



Insights into Holocene megafauna survival and extinction in southeastern Brazil from new AMS ^{14}C dates

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ABSTRACT

The extinction of late Quaternary megafauna in South America has been extensively debated in past decades. The majority of the hypotheses explaining this phenomenon argue that the extinction was the result of human activities, environmental changes, or even synergism between the two. Although still limited, a good chronological framework is imperative to discuss the plausibility of the available hypotheses. Here we present six new direct AMS ^{14}C radiocarbon dates from the state of São Paulo (Brazil) to further characterize the chronological distribution of extinct fauna in this part of South America. The new dates make evident that ground sloths, toxodonts, and saber-toothed cats lived in the region around the Pleistocene/Holocene transition, and, in agreement with previous studies, also suggest an early Holocene survival for the ground sloth *Catonyx cuvieri*. Taken together with local paleoclimatic and archaeological data, the new dates do not support hunting or indirect human activities as a major cause for megafauna extinction. Although more data are required, parsimony suggests that climatic changes played a major role in this extinction event.

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Introduction

The cause of late Quaternary megafauna extinction has been contested since the 19th century (Grayson, 1984; Koch and Barnosky, 2006; Borrero, 2008; Rule et al., 2012), and current hypotheses explaining this process range from factors such as environmental changes to human activities, or even synergy between these two (see Koch and Barnosky, 2006 for a review). Despite the growing number of studies, relatively little attention has been paid to the South American case (Borrero, 2008, 2009), even though this continent lost more megafauna genera during this period than any other continent (Barnosky and Lindsey, 2010).

Nevertheless, the available studies based on South America data show a diverse range of hypotheses. For instance, Brazilian megafaunal records have been used to argue that the extinction occurred at the very end of the Pleistocene due to the cold and dry conditions of the last interglacial period (Cartelle, 1999). Ecuadorian data, on the other hand, suggest that increased aridity followed by high humidity and specific geographic factors during the end of the

Pleistocene and beginning of the Holocene were major conditions responsible for this extinction event (Ficcarelli et al., 2003). De Vivo and Carmignotto (2004) contrasted extant and extinct South American and African mammal faunas and suggested that the increase in the proportion of closed vegetation physiognomies in response to a more humid climate (associated with the end of the Pleistocene and the Holocene) resulted in the extinction of large-sized mammal lineages adapted to open landscapes.

Against this background, Steadman et al. (2005) compiled chronological data from the Americas, concluding that human hunters were the pivotal cause for the extinction of sloths in South America at the end of the Pleistocene. Other studies (Cione et al., 2003, 2009) proposed that under a scenario of shortage of preferential habitats (resulting from climatic fluctuations related to the last interglacial period), megafauna species were more prone to extinction, primarily due to human hunting. Barnosky and Lindsey (2010) also favor a synergistic effect between humans and climate changes, arguing that human impact coupled with rapid climate change at the end of the Pleistocene and beginning of Holocene motivated the extinctions. Finally, it has been suggested that this extinction could be related to the action of new pathogens (Ferigolo, 1999), providing yet another possibility for the extinction of megafauna in South America.

The myriad models used to explain the South American late Quaternary mammal extinction clearly demonstrate the lack of consensus

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regarding the processes of this disappearance. This is largely due to the lack of well-defined chronological distributions for megafauna species (Hubbe et al., 2007, 2009; Barnosky and Lindsey, 2010). Considering Brazil, for instance, although the megafaunal chronological framework has been substantially improved in the past decade (Rossetti et al., 2004; Auler et al., 2006; Neves et al., 2007; Hubbe et al., 2009, 2011), it is still developing and limited to a few regions of the country (Auler et al., 2006). Herein is presented six new direct AMS ^{14}C dates from two cave sites in São Paulo State (SE Brazil), a rich paleontological region with only two AMS dates reported so far, that will contribute to the growth of these chronologies. Based on these dates, it is possible to determine which extinct species inhabited the region around the Pleistocene/Holocene boundary. Furthermore, when combined with paleoclimatic and archeological data, these new dates contribute to the discussion of the possible processes for local megafauna extinction.

