# Defaunation and species introductions alter long-term functional trait diversity in insular reptiles

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Biodiversity loss poses a major threat to ecosystem function, which has already been severely impacted by global late-Quaternary defaunation. The loss of mammalian mega-fauna from many insular systems has rendered reptiles into key modulators of many ecosystem services, such as seed dispersal and pollination. How late-Quaternary extinction events impacted reptile functional diversity remains unclear but can provide critical guidance on traits that render reptiles vulnerable to extinction, as well as anthropogenic, environmental, and evolutionary histories that may promote stability and resilience. This study reconstructs the trajectory of functional diversity change in the Caribbean reptile fauna, a speciose biota distributed over a diverse set of islands with heterogeneous histories of human habitation and exploitation. Human-induced Quaternary extinctions have completely removed key functional entities (FEs)—groupings of species with similar traits that are expected to provide similar ecosystem services—from the region, but functional redundancy on large islands served as a buffer to major functional diversity loss. Small islands, on the other hand, lose up to 67% of their native FEs with only a few exceptions, underscoring the importance of a place's anthropogenic history in shaping present-day biodiversity. While functional redundancy has shielded ecosystems from significant functional diversity loss in the past, it is being eroded and not replenished by species introductions, leaving many native FEs and the communities that they support vulnerable to extinction and functional collapse. This research provides critical data on long-term functional diversity loss for a taxonomic group whose contributions to ecosystem function are understudied and undervalued.

reptiles | functional diversity | Quaternary | Caribbean | extinctions

Biodiversity loss is one of the biggest challenges facing humanity today, threatening many known and unknown ecosystem services that we depend upon, such as food production, pest control, and nutrient cycling (1). There is an urgent need to quantify recent biodiversity loss, characterize existing biodiversity, and determine how species and ecosystems will be impacted by ongoing and future global change. Species richness has been the principal metric for measuring biodiversity, but species richness does not consider the functional capabilities of species within an ecosystem, which may be a better proxy for ecosystem health. Two ecosystems with the same species richness may have very different levels of functional diversity and support disparate ecosystem services, rendering one ecosystem stable, whereas the other could be on the brink of collapse. By emphasizing function over species, trait-based approaches allow for studies of biodiversity to occur over temporal and spatial scales where there is species turnover but continuity in functional traits, and functional diversity studies may draw attention to important organisms that are often overlooked in species-based approaches.

Reptiles are one such group that play important, albeit understudied, roles in ecosystem function, including seed dispersal, pollination, ecosystem engineering (2–4), and nutrient cycling (5). Whereas mammals and birds are widely recognized as important pollinators and seed dispersers, turtles and lizards also contribute to these services. Seed dispersal services provided by tortoises are well documented, as are giant tortoise-plant mutualisms in insular settings (6). Like giant tortoises, most lizards pass intact seeds, and experimental studies show a high rate of enhanced seed germination (25%) after gut passage, a number comparable to studies in birds, nonvolant mammals, and bats (7). According to (7), roughly 7% of lizards incorporate fleshy fruits into their diet, although this number may be an underestimate due to limited dietary studies, limited reporting on diet components, and prevailing narratives that lizards are largely (and often exclusively) carnivorous.

Compared to other terrestrial vertebrates, reptiles lack comprehensive studies of functional diversity and functional diversity loss, which would be helpful in determining the role that reptiles have played in ecosystems past and present. Given widespread

## Significance

Reptiles serve a host of ecological functions, but how functional diversity has changed through time remains unclear. Here, functional diversity in Caribbean reptiles is quantified using functional entities (FEs): groupings of species with similar traits that are expected to provide similar ecosystem services. Quaternary extinctions erode the number of FEs most severely on small islands, which lose up to 67% of their native FEs. While species introductions restore functional richness on small islands, lost FEs are not being replaced by species introductions, which are shifting Caribbean biotas into novel functional trait space and leaving native FEs vulnerable to further loss. This study highlights the importance of investigating functional diversity in reptile faunas, which remain understudied relative to other vertebrate taxa.

