Symposium

Assembly, Persistence, and Disassembly Dynamics of Quaternary Caribbean Frugivore Communities*

Melissa E. Kemp[†]

Department of Integrative Biology, University of Texas at Austin, Austin, Texas 78712

Submitted July 16, 2023; Accepted April 2, 2024; Electronically published September 4, 2024

abstract: How communities assemble and restructure is of critical importance to ecological theory, evolutionary theory, and conservation, but long-term perspectives on the patterns and processes of community assembly are rarely integrated into traditional community ecology, and the utility of communities as an ecological concept has been repeatedly questioned in part because of a lack of temporal perspective. Through a synthesis of paleontological and neontological data, I reconstruct Caribbean frugivore communities over the Quaternary (2.58 million years ago to present). Numerous Caribbean frugivore lineages arise during periods coincident with the global origins of plant-frugivore mutualisms. The persistence of many of these lineages into the Quaternary is indicative of long-term community stability, but an analysis of Quaternary extinctions reveals a nonrandom loss of large-bodied mammalian and reptilian frugivores. Anthropogenic impacts, including human niche construction, underlie the recent reorganization of frugivore communities, setting the stage for continued declines and evolutionary responses in plants that have lost mutualistic partners. These impacts also support ongoing and future introductions of invader complexes: introduced plants and frugivores that further exacerbate native biodiversity loss by interacting more strongly with one another than with native plants or frugivores. This work illustrates the importance of paleontological data and perspectives in conceptualizing ecological communities, which are dynamic and important entities.

Keywords: frugivory, Caribbean, Quaternary, community ecology, human niche construction, plant-animal mutualisms.

Introduction

The community—populations of different species that co-occur spatially and temporally—is often conceptualized as an important level of biological organization, as it is the first level at which we move away from one organism and toward an understanding of how different organisms interact with one another, facilitating higher-level studies of how organisms interact with their abiotic environment. But many have asked, are ecological communities—particularly the interactions of the species within them—biologically meaningful? This is a contentious topic in both neontological and paleontological circles, each of which have different perspectives on communities that are in part shaped by available research methods and limitations in taxonomic, spatial, and temporal scales. Neontologists can observe species interactions in real time and experimentally manipulate communities to characterize the processes underlying community structure and patterns. The lack of generalizable rules in community ecology has been billed as a fatal flaw that warrants abandoning the discipline (Lawton 1999), but others have argued that adherence to general rules is less important than the discipline's ability to shed light on conservation practice, evolutionary theory, and ecological theory (Shrader-Frechette and McCoy 1993; Simberloff 2004). That traditional community ecology is "intensely local in focus" (Lawton 2000, p. 15) is another sticking point, as the local community represents a point in space that is not inclusive of entire populations that are geographically distributed over variable environments (Ricklefs 2008). Finally, the short timescales at which neontology—and, consequently, traditional community ecology—operates begs the question, are observed patterns truly meaningful?

Paleontologists face the challenge of not being able to observe species interactions directly. Instead, they must use patterns in the fossil record to infer interactions and the underlying ecological and evolutionary processes that structure communities. Because of temporal and spatial averaging in the fossil record, paleocommunities are more aptly called assemblages, which are collections of co-occurring species that may or may not interact (Underwood 1986). But paleobiology recognizes that spatial distributions of species are contingent on temporal processes and that a

* This article originated as part of the 2023 Vice Presidential Symposium, which was presented at the annual meetings of the American Society of Naturalists in Albuquerque, New Mexico.

† Email: mkemp@austin.utexas.edu.
ORCIDs: https://orcid.org/0000-0003-0668-3458.

American Naturalist, volume 204, number 4, October 2024. Published by The University of Chicago Press for The American Society of Naturalists. https://doi.org/10.1086/731994

species assemblage at any given time point is the result of spatial distributions and environmental processes. Furthermore, the temporal perspective afforded by the fossil record "reveals patterns and dynamics to which ecologists are otherwise blind" (Jackson and Blois 2015, p. 4916). Paleontology capitalizes on the multitude of community ecology case studies afforded by neontology, bringing temporal depth to singular observations and advancing theory. A major takeaway of paleontological conceptualizations of communities is that they are dynamic; there exists paleontological evidence of communities that persist unchanged for millennia as well as much shorter periods of time, and the extent and nature of biotic change runs the gamut from small abundance shifts to complete turnover. The reoccurrence of no-analogue communities, which are species that co-occur in the past with no modern analogues, suggests that species interactions are ephemeral. Because communities come and go, trait-based approaches to understanding communities and the processes that govern them are highly emphasized in paleobiology; the fact that species are not always a tractable unit of study given issues of taxonomic resolution in the fossil record also motivates trait-based inquiry. Over geologic timescales, functional diversity and the ecological functions provided through taxonomic interactions persist, suggesting that who performs the interaction is less important than the occurrence of the interaction itself (Järvinen et al. 1986). This idea, which analogizes as "different actors, same drama" (Järvinen et al. 1986), is particularly relevant in conservation biology, where conserving ecosystem function may be more urgent and realistic than conserving individual species (Barnosky et al. 2017).

Despite differences, there are commonalities in the conceptualization of ecological communities across intellectual communities. Both neontologists and paleontologists stress the importance of taxonomic interactions and the environment in community assembly (Ricklefs 2008; Jackson and Blois 2015); structure and organization are critical components too. The processes that modulate these tenets of communities are not readily discernible from either intellectual standpoint alone, although a synthesis of perspectives may provide some insight into the small-scale biotic and abiotic processes that establish and shape ecological communities through time and across space. Here I pose the question, what can we infer about the abiotic and biotic processes underlying community structure and assembly dynamics from the fossil record? I turn to Quaternary frugivore communities of the Caribbean for answers.

As species interactions are central to both neontological and paleontological conceptualizations of communities, studying frugivores uniquely positions us to address the stability and strength of species interactions and ecological communities over long timescales. Frugivory is critical for maintaining plant diversity and ecosystem function, particularly in tropical insular systems like the Caribbean (Smith 2001; Moran-Lopez et al. 2018; Villar et al. 2021). Not only do frugivores disperse seeds great distances, but many frugivores have been shown to enhance seed germination (Torres et al. 2020). A recent study of plant-frugivore interactions across the Caribbean identified interactions between 486 plants and 178 frugivore species (Vollstädt et al. 2022). An estimated 2.1% of angiosperm species in the Caribbean are at risk of losing all vertebrate pollinators (Aslan et al. 2013), but plant-frugivore relationships remain poorly characterized, meaning that even more species may be at risk. Furthermore, the Caribbean's dynamic history of diversification, coupled with recent extinction and colonization events throughout the Quaternary (2.58 million years ago [mya] to present), render it a unique system to characterize assembly, disassembly, and persistence dynamics of frugivore communities and the impacts of extinctions and introductions on Caribbean ecosystems more broadly.

Conceptual Framework

Here I synthesize ecological data from the fossil record, historical accounts, and recent ecological surveys to reconstruct ancient and modern frugivore communities of the Caribbean and characterize the impacts of Quaternary extinction and colonization processes on the functional and taxonomic diversity of Caribbean frugivores. For this study, I focus on body size as a measure of functional diversity, as it is tractable in the fossil record and has been shown to correlate with seed size in a variety of frugivorous taxa (Herrel et al. 2004; Lim et al. 2020; Naniwadekar et al. 2021). I contextualize Caribbean frugivore diversity with literature on the evolution of frugivory to characterize the biotic and abiotic processes that contribute to the assembly of Caribbean frugivore communities. Then, using taxonomic and functional data for extinct and extant frugivores, I test two hypotheses about community disassembly dynamics and the underlying processes that produce observed patterns. First, I hypothesize that extant native Caribbean frugivores are a subset of ancient frugivore communities, which have undergone nonrandom taxonomic and functional diversity loss largely due to anthropogenic activity. Second, I hypothesize that introduced species do not restore taxonomic or functional diversity loss, further altering the evolutionary trajectories of frugivore communities and plant-frugivore interactions in the Caribbean. In evaluating these hypotheses, I review the abiotic and biotic processes that contribute to patterns of frugivore loss, including anthropogenic impacts. Finally, changes in frugivore community structure are expected to have significant impacts on Caribbean plant diversity; I highlight existing research on this topic, identify knowledge gaps, and describe prospects for future research. Through these analyses and synthesis, I provide paleobiological perspectives on the processes that shape biological communities and the overall utility of communities as an ecological concept.

Inferring the Evolutionary Origins of Caribbean Biodiversity and Frugivore Community Assembly

Encompassing a land area around 229,550 km^2 and stretching nearly 3,200 km in length, the Caribbean is a biodiversity hotspot and replicate insular system continually shaped by colonization, extinction, and diversification dynamics (Ricklefs and Bermingham 2008; Gillespie et al. 2009). Various types of ecological communities are found throughout the archipelago, which is traditionally broken up into three regions: the Greater Antilles, the Bahamas, and the Lesser Antilles. As is the case with many insular systems, the Caribbean is home to multiple magnificent evolutionary radiations. The most well-known radiation is that of the *Anolis* lizards, which total more than 150 species in the Caribbean. In the Greater Antilles, *Anolis* converge onto six ecomorphs, each of which has morphological features that are suited toward navigating specific environmental niches. Other notable vertebrate radiations include that of *Sphaerodactylus* geckos and *Eleutherodactylus* frogs. However, many vertebrate radiations have been heavily impacted by extinction, and extant diversity is only a fraction of what once existed a few thousand years ago. Entire radiations of sloths, primates, heptaxodontid rodents, and giant tortoises were lost during the Quaternary, and the extant capromyid rodents of the Greater Antilles are only a subset of what they used to be. Invertebrates and plants have also radiated extensively, leading to high endemicity. Indeed, 2.3% of global plants are endemic to the Caribbean (Myers et al. 2000). The extent to which these lineages have been impacted by extinction relative to vertebrate lineages remains unclear.

