RESEARCH ARTICLE

The bat community of Haiti and evidence for its long-term persistence at high elevations

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Abstract

Accurate accounts of both living and fossil mammal communities are critical for creating biodiversity inventories and understanding patterns of changing species diversity through time. We combined data from 14 new fossil localities with literature accounts and museum records to document the bat biodiversity of Haiti through time. We also report an assemblage of late-Holocene (1600–600 Cal BP) bat fossils from a montane cave (Trouing Jean Paul, ~1825m) in southern Haiti. The nearly 3000 chiropteran fossils from Trouing Jean Paul represent 15 species of bats including nine species endemic to the Caribbean islands. The fossil bat assemblage from Trouing Jean Paul is dominated by species still found on Hispaniola (15 of 15 species), much as with the fossil bird assemblage from the same locality (22 of 23 species). Thus, both groups of volant vertebrates demonstrate long-term resilience, at least at high elevations, to the past 16 centuries of human presence on the island.

Introduction

Caribbean islands (the West Indies) are among the top ten biodiversity hotspots and currently sustain some of the highest levels of endemism in the world [1]. These islands have sustained massive losses of species in many mammalian taxa since the last glacial maximum (~25–18ka). For example, the Caribbean islands once hosted a terrestrial, non-volant mammal diversity of ±95 species including insectivores, primates, rodents, and sloths, but at least ~80% of these became extinct in the late Quaternary [2,3]. Many of these losses took place during the mid- to late Holocene, a time interval characterized by climates, sea levels, and island areas similar to those of today [2–6].

Unlike in the nearby Bahamas, the island of Hispaniola (Dominican Republic + Haiti) remained largely unaffected in physical geography by climate driven sea-level changes during the Pleistocene-Holocene transition (PHT, centered around 15–9 ka) because of its high topographic profile and deep surrounding seas [7]. It is estimated that land area loss resulting from sea-level rise from the Last Glacial Maximum to the present in Hispaniola was as little as 6% [7]. Thus, Hispaniola is an ideal place to study the loss vs. long-term persistence of species without the need to consider changing island area or the loss of available terrestrial habitats. In this context, paleontological studies can help us understand the patterns, causes, and timing of...
faunal change, thereby providing a long-term perspective useful to improve our knowledge of current biodiversity. Documentation of fossil diversity and its comparison with modern biotas can help assess how abiotic (e.g., climate) and biotic (e.g., anthropogenic disturbance) historical events affected these insular communities.

Bats are the most species-rich native mammals in the Caribbean. The bat fauna of the Caribbean once featured at least 67 species, of which 12 (18%) became extinct sometime during the late Quaternary [2,8]. The island of Hispaniola today supports 18 (32%) of the 56 extant species of Caribbean bats [9–11]. The Hispaniolan fossil bat fauna has been studied in some detail from 10+ fossil sites, including two recently discovered flooded sinkholes in the Dominican Republic [12–15]. The bat fauna of adjacent Haiti has received less attention. Klingener et al. [16] compiled a comprehensive dataset of extant bats encompassing 17 localities surveyed between 1973 and 1975 along the Tiburon Peninsula in southern Haiti. While other authors have studied the Haitian fossil bat fauna from various localities [12,13,17–19], documentation of the fossil bat fauna of Haiti is scant and lacks a comparison with modern inventories. Furthermore, the chronological control on these fossil assemblages has been poorly resolved beyond being "late Quaternary.”

The combination of extant and fossil species inventories with a chronological framework for a paleontological site can yield crucial data on such interrelated topics as species turnover, population changes, range shifts, and species and community composition. For example, a radiocarbon dated set of fossil bats from Abaco (The Bahamas) demonstrated that this island lost five (50%) of its species within the past four millennia [8]. In this paper, we present a comprehensive literature review of the bats of Haiti, including all previous records of living and fossil species. Our compilation builds on that of Velazco et al. [15] for bats from the Dominican Republic. We also report bat fossils from 14 Haitian localities not previously documented, including a detailed description and chronology for the fossil bats of Trouing Jean Paul, a rich deposit in a limestone sinkhole in the mountains of southeastern Haiti.

**Materials and methods**

**Literature and museum records**

To develop a complete list of the documented extant and fossil bat species from Haiti, we performed three independent literature searches during August 2016. The first consisted of an Internet search in Web of Science across all years using the key words “Haiti” and “Hispaniola” within the title (TI) or as a topic (TS), and refined by “Mammalia.” A second Internet search was performed in Google Scholar using the key words “Haiti OR Hispaniola” and “bat OR Chiroptera.” Sources including extant or fossil species inventories and biogeographic or species accounts within the geographic scope of the Caribbean were considered relevant in our search, which resulted in eight articles fitting these criteria (Table 1). The third search consisted of a more classical approach scanning the references included in the literature cited of each of the relevant articles.

