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The importance of late Quaternary climate change and karst on distributions of Caribbean mormoopid bats

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ABSTRACT

The bat family Mormoopidae includes three species with distributions in the Caribbean. These taxa—*Mormoops blainvillei, Pteronotus parnellii, and P. quadridens*—roost predominantly in hot cave chambers where temperatures may reach 40° C and humidity is close to 100%. We tested the hypothesis that mormoopid bat extirpations in this region were due to climatic changes and the loss of suitable cave environments due to flooding caused by sea level rise associated with the late Pleistocene to Holocene (ca. 10 ka) climate change transition. Ecological niche models (ENMs) were developed to estimate the current, mid-Holocene, and Last Glacial Maximum distributions of these three bat species and to assess whether suitable climatic habitat for these taxa had been stable across time in the Caribbean. Additionally, we examined the importance of karst formations (where hot caves typically form) as a predictor for the distributions of Caribbean mormoopid bats. Our results show that mormoopid bat distributions in the Caribbean have remained relatively stable over time with climate ENMs indicating up to a 19% expansion in the amount of suitable habitat from late Pleistocene to the present. Presence of karst was a good predictor when used alone or when combined as karst-climate ENMs. Fossil evidence shows that some populations of mormoopids became extirpated as recently as 3.6 ka. These data, taken together with our conclusion that suitable climate habitat for mormoopid bats existed in the Caribbean beyond late Pleistocene to Holocene transition, suggest that these bats may have survived this climate change event by roosting outside their characteristic hot cave environment.

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INTRODUCTION

The climate of the Earth has been characterized by multiple glacial-interglacial cycles occurring over millions of years (Paillard, 1998). Much attention has been paid to the transition from the cold climate of the Last Glacial Maximum (LGM; ca. 25–18 ka) to the warmer interglacial climate of the Holocene (HOL; ca. 10–0 ka) because this period includes events in human history and it lies within a time interval that can be easily radiocarbon dated. Isotopic evidence indicates that during the LGM, climate in the Caribbean was more arid with temperatures about 5°–8° C colder than today (Curtis et al., 2001). In contrast, mid-Holocene (ca. 6 ka) temperatures were about 1°–2° C warmer than today and habitats changed from xerophytic to mesophytic after the last glaciation (Pregill and Olson, 1981; Foley et al., 1994; Huang et al., 2008). Sediment cores from mainland and insular Caribbean localities indicate major shifts from extensive dry scrubland to more moisture-tolerant vegetation following climate change at the Pleistocene-Holocene transition (PHT, ca. 11–9 ka; Leyden, 1984, 1985; Higuera-Gundy et al., 1999). Faunal changes are also associated with the PHT; for example, some birds such as the Bahama mockingbird (*Mimus gundlachi*) and the burrowing owl (*Athene cunicularia*) are known to have experienced range contractions and extirpation in the Bahamas with the loss of xeric environments (Pregill and Olson, 1981).

Several hypotheses have been proposed to explain the effect that the PHT had on the biotic diversity in the Caribbean (Pregill and Olson, 1981). Fossil evidence indicates that about 80% of the land mammals in the Caribbean became extinct sometime after the LGM (MacPhee, 2009; Dávalos and Turvey, 2012). Many of these taxa (e.g., sloths and insectivores) disappeared shortly after the last glaciation (Pregill and Olson, 1981; Steadman et al., 2005). In contrast, only about 18% of Caribbean bats became extinct during the same period (Pregill and Olson, 1981; Morgan, 2001; Dávalos and Turvey, 2012). Changes in island area due to rising sea level and concomitant changes in cave availability due to flooding and loss of roosting habitats after the PHT have been proposed to explain Caribbean bat extinctions (Morgan, 2001; Dávalos and Russell, 2012). However, recent evidence from radiocarbon chronology has indicated that many bat fossils in the Caribbean are younger than previously thought, and that many species of bat survived the PHT by 5–7 ky (Soto-Centeno and Steadman, 2015). Furthermore, evidence from time-scaled ecological niche models (ENM) covering the LGM to the present have revealed that climate-based distributions for the bats *Monophyllus redmani*, *Macrotus waterhousii*, and *Pteronotus parnellii* remained largely stable over time (Soto-Centeno and Steadman, 2015). This evidence from fossils and ENMs suggests that some species of bats were able to maintain viable populations until the late Holocene despite habitat loss due to rising sea level after the PHT.

Ecological niche models combine species localities and environmental data to estimate the predicted distributions of organisms based on available suitable habitat (Franklin, 2009). ENMs have been used to study biogeographic, ecological, and evolutionary questions (Carnaval et al., 2009; Soto-Centeno et al., 2013) and are an exceptional tool for understanding how climate may influence the distribution of a species. ENMs can use current and past climate datasets to hindcast species distributions across time (Elith and Leathwick, 2009). These time-scaled ENMs, in combination with fossil data, provide a strong framework for testing hypotheses of climate-based extinction or extirpation (Soto-Centeno and Steadman, 2015).

As with all mammals, the distributions of bats are dependent on many variables of which climate is just one factor (Peterson et al., 2011; Anderson, 2013). For many bat species, the availability of suitable roost sites may be a significant factor that influences population distributions and, ultimately, the geographic range of species (Peterson et al., 2011; Anderson, 2013). For example, cave-roosting bat species may be limited by the availability of suitable caves in which to roost (Rodríguez-Durán, 2009). Hot caves, where temperatures range from 28°–40° C and humidity exceeds 90%, are preferred roosts of some bat species of the Neotropics, but their development depends upon the underlying geology of a region (Ladle et al., 2012). Neotropical hot caves are known from northeastern Brazil, the Greater Antilles, Mexico, and Venezuela (Rodríguez-Durán, 2009; Ladle et al., 2012).

The Caribbean is rich in calcium carbonate ($CaCO_3$) and calcium-magnesium carbonate ($CaMg[CO_3]$) deposits (Mylroie and Mylroie, 2007). These deposits, commonly known as karst or limestone, have a high prevalence of caves that are formed by dissolution of minerals by water moving through the deposits (Mylroie and Mylroie, 2007; Rodríguez-Durán, 2009). Although caves are common geological features worldwide, only some have the geomorphology necessary to become hot caves (Ladle et al., 2012). Fluviokarst caves—caves formed by rivers or precipitation that percolates through limestone—provide the most suitable conditions for hot cave formation (Rodríguez-Durán, 2009). In the Caribbean region, fluviokarst caves are found only in the Greater Antilles (Rodríguez-Durán, 2009).

The microclimatic conditions of hot caves are thought to be caused mainly by the radiating body heat from large colonies of bats and heat/humidity associated with decomposing guano (Rodríguez-Durán, 2009; Ladle et al., 2012). Species of Caribbean bats in the families Mormoopidae, Natalidae, and some members of Phyllostomidae primarily roost in hot caves, where the range in temperatures promotes the segregation of species (Rodríguez-Durán and Soto-Centeno, 2003; Rodríguez-Durán, 2009). Thus, given their specific microclimatic conditions, hot caves in the Caribbean play a significant role as roosts for many species of bats. Indeed, some bats such as *Chilonatalus micropus*, *Erophylla bombifrons*, *Monophyllus redmani*, and *Pteronotus quadridens* have been posited to roost only in hot caves (Rivera-Marchand and Rodríguez-Durán, 2001; Rodríguez-Durán and Soto-Centeno, 2003; Tejedor et al., 2005a).

In contrast to Greater Antillean fluviokarst caves, karst in the Bahamas is predominantly eolianite (Brooke, 2001). This type of karst results from the lithification of sediment that is deposited by wind processes in shallow banks, such as those in the Bahamas (Brooke, 2001). The flooding of carbonate platforms during the middle to late Pleistocene sea level high stands shaped large expanses of eolianite karst in the Bahamas (Brooke, 2001). Weathering of exposed eolianite by glacial-interglacial sea level changes aided in the formation of numerous small caves but not the large, complex caves commonly found in fluviokarst. Consequently, even though caves are common throughout the Bahamas, these caves usually lack the geomorphology and distinctive features of Greater Antillean hot caves.

We studied three species of bats in the family Mormoopidae that are codistributed in the Caribbean (fig. 1A). The ghost-faced bat (*Mormoops blainvillei* Leach, 1821; fig. 1B), Parnell's mustached bat (*Pteronotus parnellii* Gray, 1843; fig. 1C), and sooty mustached bat (*Pteronotus quadridens* Gundlach, 1840; fig. 1D) are small- to medium-sized aerial insectivores that prefer
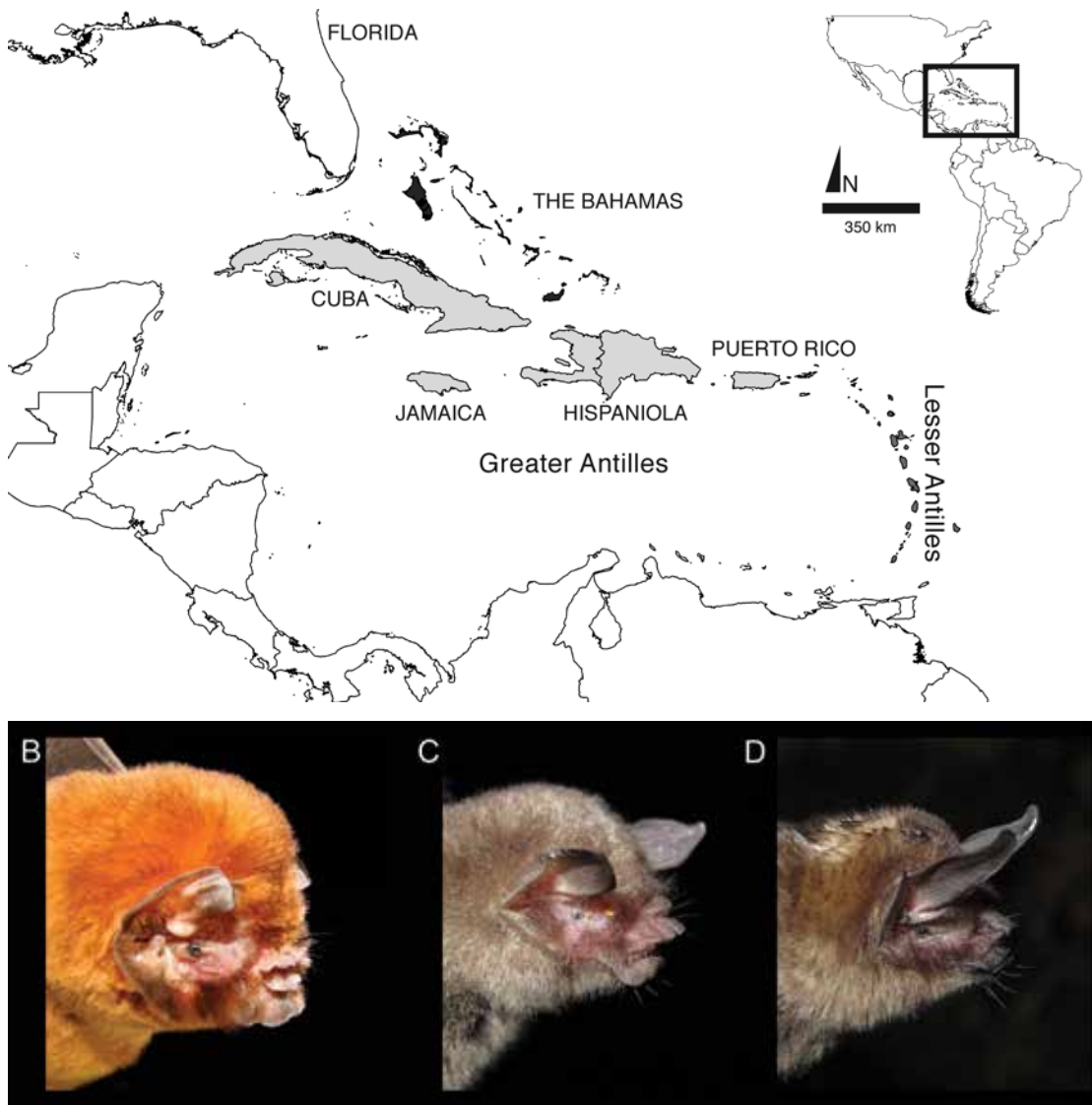
FIGURE 1. (**A**) Map of the Caribbean region showing locations of major islands and archipelagos discussed in the text. Portraits of the mormoopid species that are the focus of this study: (**B**) *Mormoops blainvillei*, (**C**) *Pteronotus parnellii*, and (**D**), *Pteronotus quadridens*. All photographs by J.A.S.-C.

to roost in hot caves (Rodríguez-Durán and Soto-Centeno, 2003; Mancina et al., 2007; Ladle et al., 2012). Given the recent evidence from radiocarbon-dated fossils and ENMs, we hypothesized that climate-based distributions of mormoopid bats will show stability in the Caribbean similar to other species of bats. However, Morgan (2001) suggested that rising sea level following the PHT damaged the structure of many caves, rendering them unable to maintain a warm microclimate. If so, PHT change in climate could have affected the distribution of mormoopid bats in the Caribbean because of the lack of suitable hot cave roosts (Morgan, 2001). We tested this hypothesis in two ways: first, we developed a series of buffers around karst outcrops to

estimate the proportion of bat sampling localities within karst as well as outside of karst; second, we created ENMs of the intersection of climate and karst to examine the role of karst (i.e., where hot caves are likely to exist) in the distributions of mormoopid bats.

