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The Brazilian megamastofauna of the Pleistocene/Holocene transition and its relationship with the early human settlement of the continent

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ABSTRACT

One of the most intriguing questions regarding the Brazilian Late Quaternary extinct megafauna and *Homo sapiens* is to what extent they coexisted and how humans could have contributed to the former's extinction. The aim of this article is to review the chronological and archaeological evidences of their coexistence in Brazil and to evaluate the degree of direct interaction between them. Critical assessment of the Brazilian megafauna chronological data shows that several of the late Pleistoscene/early Holocene dates available so far cannot be considered reliable, but the few that do suggest that at least two species (*Catonyx cuvieri*, ground sloth; *Smilodon populator*, saber-toothed cat) survived until the beginning of the Holocene in Southeast Brazil. Archaeological data indicates that the first human groups arrived in Brazil and were inhabiting this region during the last millennia of the Pleistocene and, consequently, they coexisted with the extinct fauna in some parts of Brazil for at least one thousand years. There is no robust evidence favoring any kind of direct interaction between humans and megafauna prior to their extinction. To date, it is not possible to properly judge the indirect influence of humans (landscape transformation, introduction of predators, among others) in this extinction event. Intense and to some extent unique climate changes between the Last Glacial Maximum and the Holocene favors the interpretation that they had a major contribution to the megafauna extinction, although the scarcity of data impedes the proper testing of this hypothesis.

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1. Introduction

When the first human groups arrived in the Americas, they encountered a vast diversity of large sized mammals (late Quaternary extinct megafauna; hereafter just megafauna), nowadays extinct, that inhabited the continent until the very end of the Pleistocene and in some places the beginning of the Holocene (Barnosky et al.,

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2004). In North America, distinct cultures systematically hunted this fauna (Haynes, 1995; Waguespack, 2007). In South America, despite the growing evidence that early humans coexisted with at least some of the extinct fauna's species for a few millennia (Barnosky and Lindsey, 2010; Hubbe et al., 2007, 2009), evidences of hunting are scant (Borrero, 2009).

Here, we review the evidence supporting the chronological coexistence between humans and megafauna in the Brazilian territory, as well as the archaeological evidence of direct interaction between them. Only incipient information on these subjects is available for Brazil, but when complemented with existing data for other regions of South America (especially Argentina), it can contribute to the growing body of evidence favoring a chronological overlap between the first South Americans and some megafauna species and to the discussion of the possible causes for the extinction of this fauna.

2. Megafauna context

2.1. Brief overview

Systematic paleontological studies of Brazilian megafauna began during the 1830 s with the excavations of the Danish paleontologist Peter Wilhelm Lund (Lund, 1840; Cartelle, 1999). Following Lund's pioneer work, there were significant advances in paleontological studies in the country and, as a result, extensive knowledge regarding the taxonomy and geographic distribution of several species is currently available (Paula Couto, 1979; Cartelle, 1999; Cartelle et al., 2009; Ghilardi et al., 2011). From the more than 50 genera of large mammals that became extinct in South America (Martin and Steadman, 1999), the Brazilian records present over 25. However, despite the large number of Quaternary fossils deposited in museum collections, only a small fraction of these was retrieved from paleontological excavations with some type of stratigraphic control (Kipnis, 1998; Hubbe et al., 2011a). This is especially limiting because most of our knowledge about Brazilian megafauna comes from cave deposits (Auler et al., 2006), which present complex sedimentary accumulation processes (Neves and Piló, 2003; Auler et al., 2006, 2009; Hubbe et al., 2011a), further limiting any contextualization of the fossils recovered from them.

Consequently, most of the Brazilian paleontological collections available to date allow only for taxonomic and descriptive studies. Critical data about the spatiotemporal distribution of these extinct animals cannot be addressed due to the lack of reliable stratigraphic information, hindering the research of relevant topics such as: the synchronism (or lack thereof) of the megafauna extinction at the Pleistocene/Holocene transition (Cartelle, 1999); the survival of some groups into the middle Holocene (Baffa et al., 2000; but see Neves et al., 2007); the type of social organization of these animals (Cartelle and Bohorquez, 1982; Rossetti et al., 2004); and the reason(s) behind the extinction of the megafauna (Ferigolo, 1999; de Vivo and Carmignotto, 2004; Cartelle et al., 2009; Hubbe et al., in press).

2.2. Spatiotemporal distribution

Table 1 and Fig. 1 show the chronological data available in the literature based on ^{14}C (radiocarbon), U/Th (uranium/thorium) on calcite speleothems and TL (thermoluminescence) methods for the Brazilian megafauna. Although ESR (electron spin resonance) and U/Th on bone dates are available as well (e.g. Vialou et al., 1995; Baffa et al., 2000; Kerber et al., 2011), they are not considered here since they still lack the reliability of the other methods (Skinner, 2000; Auler et al., 2006; Neves et al., 2007). The dates presented are either direct (i.e. age determined on the fossil material), correlative (i.e. age determined on material other than the fossil but in the same stratigraphic layer) or minimum ages (i.e. age determined on material other than the fossil but younger than it by stratigraphic correlation). Table 1 demonstrates the paucity of the spatiotemporal data record for the Brazilian megafauna: only 33 dates are available for the entire country, and they come from only a few states (Fig. 2), despite the widespread occurrence of this fauna in the Brazilian territory (e.g. Cartelle, 1999; Rossetti et al., 2004; Holanda and Cozzuol, 2006; Ribeiro and Scherer, 2009; Hubbe et al., 2011b). From the states with chronological data, Minas Gerais alone has almost one third of the existing megafauna's dates. Also, the chronology available is mainly restricted to fossils recovered from cave deposits. Other types of late Quaternary fossil sites (e.g., floodplains, cacimbas, caldeirões, lagoon-barrier systems; Cartelle, 1999; Rossetti et al., 2004; Scherer et al., 2007) are almost not represented in the paleontological chronological record.

Available fossil ages range from mid Pleistocene to early Holocene, even though most dates (27) are younger than the Last Glacial Maximum (LGM). Of special interest are the dates between the very end of the Pleistocene and the Holocene, since they are within the time span of the human occupation of the country (see chronology of human occupations below). However, most of these dates have to be seen with caution. When the available dates are accessed critically, most cannot be held as undeniable proof of the temporal coexistence between humans and megafauna (i.e. are not reliable evidence of late survival of megafauna specimens).

From the four correlative dates presented here (all within the end of the Pleistocene and the Pleistocene/Holocene boundary) only one is considered reliable by us: the 20.2–12.2 ka for an *Eremotherium* (ground sloth) from Bahia. Similar ages were obtained from three distinct calcite speleothem layers, one above, one across and one below the fossil, which constrained the age to the interval reported (Auler et al., 2006). Nevertheless, the age interval is relatively wide and therefore cannot be used to attest the coexistence between humans and megafauna. The other three correlative dates, although retrieved from excavations with stratigraphic and chronological control, suffer from uncertainties related to the complexity of cave deposits (Auler et al., 2006, 2009; Hubbe et al., 2011a). According to Prous (2002) the association of the few *Catonyx* remains found at Lapa Vermelha IV, Minas Gerais, to the same stratigraphic level of the charcoal dated to 11,400–10,270 cal yr BP could be accidental. Since only few bones (and not an articulated or well represented specimen) were found, possible explanations to the potential (and probable) spurious association between bones and charcoal are as follow: (1) different taphonomic agents could have caused both vertical and horizontal movement of the fossil material (e.g. Andrews, 1990; Lyman, 1994; Araujo and Marcelino, 2003; Kos, 2003), placing those few remains near the dated sample (or vice-versa); and (2) caves are very active environments usually presenting reworking events of the sediments (and consequently fossils; Auler et al., 2009; Hubbe et al., 2011a). These associations would be harder to refute, if the fossil found was articulated or at least well represented and if the charcoal was retrieved from a structured hearth, since this would indicate that neither bones nor charcoals dislocated significantly after deposition in the site.

Similarly, the date of 11,990–11,400 cal yr BP on a fireplace's charcoal at the same stratigraphic level of few bones and hundreds of osteoderms from a *Glossotherium* at Santa Elina Rock Shelter, Mato Grosso, is not considered reliable by us, since a typical animal would have many bones and thousands of osteoderms and only those few remains were found at this level. Actually, bones from the same species (and possibly from the same specimen) were found in deeper levels of the excavation, probably older than 20 cal kyr BP (Vialou et al., 1995). Lastly, Faure et al. (1999) argued for a Holocene age (between ~7.6 and 9.7 cal kyr BP) for several megafauna taxa based on soil organic matter concentration ^{14}C dates at the top and the bottom of a fossiliferous facies at Toca do Serrote do Artur, Piauí. However, this evidence can also be questioned in two ways. Firstly, most species are represented by scant material found not only within the facies dated, but also below it. Thus, the same

Table 1
Available dates for the Late Quaternary Brazilian megafauna.