We also searched for all museum specimens of bats in VertNet (www.vertnet.org; accessed on 1 December 2016) to complement our extant species list. This search included specimen data from 12 institutions (American Museum of Natural History, AMNH; University of Kansas Biodiversity Institute, KU; Natural History Museum of Los Angeles County, LACM; Museum of Comparative Zoology, MCZ; Muséum d’histoire naturelle de la Ville de Genève, MHNG; UC Berkeley Museum of Vertebrate Zoology, MVZ; Natural History Museum, NHMUK; Museum of Texas Tech University, TTU; Florida Museum of Natural History, UF; University of Michigan Museum of Zoology, UMMZ; National Museum of Natural History Smithsonian Institution, USNM; and Yale Peabody Museum, YPM).
Table 1. Bat diversity of Hispaniola (Dominican Republic + Haiti).

| Family | All bat species reported in Hispaniola | Extant Hispaniola\(^{[15,16,20]}\) | Extant Parc National La Visite\(^{[21]}\) | Trouing Jean Paul\(^{b}\) | Diquini\(^{[14,18]}\) | Gonâve Island\(^{[13,19]}\) | Port-de-Paix\(^{[17]}\) | Saint-Michel-de-l’Atalaye\(^{[14,18]}\) | La Selle\(^{[17]}\) |
|--------|---------------------------------------|--------------------------------------|------------------------------------------|--------------------------|-------------------|-----------------|--------------------------|--------------------------|--------------------------|
| Molossidae | Molossus molossus | x | | | | | | | |
| | Nyctinomops macrotis | x | x | | | | | | |
| | Tadarida brasiliensis | x | x | x | x | | | | |
| | [Tadarida sp.] | | | | | | | | x |
| Mormoopidae | Mormoops blainvillii | x | x | x | | | | | |
| | Mormoops magnifica | | | | | | | | |
| | Mormoops megalophylla | | | | | | | | |
| | Pteronotus maclearyi | ? | | | | | | | |
| | Pteronotus pamelli | x | x | x | x | | | | |
| | Pteronotus quadridens | x | x | | | | | | |
| | Pteronotus sp.\(^{1}\) | | | | | | | | |
| Natalidae | Chilonatalus micropus | x | x | | | | | | |
| | Natalus major | x | x | | | | | | |
| Noctilionidae | Noctilio leporinus | x | | | | | | | |
| Phyllostomidae | Brachyphylla nana | x | x | x | x | | | | |
| | Erophylla bomferrons | x | x | | x | x | | | |
| | Monophyllus redmani | x | x | x | x | x | | | |
| | Phyllonycteris poeyi | x | x | x | x | | | | |
| | Macrotus waterhousii | x | x | x | x | | | | |
| | Artibeus jamaicensis | x | x | x | x | x | | | |
| | Phyllops falcatus (= haitiensis\(^{3}\)) | x | x | x | x | | | | |
| Vespertilionidae | Eptesicus fuscus | x | x | x | | | | | |
| | Lasiurus cinereus | ? | | | x | | | | |
| | Lasiurus intermedius | | | | | | | | |
| | Lasiurus minor | x | x | | | | | | |

\(^{a}\) Species reported in VertNet (accessed 1 December 2016) and reported in the literature
\(^{b}\) fossil bats reported by this study
\(^{c}\) fossil reported in the literature.
Extinct species = †
species extirpated in the Caribbean = #
species extirpated in Hispaniola = *
specific epithet synonym in previous publications = §
species of unknown status = ?.
Taxa in brackets not necessarily different from those identified more precisely.

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Trouing Jean Paul cave site

Trouing Jean Paul (TJP) is a limestone sinkhole cave located ~22 km south of Port-au-Prince in Parc National La Visite, Massif de la Selle, Haiti (18.33˚N, -72.28˚W; Figs 1 and 2). TJP is a high elevation site (~1825 m) that was discovered in 1983 and excavated primarily in February 1984 by a field team led by Charles A. Woods. Relevant permits and documentation associated with the fossil excavations were obtained by C. A. Woods at the Florida Museum of Natural History, University of Florida (UF) from 1978 to 1984. These fossils were loaned to us for study by the UF Division of Vertebrate Paleontology, where permits and field notes are

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Fig 1. Map of the Caribbean (A). Major island groups highlighted as: Greater Antilles = light gray, Lesser Antilles = dark gray, and The Bahamas = black. The inset indicates the island of Hispaniola as reference including the locality of Trouing Jean Paul (B).

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archived. This cave is rich in vertebrate fossils including specimens of the insectivorans *Neso-
phontes* sp. (Nesophileidae) and *Solenodon paradoxus* (Solenodontidae), and the rodents *Brot-
omys voratus* (Echimydae) and *Plagiodontia aedium* (Capromyidae). Additionally, the non-
passerine fossil bird community of TJP includes 23 species, only one of which (the woodcock *Scolopax brachycarpa*) is extinct [22,23].