Pleistocene extinctions of mammalian megafauna that are often associated with the aforementioned ecosystem services, extant reptiles play an outsized role in modulating ecosystems. Megafaunal extinctions have left many plants involved in vertebrate-plant mutualisms widowed, though the extent to which megafaunal extinctions have led to extinction cascades in plant communities has not been fully quantified because plant-reptile mutualisms have not been adequately explored. A recent study found that reptile species richness was an important predictor for the distribution of zoochoric plants in the Caribbean (8). Globally, at least 1.1% of all angiosperm species are at risk for losing their vertebrate mutualist partners, and in insular settings like the Caribbean, the risk is even higher (9). Studies dating back to the Paleogene show large-bodied reptiles occupying trophic space traditionally associated with mammals (10), and in many insular systems, particularly oceanic islands like the Galapagos, reptiles have always been the largest native herbivores. The cascading effects of reptile extinctions go well beyond that of plant-reptile mutualisms, however, and other species such as scavengers and predators were also likely impacted by these losses (11).

Quaternary reptile extinctions are thought of as less extensive than extinctions in other taxonomic groups, and while many species did persist through the Pleistocene-Holocene transition, emerging datasets indicate nonrandom and at times extensive biodiversity loss (12–14). Several challenges hinder the long-term quantification of biodiversity loss in reptiles. Reptile biodiversity peaks in the tropics, which are more inhospitable to fossil preservation than temperate regions (15). But regardless of geographic focus, research programs in Quaternary vertebrate paleontology have historically emphasized mammals and large-bodied organisms; at worst this has resulted in excavation and sediment screening processes that bias results toward larger fossils and particular taxa, and at best nonmammalian taxa are put aside for future study by specialists.

The Caribbean serves as an exceptional system to query reptile functional diversity through time. A wealth of zooarchaeological and paleontological data exists with which researchers have characterized ancient biodiversity, extinction patterns, and species introductions throughout the Bahamas, Greater Antilles, and Lesser Antilles. It is also an epicenter for ecological, behavioral, and evolutionary biology studies on extant reptiles. Detailed reptile occurrence data exists for many of the islands (16), and decades of natural history research has yielded extensive trait data for extant taxa (17). The many islands of the Caribbean also serve as natural replicates to test hypotheses about the relationship between island area and functional diversity, and the heterogeneous, long-term history of humans across the landscape provides critical information on the role that humans have played in modulating functional diversity over long time scales and different land-use strategies.

Here, Caribbean reptile communities are disaggregated into their ancient, extant native, and modern (extant native plus introduced) components to answer the question: how has functional diversity changed over the Quaternary? Functional entities (FEs), which are multivariate groups of species that share the same trait values, are especially useful for quantifying functional diversity in species-rich systems like the Caribbean reptile fauna. Large FEs indicate that many species within an ecosystem share a suite of functional traits, meaning that they might fill similar ecological roles. It is expected that FE redundancy, the mean number of species per FE, and FE richness, the number of FEs within an assemblage, will be higher on large, species-rich islands because on large islands in situ diversification plays a larger role in building species richness than

colonization, and closely related species are likely to have similar functional traits. Additionally, functional diversity, measured as FE richness and functional richness (the proportion of functional trait space that an assemblage occupies), is hypothesized to decrease over the Quaternary. To date, the extent to which Quaternary extinction and extirpation events have led to FE loss remains unknown, although functional redundancy may buffer ecosystems from the detrimental impacts of extinction, and large reserves of functional redundancy may facilitate an ecosystem's adaptive capabilities. Additionally, species introductions might restore FE richness and functional richness to prehistoric levels or shift the functional trait space entirely (18). Through quantifying functional diversity through time, the interplay of island size, anthropogenic impact, and species introductions is investigated, and features that may promote community stability and resiliency—as well as traits that are most vulnerable to impending changes—are identified.