Sample context

The samples dated in this study were recovered from caves located in the Upper Ribeira River karst, in southern São Paulo State. The karst developed in Middle Proterozoic low-metamorphosed limestones of the Açungui Group (Ribeira Fold Belt) and it lies in the transition zone between the Atlantic Plateau (800–1200 m a.s.l.) and the Coastal plains, with altitudes reaching 600 m a.s.l. This karstic system stands out for its steep hydraulic gradient, significant allogenic recharge and incised underground drainage with vadose canyons up to 80 m deep, where vertical caves and huge collapse halls are common. Polygonal karst outcrops with blind valleys characterize the surface.

The initial studies of the Upper Ribeira karst date to the early 20th century, done by German naturalist Richard Krone who investigated local caves in search of paleontological, archaeological and ethnological material. The results of his studies were published in “Exploração do Rio Ribeira de Iguape”, published by the Geographic and Geological Commission in 1914. Later, Krone (1950) recounted the discovery of 41 caves where he found bones of extinct megafauna and called attention to the natural beauty of the region.

The fossil remains dated here were collected in two caves: Abismo do Fossil and Abismo Iguatemi, both near the city of Iporanga (Fig. 1). The entrance of the Abismo do Fossil cave is a 100–150 m radius

sinkhole of a centripetal drainage of an ancient polygonal closed depression. The cave is composed of a main vertical pit of 45 m and two subhorizontal passages, one at the bottom and another in an upper level. The latter is currently connected to the bottom of a small doline. Abismo do Fossil was discovered in 1976, during speleological explorations of the Iporanga karst area. During cave surveying, several large bones were documented on the surface of the sediments. In 1977, a group of geologists, biologists and students conducted a systematic excavation of the main sedimentary deposits of this cave, applying archeological techniques in order to locate material and observe the deposit's stratigraphy (Lino et al., 1979). All the material recovered during this project is housed at the Museu de Zoologia, Universidade de São Paulo.

Abismo Iguatemi's entrance is the sinkhole of a blind valley developed along the contact zone between the cave limestone and underlying phyllites. The cave is also mainly vertical, with a 16-m pit that is connected to an inclined passage at the bottom (Fig. 2). Abismo Iguatemi was discovered and surveyed in 1999 (Ferreira and Karmann, 2002). The dated material was collected from the surface of the sediment during this survey and is housed at the Instituto de Geociências, Universidade de São Paulo. A more systematic excavation was conducted later (Castro and Langer, 2011), but materials from that excavation are not included in this study.

In both caves clastic sediments are very poorly sorted, and coarse angular material (boulder to granule size) is found together with finer sediments (sand to silt size) of dark brown color, rich in organic matter (humus) and clay, characterizing a breccia facies. The input of these breccias was mainly by gravitational process, representing a mixture of clastic material from the caves (breakdown debris) together with sediment washed from the surface into the sinkholes. Portions of these materials were preserved in depressions along the floor and walls of these cave passages. The sediment characteristics suggest that recurrent storm events reworked cave deposits as well as flushed new sediment and water into cave passages. Fossil remains were found wherever sediments accumulated (see Fig. 2 and Table 1 for details). Extinct fossil remains were found together with extant species. From Abismo do Fossil, faunal remains were found representing extinct taxa: *Glyptodon*, *Toxodon*, Tardigrada (ground sloths) and extant ones: Didelphidae, Dasipodidae, Atelidae, Felidae, Canidae, Mustelidae, Cervidae, Tayassuidae, Chiroptera and Rodentia (Lino et al., 1979).