The entrance chamber of TJP is about 20 m long at an incline of 30˚, and opens to passages
that lead to five rooms. The fossils reported herein were obtained from Room 1, which is about
5 m wide by 9 m long, and divided in three main areas: Eastern, Southern, and Western Pock-
ets. Surface fossils were collected and mapped in four-part grid coordinates, as explained in
Steadman and Takano [22]. We identified all diagnostic bat fossils to species via direct com-
parison with modern bones (e.g. dentaries, humeri, and skulls) from the UF and AMNH col-
lections. Reference material included all species of bats listed as resident to Hispaniola in
[10,11,15,24]. We estimated the overall minimum number of individuals (MNI) for each spe-
cies from the number of unique bones (e.g., left humerus) assigned to it in the fossil material.
The total of the most abundant bone for each species is its MNI value. The bat fossils from TJP
are housed in the UF Vertebrate Paleontology Collection in Gainesville, FL, and openly acces-
sible through the VertNet portal (www.vertnet.org).

Fig 2. Map of Haiti indicating localities of living bat species (squares) and fossil bat species (circles). Boundaries of Parc National Pic Macaya and Parc National La Visite are indicated with light gray polygons. The locality of Trouing Jean Paul is indicated by a triangle (23) within Parc Nacional La Visite. Inset map shows detail of localities in the Province of Nippes. Numbers refer to the specific localities listed in S1 Table.

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Detailed radiocarbon (\(^{14}\text{C}\)) chronologies allow us to understand how the timing of changes in populations or species may be related to specific historical events \([6,25]\). From TJP, six Accelerator Mass Spectrometer (AMS) \(^{14}\text{C}\) dates were obtained from purified collagen of individual bones of the extinct woodcock \((\text{Scolopax brachycarpa}\ [22,23])\). These six bones, each representing a different individual woodcock, were selected from scattered locations across the surface of Room 1 in TJP, with each of these locations also having abundant identified bat fossils. Thus, the \text{Scolopax} AMS \(^{14}\text{C}\) dates can be used to estimate the age of the bat fossils from TJP. All AMS \(^{14}\text{C}\) dates, reported in calendrically calibrated years before present (Cal BP), represent 95% (2\(\delta\)) estimates and were performed at Beta Analytic, Inc., Miami, FL. Specific details of laboratory and calibration methods can be found at www.radiocarbon.com.

Results

A total of 24 bat species have been reported for Hispaniola including extant and fossil records \((\text{Table 1})\). Three species of Mormoopidae \((\text{Mormoops magna}, \text{M. megalophylla}, \text{and Pteronotus sp.})\) and one member of Vespertilionidae \((\text{Lasiurus intermedius})\), each known only from Dominican Republic are extinct on Hispaniola \([15]\). The report of \text{Tadarida} sp. \((\text{Molossidae})\) by Miller \([19]\), based on two mandibles, most likely represents \text{Tadarida brasiliensis} and not a taxon new for the island. Recent published accounts of the complete list of extant bats in Hispaniola (including both the Dominican Republic and Haiti) reported 18 species for the island, \([10,11,26]\), but we found modern records of 20 species \((\text{Table 1})\). The two species on our list that were not documented in previous studies are \text{Pteronotus macleayii} \((\text{Mormoopidae}; \text{NHMUK 1842.11.24})\) in Haiti and \text{Lasiurus cinereus} \((\text{Vespertilionidae}; \text{USNM 105704})\) in Dominican Republic, each represented by a single specimen.

Our study of museum collections and published records reveals that 36 localities have been sampled for bats in Haiti \((\text{Fig 2}; \text{S1 Table})\). Extant bats have been documented from 17 localities \([16,20,21]\). Fossil remains from five localities have been published \([13,17–19]\) and 14 additional fossil localities are documented herein from the Vertebrate Paleontology Collection at UF \((\text{Table 1})\). Detailed information on each locality, including the 14 fossil sites, is provided in S1 Table.

An unusually rich source of data on prehistoric faunas of Haiti is the fossil assemblage from TJP, which consists of many thousands of bones of small vertebrates (bats, insectivores, rodents, birds, frogs, lizards, and snakes). This site is a roost of the two extant species of tytonid owls on Hispaniola, which are also found as fossils at TJP \([22]\). \text{Tyto alba} \((\text{Barn Owl})\) is widely distributed across the Caribbean, whereas \text{T. glaucops} \((\text{Ashy-faced Owl})\) is endemic to Hispaniola \([27,28]\).

We identified 15 species of bats in five families from 2940 fossil elements at TJP \((\text{Table 2}, \text{Figs 3–5})\). UF catalog numbers for each specimen examined are provided in S2 Table. This bat community represents about 27% and 83% of the diversity of bats in the Caribbean at the level of species and family, respectively. In all, 75% of the extant bat species of Hispaniola and all families except Noctilionidae are represented in in the TJP assemblage. Four abundant species \((\text{Eptesicus fuscus}, \text{Lasiurus minor}, \text{Monophyllus redmani}, \text{and Phyllonycteris poeyi})\) make up 94% of the bat fossils identified from TJP. Crania and dentaries were the most prevalent diagnostic elements in the fossil sample, but we also identified femora, humeri, pelves, and radii.