## Results and Discussion

Functional diversity through time was reconstructed for seventeen islands in the Caribbean that have published paleontological records of reptiles and/or historical records of reptile extinctions. These islands encompass a large proportion of Caribbean reptile species richness, with 418 species that are distributed across 123 FEs. The number of species per FE is right-skewed, indicating that there are many FEs with few species (Fig. 1A). Such FE distributions are indicative of faunas with high extinction vulnerabilities because many functions are only supported by one species (19). Across all temporal bins, island area is positively correlated with both FE richness and species richness (Fig. 1B), though species richness increases at a faster rate than FE richness increases, signifying that species are packing into existing FEs instead of partitioning into new FEs. Functional redundancy, the state of having more than one species in a FE, is highest on the large islands of the Greater Antilles, which is also where many of the in situ evolutionary radiations of reptiles occurred (20). Functional redundancy peaks in Cuba, the largest island in the Caribbean (105,806 km$^2$), where there are on average 2.67 species per FE in the ancient assemblage compared to on average 1.2 species per FE in the ancient assemblage of Grande-Terre (590 km$^2$), one of the larger islands in the Lesser Antilles archipelago. High levels of functional redundancy may buffer functional diversity loss because it signals that multiple species are present to fill an ecological role in the event of one species' extinction, though if extinction is nonrandom and selecting against a particular suite of traits, an entire FE could be eliminated. Some islands (7 of 17) never have functional redundancy, and for places that do, functional redundancy exhibits a trend of decreasing through time, either due to the extinction of species within an FE, the introduction of FEs composed of one species (henceforth referred to as singleton FEs), or a combination of these dynamics. The extinction of native species, particularly if the species is a singleton FE or the sole representative of an FE on an island, may drive an increase in functional redundancy for native, extant assemblages, as is the case for Culebra, which lost its only crown-giant anole, *Anolis roosevelti*, in the early 20th century (17). Functional redundancy in the Lesser Antilles is limited to the ancient assemblages of Antigua, Barbuda, Marie-Galante, and Grande-Terre, which eventually lose all functional redundancy.

Throughout the region, 32 FEs have been impacted by extinction or extirpation events (Fig. 2). While nine of these FEs represent FE singletons, two larger FEs (containing 3 and 6 species
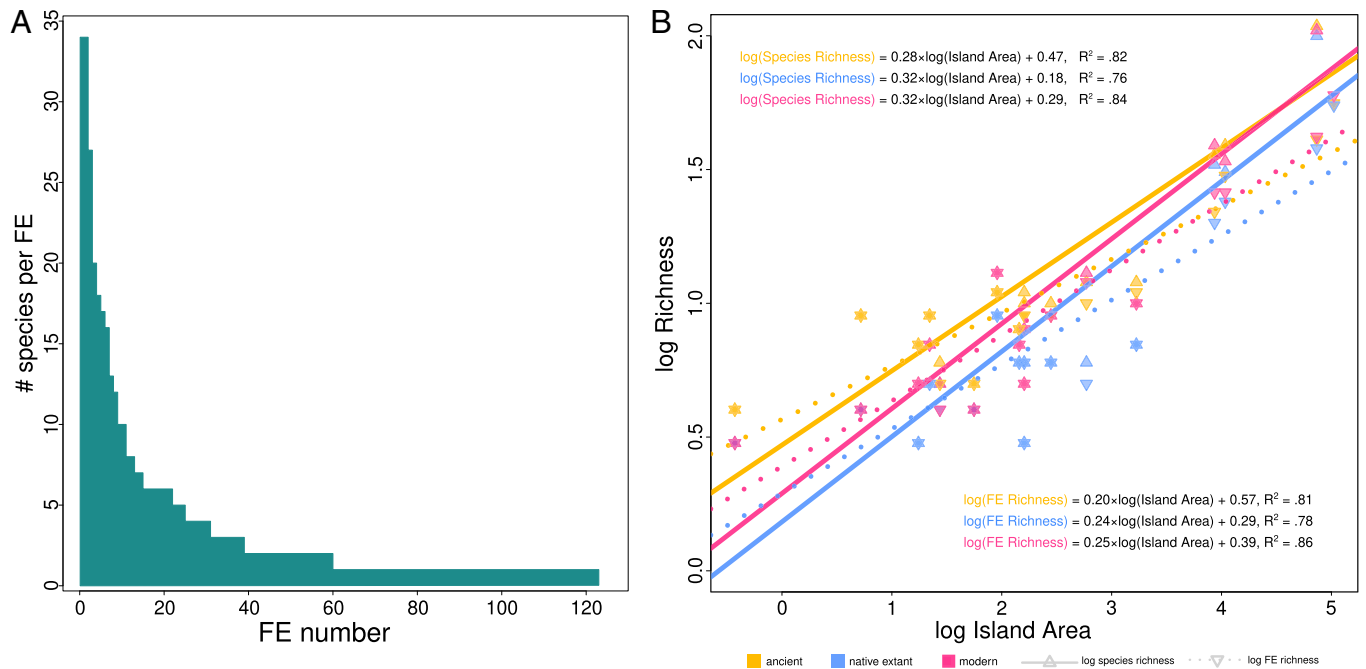
**Fig. 1.** FEs and FE Richness of Caribbean Reptiles. (*A*) The distribution of Caribbean reptiles into FEs. (*B*) log-log plots of island area versus FE richness (dotted lines) and island area versus species richness (solid lines) for ancient (orange), native extant (blue), and modern (pink) Caribbean reptile assemblages. Linear regressions for FE richness and species richness, along with the adjusted $R^2$ value, are plotted for each assemblage type. All regressions are highly significant ($P < 0.001$).

