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Isotopic ecology and extirpation chronology of the extinct Lesser Antillean native rodent *Antillomys rayi* Brace et al. (2015)

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ABSTRACT— The Lesser Antilles is a string of islands stretching from Grenada in the south to Sombrero in the north, which was once home to at least 20 insular populations of native rodents scattered across the different islands. Despite their relative ubiquity on the archipelago, these now extinct rodents remain poorly understood. In Guadeloupe (Basse-Terre and Grande-Terre), Marie-Galante, Barbuda and Antigua, fossil specimens of a large Lesser Antillean native rodent have recently been described as a distinct species, *Antillomys rayi* Brace et al. 2015. In order to shed new light on the processes leading to the extinction of this species, we use stable carbon and oxygen isotopes to better constrain its ecology, along with a series of radiocarbon dates to narrow its last-occurrence date in Guadeloupe and Marie-Galante. First, we built a reference collection of present-day isotopic data based on carbon and oxygen isotopes from black rats captured in different natural environmental contexts of Guadeloupe. Here, we show *A. rayi* to have occupied multiple distinct environments ranging from semi-deciduous dry forest to seasonal evergreen or mountain forests. New direct radiocarbon dates obtained on fossil material considerably bring forward the last occurrence of *A. rayi* in Guadeloupe and Marie-Galante, making it roughly coincident with European contact. However, our new calibrated age intervals place the last occurrence of *A. rayi* no later than the 16th century AD. Taken together, our results suggest that *A. rayi* became exceedingly rare, if not extirpated, in Guadeloupe and Marie-Galante shortly after European contact. While the overexploitation of *A. rayi* by Amerindian populations and the deforestation by European colonists could have impacted *A. rayi* populations, the consequences (biological competition, disease) of the introduction of black rat most likely explains the early decline of *A. rayi* and its ultimate extirpation from the islands of Guadeloupe.

Key words: Holocene, Lesser Antilles, Rodent, Radiocarbon, Stable isotope

1. Introduction

The Lesser Antillean native rodents form part of a wider mainland South-American rodent radiation, the tribe Oryzomyini (family Cricetidae, subfamily Sigmodontinae), which comprises 29 extant genera, from which around 141 species are currently recognized (Pardiñas et al., 2017). Species of this tribe are sometimes referred to as “rice rats”. Oryzomyine rodents probably colonized the island

chain during the Late Miocene (Brace et al., 2015). Their skeletal remains are frequently found in both archaeological and palaeontological sites and provide evidence for the presence of around 20 separate oryzomyine populations across the Lesser Antillean islands, which include different endemic genera and species (Turvey et al., 2010, 2012; Brace et al., 2015). The Lesser Antillean native rodents are now extinct, disappearing as part of a larger Holocene Caribbean extinction event most likely driven by anthropogenic causes (Cooke et al., 2017). These extinctions probably occurred during the last millennium, with several following European contact, and the last-occurrences of Lesser Antillean native rodents documented in the late 19th or very early 20th century. Because last-occurrence dates are not available for most species and/or rarely rely on direct radiocarbon dating, the dynamics, drivers and timing of these disappearances, however, remain elusive and potentially differ between regions and populations (Turvey et al., 2010; Cooke et al., 2017). Several hypotheses have been advanced to explain them, including biological competition with introduced species and human impact on oryzomyine populations or their habitats, initially by Amerindian populations and/or by subsequent European colonists.

Several studies of oryzomyine bones recovered from archaeological sites indicate they constituted an important component of the Amerindian diet (Wing et al., 2001; Wing, 2001; Newsom and Wing, 2004). Such practices could have led to the extirpation of some populations during the region's prehistoric period (e.g., Wing et al., 1968; Jones, 1985; Wing, 1995; Wing and Wing, 1997; Nokkert, 1999). On the contrary, several authors consider that most of these extirpations were driven either directly or indirectly by European colonists (Turvey et al., 2010). For instance, Lesser Antillean native rodents may have been overexploited for their meat. Historical accounts do, in fact, mention that they were still consumed during the historical period on several islands (Du Tertre 1667, Rochefort 1667, Labat, 1722, Turvey et al., 2010). Another potential cause could be the large-scale transformation of island's forests into agricultural areas, potentially destroying the natural habitats of Lesser Antillean native rodents. The introduction of invasive species may have equally played a role in these extinctions. For example, the last known records of several Lesser Antillean native rodent species (*Megalomys desmarestii*, *M. luciae* and *Oligoryzomys victus*) all date to between 1880 and 1890 and are concomitant with the introduction of the Indian mongoose (*Urva auropunctata*; Horst et al., 2001; Turvey et al., 2010). The impact of the invasive black rat (*Rattus rattus*) as a biological competitor has equally been suspected for older extirpations (Pinchon, 1967; Wing, 2008; Turvey et al., 2010). However, all of these hypotheses are currently difficult to test in view of the paucity of data, including reliable last-occurrence dates and a precise understanding of Lesser Antillean native rodent ecology.

In Guadeloupe (Basse-Terre and Grande-Terre), Marie-Galante, Barbuda and Antigua, fossil specimens of a large Lesser Antillean native rodent have recently been described as representing a distinct species, *Antillomys rayi* Brace et al. (2015). Fossil remains of *A. rayi* have been identified from very few Amerindian archaeological sites on the Eastern coasts of Guadeloupe and Marie-Galante (Brace et al., 2015). However, this species occurrence appears to have been larger, including the pre-Columbian sites of Roseau on Basse-Terre and Folle-Anse on Marie-Galante, as well as natural accumulations preserved in the caves of Grotte des Bambous, Pointe-des-Châteaux, and Blanchard 2 (Fig. 1 and SI 1). The mechanisms underlying the extirpation of *A. rayi* from both islands currently remain unexplained. This is partly due to the lack of chronological data for the remains of this species from archaeological deposits.

Surprisingly, early chroniclers who described the Guadeloupe fauna do not mention any oryzomyine rodent (Ballet, 1895), raising the possibility of a relatively early extirpation during the prehistoric period. The only mentions of an oryzomyine rat on these islands come from an anonymous early 19th text indicating the persistence of a "pilori rat" on the tiny islet of Petite Terre (Anonyme, 1829) and the suspicion of its presence in the deep forests from Basse-Terre in the 1960s (Pinchon, 1967). Unfortunately, the scarcity of these observations and the lack of associated specimens make it difficult to lend credibility to these observations, therefore hinting at an early extirpation of *A. rayi* from the main Guadeloupe Islands.

Nonetheless, in the early colonial period of the Lesser Antillean islands, like Guadeloupe, increased agriculture activity resulted in a massive transformation of natural habitats, with most

lowland forest cleared for cane cultivation, and middle elevation forest for coffee and cocoa crops (Lasserre, 1961; Lugo et al., 1981). Furthermore, the introduction of the black rat in the Lesser Antilles is relatively old, contemporary with the arrival of the first Europeans (prior to 1647, Du Tertre 1667, Breton, 1978; Lorvelec et al., 2007). This species could have colonized Guadeloupe as early as the 16th century with the arrival of the first Spanish ships, as is the case for Hispaniola (MacPhee et al., 1999; Wing et al., 2001). In this scenario, the extinction of *A. rayi* could also have been driven by direct or indirect human pressure during the historical period.

Information concerning the ecology of *A. rayi*, as well as precise last-occurrence dates is required to further test these different scenarios. To this end, we first measured both the oxygen and carbon isotopic compositions of present-day black rat tooth enamel from different natural environments of Guadeloupe (Basse-Terre and Grande-Terre (Goedert et al., 2020); in order to establish present-day isotopic reference values and compare them with oxygen and carbon isotopic compositions of fossil *A. rayi* tooth enamel (Fig. 2; SI 2, 3). In parallel, we obtained radiocarbon dates from *A. rayi* tooth enamel samples complemented by dates from other *A. rayi* skeletal elements from multiple sites in Guadeloupe (Basse-Terre and Grande-Terre) and Marie-Galante (Fig. 1) in order to better constrain the extirpation chronology of this species on these Lesser Antillean islands (Fig. 3; SI 4).

2. Present-day isotopic referential

2.1 Climatic and geographic context

Guadeloupe comprises two main islands: the volcanic and mountainous Basse-Terre Island, to the west, and the carbonated low-lying island of Grande-Terre to the east. Guadeloupe experiences a marked precipitation gradient (e.g., Lasserre, 1961); the north-eastern region of Grande-Terre receives no more than 1300 mm of mean annual precipitation compared to the 10,000 mm mean annual precipitation of the volcanic summit of La Soufrière on Basse-Terre. Variations in soil type and climatic conditions define four main types of native forests: semi-deciduous dry forest, seasonal evergreen forest, mountain rainforest, and swamp forest (Rousteau et al., 1994, Fig.1). Guadeloupe equally experiences seasonal weather variations comprising a dry season from January to April and a wet season from August to November that affects the seasonal evergreen forest and, to an even greater extent, the semideciduous dry forest.

