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Annual Review of Ecology, Evolution, and Systematics

Anthropogenic Extinction Dominates Holocene Declines of West Indian Mammals

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Annu. Rev. Ecol. Evol. Syst. 2017. 48:301–27

First published online as a Review in Advance on August 23, 2017

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

https://doi.org/10.1146/annurev-ecolsys-110316-022754

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Keywords

extinction, Caribbean, West Indies, Holocene, megafauna, mammal, Quaternary

Abstract

The extensive postglacial mammal losses in the West Indies provide an opportunity to evaluate extinction dynamics, but limited data have hindered our ability to test hypotheses. Here, we analyze the tempo and dynamics of extinction using a novel data set of faunal last-appearance dates and human first-appearance dates, demonstrating widespread overlap between humans and now-extinct native mammals. Humans arrived in four waves (Lithic,

Archaic, Ceramic, and European), each associated with increased environmental impact. Large-bodied mammals and several bats were extinct by the Archaic, following protracted extinction dynamics perhaps reflecting habitat loss. Most small-bodied rodents and lipotyphlan insectivores survived the Ceramic, but extensive landscape transformation and the introduction of invasive mammals following European colonization caused further extinctions, leaving a threatened remnant fauna. Both large- and small-bodied nonvolant mammals disappeared, reflecting complex relationships between body size, ecology, and anthropogenic change. Extinct bats were generally larger species, paralleling declines from natural catastrophes.

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1. INTRODUCTION

During the Holocene epoch (11,700 years ago–present), the relatively climatically stable period following the last Ice Age glaciation, the archipelagos of the Caribbean, collectively known as the West Indies, experienced more mammalian extinctions than any other global region (Turvey 2009). From a diverse Late Quaternary terrestrial fauna containing more than 130 currently recognized species, including megalonychid sloths, lipotyphlan insectivores, primates, and multiple rodent and bat lineages, only 13 nonvolant mammal species and 60 bat species probably survived into the present (Dávalos & Turvey 2012, Turvey et al. 2017). Research on these extinctions has focused mainly on nonvolant mammals (Morgan & Woods 1986), but numerous bat populations also disappeared (Soto-Centeno & Steadman 2015, Stoetzel et al. 2016, Valente et al. 2017). For context, only ~255 mammal species are thought to have become globally extinct during the postglacial period (Turvey 2009). Although species-level taxonomy of several West Indian groups remains subject to revision, complicating how prehuman diversity is estimated (Hansford et al. 2012), previously unknown extinct species from the region's Quaternary record are described regularly (e.g., Brace et al. 2015; Cooke et al. 2011; Turvey et al. 2010, 2012), suggesting true extinction levels may be even higher than currently recognized. Clarifying the dynamics and drivers of this uniquely severe extinction event can provide critical insights for understanding mammalian biodiversity loss in general, as well as novel information to aid conservation of surviving but highly threatened West Indian mammals.

Climate change and both direct and indirect human activities (e.g., hunting, habitat transformation, and introduction of invasive species) have been the main explanations for West Indian mammal extinctions (Dávalos & Russell 2012, Turvey et al. 2007). This discussion mirrors the long-standing debate on drivers of the Late Pleistocene continental megafaunal extinctions, for which potential climatic and anthropogenic factors are often correlated in time (Martin 1984, Stuart 2015). However, humans did not reach the West Indies until after the major climatic shift at the glacial-interglacial transition, and so glacial and anthropogenic impacts are temporally decoupled. Understanding prehistoric extinction dynamics in this island system may therefore clarify causes of earlier continental extinctions. In the West Indies, the precise timing of extinctions and human arrival remains disputed, leading to uncertainty concerning the causes of these extinctions (Fitzpatrick 2006, Soto-Centeno & Steadman 2015). New radiocarbon dates for extinct West Indian mammals (Brace et al. 2016, Stoetzel et al. 2016, Turvey et al. 2007), together with an improved understanding of the timing of regional human colonization and associated environmental changes (Giovas & Fitzpatrick 2014, Rick et al. 2013, Rivera-Collazo 2015), provide increasing evidence that humans were the primary agents behind the fauna's demise. Here, we synthesize available faunal last-appearance dates (LADs) and human first-appearance dates (FADs) and use statistical approaches to develop a coherent historical ecology of West Indian mammal extinction.

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2. WEST INDIAN EXTINCTION: A MATTER OF TIMING

A review of the evidence of the causes of West Indian mammal extinction requires establishing a chronology of species disappearance and human settlement, which in turn depends on a robust radiometric framework. We review previously published radiocarbon dates [both accelerator mass spectrometry (AMS) and non-AMS] associated with extinct species or prehistoric human arrival on different islands, as well as previously unpublished AMS dates available to the authors. All dates have been calibrated with the IntCal13 or MarineCal13 calibration curve in OxCal 4.2 (Bronk Ramsey 2009) and are reported in calendar, not radiocarbon (^{14}C), years.

2.1. Extinction of Mammals and the Pleistocene–Holocene Transition

The end of the last glaciation heralded massive environmental change, even at low latitudes, leading researchers to relate many regional extinction events to natural climate change. Three main natural extinction drivers have been proposed: shifts from xeric to mesic ecosystems, loss of island area, and flooding of critical habitats such as caves (Dávalos & Russell 2012, Morgan 2001, Morgan & Woods 1986, Pregill & Olson 1981).

The West Indian Quaternary record, particularly bird and herpetological subfossils, has revealed that Late Pleistocene ecosystems contained many species associated with cooler, drier conditions instead of mesic habitats; these species may have been unable to survive in newly mesic ecosystems (Pregill & Olson 1981). The glacial-interglacial transition was also abrupt; coral reef data suggest the sea level rose ~120 m from 20,000 years before present (BP) (Blanchon & Shaw 1995), including three catastrophic events (13.5-m rise at 14,200 BP, 7.5-m rise at 11,500 BP, and 6.5-m rise at 7,600 BP). With shallow banks surrounding the Bahamas, Cuba, Puerto Rico, and many northern Lesser Antillean islands (**Figure 1**), deglaciation dramatically reduced the area of many islands. Bathymetric analyses suggest some islands (e.g., Abaco in the Bahamas) lost up to 85% of their original area, whereas others lost only 20% or less (e.g., Hispaniola, Jamaica) (Dávalos & Russell 2012). Assuming at least some of this previously exposed area supported terrestrial habitats, sea-level rise would have driven large-scale habitat loss. Species-area relationships for modern faunas indicate such loss could have driven extinctions among island endemics (Dávalos & Russell 2012).

Habitat loss induced by climate change could also include loss of ecologically critical geographic features. For example, hot caves (which harbor closed chambers with dense bat populations, generating stable hot, humid atmospheres) are a scarce resource required by many West Indian bats (Dávalos & Turvey 2012). Loss of even one hot cave can be catastrophic for individual populations. For example, *Natalus primus*, known only from subfossils until 1992, persists as a single extant population dependent on one roost near the shore in southwestern Cuba (Tejedor et al. 2004). Flooding of low-lying caves by rising seas is therefore a third mechanism of climate-driven extinction, after habitat change and reduced island area (Morgan 2001).

Environmental shifts at the Pleistocene-Holocene boundary represent only the most recent event in a long history of glacial cycles, and all climate-based Quaternary extinction hypotheses must explain why comparable extinctions are not seen during previous glacial-interglacial transitions (Soto-Centeno et al. 2015, Stuart 2015). However, such hypotheses have one good precedent in the West Indies. On the basis of chronostratigraphic records from its Quaternary distribution on the Anguilla Bank and the likely demands of a land mammal weighing ~60–200 kg (Biknevicius et al. 1993), the extinction of the rodent *Amblyrhiza inundata*, the largest West Indian Quaternary land mammal, apparently followed a 93% decrease in island size during the previous (Sangamonian) interglacial (McFarlane et al. 1998). Population models incorporating body mass and related demographic parameters estimate the cumulative probability of *Amblyrhiza*

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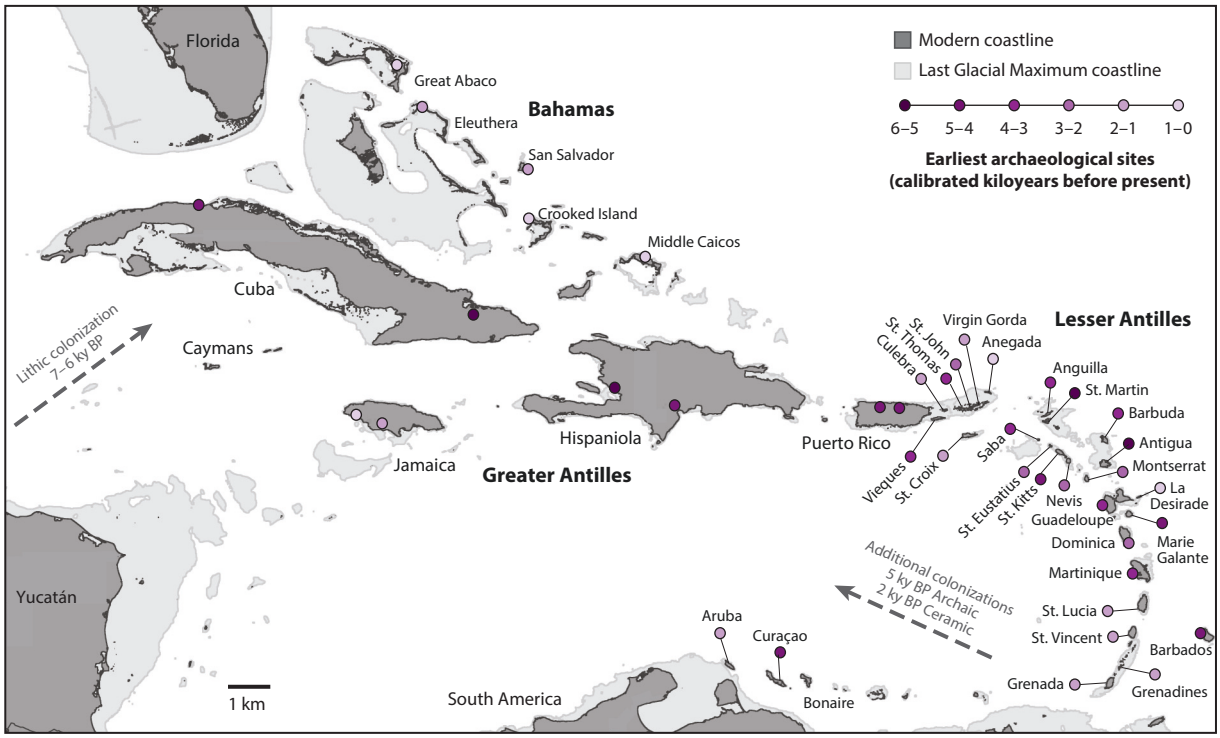