each) composed of giant tortoises are lost completely. These two FEs represent the largest herbivorous reptiles that ever existed in the Caribbean (ranging between 9 kg and 135 kg estimated body mass). Nonsingleton FEs impacted by extinction lost on average 2.4 species, or 35% of the FE. While not extinct, several of the FEs containing large-bodied, terrestrial, herbivorous iguanas

(*Cyclura* sp. and *Iguana delicatissima)* have been extirpated from islands where they previously occurred.

Functional richness scales with island area similar to FE richness and species richness (*SI Appendix*, Fig. S1) but significant losses in native functional richness are only seen on small islands (<2,000 km²) (Fig. 3) where on average 5.4% of an island's
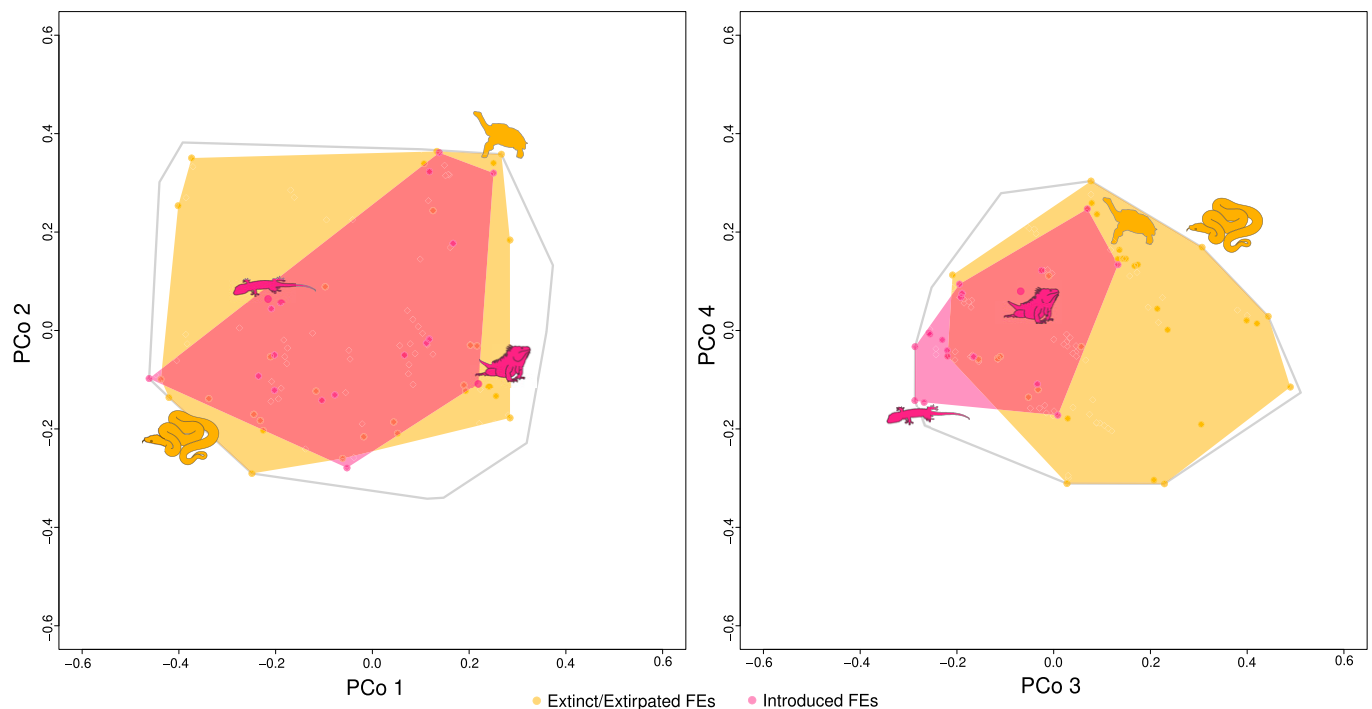