Taxon	Common name	State[a]	Environment	Method	Material dated	Date interval[b]	Originally proposed date category	Reference
Eremotherium	Ground sloth	AM	Fluvial	^{14}C	Collagen	13,330–13,110	Direct	Rossetti et al. (2004)
Haplomastodon	Mastodont	AM	Fluvial	^{14}C	Collagen[c]	18,330–18,120	Direct	Rossetti et al. (2004)
Nothrotherium	Ground sloth	BA	Cave	U/Th	Speleothem	14,570–13,260[d]	Minimum	Auler et al. (2006)
Nothrotherium	Ground sloth	BA	Cave	^{14}C	Dung	14,860–13,770	Direct	Czaplewski and Cartelle (1998)
Nothrotherium	Ground sloth	BA	Cave	U/Th	Speleothem	15,410–14,660[d]	Minimum	Auler et al. (2006)
Eremotherium	Ground sloth	BA	Cave	U/Th	Speleothem	20,000–12,200[e]	Correlative	Auler et al. (2006)
Eremotherium	Ground sloth	BA	Tanque	^{14}C	Collagen	19,280–18,730	Direct	Drehfal (2010)
Palaeolama	Paleolama	MG	Cave	U/Th	Speleothem	>450,000	Minimum	Auler et al. (2006)
Smilodon	Saber-toothed cat	MG	Cave	^{14}C	Collagen	11,080–10,160	Direct	Neves and Piló (2003)
Catonyx	Ground sloth	MG	Cave	^{14}C	Charcoal	11,400–10,270	Correlative	Laming-Emperaire et al. (1975), Prous (2002)
Catonyx	Ground sloth	MG	Cave	^{14}C	Collagen	11,690–11,270	Direct	Neves and Piló (2003)
Smilodon	Saber-toothed cat	MG	Cave	^{14}C	Collagen	12,850–12,570	Direct	Hubbe et al. (2009)
Catonyx	Ground sloth	MG	Cave	U/Th	Speleothem	125,570–122,230	Minimum	Auler et al. (2006)
Valgipes	Ground sloth	MG	Cave	^{14}C	Collagen	13,090–12,710	Direct	Hubbe et al. (2009)
Hoplophorus	Glyptodont	MG	Cave	U/Th	Speleothem	15,560–14,140	Minimum	Auler et al. (2006)
Catonyx	Ground sloth	MG	Cave	^{14}C	Collagen	17,390–16,800[f]	Direct	Neves and Piló (2003)
Equus	Horse	MG	Cave	^{14}C	Collagen	19,870–19,420[g]	Direct	Neves and Piló (2003)
Catonyx	Ground sloth	MG	Cave	U/Th	Speleothem	30,500–23,700	Minimum	Auler et al. (2006)
Palaeolama	Paleolama	MG	Cave	U/Th	Speleothem	327,860–294,880[d]	Minimum	Auler et al. (2006)
Hoplophorus, Pampatherium	Glyptodont, Armadillo	MG	Cave	U/Th	Speleothem	80,750–47,680[d]	Minimum	Auler et al. (2006)
Glossotherium	Ground sloth	MT	Cave	^{14}C	Charcoal	11,990–11,400	Correlative	Vialou et al. (1995)
Hippidium, Palaeolama, Pampatherium, Toxodon, Catonyx	Horse, Paleolama, Armadillo, Toxodont, Ground sloth	PI	Cave	^{14}C	Charcoal	12,530–10,750	Minimum	Guérin et al. (1996)
Hoplophorus, Glyptodon, Palaeolama, Propraopus	Glyptodont, Glyptodont, Paleolama, Armadillo	PI	Cave	^{14}C	Organic matter	7910–7610	Correlative	Faure et al. (1999)
Glossotherium	Ground sloth	RS[h]	Fluvial	^{14}C	Probably collagen	16,340–14,190	Direct	Miller (1987), Ribeiro, pers. comm., 2011
Pampatherium,Glyptodon, Propraopus, Macrauchenia, Hippidion, Hemiauchenia	Armadillo, Glyptodont, Armadillo, Long llama, Horse, Long llama	RS[h]	Fluvial	TL	Sediment	15,580–14,080	Minimum	Scherer et al. (2007), Kerber and Oliveira (2008a)
Catonyx	Ground sloth	SP	Cave	^{14}C	Collagen	12,860–12,580	Direct	Hubbe et al. (in press)
Toxodon	Toxodont	SP	Cave	^{14}C	Collagen	13,120–12,770[d]	Minimum[i]	Neves et al. (2007)
Toxodon	Toxodont	SP	Cave	^{14}C	Collagen	13,860–13,460	Direct	Hubbe et al. (in press)
Eremotherium	Ground sloth	SP	Cave	^{14}C	Collagen	15,130–14,240	Direct	Hubbe et al. (in press)
Smilodon	Saber-toothed cat	SP	Cave	^{14}C	Collagen	18,030–17,260	Direct	Hubbe et al. (in press)
Tardigrada	Ground sloth	SP	Cave	^{14}C	Collagen	18,680–18,060	Direct	Hubbe et al. (in press)
Scelidotheriinae	Ground sloth	SP	Cave	^{14}C	Collagen	19,310–18,710	Direct	Hubbe et al. (in press)
Glyptodon	Glyptodont	SP	Cave	^{14}C	Collagen	21,530–20,620	Direct	Hubbe et al. (2011b)

[a] States are as follow: AM: Amazonas; BA: Bahia; MG: Minas Gerais; MT: Mato Grosso; PI: Piauí; RS: Rio Grande do Sul; SP: São Paulo.
[b] Date interval presented here is as follows: for ^{14}C dates, the two sigma calibration date interval; for U/Th and TL, the date obtained added and subtracted the associated error. The two sigma ^{14}C calibrated age interval was generated using Calib 6.0html (http://calib.qub.ac.uk/calib/calib.html; Stuvier and Reimer, 1993).
[c] May contain exogenous carbon (Rossetti et al., 2004).
[d] More than one date was originally presented for the same specimen. Only the youngest one is shown here.
[e] three ages are reported by Auler et al. (2006) for this specimen. The date presented here is the one based on the calcite speleothem found across the fossil (Auler et al., 2006; pp. 517).
[f] Two similar dates were presented by Neves and Piló (2003) for this species at the same locality. Due to uncertainties about if the same specimen was dated twice or if two different specimens were dated, only the younger date for the species and locality is shown here.
[g] Four similar dates were presented by Neves and Piló (2003) for this species (or Family) at the same locality. Due to uncertainties about if the same specimen was dated four times or if several different specimens were dated, only the younger date for the species and locality is shown here.
[h] Other dates are available for the fauna from Rio Grande do Sul, but there is a general lack of congruence between dates obtained for the same deposit or correlative formation, therefore we decided not to include them here (see Scherer et al., 2007; Kerber and Oliveira, 2008a, 2008b; Ribeiro and Scherer, 2009 for more information about the available dates).
[i] Although the date reported here could be a direct date (Neves et al., 2007; Hubbe et al., in press), under a conservative approach should be considered as a minimum age.