2.2 Environmental isotopic variations

In natural environments, annual rainfall controls oxygen isotope composition of water (Dansgaard, 1964; Rozanski et al., 1993) and also influences the carbon isotope composition of plants (e.g., Kohn, 2010; Basu et al., 2019). This being the case, the different environments of Guadeloupe should bear marked isotopic differences that potentially vary seasonally. These environmental oxygen and carbon isotopic signals can be integrated in bioapatite ($\text{Ca}_5[(\text{PO}_4)_{3-x}(\text{CO}_3)_x](\text{OH})$), the mineral fraction that constitutes the skeletal tissues of vertebrates. For instance, the oxygen isotope composition of phosphate ($\delta^{18}\text{O}_p$) bioapatite has been shown to principally reflect the oxygen isotope composition of environmental water ($\delta^{18}\text{O}_w$) (e.g., Longinelli, 1984; Luz et al., 1984). Whereas the carbon isotope composition of carbonate ($\delta^{13}\text{C}_c$) bioapatite has been shown to principally reflect the carbon isotope composition of ingested food, in particular plants consumed by herbivores ($\delta^{13}\text{C}_{vg}$) (e.g., Lee-Thorp et al., 1989; Cerling and Harris, 1999), which is in turn controlled by climatic conditions (Kohn, 2010). The integration of isotopic compositions in bioapatite tissues of different vertebrate species living in the same environment can, however, vary according to their specific ecology, physiology, and diet.

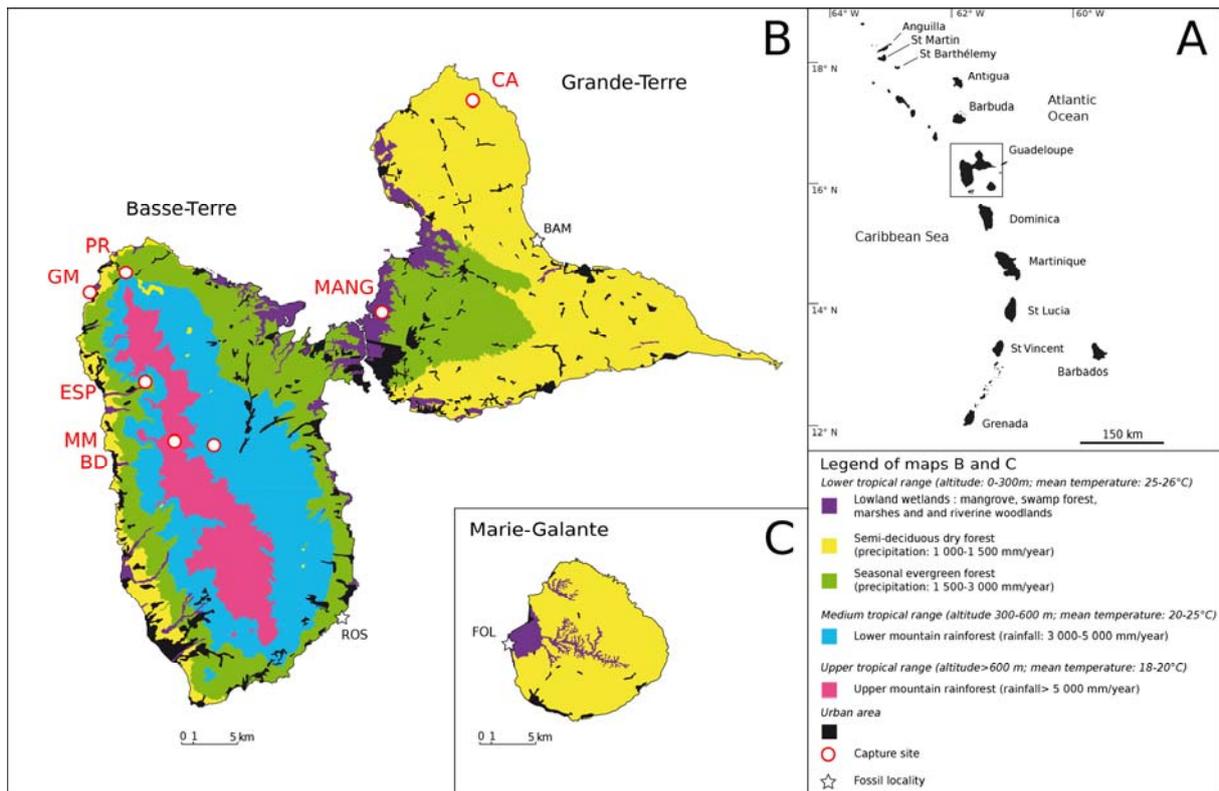


Figure 1. Geographical maps. A Location of the Guadeloupe Islands within the Lesser Antilles. B Ecological map of Guadeloupe (Basse-Terre and Grande-Terre) C Ecological map of Marie-Galante. The legend and ecological map are based on (Rousteau et al., 1994). The different capture sites of present-day black rats are indicated with red circles and the different fossil localities studied in this study as black stars. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.3 Black rats (*Rattus rattus*)

In the case of small rodents, such as rats, several studies have shown that stable isotope compositions recorded in teeth accurately reflect local environmental and climatic parameters (e.g., Royer et al., 2013a; Jeffrey et al., 2015). Their small size implies both a rapid body water turnover (Podlesak et al., 2008) and tooth mineralisation during a brief time interval (Hillson, 2005). Therefore, isotope compositions from rodent teeth are sound indicators of seasonal climatic information (Royer et al., 2013a, 2013b); moreover, for continuously growing teeth such as incisors, this seasonal period corresponds to the last weeks before animal death. In the case of the black rat, this represents about two months. Three introduced rodent species are currently present in Guadeloupe: the black rat (*Rattus rattus*), the Norwegian rat (*Rattus norvegicus*) and the house mouse (*Mus musculus*) (Lorvelec et al., 2007), all of which are relatively small-bodied rodents (<0.48 kg; Cooke et al., 2017). Adult black and Norwegian rats have mean body weights of around 0.085-0.165 and 0.195-0.485 kg (data for Central America), respectively (Burgin et al., 2017a, 2017b). *A. rayi* is comparatively heavier, with body weight estimates ranging from 0.320 to 0.630 kg (SI 5). Therefore, they have comparable metabolic turnovers and thus similar residence times regarding the integration of environmental isotopic signals (Podlesak et al., 2008; Royer et al., 2013a). Furthermore, the black rat is present in all natural environments of Guadeloupe (Delattre and Le Louarn, 1980; Pascal et al., 2004b; Goedert et al., 2020), whereas the Norwegian rat and House Mouse are more restricted to human-dominated environments (Pascal et al., 2004b). The black rat therefore appears to be the most appropriate species for building a present-day isotopic reference series for comparisons with fossil *A. rayi*.

To this end, we analysed the carbon and oxygen isotope compositions of black rats captured in the five distinct natural environments of Guadeloupe (Goedert et al., 2020), as well as several

specimens from Hardy Islet of Martinique (Pascal et al., 2004a). For each Guadeloupe environment, except for the swamp forest, two sampling localities were selected (Fig. 1). Black rats were captured both during the wet season (October 2017) and dry season (March 2018) in order to document seasonal isotopic variability. Five specimens from Martinique were captured during eradication efforts in November 1999 (wet season; Pascal et al., 2004a).

3. Material and methods

Sample sizes follow Royer (2013), Royer et al. (2013a), and Peneycad et al. (2019), who found that mean isotopic values from a subsample of $n > 5-10$ rodent individuals is accurate enough to confidently (>90 %) reflect mean isotopic values of larger populations. Consequently, we selected five black rat lower incisors per locality and per season to establish a present-day isotopic referential and at least ten *A. rayi* lower incisors per locality, representing at least six different individuals.

3.1 [Collection of present-day material](#)

Skeletal elements of present-day black rats analysed in this study come from the “Caribbeetek” osteological collection housed at the PACEA laboratory of the University of Bordeaux (Guimaraes et al., 2019). Details concerning the protocol and capture data can be found in Goedert et al., 2020. Black rats come from the four different natural environments of Guadeloupe: semi-deciduous dry forest, seasonal evergreen rainforest, mountain forest and swamp forest (Ecological Map of Rousteau et al., 1994). Except for the swamp forest, black rats were captured at two localities for each type of environment (Fig. 1). These 7 localities were selected both because they were at least 500m away from all human activity (e.g. habitations, crops, picnic areas) and because they represent the most indigenous environmental conditions.

Two capture sessions were carried out in the same area for each locality, one during the wet season (October 2017) and one during the dry season (March 2018). At least five black rats were sampled for each locality and season (SI 2), except for the dry season at Barre-de-Cadoue, where only three individuals were available in the collection. In addition, black rats captured during the wet season from a small creole garden near the locality of Espérance were sampled in order to test the potential enrichment of enamel in ^{13}C due to the consumption of C4-plants.

Similarly, we included five black rats captured during eradication attempts (Pascal et al., 2004a) on the Hardy Island (0.02526 km²; Martinique) in order to test the potential ^{13}C enrichment of black rat enamel due to the consumption of marine resources. The overall present-day stable isotopic reference collection comprises 78 individuals (SI 2).