MATERIALS AND METHODS

Species Localities and Climate Data

Bat-sampling locality records with decimal latitude and longitude coordinates were obtained from the Global Biodiversity Information Facility (GBIF; www.gbif.org) and from the literature. We plotted all points in ArcGIS v10.2 (ESRI, Redlands, CA) to assess the quality of the spatial data and we corrected localities that were clearly erroneously georeferenced (e.g., lying in the ocean). Localities georeferenced from the literature were recorded at a resolution of 0.0001 decimal degrees, while points obtained from GBIF were kept at their original resolution. Information on fossil localities was obtained from the literature and from collections held at Florida Museum of Natural History, and localities were subsequently georeferenced. Via these methods, we obtained a total of 95 current and 12 fossil localities for *Mormoops blainvillei*, 109 current and 13 fossil localities for *Pteronotus parnellii*, and 75 current and 10 fossil localities for *P. quadridens* (figs. 2–3; appendix table A1). A recent search after the submission of this article produced two additional locality records: *Pteronotus quadridens*, Mona, Puerto Rico (recent; Lancaster, 2010), and *Mormoops blainvillei*, Exuma, Bahamas (fossil; Koopman, 1951). Careful examination of the climate models revealed that the addition of these localities did not have a significant impact on or change our interpretation of the climate models. To maintain the integrity of the dataset used for producing the models, we did not include these points in our database.

We used climate data from 19 WorldClim variables at 30 sec (ca. 1 km^2) spatial resolution for current, mid-Holocene (HOL, ca. 6 ka), and Last Glacial Maximum (LGM, ca. 21 ka) climate (Hijmans et al., 2005). Both paleoclimate conditions were obtained as statistically downscaled estimates of past conditions from the ESCHAM3 and CCSM models available in WorldClim (see www.woldclim.org for downscaling details). Each variable was clipped to the extent of the Caribbean using ArcGIS v10.2. We performed a Pearson correlation analysis in ENMTools v1.4.3 (Warren et al., 2010) on the 19 climate variables to avoid issues with collinearity and chose seven uncorrelated variables to represent regional temperature and precipitation (correlation coefficient >0.8; Peterson, 2011). The seven climate variables chosen were annual mean temperature (Bio1), mean diurnal temperature range (Bio2), isothermality (Bio3), temperature annual range (Bio7), annual precipitation (Bio12), precipitation of driest month (Bio14), and precipitation of warmest quarter (Bio18; see Hijmans et al., 2005).

We extracted climate information for our species localities using ArcGIS v10.2. A high volume of background climate points has the potential to overfit models to the locality data because of the high abundance of absence points surrounding presence localities (Elith et al., 2011). To correct for this, we ran models by randomly sampling 3000 background localities within the Caribbean region. We used a 2 km buffer around species locality points and removed background points located within this buffer to prevent bias in our background climate dataset.
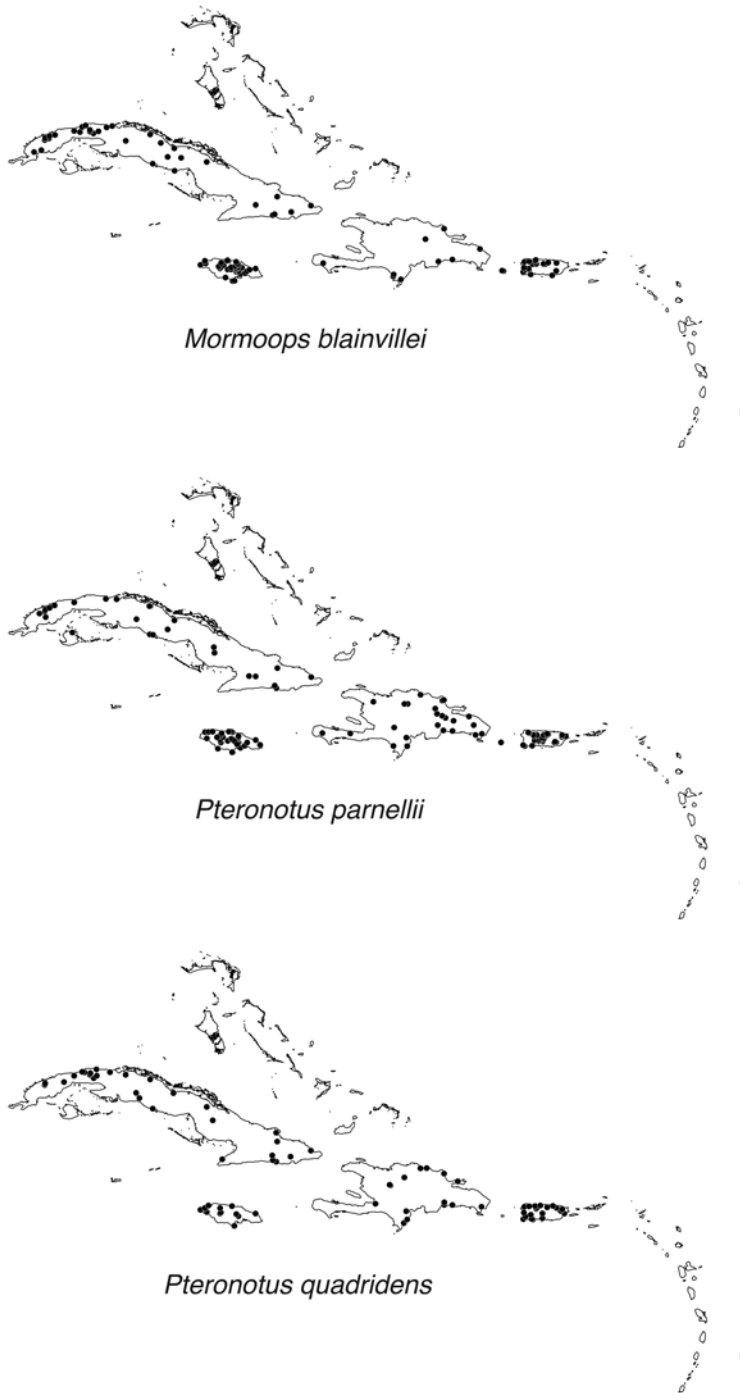
FIGURE 2. Current localities (black dots) used to develop and evaluate ecological niche models of current climate conditions for *Mormoops blainvillei*, *Pteronotus parnellii*, and *Pteronotus quadridens* in the Caribbean. See figure 1 for geographic reference.

Mormoops blainvillei

Pteronotus parnellii
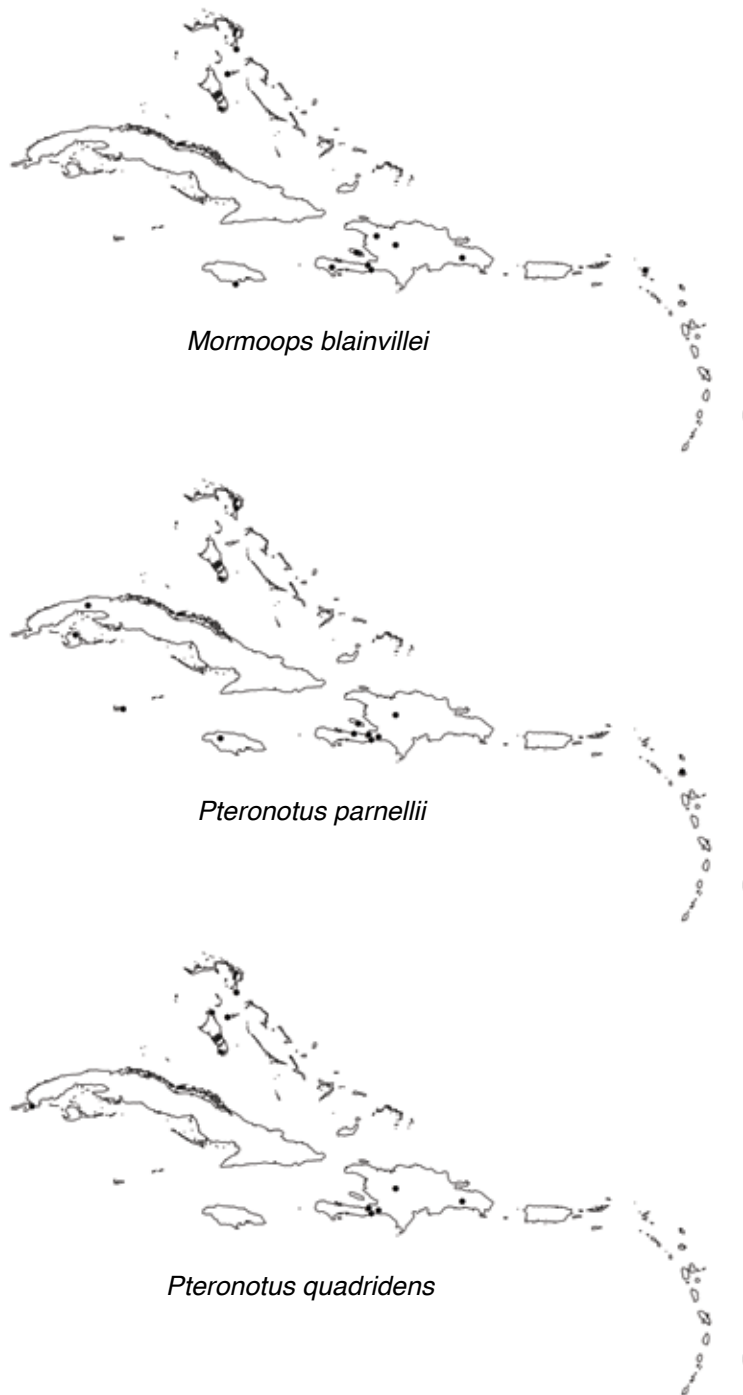
Pteronotus quadridens

FIGURE 3. Fossil localities (black dots) used to develop and evaluate hindcasted ecological niche models for *Mormoops blainvillei*, *Pteronotus parnellii*, and *Pteronotus quadridens* in the Caribbean. See figure 1 for geographic reference.

Ecological Niche Modeling

We developed ecological niche models (ENM) in Maxent v3.3, which uses a maximum entropy algorithm to predict the relationship between a species locality and the environmental and spatial characteristics of those localities (Elith et al., 2011). Previous studies suggest that the use of default parameters in Maxent for every species is not appropriate (Anderson and Gonzalez, 2011). Therefore, for each species of bat we explored multiple values of regularization, which controls the ability of a model to be more restricted or relaxed. We tested which regularization value showed better predictive ability for each of the species datasets using two threshold rules: minimum training presence threshold (MTP) and the 10th percentile training presence threshold (10PTP), estimated within Maxent. The MTP is the lowest threshold value that is able to accurately predict all training locality points (Radosavljevic and Anderson, 2014). We used MTP because previous studies suggest that relaxed thresholds provide useful estimates when hindcasting distributions (Waltari and Guralnick, 2009). The 10PTP is a more restrictive threshold that attempts to exclude only 10% of the training locality points (Radosavljevic and Anderson, 2014). We compared the number of correctly predicted localities (i.e., true positive fraction) against the theoretical expectation of correctly predicted localities for each threshold to test for model overfitting. Using this method we estimated regularization values, which were kept constant when developing hindcasted model projections (table 1).