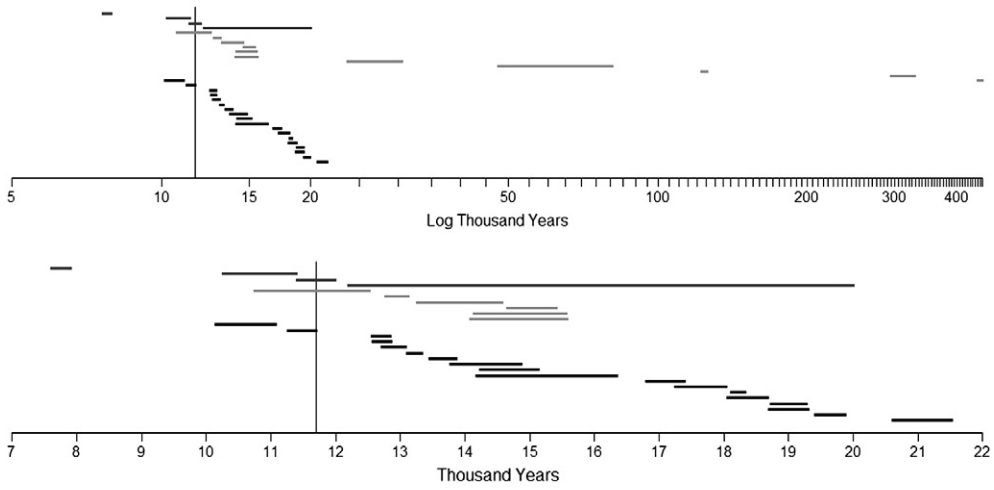

Fig. 1. Brazilian megafauna chronological dispersion. The vertical line indicates the limit between the Pleistocene and Holocene. Each horizontal line represents a date interval. For details refer to Table 1. Dark grey lines: correlative dates; light grey lines: minimum dates; black lines: direct dates.

rationale presented above for Santa Elina applies here. Secondly, ^{14}C dates based on organic matter are not as reliable as on other materials (Mead and Meltzer, 1984; Pessenda et al., 2001; Barnosky and Lindsey, 2010). Therefore, a more conservative approach is recommended and the dates for the fossils found at Toca do Serrote do Artur should be considered minimum ages.

Minimum ages, even when they fall within the Holocene/Pleistocene transition, also cannot be used to determine the last dated appearance (LDA) of megafaunal species, since they are not associated with a maximum age for the fossils. In other words, even when minimum ages are within the period of human presence in Brazil, the real age of the fossil might be considerably older than the human arrival. Consequently, they cannot be used for the discussion of human and megafauna interaction. In summary, from the 33 dates presented in Table 1, we rely solely on the 18 direct dates (besides the one acceptable correlative date) to discuss the LDAs of the Brazilian megafauna. The small number of direct dates per species in each region is a major drawback, since it hampers the detection of outliers and the precise determination of the LDAs (Barnosky and Lindsey, 2010). Also, even though the majority of the direct dates were obtained on reliable materials (i.e., collagen and dung; Mead and Meltzer, 1984; Barnosky and Lindsey, 2010) and they reached the standards of ^{14}C dating protocols (e.g. well preserved collagen, acceptable values for the $\delta^{13}C$), most of them are based on isolated bones (or specimens; but see Hubbe et al., 2009, 2011a). This substantially limits the possibility of generating chronological contexts for the fossiliferous packages from where the specimens were recovered and makes the correlation of the date with other fossils of the same package very unreliable.

Despite all these limitations, the data available suggests that some species survived into the Pleistocene/Holocene transition and beginning of the Holocene, and consequently shared the Brazilian territory with the first local human groups. Two species have direct dates in this time interval: the saber-toothed cat (*Smilodon populator*), with a specimen from Minas Gerais dated to 11,080–10,160 cal yr BP; and a ground sloth (*Catonyx cuvieri*) with a specimen from the same state dated to 11,690–11,270 cal yr BP (Neves and Piló, 2003). Since we are advocating a very cautious approach to the acceptance of evidence of megafauna and human coexistence, it could be argued that these dates were biased by contaminants and are, therefore, not reliable. However, we do not believe this is the case mainly due to three reasons:

First, there is no a priori reason to suspect of the quality of the dates obtained, since the material dated reached the standards of the radiocarbon dating laboratory (among other things they provided plenty of well-preserved collagen and provided $\delta^{13}C$ values in accordance to the expectations). Secondly, following the rationale that LDAs likely reflect the last moments that animals were abundant and that a few dates per species are 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 existence of other dates for these species from distinct localities with slightly older ages support the early Holocene ages: a ^{14}C date of 12,850–12,570 cal yr BP for a *Smilodon* from Minas Gerais and another of 12,860–12,580 cal yr BP for a *Catonyx* from São Paulo (Hubbe et al., 2009, 2011a, 2013). This argument is strengthened by (1) the fact that the *Smilodon* dated was retrieved from excavations with rigid stratigraphic control and the age obtained is in accordance with the stratigraphic position where it was found (Hubbe et al., 2009, 2011a), and (2) the samples from the two *Smilodon* and two *Catonyx* were collected in distinct localities and had similar dates. This could be because the specimens truly died around the Pleistocene/Holocene transition or because the four different places suffered the effects of contaminants that coincidently biased the dates of animals that died at different times to a similar age. Although it is possible to speculate different situations where contaminants were responsible for the dates obtained it is safe to assume the very likely possibility that the ages are correct. Thirdly, and following the same argumentation presented above, there are Holocene dates for other megafauna species in other places of South America as well, making the late Brazilian Holocene dates not unique when seen in a continental perspective (Hubbe et al., 2007; Messineo and Politis, 2009; Barnosky and Lindsey, 2010; Cruz et al., 2010; but see Steele and Politis, 2009 for updated non Holocene ages for the megafauna at Arroyo Seco 2, and Cione et al., 2001; Rossello et al., 2001 for a dispute about a mid-Holocene megafauna age).

In short, compelling evidence exists favoring the idea of a Holocene megafauna survival in Brazil (more specifically in Minas Gerais and São Paulo) for at least *C. cuvieri* and *S. populator*. In virtue of the scarcity of dates and the fact that they do not probably represent accurate LDAs for the species (Barnosky and Lindsey, 2010), one can speculate that these species survived even further. Following the same logic, it is possible to envisage that *Eremotherium*, *Valgipes* (ground sloth) and *Toxodon* (toxodont), whose current LDAs are in the late Pleistocene, might have also survived until the Pleistocene/Holocene transition, although plenty of new dates will be required to evaluate this hypothesis. Finally, with the scant number of dates available, it is not possible at this moment to evaluate (1) if megafauna species survived into the Holocene in all the Brazilian territory or only in some regions and (2) the abundance of these species prior to their extinction. They could either be suffering a slow reduction in population size for a relatively long period of time, which means that near the extinction they

Fig. 2. State names and schematic location of the Brazilian sites with dates for megafaunal remains.

were quite scarce in the landscape, or their population size could have declined abruptly in the last few millennia of their existence. Despite the preponderance of this information to explain the reason(s) of their extinction, nothing can be assumed about it at the present, and additional efforts in generating reliable chronological contexts will be of uttermost significance to further understand the fate of this fauna.

2.3. Megafauna ecology

The Brazilian megafauna is usually described as inhabiting predominantly open vegetation physiognomies, such as savannas, and the majority of the species are considered herbivores (e.g., giant sloths, toxodonts, glyptodonts, mastodonts, horses, palaeolamas, some armadillos) with few carnivores or omnivores (saber-toothed cat, bears, dogs, some armadillos; Cartelle, 1999; Rancy, 1999; de Vivo and Carmignotto, 2004; Rossetti et al., 2004; Prevosti and Vizcaíno, 2006; Asevedo et al., 2012). However, this description might be oversimplistic for some species. MacFadden (2005) for example argued based on dietary preferences that *Toxodon platensis* inhabited distinct biomes, ranging from dense forested areas to grasslands. Also Hubbe et al. (2013) attested the presence of some genera (*Glyptodont* and *Smilodon*) in São Paulo State during relatively humid and forested phases of the end of the Pleistocene. Some authors also suggested that ground sloths species might have been opportunist flesh eaters or even carnivores (Farina, 1996; Farina and Blanco, 1996; but see Prevosti and Vizcaíno, 2006 for a different point of view).

Besides that, it is hard to understand how the megafauna species were inserted in the ecosystems (e.g., habitat and food preferences, abundance, general behavior, interaction with other species), because ecological data for the Brazilian megafauna is scant. Part of this deficiency is due to a local research tradition focused on the description of new species, definition of their geographic distribution and understanding of their phylogenetic relationships, a situation also seen in other parts of South America (Bargo, 2003). To this limitation, we add the fact that most of the extinct megafauna species do not exhibit a modern analogue, which impedes the reconstruction of their habits based on extant species correlatives (Vizcaino et al., 2009).

More specifically, regarding the species that are known to have (or potentially have) temporally coexisted with the first Brazilians, it is suggested that *S. populator* preyed on large mammals (100–1000 kg; Prevosti and Vizcaíno, 2006) and lived in open areas (Turner and Anton, 1997; Vizcaino et al., 2009), even though it could have lived in more forested areas too (Hubbe et al., in press). Based on studies of a close related species (*S. fatalis*), it is even possible that *S. populator* could have been social animals (Van Valkenburgh et al., 2009).

