Quaternary Research 85 (2016) 54–65

Contents lists available at ScienceDirect

Quaternary Research

journal homepage: www.elsevier.com/locate/yqres

Evidence for historical human-induced extinctions of vertebrate species on La Désirade (French West Indies)

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ARTICLE INFO

Article history:
Received 27 April 2015
Available online 8 December 2015

Keywords:
West Indies
Caribbean archaeology
Palaeontology
Herpetofauna
Biodiversity
Palaeoecology

ABSTRACT

Pit cave 6 on Pointe Gros Rempart (Baie-Mahault, La Désirade, French West Indies) is a stratified fossil-bearing site. While the archaeological material and faunal remains from the oldest assemblage demonstrate it to have formed during the Amerindian period, the second assemblage dates to the first one-hundred years of the island's colonial period (mid-18th to mid-19th centuries). Faunal analysis revealed the presence of 4 now locally extinct or extinct species, three of which have never before been documented on La Désirade (*Ameiva* sp., *Leiocephalus* cf. *cuneus* and *Alsophis* sp.). Changing faunal spectrums (invertebrates and vertebrates) due to environmental destabilisation combined with aspects of the island's colonial economy demonstrate habitat degradation and over-grazing to be the principal causes of extinctions and or extirpations.

Introduction

The Lesser Antilles are one of 34 hot spots of world biodiversity (Myers et al., 2000) whose indigenous flora and fauna have been dramatically affected by human activity. In fact, this region has lost a substantial portion of its indigenous amphibian, reptile (Henderson, 2004; Powell and Henderson, 2005), bird (Greenway, 1967; Wiley, 1986; Wiley et al., 2004), and mammal species (Morgan and Woods, 1986; Grouard, 2010). Moreover, these numbers probably underestimate the actual loss of vertebrate species, as they are based on comparisons with species documented by 18th century naturalists, although the majority of available information unfortunately derives from early 20th century sources. The earliest extinctions, such as the *Ara* on Martinique (Williams and Steadman, 2001) and the *Boa* on Guadeloupe (Lorvelec et al., 2007; Breuil, 2009), also remain the most debated. For example, recent work with fossil-bearing cave deposits on the island of Marie-Galante in the centre of the Lesser Antilles archipelago documented several extinct taxa (e.g. boa, curly-tailed lizard) that provide evidence for a much richer faunal spectrum than is evident from records concerning the earliest period of European colonisation (Sierpe, 2011; Stouvenot et al., 2014; Bochaton et al., 2015).

Addressing the multiple factors contributing to the disappearance of a species relies on the most precise understanding possible of its historical context (Fritts and Rodda, 1998). The study of abundant faunal remains often preserved in archaeological sites (e.g. Wing, 2001; Olson and Máiz López, 2008; Turvey et al., 2010) alongside natural, often better fossilised accumulations in karstic contexts (e.g. Pregill et al., 1994; Steadman and Hilgartner, 1999), provide an ideal source of information for addressing this issue. Karstic contexts are also likely to record substantial periods of time prior to or contemporary with an island's prehistoric occupation. As such, they can furnish new data concerning the composition and evolutionary history of past faunal communities as well as accompanying natural or anthropogenic modifications of local environments.

A focus on archaeological or natural faunal assemblages may, in fact, represent the only means for addressing extinctions in many island contexts. This is certainly true when historical sources or the work of early naturalists are unavailable, as is typically the case with La Désirade. Located 10 miles off the coast of Grande Terre, this small island was colonised by Europeans relatively late but not before the eighteenth century. Visited only occasionally by fisherman, the island remained isolated for a substantial period and, unlike the larger islands of Guadeloupe, did not receive detailed attention by naturalists who visited the

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http://dx.doi.org/10.1016/j.yqres.2015.11.001
0033-5894/

archipelago in the 18th and 19th centuries. The first descriptions of the island's indigenous fauna therefore appeared as late as the mid-20th century, in particular the work of Father Pinchon (Danforth, 1939; Pinchon, 1953, 1967).

Here we present an analysis of vertebrate remains recovered from pit cave 6 on Pointe Gros Rempart. Bone and teeth from the site demonstrate the presence of three squamate taxa and a mammal that have since disappeared from La Désirade. The combination of sedimentological, malacological, and archaeological data supports the local extinction of this fauna being associated with the European colonisation of the island and ensuing deterioration of natural habitats. The comparison of our data with the economic history of the island allow us to investigate the environmental factors involved in human-driven extinction of several terrestrial species on a small island untouched by substantial historical plantation.

Geographic context

The small island of La Désirade (31 km^2) forms part of the Guadeloupe island group (Fig. 1), with one-third of its surface covered by a large plateau ringed to the west, south, and east by a series of raised marine terraces cut by erosion. The island's original dry forest vegetation is related to the low relief (highest point 276 m) that limits annual rainfall. The current landscape is composed of parcels of land dedicated to subsistence agriculture or savanna with cacti or croton coppices supporting browsing goats. Although several patches of forest do survive in the ravines that incise the flanks of the plateau, the majority of wooded areas represent secondary forest growth on disused agricultural fields (Rousteau et al., 1994).

Historically, La Désirade was home to an indigenous Amerindian population as illustrated in the island's 43 pre-Columbian evidences of occupation including lithic workshops, ceremonial sites, and villages (De Wall, 2006). Although several date to the Early Ceramic Age (~550 BC–AD 500), the majority dates from the Late Ceramic Age (~AD 500–1500). The lack of archaeological evidence leaves the occupation of the Island after the first European populations arrived in the West Indies poorly documented. Some authors argue nevertheless that Amerindian populations continued to occupy the island for several centuries (Barbotin, 2010). French colonisation from neighbouring Guadeloupe did not begin before 1728, when a leper hospital was established on the Island (Lasserre, 1957). The human-induced modification of La Désirade's natural environment likely began shortly after the arrival of European colonisation. For example, *Lignum vitae* was exploited throughout the 18th century to meet the needs of European navies (Moreau, 1992; Barbotin, 2010) to such a point that today it is listed as endangered.

The population of the island was never very high (Barbotin, 2010), reaching 40 to 50 inhabitants/km^2 in the second half of the 18th century, and increasing again to 70 inhabitants/km^2 in the middle of the 19th century (Lasserre, 1957). Population levels remained relatively stable until the 1950s, being conditioned by the island's extremely limited economic resources connected to poor soil quality. Subsistence economies therefore centred around fishing and small-scale farming as well as cotton cultivation, sheep herding and creole gardens (Lasserre, 1957).

Geologically, La Désirade consists of a Mesozoic basement of volcanic, plutonic and siliclastic rocks surmounted by Cenozoic limestones. The littoral zone is skirted by remnant Pleistocene limestones, which form the youngest marine terraces. One of these terraces, Pointe Gros Rempart, not far from the town of Baie-Mahault, juts 200 m into the ocean and rises no more than a dozen metres above sea level (Fig. 1). No less than 25 caves and depressions have been documented on this heavily karstified landform and consist either of vadose shafts or collapsed dissolution features opening onto the surface (i.e. banana holes, Harris et al., 1995).

Pit cave 6 on Pointe Gros Rempart (16°19′41.56″ N, 61° 0′49.18″ O WGS 84), hereafter referred to simply as PGR6, is a banana-hole (Fig. 2) with a partially preserved roof forming a 2 to 3 m deep rock shelter. While the 2 m high ceiling allows for easy movement, collapsed blocks at the entrance protect the rock shelter from the elements. The combination of easy access and protection from the elements makes for an ideal setting for denning animals or human occupation.