Vicariant events and overwater dispersal are both thought to contribute to the colonization and subsequent speciation of Caribbean lineages, although the relative contributions of these phenomena remain a topic of debate, in part because of the complex geology of the region. The islands themselves originated through volcanism, tectonic activity, and sea level fluctuation. Iturralde-Vinent and MacPhee (1999) proposed a late Eocene–early Oligiocene land bridge between South America and the Caribbean via the Aves Ridge (GAARlandia), which would have allowed South American lineages to colonize the Greater Antilles. While phylogenetic analyses indicate that many extant Caribbean lineages are monophylic and derive from South American ancestors, the timing of these splits are not always consistent with the GAARlandia land-bridge hypothesis, leading many researchers to favor overwater dispersal hypotheses (Cano et al. 2018; Ali and Hedges 2021).

Connections between North America and the Proto-Antilles during the Late Cretaceous also yielded flora and fauna derived from North American lineages, such as the rhinoceros-like perissodactyl (*Hyrachys* sp.) known from the Eocene of Jamaica. The evolutionary trajectories of some of these early communities were squashed by changing environments. The rich Eocene community of Jamaica, for example, was lost when the island became submerged from the middle Eocene to the middle Miocene (Buskirk 1985). Thus, the biological communities presently found on Jamaica are evolutionarily younger and much less diverse than those found on other islands in the Greater Antilles. Pleistocene ice age cycles played an outsized role in shaping ecological communities in the Bahamas and the Lesser Antilles. During periods of low sea level, many present-day islands would have been connected to one another as significantly larger land masses. Decreases in island area at the Pleistocene-Holocene transition may have played a role in population differentiation of extant fauna and contributed to the extinction of many taxa. Conversely, partial submergence can also contribute to speciation; the fusion of paleoislands and repeated Pleistocene submergence of low-elevation sites on Hispaniola and Cuba have influenced lineage diversification and genetic structure (Nieto-Blázquez et al. 2022). Despite significant dynamism, there is also evidence of deep-time stability in ecological communities of the Caribbean. Miocene amber from Hispaniola reveals the ancient presence of *Anolis* ecomorphs that are presently found in the Greater Antilles (Sherratt et al. 2015). Living fossils like the solenodon, which separated from other placental mammals approximately 76 mya (Roca et al. 2004), likely colonized the Caribbean through vicariance and also point to environmental continuity.

The initial formation of parts of the Caribbean during the Late Cretaceous coincides with the global origin of plant-frugivore interactions, and both angiosperms and frugivores may have played a significant role in early Caribbean ecosystems. In a comprehensive review of the evolution of plant-frugivore interactions, Eriksson (2016) concludes that the evolution of frugivory occurred in two phases, whereby plants and animal lineages evolved into novel niche spaces. The first phase began 80 mya and was marked by the diversification of angiosperm seed size and fleshy fruits. This diversification event peaked around the time of the Paleocene-Eocene Thermal Maximum (~55 mya), a period where global temperatures significantly increased (Dunkley Jones et al. 2013). As this niche space developed, so did the first frugivores, which likely included rodents, primates, and extinct multituberculate mammals. The second phase coincides with the Eocene-Oligocene boundary (~34 mya) and climate shifts that led to more semiopen woodland habitats. The

Table 1: Divergence dates for important Caribbean frugivore lineages

Group	Divergence date (mya)	Reference
Caribbean sloths	Late Eocene (35)	Delsuc et al. 2019
Short-faced bats	Miocene (10.8–20.3)	Dávalos 2007
Capromyid rodents	Early Miocene (16.5)	Fabre et al. 2014
Giant tortoises	Early Miocene (15.5)	Kehlmaier et al. 2017
Rock iguanas	Late Miocene (9.91)	Reynolds et al. 2022
Caribbean parrots	Pliocene (3.47)	Kolchanova et al. 2021
Crows and ravens	Middle Miocene (17.5)	Jønsson et al. 2012

Note: mya = million years ago.

patchy occurrence of food resources for frugivores resulting from this environment promoted the evolution of a "flying frugivore niche" in the Oligocene and Miocene. While fossils from the Oligocene of Puerto Rico (Vélez-Juarbe et al. 2014) point to an early presence of rodents in the region, the incompleteness of the pre-Quaternary Caribbean fossil record, coupled with mass extinctions of rodents and other mammals during the Quaternary, obfuscate both ancient and extant patterns of diversification and hinder our ability to infer the process of plant-frugivore coevolution in the Caribbean from fossil data alone. Nevertheless, phylogenetic data reveal that many Caribbean frugivore lineages arose and diversified in novel Miocene environments, concordant with Eriksson's conclusion (table 1). For example, a lineage of obligate frugivore bats (Phyllostomidae: Stenodermatina) arose in the Miocene during a period when phyllostomid bats more generally began to show an increase in morphological disparity associated with dietary diversification (Dávalos 2007; Monteiro and Nogueira 2011). Interestingly, several nonvolant groups, including the rock iguana genus *Cyclura* and the giant tortoises (*Chelonoidis*), also originate during the expansion period of the flying frugivore niche (Kehlmaier et al. 2017; Reynolds et al. 2022). These large-bodied terrestrial species can travel long distances and may have also capitalized on open habitats to begin exploiting fruits.

Despite the poor fossil record, phylogenetic data from Caribbean frugivores are consistent with global patterns of plant-frugivore coevolution. However, fossil data are critical to some of these phylogenetic reconstructions because the paucity of modern frugivores means that ancient DNA from Quaternary fossils must be employed in order to reconstruct diversification patterns and clade ages for groups that are now largely extinct (Fabre et al. 2014; Delsuc et al. 2019). The rich Quaternary fossil record of the Caribbean can be used further to quantify changes in functional and taxonomic diversity of frugivore communities during periods of environmental change, providing essential information on the past vulnerabilities of specific archipelagos, taxonomic groups, and functional groups while also elucidating the abiotic and biotic processes responsible for structuring modern-day communities.

Methods

To characterize the functional and taxonomic diversity of Caribbean frugivore communities over the Quaternary, I collated body size data for frugivorous birds, mammals, and reptiles in the Caribbean past and present. Our knowledge of diet varies greatly across taxa, ranging from direct observation to inference. Many of the species included in this study are classified in databases as omnivores but include a significant portion of fruits and seeds in their diets; others are obligate frugivores. Stable isotopes help clarify the diet of extinct species (Cooke and Crowley 2018; Shev et al. 2021), as do observations in extant congeners.

Extinct and extant frugivores were identified through literature review of previously published datasets (Dávalos and Russell 2012; Lyons et al. 2016; Kim et al. 2022; Vollstädt et al. 2022; Kemp 2023) and natural history accounts (Henderson and Powell 2009; Powell and Henderson 2012; Gerbracht and Levesque 2019; Kurta et al. 2023). Reptile data come from recent studies published by Kemp (2023) and Kim et al. (2022) that focus on reptile functional traits and modern Caribbean frugivores, respectively. Caribbean faunal lists of birds and mammals, along with paleontological descriptions of extinct taxa, were cross-referenced with trait databases (Jones et al. 2009; Wilman et al. 2014) to identify birds and mammals that practice frugivory; body size data were also taken from these databases if not available in the other published datasets I referenced. In a few instances, body mass was estimated using previously reported allometric scaling relationships (Hopkins 2008; Meiri 2018; Sayol et al. 2021). Taxa were then classified on the basis of their geographic distribution within the Caribbean (Greater Antilles, Bahamian Archipelago, and/or Lesser Antilles), their extinction status, and their status as either a native or an introduced species. The full dataset used in this study can be found in supplementary table 1 in the Dryad Digital Repository (https://doi.org/10.5061/dryad.1ns1rn92f; Kemp 2024).

Results

New Insights from New Data: Shifting Caribbean Frugivore Communities

I compiled data on 500 frugivores in the Caribbean, 447 of which are native. Fifty-six (12.5%) of all native frugivores have become extinct, and several species have experienced significant range contraction (e.g., *Amazona leucocephala*, *Brachyphylla cavernarum*, *Geocapromys ingrahami*, *Iguana delicatissima*, *Macrotus waterhousii*, *Monophyllus plethodon*, *Phyllonycteris poeyi*). The loss of native frugivores is most acute in the species-rich Greater Antilles, where 12.6% of native frugivores became extinct; the Bahamas and Lesser Antilles lose 5.9% and 8.2% of their native frugivores, respectively.

My analyses uncovered region-wide and archipelago-specific patterns for how native frugivore diversity has changed across the Caribbean. Extinct frugivores are significantly larger than extant native frugivores in the Greater Antilles (Mann-Whitney test, $P < .0001$), the Bahamas (Mann-Whitney test, $P < .01$), and the Lesser Antilles (Mann-Whitney test, $P < .01$), leading to truncated native frugivore body size distributions in the present (fig. 1). Throughout all regions, birds are the most common native frugivores (table 2). The frugivore community of the Greater Antilles, which is consistently the most species rich, lost a disproportionate number of mammals during the Quaternary: 71.7% of extinct frugivores in the Greater Antilles are mammals (table 2). Furthermore, the size-biased frugivore extinctions in the Greater Antilles result in a taxonomic transition for native frugivores, where the largest body size classes that were once dominated by mammals are now dominated by reptiles (fig. 2). The 12 largest ancient frugivores (>12,000 g) in the Greater Antilles are all extinct;