The ground sloth *Catonyx* is usually described as a bulk feeder (Toledo, 1998; Rancy, 1999), but studies with a close related species suggest it was a selective feeder (Bargo et al., 2006). Moreover, it is probable that this species had the ability to dig the substrate to

some extension (Bargo et al., 2006). Due to its widespread geographic distribution (from Rio Grande do Sul in South Brazil to Ceará in Northeast Brazil; Ghilardi et al., 2011) it is possible that *Catonyx* inhabited diversified habitats, including more forested biomes. Although little information is available for *Valgipes*, its morphological resemblance to *Catonyx* (Cartelle et al., 2009) suggests that it probably had broad similar ecological attributes.

The other ground sloth that potentially coexisted in time with *Homo sapiens* in Brazil was *Eremotherium*. Rossetti et al. (2004) proposed that this species probably lived in diversified habitats and was a selective feeder. Based on their findings and especially on the report of Cartelle and Bohorquez (1982) these authors sustain the idea that this species might have had gregarious social behavior. However, this idea rests on Cartelle and Bohorquez's (1982) finding of *Eremotherium*'s specimens in a pitfall conduct without a good chronological contextualization. Since it is unfeasible to estimate the amount of time the deposit was actively receiving faunal remains, it is possible that they represent the accumulation of specimens over a relatively long period of time rather than a single event of several animals dying simultaneously (see also discussion in Hubbe and Auler, 2012). Lastly, *Toxodon* probably had different diets and habitats in accordance to its geographic location (MacFadden, 2005). Therefore, since this species shows a wide distribution in Brazil (Ghilardi et al., 2011), it probably inhabited different habitats throughout the country. Furthermore, *Toxodon* is considered semi-aquatic by some authors (see a brief discussion in MacFadden, 2005).

This information illustrates well the uncertainties regarding the ecology of these extinct mammals, which makes any reconstruction of their life habits a rather precarious enterprise. As will be stressed out below, this severely hinders the discussion about their extinction.

3. Human context

3.1. The settlement of South America and initial occupation of the Brazilian territory.

The initial occupation of South America dates to at least ~14.5 cal kyr BP (Dillehay et al., 2008; Dillehay, 2009; Rothhammer and Dillehay, 2009) with the Pacific coast showing the earliest accepted archaeological evidence for human groups on the continent (Sandweiss et al., 1998; Dillehay, 2000; Dillehay et al., 2008). Early accepted human evidence on the continent is common in the Pacific rim and Andean regions (Dillehay, 2008), although there is no doubt that by ~13 cal kyr BP most of the continent was already occupied (Salemme and Miotti, 2003), with groups dwelling in forest environments (Roosevelt et al., 1996; Guidon et al., 1998), bushy savannahs (Correal, 1990; Araujo and Feathers, 2008; Araujo et al., 2008) and cold and semi-arid steppes and plains (Steele and Politis, 2009; Bayón et al., 2011).

In the Brazilian territory, the archaeological scenario fits perfectly well the continental perspective. Although some sites older than ~15 cal kyr BP have been reported, their age are still contested by most archaeologists (see Prous and Fogaça, 1999 for a review). However, evidence of human occupation in the last millennia of the Pleistocene has been reported in Northern (Amazonia; Silveira, 1994), Northeastern (Piauí; Parenti, 1993), Central-Western (Mato Grosso; Vialou et al., 1995; Goiás; Barbosa, 1991), Southeastern (Minas Gerais; Prous, 1986) and possibly Southern Brazil (Rio Grande do Sul; Miller, 1987).

These early settlements differ considerably from those described for North America (Dillehay, 2000, 2009; Rothhammer and Dillehay, 2009), and were probably occupied by generalized Hunter-Gatherers, with a life style characterized by low population density, high mobility with short-term stays, preference for favorable habitats and seasonal exploitation of diverse resources (Prous and Fogaça, 1999; Dillehay, 2008). Coastal groups might have shown a further specialization toward maritime exploitation, but Pleistocene coastal occupations are only known in the Pacific rim of the continent (Sandweiss et al., 1998; Dillehay, 2000), since the Pleistocene Atlantic shores are now submerged (Martin et al., 1988; Angulo and Lessa, 1997). The life-style of early South Americans probably changed around 10,000 cal yr BP when more permanent settlements started to appear in distinct regions of the continent (e.g., Dillehay et al., 2003; Piperno and Stothert, 2003; Arriaza et al., 2008; Araujo et al., 2008; Dillehay, 2008; among others). This shift, that predates the domestication of plants and animals in South America, probably involved the establishment of logistic centres around which mobile groups organized themselves (Dillehay, 2008). These can be seen as the precursors of the diverse local cultural traditions that developed during the middle Holocene.

3.2. Human–megafauna interaction

The possible window of interaction between human groups and megafauna refers to the Pleistocene's final millennia and Holocene's first few millennia, when human presence in the continent was probably still represented by groups of small size and high mobility (Prous and Fogaça, 1999; Dillehay, 2008). In the Brazilian territory as well as in South America, there are very few evidences of human groups interacting directly with the extinct megafauna (Borrero, 2009). In Brazil, all evidences of interaction between human groups and megafauna are associated to the finding of individual (or very few) bones or bone fragments that have either been found in human occupation levels (or near archaeological evidences) or that show marks that suggest their usage by human hunters. However, few of those, if any, can be considered as reliable evidence of interaction and are probably spurious associations of elements at a same stratigraphic level or do not show unequivocal human made marks (see below). Details about most of these cases can be found in Prous (2002), and for this reason we present here only a brief summary.

In South Brazil, Miller (1987) and Marshall et al. (1984) reported the finding of extinct megafauna specimens (*Glossotherium, Scelidotherium, Pampatheirum, Glyptodon, Toxodon* and *Equus*) associated to stratigraphic levels with the presence of stone tools or human remains. However, the suggested association is due to general proximity with the remains and there is no evidence of real interaction. Prous (2002) discarded these findings as reliable evidence of human and megafauna interaction or even of coexistence. In Southeast Brazil (São Paulo), Barreto et al. (1982) found cut marks in bone fragments of a cave deposit that they associate to humans. Among these fragments, they report a *Toxodon platensis*' pre-molar with cut marks near to its root base. This tooth was dated to between 5 and 6.7 ka by ESR (Baffa et al., 2000), but this date has been shown to be unreliable (Neves et al., 2007). Also, the alleged cut marks are located in a place that is not consistent with butchering, and have been considered questionable for this reason as evidence of direct interaction (i.e. not considering scavenging on already defleshed carcasses; Prous, 2002; Hubbe et al., in press).

In the Lagoa Santa region, despite the presence of megafauna species lasting into the Holocene, there is no clear evidence of human and megafauna interaction. Prous (2002) discussed the case of a gomphothere's iliac that appears to have cut marks that are consistent with butchering activities, as well as fractures that were potentially caused by blunt strikes to recover bone shards for tools. However, the specimen was found in a site that shows no human activity whatsoever and part of the cut marks are covered by rodent gnawing marks. Moreover, the interpretation presented by Prous is not a consensus (Prous, 2002; pp. 54). Consequently, the author recommended caution before accepting this specimen as evidence of human–megafauna interaction. In Mato Grosso, Vialou et al. (1995) reported the finding of *Glossotherium* remains associated to stone tools in a level dated to around 11.5 cal kyr BP. As discussed before, the correlative date is questionable. However, Vialou et al. (1995) also describes one perforated osteoderm, which the authors suggest might be the result of human action. Prous (2002) questioned

this interpretation by suggesting that it could be the result of small invertebrates, reported to produce similar marks in non-archaeological contexts (e.g., Dominato et al., 2009).

In Northeast Brazil (Piauí State), Guidon (1989) reported the association between megafauna remains (*Eremotherium*, mastodonts and horses) and human tools in rockshelters at the São Raimundo Nonato region. However, again there is no evidence of use of the megafauna remains and the chronological association between them is not certain (Prous, 2002). Also, in Pernambuco State, associations between megafauna and stone tools have been reported, but the material came from a site that is the result of erosion from nearby lagoon shores, and the stratigraphic association is not certain (Prous, 2002). Recently an *Eremotherium*'s tooth recovered in Sergipe State was reported as presenting human cut marks (Dantas et al., 2012). However, the evidence has been questioned due to the nature and location of the marks and the lack of archaeological and paleontological context of the finding (Hubbe et al., 2012).