Final models were created using 100 bootstrap replicates and projected to current, HOL, and LGM climate in the Caribbean. Bootstrap replicates consisted of sampling with replacement of each training dataset (i.e., 75% of the presence localities for each species). Because bootstrap iterations are generated as pseudoreplicates from the original dataset, we took the average of each threshold in each replicate to determine a MTP and a 10PTP threshold value for each model. We used the logistic output created by Maxent, which represents a continuous model, and applied thresholds in ArcGIS v10.2 to convert it into a binary (i.e., presence-absence) model. The resulting binary distributions for the three time periods were summed and corrected for the current island area to develop stability maps for each species. Predicted areas of stability show suitable areas where each species is predicted to occur across the current, HOL, and LGM time periods.

The Importance of Karst

It is difficult to distill all factors that rule the distribution of a species into one abiotic variable such as presence of karst because species geographic distributions are governed by complex interactions among many abiotic and biotic variables (Hutchinson, 1957; Holt, 2009; Peterson et al., 2011). Nonetheless, we wanted to assess whether the presence of karst outcrops, and thus the potential availability of hot caves, is a useful predictor in the distribution of Caribbean mormoopid bats. Data on presence and absence of karst were obtained from the KROW database (Hollingsworth, 2006), which to our knowledge is the only readily available digital map of karst that includes the Caribbean. This database includes areas of fluviokarst formations in the Greater Antilles, but not areas of eolianite karst that occur in shallow banks, such as those in the Bahamas. Developing an ENM using presence and absence of karst alone would

TABLE 1. Model statistics estimated for current (CUR), mid-Holocene (HOL), and Last Glacial Maximum (LGM) climate using a minimum training presence threshold (MTP) for *Mormoops blainvillei*, *Pteronotus parnellii*, and *Pteronotus quadridens* in the Caribbean. True-positive fraction (TPF) estimates were based on climate-only and climate-plus-karst models (i.e., karst-clim). Karst-climate models are based on the intersection of climate and occurrence of karst in the Caribbean. Statistics: Regularization value (β), area under the curve (AUC), and true-positive fraction (TPF).

Species	Time	β	Threshold value	AUC	TPF	TPF (karst-clim)[a]
M. blainvillei	CUR	2	0.191	0.751	94/95 (99%)	64/65 (98%)
	HOL				11/12 (92%)	4/5 (80%)
	LGM				11/12 (92%)	4/5 (80%)
P. parnellii	CUR	4	0.197	0.740	109/109 (100%)	56/56 (100%)
	HOL				12/13 (92%)	7/7 (100%)
	LGM				12/13 (92%)	7/7 (100%)
P. quadridens	CUR	7	0.362	0.715	75/75 (100%)	46/46 (100%)
	HOL				8/10 (80%)	3/3 (100%)
	LGM				6/10 (60%)	3/3 (100%)

[a] True-positive fraction estimated as the number of localities occurring within karst.

not answer our question effectively because bats fly and a preliminary assessment showed that many localities from the three species of bat studied lie outside karst areas across the Caribbean. As a result, the model considered areas inside and outside karst areas as equally suitable. Instead, we estimated the proportion of localities of each species that lie within and outside karst areas as well as their distance from karst by creating a series of buffers at 5 km intervals. This approach is justified because many species of bats are known to routinely fly long distances from their roosts while foraging. In the Neotropics, movement between day roosts and foraging areas has been reported to range from 2.5 km in *Carollia perspiscillata* (Phyllostomidae; Bernard and Fenton, 2003) to 18 km in *Tadarida brasiliensis* (Molossidae; Horn and Kunz, 2008) and even 30 km in *Leptonycteris yerbabuenae* (Horner et al., 1998). On Cuba and Puerto Rico, *Pteronotus quadridens* has been reported to disperse up to 9 km to their feeding grounds (Rodríguez-Durán, 1984) and are also able to return to their roost on a single night from distances up to 30 km (Silva-Taboada, 1979). It is likely that *Mormoops blainvillei* and *Pteronotus parnellii* are also capable of long-distance flight (e.g., Bateman and Vaughan, 1974). Thus, karst might be important (i.e., for providing cave roost sites) even to bats captured in nonkarst areas if foraging areas are located many kilometers away from roost sites.

To determine how karst affected each species' climate-based distribution, we used the karst layer to estimate the intersection of karst and climate. This indicated where both climatic and habitat suitability cooccurred in the Caribbean at each time scale. The relaxed nature of the MTP threshold used in the climate models combined with karst provided conservative estimates suitable for hindcasting distributions while reducing the probability of overfitting. We projected the KROW database from World Eckert IV into World Geodetic System 1984 (WGS 84) datum to match our climate data and adjusted irregularities of the karst map to match the boundaries of the Caribbean in ArcGIS v10.2.

Evaluating Model Performance

Model performance was assessed using the area under the receiving operating characteristic curve (AUC) statistic from Maxent. AUC is a threshold independent measure of performance where a value of 1 indicates perfect model performance and a value of 0.5 indicates a model performing no better than random (Peterson et al., 2011). Values greater than 0.7 indicate good model performance (Swets, 1988; Peterson et al., 2011). AUC values do not take into account whether a model is overfit (Radosavljevic and Anderson, 2014). Therefore, we also examined the true-positive fraction using the MTP and 10PTP thresholds as an additional measure of performance. True-positive fractions for the karst-climate models were estimated using only localities that fell within karst to avoid bias in the estimates of correctly predicted localities.

One goal of this study was to determine whether recent climate change had an effect in the distributions of each species. Therefore, for the climate-only models we estimated two indices: relative range size (current ≥ past RRS = $c/m − 1$ or current ≤ past RRS = $-1×[m/c − 1]$) and overlap index (OI = o/m; where m = current climate conditions, c = past climate conditions, and o = amount of overlap between current and paleo-ENMs; Hijmans and Graham, 2006). We used RRS to estimate the magnitude and directionality of change in distributions, where an RRS value of zero indicates no change in distributions across time. Conversely, a positive RRS means that the past range size was larger than the current one and a negative value indicates that the past range size was smaller than the current one (Hijmans and Graham, 2006). Overlap index was used to understand the proportion of overlap between the present distribution and past distributions (Hijmans and Graham, 2006).

RESULTS

Climate-only Current and Paleo-ENMs

ENMs that estimated the current distributions performed well based on AUC values in all three bat species that we evaluated (table 1). Moreover, all current models had true-positive fractions over 99% for the MTP threshold (table 1). ENM projections to HOL and LGM had true-positive fractions over 91% for *Mormoops blainvillei* and *Pteronotus parnellii*. However, the true-positive fractions of paleo-ENMs for *P. quadridens* showed lower and variable performance when projected to the past, with 80% in the HOL and 60% in the LGM models (table 1). Models generated using the 10PTP threshold performed well considering their theoretical expectation and resulted in true-positive fraction values under 93% for the present and as low as 16% for the HOL predictions in all three species of bat (table 2). Below we focus our discussion of results based on the MTP threshold models because they show the best performance based on true-positive fractions.

The Effect of Climate on Caribbean Mormoopids

Climate-based ENM projections showed relative range sizes (RRS) that indicate range contraction from the LGM to the HOL followed by a range expansion from HOL to the present in two

TABLE 2. Alternative climate-only model statistics using 10th percentile training presence threshold (10PTP) for three species of mormoopid bat on the West Indies. Models using 10PTP also showed a range expansion from mid-Holocene to the present (see table 1). Overlap indexes in the 10PTP models were lower than when using a minimum training presence threshold (MTP), indicating that 10PTP is more restrictive. Statistics: Regularization value (β), area under the curve (AUC), overlap index (OI), relative range size (RRS), true-positive fraction (TPF).

Species	Time	β	Threshold type	Threshold value	AUC	OI	RRS	TPF
Mormoops blainvillei	Current	2	10PTP	0.310	0.751	0.855	-1.167	85/95
	Holocene	2	10PTP	0.319				2/12
Pteronotus parnellii	Current	4	10PTP	0.279	0.740	0.777	-1.285	97/109
	Holocene	4	10PTP	0.285				10/13
Pteronotus quadridens	Current	7	10PTP	0.398	0.715	0.577	-1.713	70/75
	Holocene	7	10PTP	0.404				5/10

of the three species of bats (table 3; figs. 4–6). A comparison of the overall RRS from LGM to the present reveals a trend of range contraction in *Mormoops blainvillei* and *Pteronotus parnellii*, which exemplifies the loss of habitat (i.e., land area) due to sea level rise after the end of the Pleistocene (table 3; figs. 4–5). Despite these observed changes, the amount of overlap (OI) in distribution across time (a measure of geographic range stability through time) was at least 81% in *Mormoops blainvillei* and 73% in *Pteronotus parnellii*, indicating relative stability despite loss of habitat. In contrast, the overall trend in *P. quadridens* showed a range expansion more or less continuously from LGM to the present (table 3; fig. 6). The overlap through time was 47% in *P. quadridens* (table 3), but in this case the low value reflects that new areas of suitable habitat became available after the LGM. We represent the areas of overlap as stability maps that show the intersection of predicted distributions across the three time periods for each species of bat (fig. 7).

We also estimated RRS corrected for the present-day island area to examine the amount and directionality of change for land areas that have not been affected by sea level rise. These estimates show a trend of range expansion from the LGM to the present for all three bat species. The magnitude of this change for *Mormoops blainvillei* and *Pteronotus parnellii* was <0.32, while the range expansion in *P. quadridens* was >0.5 (table 3).

Karst and ENMs of the Intersection of Karst and Climate

We generated a series of buffers at 5 km intervals to obtain the proportion of localities of each species that lie outside of fluviokarst as well as their distance from karst for each species of bat (fig. 8). These data are summarized in table 4. Only 50%–70% of modern sampling localities for the three focal species actually occur in karst areas (table 4). However, >90% of known capture localities for these taxa occur within 15 km of karst (table 4). Only 1% of modern localities for *Pteronotus quadridens* and 4% of capture localities for *P. parnellii* and *Mormoops blainvillei* occur farther than 25 km from karst.

For *Mormoops blainvillei*, 96% of current localities and 83% of fossil localities occur within 15 km of karst outcrops. *Pteronotus parnellii* is known from somewhat more localities, but the

TABLE 3. Overlap index (OI) and relative range size (RRS) estimates for *Mormoops blainvillei*, *Pteronotus parnellii*, and *Pteronotus quadridens* in the Caribbean. Time of the predicted distributions is indicated as current (CUR), Holocene (HOL), and Last Glacial Maximum (LGM). Threshold values were determined using the minimum training presence threshold (MTP). RRS for LGM distributions corrected for current island area are indicated with an asterisk (*). Negative RRS values indicate that the more recent range is bigger than the past (i.e., range expansion). Conversely, positive RRS values indicate that the more recent range is smaller than the past (i.e., range contraction).

Species	Threshold Value	OI			RRS		
		CUR-HOL	HOL-LGM	CUR-LGM	CUR-HOL	HOL-LGM	CUR-LGM
M. blainvillei	0.191	0.983	0.825	0.815	-0.016	0.892	0.862
						-0.155*	-0.174*
P. parnellii	0.197	0.875	0.831	0.739	-0.142	0.803	0.578
						-0.158*	-0.322*
P. quadridens	0.362	0.808	0.532	0.474	-0.234	0.201	-0.027
						-0.670*	-1.061*

pattern remains the same: 93% of modern localities and 85% fossil localities occur within 15 km of karst (table 4). A total of 93% of modern localities and 70% of fossil localities for *P. quadridens* are within 15 km of karst (table 4). For all three species, the totals for fossil localities are affected by exclusion of localities from Bahamas and Cayman Islands, because eolianite karst is not included in the KROW database. To be conservative, we treated eolianite karst in these areas as nonkarst for this analysis because its geomorphology is different than that of fluviokarst.