Figure 1

Human colonization of the West Indies did not follow a simple minimal-distance pattern. Instead, there were at least three indigenous waves of colonization (Lithic, Archaic, and Ceramic); the earliest (*darkest hues* for settlements) was probably from Mesoamerica, and the later two were likely from South America. Paradoxically, the southern islands of the Lesser Antilles were colonized relatively late (*lighter hues*). The Cayman Islands were not settled until the European arrival. Lighter outlines indicate banks emergent at the Last Glacial Maximum (Dávalos & Turvey 2012).

extinction during the Sangamonian at >0.99, linking island area to population dynamics, despite many unknowns (McFarlane et al. 1998).

The only other quantitative test of the hypothesis that West Indian extinctions were driven by habitat loss following sea-level rise was conducted recently for bats. Using species-area relationships to estimate species richness lost by island, Dávalos & Russell (2012) found that island area declines in the Bahamas and Greater Antilles predicted numbers of postglacial bat species losses, explaining ~85% of the change in species numbers. Area loss as a cause of bat species loss is therefore well supported, assuming that extinctions track deglaciation. However, testing this hypothesis requires knowledge about LADs for extirpated populations and associated human FADs (Soto-Centeno & Steadman 2015), which were then unavailable.

2.2. The Signature of Human Activity on Extinction

Human activity has been viewed as a complementary or alternative explanation for West Indian extinctions (Morgan & Woods 1986). Contemporary anthropogenic transformation of the biosphere is responsible for catastrophic species declines and disruptions to ecosystem structure and functioning, and human activities are also linked to earlier biodiversity change (Barnosky et al.

2016). Possible human involvement in the loss of ~97 continental megafaunal vertebrate genera, which disappeared ~47,000 BP in Australia and 14,000–11,700 BP in the Americas and Eurasia, is still debated (Stuart 2015). Some form of human involvement in these extinctions is now widely accepted, as the stepwise nature of these extinctions across different continents correlates with the regional arrival of technologically modern humans instead of with any spatiotemporally staggered environmental change (Steadman et al. 2005, Stuart 2015). Extensive vertebrate extinctions also occurred under broadly modern environmental and climatic conditions during the subsequent Holocene, when evidence for human involvement is not confounded by climatic factors. Most postglacial species losses occurred in island faunas and are associated with the regional arrival of prehistoric settlers, providing important circumstantial evidence for human involvement (Turvey 2009).

The mechanisms by which humans may have driven prehistoric losses are unclear at a global level and likely differed between regions. Explanations vary between the original model of rapid, direct overhunting (Alroy 2001, Martin 1984) and models of more protracted extinction associated with less intensive hunting, typically coupled with indirect interactions such as habitat modification, e.g., through landscape burning (Stuart 2015). Life history is also critical to understanding and predicting effects of hunting pressure, as species with low reproductive rates—an ecophysiological characteristic typical of island endemics (McNab 2001)—are more vulnerable to hunting pressure (Zuo et al. 2013). Insular mammal faunas typically lack native mammalian predators and contain few sympatric species filling closely similar niches; consequently, they are also vulnerable to invasive mammalian predators and competitors.

Levels and rates of prehistoric faunal collapse also vary between regions. Some island systems (e.g., New Zealand) suffered rapid, severe vertebrate losses within centuries or decades of human arrival (Holdaway et al. 2014), but human arrival was not always associated with landscape changes or unsustainable exploitation of vertebrate populations (Rick et al. 2013). Other systems (e.g., Madagascar) experienced coexistence between humans and endemic megafauna for millennia and apparently lost now-extinct taxa only in recent centuries (Goodman & Jungers 2014). The latter pattern is similar to the human-megafauna overlap period in some continental regions, estimated at ~3,900 years in Australia and ~1,570 years across the Americas (Gillespie et al. 2006, Johnson et al. 2013, Stuart 2015). Therefore, complex variation in dynamics, rates, and probable mechanisms of human-caused Late Quaternary extinctions suggests there is no one-size-fits-all mechanism; rather, close appraisal of available long-term archives is required for individual systems.

2.3. Tempo and Mode of Human Colonization and Resource Use in the West Indies

The timing and effects of human arrival in the West Indies are critical to the New World extinction debate, as colonization of the West Indies occurred millennia after the Pleistocene-Holocene transition (Steadman et al. 2005). Colonization was a complex process, and many details remain unclear. Although a map of earliest dated human presence suggests continuous geographic progression between islands (**Figure 1**, **Supplemental Figure 1**), the peopling of the West Indies proceeded in stages and waves and was more influenced by seafaring technology and ocean currents than by geographic distance (Fitzpatrick 2015).

Supplemental Material

Archaeologists recognize four colonization waves associated with increasingly complex material culture (Fitzpatrick 2006, Keegan 1994): Lithic (~7,000–4,000 BP), Archaic (~5,000–2,000 BP), Ceramic (~2,500 BP in Puerto Rico and the Virgin Islands, later elsewhere), and historical [since 1492 Common Era (CE), i.e., ~500 BP]. Only the earliest Lithic sites, on Cuba (Levisa 1, 5,911 ± 191 BP; Cooper 2010) and Hispaniola (Vignier II, 6,028 ± 85 BP; Moore 1991), may represent

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migration from Mesoamerica, although a South American origin remains possible (Keegan 1994). Archaeological and genetic evidence supports a South American origin for subsequent waves of Amerindian migration (Lalueza-Fox et al. 2001), with the Ceramic wave bringing alleles from Amazonian groups (Moreno-Estrada et al. 2013).

Whether Lithic sites were inhabited or represent transient tool-making sites is unknown, and no animal remains from these sites have been reported. Population dynamics of early Lithic populations therefore cannot be inferred. The environmental footprint and capacity to transform terrestrial landscapes increased with each successive migration wave and its technology (Rick et al. 2013). However, local sites and entire islands were sometimes abandoned and recolonized, pauses in migration suggest human populations increased nonlinearly, and interactions between population growth and local carrying capacity likely determined the sustainability of resource use (Giovas & Fitzpatrick 2014, Newsom & Wing 2004).

Little is also known about population size and distribution of Archaic peoples, but a diverse material culture is known from Cuba, Hispaniola, Puerto Rico, and several Lesser Antillean islands (Fitzpatrick 2015). The shoreline location of most Archaic sites, evidence of seasonal occupation, and reliance on marine resources have led researchers to characterize pre-Ceramic peoples as mobile hunter-gatherers with little influence on terrestrial faunas (Veloz Maggiolo 1991). However, sites in Puerto Rico, Antigua, and Saba reveal extensive effects on terrestrial habitats. Excavations in Angostura, Puerto Rico, have revealed both paleobotanical and geoarchaeological evidence of sustained cultivation and burning, including the presence of anthropogenic soils similar to Amazonian dark soils approximately 3,000 BP (Rivera-Collazo 2015). Together with the Hispaniolan rodent *Isolobodon portoricensis* (dated at Angostura from ~4,000 BP), Archaic peoples introduced wild avocado (*Persea americana*), yellow sapote (*Pouteria campechiana*), wild fig (*Ficus* sp.), primrose (*Oenothera* sp.), and West Indian cherry (*Malpighia* sp.) to Puerto Rico, and also cultivated native yams, the starchy roots marunguey (*Zamia* sp.) and arrowroot (*Calathea allouia*), and edible seeds of the corozo palm (*Acrocomia media*) (Newsom & Wing 2004, Rivera-Collazo 2015). Wild beans (*Phaseolus*) were introduced to Cuba ~3,000 BP (Fitzpatrick 2015). A midden rich in mountain crab and bird bones, but largely lacking fish or mollusks, shows intense terrestrial resource use from ~3,500 BP in Plum Piece, Saba, and has been interpreted as representing a seasonally sedentary community that periodically relocated inland to maintain a diverse food base (Hofman et al. 2006).