The most abundant species in the TJP fauna is \text{Eptesicus fuscus} \((\text{Big Brown Bat}; N = 1944; \text{Fig 3})\), which has a Caribbean distribution that includes the Greater Antilles and The Bahamas. This aerial insectivore also has a wide continental distribution in North, Central, and northern South America \([31]\). The second most common species is \text{Lasiurus minor} \((\text{Minor Red Bat}; N = 401; \text{Fig 3})\), a solitary insectivorous species that roosts primarily in trees and is known to
occur at high elevations in the Caribbean [30]. The third and fourth most abundant species found in TJP are the Caribbean phyllostomid endemics Monophyllus redmani (Greater Antillean Long-tongued Bat; N = 277) and Phyllonycteris poeyi (Cuban Flower Bat; N = 134; Fig 4). These primarily nectarivorous bats are distributed throughout the Greater Antilles, are strictly cave-dwelling, and often roost together in the same caves [9]. Both of these species form colonies up to tens of thousands of individuals and are associated with hot caves [9,30]. “Hot caves” are characterized by their high temperatures (28–40˚C) and humidity (>90%) that are believed to be caused mainly by the radiating body heat from large colonies of bats and heat/humidity associated with decomposing guano [32,33].

The remaining 11 fossil bat species from TJP are represented by fewer than 50 elements each and include members of the families Molossidae, Mormoopidae, Natalidae, Phyllostomidae, and Vespertilionidae (Table 2, Figs 3–5). Two of these species are especially noteworthy. First, although commonly included in lists of the bats of Haiti due to its presence in Dominican Republic, we report here the first record of Chilonatalus micropus from Haiti identified from three fossil elements (Table 2; Fig 5). Second, Lasiurus cinereus has been documented only once in the Caribbean from a single specimen collected in Dominican Republic, which was believed to be a wayward migrant [34]. The presence of 35 fossils of L. cinereus in TJP suggests that this species is more likely a resident than a migrant (Table 2; Fig 3).

Sixty percent of the bats at TJP (9 of 15) are Caribbean endemics and include extant phytotrophous and insectivorous species. Nine of the 15 TJP bat species roost exclusively in caves, of which seven use primarily hot caves (Table 2). In addition to the strict cave-dwelling bats, three of the species found in TJP roost in vegetation, and three of them facultatively use caves and man-made structures (Table 2).

Table 2. Fossil bat species identified in this study from Trouing Jean Paul, Parc National La Visite, Massif de la Selle, Haiti.

| Family          | Scientific name                  | Number of fossils | MNI | Status [29,30] | Roost preference |
|-----------------|----------------------------------|-------------------|-----|----------------|-----------------|
| Molossidae      | Nyctinomops macrotis             | 3                 | 2   | E              | C, S            |
|                 | Tadarida brasilensis             | 47                | 31  | E              | C, S            |
| Mormoopidae     | Pteronotus pamellii              | 7                 | 2   | E              | HC              |
|                 | Pteronotus quadridens*           | 1                 | 1   | E              | HC              |
| Natalidae       | Chilonatalus micropus*           | 3                 | 1   | U              | HC              |
|                 | Natalus major*                  | 2                 | 2   | E              | HC              |
| Phyllostomidae  | Brachyphylla nana*               | 21                | 12  | E              | C               |
|                 | Erophylla bombilrons*            | 39                | 21  | E              | HC              |
|                 | Macrotrus waterhousii            | 21                | 10  | E              | C, S            |
|                 | Monophyllus redmani*             | 277               | 182 | E              | HC              |
|                 | Phyllonycteris poeyi*            | 134               | 117 | E              | HC              |
|                 | Phyllops falcatus*               | 4                 | 3   | E              | V               |
| Vespertilionida | Eptesicus fuscus                 | 1944              | 1086| E              | C               |
|                 | Lasiurus cinereus                | 35                | 22  | U              | V               |
|                 | Lasiurus minor*                  | 401               | 280 | E              | V               |
| Totals          | 15 species                       | 2940              | 1772|                |                 |

Asterisks (*) represent species that are endemic to the Caribbean. Status of each species in Haiti listed as extant (E) and unknown (U). Roost preference categories listed as cool cave (C), hot cave (HC), man-made structure (S), and vegetation (V). See methods for description of estimates of minimum number of individuals (MNI).

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Fig 3. Fossil crania of bats from Trouing Jean Paul, Haiti, shown as dorsal (top), lateral (middle), and ventral (bottom) views. Left to right: Vespertilionidae—*Eptesicus fuscus* (A; UF 281797), *Lasiurus cinereus* (B; UF 282166), *Lasiurus minor* (C; UF 307426), Natalidae—*Natalus major* (D; UF 307471), and Molossidae—*Tadarida brasiliensis* (E; UF 282589).

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Fig 4. Fossil crania of bats from Trouing Jean Paul, Haiti, in the family Phyllostomidae shown as dorsal (top), lateral (middle), and ventral (bottom) views. Left to right: *Brachyphylla nana* (A; UF 307430), *Phyllonycteris poeyi* (B; UF 307397), *Erophylla bombilons* (C; UF 282439), *Monophyllus redmani* (D; UF 282169), and *Macrotus waterhousii* (E; UF 282171).