To estimate the importance of karst, and how PHT change in climate and the resulting loss of suitable hot cave roosts could have affected the distribution of mormoopid bats in the Caribbean, we constrained climate-based distributions to the consistently exposed areas of karst on the Greater Antilles. Similar to the ENMs produced using climate data alone, the karst-climate ENMs using the MTP threshold showed good overall performance in all species for localities occurring within karst (table 1). True-positive fractions for *Mormoops blainvillei*, *Pteronotus parnellii*, and *P. quadridens* for the current karst-climate models were 98%, 100%, and 100%, respectively. Past projections to the HOL and LGM of the karst-climate ENMs had a true-positive fraction of 80% for *Mormoops blainvillei* and 100% for *Pteronotus parnellii* and *P. quadridens* (table 1). As noted previously, in contrast to the Greater Antilles, the Bahamas are part of two shallow banks and eolianite karst in these islands has been consistently eroded by glacial-interglacial changes in sea level. As a result, karst-climate ENMs were unable predict the fossil localities in the Bahamas (fig. 9).

DISCUSSION

Bats are widely distributed across the Caribbean, and for many islands they are the only extant native mammals (Morgan, 2001; Rodríguez-Durán and Kunz, 2001; MacPhee, 2009). Examining the effects of recent climatic changes and the availability of suitable roosting habitat may illuminate our understanding of causes contributing to extirpation of populations of insu-
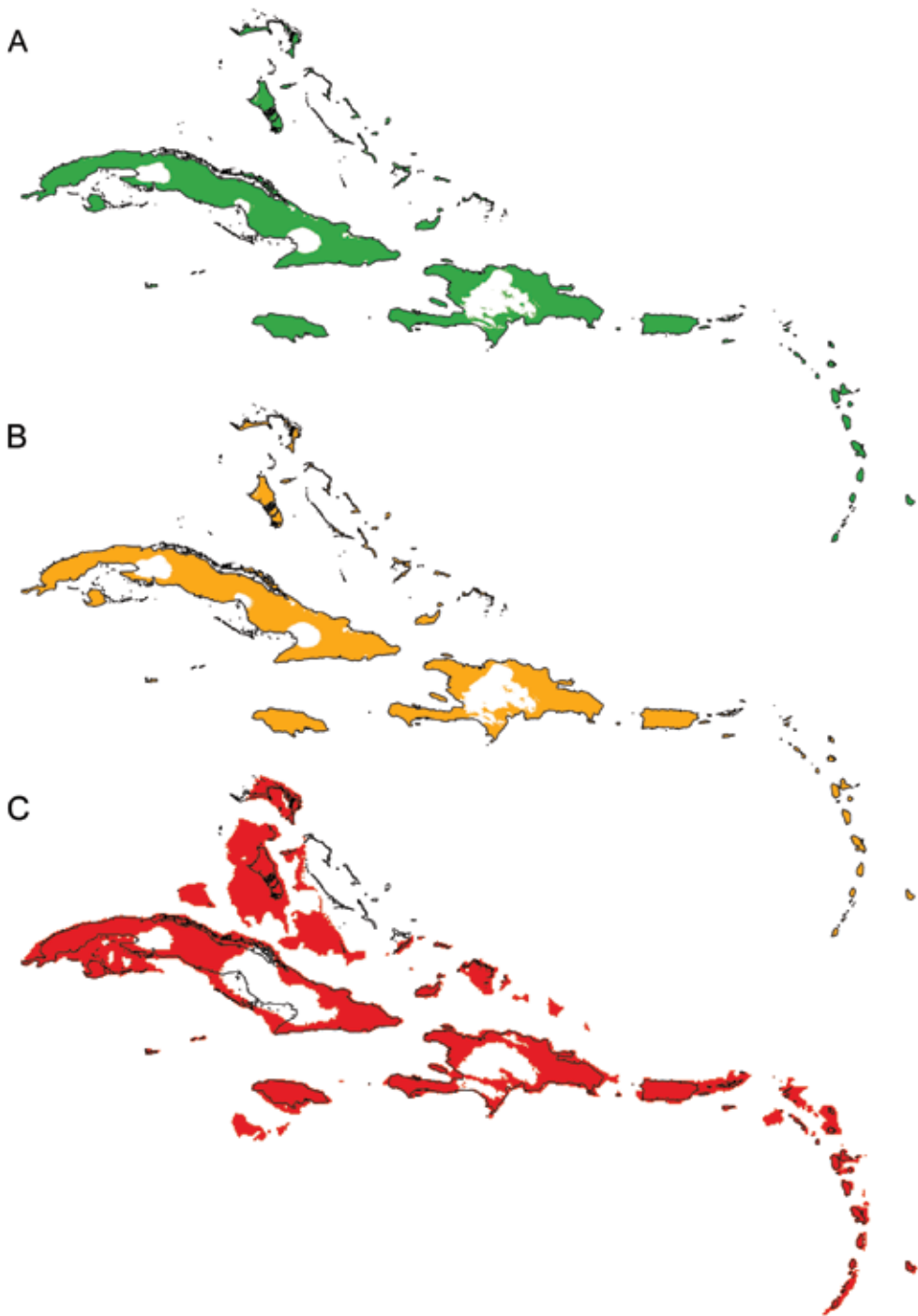
FIGURE 4. Current (**A**), Holocene (**B,** ca. 6 ka), and Last Glacial Maximum (**C,** ca. 21 ka) ecological niche model projections for *Mormoops blainvillei* in the Caribbean. Models were developed using Maxent v3.3.3 and projected as binary distributions in ArcGIS v10.2. Island boundaries (black outlines) are based on current land areas. See figure 1 for geographic reference.

FIGURE 5. Current (**A**), Holocene (**B,** ca. 6 ka), and Last Glacial Maximum (**C,** ca. 21 ka) ecological niche model projections for *Pteronotus parnellii* in the Caribbean. Models were developed using Maxent v3.3.3 and projected as binary distributions in ArcGIS v10.2. Island boundaries (black outlines) are based on current land areas. See figure 1 for geographic reference.
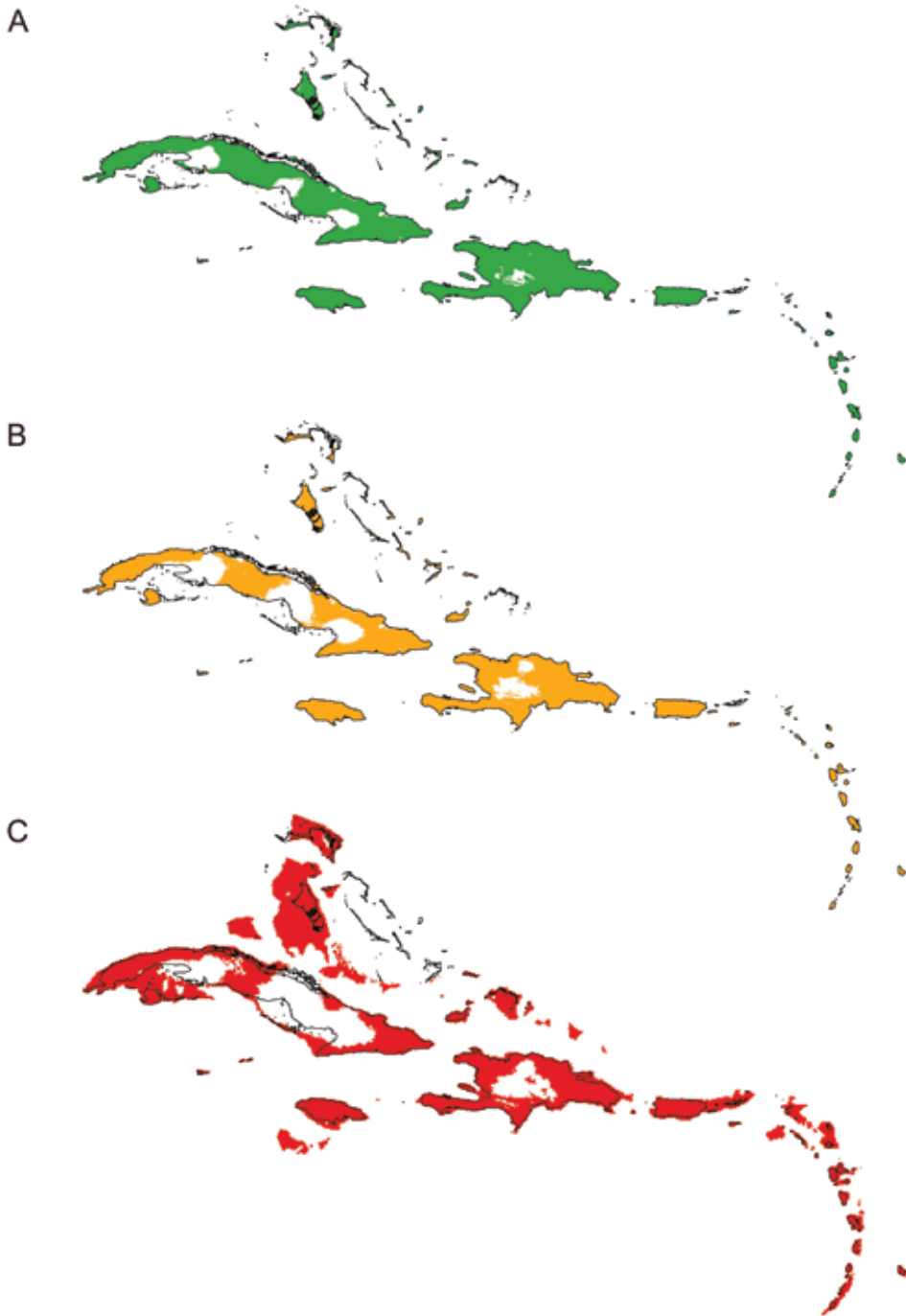
FIGURE 6. Current (**A**), Holocene (**B,** ca. 6 ka), and Last Glacial Maximum (**C,** ca. 21 ka) ecological niche model projections for *Pteronotus quadridens* in the Caribbean. Models were developed using Maxent v3.3.3 and projected as binary distributions in ArcGIS v10.2. Island boundaries (black outlines) are based on current land areas. See figure 1 for geographic reference.
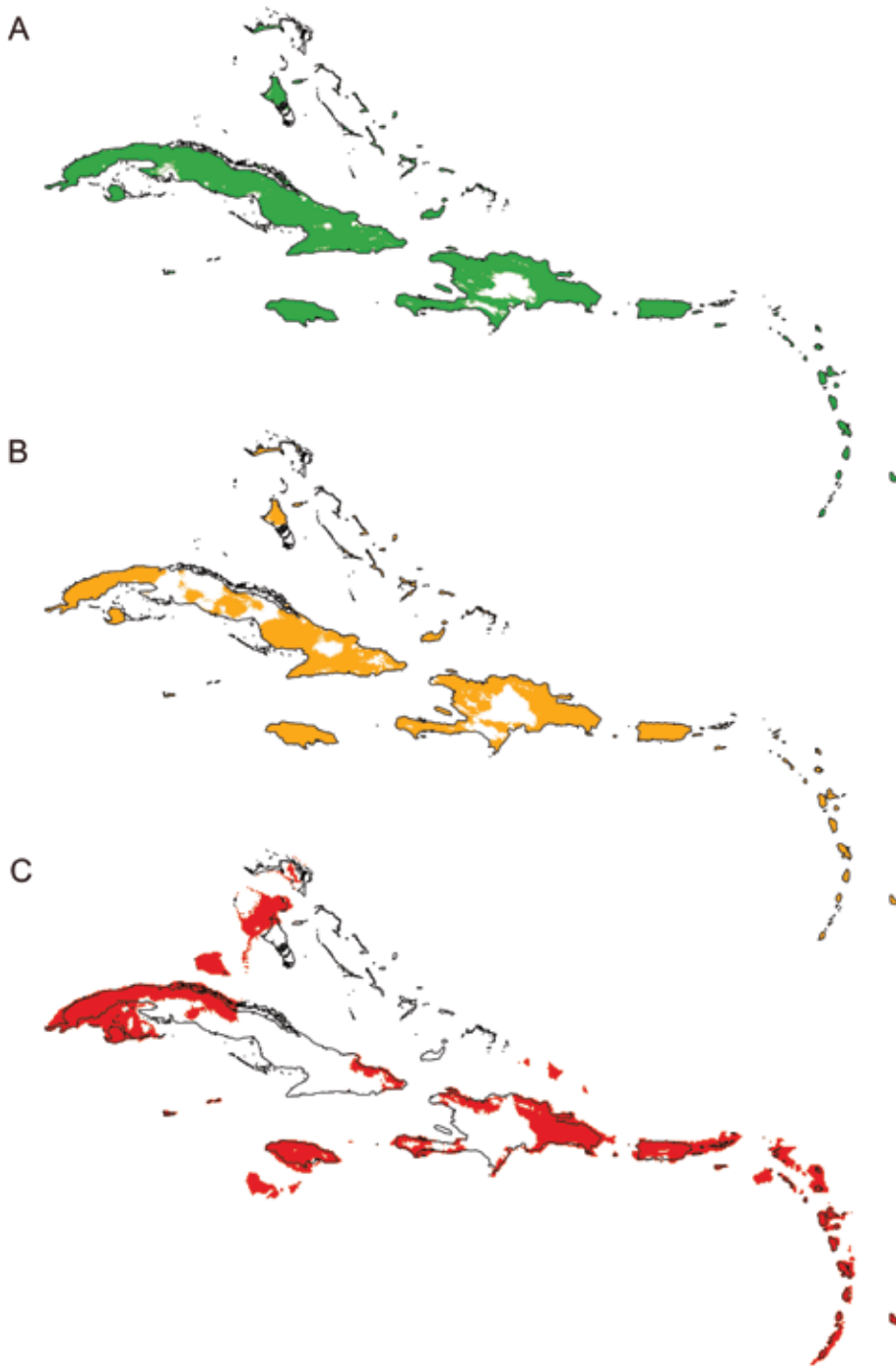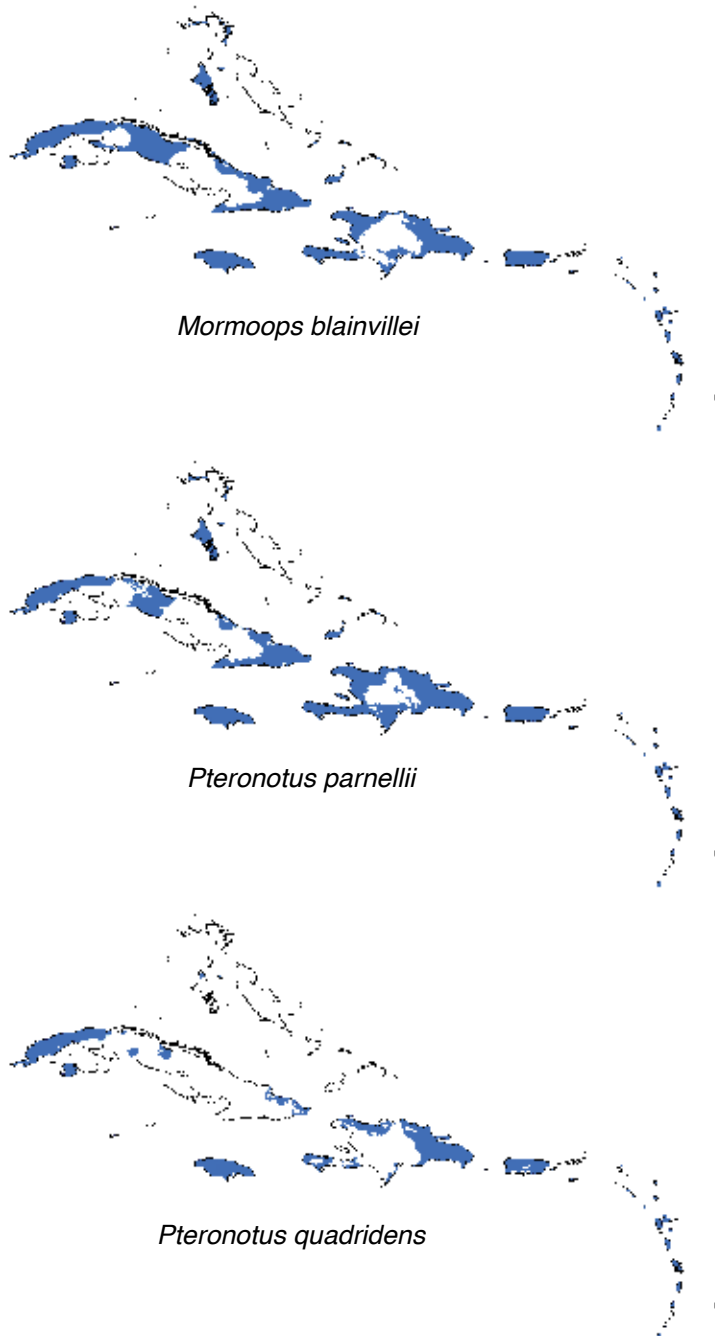
FIGURE 7. Predicted habitat suitability in the Caribbean for *Mormoops blainvillei*, *Pteronotus parnellii*, and *Pteronotus quadridens* represented as stability maps of the intersection of ecological niche model climate projections at three time periods: current, Holocene (HOL, ca. 6 ka), and Last Glacial Maximum (LGM, ca. 21 ka). Blue shading indicates areas where each species could have maintained viable populations across time. See figure 1 for geographic reference.