**Fig. 2.** Extinct, Extirpated, and Introduced FEs in global functional trait space. The global functional trait space of 418 species (123 FEs) is represented by the gray outline and plotted along the first four PCo axes from a PCo analysis. The orange convex hulls represent the 4D volume of functional trait space (functional richness) occupied by FEs that have undergone extinction and/or extirpation, whereas the pink convex hulls represent the 4D volume of FEs that have been introduced. Circles represent the individual FEs of each type in the global functional trait space. The introduced FEs are significantly different from the extinct/extirpated ones along PCo axis 3 (Mann-Whitney *u* test, $P < 0.001$). The relative positions of several key introduced (e.g., *Iguana iguana* and *Gecko gecko)* and extinct (e.g., *Chelonoidis* sp. and *Boa* sp.) reptiles are denoted with images from phylopic (http://www.phylopic.org).
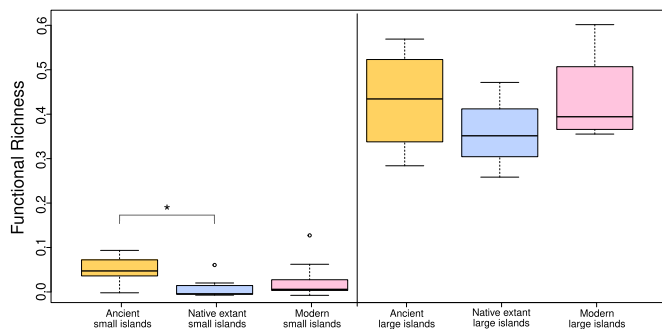
**Fig. 3.** Differential loss of native functional richness on small islands. The three barplots on the left represent functional richness values of ancient, native extant, and modern assemblages for islands with an area less than 2,000 km². The three barplots on the right represent functional richness values of ancient, native extant, and modern assemblages for islands with an area greater than 2,000 km². Mann-Whitney $u$ tests were used to compare functional richness across ancient, native extant, and modern assemblages in each size bin. "*" indicates $P < 0.05$.