The only evidence of human–megafauna interaction that is considered unquestionable by Prous (2002) is a *Glossotherium* humerus recovered from a paleontological context in Bahia State: "the specimen shows unquestionable marks of human action done while the bone was still fresh" (Prous, 2002; pp. 55), and was subsequently abandoned and carried into the cave by the action of water. The bone also presents many impact marks as a result of its transport inside the cave as well as rodent gnawing marks covering part of the human cut marks. However, even if this represents an undeniable evidence of human–megafauna interaction, the fact that it was recovered in a paleontological context precludes any discussion about the nature of this interaction.

In summary, despite the fact that at least in some regions some megafauna species survived into the Pleistocene/Holocene transition and beginning of the Holocene, the absence of reliable evidence of humans interacting with this fauna, suggests that if human groups exploited megafauna species it was in a very sporadic and opportunistic way. This situation is not peculiar to the Brazilian territory. Borrero (2009) reviewed the reports of megafauna and human interaction in South America and concluded in a continent-wide level that, besides the chronological overlap between megafauna extinction and first human arrival (sometimes of thousands of years), only in a few cases did this coexistence lead to some interaction. Similar to the Brazilian scenario, the South American record for human–megafauna interaction is uneven and in most cases reports of associations between them are unreliable. Even in the regions where more information is available, namely the Argentine Pampas, evidence of interaction is uncommon and extant species have a much higher presence in early archaeological sites than the megafauna taxa (Politis et al., 1995; Borrero, 2009).

4. Final remarks

This review about the pieces of evidence of the coexistence between megafauna and *H. sapiens* in the Brazilian territory served two purposes: 1) to show that research on this topic is still very incipient in the country and that most of the available data to date is rather unreliable to properly discuss human and megafauna coexistence; and 2) to demonstrate that even with such scant data there is evidence suggesting that at least two extinct megafauna genera (*Smilodon* and *Catonyx*) survived into the Holocene. Human settlements in the same area of the late megafauna findings have been dated to the Pleistocene/Holocene boundary, suggesting that humans coexisted with megafauna for no less than one thousand years. Indeed, this situation is not exclusive to Brazil and fits perfectly well the scenario observed in other countries of South America (Barnosky and Lindsey, 2010).

Even in face of the limitation of the data, the existence of such relatively long coexistence in Brazil between humans and megafauna may shed some light on the role of humans in the extinction of the late Pleistocene megafauna. The discussion about this fauna extinction dates back to the beginning of the 19th century (Grayson, 1984) and the available hypotheses can be divided in two major categories: one arguing that the extinction was driven by environmental changes (usually related to climate changes) and another suggesting that *H. sapiens* had a decisive role in the extinction, either directly (hunting) or indirectly (e.g., landscape alteration, introduction of predators and/or diseases). Some authors also argue for a model combining both factors (see Koch and Barnosky, 2006, for general descriptions about late Quaternary extinction hypotheses. For discussions about late Quaternary extinction in Brazil and South America, see Cartelle, 1999; Ferigolo, 1999; Cione et al., 2003; Ficcarelli et al., 2003; Araujo et al., 2004; de Vivo and Carmignotto, 2004; Steadman et al., 2005; Hubbe et al., 2007, in press; Cione et al., 2009; Barnosky and Lindsey, 2010).

The data reviewed here do not favor, at least on a regional scale, hypotheses that consider specialized hunting an important factor in megafauna extinction (e.g., Steadman et al., 2005; Cione et al., 2009). On the contrary, as described above, the data supports the available South American archaeological evidence that there is no empirical support for humans hunting megafauna systematically (Borrero, 2009). Moreover, if the suggestion that human density was very low during the final millennia of the Pleistocene is correct (Prous and Fogaça, 1999; Dillehay, 2008), the role of human groups as an indirect agent on megafauna extinction due to landscape modification and predators/competitors introduction (and the degree of its synergistic effect with climate changes on this extinction as suggested by Barnosky and Lindsey, 2010) cannot be supported. However, studies on the actual density of human occupation during this period and their impact on the landscape are still very preliminary and future work will be required to properly test this idea.

Although more data is required to fully comprehend the ecology (autoecology and sinecology) of the extinct fauna, which would help to understand the effects of climate changes toward them, it is known that climate in South America changed markedly over the past 20 thousand years (Cruz et al., 2006; Vimeux et al., 2009; Barnosky and Lindsey, 2010; Cheng et al., 2012). It is argued here, therefore, that these climatic changes probably had a major contribution to the megafauna disappearance. Nevertheless, as pointed out by Barnosky and Lindsey (2010), in some cases there is no straightforward association between major climatic changes and LDAs of megafauna species in South America (some species survived for relatively long periods after major climatic shifts). One explanation for this mismatch could be that relatively widespread megafauna species (like *Smilodon*, *Toxodon*, *Catonyx*, *Eremotherium*) suffered major population decline during more intense climatic shifts, but retained some long lasting isolated populations (for example, hypothetically in São Paulo and Minas Gerais). These once widespread populations, while reduced and isolated, were more prone to extinction than the usual (less thread tolerant; Waldron, 2010) and later minor climatic changes could have led them to extinction. Consequently, there is no need to expect that extinction would immediately follow major climatic changes. In fact, the mechanisms through which climate changes might have triggered this extinction event are poorly understood (Koch and Barnosky, 2006) and might even be species-specific (Lorenzen et al., 2011).

It is generally argued, though, that climate changes during the transition from the LGM to the Holocene were not different from previous glacial/interglacial periods and consequently would not justify the extinction by itself (Koch and Barnosky, 2006; Cione et al., 2009). However, there was an unusual fast alternation between wet and dry phases between ~20 and 10 ka in most of the South American continent that differs from previous events (Cruz et al., 2009; Cheng et al., 2012) and could be related to the megafauna extinction. However, further research on this topic is required before this

humidity fluctuation can be properly related to the disappearance of megafauna in South America. Moreover, theoretically it is also possible that the extinction process had its foundations in previous and successive glacial/interglacial periods. Evolutionary processes act upon population variability (Darwin and Wallace, 1858; Darwin, 1859; Wright, 1931) and sequential glacial/interglacial periods might have been shaping those lineages in such a way that they succumbed between the LGM and Holocene.

In conclusion, the empirical data available to date for Brazil supports the chronological coexistence between *H. sapiens* and megafauna but does not support a major direct influence of humans on its demise. Despite the data pointing toward a coexistence of megafauna and humans for at least a thousand years in Brazil, archaeological evidence shows a general lack of systematic exploitation of megafauna in all Brazilian sites (Prous, 2002). Even in the few sites in South America where interaction between humans and megafauna is unequivocal, small and medium sized extant fauna still had a much more preponderant role in the subsistence of these groups (Politis et al., 1995; Borrero, 2009). The scant available archaeological evidence suggests that, during the initial human occupation of the continent, population density was low and human groups had a very mobile strategy, with a diversified diet, and colonized a variety of ecological zones (Prous and Fogaça, 1999; Dillehay, 2008). It is not clear the degree of the impact of these groups in the local ecosystems and therefore it is hard to properly address the indirect influence of humans on the megafauna extinction. On the other hand, climate changed markedly during the end of the Pleistocene and Holocene and to some extent in an unusual way, favoring the idea that climate had a major contribution to this extinction event.

Evidently, further efforts in generating more reliable chronological framework for megafauna in the country as well as the identification of new early sites with potential evidence of human–megafauna interaction and better understanding of climate changes during the period of interest will certainly reshape and refine the conclusions drawn here. Nonetheless, the fact that the Brazilian record suggests the same scenario seen in other regions of the continent strengthens the general conclusion that humans did not play a major direct role in the process of local megafauna extinction.

