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CONCEPTUAL CHALLENGES FOR THE PALEOECOLOGICAL RECONSTRUCTION OF THE PLEISTOCENE PAMPEAN MEGAFAUNA AND THE CONSEQUENCES OF ITS EXTINCTION

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Abstract. The Pleistocene Pampean Megafauna (PPM) may be considered as the assemblage consisting mainly of large mammals (*i.e.*, body-mass ≥ 45 kg) that inhabited what is currently considered the Pampean Region during the Pleistocene and became extinct near the Pleistocene–Holocene transition. This contribution addresses several conceptual issues that may guide future efforts in its reconstruction and to consider potential consequences of its extinction. First, we approach the concept of megafauna by urging its explicit definition and contextualization in every investigation as a means of avoiding conceptual ambiguity. Second, we call attention to the risks of succumbing too readily to the temptation of employing a simplistic approach that assumes that extinct taxa had virtually the same biological requirements as those of their extant counterparts. We claim that within the PPM the abundance of taxa distantly related to or markedly distinct morphologically from their living counterparts poses significant challenges for understanding their paleobiology. Paleobiological interpretations need not be rigidly phylogenetically restricted, and phylogenetically based interpretations require critical assessment before their application. Third, we consider the paleoecology of the PPM from a metabolic perspective: as it was clearly dominated by allegedly hypometabolic megaherbivores (xenarthrans), there is no clear counterpart among living faunas. Fourth, we call attention to the fact that the loss of the PPM may have left in its wake an enduring but little-recognized legacy on the functioning of the contemporary ecosystem of the Pampean Region. Extinction of the PPM opened an enormous ecological chasm in the herbivore guild during the Holocene that persisted for about 6000 years, until it was filled, at least in part, by herds of cattle introduced since the sixteenth century.

Key words. Quaternary. Pampean Region. Mammals. Actualism. Paleobiology. Metabolism.

Resumen. DESAFÍOS CONCEPTUALES PARA LA RECONSTRUCCIÓN PALEOECOLÓGICA DE LA MEGAFAUNA PAMPEANA Y LAS CONSECUENCIAS DE SU EXTINCIÓN. La Megafauna Pampeana del Pleistoceno (MPP) puede considerarse como el conjunto formado principalmente por grandes mamíferos (*i.e.*, masa corporal ≥ 45 kg) que habitaron lo que actualmente se considera región pampeana durante el Pleistoceno y se extinguieron cerca de la transición Pleistoceno–Holoceno. Esta contribución aborda varias cuestiones conceptuales que pueden orientar los esfuerzos futuros en su reconstrucción y considerar las posibles consecuencias de su extinción. Primero, abordamos el concepto de megafauna, instando a su definición explícita y contextualización en cada investigación, como un medio para evitar la ambigüedad conceptual. En segundo lugar, llamamos la atención sobre los riesgos de sucumbir demasiado fácilmente a la tentación de emplear un enfoque simplista que asuma que los taxones extintos tenían prácticamente los mismos requisitos biológicos que los de sus contrapartes existentes. Señalamos que dentro de la MPP, la abundancia de taxones relacionados lejanamente o muy distintos morfológicamente de sus homólogos actuales plantea desafíos importantes para comprender su paleobiología. Las interpretaciones paleobiológicas no necesitan ser estrictamente restringidas filogenéticamente y las interpretaciones basadas en la filogenia deben aplicarse después de una revisión crítica. En tercer lugar, consideramos la paleoecología de la MPP desde una perspectiva metabólica: dado que estaba claramente dominada por megaherbívoros supuestamente hipometabólicos (xenartros), no existe una contraparte clara entre las faunas vivientes. En cuarto lugar, llamamos la atención sobre el hecho de que la pérdida de la MPP puede haber dejado un legado perdurable pero poco reconocido sobre el funcionamiento del ecosistema contemporáneo de la región pampeana. La extinción de la MPP produjo un enorme vacío ecológico en el gremio de herbívoros durante el Holoceno que persistió durante unos 6.000 años, hasta que fue ocupado, al menos en parte, por rebaños de ganado introducido desde el siglo XVI.

Palabras clave. Cuaternario. Región pampeana. Mamíferos. Actualismo. Paleobiología. Metabolismo.