functional richness is lost. However, there is no difference between native and modern richness for these islands, indicating that species introductions may have restored some of the functional diversity lost through extinction. However, a comparison of functional trait space for all extinct/extirpated FEs and for all introduced FEs shows that introduced FEs do not occupy the breadth of functional trait space occupied by extinct/extirpated FEs and are shifting Caribbean communities into novel trait space (Fig. 2). Introduced FEs occupy a mere 11% of the global functional trait space, whereas extinct/extirpated FEs occupy 64% of the global functional trait space. Instead of filling existing FEs that have been depleted, the majority of introduced species are FE singletons (67%). Introduced species are putting FEs on islands where they did not exist previously (11 instances spread across 5 FEs) or adding new FEs to the regional pool (35 instances spread across 13 FEs). Some of these introduced FEs, such as that of the green iguana (*Iguana iguana*), cluster in trait space with several FEs containing large-bodied herbivorous native iguanas that have undergone extinction or extirpation, suggesting that there is some similarity between a few introduced and native FEs. Introduced FEs that cluster in functional trait space with native FEs may provide similar ecological functions as native FEs, thereby serving as another buffer against functional diversity loss. However, the fact that several introduced FEs are outside of the functional trait space occupied by both extinct and extant native FEs for both the entire Caribbean region and for individual islands (*SI Appendix*, Fig. S2) and that a small number of introduced FEs are spreading across multiple islands where they did not exist previously supports the notion that species introductions are restructuring biological communities and contributing to the biotic homogenization of the Caribbean (21).

Small islands (< 2,000 km²) also lose a greater percentage of their native FEs than large islands: Cuba, Jamaica, Hispaniola, and Puerto Rico retain between 80–98% of their native FEs (Fig. 4). This result is not surprising as larger islands have some degree of functional redundancy within FEs in addition to more FEs. Four small, relatively isolated islands—which vary from being sparsely populated (Culebra and Middle Caicos) to uninhabited (Mona and Sombrero)—retain at least 75% of their native FEs. These islands provide evidence that the intensity of long-term anthropogenic impacts can lead to different biodiversity outcomes. Mona has a long-term history of human activity dating to at least 5,000 ybp, and its position in the Anegada passage between Hispaniola and Puerto Rico rendered it a historical nexus for trade and migration. Pre-Columbian Indigenous

people utilized both inland and coastal resources on the island, but after European colonization, exploitation shifted toward the coasts and the extensive cave networks where phosphate mining occurred until the early 20th century (22). Sombrero, which also sits at a biogeographical and trading crossroads, was extensively mined for guano until the late 19th century. Culebra was also an important trading post during colonial times. For much of their colonial and modern history, Culebra, Sombrero, and Mona have had sex- and age-biased human populations that lacked women and children due to the type of human activity being supported (piracy, mining, fishing, and military exercises) (22). These population structures are common on small islands around the world, and while the extractive activities that coincide with these occupation types can have negative impacts on biodiversity, these islands are typically spared from large-scale agriculture and deforestation for long-term settlements and sustenance. The lack of dense human populations and agricultural development for at least the past 400 years also means that several invasive species that have had negative impacts on reptiles elsewhere, such as the mongoose, were never introduced to these islands.

Marie-Galante has had the most extensive FE loss, with only 33% of its native FEs remaining. Marie-Galante and other islands in the Guadeloupe archipelago (Grande-Terre and La Desirade) have undergone several extensive excavations in recent years which have yielded detailed systematic paleontological accounts of the ancient herpetofauna (23–25). These studies reveal that ancient reptile assemblages were much more diverse than present-day assemblages indicate, and diversity declines coincide with European colonization (14). While the Caribbean has more detailed paleoherpetological accounts than many other tropical insular systems, the records of many islands warrant revisiting with a specific focus on reptile fossils, as many of the earliest described sites were preferentially excavated for mammals. Small island size and low habitat diversity certainly constrain species richness (26), but emerging datasets from Guadeloupe and elsewhere support the notion that ancient biodiversity has not been fully quantified. Several taxa exhibit disjunct distributions: *Boa* fossils have been found in both zooarchaeological and paleontological contexts throughout Guadeloupe, except on the island of Grande-Terre, even though Grande-Terre formed a continuous landmass with neighboring islands in Guadeloupe during the Pleistocene and is therefore expected to have had a species of *Boa* (14). Up until recently when fossil *Diploglossus* were discovered on Grande-Terre (27),
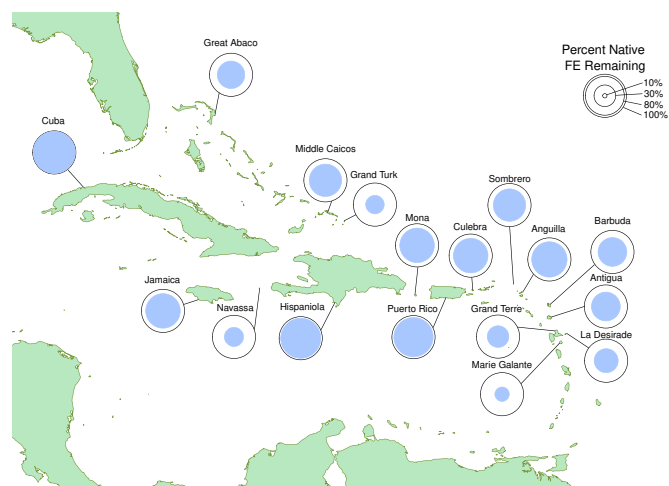