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The grid coordinates for 736 of the fossil bat specimens, representing 14 of the 15 species in TJP, were identical to those used by Steadman and Takano [22] for AMS $^{14}$C dating. These included *Brachyphylla nana* (N = 5), *Chilonatalus micropus* (N = 3), *Eptesicus fuscus* (N = 443), *Erophylla bombifrons* (N = 10), *Lasius cinereus* (N = 9), *L. minor* (N = 121), *Macrotus waterhousei* (N = 12), *Monophyllus redmani* (N = 85), *Natalus major* (N = 1), *Nyctinomops macrotis* (N = 2), *Phyllonycteris poeyi* (N = 29), *Phyllops falcatus* (N = 1), *Pteronotus parnellii* (N = 2), and *Tadarida brasiliensis* (N = 13). The $^{14}$C dates from these grid coordinates ranged from 1690–1530 Cal BP to 680–570 Cal BP with 95% confidence ($\delta\$; Table 3), i.e., from about 1600 to 600 years ago.

**Discussion**

The study of islands and their biodiversity has contributed to important ecological and evolutionary theories focusing on dispersal, colonization, extinction, and speciation [35,36]. Given
the fast pace of human-induced global change, combining data from both living species and fossils provides important insight into how communities have been shaped across time. As the second largest island of the Caribbean, Hispaniola supports some of the greatest diversity of habitats and highest levels of endemism [37–40]. Coincidently, Haiti has one of the highest levels of habitat loss due to farming and logging, and has lost about 98% of its native forest cover [37]. Understanding the effects of such large-scale human alterations of the environment is critical to predicting the biotic future of the island.

Our study compiled data from 36 localities, described the fossil bat community of Trouing Jean Paul (TJP), Haiti, and provides a thorough review of the living and fossil bat biodiversity of one of the most environmentally imperiled countries in the Neotropics. Previous accounts of Hispaniolan bats documented 18 species in both countries (Dominican Republic and Haiti). Herein we add two recent records, *Lasiurus cinereus* and *Pteronotus macleayii*, which have not been previously included. The prevalence of remains of *L. cinereus* in Trouing Jean Paul, Haiti (TJP) shows that this species resides in Hispaniola (Table 2). Based on a single record, *Pteronotus macleayii* is currently known only from Haiti, and together with *L. cinereus*, brings the number of bat species in Haiti to 20 (Table 1). Our results, combined with those of previous studies, increase the total number of bats currently occurring on Hispaniola to 20 species.

The fossil bat assemblage of Trouing Jean Paul (TJP) accumulated during an 1100-year interval in the late Holocene (~1690–570 Cal BP). The bat fossils were deposited before the arrival of Europeans and Africans to Hispaniola, which occurred in 1492 AD (which equals 458 Cal BP [41]), although the fossils postdate the colonization of Hispaniola by Amerindians (6–5 ka [42,43]) by about 4 ky. The late Holocene montane bat fauna around TJP was likely sampled by two species of owl, *Tyto alba* and *T. glaucops*. While some studies suggest fossil biases in predator-derived sites due to feeding preference of the predator [44,45], we are confident that the bat diversity sampled by these owls is representative of the bat fauna of TJP because all species have been previously documented in the diets of tytonid owls and are well within the range of prey body mass taken by the owls [28]. The foraging radius of *T. alba* is up
to 5.6 km but usually less [46]; that of the smaller *T. glaucops* is unknown but unlikely to be greater than in *T. alba*.

The two most common species of bats in the TJP community belong to the family Vespertilionidae and are either found in a few localities or considered uncommon on most Caribbean islands (Table 1). *Eptesicus fuscus* in the Caribbean forms small colonies of a few hundred individuals that are frequently found near the entrance of caves [29,30]. In contrast, *Lasiusurus minor* is solitary and roosts among the leaves of trees but apparently never in tree hollows, buildings, or caves [29]. Because of its roosting preference, *L. minor* is seldom captured by scientists in the Caribbean, and is represented by fewer than 10 records from Hispaniola in museum collections (www.vertnet.org). Both *Eptesicus fuscus* and *Lasiusurus minor* have a swift flight pattern with low maneuverability and typically forage in open areas [29]. Ashy-faced owls (*Tyto glaucops*) and barn owls (*T. alba*) routinely roost in caves and sinkholes where they can capture bats in flight, and they are also known prey upon bat species that do not live in caves [28,30]. It is therefore likely that the roosting and foraging habitat preferences of *Eptesicus fuscus* and *Lasiusurus minor* render them easy prey to aerial predators such as owls. The TJP sample of *L. minor* is the largest documented so far for the Caribbean. Given the high incidence of *Eptesicus fuscus* fossils found at TJP, it is plausible that a colony of this bat was present within TJP.