TABLE 4. Proportion of present and fossil localities occurring within karst (i.e., karst buffer = 0 km) and at increasing 5 km distances away from karst (i.e., karst buffer = 5, 10, 15, 20, 25, and >25 km).

Species	Karst Buffer (km)	Proportion of present localities	Proportion of fossil localities
M. blainvillei	0	65/95 (68%)	5/12 (41%)
	5	83/95 (87%)	9/12 (75%)
	10	88/95 (92%)	9/12 (75%)
	15	91/95 (96%)	10/12 (83%)
	20	91/95 (96%)	10/12 (83%)[a]
	> 25	95/95 (100%)	
P. parnellii	0	56/109 (51%)	7/13 (54%)
	5	88/109 (81%)	11/13 (85%)
	10	100/109 (92%)	11/13 (85%)[a]
	15	101/109 (93%)	
	20	102/109 (94%)	
	25	105/109 (96%)	
	> 25	109/109 (100%)	
P. quadridens	0	46/75 (61%)	3/10 (30%)
	5	59/75 (79%)	6/10 (60%)
	10	67/75 (89%)	6/10 (60%)
	15	70/75 (93%)	7/10 (70%)
	20	72/75 (96%)	7/10 (70%)[a]
	25	74/75 (99%)	
	> 25	75/75 (100%)	

[a] Remaining fossil localities occur in the Bahamas or Cayman Islands, where karst has been exposed to erosion by glacial-interglacial cycles and not included in the KROW database.

lar bats. In this regard, estimating the intersection of karst with climate-based models can provide insight into the importance of karst and whether the loss of suitable hot caves due to climatic changes and associated sea level changes could explain the extirpation of bat populations in the Caribbean.

Previous studies have addressed the usefulness of ENMs to estimate the effect of recent climate change on species distributions and population structure (Waltari et al., 2007; Carnaval et al., 2009; Waltari and Guralnick, 2009). In this study, we developed time-scaled ENMs from the current to the LGM climate and validated them using fossil information for three species of Caribbean bats. Based on previous studies of other Caribbean bats, we hypothesized that climate-based distributions of mormoopid bats would show stability across time. ENMs developed for current climate were highly accurate in all three species of bat with true-positive fractions ranging from 99%–100%. ENM projections to the HOL and LGM for *Mormoops blainvillei* and *Pteronotus parnellii* also performed well and showed true positive fractions of 91% and 92%, respectively. This suggests that our model projections accurately represent the known distribution in the present and past (as evidenced by fossils) of these two mormoopid bats in the Caribbean. RRS for *Mormoops blainvillei* and *Pteronotus parnellii* suggest a range

contraction from LGM to the present. This supports the hypothesis that loss of land area had a negative effect on populations of bat in the Caribbean (Dávalos and Russell, 2012). However, when corrected for island area, changes in RRS are small for land areas that were not affected by sea level change over time, such as the Greater Antilles, and in all species indicate a range expansion from past to present (table 1). At least 73% of the distribution estimates in *Mormoops blainvillei* and *Pteronotus parnellii* represent areas of stability and distribution overlap, indicating that a large portion of the land area available over time has been part of the suitable climatic habitat for these species (fig. 7). These results support our hypothesis that climate-based distributions of mormoopid bats show stability in the Caribbean, and also support the hypothesis that extirpation of these bats from localities in the Bahamas was unlikely driven by PHT climate change alone (Soto-Centeno and Steadman, 2015).

In the case of *Pteronotus quadridens*, we observed hindcasted models with a low level of accuracy and true-positive fractions of 80% for HOL and 60% for LGM. RRS estimates show little change from the LGM to the present. In contrast, there was a trend of range expansion from LGM to the present in RRS estimates corrected for island size, which suggests that estimates of the LGM distribution of *P. quadridens* for areas not affected by sea level change were much smaller than for the present. This is also shown by our estimates of stability and distribution overlap, where at most 47% of the available suitable climatic habitat was shared with LGM distribution, whereas 80% was shared between CUR and HOL distributions. Fossil evidence indicates that *P. quadridens* was once extant on north Andros, Great Abaco, and New Providence in the Bahamas—all areas where it is no longer found (Morgan, 2001; Dávalos and Turvey, 2012). However, the age of these Bahamian fossils is uncertain because they have not been radiocarbon dated. Most bat fossils from extirpated populations in the Bahamas are not older than late Holocene (i.e., <4 ky; Soto-Centeno and Steadman, 2015). If *P. quadridens* fossils were the same age, this pattern may be evidence that this species was able to colonize the Bahamas in the Holocene when climatic conditions were favorable to sustain viable populations, but then became extinct shortly after during the same time period.

Extant mormoopid bats in the Caribbean are known for their nearly exclusive use of hot caves (Silva-Taboada, 1979; Rodríguez-Durán and Soto-Centeno, 2003; Mancina et al., 2007). Because of this tight association, Morgan (2001) hypothesized that the disappearance of mormoopids in the Bahamas was due to the loss of large cave systems and their associated hot microclimate following sea level rise at the end of the Pleistocene. We tested this hypothesis by examining the importance of karst to the distribution of mormoopid bats in the Caribbean. Although karst may seem to be a poor predictor for mormoopid distributions in the Caribbean (i.e., at most 68% of modern localities occur within karst areas), our karst buffer analysis show that >90% of all modern localities lie either in karst areas or within 15 km of the karst edge (fig. 8). Furthermore, the current and hindcasted karst-climate ENMs performed well in each species when corrected for karst area (table 1; fig. 9). This makes sense given that bats are volant animals, and that many bat species have large home ranges and are known to travel long distances from their roost to foraging sites (Rodríguez-Durán, 1984; Horner et al., 1998; Frick et al., 2007; Safi et al., 2007; Zeale et al., 2012). In the Greater Antilles, a region known for exten-
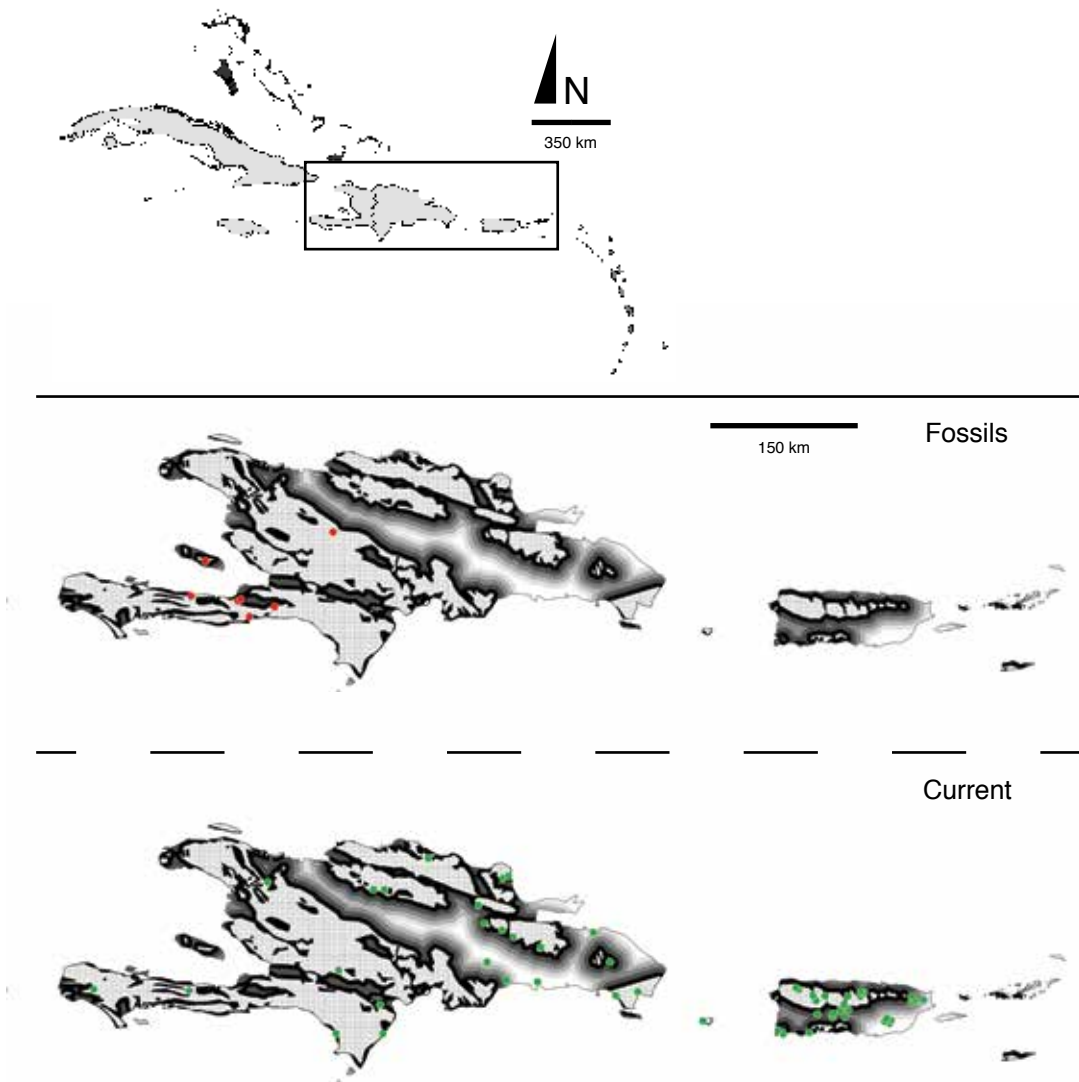
FIGURE 8. Map of karst in the Caribbean and localities of *Pteronotus parnellii*. Fossils are shown in red dots, present localities in green dots, and stippling represents areas of karst. Outlines show buffers around karst at 5 km intervals from 0–25 km (black to light gray shading). Insets represent Hispaniola and Puerto Rico for fossils and present localities to show detail.