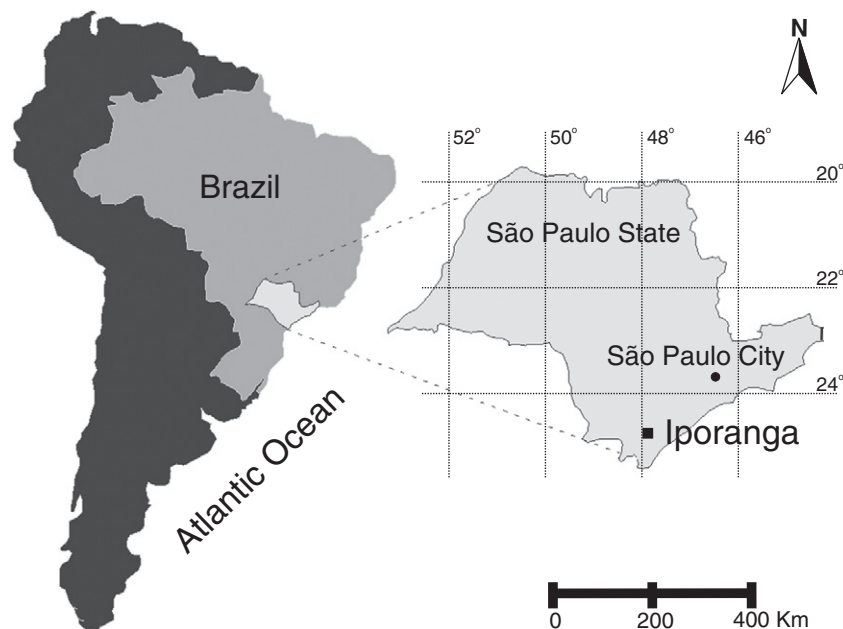


Figure 1. Map indicating São Paulo and Iporanga (detail), where Abismo Iguatemi Cave and Abismo do Fossil Cave (SP-145) are located.

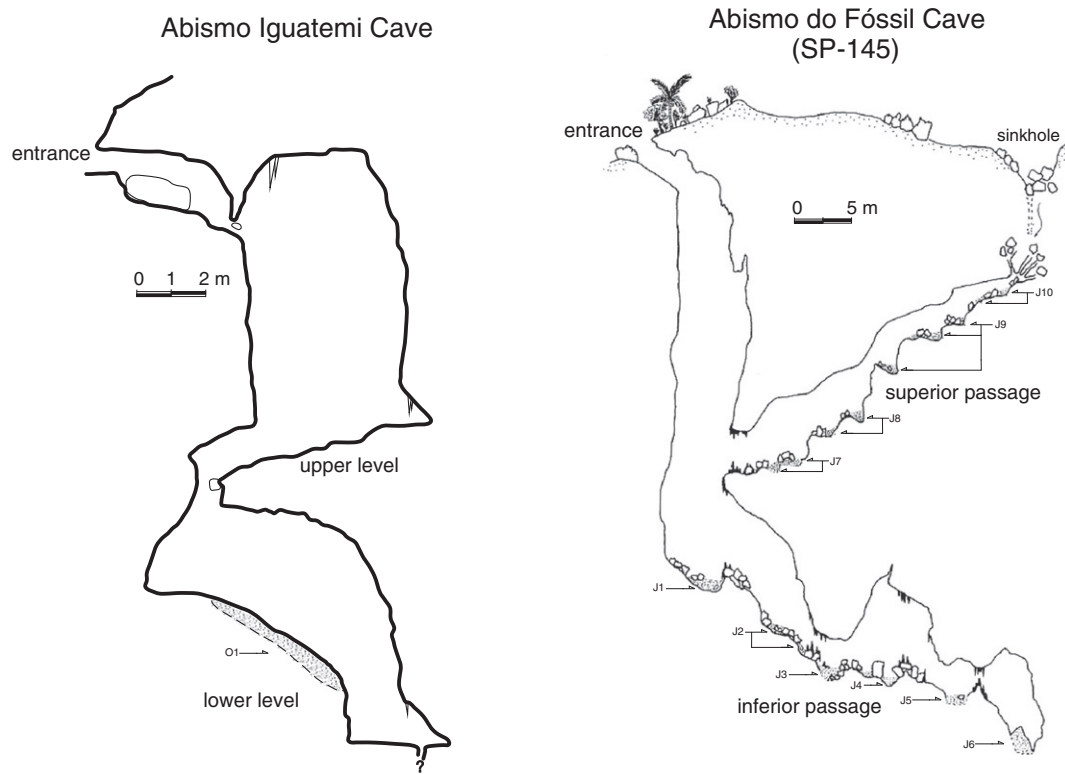


Figure 2. Schematic cross section of Abismo Iguatemi Cave (adapted from Ferreira and Karmann, 2002) and Abismo do Fossil Cave (SP-145; adapted from Lino et al., 1979). Dense spotted areas (highlighted by arrows; the acronym beside each arrow identifies stratigraphic locations) in the lower level of Abismo do Iguatemi Cave and in both passages of Abismo do Fossil Cave represent the areas where sediments were found.