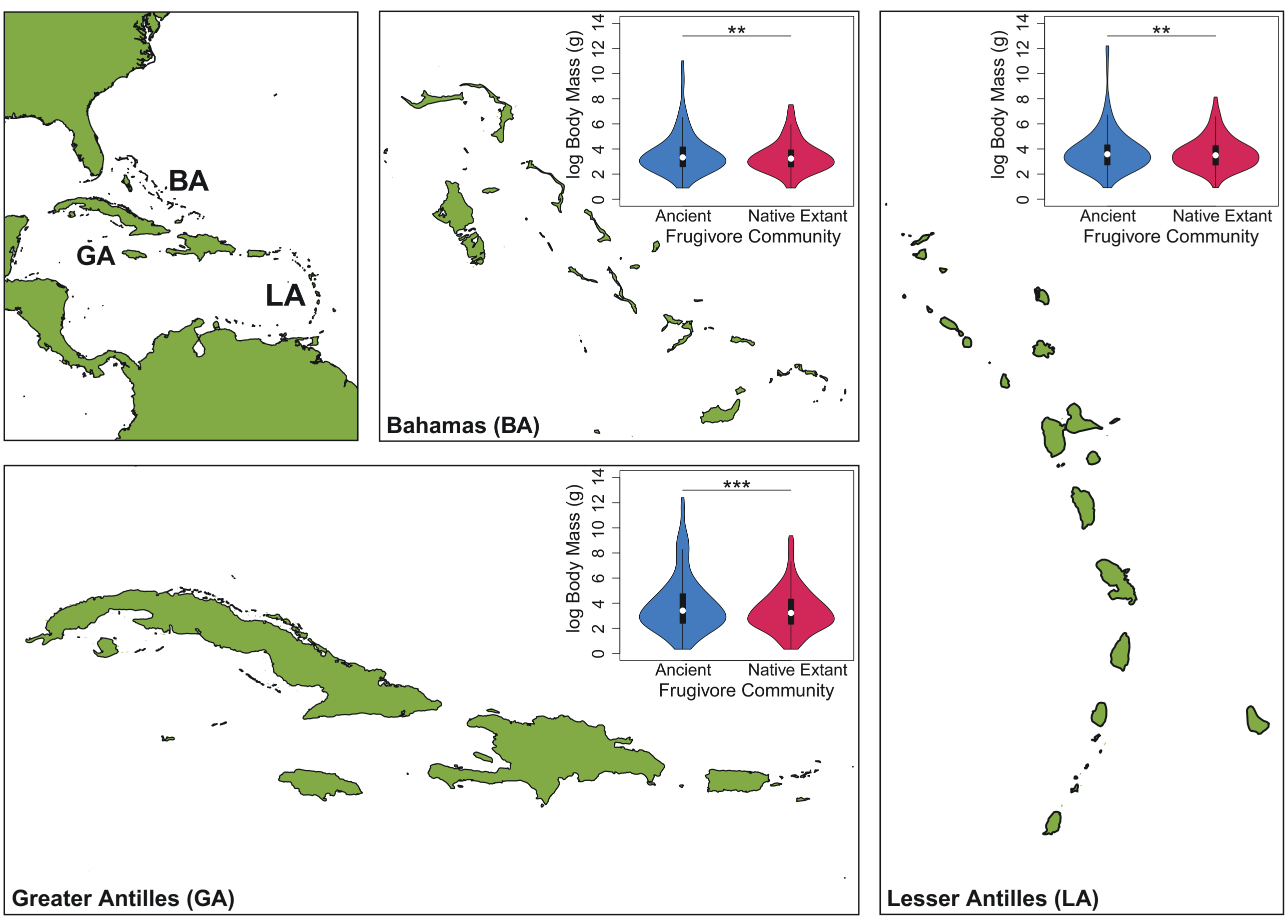

Figure 1: Map of the Caribbean archipelago with its three principal regions: the Bahamas, the Greater Antilles, and the Lesser Antilles. In each regional panel, the body size distributions of the ancient and native extant frugivore communities are shown as violin plots. $^{**}P < .01$, $^{***}P < .001$ (Mann-Whitney test).

Table 2: Taxonomic percentages of Caribbean frugivores across extinct, native extant, and introduced communities

	Bahamas			Greater Antilles			Lesser Antilles		
Community	Birds	Mammals	Reptiles	Birds	Mammals	Reptiles	Birds	Mammals	Reptiles
Extinct	16.7	33.3	50	13	71.7	15.2	18.2	63.6	18.2
Native extant	82.1	4.2	13.7	56.4	6.3	37.3	73.2	10.6	16.3
Introduced	52.9	29.4	17.6	54.5	40.9	4.5	50	40.6	9.4

they include six sloths, four tortoises, one rodent, and one iguana. At present, the 10 largest native frugivores of the Greater Antilles include nine species of *Cyclura* iguanas, ranging in size from 2,624.2 to 11,803.2 g, and one rodent, *Capromys pilorides*, which is endemic to Cuba and is the sixth-largest native frugivore remaining in the Greater Antilles.

The largest native frugivores of the Bahamas have been reptiles throughout the Quaternary (fig. 3), although the extinction of all giant tortoises of the genus *Chelonoidis* (9,180–61,329 g) has left the substantially smaller rock iguana *Cyclura carinata* (1,860 g) as the largest native frugivore. Native birds comprise 82.1% of all native extant frugivores, and eight bird species ranging in size from 171.5 to 1,150 g are among the 10 largest native extant frugivores of the Bahamas.

The largest Quaternary frugivores in the Lesser Antilles were *Amblyrhiza inundata*, a giant rodent endemic to the Anguilla Bank, and a giant tortoise (*Chelonoidis sombrerensis*) endemic to Sombrero, an isolated 0.38-km^2 island north of Anguilla (fig. 4). Both *Amblyrhiza inundata* and *Chelonoidis sombrerensis* are likely part of Greater Antillean radiations of heptaxodontid rodents and giant tortoises, as Sombrero and Anguilla are the northernmost islands of the Lesser Antilles. Throughout most of the Lesser Antilles, the largest frugivore throughout the Quaternary was *Iguana delicatissima*, a species that has undergone significant range contraction throughout the Holocene as human populations have migrated throughout the region. The extant native fauna continues to be dominated by birds and reptiles (table 2).

Biodiversity loss in native frugivore communities—and the downstream impacts on seed dispersal and ecosystem structure—may be ameliorated by introduced frugivores. While the vast majority of frugivore losses in all Caribbean regions are of mammals and reptiles, the majority of introduced frugivores are birds. Birds account for anywhere between 50% of introduced frugivores in the Lesser Antilles to 54.5% of introduced frugivores in the Greater Antilles. Frugivorous reptiles are least commonly introduced across all regions (table 2). Throughout the Caribbean there is an influx of mammalian frugivores such that the largest frugivores in all regions are now mammals (figs. 2*C*, 3*C*, 4*C*)—a first for the Bahamas and most islands of the Lesser Antilles, excluding the Anguilla Bank islands. Despite these shifts in taxonomic diversity, introduced Caribbean frugivores are significantly smaller than extinct Caribbean frugivores (fig. 5; Mann-Whitney test, $P < .005$), indicating that modern-day frugivore communities are still missing large-bodied frugivores.

Discussion

Relating Pattern to Process: The Role of Humans in Restructuring Frugivore Communities

The Quaternary fossil record reveals patterns of nonrandom extinction and colonization that results in a loss of large-bodied mammal and reptile frugivores and an influx of new avian and mammal frugivores that are significantly smaller than their extinct counterparts. While I document a vast number of frugivores in the Caribbean past and present, there is a possibility that ancient frugivore diversity is still underestimated across all taxonomic groups. The taxonomy of several rodent groups in the Greater Antilles is still unresolved; reptile taxa are still being described from excavations that occurred decades ago; and there exist a number of hypothetical extinct species of birds that various European naturalists described but for which specimens or fossil evidence does not exist (Olson 2005; Oswald et al. 2023). Thus, there is a continued need for field- and collections-based paleontological research to ensure that we have a complete biodiversity baseline for frugivores.

While clear patterns of frugivore extinction exist, disentangling the processes that contribute to this biodiversity loss is more complicated and is situated within long-standing debates about the relative impacts of climate and humans in driving Quaternary extinctions (Koch and Barnosky 2006). Unlike many continental systems, the climatic events of the end of the Pleistocene are temporally decoupled from human colonization in the Caribbean. In theory, this decoupling allows for a more nuanced characterization of the abiotic and biotic processes at play in Quaternary extinctions. This can be achieved through radiocarbon dating both extinct taxa and archaeological sites and comparing the last appearance dates of extinct fauna to paleoenvironmental data and human first appearance dates.