sive fluviokarst deposits, it seems clear that proximity to karst is an important factor driving distribution of mormoopid bats.

The Bahamas present a different problem. Roughly 22 glacial-interglacial cycles that altered sea level and island size in the Caribbean have been documented in the past 2.5 my (Cuffey and Marshall, 2000; Lambeck and Chappell, 2001). Rising and falling sea level during these cycles repeatedly inundated the shallow platforms of the Bahamian banks and likely precluded the formation or long-term existence of hot caves in this archipelago. The KROW database
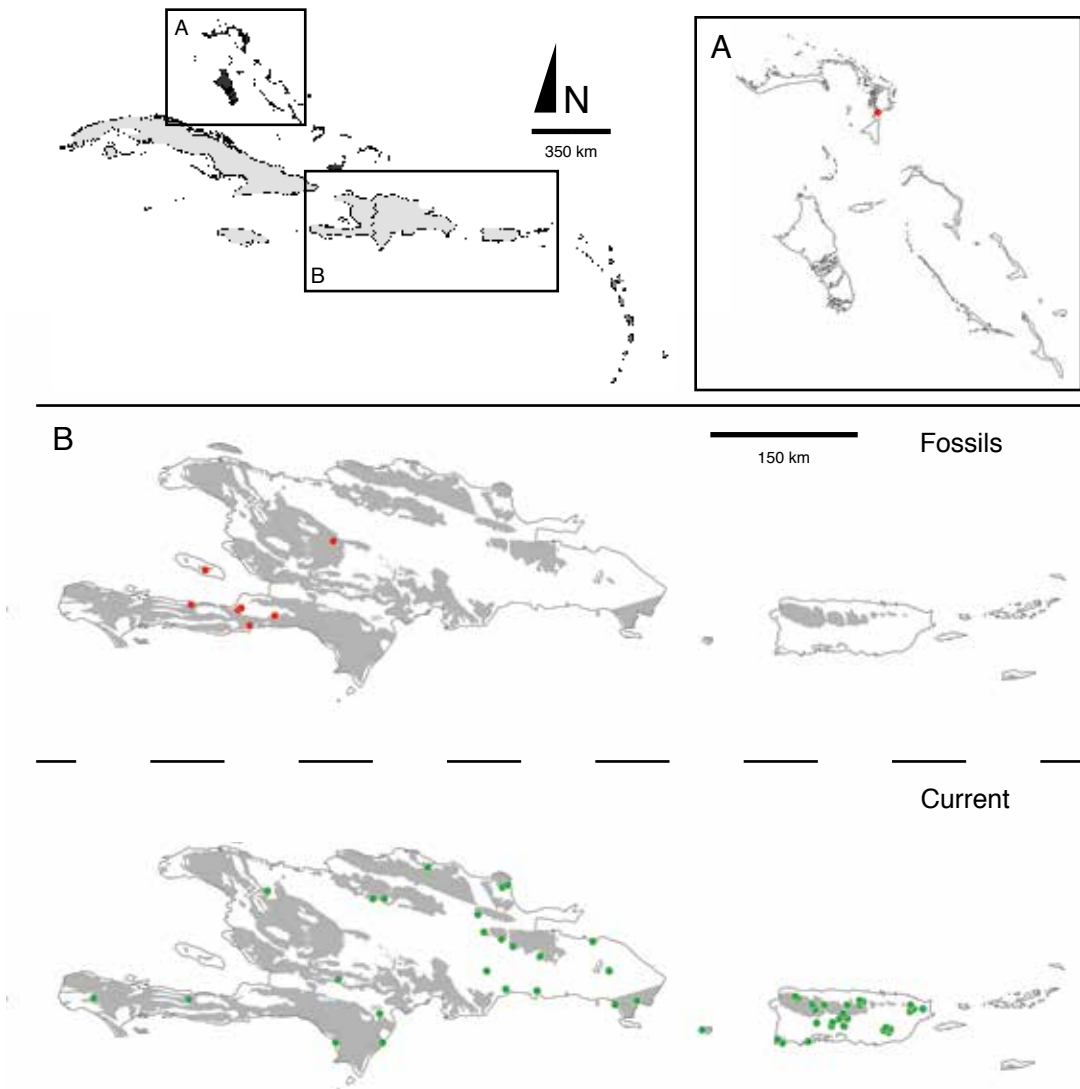
FIGURE 9. Ecological niche model of the intersection of karst and climate in the Caribbean for *Pteronotus parnellii*. Gray shading indicates areas where karst is available and climate is suitable for *P. parnellii*. Insets represent (**A**) the Bahamas and (**B**) Hispaniola and Puerto Rico to show detail. Locality distributions represent fossils (red dots) and current (green dots) samples.

includes Caribbean karst formations that have not been affected by erosion caused by sea level change—i.e., it does not include eolianite karst deposits such as those characteristic of the Bahamas (Hollingsworth, 2006). Therefore, our evaluation involving karst using the KROW database could not be extended to the Bahamas.

It is important to point out that caves do exist in the Bahamas even though eolianite karst does not have the geomorphological features that allow hot caves to form as in the Greater Antilles (Brooke, 2001; Mylroie and Mylroie, 2007; Ladle et al., 2012). The colonization of the Caribbean by mormoopids (ca. 3 ma; Dávalos, 2009) predates the last 22 glacial-interglacial

cycles and our ENM results suggest that a large proportion of the available suitable climatic habitat remained stable at least since the LGM. Furthermore, recently radiocarbon-dated fossils show that the extirpation of *Pteronotus parnellii* in the Bahamas occurred in the late Holocene (ca. 3.4 ka; Soto-Centeno and Steadman, 2015). Contrary to Morgan's (2001) hypothesis, this evidence suggests that mormoopid bats could and did survive glacial-interglacial cycles across long time scales in the Caribbean, and that climate change and associated sea level changes might not have contributed directly to extirpation of populations. Although mostly associated with hot cave environments, *Mormoops blainvillei* and *Pteronotus parnellii* have been reported to occasionally roost in cool cave conditions (Silva-Taboada, 1979; Gannon et al., 2005). Some bat species typically associated with hot caves (e.g., *Nyctiellus lepidus* and *Pteronotus parnellii*) are known to change their roosting behavior by forming tight clusters in bell holes or spreading out on ceilings depending on the temperature and humidity of the cave (Gannon et al., 2005; Tejedor et al., 2005b). In the absence of large hot caves, we suggest that mormoopid bats in the Bahamas were able to use alternative cave roosts, perhaps behaviorally creating suitable roosting conditions by forming tight clusters in bell holes or using small chambers within the eolianite caves characteristic of the Bahamian region.

Our climate-only, karst buffer, and karst-climate analyses suggest that karst is a good predictor for the distribution of mormoopid bats in the Caribbean based on their present distribution. However, evaluating the importance of karst for *Mormoops blainvillei*, *Pteronotus parnellii*, and *P. quadridens* based on climatic and habitat suitability alone cannot account for changes in microclimate within roost sites. Further research is necessary to fully understand the use and importance of hot caves for Caribbean bat populations, and to investigate more thoroughly the possibility that some or all species may use alternative roosts under some circumstances. In this regard, studies of physiology and roosting behavior, as well as more detailed analyses of fossil sites including radiocarbon dating, may shed additional light on the causes of recent change and extirpation of mormoopid bats in the Caribbean islands.

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APPENDIX

Unique localities with geographic coordinates (decimal degrees) and locality descriptions used to construct ecological niche models for *Mormoops blainvillei*, *Pteronotus parnellii*, and *Pteronotus quadridens* in the Caribbean.

Species	Country/island	Locality	Latitude	Longitude
Mormoops blainvillei	Cuba	Camagüey	21.856561	-78.111381
Mormoops blainvillei	Cuba	La Habana	23.118181	-82.300233
Mormoops blainvillei	Cuba	La Habana	23.067617	-82.421394
Mormoops blainvillei	Cuba	Granma	20.3724	-76.422056
Mormoops blainvillei	Cuba	Guantánamo	20.348559	-74.510627
Mormoops blainvillei	Cuba	Guantánamo	20.130133	-75.18937
Mormoops blainvillei	Cuba	Holguín	20.659103	-75.678434
Mormoops blainvillei	Cuba	La Habana	22.843899	-82.034384
Mormoops blainvillei	Cuba	La Habana	22.906782	-82.154048
Mormoops blainvillei	Cuba	La Habana	22.966776	-82.155701
Mormoops blainvillei	Cuba	La Habana	22.915913	-81.857271
Mormoops blainvillei	Cuba	La Habana	22.888889	-82.498889
Mormoops blainvillei	Cuba	La Habana	22.93	-82.7
Mormoops blainvillei	Cuba	Matanzas	22.587052	-80.913856
Mormoops blainvillei	Cuba	Matanzas	23.099539	-81.381397
Mormoops blainvillei	Cuba	Matanzas	23.050968	-81.575283
Mormoops blainvillei	Cuba	Pinar del Río	22.200429	-84.083902
Mormoops blainvillei	Cuba	Pinar del Río	22.670556	-83.568056
Mormoops blainvillei	Cuba	Pinar del Río	22.7491667	-83.5538889
Mormoops blainvillei	Cuba	Pinar del Río	22.79	-83.36
Mormoops blainvillei	Cuba	Pinar del Río	22.265334	-83.833333
Mormoops blainvillei	Cuba	Pinar del Río	22.615233	-83.715834
Mormoops blainvillei	Cuba	Pinar del Río	22.68	-83.7
Mormoops blainvillei	Cuba	Sancti Spíritus	22.03333	-79.46667
Mormoops blainvillei	Cuba	Sancti Spíritus	22	-79
Mormoops blainvillei	Cuba	Sancti Spíritus	21.797037	-79.980651
Mormoops blainvillei	Cuba	Sancti Spíritus	22.330177	-79.237437
Mormoops blainvillei	Cuba	Sancti Spíritus	21.553103	-79.224918
Mormoops blainvillei	Cuba	Santiago de Cuba	20.016847	-75.830175
Mormoops blainvillei	Cuba	Santiago de Cuba	20.05	-75.76667
Mormoops blainvillei	Cuba	Villa Clara	22.515228	-79.701958
Mormoops blainvillei	Cuba	Villa Clara	22.809114	-80.070934
Mormoops blainvillei	Dominican Republic	La Altagracia	18.85	-68.66667
Mormoops blainvillei	Dominican Republic	La Vega	19.19	-70.55
Mormoops blainvillei	Dominican Republic	María Trinidad Sánchez	19.551011	-69.905938
Mormoops blainvillei	Dominican Republic	Pedernales	17.797227	-71.398046