From Abismo Iguatemi, remains of Marsupialia, Xenarthra, Carnivora, Chiroptera, Primates, Artiodactyla and Rodentia were recovered, including the extinct genera *Catonyx*, *Smilodon* and *Glyptodon* (Castro and Langer, 2011).

Four radiocarbon dates from Abismo do Fossil Cave were obtained: one undetermined ground sloth species (Tardigrada), one *Toxodon platensis*, one *Eremotherium laurillardi* and one Scelidotheriinae. Hubbe et al. (2011) recently reported a radiocarbon date for one *Glyptodon clavipes* from the same cave. The dated remains from the Abismo do Iguatemi Cave come from one *Smilodon populator* and one *Catonyx cuiveri*, both found at the lower level of the cave.

Methods

Bone samples were collected from the fossil collections of the Museu de Zoologia and the Instituto de Geociências, Universidade de São Paulo, Brazil, with the help of a dental drill. Bone collagen samples were dated by Accelerator Mass Spectrometry (AMS ^{14}C) at the Beta Analytic Radiocarbon Dating Laboratory (Miami, Florida, USA)

Table 1
AMS ^{14}C dates obtained from two cave localities at Iporanga, Southern São Paulo, Brazil.

Sample	Laboratory #	Taxon	Common name	Skeletal element dated ^a	Cave name	Species stratigraphic location ^b	$\delta^{13}\text{C}\text{‰}$	Conventional age (^{14}C yr BP)	2σ calibration (cal yr BP)
GP/2E-706 ^c	BETA230974	<i>Catonyx cuiveri</i>	ground sloth	rib	Abismo Iguatemi	O1	-22.7	10,800 ± 60	12,860–12,580
GP/2E-716 ^c	BETA183566	<i>Smilodon populator</i>	saber-toothed cat	skull	Abismo Iguatemi	O1	-18.3	14,580 ± 90	18,030–17,260
MZSP-PV454 ^d	BETA237347	<i>Toxodon platensis</i>	toxodont	tooth	Abismo do Fossil	J3, J4, J5, J8, J9	-23	11,850 ± 70	13,860–13,460
MZSP-PV610 ^d	BETA237348	<i>Eremotherium laurillardi</i>	ground sloth	tooth	Abismo do Fossil	J4	-21.5	12,550 ± 60	15,130–14,240
MZSPV773 ^d	BETA246245	Tardigrada	ground sloth	vertebra	Abismo do Fossil	J6	-22.7	15,230 ± 70	18,680–18,060
MZSP-PV642 ^d	BETA237349	Scelidotheriinae	ground sloth	vertebra	Abismo do Fossil	J2, J3, J4	-21.4	15,780 ± 80	19,310–18,710

^a Material dated: collagen. Treated with multiple alkali extractions and ultra-purified prior to dating.

^b Please see Fig. 2 for stratigraphic locations.

^c Housed at Instituto de Geociências, Universidade de São Paulo, Brazil.

^d Housed at Museu de Zoologia, Universidade de São Paulo, Brazil.

using their laboratory protocols for collagen extraction and dating. According to the $^{13}\text{C}/^{12}\text{C}$ ratio obtained, the measured date was corrected to the conventional age (radiocarbon years before present; ^{14}C yr BP). These dates were then calibrated in accordance with Reimer et al. (2009). The two-sigma calibration age interval was generated using Calib 6.0 (based on the IntCal09 calibration curve; <http://calib.qub.ac.uk/calib/calib.html>; Stuiver and Reimer, 1993) and is presented as calibrated years before present (cal yr BP).

Results

The new radiocarbon dates from Abismo do Fossil Cave and Abismo Iguatemi Cave are presented in Table 1. They range from approximately the last glacial maximum (LGM) to the very end of the Pleistocene, between ~19.3 and 12.5 cal kyr BP. The ages are within the span of the available direct radiocarbon dates for megafaunal remains from the Brazilian territory (see Hubbe et al., 2011 and references therein).