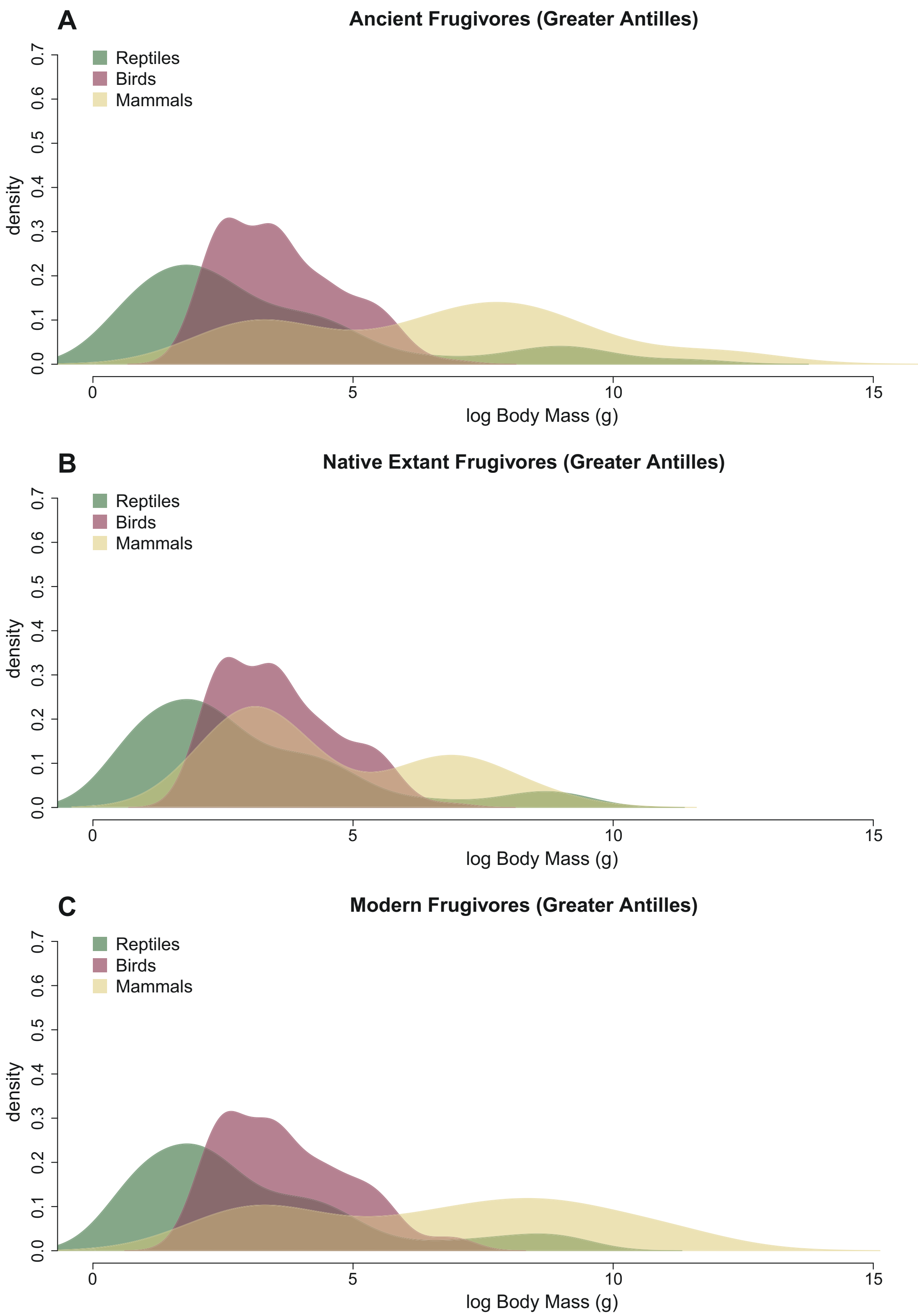

Figure 2: Body size distributions of ancient, native extant, and modern (native extant plus introduced) frugivore communities of the Greater Antilles.

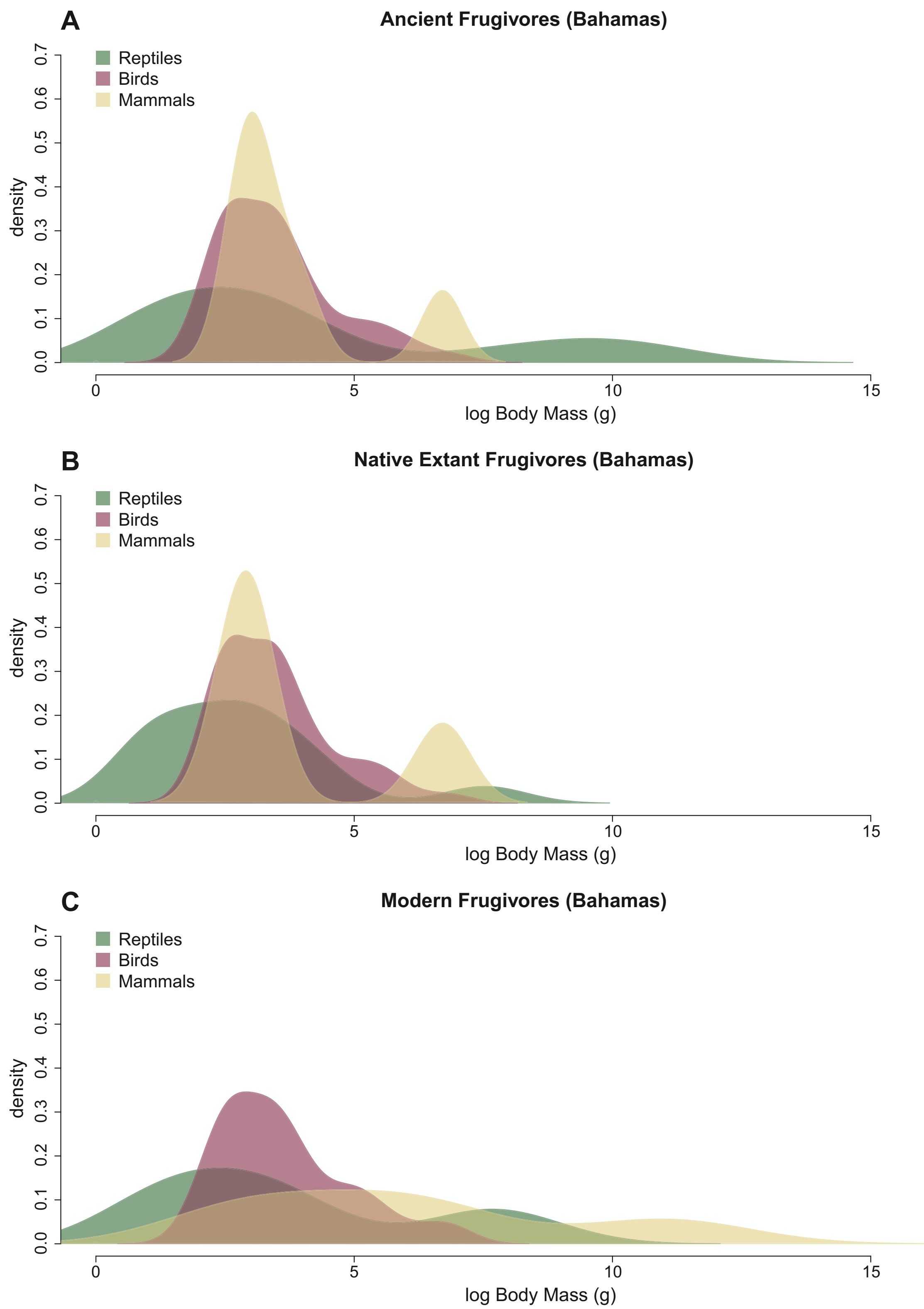

Figure 3: Body size distributions of ancient, native extant, and modern (native extant plus introduced) frugivore communities of the Bahamas.

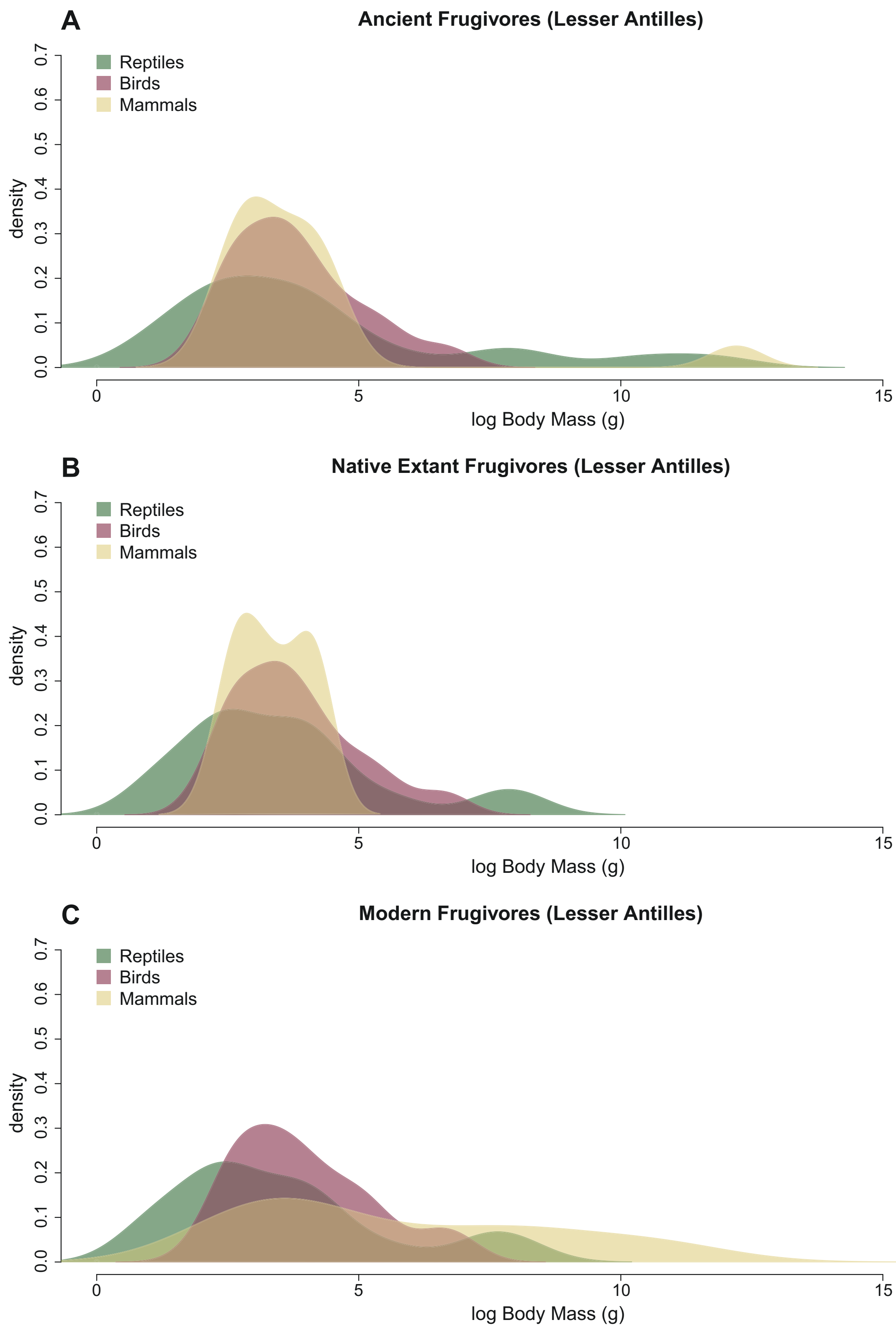

Figure 4: Body size distributions of ancient, native extant, and modern (native extant plus introduced) frugivore communities of the Lesser Antilles.