Species	Country/island	Locality	Latitude	Longitude
Mormoops blainvillei	Dominican Republic	Pedernales	17.9	-71.664
Mormoops blainvillei	Dominican Republic	Pedernales	17.97	-71.65
Mormoops blainvillei	Dominican Republic	San Cristóbal	18.41667	-70.1
Mormoops blainvillei	Dominican Republic	Santo Domingo	18.48333	-69.61667
Mormoops blainvillei	Haiti	Sud	18.356954	-74.085955
Mormoops blainvillei	Jamaica	Clarendon	17.74	-77.215
Mormoops blainvillei	Jamaica	Clarendon	17.75	-77.15
Mormoops blainvillei	Jamaica	Clarendon	18.14	-77.39
Mormoops blainvillei	Jamaica	Clarendon	18.14217	-77.276
Mormoops blainvillei	Jamaica	Hanover	18.442047	-78.178724
Mormoops blainvillei	Jamaica	Manchester	17.86031	-77.466228
Mormoops blainvillei	Jamaica	Manchester	18.206944	-77.625833
Mormoops blainvillei	Jamaica	Manchester	18.207	-77.626
Mormoops blainvillei	Jamaica	Portland	18.0833	-76.7167
Mormoops blainvillei	Jamaica	Portland	18.133215	-76.63334
Mormoops blainvillei	Jamaica	Portland	18.168737	-76.425077
Mormoops blainvillei	Jamaica	Saint Andrew	18.010556	-76.784722
Mormoops blainvillei	Jamaica	Saint Ann	18.21383	-77.27028
Mormoops blainvillei	Jamaica	Saint Ann	18.257048	-77.115479
Mormoops blainvillei	Jamaica	Saint Ann	18.33175	-77.052583
Mormoops blainvillei	Jamaica	Saint Ann	18.405551	-77.096769
Mormoops blainvillei	Jamaica	Saint Ann	18.4333	-77.3667
Mormoops blainvillei	Jamaica	Saint Ann	18.4333	-77.42718
Mormoops blainvillei	Jamaica	Saint Ann	18.45833	-77.39267
Mormoops blainvillei	Jamaica	Saint Catherine	17.983096	-76.94998
Mormoops blainvillei	Jamaica	Saint Catherine	18.066696	-77.098056
Mormoops blainvillei	Jamaica	Saint Catherine	18.08	-77.02
Mormoops blainvillei	Jamaica	Saint Catherine	18.127188	-77.144879
Mormoops blainvillei	Jamaica	Saint Catherine	18.15	-77.08333
Mormoops blainvillei	Jamaica	Saint Catherine	18.18333	-77.1
Mormoops blainvillei	Jamaica	Saint Catherine	18.21	-77.03
Mormoops blainvillei	Jamaica	Saint Elizabeth	18.171874	-77.650724
Mormoops blainvillei	Jamaica	Saint Mary	18.2	-76.9
Mormoops blainvillei	Jamaica	Saint Mary	18.3	-77.0167
Mormoops blainvillei	Jamaica	Trelawny	18.245033	-77.702272
Mormoops blainvillei	Jamaica	Trelawny	18.291276	-77.531755
Mormoops blainvillei	Jamaica	Trelawny	18.3667	-77.6167
Mormoops blainvillei	Jamaica	Westmoreland	18.299	-78.33
Mormoops blainvillei	Jamaica	Westmoreland	18.350278	-78.152917
Mormoops blainvillei	Puerto Rico	Aguadilla	18.402125	-67.132873

Species	Country/island	Locality	Latitude	Longitude
Mormoops blainvillei	Puerto Rico	Arecibo	18.333412	-66.715849
Mormoops blainvillei	Puerto Rico	Arecibo	18.41543	-66.75633
Mormoops blainvillei	Puerto Rico	Arecibo	18.469	-66.734
Mormoops blainvillei	Puerto Rico	Cabo Rojo	18.052716	-67.171753
Mormoops blainvillei	Puerto Rico	Ciales	18.3381	-66.4692
Mormoops blainvillei	Puerto Rico	Guánica	17.969462	-66.910892
Mormoops blainvillei	Puerto Rico	Guayama	17.937	-66.168
Mormoops blainvillei	Puerto Rico	Isabela	18.418755	-66.967505
Mormoops blainvillei	Puerto Rico	Lares	18.325313	-66.842437
Mormoops blainvillei	Puerto Rico	Maricao	18.170662	-66.980338
Mormoops blainvillei	Puerto Rico	Mayagüez	18.200774	-67.145181
Mormoops blainvillei	Puerto Rico	Mona	18.084759	-67.851208
Mormoops blainvillei	Puerto Rico	Mona	18.1	-67.9
Mormoops blainvillei	Puerto Rico	Morovis	18.32576	-66.406556
Mormoops blainvillei	Puerto Rico	Patillas	18.0933	-66.0314
Mormoops blainvillei	Puerto Rico	Sabana Grande	18.13815	-66.9671
Mormoops blainvillei	Puerto Rico	San Germán	18.128066	-67.079702
Mormoops blainvillei	Puerto Rico	Toa Alta	18.375696	-66.305561
Mormoops blainvillei	Puerto Rico	Trujillo Alto	18.364167	-66.020278
Mormoops blainvillei	Anguilla		18.227445	-63.063873
Mormoops blainvillei	Bahamas	New Providence	25.003318	-77.499091
Mormoops blainvillei	Bahamas	South Abaco	25.860793	-77.189764
Mormoops blainvillei	Dominican Republic	Hato Mayor	18.652906	-69.387167
Mormoops blainvillei	Dominican Republic	La Estrelleta	19.093922	-71.68709
Mormoops blainvillei	Haiti	L'Artibonite	19.401333	-72.348675
Mormoops blainvillei	Haiti	Ouest	18.805733	-72.946928
Mormoops blainvillei	Haiti	Ouest	18.836522	-73.041047
Mormoops blainvillei	Haiti	Ouest	18.395233	-72.650094
Mormoops blainvillei	Haiti	Sud	18.322078	-73.887606
Mormoops blainvillei	Haiti	Sud-Est	18.23825	-72.534214
Mormoops blainvillei	Jamaica	Clarendon	17.74	-77.215
Pteronotus parnellii	Cuba	Camagüey	21.37826	-77.868734
Pteronotus parnellii	Cuba	Camagüey	21.1833333	-77.85
Pteronotus parnellii	Cuba	Cienfuegos	22.346755	-80.546293
Pteronotus parnellii	Cuba	Granma	20.367398	-76.425036
Pteronotus parnellii	Cuba	Granma	20.379115	-76.653459
Pteronotus parnellii	Cuba	Guantánamo	20.345055	-74.504196
Pteronotus parnellii	Cuba	Holguín	20.655898	-75.671979
Pteronotus parnellii	Cuba	Isla de la Juventud	21.88379	-82.764021
Pteronotus parnellii	Cuba	La Habana	22.93	-82.7

Species	Country/island	Locality	Latitude	Longitude
Pteronotus parnellii	Cuba	Matanzas	23.038411	-81.233049
Pteronotus parnellii	Cuba	Matanzas	23.050189	-81.605457
Pteronotus parnellii	Cuba	Pinar del Río	22.54377	-83.899318
Pteronotus parnellii	Cuba	Pinar del Río	22.67	-83.7
Pteronotus parnellii	Cuba	Pinar del Río	22.740422	-83.551347
Pteronotus parnellii	Cuba	Pinar del Río	22.827554	-83.379809
Pteronotus parnellii	Cuba	Pinar del Río	22.419994	-83.686846
Pteronotus parnellii	Cuba	Pinar del Río	22.616513	-83.718045
Pteronotus parnellii	Cuba	Sancti Spíritus	21.993775	-79.470375
Pteronotus parnellii	Cuba	Sancti Spíritus	22.308344	-79.233746
Pteronotus parnellii	Cuba	Sancti Spíritus	21.822629	-80.083468
Pteronotus parnellii	Cuba	Sancti Spíritus	21.805438	-79.974238
Pteronotus parnellii	Cuba	Santiago de Cuba	20.05	-75.7666667
Pteronotus parnellii	Cuba	Santiago de Cuba	19.962387	-75.708702
Pteronotus parnellii	Cuba	Villa Clara	22.797666	-80.067178
Pteronotus parnellii	Cuba	Villa Clara	22.8	-80.1
Pteronotus parnellii	Dominican Republic	Barahona	18.251546	-71.213792
Pteronotus parnellii	Dominican Republic	Barahona	17.959046	-71.184159
Pteronotus parnellii	Dominican Republic	Distrito Nacional	18.5	-69.9333333
Pteronotus parnellii	Dominican Republic	Duarte	19.25638	-70.21667
Pteronotus parnellii	Dominican Republic	El Seybo	18.98333	-69.05
Pteronotus parnellii	Dominican Republic	Independencia	18.6	-71.6333333
Pteronotus parnellii	Dominican Republic	La Altagracia	18.342936	-68.82117
Pteronotus parnellii	Dominican Republic	La Altagracia	18.68474	-68.88333
Pteronotus parnellii	Dominican Republic	La Altagracia	18.3833333	-68.6
Pteronotus parnellii	Dominican Republic	María Trinidad Sánchez	19.531275	-69.968486
Pteronotus parnellii	Dominican Republic	María Trinidad Sánchez	19.552538	-69.912837
Pteronotus parnellii	Dominican Republic	Monte Plata	18.8333333	-69.5833333
Pteronotus parnellii	Dominican Republic	Monte Plata	18.93546	-69.86112
Pteronotus parnellii	Dominican Republic	Pedernales	17.961605	-71.66022
Pteronotus parnellii	Dominican Republic	Puerto Plata	19.73333	-70.72434
Pteronotus parnellii	Dominican Republic	Sánchez Ramírez	19.006859	-69.975467
Pteronotus parnellii	Dominican Republic	Sánchez Ramírez	19.077381	-70.155181
Pteronotus parnellii	Dominican Republic	Santiago Rodríguez	19.4166667	-71.1666667
Pteronotus parnellii	Dominican Republic	Santiago Rodríguez	19.41667	-71.28092
Pteronotus parnellii	Dominican Republic	Santo Domingo	18.4833333	-69.6166667
Pteronotus parnellii	Dominican Republic	Santo Domingo	18.68387	-70.12762
Pteronotus parnellii	Haiti	Grand'Anse	18.408981	-74.116227
Pteronotus parnellii	Haiti	L'Artibonite	19.493093	-72.35487
Pteronotus parnellii	Haiti	Nippes	18.39719	-73.15