*Chilonatalus micropus* in TJP represents the first record of this species from Haiti. This bat exclusively roosts in small colonies in hot caves and typically forages in densely cluttered mesic environments [47]. In Dominican Republic, *C. micropus* is considered rare and has been documented in two northeast localities in Samaná Province and two southwest localities in Barahona Province. Both *Tyto alba* and *T. glaucops* frequently prey upon very small vertebrates such as the 0.6 g Tuck-weep Frog (*Eleutherodactylus abbotti* [28]), suggesting that they could effectively capture *Chilonatalus micropus*, which weighs only 2.6 g and has a characteristic slow flight pattern [47,48]. The relatively low numbers of *C. micropus* in TJP may result from its preference for roosting in hot caves, and because this species typically forages in densely forested areas where it is less likely to be captured by the owls.

The presence of *Lasiusurus cinereus* in TJP stands out among this diverse bat fauna. This bat is solitary, insectivorous, and roosts primarily among the foliage in trees [34]. It is one of the most widespread of American bats and occurs from Canada (North America) to Brazil, northern Argentina, and Chile (South America; [34]). *Lasiusurus cinereus* also occurs in the Galápagos Islands (Ecuador) and is the only bat that has colonized Hawai‘i, which is one of the longest dispersal distances known to have been traversed by bats [49]. *Lasiusurus cinereus* has been reported from Bermuda (3 specimens) and Hispaniola (1 specimen) but, until now, these individuals were considered migrants [34]. The verbatim locality for the single Hispaniolan specimen (USNM 105704) is “Dominican Republic” and lacks specific details to accurately determine its provenance. The estimated minimum number of individuals of *L. cinereus* (MNI = 22) in the TJP sample is comparable to some colonial cave-dwelling species that are considered common in the Caribbean (e.g., *Tadarida brasiliensis*, MNI = 31; *Brachyphylla nana*, MNI = 12; *Erophylla bombifrons*, MNI = 21; Table 2). Although only a single living specimen has been collected, the relatively young radiocarbon dates of *L. cinereus* samples (~930–780 Cal BP; Table 3) at TJP suggest that resident (non-migratory) populations of this species are likely present. The paucity of living records of *L. cinereus* in the Caribbean probably reflects the difficulty of catching these bats in mist nets and lack of adequate biodiversity inventory efforts in Hispaniola.

Both *Lasiusurus minor* and *L. cinereus* were found commonly in TJP, yet they are considered rare in the Caribbean. TJP lies at about 1800 m elevation within a 3000 ha area of pine forest, broadleaf cloud forest, savanna, and juniper forest in Massif de la Selle [21,50]. Substantial
areas to the east of Massif de la Selle (e.g., Calalo and Savane Bourrique in Haiti, and Peder-nales and Bahoruco in Dominican Republic) are also characterized by mountain ranges over 1500 m. While Caribbean records of *L. minor* do not necessarily represent high elevation local-

ties, the majority are from topographically heterogeneous forested habitats with steep eleva-

tional gradients that drastically increase in elevation. The single *L. cinereus* specimen from

Dominican Republic lacks specific locality information. Nonetheless, the occurrence of *L.

cinereus* in the TJP deposits suggests that it inhabits high elevation forests in Haiti and, given

the size of the foraging range of the owls, this species was likely part of the resident bats of the

area. It therefore seems likely that the mountain ranges of southeastern Haiti and southwestern

Dominican Republic contain adequate habitat to sustain populations of *L. minor* and *L. ciner-

eus* that have eluded modern scientific surveys but are efficiently sampled by owls.

The long-term persistence of most species of bats in Haiti (and in Hispaniola in general) stands in sharp contrast to the situation with non-volant mammals, about 80% of which have become extinct during the late Quaternary [2,3]. Two likely factors in the greater resilience of bats may be their roosting habits in caves (which are less subjected to human impact than non-cave habitats) and their lack of appeal to humans as food. The considerable late Holocene extirpation of bats found on the Bahamian island of Abaco [8], however, demonstrates that even bat communities can be highly vulnerable to loss on relatively small islands. The large size and high relief of Hispaniola has apparently buffered its bat communities from rapid declines. However, persistence of high-elevation forests may have been key in the preservation of the bat fauna. Ongoing deforestation, if it encompasses higher elevation areas, may have a rapid and devastating effect on the bats of Hispaniola.

**Supporting information**

S1 Table. Descriptions for all localities where living or fossil bats have been documented in Haiti. Verbatim elevation (in meters) provided for previously published localities if available. Elevation for new localities reported in this study estimated via GoogleEarth.

(XLSX)

S2 Table. List of specimens examined per species for Trouing Jean Paul, Haiti, from the UF Vertebrate Paleontology collection in Gainesville, FL.