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References

Andrews, P., 1990. Owls, Caves, and Fossils. University of Chicago Press, Chicago.
Angulo, R.J., Lessa, G.C., 1997. The Brazilian sea level curves: a critical review with emphasis on the curves from Paranaguá and Cananéia regions. Marine Geology 140, 141–166.
Araujo, A.G.M., Feathers, J.K., 2008. First Notice of Open-Air Paleoamerican Sites at Lagoa Santa: Some Geomorphological and Paleoenvironmental Aspects, and Implications for Future Research. Current Research in the Pleistocene 25, 27–29.
Araujo, A.G.M., Marcelino, J.C., 2003. The role of armadillos in the movement of archaeological materials: an experimental approach. Geoarchaeology 18, 433–460.
Araujo, A.G.M., Neves, W.A., Pilo, L.B., 2004. Vegetation changes and megafaunal extinction in South America: comments on de Vivo and Carmignotto. Journal of Biogeography 31, 2039–2040.
Araujo, A.G.M., Feathers, J.K., Arroyo-Kalin, M., Tizuka, M.M., 2008. Lapa das boleiras rockshelter: stratigraphy and formation processes at a paleoamerican site in Central Brazil. Journal of Archaeological Science 35, 3186–3202.
Arriaza, B., Standen, V.G., Cassman, C., Santoro, C.M., 2008. Chinchorro culture: pioneers of the coast of the Atacama Desert. In: Silvermann, H., Isbell, W.H. (Eds.), Handbook of South American Archaeology. Springer, New York.
Asevedo, L., Winck, G.R., Mothe, D., Avilla, L.S., 2012. Ancient diet of the Pleistocene gomphothere *Notiomastodon platensis* (Mammalia, Proboscidea, Gomphotheriidae) from lowland mid-latitudes of South America: Stereomicrowear and tooth calculus analyses combined. Quaternary International 255, 42–52.
Auler, A.S., Piló, L.B., Smart, P.L., Wang, X., Hoffmann, D., Richards, D.A., Edwards, R.L., Neves, W.A., Cheng, H., 2006. U-series dating and taphonomy of Quaternary vertebrates from Brazilian caves. Palaeogeography, Palaeoclimatology, Palaeoecology 240, 508–522.
Auler, A.S., Smart, P.L., Wang, X., Piló, L.B., Edwards, R.L., Cheng, H., 2009. Cyclic sedimentation in Brazilian caves: mechanisms and palaeoenvironmental significance. Geomorphology 106, 142–153.
Baffa, O., Brunetti, A., Karmann, I., Neto, C.M.D., 2000. ESR dating of a toxodon tooth from a Brazilian karstic cave. Applied Radiation and Isotopes 52, 1345–1349.
Barbosa, A., 1991. A Tradição Itaparica: Uma compreensão ecológica e cultural do povoamento inicial do planalto central brasileiro. In: Meggers, B. (Ed.), Prehistoria de Sulamerica — Nuevas perspectivas, pp. 145–160.
Bargo, M.S., 2003. Biomechanics and palaeobiology of the Xenarthra: the state of the art (Mammalia, Xenarthra). Senckenbergiana Biologica 83, 41–50.
Bargo, M.S., Toledo, N., Vizcaino, S.F., 2006. Muzzle of South American Pleistocene ground sloths (Xenarthra, Tardigrada). Journal of Morphology 267 (2), 248–263.
Barnosky, A.D., Lindsey, E.L., 2010. Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. Quaternary International 217, 10–29.
Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L., Shabel, A.B., 2004. Assessing the causes of Late Pleistocene extinctions on the continents. Science 306, 70–75.
Barreto, C., De Blasis, P., Dias Neto, C., Lino, C., Robrahn, M., 1982. Abismo Ponta de Flecha: um projeto arqueológico e geológico no médio Ribeira de Iguape, São Paulo. Revista de Pré-História 4, 195–220.
Bayón, C., Manera, T., Politis, G., Aramayo, S., 2011. Following the tracks of the first South Americans. Evolution: Education & Outreach 4, 205–217.
Borrero, L.A., 2009. The elusive evidence: the archeological record of the South American extinct megafauna. In: Haynes, G. (Ed.), American Megafaunal Extinctions at the End of the Pleistocene. Springer, New York, pp. 145–168.
Cartelle, C., 1999. Pleistocene mammals of the Cerrado and Caatinga of Brazil. In: Eisenberg, J.F., Redford, K.H. (Eds.), Mammals of the Neotropics — The Central Neotropics. University of Chicago Press, Chicago, pp. 27–46.
Cartelle, C., Bohorquez, G.A., 1982. Eremotherium laurillardi Lund, 1842: Parte I. Determinação específica e dimorfismo sexual. Iheringia 7, 45–63.
Cartelle, C., De Iuliis, G., Ferreira, R.L., 2009. Systematic revision of tropical Brazilian scelidotheriine sloths (Xenarthra, Mylodontoidea). Journal of Vertebrate Paleontology 29, 555–566.
Cheng, H., Sinha, A., Wang, X., Cruz, F.W., Edwards, R.L., 2012. The Global Paleomonsoon as seen through speleothem records from Asia and the Americas. Climate Dynamics 39, 1045–1062.
Cione, A.L., Figini, A.J., Tonni, E.P., 2001. Did the megafauna range to 4300 bp in South America? Radiocarbon 43, 69–75.
Cione, A.L., Tonni, E.P., Dondas, A., 2003. The broken Zig-zag: Late Cenozoic Large Mammal and Turtle Extinction in South America, 5. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", pp. 1–19.
Cione, A.L., Tonni, E.P., Soibelzon, L., 2009. Did humans cause the late Pleistocene–early Holocene mammalian extinctions in South America in a context of shrinking open areas? In: Haynes, G. (Ed.), American Megafaunal Extinctions at the End of the Pleistocene. Springer, New York, pp. 125–144.
Correal, G., 1990. Evidencias culturales durante el Pleistoceno y Holoceno de Colombia. Evidencias culturales durante el Pleistoceno y Holoceno de Colombia. Revista Arqueo American 1, 33–68.
Cruz, F.W., Burns, S.J., Karmann, I., Sharp, W.D., Vuille, M., 2006. Reconstruction of regional atmospheric circulation features during the late Pleistocene in subtropical Brazil from oxygen isotope composition of speleothems. Earth and Planetary Science Letters 248, 494–507.
Cruz, F.W., Wang, X., Auler, A., Vuille, M., Burns, S.J., Edwards, R.L., Karmann, I., Cheng, H., 2009. Orbital and millennial-scale precipitation changes in Brazil from speleothem records. In: Vimeux, F., Sylvestre, F., Khodri, M. (Eds.), Past Climate Variability in South America and Surrounding Region: From the Last Glacial Maximum to the Holocene. Springer, New York, pp. 29–60.
Cruz, L.E., Bargo, S.M., Tonni, P.E., Figini, J.A., 2010. Radiocarbon date on megafauna from the late Pleistocene–early Holocene of Cordoba province, Argentina: stratigraphic and paleoclimatic significance. Revista Mexicana de Ciencias Geologicas 27, 470–476.
Czaplewski, N.J., Cartelle, C., 1998. Pleistocene bats from cave deposits in Bahia, Brazil. Journal of Mammalogy 79, 784–803.
Dantas, M.A.T., de Queiroz, A.N., Vieira dos Santos, F., Cozzuol, M.A., 2012. An anthropogenic modification in an Eremotherium tooth from northeastern Brazil. Quaternary International 253, 107–109.
Darwin, C.R., 1859. On the Origin of the Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.
Darwin, C.R., Wallace, A.F., 1858. On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. Journal of the Proceedings of the Linean Society of London. Zoology 3, 45–62.
de Vivo, M., Carmignotto, A.P., 2004. Holocene vegetation change and the mammal faunas of South America and Africa. Journal of Biogeography 31, 943–957.
Dillehay, T.D., 2000. The Settlement of the Americas: A New Prehistory. Basic Books, New York.
Dillehay, T.D., 2008. Profiles in Pleistocene history. In: Silvermann, H., Isbell, W.H. (Eds.), Handbook of South American Archaeology. Springer, New York.
Dillehay, T.D., 2009. Probing deeper into first American studies. Proceedings of the National Academy of Sciences of the United States of America 106, 971–978.