Discussion and conclusions

Continental chronological context

All genera dated for this study have less than four direct radiocarbon dates reported in South America, and the new data presented in Table 1 significantly improve our knowledge of their chronological distribution in the region and in the continent as a whole. The date obtained for *Eremotherium* (15,130–14,240 cal yr BP; 12,550 ± 60 ¹⁴C yr BP; BETA 237348) is around 1–2 thousand years older than the youngest direct date available for this giant ground sloth (from Pará State, Brazil; ~13,000 cal yr BP; Rossetti et al., 2004). The other direct date available for this genus comes from Bahia State, Brazil, and is ~19,000 cal yr BP (Drehfal, 2010). The first two *Eremotherium*'s ages show that this widespread ground sloth species (Cartelle and De Juliis, 2006) was still living in different regions of Brazil (more than 2000 km apart) during the last few millennia of the Pleistocene. The date of 13,860–13,460 cal yr BP (11,850 ± 70 ¹⁴C yr BP; BETA 237347) obtained for *Toxodon* is similar to the only other direct date (~13,000 cal yr BP; Neves et al., 2007) available for this genus. Both ages were assessed on fossils from the Iporanga region and they indicate that this species might have survived in Southeast Brazil till at least the very end of the Pleistocene. The date obtained for the *Smilodon* (18,030–17,260 cal yr BP; 14,580 ± 90 ¹⁴C yr BP; BETA 183566) is the oldest in relation to the other two published dates available for this genus in South America (from Minas Gerais State, Brazil; ~10,500 and ~12,700 cal yr BP; Neves and Piló, 2003; Hubbe et al., 2009).

The date obtained for the *Catonyx cuvieri* of 12,860–12,580 cal yr BP (10,800 ± 60 ¹⁴C yr BP; BETA 230974) is the latest one available for the megafauna in the southern portion of Brazil. In addition, Neves and Piló (2003) reported for Minas Gerais State, Brazil, three dates for this species. Two are dated to around 17,000 cal yr BP (however, it is unclear whether the samples dated belong to a single specimen or not) and another dates to the Pleistocene/Holocene transition (~10,900 cal yr BP). Based on the latter, the authors suggested that this species survived until the Holocene. Following the rationale that last appearance dates likely reflect the last moments that the animals were abundant and that a few dates per species is simply not sufficient to properly constrain the age of a particular species' last appearance (Signor-Lipps effect; Signor and Lipps, 1982; Barnosky and Lindsey, 2010), the date at the very end of the Pleistocene for the São Paulo specimen gives further support to an early Holocene survival for this species and expands its late occurrence southwards.

Furthermore, this new result is consistent with a growing body of evidence that at least some megafauna genera, such as the saber-toothed cat (*S. populator*; Neves and Piló, 2003; Hubbe et al., 2009), survived into the early Holocene in Brazil. These results also indirectly reinforce Holocene survival for megafauna in other South American regions as well (Cione et al., 2001; Rossello et al., 2001; Hubbe et al., 2007; Messineo and Politis, 2009; Steele and Politis, 2009; Cruz et al., 2010).

Table 1 also shows that some undetermined ground sloth genera (Tardigrada; 18,680–18,060 cal yr BP; 15,230 ± 70 ¹⁴C yr BP; BETA 246245; and Scelidotheriinae; 19,310–18,710 cal yr BP; 15,780 ± 80 ¹⁴C yr BP; BETA 237349) inhabited São Paulo State between ~18,500 and 19,000 cal yr BP. Finally, there is a date for *Glyptodon* (21,530–20,620 cal yr BP; 17,800 ± 70 ¹⁴C yr BP; BETA 237350) reported by Hubbe et al. (2011) from Abismo do Fóssil that is the sole direct date for this genus in Brazil and attests that it lived at least until the LGM in São Paulo State. Besides this date, there are two other direct dates from elsewhere in South America. The first comes from Venezuela, dated to ~30,000 cal yr BP (Jull et al., 2004), and the other is a disputed Argentinean fossil age of ~5,000 cal yr BP (Cione et al., 2001; Rossello et al., 2001).

Megafaunal extinction in SE Brazil

Before this study, only two fossil specimens were directly dated from São Paulo State (Neves et al., 2007; Hubbe et al., 2011) and together with the new dates presented here they offer the first glimpse of which extinct species were actually present in São Paulo at the end of the Pleistocene. It is possible to envision, for instance, a landscape inhabited by ground sloths (*Catonyx* and *Eremotherium*), toxodonts and saber-toothed cats near the Pleistocene/Holocene transition. Although these few dates are not enough to confidently determine the dates of last appearance of the extinct megafauna in São Paulo, it is likely, following the Signor-Lipps effect (Signor and Lipps, 1982; Barnosky and Lindsey, 2010), that all dated species survived into later moments indicating that *C. cuvieri* and perhaps *T. platensis* became extinct during the early Holocene. If this holds true, the new data from São Paulo State agree with previous studies that suggest that extinction processes in South America lasted until the Holocene (Ficcarelli et al., 2003; Cione et al., 2009; Barnosky and Lindsey, 2010).