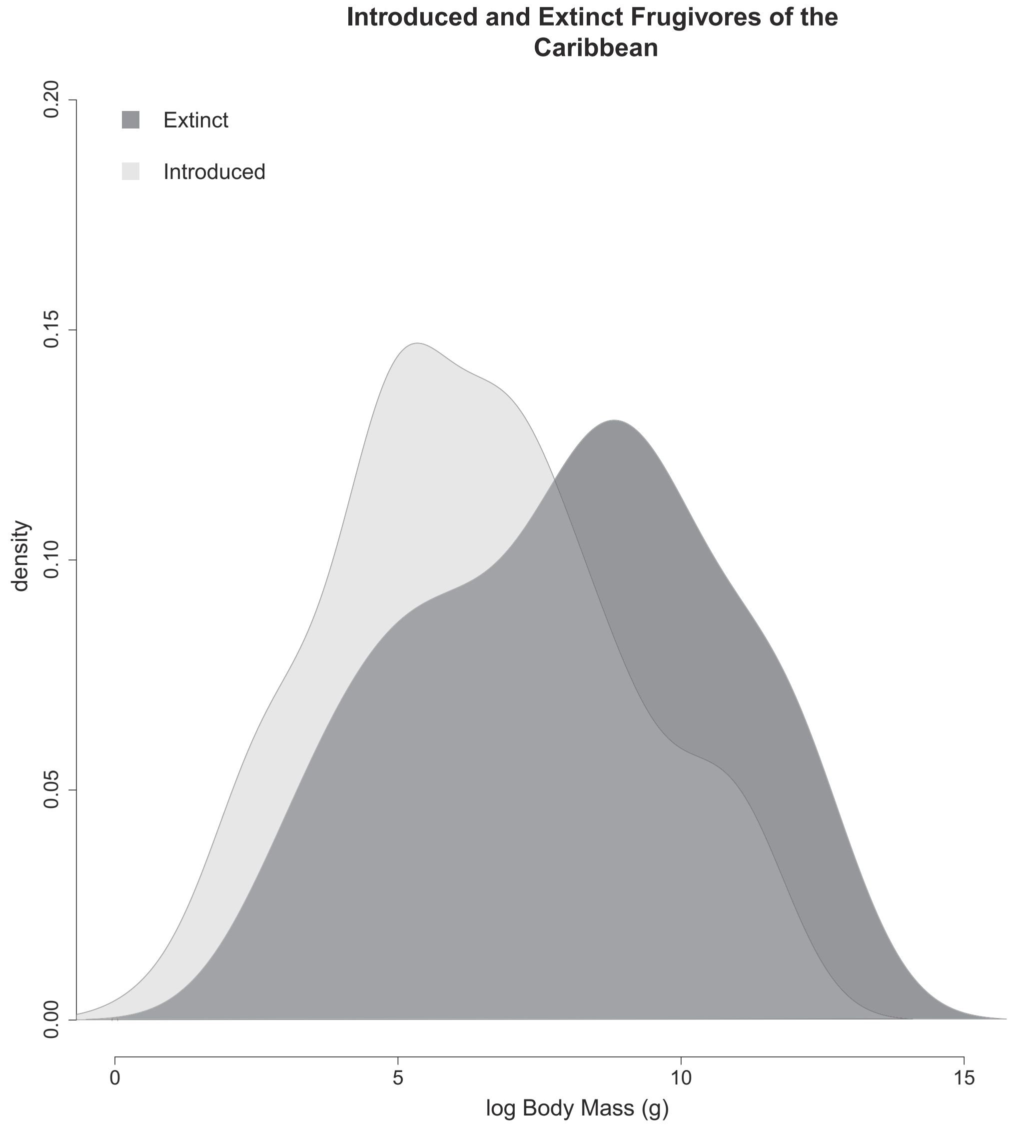

Figure 5: Body size distributions of introduced and extinct Caribbean frugivores.

In practice, obtaining direct radiocarbon dates for extinct fauna has been difficult, especially for birds and reptiles. Indirect dates made from associated fauna and charcoal are often employed but necessitate knowledge of the stratigraphic positions of extinct taxa relative to the associated material, which is not always available for previously excavated sites. In a comprehensive review of Caribbean mammal extinctions, Cooke et al. (2017) synthesized data from paleontological and archaeological literature to compile mammal last-appearance dates and human first-appearance dates across the Caribbean. Several extinction events appear to occur prior to human colonization, such as that of *Amblyrhiza inundata* in Anguilla, and may be related to Pleistocene climatic cycles, as sea level fluctuations reduced island area significantly in the Lesser Antilles and Bahamas, which could have led to extinction (McFarlane et al. 1998). However, their meta-analyses corroborate what many have long suspected: that many Caribbean mammals survived well into the Holocene, implicating humans in these extinctions. While such systematic studies of bird and reptile extinctions have not been performed (but see Bochaton et al. 2021; Oswald et al. 2023), the presence of museum voucher specimens for many extinct species indicate that various extinct reptiles, birds, and mammals persisted until European colonization.

Given the timing and nature of community change, the extinction and colonization events that shape Quaternary frugivore communities are a consequence of human niche construction. Humans are highly efficient ecosystem engineers who actively modify their environment, catalyzing extinctions, extirpations, species introductions, and shifts in community structure (Boivin et al. 2016). Ethnohistoric data and archaeological records indicate that many Indigenous populations directly exploited native fauna, including frugivores, through hunting and translocation (Bochaton et al. 2016; Kemp et al. 2020; Oswald et al. 2023). Large-bodied frugivores, such as sloths, giant hutias, tortoises, and iguanas, were likely a prized food source for the first inhabitants of the Caribbean; hutias and iguanas are still consumed in various parts of the Caribbean today. Indirect anthropogenic impacts, such as habitat modification and introduced species, also likely contributed to frugivore loss. Lake and sediment cores indicate increased fire activity and changes in plant communities consistent with disturbance and deforestation concomitant with human colonization events (Burney et al. 1994; Hooghiemstra et al. 2018). Since European colonization, the Caribbean has undergone massive deforestation: by the early twentieth century, Puerto Rico was estimated to have lost >99% of its primary forest (Brash 1987), and at present Haiti retains approximately 0.32% of its primary forest (Hedges et al. 2018). Deforestation, most acute at low-elevation sites, represents a major threat to native biodiversity and would particularly impact habitat and dietary specialists like frugivores and large-bodied species, which require larger home ranges. Fifty-one percent of native extant Caribbean frugivores are threatened or near threatened (IUCN 2023), and the anthropogenic processes that contribute to population decline and extinction also render these species more vulnerable to abiotic processes such as hurricanes, which have been shown to affect frugivorous and nectivorous species of birds and bats more strongly than other dietary groups (Jones et al. 2001 and references therein), and sea level rise, which is expected to impact the Caribbean quite significantly (Bellard et al. 2014).

The novel frugivore communities of the present result directly from human agency. While abiotic factors influence invasiveness and the establishment likelihood of introduced species, humans have intentionally introduced a significant number of birds and mammals to the Caribbean, particularly after European colonization, with reptile introductions increasing only more recently (Kemp et al. 2020). Some of these species, such as the mongoose and the black rat, participate in frugivory (Vollstädt et al. 2022) but are also linked to native species declines through predation or competition (Borroto-Páez 2009; Lewis et al. 2011).

Importantly, these patterns and processes are not specific to the Caribbean. A study of 33 Pacific islands that experienced anthropogenic extinctions also found a decline in native frugivore functional diversity as quantified through body size (Heinen et al. 2018). Furthermore, a study of ancient frugivore diversity on Mauritius showed that species introductions do not restore preextinction functional diversity (Heinen et al. 2023). Data from other systems can inform the impact of introduced frugivores on native plants and native seed dispersal, an area where data are lacking in the Caribbean. A comprehensive study of ancient and modern plant frugivore networks on Mauritius found that while introduced frugivores interacted with native plants, a closer examination of seed-handling behavior indicated that many introduced frugivores are also seed predators (Heinen et al. 2023). Two introduced frugivores now common in the Caribbean—pigs (*Sus scrofa*) and rats (*Rattus rattus*)—have been reported to destroy up to 86% (O'Connor and Kelly 2012) and ~65% (Shiels and Drake 2011) of handled seeds in other insular systems. In Puerto Rico, gnaw marks consistent with rats have been observed on the seeds of *Zamia* (Negrón-Ortiz and Breckon 1989); while it has been conjectured that rats are a novel dispersal agent of *Zamia*, it is unclear how much of their seed-handling activity is antagonistic toward *Zamia*. More behavioral data are necessary to characterize the ecosystem service potential of introduced frugivores.

Implications of Frugivore Loss on Plant Diversity

If plant-frugivore interactions are strong, frugivore loss is expected to impact plant species in several predictable ways. We expect to see declines in plant diversity, decreases in seed dispersal distance from maternal plants, and restricted gene flow in affected plant species (Guimarães et al. 2008; Pérez-Méndez et al. 2016; Galetti et al. 2018). Patterns of diversity loss should be particularly pronounced in plants exhibiting traits consistent with the Neotropical anachronism hypothesis (Janzen and Martin 1982), whereby fruit traits are best explained by interactions with extinct megafauna. The fruits of these plants, referred to in the literature as megafaunal fruits, tend to fall into two classes: class I fruits, which are 4–10 cm in diameter with up to five large seeds, and class II fruits, which are larger than 10 cm in diameter and contain many small seeds (Guimarães et al. 2008). In both cases, large fruit size hinders effective dispersal by small frugivores. Indeed, large frugivore loss has had cascading effects on seed dispersal patterns and the population genetics of the fleshy-fruited shrub *Neochamaelea pulverulenta* in the Canary Islands (Pérez-Méndez et al. 2016). The fruits of *N. pulverulenta* are consistent with a type I megafaunal fruit and its seeds are exclusively dispersed by lizards, but the largest species of lizards became extinct shortly after human colonization of the archipelago (Barahona et al. 2000). Researchers have shown that the frequency of short-distance dispersal events for *N. pulverulenta* is significantly higher for populations dispersed by small- and medium-bodied lizards; these populations also exhibit more fine-scale genetic structure and reduced effective population sizes relative to the populations that are dispersed by larger species (Pérez-Méndez et al. 2016). The paucity of population genetic and demographic data for Caribbean plants makes it difficult to link changes in plant diversity to past frugivore extinction, but given that 44.6% of Caribbean plants are dispersed through frugivory (Kim et al. 2022), future frugivore loss is likely to contribute to plant diversity declines.