There is also increasing evidence of land management to establish horticultural landscapes during the Archaic. Pre-Columbian peoples used fire to bring natural habitats into production, and sedimentary records show geographic variation in fire regimes consistent with anthropogenic fires, with timing corresponding to Archaic expansion on Hispaniola and Puerto Rico (Keegan 1994, Rivera-Collazo 2015). Fire is also directly associated with a now-extinct fauna, although the anthropogenic nature of these fires is unconfirmed. In Burma Quarry, Antigua, analyses of charcoal date three species of bats all now extirpated from Antigua, and the extinct rodent *Antillomys rayi*, to 4,300–2,500 BP (Steadman et al. 1984). The loss of small bats from Antigua could be the result of landscape transformation as documented by charcoal.

Mammals were apparently not prominent in the diet of Archaic peoples—records of mammals in Archaic sites, though limited, include the echimyid rodent *Heteropsomys insulans* in Puerto Rico, the plant-visiting bat *Brachyphylla* spp. in Antigua (although whether bats were eaten is unknown), and oryzomyine rodents in Barbados, Nevis, and Antigua (Newsom & Wing 2004). Importantly, there is virtually no evidence of direct exploitation of large mammals such as sloths or monkeys. One published record (Miller 1929) documents the presence of a primate tibia together with rodents and lipotyphlans in a midden, but the association with the archaeological material is dubious. Although there is no evidence for intensive hunting of mammals during this period (i.e., rapid extinction model), landscape changes associated with fires, combined with potentially

undetected hunting of slowly reproducing mammals, may be a more relevant model (i.e., protracted extinction model) to explain the loss of sloth and monkey populations by this period (**Figure 2**).

The last indigenous wave of migration, known as the Ceramic after the high prevalence of pottery in archaeological sites, comprises the ancestors of the Taíno peoples (Keegan 2000). Beginning ~2,500 BP in Puerto Rico and the northern Lesser Antilles and reaching other islands ~1,000 years later (**Figure 2**), the Ceramic peoples introduced dogs (*Canis lupus familiaris*) and guinea pigs (*Cavia porcellus*) throughout the West Indies, and agouti (*Dasyprocta* sp.), peccary (*Tayassu* sp.), and other mammals to several Lesser Antillean islands, along with *Phaseolus* beans, maize (*Zea mays*), cassava (*Manihot esculenta*), peanuts (*Arachis hypogaea*), sweet potatoes (*Ipomoea batatas*), tobacco (*Nicotiana tabacum*), chilis (*Capsicum* sp.), and guava (*Psidium guajava*), caimito (*Chrysophyllum cainito*), annona or sweetsop (*Annona squamosa*), and jobo (*Spondias mombin*) trees (Rick et al. 2013, Rivera-Collazo 2015). Early Ceramic peoples established sedentary villages, including inland sites along rivers, and systematically practiced horticulture and agriculture (Rick et al. 2013). Habitat change linked to this new economic assemblage was unprecedented in scale and had lasting effects on biotic communities (Rick et al. 2013). Early Ceramic (Saladoid) layers on Puerto Rico and the Virgin Islands show abundant land crabs, later displaced by marine mollusks, presumably reflecting exhaustion of land crab populations (Newsom & Wing 2004). Reef fish from post-Saladoid sites have a lower mean trophic level and body mass than those from Saladoid deposits in Nevis, indicating overfishing (Newsom & Wing 2004). Changes in terrestrial animal populations are harder to document. Early Ceramic peoples exploited amphibians, reptiles, seabirds, and rodents, including capromyid hutias in the Greater Antilles and oryzomyine rodents in the Lesser Antilles (Newsom & Wing 2004). But despite the abundance of the capromyid *Isolobodon portoricensis* in middens throughout the Greater Antilles, and of several oryzomyines in middens in the Lesser Antilles, these populations all apparently survived until close to or after European arrival (Turvey et al. 2010, 2012).

By ~2,000–1,500 BP, Saladoid cultures had reached the entire West Indian archipelago excluding the Cayman Islands (**Figure 2**). A new pottery series (Ostionoid) emerged ~1,000 BP (Keegan 2000), in which pottery-lined wells allowed people to settle at sites that lacked consistent rivers (e.g., Barbados, Carriacou, Mustique, and Saint Vincent) (Fitzpatrick 2015), and further inland expansion occurred on larger islands as evidenced by the remains of ball courts (Veloz Maggiolo 1991). This cultural transition was associated with intensification of natural resource exploitation; marine mollusks replace land crabs in deposits throughout the Greater Antilles, presumably because of terrestrial resource decline (Keegan 2000); reef fish in Puerto Rican middens decline in size and trophic level (Wing & Wing 2001); and sites in St. Thomas, St. Martin, Saba, and Nevis also show unsustainable resource use (Wing & Wing 2001), despite evidence of sustainable fishing in Anguilla (Carder et al. 2007). During the Ostionoid period overharvesting of mollusks on Jamaica is evident (Keegan et al. 2003), but mollusk size increases on Nevis indicate sustainable harvesting (Giovas et al. 2013). Use of mammals is poorly documented, but general shifts toward less sustainable use reflect increases in human population that likely affected all natural resources.

By the time of European contact, the Taíno had complex forms of social organization suitable to transforming landscapes for productive use. Eighty species of plants were cultivated on land, and intensification included terracing on hillsides and earth mounds replacing slash-and-burn agriculture in some places (Ortiz Aguilú et al. 1991). Estimates of the indigenous population in the West Indies at the time of European contact vary by almost two orders of magnitude, from 100,000 to 6–8 million (Keegan 1996). Low estimates are associated with demographic models scaling to dwellings or agricultural productivity (Curet 1998), and high estimates with models incorporating disease-driven declines that followed contact (Cook 1998). The disparity among these estimates reflects uncertainty inherent to the archaeological record, and the heterogeneity of

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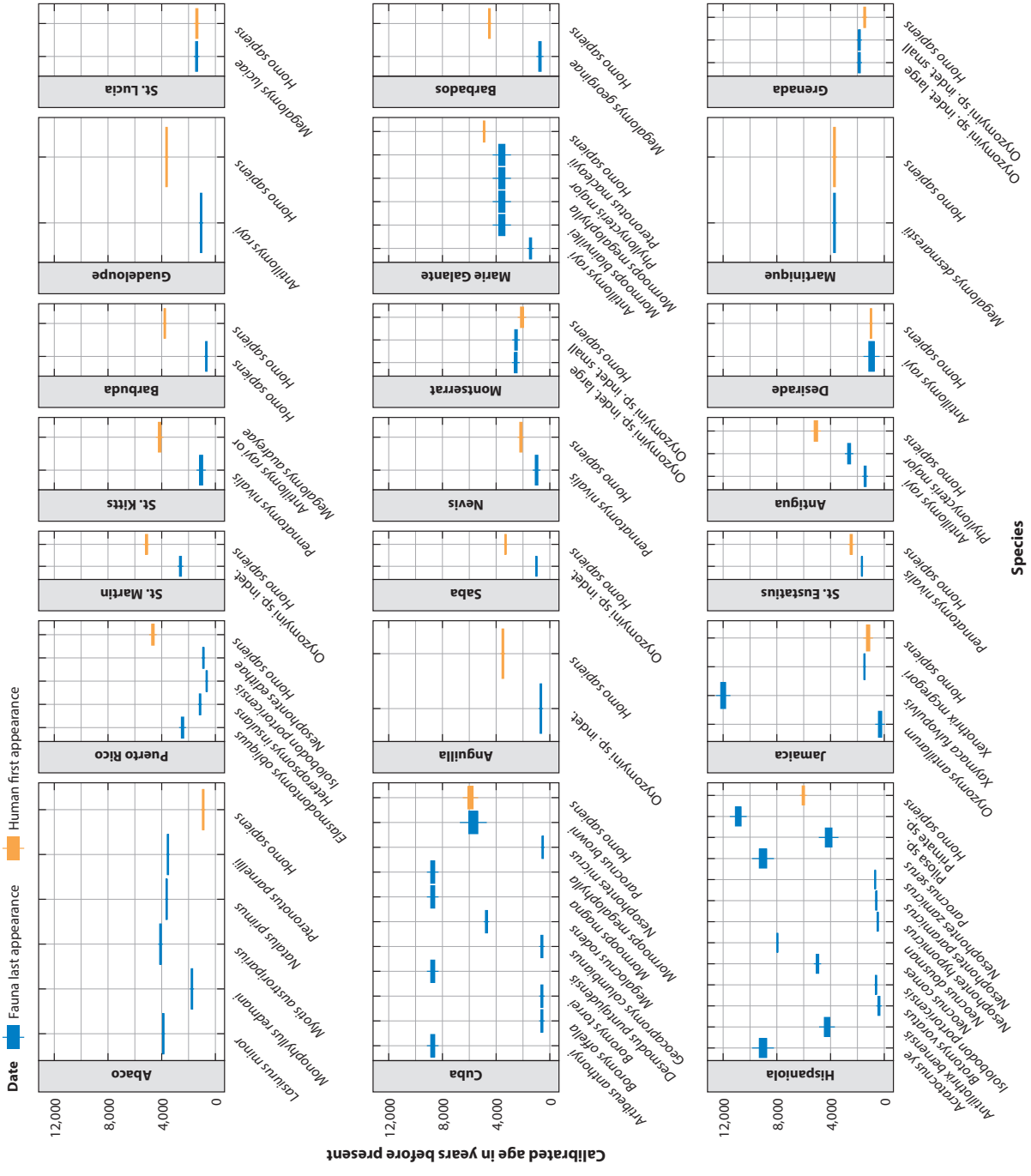

the islands and their cultures that together determine carrying capacity. This variation compounds uncertainty over the extent of prehistoric anthropogenic pressure on West Indian ecosystems.