3.2 [Collection of fossil material](#)

Fossil material comes from five localities: Grotte des Bambous and Pointe-des-Châteaux on Grande-Terre, Roseau on Basse-Terre, and Folle-Anse and Blanchard 2 on Marie-Galante (Fig. 1). Grotte des Bambous (WGS 84: 61°23'30'' W, 16°21'01'' N) is a small cave formed in the carbonated substratum by phreatic karstification. The site is located in a small ravine near Le Moule, about 1 km from the eastern shore of Grande-Terre Island (Cochard et al., 2019). Pointe des Châteaux lies at the southeastern most point of Grande-Terre and comprises numerous archaeological sites (De Waal, 2006) and natural cavities. Several bones, including a *A. rayi* mandible (Lenoble et al., 2017), were collected from the surface of one of these natural cavities (61°10'31,5'' W, 16°14'44'' N). Blanchard 2 (61°14'2.27'' W, 15°52'55.82'' N) is a small cavity on Marie-Galante that preserves a natural deposit that accumulated over the last millennium (Mallye et al., 2018). Roseau and Folle-Anse are both Amerindian archaeological sites documenting the Ceramic Age (ca. 500 BC e 1500 AD), the period

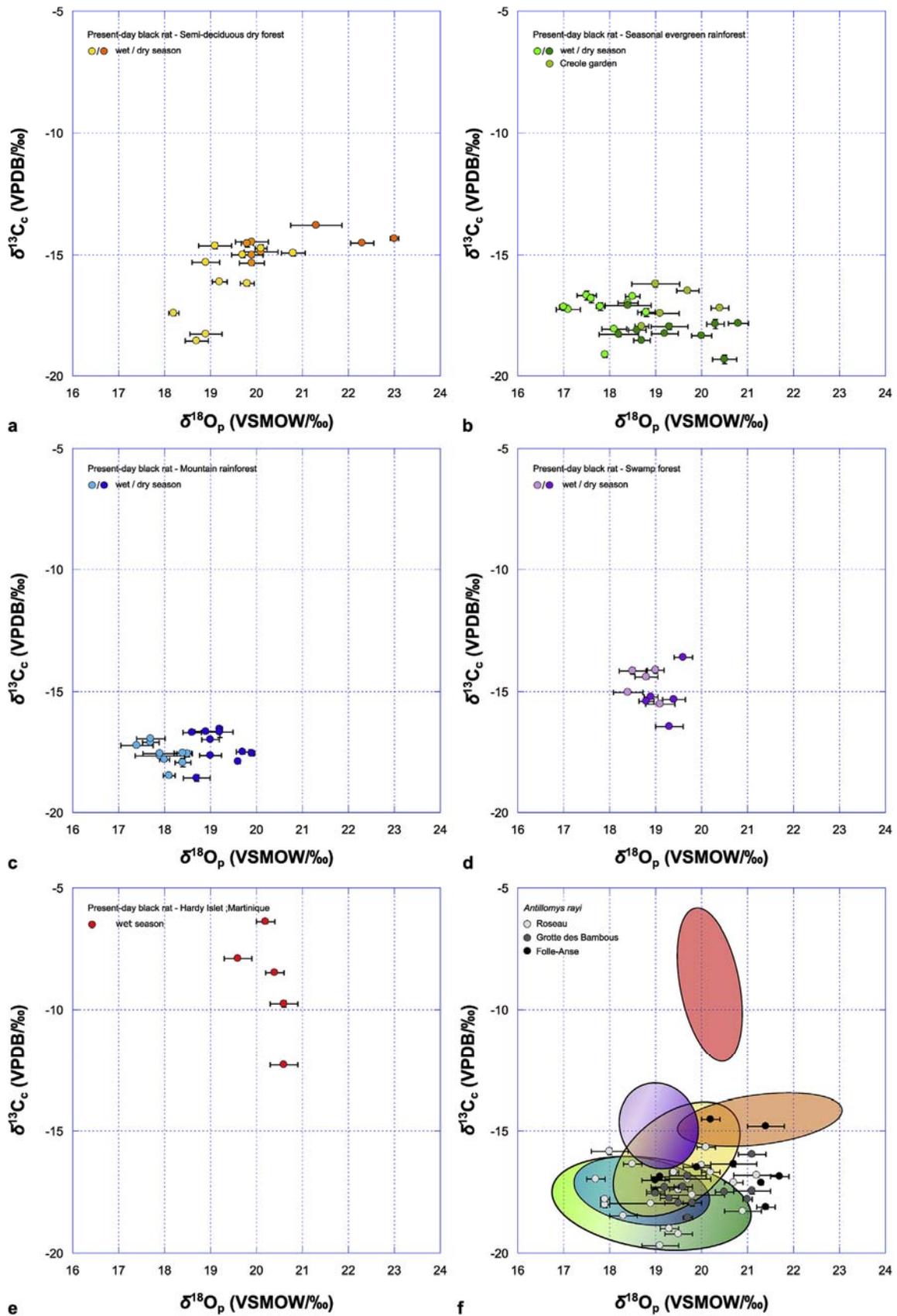


Figure 2. Present-day and fossil stable isotopic data. Stable isotope composition of carbon of carbonate ($\delta^{13}\text{C}_c$) bioapatite and stable isotope composition of oxygen of phosphate ($\delta^{18}\text{O}_p$) bioapatite of present-day black rats captured in: a semi-deciduous dry forest; b seasonal evergreen forest; c mountain rainforest; d swamp forest; and e Hardy Islet, Martinique. And f Stable isotope composition of carbon and oxygen of fossil *A. rayi*. For comparison,

*different ellipses corresponding to the present-day isotopic values of each natural environment are drawn in the background. The semi-deciduous forest environment is represented by two ellipses corresponding to the dry and wet season. $\delta^{13}\text{C}_c$ values measured for *A. rayi* and black rats coming from Martinique samples are corrected in order to directly compare them with present-day $\delta^{13}\text{C}_c$ values obtained for black rats captured in 2017-2018 (cf. Method section and SI 7). In a, b, c, d and e each dot represents a biologically independent individual ($n = 78$) and corresponds to the average value of two and five repeated measurements for carbon and oxygen isotope, respectively. Each error bar corresponds to 1 s.d. (SI 2). In f, each dot represents an independent fossil samples ($n = 42$) that may not represent a biologically independent individual given the disarticulated nature of the material (cf. Method section and SI 3) and corresponds to the average value of two and five repeated measurements for carbon and oxygen isotope, respectively. Each error bar corresponds to 1 s.d. (SI 3). $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_p$ results are given as variations in ‰ from the ratio of $^{13}\text{C}/^{12}\text{C}$ in Vienna Pee Dee Belemnite (VPDB/‰) and $^{18}\text{O}/^{16}\text{O}$ in Vienna Standard Mean Ocean Water (VSMOW/‰), respectively.*

succeeding the Archaic Age (ca. 3000-500 BC) which witnessed the first settlement of the Lesser Antilles (Napolitano et al., 2019). Roseau (61°33'35.39" W, 16°50'41.21" N) is a late and Final Ceramic stratified midden on the southeast coast of Basse-Terre Island (Richard, 2005; Bochaton et al., 2019), and Folle-Anse (61°20'09" W, 15°56'13" N) is Late Ceramic midden buried in the coastal sand ridge off the northwest coast of Marie-Galante (Chenorkian, 1999).

3.3 Skeletal elements for stable isotopic analyses

Sampling procedure follows the protocol described by Royer et al. (2014). We focused systematically on incisors to avoid variation in isotopic compositions related to patterns of tooth/bone formation (Gehler et al., 2012; Royer et al., 2013a; Peneycad et al., 2019). For each individual, the right lower incisor was extracted from the hemimandible for isotopic analyses of the enamel fraction. We selected lower incisors as they are regularly preserved in the fossil record and their enamel fraction is easily extractable. Enamel tissue is also much more resistant than dentine or bone tissue to post-mortem chemical alterations that are susceptible to alter pristine isotopic signals (e.g., Lee-Thorp et al., 1989; Koch et al., 1997; Zazzo et al., 2004). The low porosity of enamel tissue due to the large and heavily packed enamel crystals limits the circulation of fluids or the precipitation of exogenous material that could modify the pristine isotopic signal. Rodent lower incisors are particularly interesting as they record an isotopic signal that generally corresponds to the 30e60 days that precede an individual's death (Royer et al., 2013a). This short interval is connected to the generally small size of the rodents and thus their rapid metabolic turnover (Podlesak et al., 2008), as well as the fact that the lower incisor grows continuously throughout the individual's life (Hillson, 2005). For instance, black rat lower incisors augment around 0.4 mm/day (e.g., Coady et al., 1967). The samples comprising the present-day referential reflect the integrated isotopic record around 2 months before death, with the carbon and oxygen isotope compositions corresponding to the incorporation of environmental isotopic compositions during February-March (dry season) and September-October (wet season).

For fossil material, the sampled lower incisors were mostly still associated with their hemimandible. A total of 42 *A. rayi* lower incisors were sampled (SI 3), which, based on the laterality of the lower incisor, represent at least six individuals from Folle-Anse, fifteen from Roseau, and seven from Grotte des Bambous (SI 3).