More natural history observations, coupled with seed transport and germination studies, are needed to identify and characterize remaining plant-frugivore interactions, particularly for seed dispersal–limited plants and for reptiles, where frugivory is understudied and likely underestimated (Valido and Olesen 2019). Given the large radiations of reptiles and birds that commonly occur on oceanic islands, it should come as no surprise that birds and reptiles are significant seed dispersal agents in the Caribbean (Kim et al. 2022). However, it is unclear how large-bodied reptiles like *Cyclura*, which are now the largest native frugivores in most communities, may modulate seed dispersal for megafaunal fruits. Recent studies of *Cyclura* scat from the Dominican Republic identified seeds in high abundance from several plant species that had not been previously recorded as food sources for *Cyclura*, despite co-occurring with other species of *Cyclura* (Pasachnik and Martin-Velez 2017). This includes *Consolea moniliformis*, a keystone species in the dry forest ecosystem (García-Fuentes et al. 2015), which has experienced severe degradation due to colonial agricultural practices (Maunder et al. 2008). Several endangered plants were also found in the diet of *Cyclura*, including *Guaicacum* spp., which is represented by two IUCN redlisted species in the Caribbean (Pasachnik and Martin-Velez 2017). Understanding mutualisms between endangered plants and endangered frugivores may contribute to the development of coordinated management plans, including tropic rewilding, that target both species and the ecosystems they support (Stark and Galetti 2024).

Cycads are one such group that might benefit from coordinated management of plants and frugivores. Cycads are highly threatened gymnosperms that produce brightly colored fleshy fruits. Presently, there are six cycad species in the Caribbean, all of which are redlisted by the IUCN. The monotypic, critically endangered *Microcycas calocoma* is restricted to Cuba and has no known zoonotic disperser, although researchers have suggested that the beetle *Pharaxonotha esperanzae* may be a dispersal agent (Chaves and Genaro 2005). The other five belong to the genus *Zamia*, which was previously described by Janzen and Marten (1982) as having megafaunal fruit traits. Based on the literature review performed by Kim et al. (2022), reptiles are an important zoonotic dispersal agent for *Zamia*; however, many of the rock iguana species that would co-occur with *Zamia* are highly threatened and may be functionally extinct, further limiting seed dispersal.

Are Plant-Frugivore Interactions Important?

Although I have highlighted declines in plants with zoochoric dispersal syndromes, these patterns alone do not prove that plant-frugivore interactions are strong—and therefore important—because in addition to altered mutualistic networks, other global change phenomena, such as habitat destruction and climate change, are contributing to plant diversity declines. Introduced frugivores hint at the strength of plant-frugivore interactions and coevolution, as they are more likely to interact with introduced plants than expected at random (Vollstädt et al. 2022). These interactions, referred to in the literature as "invader complexes," may negatively impact native communities, as both introduced plants and introduced frugivores propel one another toward range expansion at the expense of native flora and fauna. Invader complexes lend credence to the idea that these interactions are biologically meaningful because they persist even in novel environments. By reciprocally advancing ranges at local scales, invader complexes further contribute to large-scale patterns of biotic homogenization that typify environments with strong anthropogenic impacts. On the other hand, native frugivores have been shown to interact with nonnative plants (Burgos-Rodríguez et al. 2016), and under future climate change scenarios they may support range expansion of introduced plant species (Ellis-Soto et al. 2017).

Despite declines in plants with zoochoric dispersal syndromes, plant-frugivore interactions are generally considered weak and diffuse (Eriksson 2016). Indeed, in their study of modern plant-frugivore networks in the Caribbean, Vollstädt et al. (2022) found plant-frugivore networks to be highly modular, with the smallest network containing eight plant species and one frugivore and the largest containing 60 plants and 38 frugivores. However, in a system whose biodiversity is defined by multiple evolutionary radiations, it is unsurprising that there is redundancy in interaction networks, particularly because the evolution of frugivory is marked by different species repeatedly taking advantage of fruits in novel environments. Furthermore, it is important to keep frugivore extinctions in mind when evaluating the evolution and strength of plant-frugivore interactions in the present day: the high level of trait mismatch between bird gape size and palm fruit size observed in modern Caribbean communities (McFadden et al. 2022) may be indicative of diffuse evolution, but if we instead consider the more taxonomically diverse frugivore communities that the fossil record elucidates, we are forced to ask whether trait mismatch between bird gape size and fruit size may be an artifact of Quaternary extinctions that differentially impacted the large-bodied reptilian and mammalian frugivores that would have dispersed the largest fruits.

While interactions are considered weak and diffuse, Eriksson (2016) posits that significant environmental change can alter plant-frugivore interactions, "initiating directional and reciprocal selection on fruit and frugivore traits" (p. 180). The impact of habitat fragmentation on coevolution has been shown empirically in Brazil, where palm seed size was reduced in forest fragments where toucans were extirpated (Galetti et al. 2013), but perhaps we can go back even further to characterize the strength and nature of plant-frugivore coevolution. Tethering the recent past to the present and a rapidly approaching future, Quaternary communities provide critical baseline data for characterizing coevolutionary networks in changing environments. Frugivore extinctions, climate change, and ongoing anthropogenic impacts are likely to have elicited evolutionary changes in surviving lineages of frugivores and plants, and the Quaternary fossil record documents morphologies, abundances, and distributions of mutualistic partners during periods of environmental stasis and environmental change. There are certainly limitations in the Quaternary fossil record, the largest being that characterizing plant-frugivore interactions from fossil data alone is difficult. Interactions between extinct frugivores and plants can be inferred through observations of extant closely related taxa. Plant microfossils, isotopic data, and genetic data may also clarify some ancient plant-frugivore interactions if preserved in dental calculus or coprolites. The poor preservation of plants in the tropics largely precludes detailed morphological analyses, but early museum specimens collected by European naturalists may fill this gap and are especially valuable for species that lost their frugivore mutualists recently.

Quaternary extinctions opened niche space for frugivores that has yet to be filled through evolution or species introductions. Human niche construction may have rendered this niche space inaccessible to other frugivores regardless of geographic origin while simultaneously priming other niche space for species introductions and establishment. The successful establishment of an introduced species is a multistaged process, and members of invader complexes help one another negotiate various barriers to establishment, including reproductive, survival, and dispersal barriers (Blackburn et al. 2011). Interestingly, anthropogenic impacts create persistence barriers for native plant-frugivore interactions, rendering processes like dispersal insurmountable because of the loss of mutualistic partners. Not only are Quaternary invader complexes another example of reciprocal coevolution in altered environments, but they also appear to be part of larger cycles of community turnover and biological homogenization triggered by anthropogenic impacts that began in the Pleistocene and Holocene. Both paleontological and archaeological data from the Quaternary can be harnessed to test the prevalence of invader complexes and their impact on community structure across spatial and temporal scales.

Conclusions

Through interrogation of the fossil record, I show that both abiotic and biotic processes underlie patterns of community assembly, persistence, and disassembly. Caribbean biodiversity is the result of dynamic biogeographic processes, and the evolution of plant-frugivore interactions appears to be closely linked to the presence of novel environments formed during periods of environmental change. During the Quaternary, frugivore communities were both functionally and taxonomically diverse, and present-day frugivore communities represent a nonrandom subset of the diversity that had accumulated prior to the mid-Holocene. I find that throughout the Quaternary, birds have been the most abundant frugivores and have not been impacted by extinction as much as some other vertebrate taxa, although further investigations of paleontological and archaeological data may reveal additional extinct birds. While birds dominate extant native communities and species introductions, mammals and reptiles dominate frugivore extinctions, which are concentrated in the largest size classes. Regardless of taxonomic identity, introduced frugivores remain significantly smaller than extinct frugivores, which may have adverse effects on native plants and overall ecosystem structure and function. While abiotic processes largely structured Quaternary communities prior to human colonization, biotic processes in the form of human niche construction played an outsized role in restructuring frugivore communities in the Holocene. Fossils and museum collections have immense potential to (1) reveal patterns of selection in plant-frugivore traits in changing environments and (2) demonstrate the strength of plant-frugivore interactions.

What do these data say about the overall importance and strength of species interactions and, in turn, the utility of ecological communities? Data from this study and other systems indicate that plant-frugivore interactions are important, with species responding to the loss of mutualistic partners through rapid evolution or extinction, but quantifying the strength of these interactions is difficult and confounded by anthropogenic impacts. The different timescales at which plants and animals respond to changes must also be considered when evaluating the strength of plant-frugivore interactions. For example, with the exception of the Neotropics, global variation in fruit size is better explained by present-day frugivore assemblages than by late Pleistocene assemblages, indicating that interactions are important because communities reorganize rapidly when interactions are lost (Lim et al. 2020). But the Neotropics, which experienced human impacts much later than other biogeographic realms, are likely still undergoing a reorganization of fruit traits, providing ecologists with a rare opportunity to observe plant responses to novel frugivore communities in real time.

The conservation of species interactions has been promoted as critical for ecosystem conservation (Heinen et al. 2020) and is in line with paleontological conceptualizations of communities that emphasize tracking functional diversity over long timescales. Through studying plant-frugivore interactions over geologic timescales, we see species change and are forced to ask whether the interactions are preserved. In the case of the Quaternary plant-frugivore drama, the script is changing significantly. The differential loss of large-bodied frugivores, ongoing and intensifying anthropogenic impacts, and the influx of invader complexes is leading to a less morphologically and taxonomically diverse frugivore fauna alongside declining native plant diversity. The show goes on, but the play itself is less illustrious than it once was.