Dillehay, T.D., Rossen, J., Maggard, G., Stacketback, K., Netherly, P., 2003. Localization and possible social aggregation in the Late Pleistocene and Early Holocene on the north coast of Peru. Quaternary International 109–110, 3–11.
Dillehay, T.D., Ramírez, C., Pino, M., Collins, M.B., Rossen, J., Pino-Navarro, J.D., 2008. Monte Verde: seaweed, food, medicine, and the peopling of South America. Science 320, 784–786.
Dominato, V.H., Mothé, D., Avilla, L.S., 2009. Ação de insetos em vértebras de Stegomastodon waringi (Mammalia, Gomphotheriidae) do Pleistoceno de Águas de Araxá, Minas Gerais, Brasil. Revista Brasileira de Paleontologia 12, 77–82.
Drehfal, M., 2010. Implicações paleoambientais preliminares da análise de d13C em osso de paleomastofauna procedente de Quijingue, Bahia, Boletim de Resumos. Simpósio Brasileiro de Paleobotânica e Palinologia. ALPP, Bahia, Salvador, p. 239.
Farina, R.A., 1996. Trophic relationships among Lujanian mammals. Evolutionary Theory and Review 11, 125–134.
Farina, R.A., Blanco, R.E., 1996. Megatherium, the stabber. Proceedings of the Royal Society of London 263, 1725–1729.
Faure, M., Guérin, C., Parenti, F., 1999. Découverte d'une mégafaune holocène à la Toca do Serrote do Artur (aire archéologique de São Raimundo Nonato, Piauî, Brésil). Comptes Rendus de l'Académie des Sciences 329, 443–448.
Ferigolo, J., 1999. Late Pleistocene South-American land-mammal extinctions: the infection hypothesis. Quaternary of South America and Antarctic Peninsula 12, 279–310.
Ficcarelli, G., Coltorti, M., Moreno-Espinosa, M., Pieruccini, P.L., Rook, L., Torre, D., 2003. A model for the Holocene extinction of the mammal megafauna in Ecuador. Journal of South American Earth Sciences 15, 835–845.
Ghilardi, A.M., Fernandes, M.A., Bichuette, M.E., 2011. Megafauna from the Late Pleistocene–Holocene deposits of the Upper Ribeira karst area, southeast Brazil. Quaternary International 245, 369–378.
Grayson, D.K., 1984. Nineteenth-century explanations of Pleistocene extinctions: a review and analysis. In: Martin, P.S., Klein, R.G. (Eds.), Quaternary Extinctions: a Prehistoric Revolution. University of Arizona Press, Tucson, pp. 5–39.
Guérin, C., Curvello, M.A., Faure, M., Hugueney, M., Mourier-Chauviré, C., 1996. The Pleistocene fauna of Piaui (northeastern Brazil): palaeoecological and biochronological implications. Fumdhamentos 1, 56–103.
Guidon, N., 1989. Notas sobre dois sitios arqueológicos de São Raimundo Nonato, Piauí. Clio, Série Arqueología, 5, pp. 41–46.
Guidon, N., Parenti, F., Oliveira, C., Vergne, C., 1998. Nota sobre a sepultura da Toca dos Coqueiros, Parque Nacional Serra da Capivara, Brasil. Rev Clio Ser Arqueol, 13, pp. 187–197.
Haynes, C.V., 1995. Geochronology of paleoenvironmental change, Clovis type site, Blackwater Draw, New Mexico. Geoarchaeology 10, 317–388.
Holanda, E., Cozzuol, M.A., 2006. New records of Tapirus from the late Pleistocene of southwestern Amazonia, Brazil. Revista Brasileira de Paleontologia 9, 193–200.
Hubbe, A., Auler, A., 2012. A large cervidae Holocene accumulation in eastern Brazil: an example of extreme taphonomical control in a cave environment. International Journal of Speleology 41, 297–305.
Hubbe, A., Hubbe, M., Neves, W.A., 2007. Early Holocene survival of megafauna in South America. Journal of Biogeography 34, 1642–1646.
Hubbe, A., Hubbe, M., Neves, W.A., 2009. New Late-Pleistocene dates for the extinct megafauna of Lagoa Santa, Brazil. Current Research in the Pleistocene 26, 154–156.
Hubbe, A., Haddad-Martim, P.M., Hubbe, M., Mayer, E.L., Strauss, A., Auler, A.S., Piló, L.B., Neves, W.A., 2011a. Identification and importance of critical depositional gaps in pitfall cave environments: the fossiliferous deposit of Cuvieri Cave, eastern Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology 312, 66–78.
Hubbe, A., Vasconcelos, A.G., Vilaboim, L., Karmann, I., Neves, W.A., 2011b. Chronological distribution of Brazilian Glyptodon sp. remains: a direct ^{14}C date for a specimen from Iporanga, São Paulo, Brazil. Radiocarbon 53, 13–19.
Hubbe, A., Haddad-Martim, P.M., Hubbe, M., Neves, W.A., 2012. Comments on: "An anthropogenic modification in an Eremotherium tooth from northeastern Brazil". Quaternary International 269, 94–96.
Hubbe, A., Hubbe, M., Karmann, I., Cruz, F.W., Neves, W.A., in press. Insights into Holocene megafauna survival and extinction in southeastern Brazil from new AMS 14C dates. Quaternary Research. http://dx.doi.org/10.1016/j.yqres.2012.11.009.
Kerber, L., Oliveira, E.V., 2008a. Fósseis de vertebrados da formação Touro Passos (Pleistoceno Superior), Rio Grande do Sul, Brasil: atualização dos dados e novas contribuições. Journal of Geosciences 4, 49–64.
Kerber, L., Oliveira, E.V., 2008b. Novos fósseis de vertebrados para a Sanga da Cruz (Pleistoceno Superior), Alegrete, RS, Brasil. Revista Pesquisas em Geociências 35, 39–45.
Kerber, L., Kinoshita, A., Jose, F.A., Graciano Figueiredo, A.M., Oliveira, E.V., Baffa, O., 2011. Electron spin resonance dating of the southern Brazilian Pleistocene mammals from Touro Passo Formation, and remarks on the geochronology, fauna and palaeoenvironments. Quaternary International 245, 201–208.
Kipnis, R., 1998. Early hunter-gatherers in the Americas: perspectives from central Brazil. Antiquity 72, 581–592.
Koch, P.L., Barnosky, A.D., 2006. Late quaternary extinctions: state of the debate, annual review of ecology evolution and systematics. Annual Review of Ecology, Evolution, and Systematics 215–250.
Kos, A.M., 2003. Characterisation of post-depositional taphonomic processes in the accumulation of mammals in a pitfall cave deposit from southeastern Australia. Journal of Archaeological Science 30, 781–796.
Laming-Emperaire, A., Prous, A., Morais, A.V., Beltrão, M., 1975. Grottes et Abris de la Région de Lagoa Santa, Minas Gerais, Brésil. Cahiers d'Archeologie d'Amerique du Sud 1, Paris (185–185 pp.).
Lorenzen, E.D., Nogues-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., Marske, K.A., Ugan, A., Borregaard, M.K., Gilbert, M.T.P., Nielsen, R., Ho, S.Y.W., Goebel, T., Graf, K.E., Byers, D., Stenderup, J.T., Rasmussen, M., Campos, P.F., Leonard, J.A., Koepfli, K.-P., Froese, D., Zazula, G., Stafford, T.W., Aaris-Sorensen, K., Batra, P., Haywood, A.M., Singarayer, J.S., Valdes, P.J., Boeskorov, G., Burns, J.A., Davydov, S.P., Haile, J., Jenkins, D.L., Kosintsev, P., Kuznetsova, T., Lai, X., Martin, L.D., McDonald, H.G., Mol, D., Meldgaard, M., Munch, K., Stephan, E., Sablin, M., Sommer, R.S., Sipko, T., Scott, E., Suchard, M.A., Tikhonov, A., Willerslev, R., Wayne, R.K., Cooper, A., Hofreiter, M., Sher, A., Shapiro, B., Rahbek, C., Willerslev, E., 2011. Species-specific responses of Late Quaternary megafauna to climate and humans. Nature 479, 359–364.
Lund, P.W., 1840. View of the fauna of Brazil previous to the last geological revolution. Magazine of Natural History 4: 1–8, 49–57, 105–112, 153–161, 207–213, 251–259.
Lyman, R., 1994. Vertebrate Taphonomy. Cambridge University Press, Cambridge.
MacFadden, B.J., 2005. Diet and habitat of toxodont megaherbivores (Mammalia, Notoungulata) from the late Quaternary of South and Central America. Quaternary Research 64, 113–124.
Marshall, L., Berta, A., Hoffstetter, R., Pascua, R., Reig, O., Bombin, M., Mones, A., 1984. Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary of South America. Palaeovertebrata.Memoire Extraordinaire, Montpellier (77 pp.).
Martin, P.S., Steadman, D.W., 1999. Prehistoric extinctions on islands and continents. Extinctions in Near Time: Causes, Contexts and Consequences. (17–55 pp.).
Martin, L., Suguio, K., Flexor, J.M., Azevedo, A.E.G., 1988. Mapa geológico do Quaternário costeiro dos Estados do Paraná e Santa Catarina. Série Geol. DNPM, 28.
Mead, J.I., Meltzer, D.J., 1984. North American late Quaternary extinctions and the radiocarbon record. In: Martin, P.S., Klein, R.G. (Eds.), Quaternary Extinctions: a Prehistoric Revolution. The University of Arizona Press, Tucson, pp. 440–450.
Messineo, P.G., Politis, G.G., 2009. New radiocarbon dates from the Campo Laborde Site (Pampean region, Argentina) support the Holocene survival of giant ground sloth and glyptodonts. Current Research in the Pleistocene 26, 5–9.
Miller, E., 1987. Pesquisas arqueológicas paleoindígenas no Brasil Ocidental. Estudios Atacameños 8, 3–61.
Neves, W.A., Piló, L.B., 2003. Solving Lund's dilemma: new AMS dates confirm that humans and megafauna coexisted at Lagoa Santa. Current Research in the Pleistocene 20, 57–60.
Neves, W.A., Hubbe, A., Karmann, I., 2007. New accelerator mass spectrometry (AMS) ages suggest a revision of the electron spin resonance (ESR) Middle-Holocene dates obtained for a *Toxodon platensis* (Toxodontidae, Mammalia) from Southeast Brazil. Radiocarbon 49 (3), 1411–1412.
Parenti, F., 1993. Le gisement Quaternaire de la Toca do Boqueirão da Pedra Furada, Piauí, Brésil. Ph.D. Dissertation, EHESS, Paris.
Paula Couto, C., 1979. Tratado de Paleomastozoologia. Academia Brasileira de Ciências, Rio de Janeiro.
Pessenda, L.C.R., Gouveia, S., Aravena, R., 2001. Radiocarbon dating of total soil organic matter and humin fraction and its comparison with ^{14}C ages of fossil charcoal. Radiocarbon 43, 595–601.
Piperno, D.R., Stothert, K.E., 2003. Phytolith evidence for Early Holocene Cucurbita domestication in southwest Ecuador. Science 299, 1054–1057.
Politis, G., Prado, J.L., Beukens, R., 1995. The human impact in Pleistocene–Holocene extinctions in South America. In: Johnson, E. (Ed.), Ancient Peoples and Landscapes. Museum of Texas Tech University, Lubbock (187–205 pp.).
Prevosti, F.J., Vizcaíno, S.F., 2006. Paleoecology of the large carnivore guild from the late Pleistocene of Argentina. Acta Palaeontologica Polonica 51, 407–422.
Prous, A., 1986. Os mais antigos vestígios arqueológicos no Brasil Central. In: Bryan, A. (Ed.), Early Man in America from a Circum Pacific Perspective. Occasional papers, 1. Department of Anthropology, University of Alberta, pp. 173–182.
Prous, A., 2002. O homem pré-histórico e a megamastofauna pleistocênica no Brasil. Uma revisão bibliográfica. O Carste 14, 52–59.
Prous, A., Fogaça, E., 1999. Archaeology of the Pleistocene–Holocene boundary in Brazil. Quaternary International 53 (54), 21–41.
Rancy, A., 1999. Fossil mammals of the Amazon as a portrait of a Pleistocene environment. In: Eisenberg, J.F., Redford, K.H. (Eds.), Mammals of the Neotropics — The Central Neotropics. University of Chicago Press, Chicago, pp. 20–26.
Ribeiro, A.M., Scherer, C.S., 2009. Mamíferos do Pleistoceno do Rio Grande do Sul, Brasil. In: Ribeiro, A.M., Bauermann, S.G., Scherer, C.S. (Eds.), Quaternário do Rio Grande do Sul: integrando conhecimentos. Sociedade Brasileira de Paleontologia, Porto Alegre, RS, pp. 171–192.
Roosevelt, A.C., Costa, M.L., Machado, C.L., Michab, M., Mercier, N., Valladas, H., Feathers, J., Barnett, W., Imazio da Silveira, M., Henderson, A., Sliva, J., Chernoff, B., Reese, D.S., Holman, J.A., Toth, N., Schick, K., 1996. Paleoindian cave dwellers in the Amazon: the peopling of the Americas. Science 272, 373–384.
Rossello, E.A., Jahn, B., Liu, T., Petrocelli, J.L., 2001. The 4300-yr 14 C age of glyptodonts at Luján River (Mercedes, Buenos Aires, Argentina) and comments on 'Did the megafauna range to 4300 BP in South America' by Cione et al. Radiocarbon 43, 77–81.
Rossetti, D.D.F., Toledo, P.M.D., Moraes-Santos, H.M., Santos Jr., A.E.d.A., 2004. Reconstructing habitats in central Amazonia using megafauna, sedimentology, radiocarbon, and isotope analyses. Quaternary Research 61, 289–300.
Rothhammer, F., Dillehay, T.D., 2009. The late Pleistocene colonization of South America: an interdisciplinary perspective. Annals of Humans Genetics 73, 540–549.
Salemme, M., Miotti, L., 2003. South America: long and winding roads for the first Americans at the Pleistocene/Holocene transition. Quaternary International 109–110, 1–179.
Sandweiss, D., Mcinnis, H., Burger, R.L., Cano, A., Ojeda, B., Paredes, R., Sandweiss, M.C., Glascock, M.D., 1998. Quebrada Jaguay: early South American maritime adaptations. Science 281, 1830–1832.