3.4 Enamel sampling

Present-day and fossil lower incisors were cleaned in an ultrasonic bath using double-deionized water. The base of the enamel was then systematically removed under a binocular microscope (as described in Royer et al., 2014 and Calandra et al., 2015). The $\delta^{18}\text{O}$ values of this not yet fully mineralized enamel (Hiller et al., 1975) have been shown to be significantly lower than those of fully

mature enamel (Barham et al., 2017). The remaining tooth was gently crushed in an agate mortar in order to separate the enamel from the dentine. Enamel fragments were then separated from dentine by hand under a binocular microscope and then crushed in an agate mortar into a fine enamel powder. Each enamel powder sample was subdivided into two aliquots of 10 and 3 mg for carbon and oxygen isotope analysis of carbonates and oxygen isotope analysis of phosphates, respectively. The remaining dentine was preserved for radiocarbon dating.

3.5 [Carbon and oxygen isotope analysis of carbonates](#)

Each 10 mg enamel powder aliquot was pre-treated according to the protocol described by Koch et al. (1997). For each sample, enamel powder was washed with a 2 % NaOCl solution to remove possible organic matter, followed by a 0.1 M acetic acid solution to remove diagenetic carbonates in the case of fossil samples. The volume of solution/mass of powder ratio was held constant at $25 \mu\text{mg}^{-1}$ for both treatments. Each treatment lasted for 24 h, and samples were rinsed 5 times with double-deionized water.

Carbon and oxygen isotope analysis of bioapatite carbonate was performed at the Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés (LEHNA; UMR CNRS 5023) in Lyon using an isoFLOW system connected on line in continuous flow mode to a precisiON mass spectrometer operated by a visION software from Elementar UK Ltd. Sample powders were loaded in roundbottomed, non-evacuated LABCO Exetainer® 3.7 ml soda glass vials. For each pre-treated sample, two aliquots of approximately 2 mg were automatically reacted with anhydrous oversaturated phosphoric acid prepared according to the protocol described by McCrea (1950). Phosphoric acid was automatically introduced to the sample using an acid pump. The reaction took place at 90° C in a temperature regulated sample tray. The CO₂ gas generated during the acid digestion of the carbonate sample was then transferred to the mass spectrometer via a centrION interface. A calibrated CO₂ gas was used as a monitoring gas.

Carrara Marble ($\delta^{18}\text{O}_{\text{VPDB}} = -1.841\text{‰}$; $\delta^{13}\text{C}_{\text{VPDB}} = +2.025\text{‰}$) (Fourel et al., 2016) and NBS18 ($\delta^{18}\text{O}_{\text{VPDB}} = -23.2\text{‰}$; $\delta^{13}\text{C}_{\text{VPDB}} = -5.01\text{‰}$) (Friedman et al., 1982; Hut, 1987; Stichler, 1995; Coplen et al., 2006) were used as calibration materials. The normalization incorporates the CO₂-carbonate acid fractionation factor for calcite. Additionally, aliquots of NBS120c (Natural Miocene phosphorite from Florida), a standard of chemical composition similar to bioapatite, were placed at the beginning of each analytical batch to check that analytical conditions were suitable to analyse bioapatite samples. Aliquots of Carrara Marble were placed at the beginning and at the end of each analytical batch to check instrumental drift over time. No significant drift was recorded during experiments (Unpaired *t*-test: *p*-value = 0.99). Aliquots of Carrara Marble of different weights were measured in order to estimate the carbonate content of bioapatite samples. External reproducibility (2s) was lower than $\pm 0.10\text{‰}$ for $\delta^{18}\text{O}$ and $\pm 0.05\text{‰}$ for $\delta^{13}\text{C}$. Data are reported as $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_c$ values versus VPDB/‰

3.6 [Oxygen isotope analysis of phosphate](#)

Each 3 mg enamel powder aliquot was pre-treated according to the wet chemistry protocol initially described by Crowson et al. (1991), and subsequently modified by Lécuyer et al. (1993) and then adapted by Bernard et al. (2009) for small sample weights (3 mg). This protocol involves the isolation of phosphates (PO₄³⁻) from bioapatite as silver phosphate (Ag₃PO₄) crystals using acid dissolution and anion-exchange resin. For each sample, enamel powder was dissolved in 1 ml of 2 M HF overnight. The CaF₂ residue was separated in a centrifuge and the solution neutralized by adding 1 ml of 2 M KOH. Amberlite anion-exchange resin (1.5 ml) was added to the solution to separate the PO₄³⁻ ions. After 24 h, the solution was removed and the resin was eluted with 6 ml of 0.5 M NH₄NO₃. After 4 h, 0.1 ml of NH₄OH and 3 ml of an ammoniacal solution of AgNO₃ were added and the samples were placed in a thermostated bath at 70° C for 6 h, enabling the precipitation of Ag₃PO₄ crystals.

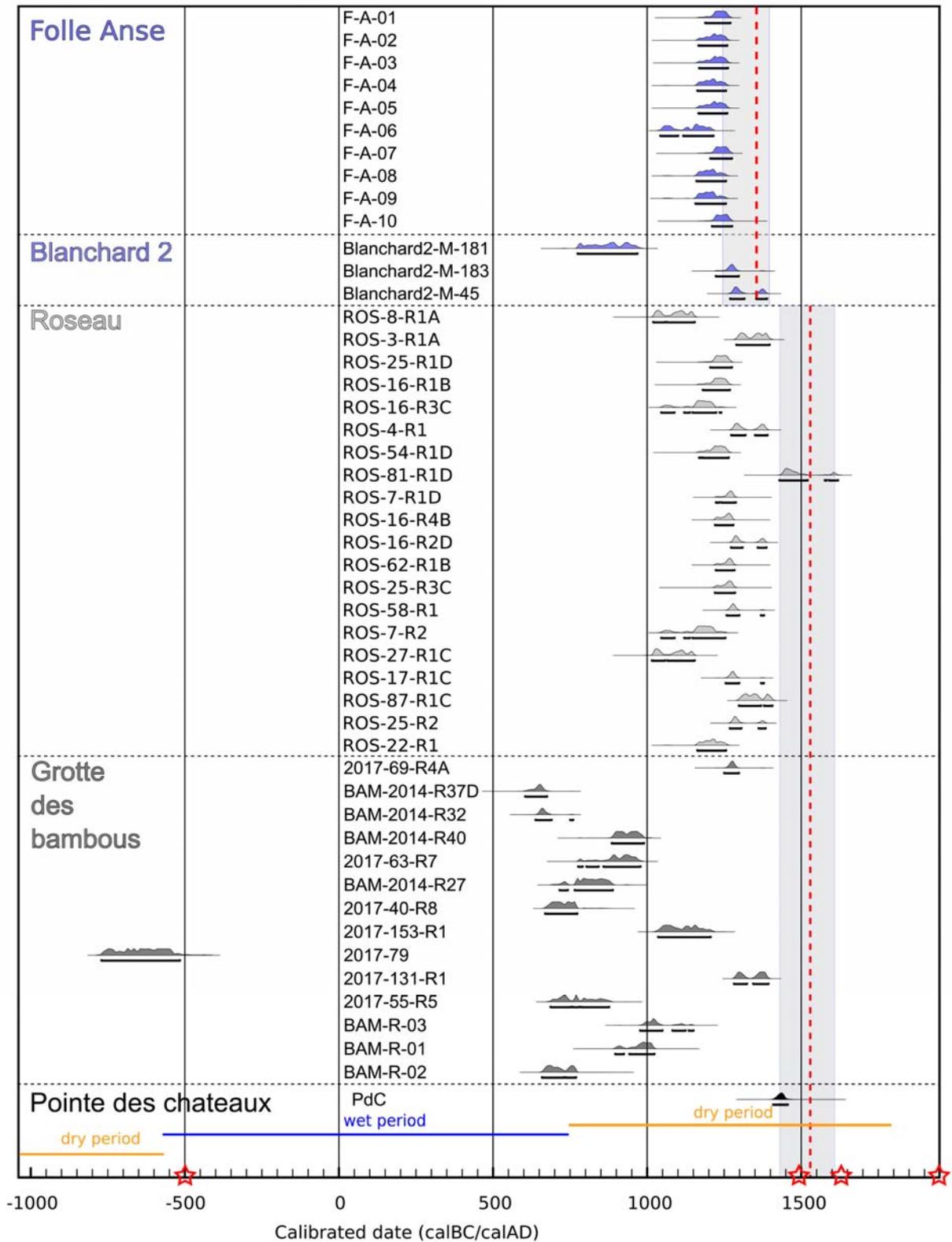


Figure 3. Radiocarbon dating of fossil *Antillomys rayi*. Calibrated time intervals obtained for *A. rayi* fossil skeletal samples from the 5 different localities of the Guadeloupe islands (Fig. 1). Each time interval represents an independent *A. rayi* fossil bioapatite sample ($n = 48$) that may not represent a biologically independent individual given the disarticulated nature of the material (cf. Method section). Red dotted lines correspond to calculated date of *A. rayi* extirpations in Guadeloupe and Marie-Galante using the GRIWM analysis and the gray shaded areas correspond to the associated 2s confidence interval. A regional climatic frame taken from Malaizé et al. (2011) has been added in red on the calendar axis, as well as important regional dates (red stars): 500 AD,