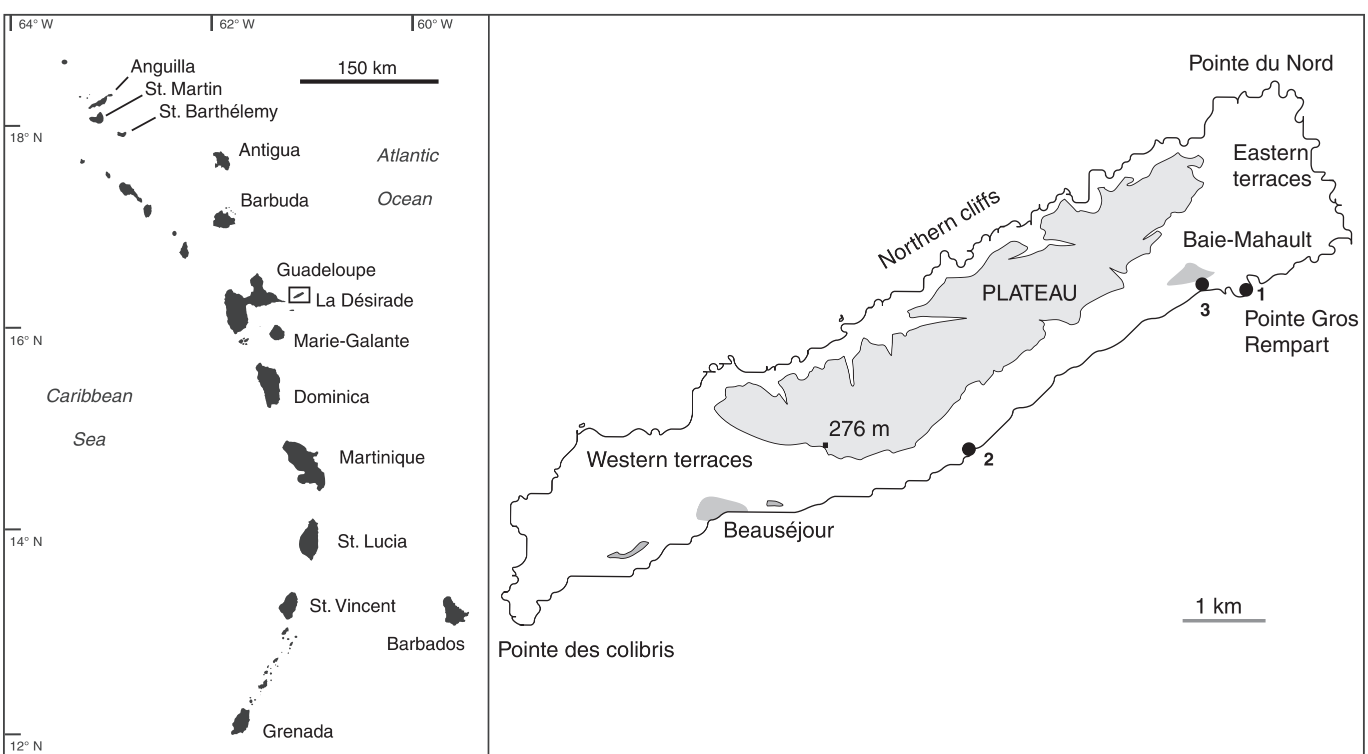

Figure 1. Left — Location of La Désirade. Right — Location of pit cave 6 on Pointe Gros Rempart (1) and Amerindian sites having produced fossil deposits: L'Escalier (2) and Petite Rivière (3).

https://doi.org/10.1016/j.yqres.2015.11.001 Published online by Cambridge University Press

Figure 2. View of the site's surroundings from the western limit of the point. The white arrow indicates the opening to PGR6.

Materials and methods

Fieldwork carried out during November 2011 consisted of a one-square metre test pit sunk in the back of the rock shelter to identify archaeological and or palaeontological deposits (Fig. 3). Excavated by flat, 5 to 10 cm spits, the fossil-bearing sediments were dry sieved with a 2.8 mm mesh, with the volume sieved adapted to the richness of the sediments as follows: fauna-poor sediments (layer 1) from a quarter-square metre area were sieved for control (spits 1–3), while all sediments from underlying fossil-bearing sediments were sieved (spits 4–9); sieving was, however, limited to a single half-square metre from spit 9 onwards. Faunal remains were identified to anatomical part and species using a reference collection housed at the Muséum national d'Histoire naturelle in Paris for each spit and in terms of number of remains (NR) for the site in general.

Sediment descriptions were based on soil (colour, texture, structure) and sedimentological criteria (bedding, clast type and orientation) complemented by the geometry of the deposits and the nature of the contact between layers. Tests with a PANDA light dynamic penetrometer were carried out to sound the absolute depth of the deposits and document layers undetected during excavations (Lenoble and Martinaud, 2003). A radiocarbon date obtained on fish bones was calibrated with Calib software 7.1 (Stuiver and Reimer, 1993) using the Marine 13 calibration curve provided by Reimer et al. (2013) assuming an averaged reservoir effect Delta R value of −27 years based on the ten nearest data points.

Results

Stratigraphy and age of the deposits

Four stratigraphic units were distinguished in the 0.9 m deep test-pit without having reached the base of the deposits (Fig. 4, Table 1). A granular, brown-grey clay-silt with little to no gravels was encountered 10 to 20 cm below the surface (layer 1). This silt contained colonial-era archaeological material reworked from the underlying layer, suggesting this deposit to be tied to the accumulation of earth remobilised by goats that today take refuge at the back of the rock shelter. Only small-sized bones were recovered from this level, which is all the more surprising given that the carbonate-rich nature of the horizon ought to preserve fossils as is evidenced by the presence of land snail (*Chondropoma crenulatum*) and whelk (*Cittarium pica*) shells alongside the remains of land crabs (Gerarcinidae) (Table 2). The predominance of bones belonging to introduced mammal species: rat (*Rattus* sp.), goat and pig (Table 3), combined with the age of the underlying levels (see below) indicates this deposit to document no more than the last 200 years of the island's settlement.

Layer 2 is 20 to 25 cm thick and composed of small limestone rubble, alongside numerous *Cittarium pica* and other marine gastropod shell fragments. Several burrows, of approximately ten centimetre wide, are likely to account for the presence of land crabs and hermit crabs (Gerarcinidae/Coenobitidae) in the sediments. Colonial-era archaeological material (Fig. 5), including Dutch Gouda clay pipe bowls, brass wire, a lead ingot, an edge-damaged bivalve shell (*Codakia orbicularis*) that likely served as a scraper, flint flakes, an andesite grinder and or millstone as well as a tubular Cornaline d'Aleppo bead with a deep red surface that was manufactured in Venice since the 17th century, were all found in the various spits of layer 2.

The origin of the ceramic elements recovered from layer 2 provides further chronological precision. Thin-walled potsherds with distinct rilling and an internal glaze are typical of English pottery that became abundant in the French Caribbean following the Franco–English treaty of 1786. A late 18th century age for layer 2 is corroborated by two further elements: the bottom of a plate with a bluish surface characteristic of late 18th century 'pearlware' (Campbell, 1984) recovered from the surface of the rock shelter and a bone button comparable to examples found at the Cluny Beach cemetery in Guadeloupe that tend to date to the same period (Pichon and Vragar, 1998). Taken together, these elements provide secure evidence for layer two representing the period spanning the late 18th to no latter than the early 19th century, in other words, a little less than a one hundred-year period following the island's initial European colonisation. In terms of faunal material, layer 2 is characterised by a limited spectrum of terrestrial snails (Table 2) represented essentially by *Chondropoma crenulatum* and *Bulimulus guadalupensis* along with the remains of birds and squamates (Table 3). A single pig is according with a wide introduction of this species in the Caribbean by first Europeans (Breton, 1647).