European arrival in 1492 CE brought further ecological disruption. Initial contact was associated with the collapse of native Taíno societies and rapid depopulation, largely through the transmission of European zoonotic diseases, temporarily reducing direct human pressure on natural resources (Cook 1998). Populations of European colonists and enslaved Taíno and later African peoples remained small for a considerable period. For example, although permanent European occupation of Puerto Rico began in 1508 CE, by 1650 CE its population was only ~880 individuals, and by 1770 CE the population was probably still below that of the Taínos at the time of European contact (Snyder et al. 1987).

European arrival was associated with the introduction of a wide range of invasive plants and animals, however, which likely had rapid and major effects on native biotas. Immediately following European arrival, the introduction from Europe, Africa, Asia, and mainland South America of a wide range of commercial field crops (e.g., sugar cane, cotton, and rice) and noncommercial invasive plants, and the establishment of feral ungulate populations (e.g., pigs, horses, cattle, and goats), would have altered plant communities and ecosystem structure (Watts 1987). Invasive black rats, house mice, and feral cats and dogs became established shortly after European arrival (Watts 1987); these species pose severe risks to insular faunas through predation, competition, and disease transfer, especially on islands lacking native mammalian predators (Courchamp et al. 2003, Wyatt et al. 2008). Even plagues of invasive ants, which can cause catastrophic shifts in tropical island ecosystems, were recorded after European colonization (Wilson 2005).

Rapid population growth occurred in the eighteenth and nineteenth centuries and is associated with massive forest clearance for sugarcane and coffee plantations, other agriculture, export of hardwoods (Funes Monzote 2008, Watts 1987), and further accidental or deliberate introductions of other highly predatory or competitive invasive mammals (e.g., brown rat, *Rattus norvegicus*, and small Asian mongoose, *Herpestes javanicus*) (Horst et al. 2001). The original forest cover of many islands, particularly low-elevation islands in the Bahamas and Lesser Antilles (e.g., Barbados), became highly degraded or almost totally cleared (Keegan 1992, Watts 1987), and larger islands were also heavily modified. Puerto Rico had lost only 6% of its primary forest in 1770 CE but >99% by 1899 CE (Brash 1987). Although forests in Puerto Rico have substantially recovered (Rudel et al. 2000), population growth across most of the West Indies has continued throughout the twentieth and twenty-first centuries, with agricultural and urban expansion, tourism development, and mining driving further land cover change and loss of natural vegetation. Many local ecoregions are now extensively disrupted and highly threatened (Olson et al. 2001, Venter et al. 2016).

2.4. The Chronology of Mammalian Extinction

Much remains unknown about the tempo, chronology, and drivers of West Indian mammal extinctions. This partly reflects the sparse record of reliable radiometric dates, especially for rodents

Figure 2

Boxplot of calibrated dates for Holocene faunal LADs and human FADs are available for only a few islands, mainly in the Greater Antilles. Faunal LADs merely represent an early boundary on the true extinction date. At least five appearance dates are necessary to estimate the true extinction date, and estimates are available for only one species with a sufficient date series (*Xenothrix mcgregori*). When sufficient data are available, statistical estimates place true extinction dates after faunal LADs, and estimates may shift to increase the temporal overlap between humans and extinct species. Abbreviations: FAD, first appearance date; LAD, last appearance date; sp. indet., species indeterminatus.

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Supplemental Material

(**Supplemental Table 2**). Only 57 of >160 extinction/extirpation events for native species have LADs derived from radiocarbon dates of identified specimens (**Figure 2**). Additional dating is a priority; however, paleontological data are often incomplete because of taphonomic factors, species distributions, life histories and behaviors, and the vagaries of collection efforts. The majority of West Indian Quaternary fossils have been recovered from cave and sinkhole sites, which are more likely to preserve cave-dwelling taxa or terrestrial organisms that become trapped. Caves are found in predominantly karstic regions (Draper et al. 1994), leading to uneven fossil distribution across islands. Hot, humid conditions typical of tropical caves also degrade organic materials used in radiocarbon dating; although fossils may be recovered, establishing their age can be difficult. Faunal associations are often used for indirect dating, but such estimates are often insecure owing to complex depositional environments in caves, with many sites spanning multiple time periods. Consequently, the absence of a particular taxon from the West Indian Quaternary record for a particular region or period does not necessarily indicate true absence. Further preservation biases also exist in the regional archaeological record, such that the absence of a taxon may only indicate that it was not consumed on-site.

Few explicit attempts to obtain direct dates for extinct West Indian mammals, or to tie LADs to dates for climatic events, human arrival, or subsequent cultural periods (MacPhee 2005), have been made. However, representatives of all West Indian mammal groups can now be demonstrated to have survived well into the Holocene, ruling out climate-only explanations for extinction. MacPhee et al. (1999) obtained dates of ~500–700 BP, close to the time of European arrival, for three *Nesophontes* (lipotyphlan insectivore) species from Cuba and Hispaniola. Steadman et al. (2005) provided 13 dates for five large- and small-bodied sloth species from Cuba and Hispaniola, which cluster around 7,000–5,000 BP, after the major Pleistocene-Holocene climatic shift, and demonstrated that some taxa persisted after the first regional human arrival (**Supplemental Table 2**). MacPhee et al. (2007) provided an additional younger LAD for the Cuban sloth *Megalocnus rodens* (~5,000 BP), again a millennium or so after human arrival (**Figure 2**). For primates, which are rare in the West Indian record, only one direct date exists: a LAD of ~1,500 BP for the Jamaican primate *Xenothrix mcgregori*, close to the time of first human arrival on this island (Cooke et al. 2017).

Many indirect dates associated with archaeological and paleontological remains for endemic rodents are available, but several lineages lack comprehensive coverage or robust data. Although Woods & Ottenwalder (1992) and Hansford et al. (2012) noted likely associations between *Rattus rattus*, *Plagiodontia spelaeum*, and *Rhizoplagiodontia lemkei* in surficial deposits, suggesting these endemic rodents may have survived until the 1500s, there are no direct dates for any extinct member of the capromyid subfamily Plagiodontinae, which include the sole living native Hispaniolan rodent, *Plagiodontia aedium*. The giant hutias (Heptaxodontidae) probably persisted into the Holocene, on the basis of indirect dating of charcoal associated with teeth of *Elasmodontomys obliquus* in Puerto Rico, indicating a LAD of ~3,500 BP for this species (Turvey et al. 2007). Work by Turvey and colleagues (Brace et al. 2015; Turvey et al. 2010, 2012) has improved knowledge of taxonomy and distribution of Lesser Antillean oryzomyines, but despite abundant dates from charcoal and other materials from sites where these rodents are common, no direct dates exist (**Supplemental Table 2**). Unfortunately, few archaeological sites provide clear reports of the stratigraphic position of now-extinct rodents, making fine temporal resolution of rodent–human interactions difficult to establish.

West Indian bats experienced fewer global extinction events than nonvolant mammals did (bats: 14% of species, with 18% extirpated from the West Indies), but local extirpation was common, with 47% of species eliminated from one or more islands. Patterns and chronologies of these extinctions are complicated; many species range across multiple islands, and some also occur into

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Central and South America. Direct dates are not available for any bat species extinct in the West Indies, but three species extinct on Cuba were recovered from an owl pellet dated to ~8,700 BP that also yielded a specimen of the extant *Monophyllus redmani* (Jiménez Vázquez et al. 2005). The best sequence for understanding regional bat survival and extinction is from Marie Galante, where Stoetzel et al. (2016) dated guano layers from ~3,500 to 37,000 BP. This series documented 12 species, of which one apparently became globally extinct (*Phyllonycteris* cf. *major*), one was extirpated from the West Indies but survived in continental America (*Mormoops megalophylla*), and four were locally extirpated but survived on other islands (*Mormoops blainvillei*, *Pteronotus macleayii* or *P. quadridens*, *P. parnellii*, and *Natalus* cf. *major*). Of these, *M. blainvillei*, *M. megalophylla*, *P. macleayii* or *P. quadridens*, and *P.* cf. *major* have LADs postdating human arrival (**Figure 2**). Soto-Centeno & Steadman (2015) provided additional data on Bahamian bat extirpations, showing that six populations extirpated from Abaco disappeared within the past 4,000 years (**Figure 2**). These data inform possible relationships between bat extirpations and anthropogenic factors, but it remains unclear whether patterns on Marie Galante hold elsewhere.

Studies of West Indian extinctions have generally relied on apparent co-occurrences of LADs and human settlement patterns or climatic events instead of models of human population. Multiple approaches for modeling demographic human settlement dynamics have been developed, and these models can generate frameworks for understanding extinction processes (Alroy 2001, Giovas & Fitzpatrick 2014, Goldberg et al. 2016, Keegan 1995). However, these approaches do not directly address gaps in the archaeological and paleontological records. Modeling population expansion requires knowledge of initial population size and settlement patterns, data frequently derived from the ^{14}C record. Other modeling approaches, such as the ideal free distribution model of Giovas & Fitzpatrick (2014), focus primarily on colonization sequences instead of population density, which would certainly affect island habitats, and remain dependent on accurate archaeological data. Although these approaches help frame the debate around causes of West Indian extinctions, additional dates and better demographic data are needed to fully implement them.