Also, considering the knowledge of human occupation in the region, there is no support for *Homo sapiens* being the major cause of this local fauna extinction as suggested continentally by Steadman et al. (2005), Cione et al. (2003, 2009) and Barnosky and Lindsey (2010). The earliest evidence for hunter-gatherers presence in the area is a small occupation at the Maximiliano Rockshelter (Collet, 1985), which was dated to 11,720–10,770 cal yr BP (9,810 ± 150 ¹⁴C yr BP; GIF-7493; McCormac et al., 2004). Not much is known about these first human groups in the region and their behavior towards megafauna is not clear. The spatiotemporal data, however, insert these groups into the Umbu archaeological tradition, which is characterized by highly mobile generalist hunter-gatherers that exploited different environments, including dense sub-tropical forests (Neves et al., 2004). Since Umbus show no evidence of megafauna exploitation, their potential association with this tradition argues against a specialization in large-sized mammal hunting in the area.

Considering the overall South American scenario, there is a generally low density of human occupations during late Pleistocene/early Holocene, when groups were very mobile and covered large territories to fill their subsistence needs (Dillehay, 2008). The population density of early South Americans probably began to change only around 10,000 cal yr BP when more permanent settlements started to appear in distinct regions of the continent (e.g., Piperno and Stothert, 2003; Araujo et al., 2008; Dillehay, 2008; among others). However, population density in São Paulo inland probably increased only during the Holocene, in association with shellmound builders (Neves et al., 2005), who seem to have replaced or assimilated the early groups. Although the peak of this occupation is seen on the coast only around 6800 cal yr BP, the earliest inland date for a shellmound is 10,160–9610 cal yr BP (8860 ± 60 ¹⁴C yr BP; Beta 153988; McCormac et al., 2004). Recently, Eggers et al. (2011) suggested, based on stable isotope analysis of the oldest human skeleton from the region (10,160–9610 cal yr BP; 8860 ± 60 ¹⁴C yr BP; Beta 153988), that the inland shellmound groups had a diet focused on C₃ plants and land animals without much access to marine protein sources. However, none of the inland or coastal shellmound archaeological records show evidence of interaction with extinct megafauna species (Collet, 1985; Collet and Loebel, 1988; Neves and Okumura, 2005; Neves et al., 2005; Eggers et al., 2011). In fact, it is argued that early humans in São Paulo were not specialized megafauna hunters (Neves and Okumura, 2005), and this can be generalized to South America (Borrero, 2009).

The only evidence of behavioral interaction between humans and megafauna in São Paulo State comes from a single *Toxodon platensis* tooth found at the Abismo Ponta de Flecha Cave (Barreto et al., 1982) that was recently dated to ~13,000 cal yr BP (Neves et al., 2007). This tooth does not present signs of major post-depositional alterations and shows apparent cutmarks on its root, a portion of

the tooth that would have been inside the massive jaw of the animal in life. The location of the apparent cutmarks, but also the fact that only this piece among several bones/teeth found shows cutmarks, are not consistent with patterns observed for food processing in ethnographic and archaeological contexts (Walker, 1978; Lupo, 2002; Lyman, 2005).

Therefore, for the moment it is more parsimonious to assume that these alleged cutmarks are the byproduct of scavenging rather than hunting by humans and cannot be considered reliable evidence of co-existence between humans and megafauna in the region, since humans can have scavenged remains significantly older than themselves. In the rest of South America, in spite of the coexistence of megafauna and early hunter-gatherers, no evidence of systematic interaction between them is found in the archaeological record (Borrero, 2009). Although the lack of evidence of interactions has been used both to favor and to deny human related extinction hypotheses (Mosimann and Martin, 1975; Grayson and Meltzer, 2003; Koch and Barnosky, 2006; Cione et al., 2009), the lack of evidence in São Paulo coupled with the non-specialized hunting of local human groups favors the argument that killing was not a major cause behind local megafauna extinction.