Layer 3 (15 to 20 cm-thick) is distinguishable by its dark brown colour resulting from the biological structure of the sediments, with the presence of numerous Hymnoptera larval tubes indicative of a fossil soil. The fact that the deposit dips towards the cave walls demonstrate that the formation of this soil is connected to a colluvial fan that developed directly below the roof collapse. Herpetofauna and fish remains are well represented, the latter comprising primarily reef species (e.g. *Sparisoma* sp., *Acanthurus* sp., *Bodianus rufus*, *Haemulon* sp.), whose habitats can be found in the site's immediate vicinity. Consequently, they may reflect predators, such as rapacious birds, being responsible for the accumulation. This likelihood is further reinforced by traces of digestion observed on certain squamate remains (*Anolis*, *Thecadactylus* and *Leiocephalus*). On the other hand, large fish vertebrae, two burnt bones towards the base of the layer (spits 11 and 12), and pelagic species (*Decapterus* sp.) may be derived to an Amerindian occupation in the vicinity of the cave. Indeed, offshore fishing is well documented during the Ameridian Period (Grouard, 2001; Wing, 2001; Grouard, 2003a, 2003b). The presence of a hand-thrown potsherd with shell temper and the absence of colonial-era archaeological material suggest an Amerindian age for layer 3. This is demonstrated by a calibrated radiocarbon age of AD 299–507 (Beta-407,191) obtained on a burnt fish bone that places the formation of level 3 several centuries to a millennium before the initial European colonisation of the island.

Layer 4 contains a silty-clay, which first appeared in spit 9 and continued to the base of the test-pit. Penetrometer tests demonstrate it to continue for approximately a metre more, bringing the total depth of layer 4 to 1.5 m. This sterile layer therefore sits directly on the rocky

https://doi.org/10.1016/j.yqres.2015.11.001 Published online by Cambridge University Press

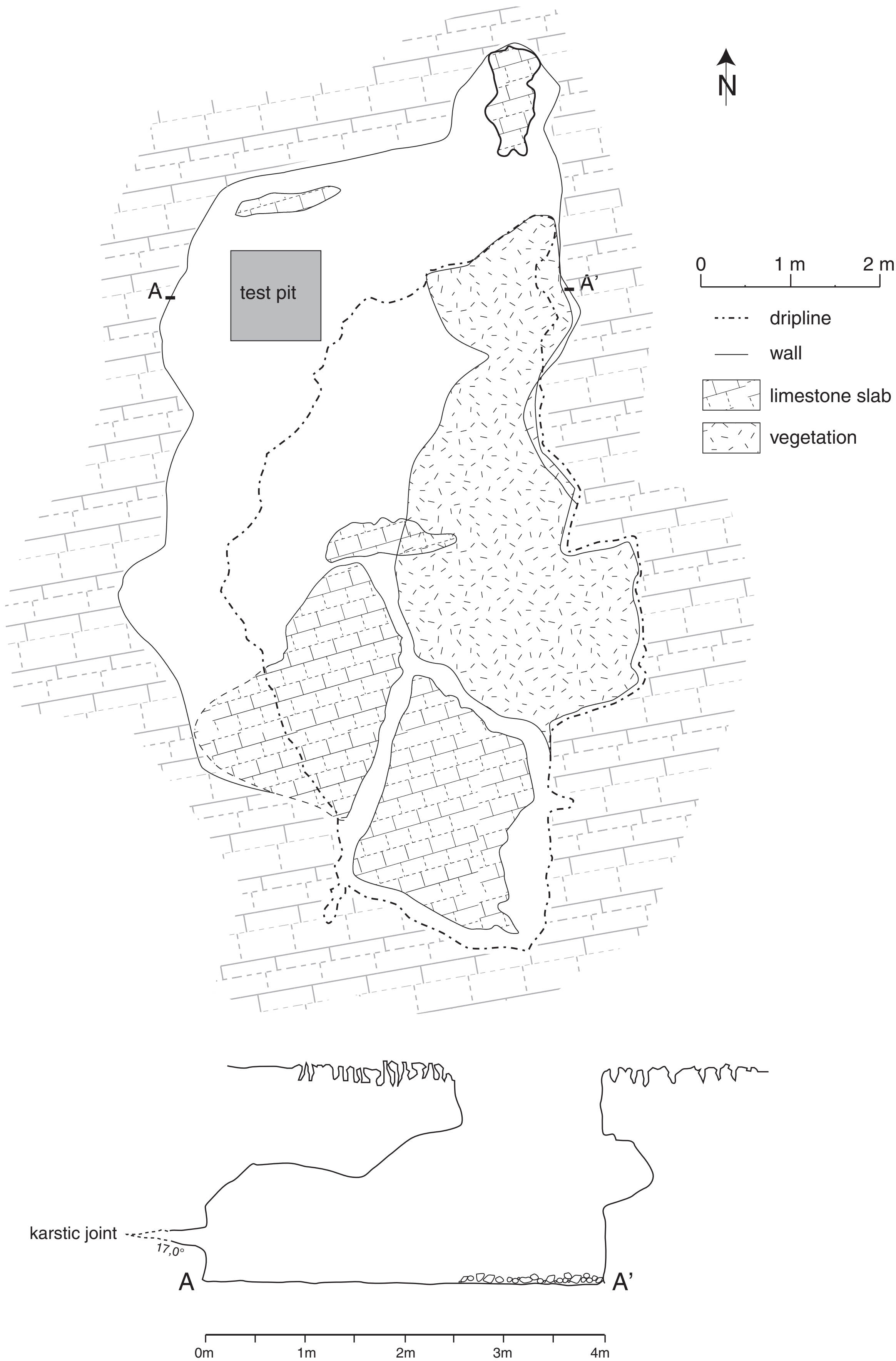

Figure 3. Plan and topographic profile of PGR6. The grey square indicates the placement of the test-pit.

https://doi.org/10.1016/j.yqres.2015.11.001 Published online by Cambridge University Press

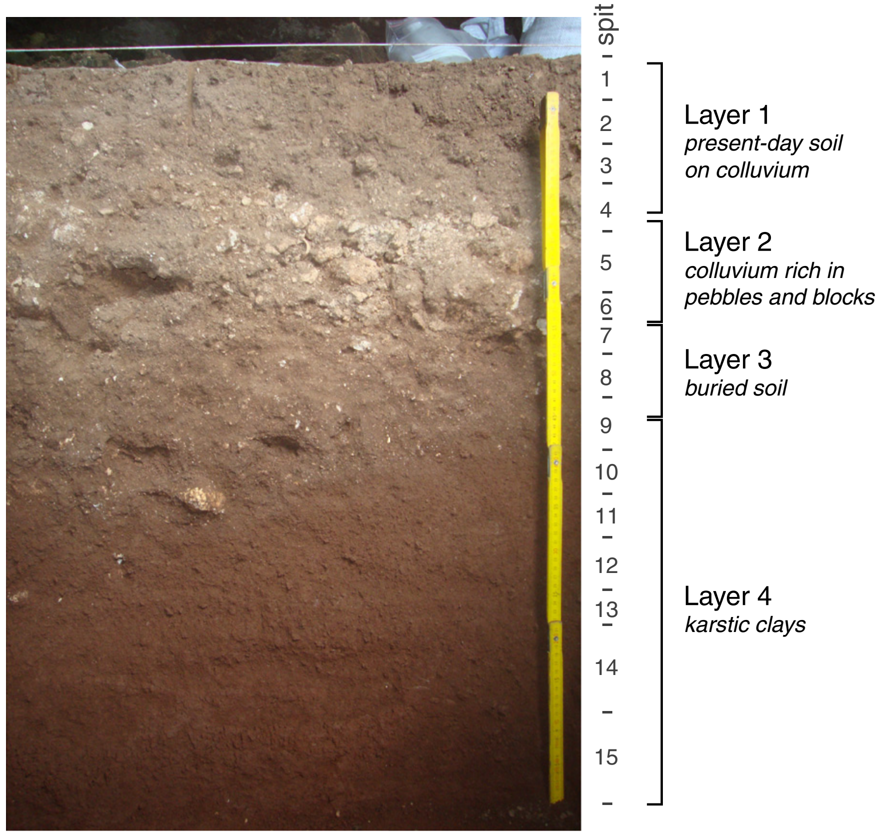

Figure 4. Northern section with the position of the stratigraphic units. The graduated scale represents 0.8 m.

substrate and represents the bulk of the cavity's fill. The decarbonated nature of the sediment and the smoothly polished surfaces of the aggregates indicate this material to be the deep horizon of a palaeosol whose upper portion is formed by layer 3. This succession of pedological horizons provides evidence for a recent, weakly-developed vertic palaeosol (Eswaran et al., 1999) that formed over a period of no more than several hundred years (Yaalon, 1971; Wilding and Tessier, 1988), and thus further constraining the formation of overlying layer 3 to a several-century long period immediately preceding the colonial era.