Recently, several authors have attempted to reconstruct extinction events with methods that account for gaps in the fossil record. A species' last record is unlikely to represent its true extinction date, and modeling approaches that assess the quality of pre-LAD records are necessary to infer post-LAD persistence. Saltré et al. (2015) compared eight such methods and found the Gaussian-resampled inverse-weighted McInerny (GRIWM) method (Bradshaw et al. 2012) to best balance misclassification with accuracy. This method incorporates Gaussian resampling to account for date uncertainty, and inversely weights older dates according to their temporal distance from the LAD to account for declining population sizes and thus decreasing detection probability. Direct and indirect dates derived from GRIWM have been used to infer the extinction chronology of the Jamaican monkey, *Xenothrix mcgregori* (Cooke et al. 2017). Unfortunately, the dating record is not dense enough for most of the 180 extirpation/extinction events recorded for West Indian mammals: Only 60 populations, comprising 40 extinct and 7 locally extirpated species, have even one direct or indirect date (**Supplemental Table 2**, **Supplemental Figure 2**). Of these, only 11 populations have the minimum five dates necessary for researchers to infer extinction timing using GRIWM (one sloth: *Neocnus comes*; one lipotyphlan: *Nesophontes edithae*; one primate: *X. mcgregori*; three locally extirpated bats from Marie Galante: *M. blainvillei*, *M. megalophylla*, and *Pteronotus macleayii* or *P. quadridens*; and six rodents: *Boromys offella*, *Geocapromys columbianus*, *Brotomys voratus*, *Oryzomys antillarum*, and *Isolobodon portoricensis* in Puerto Rico, and the undescribed *Capromys* population from Cayman Brac).

Supplemental Material

An alternative to inferring extinction dates that relies on fewer data points is meta-analysis comparing human FADs to faunal LADs, which yields approximate estimates of temporal overlap between faunal and human populations (Lima-Ribeiro & Diniz-Filho 2013). However, the results

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of meta-analyses must be interpreted with caution, as available FADs will likely be younger than the true first occurrence and available LADs will likely be older than the true last occurrence, biasing results toward underestimating overlap (Johnson et al. 2013). We used a Bayesian implementation of this method to assess relationships between available dates for regional human arrival and mammal extinction/extirpation (**Supplemental Bayesian Analyses**).

The model that explained the most variance ($R^2 = 0.61$) included only a categorical predictor describing archaeological versus paleontological dates and had similar error variance (homoscedasticity) across islands (**Supplemental Table 4**). The single predictor may reflect the presence of smaller rodents versus the general absence of other mammals from archaeological sites. Importantly, this model separates faunal LADs on Cuba and Hispaniola into two groups, one before and one after 5,000 BP, on the basis of clusters emergent from the data (**Figure 2**). This pattern indicates two waves of extinction on the largest West Indian islands with the most taxonomically and ecologically diverse prehuman faunas. The earlier cluster of Holocene LADs includes all of the largest-bodied taxa. This apparent postglacial but prehuman disappearance of some Cuban and Hispaniolan species must be interpreted with caution, as it treats limited available data at face value. Without extinction date estimates derived from analyses such as GRIWM, this apparent lack of human-faunal overlap may merely be an artifact of incomplete LADs.

Meta-analysis shows overlap between now-extinct fauna and humans on most islands (**Supplemental Figure 3**). The overlap period between humans and sloths (Steadman et al. 2005) on Hispaniola and Cuba likely lasted more than 1,000 years, and indirect dates for the Hispaniolan primate *Antillothrix bernensis* suggest co-occurrence for nearly 2,000 years (**Figure 2**). This protracted pattern of overlap between larger-bodied taxa and earliest human populations mirrors patterns across the Americas and Australia (Gillespie et al. 2006, Johnson et al. 2013). This overlap contrasts with results for Jamaica, where human settlers arrived much later (1,200 BP) than elsewhere in the Greater Antilles (Fitzpatrick 2006), and the LAD for the island's only extinct large-bodied rodent, *Clidomys osborni*, predates the Holocene (MacPhee 1984, MacPhee & Flemming 2003). Finally, Abaco, the sole Bahamian island with available LAD and FAD data, shows no overlap between extinct species and humans. Human settlement on the Bahamas occurred fairly late (**Figure 1**), and future research here should focus on finding new fossil dates to populate chronological extinction models.

3. THE BIOLOGY OF MAMMALIAN EXTINCTION EVENTS: HOW HUMANS HAVE SHAPED POPULATIONS AND COMMUNITIES

3.1. Biology of Resilience and Vulnerability

Large-scale macroecological analyses of extant and Quaternary mammals, incorporating biological, ecological, and phylogenetic data, have identified intrinsic and extrinsic variables associated with increased anthropogenic extinction risk (Cardillo et al. 2005, 2008; Turvey & Fritz 2011). The formerly species-rich West Indian fauna represents an informative system for investigating vulnerability and resilience and clarifying extinction dynamics. However, even basic ecological and life-history parameters for most species are unknown (although see Cooke 2011, McAfee 2011), phylogenies of many taxa are poorly resolved, and research has been limited and qualitative.

Body mass is an important correlate of mammalian extinction risk (Cardillo et al. 2005, 2008), and the West Indian fauna displays a clear mass-based extinction signal (Hansford et al. 2012, Steadman et al. 2005). Whereas the largest extant mammal (Cuban hutia, *Capromys pilorides*) has a mass of 3.1–5.6 kg (Borroto-Páez & Mancina 2011), the Quaternary fauna formerly contained

25 large-bodied (>3 kg) sloth, rodent, and primate species, comprising 34% of nonvolant species, with the largest weighing ~150 kg (**Figure 3**). These species were among the first to disappear following human arrival (**Figure 2**). Larger-bodied species typically have lower intrinsic population densities and population growth rates, making them more vulnerable to environmental changes, and are also disproportionately exploited by humans (Alroy 2001, Zuo et al. 2013); both direct and indirect anthropogenic activities may therefore have contributed to their disappearance. Similar size-biased extinction patterns are also seen in other West Indian vertebrates (Kemp & Hadly 2015, Steadman & Hilgartner 1999).

However, the pattern for mammals is more complex: All nonvolant species below 0.48 kg (the mass of *Mesocapromys angelcabrerai*; Borroto-Páez & Mancina 2011), representing 22% of the nonvolant fauna and including nesophontids, *Solenodon marcanoi*, echimyids, and oryzomyines, are also extinct. Some small-bodied taxa, notably oryzomyines, are abundant in pre-Columbian middens, indicating extensive prehistoric exploitation (Newsom & Wing 2004). Many representatives of small-bodied clades survived until close to or after European arrival (**Figure 2**), however, suggesting that extinction was driven by historical-era factors (Turvey et al. 2010, 2012), possibly predation by or competition with invasive rats and mongooses (Borroto-Páez 2009, Lewis et al. 2011). The medium-sized class (0.48–5.6 kg) of nonvolant mammals now contains the only surviving native species; however, this class also suffered considerable losses, with 19 species (59% of size class) extinct (**Figure 3**). The pattern of extended survival of medium-bodied species (Hansford et al. 2012) differs from a proposed pattern of elevated extinction for mammals of intermediate body mass in Australia, where native species are threatened by larger invasive species (e.g., cats and foxes) (Burbidge & McKenzie 1989, Cardillo & Bromham 2001).

Other extinction risk correlates are less well understood, although consideration of surviving West Indian species can suggest factors potentially associated with resilience. Most extant nonvolant species (e.g., capromyids and *Solenodon* spp.) exhibit traits correlated with decreased extinction risk (Colles et al. 2009, Johnson 2002), including dietary/resource generalism (generalist omnivory and herbivory), habitat generalism, arboreality, and denning behavior (Borroto-Páez & Mancina 2011, Campbell et al. 1991, Ottenwalder 1999, Woods & Ottenwalder 1992), in wide-scale studies. Geography is also a likely determinant of regional survival, with nonvolant species persisting only on large islands with inaccessible habitats (e.g., high-elevation refugia and karstic landscapes) or on tiny islets with reduced human pressures (Fisher 2011). However, several extant West Indian nonvolant mammals exhibit traits associated with elevated extinction risk, including slow life history (e.g., *Solenodon* spp.) and dietary specialization (e.g., mangrove specialist *Mesocapromys* spp.) (Borroto-Páez & Mancina 2011, Ottenwalder 1999), and some extinct taxa probably exhibited ecologically resilient traits such as arboreality (e.g., primates and smaller-bodied sloths) (Tallman & Cooke 2016, White 1993).

Proportionally fewer West Indian bats disappeared than other mammals, and bats are thought to experience lower extinction risk because they fly (18% of bats are threatened versus 25% of all mammals) (IUCN 2016). However, bats reproduce slowly (Szekely et al. 2015), and this may help explain why 78 of 472 island populations were extirpated. More LADs are needed to determine how human actions might have contributed to bat extirpations (**Figure 2**). Nevertheless, extirpation events again tended to affect larger-bodied species (**Figure 3**). Life-history traits correlated with larger size would likely have made such species (e.g., *Phyllonycteris* cf. *major*) vulnerable to human impacts, including habitat loss, and this size selectivity also matches patterns of posthurricane bat decline (Jones et al. 2001). Species feeding on plant resources are more sensitive to hurricane disturbance (Jones et al. 2001); however, roughly half of the West Indian herbivorous

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bat species remain extant (**Figure 3**). The blood specialist *Desmodus puntajudensis* possibly relied on sloths as hosts (Suárez 2005) and disappeared alongside its likely prey (**Figure 2**). Other patterns of loss and persistence are harder to understand. Short-faced bats, which are tree-roosting specialists that feed on figs, show no sympatry today in the West Indies, but up to three species seem to have coexisted on Pleistocene Cuba (definitely *Phyllops silvai* and *P. vetus* and possibly *Cubanycteris silvai*; the extant *P. falcatus* is probably a recent colonist) (Suárez & Díaz-Franco 2003).