beginning of the Ceramic Age; 1493, second voyage of C. Columbus: period of contact; 1635, settlement of the first colony; 1950, end of the colony. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Oxygen isotope compositions were measured using a high-temperature pyrolysis technique involving a VarioPYROcube elemental analyser interfaced in continuous flow mode to an Isoprime isotopic ratio mass spectrometer (the EA-PyeCFIRMS technique; Lécuyer et al., 2007; Fourel et al., 2011) performed at the LEHNA (UMR CNRS 5023). For each sample, 5 aliquots of 300 mg of Ag₃PO₄ were mixed with 300 mg of pure graphite powder and loaded in silver foil capsules. Pyrolysis was performed at 1450° C. Measurements were calibrated against NBS120c ($\delta^{18}\text{O} = +21.7\text{‰}$ VSMOW; Lécuyer et al., 1993), the international standard NBS127 (barium sulfate, BaSO₄: $\delta^{18}\text{O} = +9.3\text{‰}$ VSMOW; Hut, 1987) and a homemade standard CAL-3 (silver phosphate, Ag₃PO₄: $\delta^{18}\text{O} = +5.9\text{‰}$ VSMOW). Silver phosphate samples precipitated from standard NBS120c were repeatedly analysed ($\delta^{18}\text{O}_p = +21.2\text{‰}$; $1\sigma = 0.6$; $n = 46$) along with the silver phosphate samples derived from fossil bioapatites to ensure that no isotopic fractionation occurred during the wet chemistry. The average standard deviation was $+0.26 \pm 0.14\text{‰}$ (s.e.m). Data are reported as $\delta^{18}\text{O}$ values versus VSMOW/‰.

3.7 ¹⁴C dating

The Antilles are known to be a taphonomically “hostile” tropical region for collagen preservation (Pestle and Colvard, 2012), meaning that obtaining direct radiocarbon dates on fossil vertebrate bones is particularly problematic. Dentine is less porous than bone and therefore potentially less prone to diagenetic alteration. Nonetheless, dentine of *A. rayi* (generally weighing less than 100 mg) contains little collagen, requiring an adapted “conventional” collagen extraction protocol dedicated to the processing of smaller quantities of material. Overall, radiocarbon dates were obtained on 41 dentine samples of *A. rayi* (out of 42, one sample lost during preparation) with high analytical precision (typically $\pm 25\text{--}30$ y; SI 4). This modified protocol that makes it possible to better constrain ages obtained on material from archaeological deposits is fully detailed in SI 6.

Radiocarbon dates were also obtained on seven bones of *A. rayi* (without combined stable isotopic analyses) to complete the last occurrence dataset (SI 4). Overall, 48 bioapatite samples (out of 49) of fossil *A. rayi* were directly dated by accelerator mass spectrometry (AMS). Collagen recuperation, gelatinization and graphitization were performed on the Laboratoire d’Archéologie et d’Archéométrie (ARAR; UMR CNRS 5138). AMS radiocarbon measurements were performed at the Saclay laboratory (LMC 14) as part of the ARTEMIS program (Billard, 2008).

3.8 Comparison of present-day and fossil $\delta^{13}\text{C}_c$ values

Two corrections are required prior to comparing fossil and present-day $\delta^{13}\text{C}_c$ values of lower incisors. Since the 1800s, human activity has released substantial quantities of CO₂ into the atmosphere, modifying both the atmospheric CO₂ content and its carbon isotope composition (e.g., Francey et al., 1999, MacFarling Meure et al., 2006). However, both the atmospheric CO₂ content and its carbon isotopic composition ($\delta^{13}\text{C}_{\text{atm}}$) are known to control the $\delta^{13}\text{C}$ values of vegetation ($\delta^{13}\text{C}_{\text{vg}}$; Arens et al., 2000; Prentice and Harrison, 2009). Previous work has shown CO₂ concentrations and $\delta^{13}\text{C}_{\text{vg}}$ values to be negatively linearly related (Garten and Taylor, 1992; Feng and Epstein, 1995; Pasquier-Cardin et al., 1999; Van de Water et al., 2002). Feng and Epstein (1995) calculated $\delta^{13}\text{C}_{\text{vg}}$ values decrease 2.0 ‰ per 100-ppm increase in CO₂. In addition, the modifications of $\delta^{13}\text{C}_{\text{atm}}$ values have a direct and quantitative effect on $\delta^{13}\text{C}_{\text{vg}}$ values (Farquhar et al., 1989; Feng and Epstein, 1995; Arens et al., 2000).

The mean annual atmospheric CO₂ concentration for 2017 and 2018 was 407.54 ± 0.12 ppm (Tans and Keeling). According to the calibrated age interval obtained for each fossil sample, we estimated the corresponding atmospheric CO₂ concentrations based on atmospheric CO₂ data measured by MacFarling Meure et al. (2006) for the last two millennia. From 0 to 1800 AD the atmospheric CO₂ content did not vary dramatically, ranging from 270 to 284 ppm (MacFarling Meure et al., 2006). As atmospheric CO₂ concentrations for the fossil samples range within 278.2-283.3 ppm (SI 7), we corrected each fossil δ¹³C_c values by +0.02 ‰/ppm (Feng and Epstein, 1995) (δ¹³C_{c.corr1}; SI 7).

In the year 2017-2018, the δ¹³C_{atm} value was closed to -8.4‰ (Mauna Loa Observatory, Hawaii and South Pole, Antarctica, δ¹³C trends; Scripps Ocean Institute; Scripps CO₂ program). From 1000 AD to 1600 AD, the δ¹³C_{atm} value is stable at approximately -6.4‰ (Francey et al., 1999). All fossil samples from Roseau and Folle-Anse are from this period, but the fossil from Grotte des Bambous are, in general, older. Nonetheless, Leuenberger et al. (1992) calculated a similar δ¹³C_{atm} value at 9270 BP (-6.51‰). It is therefore reasonable to assume a similar δ¹³C_{atm} value for all fossil samples. Assuming a similar δ¹³C_{atm} value for all fossil samples, we corrected each fossil δ¹³C_{c.corr1} values by subtracting +2.0 ‰ (δ¹³C_{c.corr2}; SI 7).

3.9 Preservation of isotopic signal

Skeletal remains underwent post-mortem chemical alterations that potentially disturbed the pristine isotope compositions recorded in bioapatite. For this reason, all stable isotopic analyses were performed on enamel tissues, which are the most resistant part of the tooth to chemical alterations (e.g., Lee-Thorp et al., 1989; Koch et al., 1997; Zazzo et al., 2004). Furthermore, we also performed oxygen isotope analysis of phosphates despite the method being more time consuming and expensive than oxygen isotope analysis of carbonates. Phosphates are substantially more resistant than carbonates in terms of the inorganic oxygen exchange with water at low temperatures (Blake et al., 1997; Lécuyer et al., 1999; Zazzo et al., 2004).

The higher resistance of phosphate group in terms of diagenetic alterations is further illustrated when coexisting δ¹⁸O_c and δ¹⁸O_p values in skeletal material are compared (Fig. 4). They normally follow linear relationship and can be used to identify diagenetic bone alterations (Bryant et al., 1996; Iacumin et al., 1996). Coexisting δ¹⁸O_c and δ¹⁸O_p values measured in present-day black rat tooth enamel present a significant linear relationship (R² = 0.75; p-value = 2.553E-24; Fig. 4a). However, there is only a weak correlation in the overall fossil sample (R² = 0.07; p-value = 0.0857; Fig. 4a). This lack of a correlation appears primarily due to the fossil samples from Roseau (R² = 0.02; p-value = 0.5494) (Fig. 4b) given that those from both Grotte des Bambous and Folle-Anse have coexisting δ¹⁸O_c and δ¹⁸O_p values that present stronger and more significant correlations (R² = 0.33; p-value = 0.049845; R² = 0.53; p-value = 0.0129), although still less robust than what can be seen with the present-day material. These differences are probably connected to the geological context of each locality. Roseau is located on the volcanic Basse-Terre Island, while Grotte des Bambous and Folle-Anse both have a calcareous substratum. For Roseau, the siliceous nature of the substratum results in acidic conditions that favour the chemical alteration of bone and teeth.

Moreover, present-day lower incisor enamel samples have similar carbonate content (CO₃ wt%, estimated with the height (in nA) of the analysed CO₂ peak) to fossil specimens (Average CO₂ Height (nA) = 1.8 and 1.9, respectively; Mann-Whitney U: p-value = 0.98). Although minimal, the difference is nonetheless significant for Roseau compared to present-day data (Average CO₂ Height (nA) = 2.0 and 1.8, respectively; Mann-Whitney U: p-value = 0.02). This excludes the possibility that diagenetic alteration of oxygen isotope composition of carbonates was primarily due to the precipitation of exogenous carbonates from ambient fluid. This is further reinforced by the fact that the acidic nature of the substratum does not favour carbonate precipitation. Moreover, the very low porosity of enamel tissues impedes any substantial incorporation of exogenous material from precipitation. Hence, the apparent modifications of pristine oxygen isotope composition of carbonates in samples from Roseau probably result from isotopic substitution mechanisms. It is equally worth

noting that the chemical alteration of the oxygen isotope composition of carbonates does not necessarily imply changes in carbon isotopic composition. The carbon isotope system is, in fact, much more resistant to diagenetic modifications than oxygen isotopes (Wang and Cerling, 1994). This being the case, and bearing in mind that the carbon isotopic can be considered valid, we nevertheless based our interpretations uniquely on the oxygen isotope composition of phosphate.