Acknowledgments

I thank Priyanga Amarasekare for organizing the Vice Presidential Symposium and the other symposium participants for vibrant discussion about the intersections of our research. Mauro Galetti and two anonymous reviewers provided valuable feedback on early versions of the manuscript. M.E.K. was supported by funding from the National Science Foundation (NSF-EAR 2050228).

Data and Code Availability

Supplementary table 1 and R code are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.1ns1rn92f; Kemp 2024).

Literature Cited

Ali, J. R., and S. B. Hedges. 2021. Colonizing the Caribbean: new geological data and an updated land-vertebrate colonization record challenge the GAARlandia land-bridge hypothesis. Journal of Biogeography 48:2699–2707.

Aslan, C. E., E. S. Zavaleta, B. Tershy, and D. Croll. 2013. Mutualism disruption threatens global plant biodiversity: a systematic review. PLoS ONE 8:e66993.

Barahona, F., S. E. Evans, J. A. Mateo, M. García-Márquez, and L. F. López-Jurado. 2000. Endemism, gigantism and extinction in island lizards: the genus *Gallotia* on the Canary Islands. Journal of Zoology 250:373–388.

Barnosky, A., E. Hadly, P. Gonzalez, J. Head, P. Polly, A. Lawing, J. Eronen, et al. 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. Science 355:eaah4787.

Bellard, C., C. Leclerc, and F. Courchamp. 2014. Impact of sea level rise on the 10 insular biodiversity hotspots: sea level rise and insular hotspots. Global Ecology and Biogeography 23:203–212.

Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, et al. 2011. A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26:333–339.

Bochaton, C., S. Bailon, I. Ineich, M. Breuil, A. Tresset, and S. Grouard. 2016. From a thriving past to an uncertain future: zooarchaeological evidence of two millennia of human impact on a large emblematic lizard (*Iguana delicatissima*) on the Guadeloupe Islands (French West Indies). Quaternary Science Reviews 150:172–183.

Bochaton, C., E. Paradis, S. Bailon, S. Grouard, I. Ineich, A. Lenoble, O. Lorvelec, et al. 2021. Large-scale reptile extinctions following European colonization of the Guadeloupe Islands. Science Advances 7:eabg2111.

Boivin, N. L., M. A. Zeder, D. Q. Fuller, A. Crowther, G. Larson, J. M. Erlandson, T. Denham, et al. 2016. Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. Proceedings of the National Academy of Sciences of the USA 113:6388–6396.

Borroto-Páez, R. 2009. Invasive mammals in Cuba: an overview. Biological Invasions 11:2279–2290.

Brash, A. R. 1987. The history of avian extinction and forest conversion on Puerto Rico. Biological Conservation 39:97–111.

Burgos-Rodríguez, J. A., K. J. Avilés-Rodríguez, and J. J. Kolbe. 2016. Effects of invasive green iguanas (*Iguana iguana*) on seed germination and seed dispersal potential in southeastern Puerto Rico. Biological Invasions 18:2775–2782.

Burney, D. A., L. P. Burney, and R. D. E. MacPhee. 1994. Holocene charcoal stratigraphy from Laguna Tortuguero, Puerto Rico, and the timing of human arrival on the island. Journal of Archaeological Science 21:273–281.

Buskirk, R. E. 1985. Zoogeographic patterns and tectonic history of Jamaica and the northern Caribbean. Journal of Biogeography 12:445–461.

Cano, Á., C. D. Bacon, F. W. Stauffer, A. Antonelli, M. L. Serrano-Serrano, and M. Perret. 2018. The roles of dispersal and mass extinction in shaping palm diversity across the Caribbean. Journal of Biogeography 45:1432–1443.

Chaves, R., and J. A. Genaro. 2005. A new species of Pharaxonotha (Coleoptera: Erotylidae), probable pollinator of the endangered Cuban cycad, *Microcycas calocoma* (Zamiaceae). Insecta Mundi 19:143–150.

Cooke, S. B., and B. E. Crowley. 2018. Deciphering the isotopic niches of now-extinct Hispaniolan rodents. Journal of Vertebrate Paleontology 38:e1510414.

Cooke, S. B., L. M. Dávalos, A. M. Mychajliw, S. T. Turvey, and N. S. Upham. 2017. Anthropogenic extinction dominates Holocene declines of West Indian mammals. Annual Review of Ecology, Evolution, and Systematics 48:301–327.

Dávalos, L. M. 2007. Short-faced bats (Phyllostomidae: Stenodermatina): a Caribbean radiation of strict frugivores. Journal of Biogeography 34:364–375.

Dávalos, L. M., and A. L. Russell. 2012. Deglaciation explains bat extinction in the Caribbean. Ecology and Evolution 2:3045–3051.

Delsuc, F., M. Kuch, G. C. Gibb, E. Karpinski, D. Hackenberger, P. Szpak, J. G. Martínez, et al. 2019. Ancient mitogenomes reveal the evolutionary history and biogeography of sloths. Current Biology 29:2031–2042.e6.

Dunkley Jones, T., D. J. Lunt, D. N. Schmidt, A. Ridgwell, A. Sluijs, P. J. Valdes, and M. Maslin. 2013. Climate model and proxy data constraints on ocean warming across the Paleocene–Eocene Thermal Maximum. Earth-Science Reviews 125:123–145.

Ellis-Soto, D., S. Blake, A. Soultan, A. Guézou, F. Cabrera, and S. Lötters. 2017. Plant species dispersed by Galapagos tortoises surf the wave of habitat suitability under anthropogenic climate change. PLoS ONE 12:e0181333.

Eriksson, O. 2016. Evolution of angiosperm seed disperser mutualisms: the timing of origins and their consequences for coevolutionary interactions between angiosperms and frugivores: coevolution between angiosperms and frugivores. Biological Reviews 91:168–186.

Fabre, P.-H., J. T. Vilstrup, M. Raghavan, C. Der Sarkissian, E. Willerslev, E. J. P. Douzery, and L. Orlando. 2014. Rodents of the Caribbean: origin and diversification of hutias unravelled by next-generation museomics. Biology Letters 10:20140266.

Galetti, M., R. Guevara, M. C. Côrtes, R. Fadini, S. Von Matter, A. B. Leite, F. Labecca, et al. 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. Science 340:1086–1090.

Galetti, M., M. Moleón, P. Jordano, M. M. Pires, P. R. Guimarães, T. Pape, E. Nichols, et al. 2018. Ecological and evolutionary legacy of megafauna extinctions: anachronisms and megafauna interactions. Biological Reviews 93:845–862.

García-Fuentes, A., J. A. Torres-Cordero, L. Ruiz-Valenzuela, M. L. Lendínez-Barriga, J. Quesada-Rincón, F. Valle-Tendero, A. Veloz, et al. 2015. A study of the dry forest communities in the Dominican Republic. Anais da Academia Brasileira de Ciências 87:249–274.

Gerbracht, J., and A. Levesque. 2019. The complete checklist of the birds of the West Indies: v1.1. BirdsCaribbean Checklist Committee. http://www.birdscaribbean.org/caribbean-birds/.

Gillespie, R., R. G. Gillespie, and D. A. Clague. 2009. Encyclopedia of islands. University of California Press, Berkeley.

Guimarães, P. R., M. Galetti, and P. Jordano. 2008. Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. PLoS ONE 3:e1745.

Hedges, S. B., W. B. Cohen, J. Timyan, and Z. Yang. 2018. Haiti's biodiversity threatened by nearly complete loss of primary forest. Proceedings of the National Academy of Sciences of the USA 115:11850–11855.

Heinen, J. H., F. B. V. Florens, C. Baider, J. P. Hume, W. D. Kissling, R. J. Whittaker, C. Rahbek, et al. 2023. Novel plant–frugivore network on Mauritius is unlikely to compensate for the extinction of seed dispersers. Nature Communications 14:1019.

Heinen, J. H., C. Rahbek, and M. K. Borregaard. 2020. Conservation of species interactions to achieve self-sustaining ecosystems. Ecography 43:1603–1611.

Heinen, J. H., E. E. van Loon, D. M. Hansen, and W. D. Kissling. 2018. Extinction-driven changes in frugivore communities on oceanic islands. Ecography 41:1245–1255.

Henderson, R. W., and R. Powell. 2009. Natural history of West Indian reptiles and amphibians. University Press of Florida, Gainesville.

Herrel, A., B. Vanhooydonck, R. Joachim, and D. J. Irschick. 2004. Frugivory in polychrotid lizards: effects of body size. Oecologia 140:160–168.

Hooghiemstra, H., T. Olijhoek, M. Hoogland, M. Prins, B. van Geel, T. Donders, W. Gosling, et al. 2018. Columbus' environmental impact in the New World: land use change in the Yaque River valley, Dominican Republic. Holocene 28:1818–1835.

Hopkins, S. S. B. 2008. Reassessing the mass of exceptionally large rodents using toothrow length and area as proxies for body mass. Journal of Mammalogy 89:232–243.

Iturralde-Vinent, M., and R. D. E. MacPhee. 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. Bulletin of the AMNH, no. 238.

IUCN (International Union for Conservation of Nature). 2023. The IUCN Red List of Threatened Species. Version 2022-2. https://www.iucnredlist.org.

Jackson, S. T., and J. L. Blois. 2015. Community ecology in a changing environment: perspectives from the Quaternary. Proceedings of the National Academy of Sciences of the USA 112:4915–4921.

Janzen, D. H., and P. S. Martin. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. Science 215:19–27.

Järvinen, O., C. Babin, R. K. Bambach, E. Flügel, F. T. Fürsich, D. J. Futuyma, K. J. Niklas, et al. 1986. The neontologico-paleontological interface of community evolution: how do the pieces in the kaleidoscopic biosphere move? Pages 330–350 *in* D. M. Raup and D. Jablonski, eds. Patterns and processes in the history of life. Springer, Berlin.