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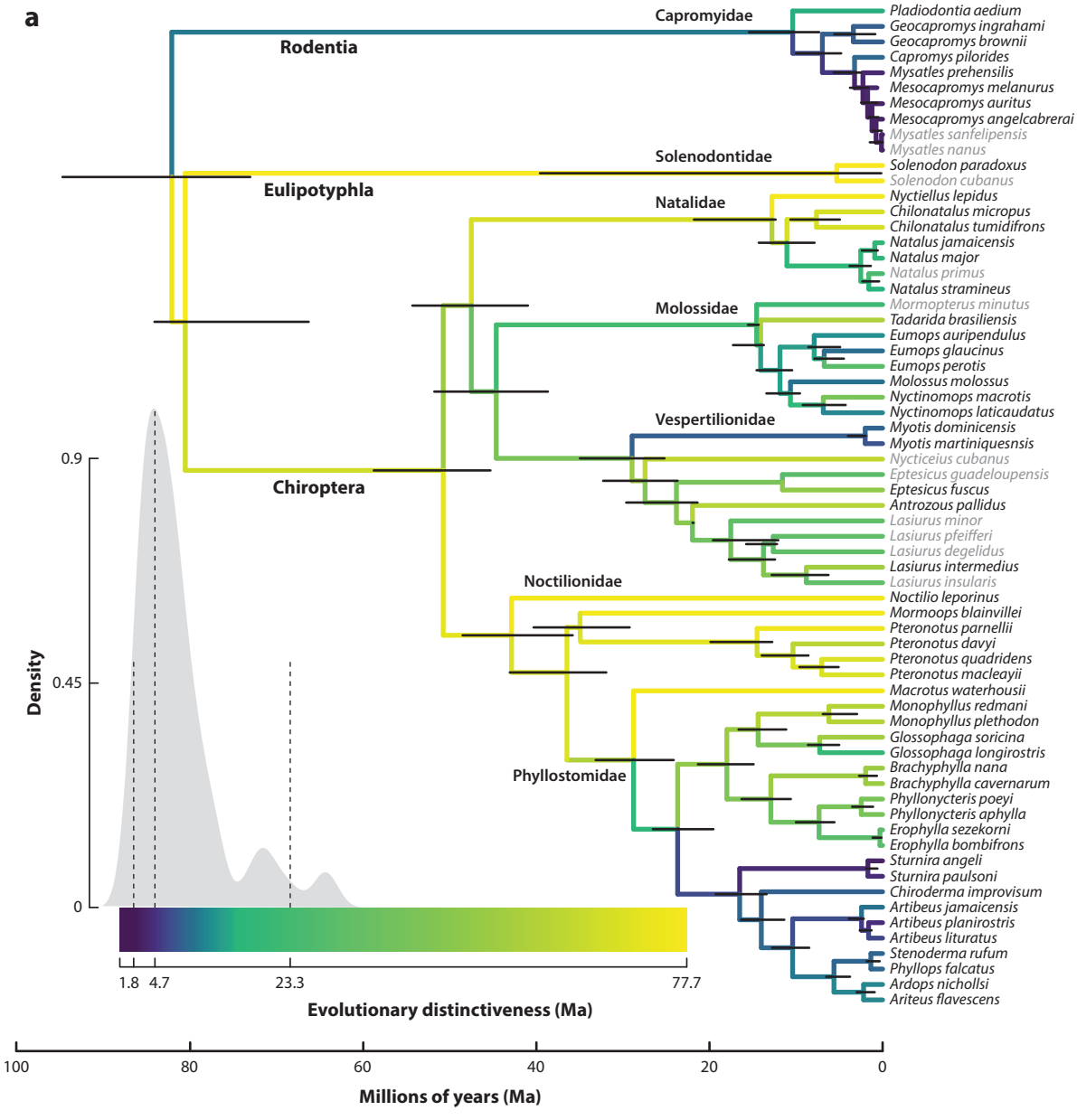

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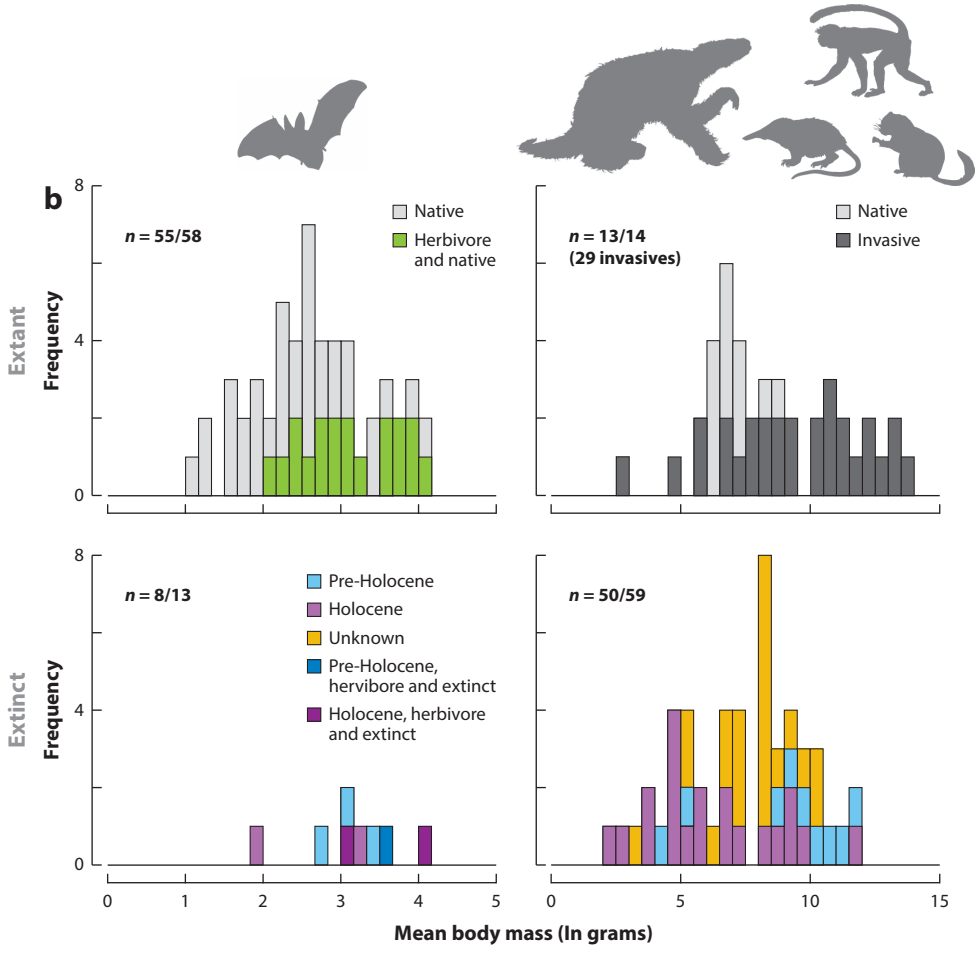

Figure 3 (*Continued*)

(*a*) The last surviving West Indian mammals comprise a diverse assemblage of ancient lineages, as shown in the dated phylogeny of living species (error bars represent 95% high probability density), including a few species lacking DNA for which positions were imputed using taxonomy (tip names in *gray*). Branch color indicates the amount of independent evolution [or evolutionary distinctiveness (ED), in millions of years (Ma)] since their last divergence from an extant relative, based on a complete species-level phylogeny of Mammalia (N.S. Upham, J. Esselstyn & W. Jetz, manuscript in preparation). The frequency distribution of ED for West Indian species (*lower left*) shows exceptionally high values for *Solenodon* species, beyond the 0.99 quantile of the ED distribution of all mammals used to calibrate the ED color scale (0.01, 0.50, and 0.99 percentiles of full distribution are represented by *dashed lines*). (*b*) The loss of West Indian mammals has not been random, as shown by the distribution of body masses for species that are extant (living) or extinct (extirpated from the region) and flying (bats) or nonvolant (all other species). For nonvolant mammals, size-selected extinctions occurred in both the smallest- and largest-bodied species, and invasive species (*dark gray bars*) have partially filled those vacant size niches. For bats, extinctions have been of smaller magnitude, not biased by size, and appear to have affected more nonherbivorous than herbivorous species. More Holocene than pre-Holocene extinctions have been recorded, but the lack of LADs for 5 bat species and 29 nonvolant species renders their timing of loss unknown. Sample sizes (*n*) of native species and the proportion with mass data are given for each plot (modified from the database of Faurby & Svenning 2016). Invasive species are those present on Cuba (Borroto-Páez 2009) with data on body mass from Jones et al. (2009). Artwork is open source from PhyloPic (**http://phylopic.org/**).