Faunal remains

Of the twenty-three vertebrate taxa identified (Table 3), lizards (anoles and ameivas), snakes (racers), marine fish (Perciformes), and birds are the most well represented. Preliminary observations indicate that the avifauna includes a yellow-crowned night-heron (*Nyctanassa violacea*), a charadriiform, an Accipitridae, an Audubon's shearwater and passerines. These bird species are accompanied by a very limited number of bats and a single frog species (*Eleutherodactylus* cf. *martinicensis*). A large rodent metapodial can be attributed to a giant rice rat (*Megalomys* sp.) given its large size. This rodent, the only Oryzomyini known from fossil sites on the island (Grouard, 2001; De Wall, 2006; Grouard, 2011) and pervasive during the Amerindian period, has now completely disappeared from the Lesser Antilles (Grouard, 2004; Turvey et al., 2010). The presence of this bone at the base of the Amerindian-age layer lends further support to its former presence on La Désirade.

The morphology of the cranial elements, teeth, and vertebrae demonstrate the presence of six different taxa of lizard and a single type of snake amongst the squamate remains. Anoles are the best represented and are clearly identifiable based primarily on maxillary, dentary, and dental morphologies (Fig. 6a, Evans, 2008; Bochaton, 2013; Bochaton et al., 2015). The morphology and size of the different elements are in good agreement with the Désirade anole (*Anolis desiradei*), the only anole species currently present on the island (Breuil, 2002).

Dentary and maxilla retaining wide, flared, fan-shaped tricuspid teeth bear witness to a species of *Leiocephalus* in the colonial and Amerindian levels (see Etheridge, 1964, 1966; Pregill, 1992 for the osteological characteristics of this genus). The Meckelian groove (Fig. 6b) is enclosed by the dentary bone along nearly its entire length, and

Table 1
Sedimentological characteristics of the stratigraphic units. Colour descriptions follow the Munsell soil colour chart (Munsell Color, 1975).

Unit	Thickness (cm)	Texture	Sedimentary structure	Pedological features	Colour	Lower boundary
Layer 1	10–20	Clayey silt poor in pebbles	Massive–planar clast fabric	Biological microaggregated structure–goat's dungs	7,5 YR 5/3	Sharp and irregular
Layer 2	15–25	Clayey silt rich in limestone Pebbles and granules and *Cittarium pica* fragments	Matrix supported–Isotropic clast fabric	Microaggregated structure–Ten cm diameter burrows	7,5 YR 6/4	Regular oblique (dipping ~5° NO)
Layer 3	15–20	Clayey silt with few limestone granules and pebbles	Massive	Microaggregated structure–Wasp burrows	7,5 YR 4/3	Gradual oblique (dipping ~10° N-NO)
Layer 4	150	Silty clay	Massive	slickensides associated to weakly developed peds	5YR 4/4	*Unrecognised*

https://doi.org/10.1016/j.yqres.2015.11.001 Published online by Cambridge University Press

Table 2
Invertebrate fauna in number of remains (NR) and by spit and level. Determinations based on Warmke and Abbott (1961), Kaas (1972), Burggren and McMahon (1988), and Pointier and Lamy (1998).

	Spit	1	2	3	4	5	6	7	8	9	10	11	12	
	Layer	1			1/2	2	2/3		3		3/4			
Family	Species													Total
Gastropoda														720
Lottiidae	*Lottia leucopleura*					1								1
Fissurellidae	*Fissurella nodosa*							1						1
Trochidae	*Cittarium pica*	17	15	19	69	85	66	69	30	26	34	4	2	436
Turbinidae	*Lithopoma* cf. *caelatum*													6
	Lithopoma tuber													2
	Litophoma sp.													15
Neritidae	*Nerita peloronta*													1
	Nerita cf. *peloronta*													8
	Nerita tessellata													10
	Nerita cf. *tessellata*													6
	Nerita versicolor													3
	Nerita sp.													23
Cerithiidae	*Cerithium* sp.						1				1			2
Littorinidae	*Echinolittorina tuberculata*		2		1	3	2	1	1					10
	Cenchritis muricata	1	1		8	4	10	4	4	3	4			39
Strombidae	*Strombus* sp.					1								1
Cypraeidae	*Luria* sp.				1			1						2
Ranellidae	*Charonia tritonis variegata*				1									1
Tonnidae	*Tonna* sp.						1							1
Muricidae	*Purpura* = *Plicopurpura patula*		3	1			1	2		2				9
	Stramonita haemastoma				1		1							2
Columbellidae	*Columbella mercatoria*		1		1									2
Buccinidae	*Pisania* = *Pollia* sp.						1							1
Conidae	*Conus* sp.						1							1
Bulimulidae	*Bulimulus guadalupensis*			1	3	6	6		2					18
Annulariidae	*Chondropoma crenulatum*		4		24	23	42	14	10	1	1			119
Bivalvia														22
Lucinidae	cf. *Lucina* sp.								1					1
	Codakia orbicularis			2	4					2				8
Tellinidae	*Tellina* sp.			3	2									5
	cf. *Tellina* sp.									1				1
Veneridae	*Chione* sp.							1						1
Dreissenidae	*Congeria* sp.								1					1
	bivalvia					4	1							5
Polyplacophora														49
Mopaliidae	*Ceratozona squalida*													1
Chitonidae	*Chiton marmoratus*													9
	Chiton tuberculatus													4
	Acanthopleura granulata													35
Crustacea														101
Coenobitidae	*Coenobita clypeatus*			1	4									6
	gen et sp. indet.				1									1
Gecarcinidae		1	7	4	30	2	51	1						96
Echinodermata										1	5			10
Indeterminate					10	9	13	8	10		2	1		53
Total Invertebrate remains		19	33	31	160	138	197	102	59	36	47	5	2	957

tricuspid teeth appear at the level of the fifth dentary tooth. These characters allow these specimens to be attributed to *L. cuneus*, an extinct species known from the Late Pleistocene and historic periods on several islands of the Lesser Antilles (Etheridge, 1964; Pregill et al., 1994; Sierpe, 2011; Stouvenot et al., 2014).

Three dentary bones, a maxilla and two pterygoids (Table 3), are attributable to a medium-sized gecko. The morphology of the pterygoids matches well with *Thecadactylus rapicauda*, which is widespread in the Caribbean. Scincid lizards are represented by a single dentary bone (Fig. 6c) recovered from the colonial-era layer 3 (Table 3). The fact that the Meckelian groove is partially enclosed by a dentary bone bearing blunt, cylindrical pleurodont teeth indicate a *Mabuya* morphology, and thus could be attributed to *Mabuya desiradae*, the only member of the skink family currently living on the island (Henderson and Breuil, 2012).