**Fig. 4.** Percentages of remaining native FEs across Caribbean islands. The inner blue circle represents the proportion of FEs that have not been lost during the late Quaternary.

the only anguid lizard known from the Lesser Antilles was *Diploglossus montiserati*, a species endemic to the small volcanic island of Montserrat which is about 90 km north of Grande-Terre. Sombrero is the only island in the Lesser Antilles known to have had a giant tortoise (*Chelonoidis sombrerensis*). Sombrero is in the northernmost Lesser Antilles near the Greater Antilles, so *C. sombrerensis* may represent the westernmost range of the *Cheolonoidis* radiation, but Anguilla did support one of the largest rodents ever described, *Amblyrhiza inundata* [∼200 kg (28)], indicating that these islands could support large-bodied herbivores, though maybe not multiple species as was the case in the Greater Antilles. Regardless, if currently available paleontological data are but a small subset of ancient biodiversity, we are likely underestimating ancient FE richness, and other islands may have lost a larger percentage of their native FEs than current data indicate.

Functional redundancy buffers functional diversity loss on large islands, as most extinctions on these islands pull from FEs with multiple species. As functional redundancy continues to be eroded, however, we will see more drastic changes in functional diversity, as FEs are being drained of taxa without being refilled. Indeed, this study reveals shifts in functional trait space occupancy and a consistent, ongoing loss of FEs that are associated with important ecological services (e.g., seed dispersal by large-bodied herbivores and frugivores) that already have a precarious fate due to Quaternary extinctions in other taxonomic groups. Insular reptiles serve as one of the last remaining reservoirs of large-bodied herbivores, and after insular mammals, insular lizards have the highest percentage of threatened seed dispersers, meaning that seed dispersal and pollination services may be further interrupted by biodiversity loss (9). While several FEs containing large-bodied herbivorous lizards still exist in the Caribbean, species within them are critically endangered and have experienced severe range contraction, rendering these FEs highly vulnerable to extinction. The contributions of reptiles to other ecological processes are still being uncovered, meaning that we may lose integral ecosystem services before they are quantified.

The replicate nature of biological communities within the Caribbean and the region's complex, heterogeneous history of human habitation also allows for key insights into land-use histories that have fostered stability and resiliency. Several culturally peripheral islands with small, demographically biased human populations retain a large proportion of native FEs even when surrounding islands of similar size do not, underscoring the role of anthropogenic processes in the erosion of functional diversity. Satellite islands like the ones identified in this study serve as important reservoirs of functional diversity that we can draw upon to restore FEs and associated ecosystem function in places where it would be most beneficial (29). Integrating paleontological data into long-term studies of functional diversity for species-rich biological communities is critical for assessing the trajectory of functional diversity in rapidly changing environments.