Patterns of mammal survival and extinction in the West Indies are therefore complex. Deciphering these patterns requires a better understanding of ecological variables of extinct and extant species within a rigorous statistical and phylogenetically explicit framework.

3.2. Demographic Collapse and Decline in Genetic Diversity

Deleterious effects of anthropogenic activities on West Indian mammals are not restricted to the past. The conservation status of extant species has been poorly understood, and limited data on population abundance, distribution, or trends are available. However, 8 of the 12 surviving described nonvolant species are now listed under an IUCN Red List category of threat (i.e., vulnerable, endangered, or critically endangered), with all others considered near threatened (Turvey et al. 2017). The remnant nonvolant fauna is therefore one of the world's most threatened mammal faunas (**Table 1**). All these species are imperiled by invasive mammals, with 10 probably also affected by hunting, habitat loss, or both; these threats remain present across the region, even inside protected areas (Turvey et al. 2017). Although conservation status is not as dire for bats, 9 of 60 extant species are listed under categories of threat, with 3 more listed as near threatened (**Table 1**). Three hot spots where West Indian bats are threatened are Cuba (*Lasiurus insularis*, *Mormopterus minutus*, *Natalus primus*, and *Nycticeius cubanus*), Jamaica (*Natalus jamaicensis* and *Phyllonycteris aphylla*), and Guadeloupe (*Chiroderma improvisum* and *Eptesicus guadeloupensis*). Habitat loss, including loss of specialized vegetation roost sites to agriculture, development, and hurricanes, threatens all populations. In Jamaica, both threatened species depend on unprotected caves within degraded habitats vulnerable to feral cats (Dávalos & Turvey 2012).

Quaternary and historical records demonstrate larger past geographic ranges, local extirpations, and range contractions for several species now surviving in restricted ranges (e.g., *Geocapromys ingrahami*, *Natalus primus*, and *Solenodon cubanus*) (Borroto-Páez & Mancina 2011, Borroto-Páez & Mancina 2017, Clough 1976, Tejedor et al. 2004). More recent and ongoing population losses are documented for other species (e.g., *Capromys pilorides*, *Geocapromys brownii*, *Mysateles prehensilis*), and three species listed as critically endangered (*Natalus jamaicensis*, *Mesocapromys nanus*, and *M. sanfelipensis*) may already be extinct (Turvey et al. 2017). At least one other rodent species, *Geocapromys thoracatus*, definitely died out during the twentieth century (Clough 1976).

Significant population structuring is also present in many species, notably those distributed across large, geotectonically complex islands or across multiple islands where geographic features provide barriers to gene flow. Such species comprise multiple geographically restricted and intrinsically vulnerable evolutionary units, with separate populations representing distinct conservation management units. For example, both of Hispaniola's native nonvolant mammals, *Plagiodontia aedium* and *Solenodon paradoxus*, comprise three subspecies associated with the island's three biogeographic provinces (Brace et al. 2012, Turvey et al. 2016). Whereas *S. paradoxus* is assessed as near threatened at the species level by IUCN (Turvey et al. 2017), two of its subspecies have extremely low estimates of effective population size, possibly indicating severe recent demographic contraction. Urgent conservation attention and a higher Red List threat status at the subspecies level are therefore needed (Turvey et al. 2016). Similarly, allopatric populations of *Capromys pilorides* distributed across Cuba and associated archipelagos are morphologically distinct and are assigned to four currently recognized subspecies (**Table 1**). Genetic studies reveal that *C. pilorides* contains at least two highly divergent mitochondrial clades, apparently corresponding to species-level genetic isolation comparable to that of sister species in *Mesocapromys* (Borroto-Páez et al. 2005, Kilpatrick et al. 2012, Upham & Borroto-Páez 2017). Populations of *Capromys* in eastern and western Cuba are estimated to have diverged ~1.1 Ma, and a further divergence occurred ~0.4 Ma within the western unit (Upham & Borroto-Páez 2017).

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Table 1 Conservation status of extant West Indian mammals (only threatened species of bats are shown) based on current IUCN assessments[a,b]

Species	Common name	Subspecies	Current range	IUCN status	Trend	Estimated size	F	L	H	P	C
Geocapromys ingrahami	Bahamian hutia	None	Bahamas: East Plana Cay, Little Wax Cay, Warderick Wells Cay	Vulnerable	Stable	12,000 individuals on East Plana Cay, 1,200 individuals on Little Wax Cay				X	
Geocapromys brownii	Jamaican coney	None	Jamaica: Hellshire Hills, John Crow Mountains, Worthy Park	Endangered	Decreasing	16 separate subpopulations identified in the 1980s		X		X	
Capromys pilorides	Desmarest's hutia	1. *pilorides* 2. *relictus* (including *ciprianoi*) 3. *doceleguas* 4. *gundlachianus*	Cuba: widely distributed across mainland Cuba, Isla de la Juventud, and archipelagos	Near threatened	Stable (decreasing)	50 individuals/ha and in some habitats up to 100 individuals/ha; one subpopulation (Sierra del Chorrillo) had 100,000 individuals prior to overharvesting in 1990s			X	X	X
Mesocapromys angelcabrerai	Cabrera's hutia	None	Cuba: Cayos de Ana Maria	Critically endangered	Unknown (decreasing)	Restricted distribution on three small islands, where it has ~380–760 individuals			X	X	X
Mesocapromys auritus	Eared hutia	None	Cuba: Cayo Fragoso, Archipiélago de Sabana	Endangered	Stable	Most recent population estimate suggests 400 individuals			X	X	X
Mesocapromys melanurus	Black-tailed hutia	None	Cuba: Granma, Guantánamo, Holguín, Santiago de Cuba	Vulnerable	Decreasing	Not abundant in its range; population reduction of 30% over the past three generations	X	X	X	X	
Mesocapromys nanus	Dwarf hutia	None	Cuba: Ciénega de Zapata (?)	Critically endangered (possibly extinct)	Unknown	Likely fewer than 50 individuals if not already extinct		X		X	

(*Continued*)

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Table 1 *(Continued)*

Species	Common name	Subspecies	Current range	IUCN status	Trend	Estimated size	F	L	H	P	C
Mesocapromys sanfelipensis	Little Earth hutia	None	Cuba: Cayos de San Felipe (?)	Critically endangered (possibly extinct)	Unknown	Likely less than 50 individuals if not already extinct			X	X	X
Mysateles prehensilis	Prehensile-tailed hutia	1. *prehensilis* 2. *gundlachi* 3. *meridionalis*	Cuba: western and central Cuba, Isla de la Juventud	Near threatened	Unknown	Locally common where it is found			X	X	X
Plagiodontia aedium	Hispaniolan hutia	1. *aedium* 2. *hylaeum* 3. *bondi*	Hispaniola: Dominican Republic, Massif de la Hotte (Haiti)	Near threatened	Decreasing	Genetic data suggest an effective population size (N_e) of ~30,000		X	X	X	
Solenodon cubanus	Almiqui, Cuban solenodon	None	Cuba: Nipe-Sagua-Baracoa Massif of eastern Cuba	Endangered	Decreasing	Unknown; all individuals found in fewer than five locations	X	X		X	
Solenodon paradoxus	Hispaniolan solenodon	1. *paradoxus* 2. *woodi* 3. *haitiensis*	Hispaniola: Dominican Republic, Massif de la Hotte (Haiti)	Near threatened	Decreasing	Genetic data suggest an effective population size (N_e) of <4,000	X	X	X	X	
Chilonatalus tumidifrons	Bahamian lesser funnel-eared bat	None	Bahamas: Abaco, Andros, San Salvador	Near threatened	Decreasing	Requires hot caves as roosts, which are threatened by changing climate		X			
Chiroderma improvisum	Guadeloupe big-eyed bat	None	Guadeloupe (Basse-Terre Island), Montserrat	Endangered	Unknown	Known only from the type locality in Guadeloupe and three records in Montserrat		X			
Eptesicus guadeloupensis	Guadeloupe big brown bat	None	Guadeloupe (Basse-Terre Island)	Endangered	Unknown	Known from five locations; acoustic monitoring suggests 30% loss over last 21 years/ three generations		X		X	

(Continued)

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Table 1 *(Continued)*

Species	Common name	Subspecies	Current range	IUCN status	Trend	Estimated size	F	L	H	P	C
Lasiurus insularis	Cuban yellow bat	None	Cuba	Vulnerable	Unknown	Known from fewer than five locations; palm roosts vulnerable to storms and habitat loss		X			
Lasiurus minor	Minor red bat	None	Hispaniola, Puerto Rico, Bahamas (eight islands)	Vulnerable	Decreasing	Known from fewer than 15 localities in its range; vulnerable to wind farming		X			
Mormopterus minutus	Little goblin bat	None	Cuba	Vulnerable	Decreasing	Known from fewer than 15 locations; requires a single palm species as roost		X			
Myotis dominicensis	Dominican myotis	None	Dominica, Guadeloupe	Vulnerable	Unknown	Known from only three localities within its range; vulnerable to habitat change		X			
Myotis martiniquensis	Schwartz's myotis	None	Martinique, Barbados	Near threatened	Unknown	Poorly known; expansion of tourism threatens habitat		X			
Natalus jamaicensis	Jamaican greater funnel-eared bat	None	Jamaica: St. Clair Cave	Critically endan-gered	Decreasing	St. Clair population estimated at ~50 individuals in 1970; single roost surrounded by feral cats		X		X	
Natalus primus	Cuban greater funnel-eared bat	None	Southwestern Cuba: Cueva La Barca	Vulnerable	Decreasing	Known from only one cave; cave roof may collapse, altering thermal balance		X			
Nycticeius cubanus	Cuban evening bat	None	Cuba	Near threatened	Unknown	Population in decline at unknown rate because of habitat change		X			
Phyllonycteris aphylla	Jamaican flower bat	None	Jamaica: reported from Marta Tick Cave (1983), Stony Hill Cave (2010)	Critically endan-gered	Decreasing	Known only from two caves; surveys failed to find in former stronghold of St. Clair Cave or other suitable caves				X	

[a]Data from IUCN (2016) and Turvey et al. (2017) for nonvolant species.
[b]Threats: F, fragmentation; L, habitat loss/degradation; H, hunting; P, predation by introduced carnivores; C, competition with introduced rodents.