Sixty-six skeletal elements can be assigned to a medium to large-sized lizard of the genus *Ameiva*. Both the maxilla and dentary contain relatively small and curved single-cusped anterior teeth, and larger, slightly recurved, bicuspid posterior teeth bearing a small anterior cusp and a well-developed principal cusp (Fig. 6d). Unlike the other lacertilians found on the site, the Meckelian groove of the *Ameiva* remains open across its entire length (cf. Estes and William, 1984; Estes et al., 1988; Kosma, 2004; Conrad, 2008; Evans, 2008; Pujos et al., 2009; Bochaton, 2013 for details concerning the characteristics of this family and genus). While the Guadeloupe *Ameiva* has disappeared from the archipelago, it has recently been shown that two species were present on the island up until the historic periods: *Ameiva cineracea* described on Basse-Terre (see Breuil, 2002) and mentioned in the fossil record of Grand-Terre by Pregill et al. (1994) and Grouard (2001), and *Ameiva major* on the small island of Petite-Terre (Breuil, 2002). The specific osteological characteristics of these two species have not yet been described and all the previous attributions were made on the basis of geographical distribution. Thus, it was not possible to attribute the remains from PGR6 to one of both species.

A single humerus of a juvenile individual from layer 3 match with the morphology of young *Iguana*; however, the early juvenile stage of this remain make us consider this attribution with caution. Today, only the Lesser Antilles iguana (*Iguana delicatissima*) is present on La

https://doi.org/10.1016/j.yqres.2015.11.001 Published online by Cambridge University Press

Table 3
Vertebrate fauna in number of remains (NR) and by spit and level.

	Spit	1	2	3	4	5	6	7	8	9	10	11	12	
	Layers	1			1/2	2	2/3		3		3/4			
Family	Species													Total
Teleostei														276
	Indeterminate		4		14	6	31	21	35	24	17	22	15	189
Carangidae	*Caranx* sp.					5	4	1	4	3	3	2	4	26
	Caranx hippos									1				1
	Decapterus sp.									1				1
Serranidae							2							2
	Epinephelus sp.						1							1
Lutjanidae											2			2
	Lutjanus sp.									3				3
Haemulidae	*Haemulon* sp.										1	3		4
Sparidae								5				1		6
Malacanthidae	*Malacanthus plumieri*						2	1	2					5
Scombridae							1							1
Acanthuridae	*Acanthurus* sp.						3	1	2	5	3	3	1	18
Scaridae											2			2
	Sparisoma sp.							1				4		5
Labridae						1	1				1			3
	Bodianus rufus													3
Perciformes		1												1
Balistidae				1	2									3
Amphibia														2
Leptodactylidae	*Eleutherodactylus* cf. *martinicensis*							1	1					2
Squamata														372
Cheloniidae												1	11	12
Lacertilia						13	5	4		5				27
Teiidae	*Ameiva* sp.			1	6	9	11	9	9	7	9	16	3	80
Polychrotidae	*Anolis* cf. *desiradei*			2	5	9		56	34	9	9	15	6	145
Tropiduridae	*Leiocephalus* cf. *cuneus*					3	2	5	2	4	2	4	1	23
Gekkonidae	cf. *Thecadactylus rapidauca*						1	1	1	1		1	1	6
Mabuyidae	*Mabuya* sp.							1						1
Iguanidae	cf. *Iguana*					1								
Xenodontidae	*Alsophis* sp.		1	1	2	7	23	20	4	7	5	4	4	78
Aves		2	0	0	16	51	74	30	22	14	36	14	1	260
Mammalia														26
	Indeterminate					6								6
Chiroptera											4			4
Phyllostomidae	*Brachyphylla cavernarum*							1	5					6
Suidae	*Sus scrofa*	2	1			1								4
Bovidae		1												1
Rodentia					1	1								2
Oryzomyini	*Megalomys* sp.												1	1
Muridae	*Rattus* sp.	2												2
indeterminated		2			25	50	92	94	55	30	77	55	7	487
Total Vertebrate remains		10	6	5	71	163	253	252	179	114	171	145	55	1423

Désirade, and its presence could be documented through the fossil from the sites of L'Escalier and Petite Rivière (*Iguana* cf. *delicatissima*, Grouard, 2001; De Wall, 2006)

A medium-sized snake in our sample is represented by two maxilla, a dentary, and 75 ribs and vertebrae, the latter of which are slightly longer than they are wide (Fig. 6e, length of the vertebral body measuring up to 5 mm). The triangular centrum bears a generally well-developed haemal keel with anterior subcentral ridges and subcotyle tubercules. The prezygapophysal processes are conical with a rounded distal extremity and are triangular in cross-section. In posterior view, the neural arch is slightly convex with fairly narrow margins. Taken together, the above characteristics are in good agreement with the members of the genus *Alsophis* in our reference collection. The morphology of the maxilla and dentary bones is also consistent with this attribution.

While the majority of the vertebrates identified at PRG6 are still present on the island, certain have seen their habitats shrink (*Puffinus* cf. *herminieri*), have completely disappeared but remain present on neighbouring islands (*Alsophis* sp.), or have gone extinct (*Megalomys* sp., *Ameiva* sp. and *Leiocephalus* cf. *cuneus*). Numerous invertebrate remains were recovered from all layers (land snails, shellfish, echinoderms, and crustaceans, Table 2), all of which are still present amongst the island's fauna.

Site formation

The stratigraphy combined with associated palaeontological and archaeological material allows for a reconstruction of the formation of the site. Once the banana-hole formed it remained connected to the surface via a network of wells and fissures, trapping exterior clay substrates introduced by percolating surface water. This process can be inferred from the same mineral facies visible in nearby caves that are connected to the surface by narrow, vertical conduits. Decalcified sediments resulting from the percolation of acid-enriched water from the surrounding soils produced unfavourable preservation conditions for both bones and shells. Not surprisingly, no palaeontological specimens were recovered from this clay (layer 4).

The enlargement of fractures in the host rock by corrosion weakened the roof and eventually led to its collapse. The resulting depression accumulated sediments remobilised by surface runoff, with the exposure of the cave floor allowing vegetation to grow and a soil to form. It is

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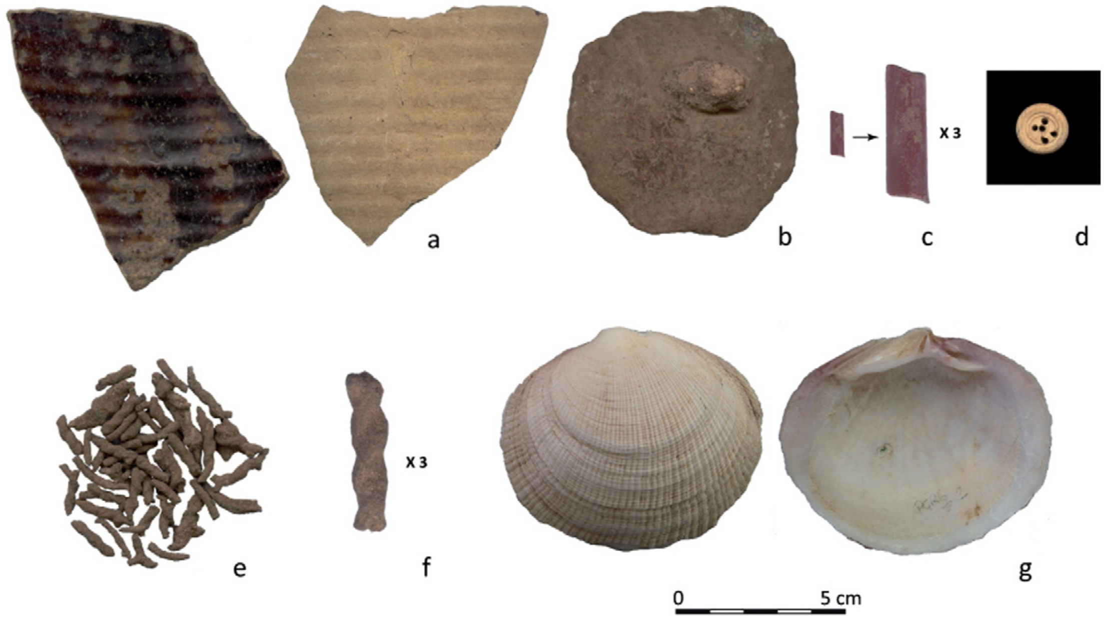