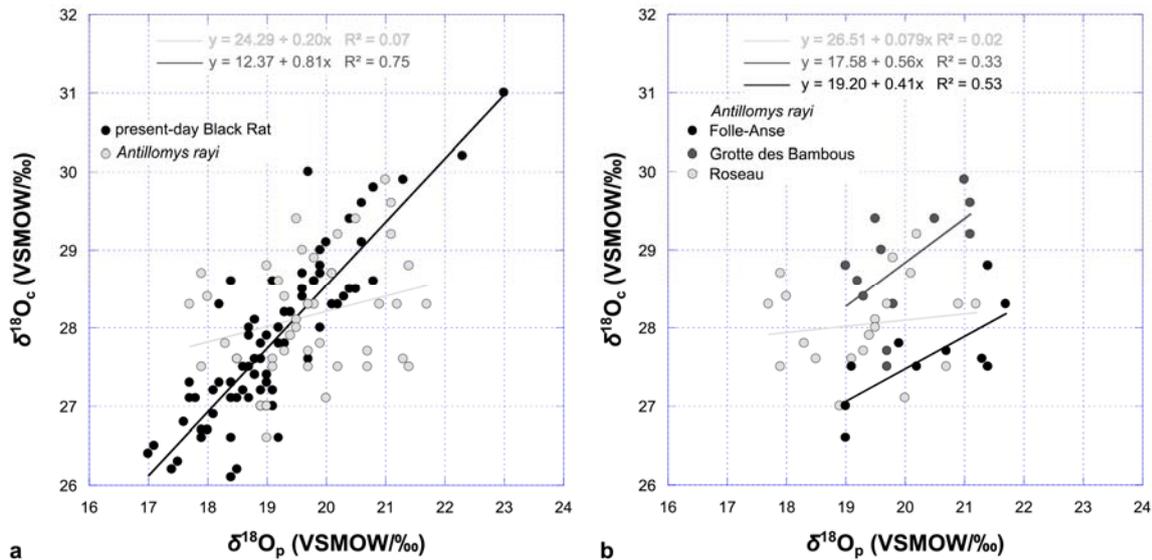


Figure 4. Preservation of pristine isotopic signal. a Oxygen isotope composition of carbonate ($\delta^{18}O_c$) and phosphate ($\delta^{18}O_p$) of present-day black rat (black dots) and fossil *A. rayi* (light gray dots). In a, each black dot represents a biologically-independent individual ($n = 78$) and each light gray dot represents an independent fossil sample ($n = 42$) that may not represent a biologically-independent individuals given the disarticulated nature of the material (cf. Method section and SI 3). In b, each dot represents an independent fossil sample ($n = 42$) that may not represent a biologically-independent individuals given the disarticulated nature of the material (cf. Method section and SI 3) In a and b, each dot corresponds to the average value of two and five repeated measurements for oxygen isotope of carbonate and phosphate, respectively. Each individual error bar (corresponding to 1 s.d.) is not reported on the figure (cf. SI 2 and SI 3). $\delta^{18}O_c$ and $\delta^{18}O_p$ results are given as variations in ‰ from the ratio of $^{18}O/^{16}O$ in Vienna Standard Mean Ocean Water (VSMOW/‰).

3.10 Chronological variability

Climate change in the Caribbean region over past millennia was driven by the position of the Inter Tropical Convergent Zone (ITCZ) (Mangini et al., 2007; Lane et al., 2011). During periods of global cooling, the ITCZ moved southward, resulting in decreased precipitation in the Lesser Antilles. The analysis of sediments from Grand-Case Pond on Saint Martin revealed alternating dry and wet periods over the last 3700 years in the Lesser Antilles (Bertran et al., 2004; Hodell et al., 2008; Malaizé et al., 2011). The majority of the fossil samples have calibrated age intervals that correspond to the current dry period that began around 800 AD (Fig. 5). The older fossil samples from Grotte des Bambous correspond to the transition between this dry period and the preceding wet period from -550 to 800 AD. The fact that most fossil samples correspond to similar calibrated age intervals, almost all of which fall at the beginning of the most recent dry period, suggests that the influence of climatic variation on fossil isotopic variability was minimal.

Moreover, the $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_p$ values of fossil samples from wet and dry periods at Grotte des Bambous are not significantly different (Mann-Whitney U: p-value (exact permutation) = 0.68571 and 0.17857, respectively). Overall, the $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_p$ values do not show any temporal trends that could be linked to climatic variations (Fig. 5). Finally, each fossil locality records carbon and oxygen isotopic variations that are comparable to those obtained from present-day localities. This demonstrates that isotopic variability recorded in fossil lower incisor enamel can be confidently attributed to differences in living environments and not the simple reflection of large-scale climatic variations.

4. Results and discussion

4.1 [Stable isotope compositions of present-day black rats](#)

Overall, $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_p$ values of black rat lower incisor distinguish the natural environments of Guadeloupe (SI 2; SI 8; Fig. 2). Apart from the swamp forest, each natural environment displays significant seasonal isotopic variations (SI 8; Fig. 2).

Black rats living in the semi-deciduous dry forest tend to have both higher $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_p$ values than those living in other environments (Fig. 2a). This is consistent with the fact that semi-deciduous dry forests receive the lowest mean annual precipitation and experience a marked dry period. These climatic conditions result in the relative enrichment of both the vegetation and meteoric water in heavy isotopes ^{13}C (Kohn, 2010) and ^{18}O (Dansgaard, 1964; Rozanski et al., 1993), respectively; and therefore, higher $\delta^{13}\text{C}_{vg}$ and $\delta^{18}\text{O}_w$ values.

In the seasonal evergreen and mountain forests, black rats are characterized by relatively lower $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_p$ values (Fig. 2b and c). Both minimal $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_p$ values are observed for black rats captured in the seasonal evergreen forest ($\delta^{13}\text{C}_c = -19.3\text{‰}$ and $\delta^{18}\text{O}_p = +17.0\text{‰}$; SI 2). It is also noteworthy that the $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_p$ values appear more variable for the seasonal evergreen forest than they are for the rainforest (Fig. 2b and c), although the difference is not significant in either case (F test: p-value = 0.20 and 0.07, respectively).

The swamp forest is characterized by a very specific combination of isotopic values having both relatively high $\delta^{13}\text{C}_c$ values and low $\delta^{18}\text{O}_p$ values (Fig. 2d). This edaphic formation, located inward of the mangrove forest, has $\delta^{13}\text{C}_c$ values comparable to those recorded for the semi-deciduous dry forest during the dry season; while the much lower $\delta^{18}\text{O}_p$ values are comparable to those recorded for the rainforest. These higher carbon isotopic values likely result from either saltwater replacing the evaporated freshwater in coastal environment during the dry season (Lambs et al., 2015) or the transfer of marine carbon to the swamp forest through the trophic chain (i.e. fish, crustacean; François-Lubin, 2005). This swamp environment also presents less seasonal isotopic variability compared to the other environmental contexts.

Black rats captured in a small creole garden (e.g. small sugar cane field, banana plantations) at Espérance have $\delta^{13}\text{C}_c$ values that tend to be significantly higher than those captured in their natural habitats at the same location during the same season (Fig. 2b; Mann-Whitney U: p-value (exact permutation) = 0.056). This isotopic shift is consistent with the incorporation of a small fraction (<10 %) of C4-plants, sugar cane for example, in the diet of black rats captured at Espérance (e.g., Bender, 1971; Smith and Epstein, 1971).

Black rats captured on Hardy Islet (Saint-Anne Islets, Martinique) recorded by far the highest $\delta^{13}\text{C}_c$ values (SI 2; Fig. 2e). These values are highly consistent with field observations corroborating the substantial intake of marine resources, such as the eggs of nesting seabirds or terrestrial crabs (Pascal et al., 2004a), a well-documented dietary behaviour for insular rats (Shiels et al., 2014).