Jones, K. E., K. E. Barlow, N. Vaughan, A. Rodríguez-Durán, and M. R. Gannon. 2001. Short-term impacts of extreme environmental disturbance on the bats of Puerto Rico. Animal Conservation 4:59–66.

Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648.

Jønsson, K. A., P.-H. Fabre, and M. Irestedt. 2012. Brains, tools, innovation and biogeography in crows and ravens. BMC Evolutionary Biology 12:72.

Kehlmaier, C., A. Barlow, A. K. Hastings, M. Vamberger, J. L. A. Paijmans, D. W. Steadman, N. A. Albury, et al. 2017. Tropical ancient DNA reveals relationships of the extinct Bahamian giant tortoise *Chelonoidis alburyorum*. Proceedings of the Royal Society B 284:20162235.

Kemp, M. E. 2023. Defaunation and species introductions alter long-term functional trait diversity in insular reptiles. Proceedings of the National Academy of Sciences of the USA 120:e2201944119.

———. 2024. Data from: Assembly, persistence, and disassembly dynamics of Quaternary Caribbean frugivore communities. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.1ns1rn92f.

Kemp, M. E., A. M. Mychajliw, J. Wadman, and A. Goldberg. 2020. 7000 years of turnover: historical contingency and human niche construction shape the Caribbean's Anthropocene biota. Proceedings of the Royal Society B 287:20200447.

Kim, S., L. Sales, D. Carreira, and M. Galetti. 2022. Frugivore distributions are associated with plant dispersal syndrome diversity in the Caribbean archipelagos. Diversity and Distributions 28:2521–2533.

Koch, P. L., and A. D. Barnosky. 2006. Late Quaternary extinctions: state of the debate. Annual Review of Ecology, Evolution, and Systematics 37:215–250.

Kolchanova, S., A. Komissarov, S. Kliver, A. Mazo-Vargas, Y. Afanador, J. Velez-Valentín, R. V. De La Rosa, et al. 2021. Molecular phylogeny and evolution of Amazon parrots in the Greater Antilles. Genes 12:608.

Kurta, A., A. Rodríguez-Durán, and A. K. Wilson. 2023. Bats of the West Indies: a natural history and field guide. Cornell University Press, Ithaca, NY.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos 84:177–192.

———. 2000. Community ecology in a changing world. Ecology Institute, Oldendorf/Luhe.

Lewis, D. S., R. van Veen, and B. S. Wilson. 2011. Conservation implications of small Indian mongoose (*Herpestes auropunctatus*) predation in a hotspot within a hotspot: the Hellshire Hills, Jamaica. Biological Invasions 13:25–33.

Lim, J. Y., J.-C. Svenning, B. Göldel, S. Faurby, and W. D. Kissling. 2020. Frugivore-fruit size relationships between palms and mammals reveal past and future defaunation impacts. Nature Communications 11:4904.

Lyons, S., J. Miller, D. Fraser, F. Smith, A. Boyer, E. Lindsey, and A. Mychajliw. 2016. The changing role of mammal life histories in Late Quaternary extinction vulnerability on continents and islands. Biology Letters 12:20160342.

Maunder, M., A. Leiva, E. Santiago-Valentín, D. W. Stevenson, P. Acevedo-Rodríguez, A. W. Meerow, M. Mejía, et al. 2008. Plant conservation in the Caribbean island biodiversity hotspot. Botanical Review 74:197–207.

McFadden, I. R., S. A. Fritz, N. E. Zimmermann, L. Pellissier, W. D. Kissling, J. A. Tobias, M. Schleuning, et al. 2022. Global plant-frugivore trait matching is shaped by climate and biogeographic history. Ecology Letters 25:686–696.

McFarlane, D., R. MacPhee, and D. Ford. 1998. Body size variability and a Sangamonian extinction model for Amblyrhiza, a West Indian megafaunal rodent. Quaternary Research 50:80–89.

Meiri, S. 2018. Traits of lizards of the world: variation around a successful evolutionary design. Global Ecology and Biogeography 27:1168–1172.

Monteiro, L. R., and M. R. Nogueira. 2011. Evolutionary patterns and processes in the radiation of phyllostomid bats. BMC Evolutionary Biology 11:137.

Moran-Lopez, T., T. Carlo, and J. Morales. 2018. The role of frugivory in plant diversity maintenance—a simulation approach. Ecography 41:24–31.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Naniwadekar, R., A. Gopal, N. Page, S. Ghuman, V. Ramachandran, and J. Joshi. 2021. Large frugivores matter more on an island: insights from island-mainland comparison of plant–frugivore communities. Ecology and Evolution 11:1399–1412.

Negrón-Ortiz, V. N., and G. A. J. Breckon. 1989. A note on the dispersal of *Zamia* (Zamiaceae) in Puerto Rico. Caribbean Journal of Science 25:86–87.

Nieto-Blázquez, M. E., M. P. Quiroga, A. C. Premoli, and J. Roncal. 2022. *Podocarpus* in the palaeogeographically complex island of Hispaniola: a stepping-stone colonization and conservation recommendations. Diversity and Distributions 28:214–226.

O'Connor, S.-J., and D. Kelly. 2012. Seed dispersal of matai (*Prumnopitys taxifolia*) by feral pigs (*Sus scrofa*). New Zealand Journal of Ecology 36:228–231.

Olson, S. 2005. Refutation of the historical evidence for a Hispaniolan macaw (Aves: Psittacidae: Ara). Caribbean Journal of Science 41:319–323.

Oswald, J. A., B. T. Smith, J. M. Allen, R. P. Guralnick, D. W. Steadman, and M. J. LeFebvre. 2023. Changes in parrot diversity after human arrival to the Caribbean. Proceedings of the National Academy of Sciences of the USA 120:e2301128120.

Pasachnik, S. A., and V. Martin-Velez. 2017. An evaluation of the diet of *Cyclura* iguanas in the Dominican Republic. Herpetological Bulletin 140:6–12.

Pérez-Méndez, N., P. Jordano, C. García, and A. Valido. 2016. The signatures of Anthropocene defaunation: cascading effects of the seed dispersal collapse. Scientific Reports 6:24820.

Powell, R., and R. W. Henderson. 2012. Island lists of West Indian amphibians and reptiles. Bulletin of the Florida Museum of Natural History 51:85–166.

Reynolds, R. G., A. H. Miller, S. A. Pasachnik, C. R. Knapp, M. E. Welch, G. Colosimo, G. P. Gerber, et al. 2022. Phylogenomics and historical biogeography of West Indian rock iguanas (genus *Cyclura*). Molecular Phylogenetics and Evolution 174:107548.

Ricklefs, R. E. 2008. Disintegration of the ecological community. American Naturalist 172:741–750.

Ricklefs, R., and E. Bermingham. 2008. The West Indies as a laboratory of biogeography and evolution. Philosophical Transactions of the Royal Society B 363:2393–2413.

Roca, A., G. Bar-Gal, E. Eizirik, K. Helgen, R. Maria, M. Springer, S. O'Brien, et al. 2004. Mesozoic origin for West Indian insectivores. Nature 429:649–651.

Sayol, F., R. S. C. Cooke, A. L. Pigot, T. M. Blackburn, J. A. Tobias, M. J. Steinbauer, A. Antonelli, et al. 2021. Loss of functional diversity through anthropogenic extinctions of island birds is not offset by biotic invasions. Science Advances 7:eabj5790.

Sherratt, E., M. del Rosario Castañeda, R. J. Garwood, D. L. Mahler, T. J. Sanger, A. Herrel, K. de Queiroz, et al. 2015. Amber fossils demonstrate deep-time stability of Caribbean lizard communities. Proceedings of the National Academy of Sciences of the USA 112:9961–9966.

Shev, G. T., J. E. Laffoon, and C. L. Hofman. 2021. Human and hutia (*Isolobodon portoricensis*) interactions in pre-Columbian Hispaniola: the isotopic and morphological evidence. Journal of Archaeological Science Reports 37:102913.

Shiels, A. B., and D. R. Drake. 2011. Are introduced rats (*Rattus rattus*) both seed predators and dispersers in Hawaii? Biological Invasions 13:883–894.

Shrader-Frechette, K. S., and E. D. McCoy. 1993. Method in ecology: strategies for conservation. Cambridge University Press, Cambridge.

Simberloff, D. 2004. Community ecology: is it time to move on? American Naturalist 163:787–799.

Smith, J. 2001. High species diversity in fleshy-fruited tropical understory plants. American Naturalist 157:646–653.

Stark, G., and M. Galetti. 2024. Rewilding in cold blood: restoring functionality in degraded ecosystems using herbivorous reptiles. Global Ecology and Conservation 50:e02834.

Torres, D., J. Castano, and J. Carranza-Quiceno. 2020. Global patterns in seed germination after ingestion by mammals. Mammal Review 50:278–290.

Underwood, A. J. 1986. What is a community? Pages 351–367 *in* D. M. Raup and D. Jablonski, eds. Patterns and processes in the history of life. Springer, Berlin.

Valido, A., and J. M. Olesen. 2019. Frugivory and seed dispersal by lizards: a global review. Frontiers in Ecology and Evolution 7:49.

Vélez-Juarbe, J., T. Martin, R. D. E. Macphee, and D. Ortega-Ariza. 2014. The earliest Caribbean rodents: Oligocene caviomorphs from Puerto Rico. Journal of Vertebrate Paleontology 34:157–163.

Villar, N., C. Paz, V. Zipparro, S. Nazareth, L. Bulascoschi, E. Bakker, and M. Galetti. 2021. Frugivory underpins the nitrogen cycle. Functional Ecology 35:357–368.

Vollstädt, M. G. R., M. Galetti, C. N. Kaiser-Bunbury, B. I. Simmons, F. Gonçalves, A. L. Morales-Pérez, L. Navarro, et al. 2022. Plant–frugivore interactions across the Caribbean islands: modularity, invader complexes and the importance of generalist species. Diversity and Distributions 28:2361–2374.

Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. Ecology 95:2027–2027.

Vice President: Priyanga Amarasekare