Figure 5. Colonial-era artefacts from layer 2; a: glazed potsherd, b: lead lingot, c: "Cornaline d'Aleppo", d: bone button, e and f: brass wire, g: *Codakia orbicularis* shell likely used as a scraper.

likely that both processes contributed to the formation of the Amerindian layer 3. The presence of Hymenoptera larvae clearly indicates the reworking of the soil by insects, whereas the changing geometry of the deposits connected to the development of a colluvial fan provides evidence for the accumulation of colluvial deposits in the cavity. A portion of the malacofauna was recovered in primary position, as is demonstrated by the terrestrial mollusc assemblage comprising *C. crenulatum* and *B. guadalupensis*. These two species have been shown to range in all types of habitats, including heavily human-modified environments or fissured rocky substrates (Bertrand, 2001). The presence of these taxa and the very low fragmentation of their shells are consistent with the site containing primary death assemblages. On the other hand, certain elements in the Amerindian-age layer were probably introduced by colluviation.

The archaeological nature of a part of the material from this layer is clear from the presence of burnt fish remains, a large variety of marine gastropods unavailable in the site's immediate surroundings as well as a worn fragment of Amerindian pottery. The absence of combustion features, anthropic sediments or features, and the rarity of archaeological material all argue for this material being in secondary position. Fragments of Amerindian material spread across the entirety of Pointe Gros Rempart (De Wall, 2006) do, however, suggest that the reworked archaeological material in the cave derives from a nearby Amerindian site. Sediments containing both natural and archaeological materials provide evidence for the formation of a soil within the cave, with sediment input being low compared to in situ transformation.

The configuration changes with the formation of layer two, which sees the accumulation of less-organic sediments, that, while rich in

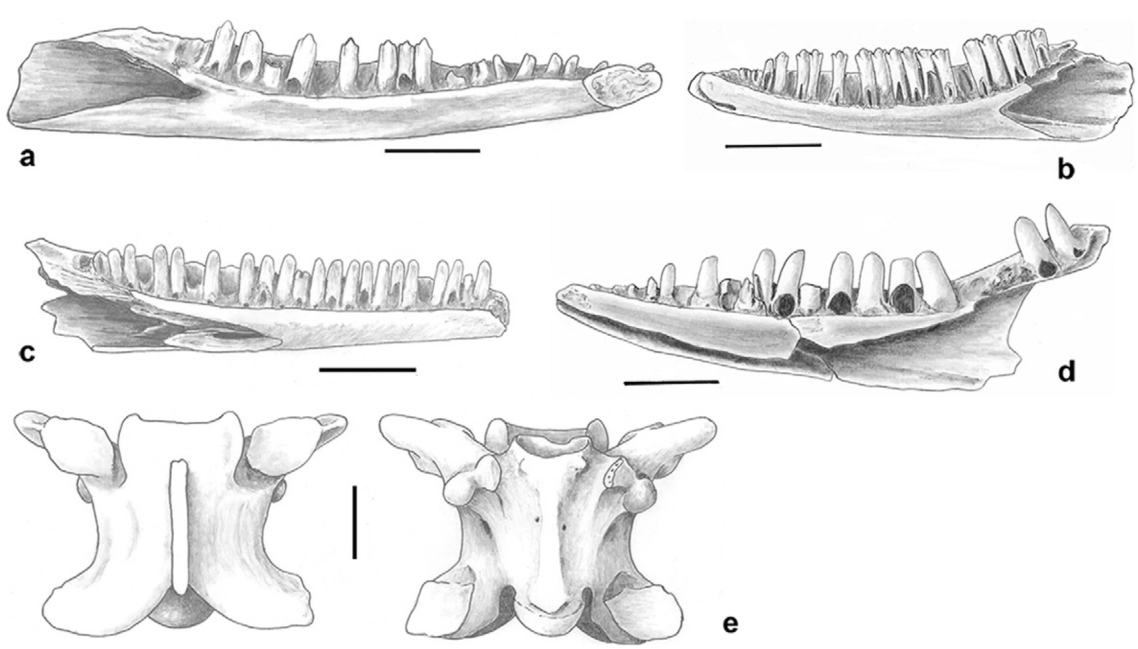

Figure 6. Squamate bones recovered from PGR6: a — left dentary of *Anolis* (cf. *desiradea*), b — right dentary of *Leiocephalus* cf. *cuneus*, c — left dentary of *Mabuya* (cf. *desiradea*), d — left dentary of *Ameiva* sp., e — *Alsophis* sp. vertebra. Scales a, b, d and e = 2 mm, and c = 5 mm (DAO, S. Bailon).

small rubble, nevertheless retain a biological microstructure. This combination is indicative of a colluvial input, which is corroborated by the unusual thickness of the resulting 60 cm thick organo-mineral horizon. This latter aspect is typical of what soil scientists refer to as a “cumulic horizon”, where sedimentary input contributes to the in situ transformation of sediments, producing unusually thick horizons (Mücher et al., 1972). The transition from a palaeosol to a soil formed by the steady contribution of material marks a clear rupture in the equilibrium of the environment, which provoked the erosion of the soils. Paradoxically, the historical remains recovered from this horizon form a coherent assemblage identifiable with the occupation of the site. While a *Codakia* shell with traces of use and a worked whorl of cone shell provide the most reliable evidence of a human presence, several invertebrate remains (land crabs, certain burgos, Nerite snails, chitons, and whelks), easily accessible in the site's vicinity, may also have been introduced to the site, perhaps as fishing bait. This possibility is in line with the use of a clamshell to scale fish as well as the presence of a roll and pieces of brass wire alongside a small lead ingot. These objects may have belonged to fishermen, who used the fine copper alloy to fashion fishtraps or impromptu hooks and the lead to make sinkers for lines or nets.

Continuing sedimentation following the site's colonial occupation is evident in the sediments reworked by goats (layer 1). The sedimentary facies and the attenuation of the debris cone morphology mark the end of materials being transported into the site. This change in the sedimentary regime linked to a barren landscape surrounding the cave demonstrates the site's current configuration in a rocky pastureland with little vegetation to have emerged following the formation of layer 2 at the end of 18th or beginning of the 19th century. Historic period sediments (layer 1) contain a less varied faunal spectrum compared to the underlying layers even when the number of remains is corrected for as a function of surface area sieved (Fig. 7). Snails are represented by a single species (*C. crenulatum*) and bones are rare. This reduction in species diversity probably reflects the desertification and mineralisation of the environment following the ‘colluvial crisis’ documented in the underlying colonial deposits.

Discussion

Locally extinct or extirpated species or a reduction in habitat sizes

Four species identified amongst the faunal material from PGR6 are today no longer present on the island (*Megalomys* sp., *Alsophis* sp., *Ameiva* sp., *Leiocephalus* cf. *cuneus*). The member of the genus *Amazona* documented at Petite Rivière, whose presence on the island is confirmed by a specimen recovered from fossil site (Grouard, 2001), adds another extirpated species (Table 4). The faunal assemblage from PGR6 thus illustrates modifications in the vertebrate population in relation to the succession of human occupations on the island. For example, the rice rat, a species common during the Amerindian period, is replaced in the upper part of the sequence by the black rat introduced by Europeans.