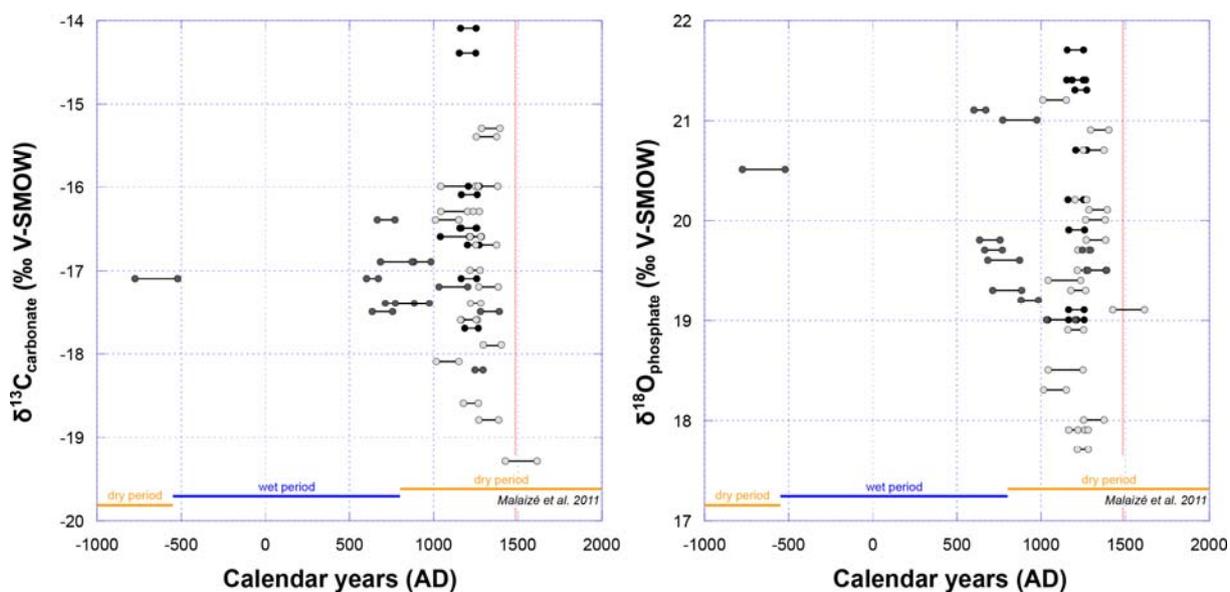


Figure 5. Fossil stable isotope compositions over time. a Carbon and b oxygen stable isotope compositions of *A. rayi* are reported over time to explore potential temporal trends that could arise, for instance, from long term regional climatic variations. To this purpose, the regional climatic frame proposed by (Malaizé et al., 2011) has been added on the calendar axis. Most of fossil samples analysed are contemporary with the more recent dry period and no clear temporal trend is observed either for carbon or oxygen isotope composition. In a and b, each dot represents an independent fossil samples ($n = 42$) that may not represent a biologically-independent individual given the disarticulated nature of the material (cf. Method section). Each dot corresponds to the average value of two and five repeated measurements for carbon and oxygen isotope, respectively. Each error bar (not reported on the figure) corresponds to 1 s.d. (SI 3). $\delta^{13}C_c$ and $\delta^{18}O_p$ results are given as variations in ‰ from the ratio of $^{13}C/^{12}C$ in Vienna Pee Dee Belemnite (VPDB/‰) and $^{18}O/^{16}O$ in Vienna Standard Mean Ocean Water (VSMOW/‰), respectively.

4.2 Stable isotope compositions of *Antillomys rayi*

Most of the fossil samples have both $\delta^{13}C_{c.corr2}$ (SI 7; cf. Method section) and $\delta^{18}O_p$ values that fall within the isotopic ranges of present-day black rats (Fig. 2f). Linear Discriminant Analysis (LDA; SI 8) attributed fossil samples to the seasonal evergreen forest ($n = 9$) and the creole-garden ($n = 7$), the semi-deciduous dry forest ($n = 4$), the mountain rainforest ($n = 2$) and the swamp forest ($n = 1$). Overall, $\delta^{13}C_{c.corr2}$ values of fossil samples are compatible with the consumption of a typical C3 plant-based terrestrial resource. These isotopic values exclude the possibility that *A. rayi* consumed C4 plants or marine resources in high proportions. In general, fossil values closely match those measured for black rats captured in the seasonal evergreen forest and rainforest, without overlapping isotope values for black rats from the swamp forest and the Martinique Islet. Several fossil samples have, however, both relatively high $\delta^{13}C_{c.corr2}$ and $\delta^{18}O_p$ values, which are more compatible with values from black rats captured in the semi-deciduous dry forest during wet and dry seasons.

For instance, fossils from Folle-Anse (Marie-Galante) have median $\delta^{13}C_{c.corr2}$ values (median $\delta^{13}C_{c.corr2} = -16.9\text{‰}$) significantly higher than those from the Grotte des Bambous (median $\delta^{13}C_{c.corr2} = -17.5\text{‰}$; Mann-Whitney U: p-value (Monte Carlo permutation) = 0.030) or Roseau, although the difference being not significant (median $\delta^{13}C_{c.corr2} = -16.8\text{‰}$; Mann-Whitney U: p-value (Monte Carlo permutation) = 0.14). They also have the highest median $\delta^{18}O_p$ value ($\delta^{18}O_p = +20.4\text{‰}$), which is significantly higher than Roseau (median $\delta^{18}O_p = +19.5\text{‰}$; Mann-Whitney U: p-value (Monte Carlo permutation) = 0.029) but lower than Grotte des Bambous (median $\delta^{18}O_p = +19.7\text{‰}$; Mann-Whitney U: p-value (Monte Carlo permutation) = 0.38). These higher values are therefore in good agreement

with the presence of dryer conditions on Marie-Galante that would have been somewhat similar to present-day semi-deciduous dry forest of the Guadeloupe mainland. Black rats captured in these environments tend to have both higher $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_p$ values than in other environments, especially during the dry season (Fig. 2a). Several fossil samples from the Grotte des Bambous also have relatively high $\delta^{13}\text{C}_{c.\text{corr}2}$ and $\delta^{18}\text{O}_p$ values. Although Folle-Anse is close to flooded areas suitable for the development of swamp forest (Fig. 1), the fossil samples, especially those from Folle-Anse, present $\delta^{13}\text{C}_{c.\text{corr}2}$ and $\delta^{18}\text{O}_p$ values incompatible with a swamp forest environment. Black rats captured in the swamp forest display very typical isotopic values, combining both relatively high $\delta^{13}\text{C}_c$ and low $\delta^{18}\text{O}_p$ values compared to other environments (Fig. 2d). This excludes the possibility that *A. rayi* exclusively inhabited this particular environment and is further supported by the LDA analysis.

Taken together, isotopic values reveal *A. rayi* to have had a rather high ecological valence, inhabiting diverse environments of Guadeloupe from the semi-deciduous dry forest to the more humid contexts or rain forests. This species did not permanently and exclusively occupy the swamp forest, which is inconsistent with hypotheses concerning a potential semi-aquatic adaptation of Lesser Antillean native rodents (e.g., Miljutin, 2010). Nonetheless, this hypothesised semi-aquatic adaptation of Lesser Antillean native rodents would be shared by species from the genera *Megalomys* and *Pennatomys* (Clade D of Weksler et al. (2006) and Turvey et al. (2010)) whereas *A. rayi* represents a distinct monophyletic clade (Brace et al., 2015). *A. rayi* is phylogenetically closer to the genus *Hylaeamys* (Clade B of Weksler et al. (2006)), which groups together most forest-dwelling species (Brace et al., 2015). Our results are consistent with this phylogenetic relationship and its environmental implications. In addition, the hypothesis of an adaptation to xeric environments, as exemplified by the Bahamian hutia (*Geocapromys ingrahami*) in cays and tiny islets in the Bahamas (Clough, 1972), can also be rejected. The $\delta^{13}\text{C}_{c.\text{corr}2}$ and $\delta^{18}\text{O}_p$ values are coherent with typical C3 plant-based terrestrial resources, and do not fit with an exploitation of resources from dry and coastal contexts.

4.3 ^{14}C -dates of *Antillomys rayi*

To date, only one Lesser Antillean native rodent fossil has been directly radiocarbon dated (MacPhee and Flemming, 1999; Cooke et al., 2017). All other radiocarbon dates used to constrain the last-occurrences of Lesser Antillean native rodent populations have been estimated from dates obtained on stratigraphically associated material. For instance, at the archaeological sites of Morel (Guadeloupe) and Taliseronde (Marie-Galante), *A. rayi* fossil remains are only indirectly associated with calibrated age intervals of 21-881 AD and 350-665 AD (Haviser, 1997).

In this study, 48 (of 49) fossil skeletal remains of *A. rayi* were directly dated by Accelerator Mass Spectrometry (AMS) (SI 4 and 6). Overall, the calibrated age intervals render the last-occurrence dates of *A. rayi* considerably later than those hitherto proposed in the literature based on indirect radiocarbon dating on both Guadeloupe and Marie-Galante (Fig. 3). The fossil samples from Roseau and Folle-Anse yielded similarly constrained calibrated age intervals, spanning from the 12th to 13th century AD. A limited number of samples from Roseau yielded younger calibrated age intervals, ranging from the 10th to the 13th century AD, and one sample produced an even younger age (from 1430 to 1620 AD) broadly contemporaneous with the European contact period. The sample from Pointe-des-Châteaux also produced calibrated age intervals corresponding to the 15th century AD, similarly close to the contact period (Fig. 3).