## Materials and Methods

**Presence-Absence and Trait Data.** A database of extinct Caribbean reptiles was created using literature sources (12–14). Fossil taxa that are described in reference to another taxa (e.g., *Cyclura cf carinata*) were coded as the referenced taxa. These reptiles are distributed across 17 islands, and present-day reptile species lists were compiled for each of these islands (16). Three presence/absence matrices were made for nonmarine reptiles of each island (henceforth referred to as assemblages): an ancient biodiversity matrix (including extinct and native extant species), a native extant biodiversity matrix (including only native extant species), and a modern biodiversity matrix (including native extant species and

introduced species). These matrices deconstruct biodiversity into three distinct time bins that do not necessarily correspond to species diversity at an actual time-point, but instead reflect the accumulation of species extinction and colonization events, as detailed chronologies for reptile species extinctions and introductions are not readily available (21). Trait data (diet, habitat affinity, foraging mode, reproductive mode, activity time, and body mass) were collected for each species using existing datasets (9, 17, 30, 31) and the paleontological literature [e.g., (24, 32–34)]. For most taxa, the habitat affinity of each species was categorized as follows: Aquatic, Semi-Aquatic, Arboreal, Semi-Arboreal, and Terrestrial. However, in recognition of the great habitat affinities exhibited by *Anolis* lizards, *Anolis* lizards were categorized as ecomorphs when applicable (e.g., Crown-Giant, Grass-Bush, Trunk, Trunk-Crown, Trunk-Ground, and Twig). Diet was categorized as Frugivorous, Herbivorous, Insectivorous, or Omnivorous. Foraging mode was categorized as Active, Mixed, or Sit-and-Wait. Reproductive mode was categorized as either viviparous or oviparous. Body mass was estimated using allometric scaling relationships reported in (13, 35), which are based on snout vent length. To enable the grouping of species into FEs, body mass data were put into six ordinated size bins of increasing size: less than 1 g, 1–10 g, 10–1 kg, 1– 5 kg, 5–45 kg, and greater than 45 kg. Body size data were $\log_{10}$ transformed prior to analysis. The trait database can be found in Dataset S1.

Missing trait data were imputed using the missForest package in R (36). To perform the trait imputation in a phylogenetic framework, species in our dataset not present in the Pyron et al. phylogeny (37) were randomly added to the root of their genus. Then, the first ten phylogenetic eigenvectors were added to the trait matrix for imputation, and each trait was weighted equally.

**FE Analyses.** Species were grouped into FEs using the function *mFD::sp.to.fe* in the R package mFD (38). This function computes FEs from a species × trait matrix, putting species that share the same suite of traits into a single FE. The 418 species were collapsed into 123 FEs varying in size from 34 species to 1 species. Three metrics based on FEs were calculated for all assemblages: FE richness, functional redundancy, and functional vulnerability. FE richness is a measure of the number of FEs in an assemblage, and functional redundancy is the average number of species per FE in an assemblage. Functional vulnerability is the proportion of FE singletons in an assemblage.

**Functional Richness Analyses.** Pairwise, trait-based distances between FEs were calculated using the Gower distance metric, which allows for both continuous and discrete traits. These pairwise functional distances were used to compute Principal Coordinates (PCo) and build a Euclidean functional space. Because the number of PCo axes may influence functional diversity metrics (39), the "best" functional trait space can be determined by measuring the quality of functional spaces, a method proposed by Maire et al. (40) that finds the number of axes with the lowest deviation between the original trait-based distances and the final Euclidian functional space distances. The first four PCos were found to define the best functional trait space, and these four PCos are used in subsequent analyses.

Functional richness, the proportion of the total possible functional space that an assemblage occupies, was calculated for assemblages with more than 4 FEs, as the number of FEs within an assemblage must be higher than the number of PCo axes. Functional richness was visualized as convex hulls in the functional trait space, and changes in functional richness were quantified across temporal and spatial scales by comparing functional richness values (the hypervolumes for the different convex hulls) for different time bins (e.g., Ancient versus Extant Native, Ancient versus modern, and Extant Native versus modern) across the whole region, as well as across specific archipelagos within the Caribbean (e.g., Greater Antilles, Bahamas, and Lesser Antilles), and separately for large (>2,000 km$^2$) and small islands. All analyses were conducted in R version 4.1.2 (41).

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