The recovery of three now-extinct squamate taxa (*Alsophis* sp., *Ameiva* sp. and *Leiocephalus* cf. *cuneus*) during excavations at PGR6 is an important element in terms of our understanding of the fauna that once inhabited La Désirade. The accounts of chroniclers, the structure of the island's biological communities (Breuil, 2002; Lorvelec et al., 2007; Breuil, 2009; Henderson and Breuil, 2012), or the hypothetical attributions of faunal remains on the basis of size criteria (De Wall, 2006; Table 4) have all been invoked as support for the previous existence of certain taxa on La Désirade. The presence of extirpated taxa at PGR6 show the make-up of herpetological populations on La Désirade during historic periods to conform to patterns described for small and medium-sized islands by Lescure (1979) and Corke (1992). Finally, the recovery of these taxa in both the Amerindian and colonial levels at PGR6 demonstrates that they disappeared no more than two centuries ago.

Unique squamate extinction events on La Désirade

The one-time presence of curly-tailed lizards, ameives and racers on La Désirade naturally poses questions as to the causes underlying their disappearance. The island was never home to the mongoose (Pinchon, 1967; Lorvelec et al., 2001), despite it being considered a primary agent for the extirpation of reptiles (Case and Bolger, 1991; Henderson, 1992;

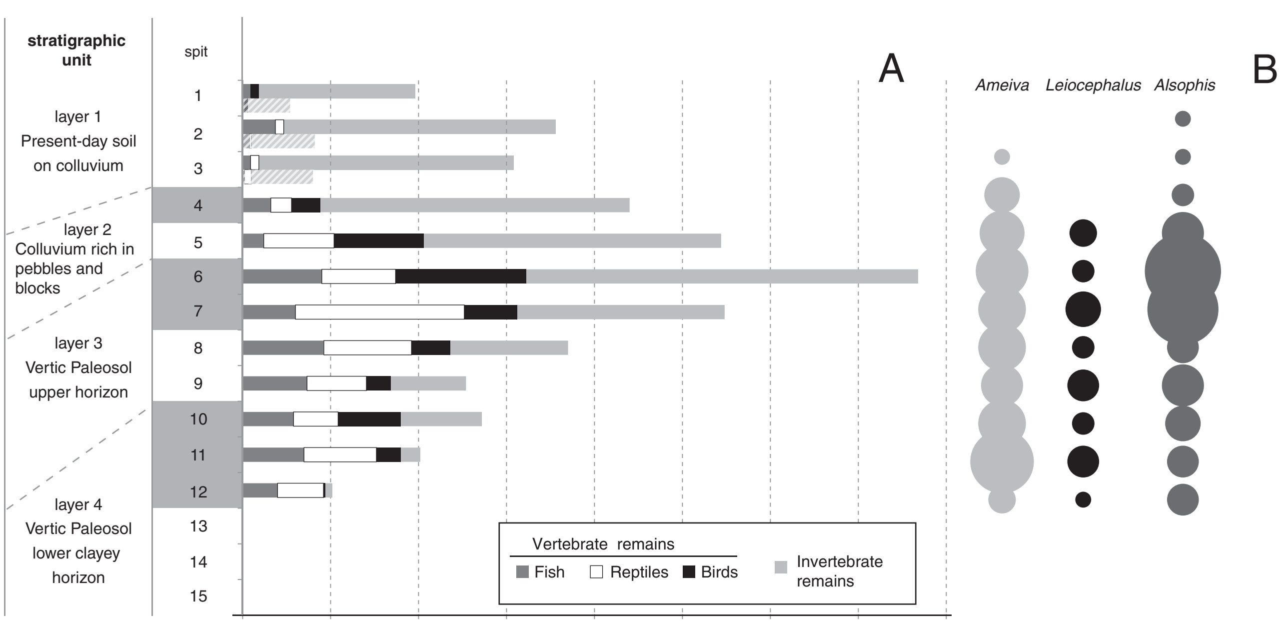

Figure 7. Stratigraphic change in the representation of the main vertebrate and invertebrate taxa (A) and stratigraphic distribution of the remains of now-extinct squamate species (B). The grey-shaded spits represent the transition between stratigraphic units. For spits 1 to 3, the bars with white lines represent the number of remains recovered, while the shaded bars represent the number of remains per square metre of sieved sediment.

https://doi.org/10.1016/j.yqres.2015.11.001 Published online by Cambridge University Press

Table 4
Vertebrate species found from fossil sites on La Désirade. (+) extirpated or extinct species. Data compiled from (1) De Wall (2006) and (2) Grouard (2001).

		Pointe Gros Rempart	A l'Escalier (1)	Petite Rivière (2)
Amphibians	*Eleutherodactylus* cf. *martinicensis*	+		
Reptiles	*Leiocephalus* cf. *cuneus* (+)	+		
	Ameiva sp. (+)	+	cf.	
	Alsophis sp. (+)	+	cf.	
	Anolis cf. *desideradei*	+		+
	Mabuya sp.	+		
	Thecadactylus rapidauca	cf.		
	Iguana sp.	cf.	+	+
Birds	*Puffinus lherminieri*	cf.		+
	Ardea herodias			+
	Nyctanassa violacea	+		
	Amazona sp. (+)			+
	Columbidae sp.			cf.
Mammals	*Brachyphylla carvernarum*	+		
	Molossus molossus			cf.
	Dasyprocta cf. *leporina*		+	+
	Megalomys sp. (+)	+	cf.	+
	Mus musculus			+
	Rattus sp.	+	+	

Powell and Henderson, 2005; Daltry, 2009; Lewis et al., 2011). This diurnal predator actively preys upon terrestrial fauna (Powell and Henderson, 2005), especially land snakes of the genus *Liophis* and *Alsophis* (Sajdak and Henderson, 1991), to such an extent that a direct causal link between the absence of racers and the presence of mongoose has been proposed: "there are no Post-columbus extirpation of *Alsophis* or *Liophis* on any island which remained mongoose-free" (Henderson, 1992, p. 4). The remains of three extirpated species recovered from PGR6 thus represents a counterexample to the traditional explanation for the regional disappearance of squamates, which is rendered all the more remarkable given that the these medium-sized diurnal species are considered the most susceptible to predation by mongoose (Corke, 1992; Henderson, op. cit.; Powell and Henderson, 2005; Lorvelec et al., 2007).

This observation is echoed by Corke (1992), who has suggested a simple *indirect* correlation between the presence of mongoose and the absence of squamates. In this view, any correlation would reflect a more important alteration of the island environments where this carnivore was introduced, notably in connection with the emergence of large plantations such as those growing sugar cane (Corke, 1992). La Désirade, however, did not see any large-scale agriculture, and the late arrival of colonial activity, alongside a more traditional subsistence farming, protected the island from environmental deterioration provoked by the development of large plantations (Pinchon, 1967).

The disappearance of squamates from La Désirade therefore represents a unique example that escapes commonly advanced models for the disappearance of island fauna. Material recovered from PGR6 nevertheless shows these species all vanished at approximately the same time, between the end of the 17th century and 1950, suggesting that their extirpation may be connected to the same combination of processes resulting from anthropogenic alterations of the environment. As these events occurred during a period for which we have but a fragmentary understanding of ecosystems, investigating this hypothesis requires combining archaeological, historical and ecological data (Burney, 1997; Fitzhugh and Hunt, 1997; Drake and Hunt, 2009).