Comparatively, the fossil samples from Blanchard 2 and Grotte des Bambous yielded much more variable calibrated age intervals. The majority are older than calculated ages for Roseau and Folle-Anse that span the 7th to 10th century AD. A small number of samples returned calibrated age intervals comparable to Roseau and Folle-Anse, while one calibrated age interval for Grotte des Bambous is older, dating to the 6th-8th century BC. To our knowledge, this Archaic Age specimen is the earliest occurrence of this taxon on the Guadeloupe Islands. It is worth noting that the outlying nature of this date cannot be attributed to the degree of collagen preservation (collagen yield: 67.9

mg/g; SI 4). This date further raises the question of a potential translocation of *A. rayi*. Brace et al. (2015) proposed an ancient (Pleistocene) inter-island oryzomyine diversification; however, their genetic data does not exclude the possibility of a translocation from Barbados to Guadeloupe in prehistoric times. Several previous studies have, in fact, suggested that the majority of translocations occurred during the Ceramic Age (e.g., Wing, 2008; Giovas, 2017; LeFebvre et al., 2019), and the calibrated age interval of this date shows *A. rayi* to occur in Guadeloupe before that time. However, the chronological overlap with the arrival of the first human groups does not definitively exclude a translocation during the Archaic Age. Further work is required to test these possibilities.

The sites of Roseau and Folle-Anse are pre-Columbian middens, while Grotte des Bambous, the cave from Pointe des Chateaux and Blanchard 2 are natural fossil-bearing deposits. Grotte des Bambous is a small cave on Grande-Terre Island that served as a nesting site for several species. Skeletal material recovered from the site most likely represents both an input from predators and natural deaths. The higher temporal variability of radiocarbon dates suggests skeletal remains to have been regularly incorporated into the deposits over a longer period compared to the two other sites. Furthermore, the vertebrate assemblage from Grotte des Bambous represents a mix of skeletal elements of species accumulated during different periods, including cane toad (*Rhinella marina*), raccoon (*Procyon lotor*) (>19th), turkey (*Meleagris* sp.) and the black rat (*Rattus rattus*) (>15th), as well as indigenous fauna, such as the burrowing owl (*Athene cunicularia*) or *A. rayi*. A direct ¹⁴C date on a bone attributed *A. cunicularia* yielded a calibrated age interval spanning the 15th to 17th AD, which postdates European contact (Cochard et al., 2019; Gala et al., 2019 submitted). Similarly, direct dates on a *A. rayi* mandible (Lyon-14110 (SacA-49752)) from Pointe des Châteaux (SI 4) and a tarsometatarsus of Audubon's shearwater (*Puffinus Iherminieri*) (Lyon-9693 (SacA-31250)) from Blanchard 2 yielded calibrated age intervals spanning the 15th and the 15th to 17th AD, respectively (Mallye et al., 2018). The nature of the accumulation at these sites leaves open the potential survival of *A. rayi* into much more recent periods at the time of European colonisation. That said, the most recent calibrated age interval for a skeletal element attributed to *A. rayi* from these sites is equally equivocal and does not support the presence of *A. rayi* after European contact. Taken together, the above suggest that *A. rayi* was already rare around the period of European contact both in Guadeloupe and Marie-Galante.

[4.4 Extirpation of *Antillomys rayi* from main Guadeloupe islands](#)

Lesser Antillean native rodent remains are often abundant in middens from archaeological sites, reflecting their forming an important component of the Amerindian diet (Wing, 1973, Wing et al., 2001; Wing and Scudder, 1983; Steadman et al., 1984; van der Klift, 1992; Wing and Wing, 1997; Newsom and Wing, 2004). Several zooarchaeological studies have assumed that native groups hunted Lesser Antillean native rodents (e.g., Newsom and Wing, 2004), while others have suggested that oryzomyine rats were managed by Amerindian groups (Wing, 1995). Isotopic values from Roseau, however, do not corroborate such a hypothesis. If *A. rayi* were bred, $\delta^{13}\text{C}_c$ and $\delta^{18}\text{O}_p$ values from the Roseau fossil should be less heterogeneous than those recorded in naturally accumulated fossil samples from Grotte des Bambous, especially given the much shorter time interval represented by the fossil remains from Roseau compared to those from Grotte des Bambous. Moreover, water and food provided to *A. rayi* would likely have been more homogeneous in terms of stable isotope composition compared to food and water sources in natural environments (e.g., Royer et al., 2013a). Although outside the scope of this paper, such a hypothesis could be further tested by analysing the isotopic compositions of fossil skeletal elements of the red-rumped agouti (*Dasyprocta leporina*), another rodent present in Guadeloupe during pre-Columbian period, which was equally assumed to have been raised by Amerindian groups.

Available radiocarbon dates, however, suggest that *A. rayi* was still present in Guadeloupe and Marie-Galante until at least the end of the 15th and the 12th-13th century AD, respectively, and became extremely rare, if not extirpated shortly afterwards. This is further supported by the most probable extirpation date calculated using the Gaussian-resampled, inverse-weighted McInerney et al.

(GRIWM) method (Bradshaw et al., 2012) that provides an estimate of 1526 AD (1438-1614; (2s)) and 1358 AD (1296-1391; (2s)) for Guadeloupe and Marie-Galante, respectively (Fig. 3).

This chronology demonstrates Amerindian groups to have not been responsible for the disappearance of *A. rayi* prior to the contact period in these regions. Of all currently available radiocarbon dates, only one is potentially contemporary with the period of European contact. Consequently, these results suggest that *A. rayi* most likely became rare if not extirpated from these regions shortly after the period of European contact in the 16th century AD.

Historical accounts of “rice rats” on the other Lesser Antillean islands support they have been consumed during historical periods (Du Tertre 1667, Rochefort 1667, Labat, 1722, Turvey et al., 2010). Early chroniclers also mentioned their strong musky smell, which helped locate their burrows (Du Tertre 1667, Rochefort 1667, Labat, 1722). Nonetheless, hunting pressure exerted by European colonists is highly unlikely to be responsible for an early and coeval rarefaction of *A. rayi* in both Guadeloupe and Marie-Galante, as hinted at by the radiocarbon dates. First, a status of heavily hunted game does not agree with the lack of mention of Lesser Antillean rat in Guadeloupe by chroniclers who were nevertheless quick to describe the prey consumed by the first settlers (Anonyme 1660, Du Tertre 1667, Labat, 1722, Ballet, 1895). Second, middle and low elevations of Guadeloupe Islands were entirely cultivated at least one century after the contact period, and up to two centuries later for some very hilly regions (e.g., “les Grands Fonds”). The time required for historic period populations to occupy and subsequently exert pressure across the whole territory is therefore incompatible with the very early rarefaction of the species. Additionally, the relatively large ecological valence of *A. rayi* reflected in the stable isotope evidence does not favour hunting pressure by European colonists as the unique cause to explain its extirpation from the islands of Guadeloupe.

Consequently, a relatively early process of decline demonstrated by the radiocarbon chronology supports the introduction of the black rat as the most plausible and determining factor accounting for the extirpation of *A. rayi* from Guadeloupe (either by competition, predation, disease, habitat modification; Turvey et al., 2010). The fact that most *A. rayi* isotopic compositions fall within the range defined for present-day black rats is in good agreement with the two species sharing the same isotopic niches, and therefore, potentially the same environmental resources. Consequently, the stable isotope results do not refute the hypotheses of the black rat being a severe biological competitor for *A. rayi*, as it has been observed in other fossil (Cooke and Crowley, 2018) or present-day Caribbean contexts (Clark, 1980; Harris and Macdonald, 2007; Borroto-Páez, 2009). Although, it has been demonstrated that black rats can exert competitive exclusion/dominance on subordinate rodent species (Harper and Cabrera, 2010), weight differences between *A. rayi* (cf. Supp. Information 1) and the black rat are too great to consider competitive exclusion/dominance between the two to be the most plausible mechanism explaining *A. rayi* extirpation (Hutchinson and MacArthur, 1959; Glazier and Keckert, 2002; Smith and Banks, 2014). Alternative hypotheses, such as competitive interaction by habitat alteration or disease transmission (e.g., Wyatt et al., 2008), may equally account for the rarefaction process that ultimately led to the extirpation of *A. rayi* in Guadeloupe and Marie-Galante.

Results and discussion

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

The following supplementary information to this article can be found in appendix.

SI 1 – *Antillomys* taxonomy and related comments

SI 2 – Present-day stable isotopic value

SI 3 – Fossil stable isotopic values

SI 4 – Radiocarbon dating results

SI 5 – Body weight estimates of *Antillomys rayi* Brace, Turvey, Weksler, Hoogland and Barnes, 2015.

SI 6 – Radiocarbon dating methodology

SI 7 – Correction of $\delta^{13}\text{C}_c$ values obtained for fossil *A. rayi* in order to be compared to $\delta^{13}\text{C}_c$ values obtained for present-day black rat (cf. Method Section).

SI 8 – Statistical tests

Author contribution statement

J. G., D. C., O. L., C. O., M.-T. C., A. R., and A. L. conceived the project. J. G. conducted stable isotopic analyses. C. O. and M.-T. C. conducted radiocarbon analyses. J. G., D. C., O. L., C. O., A. R., and A. L. wrote the manuscript.

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