Scherer, C.S., Ferigolo, J., Ribeiro, A.M., Cartelle, C., 2007. Contribution to the knowledge of *Hemiauchenia paradoxa* (Artiodactyla, Camelidae) from the Pleistocene of Southern Brazil. Revista Brasileira de Paleontologia 10, 35–52.

Signor III, P.W., Lipps, J.H., 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. Geological Society of America Special Paper 291–296.

Silveira, M.I., 1994. Estudo sobre estratégias de subsisténcia de caçadores-coletores pré-históricos do sitio Gruta do Gavião, Carajós, PA. M.A. unpublished dissertation, Universidade de São Paulo, São Paulo.

Skinner, A.R., 2000. ESR dating: is it still an 'experimental' technique? Applied Radiation and Isotopes 52, 1311–1316.

Steadman, D.W., Martin, P.S., MacPhee, R.D.E., Jull, A.J.T., McDonald, H.G., Woods, C.A., Iturralde-Vinent, M., Hodgins, G.W.L., 2005. Asynchronous extinction of late Quaternary sloths on continents and islands. Proceedings of the National Academy of Sciences of the United States of America 102, 11763–11768.

Steele, J., Politis, G., 2009. AMS ^{14}C dating of early human occupation of southern South America. Journal of Archaeological Science 36, 419–429.

Stuvier, M., Reimer, P.J., 1993. Extended ^{14}C data base and revised CALIB 3.0 ^{14}C age calibration program. Radiocarbon 35, 215–230.

Toledo, P.M.d., 1998. Locomotory Patterns within the Pleistocene Sloths. Museu Paraense Emílio Goeldi Press, Belém.

Turner, A., Anton, M., 1997. The Big Cats and their Fossil Relatives. Columbia University Press, New York.

Van Valkenburgh, B., Maddox, T., Funston, P.J., Mills, M.G.L., Grether, G.F., Carbone, C., 2009. Sociality in Rancho La Brea Smilodon: arguments favour 'evidence' over 'coincidence'. Biology Letters 5, 563–564.

Vialou, A.V., Aubry, T., Benabdelhadi, M., Cartelle, C., Figuti, L., Fontugne, M., Solari, M.E., Vialou, D., 1995. Découverte de Mylodontinae dans un habitat préhistorique daté du Mato Grosso (Brésil): l'abri rupestre de Santa Elina. Comptes Rendus de l'Academie Sciences Paris 320, 655–661.

Vimeux, F., Sylvestre, F., Khodri, M. (Eds.), 2009. Past Climate Variability in South America and Surrounding Region: From the Last Glacial Maximum to the Holocene. Springer, New York.

Vizcaino, S.F., Farina, R.A., Fernicola, J.C., 2009. Young Darwin and the ecology and extinction of Pleistocene South American fossil mammals. Revista de la Asociacion Geologica Argentina 64, 160–169.

Waguespack, N., 2007. Why we're still arguing about the Pleistocene occupation of the Americas. Evolutionary Anhtropology 16, 63–74.

Waldron, A., 2010. Lineages that cheat death: surviving the squeeze on range size. Evolution 64, 2278–2292.

Wright, S., 1931. Evolution in Mendelian populations. Genetics 16 (2), 0097–0159.