In contrast, climate in subtropical Brazil shows strong variability from the LGM to the Holocene, and is marked by abrupt fluctuations in precipitation that are synchronous with changes recorded in the northern hemisphere (Cruz et al., 2009). The climate at the LGM (~21 ka) is considered to have been as wet as it is today based on arboreal pollen records that indicate the dominance of forests characterized by species adapted to a cold and wet climate (Pessenda et al., 2009). This scenario is also supported by speleothem records (Cruz et al., 2005, 2006). A speleothem record from Santana cave, which is located in the same area as the dated fossils, shows an abrupt climate transition from glacial to the Holocene period that is marked by a very humid event between 18 and 15.5 ka. This is probably the most intense precipitation oscillation recorded in the last glacial/interglacial cycle over the region and is coincident with the Heinrich Stadial 1 event. In the study area, this event is interrupted by a dryer phase between 15.5 and 13 ka and followed by a large wet phase between 13 and 11.5 ka that are considered to be a response to the Bolling-Allerod and Younger Dryas events over precipitation in South America (Cruz et al., 2006). The abrupt nature of these millennial precipitation events may have characterized a rapid shift from dense to open forests, as attested for other part of the São Paulo State (Ledru et al., 2005). Moreover, these rapid humidity alternations were the largest observed during the last 120 ka and were also observed in different regions of South America (Cheng et al., 2012). The speleothems also suggest that climate conditions during the early to mid Holocene were relatively dryer than during the late Holocene and Younger Dryas. Unfortunately, information regarding past temperature oscillations are still incipient for this region.

Although shifts in humidity are considered an important factor in climate related extinction hypotheses, especially by relating it with changes in vegetation physiognomies (Cartelle, 1999; Ficarelli et al., 2003; De Vivo and Carmignotto, 2004), the regional climate during the transition from LGM to Holocene changed differently from the scenarios portrayed in the available hypotheses (at least locally). Climate-related extinction hypotheses are mostly criticized due to the fact that the most recent deglaciation conditions were not different from previous glacial/interglacial periods and therefore they do not, by themselves, explain why megafauna went extinct only at the last event (Koch and Barnosky, 2006; Cione et al., 2009). Nevertheless, one aspect that deserves further attention is the impact of the extraordinarily fast alternation between wet and dry phases observed in São Paulo region and in most of the South American continent from 20 to 10 ka (Cruz et al., 2009; Cheng et al., 2012) in shaping the local ecosystem.

In spite of the disagreement between the paleoclimatic data and the climate-driven extinction hypotheses, we suggest that climate must have played a major role at least in the extinction of local megafauna,

since 1) it is known that climate varied markedly between 20 and 10 ka and to some extent differently from previous glacial/interglacial cycles from the last 120 ka; 2) the archaeological record of the region does not show evidence of specialized extinct megafauna hunters occupying the territory during the Pleistocene/Holocene in concert with the lack of evidence of close interaction between humans and megafauna regionally and also suggests that human occupations were at low density during this time period; 3) Nogues-Bravo et al. (2010) suggested a larger proportion of megafaunal extinctions occurred in continents that experienced the most intense climatic changes, implying, at least on a global scale, that climate variation played a major role in this fauna's disappearance; and 4) in a recent study analyzing human fossil records, several species distribution models and ancient DNA, Lorenzen et al. (2011) concluded that the extinction of some analyzed species could be driven solely by climatic changes.

However, understanding the mechanism of how climate changes might have promoted these extinction events is still incipient (Koch and Barnosky, 2006), but it is probably associated with complex changes and interactions at different organizational levels (i.e., genome, individuals, populations, communities, ecosystems) and is perhaps related to larger time spans than just the LGM. One example of this complexity, recently proposed, is the idea that widespread species (like *Smilodon*, *Toxodon*, *Catonyx* and *Eremotherium*), when in small isolated populations (due to climatic changes), would be more prone to extinction than species that are usually characterized by small isolated populations (i.e., are less threat tolerant; Waldron, 2010). With the data presented here we cannot add anything to discussion about pathogen actions on megafauna extinction (Ferigolo, 1999), but we concur with Koch and Barnosky's (2006) view that hyper-disease hypotheses are very unlikely.

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