(PDF)

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**Author Contributions**

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References
1. Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C. Global biodiversity conservation: the critical role of hotspots. In: Zachos FE, Habel JC, editors. Biodiversity Hotspots. Berlin Heidelberg: Springer-Verlag; 2011. pp. 3–22.
2. Dávalos LM, Turvey ST. West Indian mammals: the old, the new, and the recently extinct. In: Patterson BD, Costa LP, editors. Bones, clones and biomes: the history and geography of recent neotropical mammals. Chicago, IL: University of Chicago Press; 2012. pp. 157–202.
3. MacPhee RDE. Insulae infortunatae: establishing a chronology for late Quaternary mammal extinctions in the West Indies. In: Haynes G, editor. American Megafaunal Extinctions at the end of the Pleistocene. 1st ed. Heidelberg: Springer; 2009. pp. 169–193.
4. Cuffey K, Marshall S. Substantial contribution to sea-level rise during the last interglacial from the Greenland ice sheet. Nature. 2000; 404: 591–594. https://doi.org/10.1038/35007053 PMID: 10766239
5. Lambeck K, Chappell J. Sea level change through the last glacial cycle. Science. 2001; 292: 679–686. https://doi.org/10.1126/science.1059549 PMID: 11326090
6. Steadman DW, Martin PS, MacPhee RDE, Jull AJT, Mcdonald HG, Woods CA, et al. Asynchronous extinction of late Quaternary sloths on continents and islands. Proc Natl Acad Sci USA. 2005; 102: 11763–11768. https://doi.org/10.1073/pnas.0502777102 PMID: 16085711
7. Steadman DW, Franklin J. Changes in a West Indian bird community since the late Pleistocene. Stewart J, editor. J Biogeogr. 2015; 42: 426–438.
8. Soto-Centeno JA, Steadman DW. Fossils reject climate change as the cause of extinction of Caribbean bats. Sci Rep. 2015; 5: 7971. https://doi.org/10.1038/srep07971 PMID: 25610991
9. Tejedor A, Tavares VDC, Rodríguez-Hernández D. New records of hot-cave bats from Cuba and Dominican Republic. Bioespeleología. 2005; 39: 10–15.
10. Rodríguez-Durán A, Christenson K. Brevario sobre los murciélagos de Puerto Rico, La Española, e Islas Virgenes. 1st ed. Rodríguez-Durán A, Christenson K, editors. Bayamón, PR: Publicaciones Puertorriqueñas, Inc.; 2012.
11. Nuñez-Novas MS, León YM. Análisis de la colección de murciélagos (Mammalia: Chiroptera) del Museo Nacional de Historia Natural de Santo Domingo. Novit Caribaea. 2011; 4: 109–119.
12. Morgan GS. Patterns of extinction in West Indian bats. In: Woods CA, Sergile FE, editors. Biogeography of the West Indies: patterns and perspectives. 2nd ed. Boca Raton, FL: CRC Press; 2001. pp. 369–408.
13. Koopman KF. A new subspecies of Chilonycteris from the West Indies and a discussion of the mammals of La Gonave. J Mammal. 1955; 36: 109–113.
14. Silva-Taboada G. Notas sobre los murciélagos colectados en Jamaica y Haití durante la expedición científica Cubana. Rev Arqueol y Etnol. 1952; 15: 203–214.
15. Velazco PM, O’Neill H, Gunnell GF, Cooke SB, Rimoli R, Rosenberger AL, et al. Quaternary Bat Diversity in the Dominican Republic. Am Museum Novit. 2013; 3779: 1–20.
16. Klingener D, Genoways HH, Baker RJ. Bats from Southern Haiti. Mammal Pap Univ Nebraska State Museum. 1978; 47: 81–99.
17. Miller GS. Three new bats from Haiti and Santo Domingo. Proc Biol Soc Washingt. 1918; 31: 39–40.
18. Miller GS. A second collection of mammals from caves near St. Michel, Haiti. Smithson Misc Collect. 1929; 81: 1–30.
19. Miller GS. Three small collections of mammals from Hispaniola. Smithson Misc Collect. 1930; 82: 1–16.
20. Sanborn CC. Descriptions and records of Neotropical bats. Fieldiana. 1941; 27: 371–387.
21. Woods CA. Mammals of the National Parks of Haiti [Internet]. Unpublished report for USAID/Haiti under contract No. 521–0169-C-00–3083–00. Gainesville, FL: USAID/Haiti; 1986. Available: http://pdf.usaid.gov/pdf_docs/PNAAV066.pdf
22. Steadman DW, Takano OM. A late-Holocene bird community from Hispaniola: refining the chronology of vertebrate extinction in the West Indies. The Holocene. 2013; 23: 936–944.
23. Takano OM, Steadman DW. A new species of Woodcock (Aves: Scolopacidae: Scolopax) from Hispaniola, West Indies. Zootaxa. 2015; 4032: 117. https://doi.org/10.11646/zootaxa.4032.1.6 PMID: 26624342