Species	Country/island	Locality	Latitude	Longitude
Pteronotus parnellii	Jamaica	Clarendon	17.745726	-77.236059
Pteronotus parnellii	Jamaica	Clarendon	18.14	-77.39
Pteronotus parnellii	Jamaica	Clarendon	18.17837	-77.221773
Pteronotus parnellii	Jamaica	Hanover	18.442743	-78.178636
Pteronotus parnellii	Jamaica	Hanover	18.446886	-78.052438
Pteronotus parnellii	Jamaica	Kingston	17.971209	-76.799797
Pteronotus parnellii	Jamaica	Portland	18.0833	-76.7167
Pteronotus parnellii	Jamaica	Portland	18.167637	-76.42509
Pteronotus parnellii	Jamaica	Portland	17.999254	-76.272689
Pteronotus parnellii	Jamaica	Saint Ann	18.244898	-77.026746
Pteronotus parnellii	Jamaica	Saint Ann	18.43722	-77.23009
Pteronotus parnellii	Jamaica	Saint Ann	18.459	-77.27933
Pteronotus parnellii	Jamaica	Saint Ann	18.21383	-77.27028
Pteronotus parnellii	Jamaica	Saint Ann	18.456962	-77.35504
Pteronotus parnellii	Jamaica	Saint Catherine	17.900367	-76.949945
Pteronotus parnellii	Jamaica	Saint Catherine	18.08	-77.02
Pteronotus parnellii	Jamaica	Saint Catherine	18.15	-77.0833333
Pteronotus parnellii	Jamaica	Saint Catherine	18.18053	-77.15114
Pteronotus parnellii	Jamaica	Saint Catherine	18.1833333	-77.1
Pteronotus parnellii	Jamaica	Saint Catherine	18.21	-77.03
Pteronotus parnellii	Jamaica	Saint Catherine	18.123864	-77.145018
Pteronotus parnellii	Jamaica	Saint Catherine	18.025555	-77.067333
Pteronotus parnellii	Jamaica	Saint Elizabeth	18.173026	-77.651772
Pteronotus parnellii	Jamaica	Saint Elizabeth	17.870903	-77.730313
Pteronotus parnellii	Jamaica	Saint Elizabeth	18.085268	-77.628067
Pteronotus parnellii	Jamaica	Saint James	18.459124	-77.913208
Pteronotus parnellii	Jamaica	Saint Mary	18.3	-77.017
Pteronotus parnellii	Jamaica	Trelawny	18.4	-77.6
Pteronotus parnellii	Jamaica	Trelawny	18.27	-77.56
Pteronotus parnellii	Jamaica	Trelawny	18.33492	-77.64985
Pteronotus parnellii	Jamaica	Trelawny	18.265927	-77.757807
Pteronotus parnellii	Jamaica	Westmoreland	18.225516	-78.112436
Pteronotus parnellii	Puerto Rico	Adjuntas	18.157704	-66.777671
Pteronotus parnellii	Puerto Rico	Arecibo	18.3417	-66.7
Pteronotus parnellii	Puerto Rico	Cabo Rojo	17.956419	-67.124992
Pteronotus parnellii	Puerto Rico	Cabo Rojo	17.993338	-67.175892
Pteronotus parnellii	Puerto Rico	Camuy	18.345969	-66.82491
Pteronotus parnellii	Puerto Rico	Cayey	18.1104	-66.0736
Pteronotus parnellii	Puerto Rico	Ciales	18.2529	-66.50871
Pteronotus parnellii	Puerto Rico	Ciales	18.3381	-66.4692

Species	Country/island	Locality	Latitude	Longitude
Pteronotus parnellii	Puerto Rico	Corozal	18.338185	-66.340649
Pteronotus parnellii	Puerto Rico	Fajardo	18.3	-65.7
Pteronotus parnellii	Puerto Rico	Guayama	18.082575	-66.096001
Pteronotus parnellii	Puerto Rico	Isabela	18.4062	-66.9667
Pteronotus parnellii	Puerto Rico	Isabela	18.426403	-66.995239
Pteronotus parnellii	Puerto Rico	Jayuya	18.162171	-66.616156
Pteronotus parnellii	Puerto Rico	Jayuya	18.19737	-66.54605
Pteronotus parnellii	Puerto Rico	Mona	18.087104	-67.93852
Pteronotus parnellii	Puerto Rico	Orocovis	18.203906	-66.464561
Pteronotus parnellii	Puerto Rico	Patillas	18.063084	-66.046797
Pteronotus parnellii	Puerto Rico	Patillas	18.0933	-66.0314
Pteronotus parnellii	Puerto Rico	Ponce	18.12531	-66.62604
Pteronotus parnellii	Puerto Rico	Río Grande	18.2742	-65.8297
Pteronotus parnellii	Puerto Rico	Río Grande	18.299689	-65.793044
Pteronotus parnellii	Puerto Rico	Río Grande	18.338839	-65.825771
Pteronotus parnellii	Puerto Rico	Toa Alta	18.374353	-66.305068
Pteronotus parnellii	Puerto Rico	Utuado	18.29219	-66.79215
Pteronotus parnellii	Puerto Rico	Vega Alta	18.385831	-66.342514
Pteronotus parnellii	Puerto Rico	Villalba	18.12551	-66.50049
Pteronotus parnellii	Puerto Rico	Yauco	17.9708	-66.8625
Pteronotus parnellii	Antigua and Barbuda	Saint George	17.137674	-61.784173
Pteronotus parnellii	Bahamas	South Abaco	26.24961	-77.19021
Pteronotus parnellii	Cayman Islands	East End	19.303469	-81.106584
Pteronotus parnellii	Cuba	Isla de la Juventud	21.863922	-82.750552
Pteronotus parnellii	Cuba	La Habana	22.884952	-82.321124
Pteronotus parnellii	Dominican Republic	La Estrelleta	19.093922	-71.68709
Pteronotus parnellii	Haiti	Nippes	18.446092	-73.127475
Pteronotus parnellii	Haiti	Ouest	18.395233	-72.650094
Pteronotus parnellii	Haiti	Ouest	18.414028	-72.622972
Pteronotus parnellii	Haiti	Ouest	18.79924	-72.98521
Pteronotus parnellii	Haiti	Sud-Est	18.23825	-72.534214
Pteronotus parnellii	Haiti	Sud-Est	18.3375	-72.280556
Pteronotus parnellii	Jamaica	Trelawny	18.289369	-77.741303
Pteronotus quadridens	Cuba	Camagüey	21.392591	-77.905317
Pteronotus quadridens	Cuba	Camagüey	21.856095	-78.111381
Pteronotus quadridens	Cuba	Cienfuegos	22.15995	-80.443046
Pteronotus quadridens	Cuba	Cienfuegos	22.342663	-80.555257
Pteronotus quadridens	Cuba	La Habana	23.052467	-82.345209
Pteronotus quadridens	Cuba	La Habana	23.06956	-82.421102
Pteronotus quadridens	Cuba	Granma	20.046548	-77.577958

Species	Country/island	Locality	Latitude	Longitude
Pteronotus quadridens	Cuba	Guantánamo	20.343931	-74.510117
Pteronotus quadridens	Cuba	Guantánamo	20.136722	-75.213913
Pteronotus quadridens	Cuba	Holguín	20.966154	-75.711962
Pteronotus quadridens	Cuba	Holguín	20.658905	-75.678051
Pteronotus quadridens	Cuba	La Habana	22.846398	-82.023764
Pteronotus quadridens	Cuba	La Habana	22.967611	-82.155848
Pteronotus quadridens	Cuba	La Habana	23.022058	-82.136095
Pteronotus quadridens	Cuba	La Habana	22.93333	-81.91667
Pteronotus quadridens	Cuba	La Habana	22.93	-82.7
Pteronotus quadridens	Cuba	La Habana	23.155199	-81.92664
Pteronotus quadridens	Cuba	Matanzas	23.053452	-81.457017
Pteronotus quadridens	Cuba	Matanzas	22.96667	-80.91667
Pteronotus quadridens	Cuba	Pinar del Río	22.716858	-83.051114
Pteronotus quadridens	Cuba	Pinar del Río	22.615232	-83.715824
Pteronotus quadridens	Cuba	Pinar del Río	22.67	-83.7
Pteronotus quadridens	Cuba	Sancti Spíritus	21.795979	-79.980806
Pteronotus quadridens	Cuba	Sancti Spíritus	22.33333	-79.26667
Pteronotus quadridens	Cuba	Santiago de Cuba	20.177364	-75.847998
Pteronotus quadridens	Cuba	Santiago de Cuba	19.961141	-75.709056
Pteronotus quadridens	Cuba	Santiago de Cuba	20.01516	-75.830165
Pteronotus quadridens	Cuba	Villa Clara	22.808562	-80.071109
Pteronotus quadridens	Dominican Republic	Barahona	17.96667	-71.18333
Pteronotus quadridens	Dominican Republic	Barahona	18.249722	-71.216644
Pteronotus quadridens	Dominican Republic	Distrito Nacional	18.471	-69.9
Pteronotus quadridens	Dominican Republic	La Altagracia	18.405346	-68.611304
Pteronotus quadridens	Dominican Republic	María Trinidad Sánchez	19.551011	-69.905938
Pteronotus quadridens	Dominican Republic	Pedernales	17.84	-71.3
Pteronotus quadridens	Dominican Republic	Puerto Plata	19.73333	-70.72434
Pteronotus quadridens	Dominican Republic	Puerto Plata	19.74	-70.51
Pteronotus quadridens	Dominican Republic	Samaní	19.28333	-69.43333
Pteronotus quadridens	Dominican Republic	Santiago Rodríguez	19.415649	-71.280866
Pteronotus quadridens	Dominican Republic	Santo Domingo	18.46667	-69.61597
Pteronotus quadridens	Dominican Republic	Santo Domingo	18.55701	-69.9
Pteronotus quadridens	Haiti	Centre	19.140117	-71.760258
Pteronotus quadridens	Haiti	Centre	19.164101	-71.788943
Pteronotus quadridens	Haiti	Ouest	18.51	-72.28
Pteronotus quadridens	Jamaica	Clarendon	17.742341	-77.157605
Pteronotus quadridens	Jamaica	Hanover	18.447896	-78.052508
Pteronotus quadridens	Jamaica	Manchester	18.207013	-77.625961
Pteronotus quadridens	Jamaica	Portland	18.168552	-76.425176

Species	Country/island	Locality	Latitude	Longitude
Pteronotus quadridens	Jamaica	Saint Ann	18.427303	-77.239084
Pteronotus quadridens	Jamaica	Saint Catherine	18.08	-77.02
Pteronotus quadridens	Jamaica	Saint Catherine	18.151028	-77.090889
Pteronotus quadridens	Jamaica	Saint Elizabeth	18.171771	-77.650749
Pteronotus quadridens	Jamaica	Trelawny	18.358012	-77.650749
Pteronotus quadridens	Jamaica	Westmoreland	18.223355	-78.114432
Pteronotus quadridens	Jamaica	Westmoreland	18.298236	-78.331124
Pteronotus quadridens	Jamaica	Westmoreland	18.354104	-78.173081
Pteronotus quadridens	Puerto Rico	Aguadilla	18.402125	-67.132873
Pteronotus quadridens	Puerto Rico	Arecibo	18.333412	-66.715849
Pteronotus quadridens	Puerto Rico	Arecibo	18.371667	-66.691667
Pteronotus quadridens	Puerto Rico	Arecibo	18.425562	-66.76033
Pteronotus quadridens	Puerto Rico	Barceloneta	18.448193	-66.578279
Pteronotus quadridens	Puerto Rico	Cabo Rojo	17.97483	-67.168103
Pteronotus quadridens	Puerto Rico	Canóvanas	18.265426	-65.878857
Pteronotus quadridens	Puerto Rico	Cataño	18.433481	-66.139296
Pteronotus quadridens	Puerto Rico	Guánica	17.981812	-66.878619
Pteronotus quadridens	Puerto Rico	Guayanilla	17.96	-66.84
Pteronotus quadridens	Puerto Rico	Humacao	18.1683	-65.7486
Pteronotus quadridens	Puerto Rico	Isabela	18.418755	-66.967505
Pteronotus quadridens	Puerto Rico	Juana Díaz	18.008244	-66.504347
Pteronotus quadridens	Puerto Rico	Mayagüez	18.200774	-67.145181
Pteronotus quadridens	Puerto Rico	Orocovis	18.177107	-66.505615
Pteronotus quadridens	Puerto Rico	Río Grande	18.321117	-65.819953
Pteronotus quadridens	Puerto Rico	San Germán	18.068109	-67.09324
Pteronotus quadridens	Puerto Rico	Trujillo Alto	18.364167	-66.020278
Pteronotus quadridens	Puerto Rico	Vega Alta	18.38582	-66.339727
Pteronotus quadridens	Puerto Rico	Yauco	18.131166	-66.907521
Pteronotus quadridens	Bahamas	South Abaco	25.860793	-77.189764
Pteronotus quadridens	Bahamas	North Andros	25.166667	-78.033333
Pteronotus quadridens	Bahamas	New Providence	25.003318	-77.499091
Pteronotus quadridens	Cuba	Pinar del Río	21.933333	-84.25
Pteronotus quadridens	Dominican Republic	Hato Mayor	18.652906	-69.387167
Pteronotus quadridens	Dominican Republic	La Estrelleta	19.093922	-71.68709
Pteronotus quadridens	Haiti	Ouest	18.395233	-72.650094
Pteronotus quadridens	Haiti	Ouest	18.414028	-72.622972
Pteronotus quadridens	Haiti	Sud-Est	18.23825	-72.534214
Pteronotus quadridens	Haiti	Sud-Est	18.3375	-72.280556