high densities that anoles reach in the Lesser Antilles, as high as 32,867/ha on St. Vincent (Hite et al., 2008), could be a recent phenomenon catalyzed by extinction events, synonymous to the removal of keystone species at ecological and geological timescales (Paine, 1969; Sallan et al., 2011).

The largest fossils of *A. cf. gingivinus* (80 mm) are larger than the largest *A. gingivinus* ever collected in the field (72 mm), consistent with Pregill's (1986) evaluation of dwarfism in Holocene insular lizards. However, our findings throughout the Holocene are not indicative of a persistent trend in dwarfism, and the disparity between the fossil data

and modern data is likely due to under-sampling of body size in extant *A. gingivinus*. The increased body size of *A. cf. gingivinus* could indicate a change in the population's age structure in the absence of *Leiocephalus* because anoles are indeterminate growers, so the removal of predators would allow individuals to live longer and thus grow larger. Overall, given the high abundance of *A. cf. gingivinus* throughout the unit and the increased body size, our study indicates that any detrimental impacts of ancient environmental perturbations on *A. gingivinus* were short-lived, if any occurred at all.

Conclusion

The prehistoric Katouche Bay lizard assemblage was more diverse than previous studies concluded and is in accordance with other paleontological studies from the Caribbean, which indicate range contraction for a host of taxa, including but not limited to *Leiocephalus* (Pregill and Olson, 1981). The community structure was irrevocably altered following the extinction of *Leiocephalus*, and other communities throughout the Caribbean likely underwent similar shifts in richness, evenness, and turnover. Despite a rise in relative abundance, we find no evidence of dwarfism or extirpation within *Anolis* at Katouche Bay; in contrast to previous studies, we find that at Katouche Bay, *A. gingivinus* persisted alone throughout the Holocene.

As global change renders more species vulnerable to extinction, the Katouche Bay site shows that some genera, such as *Anolis*, are resilient to environmental perturbations, and may even benefit from these pressures. On the other hand, large-bodied lizards like *Leiocephalus* have a record of extinction following climatic change and human occupation of their native lands. Although pinpointing the causes of the decline of *Leiocephalus* is out of the scope of this paper, we identify this group—and similar large, top-consumer, ground-dwelling lizards—as potential casualties to future global change forces, if the Katouche Bay site is to be treated as a premonition of what is to come.

Acknowledgments

We thank ZiXiang Zhang for assistance in sorting and measuring skeletal material of *Anolis* from Anguilla. We thank the Smithsonian National Museum of Natural History for loaning comparative specimens of *A. pogus* and *A. gingivinus*. The Hadly lab provided invaluable feedback on the research presented in this manuscript at all stages of the project, and we are especially grateful to Hannah K. Frank, Alexis M. Mychajliw, Katie A. Solari, Jeremy Dorn, and two anonymous reviewers for astute commentary on the manuscript. Melissa E. Kemp was supported by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-114747.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.yqres.2015.12.007>.