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Even among vagile bats, population structure in West Indian endemics, including *Macrotus waterhousii* (Fleming et al. 2010) and *Erophylla sezekorni* and *E. bombifrons* (Muscarella et al. 2011), is evident. The strong structuring in *M. waterhousii* explains the many extirpations in this species complex (e.g., Middle Caicos, Gonâve, Puerto Rico, and Anguilla), as interisland migration is more restricted than previously thought. Further population structure is also evidenced by recent recognition of island-endemic populations in many wide-ranging West Indian bats (e.g., the *Pteronotus parnellii* species complex) (Pavan & Marroig 2016), some of which represent island-endemic species (e.g., *Natalus primus*) (Tejedor et al. 2004).

These examples highlight the need for an improved understanding of gene flow within West Indian bats and other surviving West Indian mammals, and of the effective population sizes of different mammalian evolutionarily distinct units. Increasing evidence for substantial population structuring within the last surviving nonvolant mammals also suggests that many now-extinct species may have shown comparable evolutionary patterns, making the Holocene loss of intraisland mammalian evolutionary units probably much greater than currently appreciated from fossil morphology alone.

Effective conservation of the threatened surviving mammal fauna will require multiple management strategies, including improved population monitoring, strengthened regulation of hunting, habitat management and restoration, reduction of native mammal mortality by invasive species, community-level and national environmental education programs, and potentially ex situ approaches such as captive breeding (Turvey et al. 2017). There is still hope that the last survivors of the once-great West Indian mammal radiation have a future, but this requires carefully planned, intensive management involving coordination and expertise.

3.3. Ecological Consequences of Extinction

West Indian mammal extinctions have left a remnant endemic fauna comprising bats, hutias, and solenodons, supplemented with introduced mammals from the mainland Neotropics and the Old World (**Figure 3**). Among the endemics, bats have had the highest survival rate, but estimates of the time needed to restore communities of noctilionoid bats reveal the scope of recent losses in terms of evolutionary history. Quaternary bat extinctions have altered a long-standing equilibrium between high colonization, endemic speciation, and natural extinction rates, and restoring that equilibrium would take at least eight million years (Valente et al. 2017). These methods assume species and lineages are interchangeable, underestimating the time needed to recover functional diversity in these communities. Even the most diverse extant West Indian mammal communities, with the highest colonization rates, have therefore suffered extraordinary evolutionary losses.

The mammalian biodiversity lost in the West Indies during recent millennia also included the disappearance of ancient nonvolant clades, representing disproportionately large amounts of evolutionary history, highlighting the role of islands as museums of ancient biodiversity. The two totally extinct mammal groups, sloths and primates, have no close living relatives among mainland forms and represent unique losses of diversity. Ancient DNA analyses are not available to quantify the amount of evolutionary history lost following their extinction, or the evolutionary relationships between West Indian taxa and mainland relatives, which remain disputed on the basis of available morphological information (e.g., whether they represent single or multiple overwater colonization events); however, both groups probably represent ancient colonists (Cooke et al. 2011, MacPhee et al. 2000). Most prehuman evolutionary diversity from the West Indian rodent and lipotyphlan radiations has also been lost; these ancient mammalian clades have lost family-level lineages (e.g.,

Nesophontidae) equivalent in age to extant mammalian orders (Brace et al. 2016, Cooke et al. 2011, Fabre et al. 2014, Roca et al. 2004).

This loss of evolutionary history and higher-order clades is associated with the loss of functional and trait diversity from West Indian ecosystems and with the disappearance of several entire mammalian guilds (e.g., small-bodied insectivores, large-bodied browsers, and fruit dispersers). The consequences of this loss of functional diversity and potential keystone species for West Indian ecosystems have not been studied adequately. On the basis of better-understood extinction events, it is likely that the removal of distinct guilds would trigger wider knock-on effects, including plant coextinctions, shifts in plant community composition, or both (Barnosky et al. 2016). Further investigation of the functional ecology of now-extinct species, including inference of dietary ecology through tooth wear (Cooke 2011) and analyses of ecologically informative stable isotopes, together with additional studies of long-term West Indian Quaternary archives, particularly pollen cores, is required to understand these unknown ecological changes. The West Indies thus provides a unique opportunity to test the tools of new conservation paleobiology approaches owing to its history of recent extinctions, coupled with urgent modern management needs, and to its broad applicability to other relictual island ecosystems.

As well as eroding native West Indian mammal diversity, humans have supplemented and replaced the mammal fauna with introduced species for millennia, and the diverse invasive fauna now includes murid and caviomorph rodents, lagomorphs, artiodactyls, perissodactyls, carnivores, catarrhine primates, and marsupials. Given our limited understanding of the ecology of most extinct and extant native mammals, it remains difficult to compare the relative functional ecology of prehuman and current West Indian mammalian communities. Several novel ecological guilds (e.g., mammalian carnivores and ungulate grazers) are now present, often at high population densities (Horst et al. 2001, Lewis et al. 2011), and these invaders have likely further driven ecosystem disequilibrium. However, it is also possible that some invasive species, notably rodents and primates, may be maintaining such important ecosystem processes as seed dispersal. Further study is required to elucidate whether this might be the case and what management steps can be enacted to try to restore ecological stability to this drastically modified but unique series of island ecosystems.

SUMMARY POINTS

1. Most Quaternary nonvolant mammal species and 18% of native West Indian bats went extinct. Despite important gaps in dating the majority of these events, there is unambiguous evidence of the survival of sloths, primates, and many now-extinct lipotyphlans, rodents, and bats well into the Holocene, implicating postglacial human activities in their extinction.
2. Extinction patterns were not uniform across taxa or islands. Larger-bodied mammals on large islands went extinct early on, presumably from a combination of undetected hunting pressures—there is no archaeological evidence of overhunting—and ecosystem change, whereas heavily exploited species on small islands disappeared only after the introduction of mammalian predators and competitors.
3. The diversity in outcomes and timing of extinction among West Indian mammals illuminate the mechanisms behind both prehistoric and contemporary population declines and extinctions. The last survivors of a vast Holocene extinction wave—8 of 12 described nonvolant mammal species and 9 of 60 bat species—are threatened with extinction, and evidence of cryptic species suggests these proportions are likely underestimates.

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FUTURE ISSUES

1. Improving extinction chronologies (despite the challenges of poor preservation in tropical conditions), and wider use of quantitative methods to analyze radiometric data, is indispensable to test both natural and human influence on West Indian extinctions. As new extinct species and evolutionarily independent populations are still being discovered, taxonomic revisions are a critical component of this task.
2. Our current understanding of the systematics, phylogeny, and ecology of most West Indian extinct mammals remains limited and requires the integration of multiple data types, including those from morphometrics and stable isotopes.
3. Understanding both Holocene extinctions and the diversity of human practices and resource use, both past and present, requires integrating archeology, paleontology, paleoecology, and conservation science. Application of a conservation paleontology toolkit is necessary to conserve the remaining West Indian mammal species.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank members of the Dávalos lab for feedback and Arnaud Lenoble, Aurelien Royer, and Emmanuelle Stoetzel for help with the Marie Galante dates. S.B.C. was supported by an Explorers Fund Grant from the Explorers Club, a Professional Development Grant from the American Association of Physical Anthropologists, and National Science Foundation grant NSF-DDIG 0726134. L.M.D. was supported in part by National Science Foundation grant NSF DEB-1442142. A.M.M. was supported by a Stanford Interdisciplinary Graduate Fellowship and National Science Foundation grant NSF DEB-1600728. S.T.T. was supported by Royal Society University Research Fellowship UF130573. N.S.U. was supported by National Science Foundation grant NSF DEB-1441737. Data analyzed and presented here have been deposited in DRYAD and are available at **http://doi.org/10.5061/dryad.tj4p5**.

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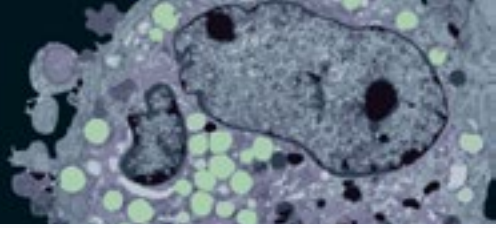

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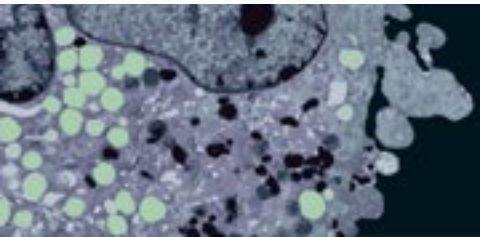

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