24. Rodríguez-Durán A, Kunz TH. Biogeography of West Indian Bats: An ecological perspective. In: Woods CA, editor. Biogeography of the West Indies: Patterns and perspectives. 2nd ed. Boca Raton, FL: CRC Press; 2001. pp. 356–368.
25. MacPhee RDE, Iturralde-Víncent MA, Jiménez-Vázquez O. Prehistoric sloth extinctions in Cuba: implications of a new “Last Appearance Date.” Caribbean J Sci. 2007; 43: 94–98.
26. Nuñez-Novas MS, León YM, Mateo J, Davalos LM. Records of the cave-dwelling bats (Mammalia: Chiroptera) of Hispaniola with an examination of seasonal variation in diversity. Acta Chiropterologica. 2016; 18: 269–278.
27. Latta SC, Rimmer C, Keith AR, Wiley JW, Raffaele HA, McFarland K, et al. Birds of the Dominican Republic and Haiti. Princeton, NJ: Princeton University Press; 2006.
28. Wiley JW. Food habits of the endemic ashy-faced owl (Tyto glaucops) and recently arrived barn owl (T. alba) in Hispaniola. J Raptor Res. 2010; 44: 87–100.
29. Gannon MR, Kurta A, Rodríguez-Durán A, Willig MR. Bats of Puerto Rico: An island focus and a Caribbean perspective. 1st ed. Lubbock, TX: Texas Tech University Press; 2005.
30. Silva Taboada G. Los murciélagos de Cuba. Silva-Taboada G, editor. La Habana: Editorial de la Academia de Ciencias de Cuba; 1979.
31. Kurta A, Baker RH. Eptesicus fuscus. Mamm Species. 1990; 356: 1–10.
32. Rodríguez-Durán A. Bat assemblages in the West Indies: the role of caves. In: Fleming TH, Racey PA, editors. Island Bats: Evolution, Ecology and Conservation. Chicago, IL: University of Chicago Press; 2009, pp. 265–280.
33. Ladle RJ, Firmino JVL, Malhado ACM, Rodríguez-Durán A. Unexplored diversity and conservation potential of Neotropical hot caves. Conserv Biol. 2012; 26: 978–982. https://doi.org/10.1111/j.1523-1739.2012.01936.x PMID: 23003344
34. Shump KA, Shump AU. Lasiurus cinereus. Mamm Species. 1982; 185: 1–5.
35. Helmus MR, Mahler DL, Losos JB. Island biogeography of the Anthropocene. Nature. Nature Publishing Group; 2014; 513: 543–546. https://doi.org/10.1038/nature13739 PMID: 25254475
36. MacArthur RH, Wilson EO. The theory of island biogeography. Princeton, NJ: Princeton University Press; 1967.
37. Woods CA, Ottenwalder JA. The natural history of southern Haiti. Gainesville, FL; 1992.
38. Sergile FE, Woods CA. Status of conservation in Haiti: a 10-year retrospective. In: Woods CA, Sergile FE, editors. Biogeography of the West Indies: Patterns and Perspectives. Boca Raton, FL: CRC Press; 2001. pp. 547–560.
39. Sly ND, Townsend AK, Rimmer CC, Townsend JM, Latta SC, Lovette IJ. Phylogeography and conservation of the endemic Hispaniolan Palm-Tanagers (Aves: Phaicnicophilus). Conserv Genet. 2010; 11: 2121–2129.
40. Schwartz A. The herpetogeography of Hispaniola, West Indies. Stud Fauna Curacao other Carrib Islands. 1980; 61: 86–127.
41. Deagan K, Cruxent JM. Archaeology at La Isabela: America’s first european town. New Haven, CT: Yale University Press; 2002.
42. Fitzpatrick SM. A critical approach to 14C dating in the Caribbean: using chronometric hygiene to evaluate chronological control and prehistoric settlement. Lat Am Antiq. 2006; 17: 389–418.
43. Wilson SM. The prehistory an early history of the Caribbean. In: Woods CA, Sergile FE, editors. Biogeography of the West Indies: Patterns and Perspectives. 2nd ed. Boca Raton, FL: CRC Press; 2001. pp. 519–527.
44. Pregill GK. Late Pleistocene herpetofaunas from Puerto Rico. Univ Kansas Museum Nat Hist Publ. 1981; 71: 1–70.

45. Steadman DW, Hilgartner WB. A new species of extinct barn owl (Aves: Tyto) from Barbuda, Lesser Antilles. Smithson Contrib to Paleobiol. 1999; 89: 75–83.

46. Marti CD. Barn Owl, Tyto alba. In: Poole A, Stettenheim P, Gill F, editors. The Birds of North America. Philadelphia: Academy of Natural Sciences; 1992.

47. Tejedor A. Systematics of funnel-eared bats (Chiroptera: Natalidae). Bull Am Museum Nat Hist. 2011; 353: 1–140.

48. Genoways HH, Baker RJ, Bickham JW, Phillips CJ. Bats of Jamaica. Spec Publ Museum Texas Tech Univ. 2005; 106: 1–154.

49. Russell AL, Pinzari CA, Vornhof MJ, Olival KJ, Bonaccorso FJ. Two tickets to paradise: multiple dispersal events in the founding of Hoary Bat populations in Hawai’i. PLoS One. 2015; 10: 1–13.

50. Dávalos LM, Brooks T. Parc National La Visite, Haiti: a last refuge for the country’s montane birds. Cotinga. 2001; 16: 36–39.