References

- Bell, C.J., Gauthier, J.A., Bever, G.S., 2010. Covert biases, circularity, and apomorphies: a critical look at the North American Quaternary herpetofaunal stability hypothesis. *Quaternary International* 217, 30–36.
- Blois, J.L., McGuire, J.L., Hadly, E.A., 2010. Small mammal diversity loss in response to late-Pleistocene climatic change. *Nature* 465, 771–U775.
- Bochaton, C., Grouard, S., Cornette, R., Ineich, I., Lenoble, A., Tresset, A., Bailon, S., 2015. Fossil and subfossil herpetofauna from Cadet 2 Cave (Marie-Galante, Guadeloupe Islands, F. W. I.): evolution of an insular herpetofauna since the Late Pleistocene. *Comptes Rendus Palevol* 14, 101–110.
- Carder, N., Reitz, E.J., Crock, J.G., 2007. Fish communities and populations during the post-Saladoid period (AD 600/800–1500), Anguilla, Lesser Antilles. *Journal of Archaeological Science* 34, 588–599.
- Cox, P.A., Elmqvist, T., 2000. Pollinator extinction in the Pacific Islands. *Conservation Biology* 14, 1237–1239.
- Daza, J.D., Bauer, A.M., Snively, E.D., 2014. On the Fossil Record of the Gekkota. The anatomical recorder: advances in integrative anatomy and evolutionary biology 297, 433–462.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345, 401–406.
- Etheridge, R., 1964. Late Pleistocene lizards from Barbuda, British West Indies. *Bulletin of the Florida State Museum Biological Sciences* 9, 43–75.
- Fay, L.P., 1988. Late Wisconsinan Appalachian herpetofaunas: relative stability in the midst of change. *Annals of Carnegie Museum* 57, 189–220.
- Grayson, D.K., 1973. Methodology of faunal analysis. *American Antiquity* 38, 432–439.
- Hite, J.L., Gomez, C.A.R., Larimer, S.C., Diaz-Lameiro, A.M., Powell, R., 2008. Anoles of St. Vincent (Squamata: Polychrotidae): population densities and structural habitat use. *Caribbean Journal of Science* 44, 102–115.
- Holman, J.A., 1991. North American Pleistocene herpetofaunal stability and its impact on the interpretation of recent faunas, a synthesis. In: Purdue, J.R., Klippel, W.E., Styles, B.W. (Eds.), *Beamers, Bobwhites, and Bluepoints: Tributes to the Career of Paul W. Parmalee* vol. 23. Illinois State Museum Scientific Papers, pp. 227–235.
- Koch, P.L., Barnosky, A.D., 2006. Late quaternary extinctions: state of the debate. *Annual Review of Ecology, Evolution, and Systematics* 215–250.
- Koehler, G., Vesely, M., 2011. A new species of *Thecadactylus* from Sint Maarten, Lesser Antilles (Reptilia, Squamata, Gekkonidae). *Zookeys* 97–107.
- Lazell, J.D.J., 1972. The anoles (Sauria, Iguanidae) of the Lesser Antilles. *Bulletin of the Museum of Comparative Zoology* 143, 1–115.
- Losos, J.B., 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. *Evolution* 44, 558–569.
- Losos, J.B., 2009. Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. Losos, J.B., Schoener, T.W., Spiller, D.A., 2004. Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. *Nature* 432, 505–508.
- McFarlane, D.A., MacPhee, R.D.E., Ford, D.C., 1998. Body size variability and a Sangamonian extinction model for *Amblyrhiza*, a West Indian megafaunal rodent. *Quaternary Research* 50, 80–89.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. (R package version 2.2-1) Community ecology package, Vegan <http://cran.r-project.org/package=vegan>.
- Paine, R.T., 1966. Food web complexity and species diversity. *American Naturalist* 100, 65 (+).
- Paine, R.T., 1969. A note on trophic complexity and community stability. *American Naturalist* 103, 91 (–&).
- Powell, R., 2004. Conservation of iguanas (*Iguana delicatissima* and *I. iguana*) in the Lesser Antilles. *Iguana* 11, 238–246.
- Pregill, G., 1981. Late Pleistocene Herpetofaunas From Puerto Rico. University of Kansas Museum of Natural History, pp. 1–72.
- Pregill, G., 1986. Body size of insular lizards – a pattern of Holocene dwarfism. *Evolution* 40, 997–1008.
- Pregill, G.K., 1992. Systematics of the West Indian Lizard Genus *Leiocephalus* (Squamata: Iguania: Tropiduridae). University of Kansas Museum of Natural History, pp. 1–69.
- Pregill, G.K., Olson, S.L., 1981. Zoogeography of West-Indian vertebrates in relation to Pleistocene climatic cycles. *Annual Review of Ecology and Systematics* 12, 75–98.
- Pregill, G.K., Steadman, D.W., Watters, D.R., 1994. Late Quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. *Bulletin of Carnegie Museum of Natural History* 30, 1–51.
- R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (URL <http://www.R-project.org/>).
- Reed, F.A., Kontanis, E.J., Kennedy, K.A.R., Aquadro, C.F., 2003. Brief communication: ancient DNA prospects from Sri Lankan highland dry caves support an emerging global pattern. *American Journal of Physical Anthropology* 121, 112–116.
- Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatte, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. INTCAL13 AND MARINE13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55, 1869–1887.
- Roughgarden, J., Pacala, S., 1989. Taxon cycle among *Anolis* lizard populations: review of evidence. In: Otte, D., Endler, J.A. (Eds.), *Speciation and its Consequences*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Roughgarden, J., 1995. *Anolis Lizards of the Caribbean: Ecology, Evolution, and Plate Tectonics*.
- Sallan, L.C., Kammer, T.W., Ausich, W.I., Cook, L.A., 2011. Persistent predator–prey dynamics revealed by mass extinction. *Proceedings of the National Academy of Sciences of the United States of America* 108, 8335–8338.
- Säterberg, T., Sellman, S., Ebenman, B., 2013. High frequency of functional extinctions in ecological networks. *Nature* 499, 468 (+).
- Schoener, T.W., Slade, J.B., Stinson, C.H., 1982. Diet and sexual dimorphism in the very catholic lizard genus, *Leiocephalus* of the Bahamas. *Oecologia* 53, 160–169.
- Schoener, T.W., Spiller, D.A., Losos, J.B., 2002. Predation on a common *Anolis* lizard: can the food-web effects of a devastating predator be reversed? *Ecological Monographs* 72 (3), 383–407.
- Simpson, G.L., 2007. Analogue methods in palaeoecology: using the analogue package. *Journal of Statistical Software* 22, 1–29.
- Simpson, G.L., Oksanen, J., 2013. Analogue: analogue matching and Modern Analogue Technique transfer function models (R package version 0.12-0). <http://cran.r-project.org/package=analogue>.
- Stuiver, M., Reimer, P.J., Reimer, R.W., 2005. CALIB 5.0. [program and documentation]. <http://calib.qub.ac.uk/calib/>.
- Wittebolle, L., Marzorati, M., Clement, L., Balloi, A., Daffonchio, D., Heylen, K., De Vos, P., Verstraete, W., Boon, N., 2009. Initial community evenness favours functionality under selective stress. *Nature* 458, 623–626.