An integrated archaeological and ecological approach

Cotton remained the island's sole exported crop, although it remained extremely limited despite attempts at industrialisation following the First World War (Lasserre, op. cit.). While this trend does not set La Désirade apart from the numerous other small islands of the Antilles archipelgo, two points are worth drawing attention to. First, more than one quarter of the island is plateau, a topography that is rare for small-sized islands (i.e. < 50 km^2). However, as is the case for most of the West Indies, the island's main settlements are in the most favourable zones comprising the coastal platform on the south coast, with all the exploitable land along this coast transformed into creole gardens (Lasserre, 1957; Pinchon, 1967). Although the plateau remained uninhabited, it regularly saw episodes of slash-and-burn farming, as had been the case in the past (Lasserre, 1957; Pinchon, 1967; Barbotin, 2010). Consequently, the relatively flat land (slopes < 15°) susceptible to agriculture during historic periods is substantial (71.3% of the landmass).

The second important point is the central role of sheep herding in the island's economy, which represents the main source of revenue for its inhabitants. In fact, La Désirade supplied much of Guadeloupe with sheep, with the standing herd numbering 2500 to 3000 head in the middle of the 20th century, to which can be added several hundred goats, bringing the total number of Caprini to twice the contemporary human population (Lasserre, 1957). Grazing on exhausted agricultural land or managed prairies led to the development of the savannas that still dominate the eastern end of the island. Moreover, goats graze freely on the islands, moving into non-agricultural land on the southern slopes of the plateau (Pinchon, 1967).

These aspects suggest that the degradation of the environment by agriculture and over grazing likely played a prominent role in the island's ecological history. Comparison with Saint-Barthélemy sheds light on the relative importance of these factors. This 21 km^2 island (maximum altitude 286 m) in the north of the Lesser Antilles is covered with xeric vegetation, making it the most suitable for comparison with La Désirade both in terms of geomorphology and physio-geography. Moreover, these two islands saw the introduction of the same predators (rats, mice, dogs, and cats), which provoked distinct ecological responses insofar as the terrestrial herpetofauna (e.g. ameive, racer) of Saint-Barthélemy persists to this day (Questel and Le Quellec, 2012).

The island of Saint-Barthélemy was colonised earlier, with the first permanent settlements dating to 1659. However, the tobacco fields that dominated in the 17th century required only small surfaces (Moreau, 1992). During this period the island's population did not surpass 21 inhabitants / km^2, the majority of which were concentrated in urban areas around the port of Gustavia. The only known census of the rural population revealed a population density comparable to La Désirade, with 30 inhabitants / km^2 during the 18th century and 70 to 80 / km^2 in the second half of the 19th (Lavoie, 1989). Two important differences nonetheless separate Saint-Barthélemy from La Désirade, moderately sloped areas (i.e. < 15°) covering less than 50% of the island, and a less substantial representation of livestock, estimated at 1500 head at the end of the 19th century. Moreover, this animal population was restricted to enclosed pastures (Robequain, 1949).

This comparison between two similar sized islands confirms the prominent role played by agriculture and grazing on La Désirade, a difference that likely accounts for the disappearance of terrestrial fauna during colonial times. Both slash-and-burn agriculture and grazing provoke the disappearance of vegetation cover, which impacts terrestrial fauna in varying ways. Slash-and-burn agriculture is likely to destroy parts of the terrestrial fauna (Russell et al., 1999), with the severe reduction in vegetation cover also leading to greater exposure to predators (Lowney et al., 2005) and temperature extremes (Russell et al., 1999). Thirdly, land degradation via slash-and-burn agriculture in a tropical area results in soil depletion (Gourou, 1946; Revert, 1949), leading to a loss of soil structure. The combination of these two processes renders soils more prone to erosion (Gourou, 1946; Revert, 1949), which is all the more important as depletion, like over-grazing, limits forest regrowth. Ultimately, this produces a reduction in invertebrates in the soil and, consequently, the vertebrates that feed upon them (Coblentz, 1978; Glor et al., 2001). This soil degradation has a greater effect on terrestrial fauna (Germano et al., 2003) whether their habitat is threatened, as in the case of plant

https://doi.org/10.1016/j.yqres.2015.11.001 Published online by Cambridge University Press

litter species (McNair and Coles, 2003), or their food source disappears, such as with carnivorous species (Lewis, 1989).

Data from the PGR6 test-pit provide supporting evidence for conclusions drawn from the island's colonial history and changing ecological contexts. The development of a cumulic soil in the colonial horizon results from the mobilisation of superficial horizons in connection with the degradation of the vegetation cover. This unusual accumulation is all the more remarkable as it contrasts with the nearby exposed bedrock where the only depressions in the limestone pavement areas permit a thin humus to develop. The colluvial accumulation contemporary with the colonial era therefore provides evidence for not only the destabilisation of the external environment but also the degradation of soils, exposing the bedrock and rendering the reestablishment of the natural environment even more difficult. This irreversible process is also shown by a hiatus in sedimentation following the formation of the colonial layer, which indicates that the landscape around the site had already assumed its present form. The impact of these environmental alterations is reflected in the range of terrestrial malacofauna, with land snails less numerous in the top layer compared to both the colonial and Amerindian layers.

It is interesting to note that extinct species documented at PGR6 are all sensitive to soil degradation, particularly carnivorous terrestrial species. The island's particular historic development thus points to the cultivation of large proportions of the land surface and over-grazing as probable causes underlying the disappearance of ameiva, curly-tailed lizards and racers from La Désirade. Although the timing is not yet clear, the extirpation of the rice rat may also have been affected by these alterations which, in addition to other factors (Pinchon, 1967; Turvey et al., 2010), led to its disappearance. The prominent role of agriculture-induced land degradation does not however exclude other, as yet unidentified factors acting in concert, favouring extirpation of some species more than others. The complexity of the faunal response is illustrated by the persistence on the island of an endemic skink species, *M. desiradae* (Paré and Lorvelec, 2012), which is also a carnivorous ground species (Vitt and Blackburn, 1991; Malhotra and Thorpe, 1999; Henderson and Powell, 2009). The persistence of this species thus underscores the complicated combination and interaction of factors involved in the disappearance of the taxa. This complexity is also well illustrated by the wide range of responses to human activity seen with endemic West Indian fauna between all the Lesser Antillean Islands , with La Désirade being a prime example of how geographic and historic particularities directly impact insular ecosystems.

In conclusion, evidence for extinctions dating to the first few centuries following the initial European colonisation of the West Indies strongly suggests that human-induced extirpations were more important in the Lesser Antilles than the picture painted by 19th or early 20th century naturalists. This is consistent with a recent study of securely dated fossil bones of birds and a reptile on Abaco in the Bahamas by Steadman et al. (2014). Moreover, the case of La Désirade also highlights the non-negligible impact of historic societies on local faunal communities, an aspect that had until now remained largely undocumented. Here we have shown the efficiency of an approach where the causes of disappearance of endemic species are sought in the specific ecological factors of each island. In the case of La Desirade, one of the factors is a topography favouring substantial cultivation, a characteristic more reminiscent of the larger islands with a history of large plantations, rather than the small West Indian islands. In this respect, questions can be raised as to the part played by historic and ecological processes in the extinction of endemic fauna of Saint-Lucia, Martinique, Guadeloupe, or Marie-Galante in which the archaeological approach advocated here is likely to provide a significant contribution.

Acknowledgments

We thank Jean-Baptiste Mallye and Alain Queffelec (PACEA, University of Bordeaux) for their participation to fieldwork reported here and helpful comments. We also want to thank the ONF and Ms Montout for permission to excavate in the protected area of Pointe Gros Rempart. This research was possible thanks to the financial support of the BIVAAG Program established by the CNRS with support from a European PO-FEDER grant 2007–2013 no2/2.4/-33456, the collective programme of research (PCR) *Cavités naturelles de Guadeloupe*, the Guadeloupe Regional Council, the DEAL of Guadeloupe, and the DAC of Guadeloupe.

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https://doi.org/10.1016/j.yqres.2015.11.001 Published online by Cambridge University Press