Paleontologists broadly regard the Pleistocene megafauna as the collection or assemblage of large and mainly mammalian vertebrates that existed during the Pleistocene and became extinct near the Pleistocene–Holocene transition. With its unique mix of gigantic representatives (*e.g.*, xenarthrans, toxodonts, and macraucheniids) of ancient endemic lineages, evolved during South America's lengthy isolation from other continental landmasses, and "newcomers" (*e.g.*, proboscideans, perissodactyls, artiodactyls, and carnivorans) arrived from North America as part of the Great American Biotic Interchange, the South American Pleistocene megafauna has played a crucial role in the development of modern biological thought. This is particularly true of the megafauna of the Pampean Region of Argentina. Indeed, the first reports announcing the discovery of elements of this fauna during the late 1700s and early 1800s caused an immediate stir among the European scientific community and contributed significantly to the establishment of scientific institutions and traditions in New World countries as they took hold of their destinies and explored their territories (Fariña *et al.*, 2013). By way of example, we may cite the giant sloth *Megatherium americanum*, recovered from deposits near Luján, then a small town in the province of Buenos Aires. Its skeleton was the first of an extinct vertebrate to be mounted in a lifelike pose (Simpson, 1984; De Iuliis, 1996). It was also the first fossil vertebrate formally described and named scientifically by the great French comparative anatomist Georges Cuvier (1796), widely considered as the founder of vertebrate paleontology as a discipline; as such, it has legitimate claim to being the subject of the seminal paper in the field. Further, it led Cuvier to forge the modern concept of extinction (Fariña *et al.*, 2013). Moreover, and perhaps most notably, its remains and those of other gigantic sloths, as well as of glyptodonts, toxodonts, and other extinct South American vertebrates, had a profound influence on the young Charles Darwin, both during and after his famous voyage aboard the HMS Beagle, as he worked through his ideas on biological evolution (Vizcaíno *et al.*, 2009). During his journey between Buenos Aires and Santa Fe, Darwin (1845, p. 155) wrote: "I believe a straight line drawn in any direction through the Pampas would cut through some skeleton or bones. Besides those which I found during my short excursions, I heard of many others, and the origin of such names as 'the stream of the animal,' 'the hill of the giant,' is obvious. At other times I heard of the marvelous property of certain rivers, which had the power of changing small bones into large; or, as some maintained, the bones themselves grew. As far as I am aware, not one of these animals perished, as was formerly supposed, in the marshes or muddy river-beds of the present land, but their bones have been exposed by the streams intersecting the subaqueous deposit in which they were originally embedded. We may conclude that the whole area of the Pampas is one wide sepulchre of these extinct gigantic quadrupeds".

Reports of Darwin's explorations spurred enthusiasm for the continued recovery of fossil remains, particularly abundant in Argentina, among both foreign and local professional and amateur fossil collectors, leading to an accumulation of a critical volume of remains and setting the stage for the eventual establishment of formal institutions and the development of studies of fossil vertebrates, especially in Argentina. Following the publication of Darwin's (1859) "On the Origin of Species", studies on the genealogical interpretation of fossil mammal lineages flourished in South America, due particularly to the intellectual influence of Florentino Ameghino during the late 19th century.

Of more direct relevance within the context of the Pampean megafauna, Darwin (1845, p. 85) further noted "That large animals require a luxuriant vegetation, has been a general assumption which has passed from one work to another; but I do not hesitate to say that it is completely false, and that it has vitiated the reasoning of geologists on some points of great interest in the ancient history of the world." Vizcaíno *et al.* (2009) suggested that Darwin thus also opened a door onto the investigation of their paleobiology and paleoecology, avenues of research that, over the past several decades, have experienced accelerated development owing largely to innovations in methodology and technology.

Although aspects of paleobiology (or paleoautoecology) —feeding and locomotion, for example— may be understood with a relatively high degree of confidence through the direct study of fossil remains (Vizcaíno *et al.*, 2016), others such as paleoecology (*i.e.*, paleosynecology) and extinction require precise and refined biostratigraphic, chronologic, and environmental frameworks. Eduardo P. Tonni is the vertebrate paleontologist who, over the past 40 years, has spearheaded the research on these issues with regard to the Pampean Region. In this sphere of research, many of his contributions (*e.g.*, Tonni & Fidalgo, 1978, 1982; Tonni *et al.*, 1985, 1992, 1999, 2003; Tonni & Cione, 1995, 1997; Tonni, 2011) are indeed required reading and his professional and personal efforts have been instrumental in the training and intellectual nurturing of more recent generations of researchers. For these and other meritorious accomplishments, recognition with this volume is wholly deserved.

The goal of this contribution honoring Eduardo is not intended as a comprehensive reconstruction of the paleoecology of the Pleistocene Pampean Megafauna (PPM) and the causes of its extinction. Rather, we view this as an opportune occasion to address several conceptual issues that may guide future efforts in its reconstruction and to consider potential consequences of its extinction.

THE CONCEPT OF MEGAFAUNA

Megafauna, derived etymologically from the combination of "mega" (from the Greek *megalos* for large) and "fauna" (from the ancient Roman nature-goddess Fauna), is defined as either "the large mammals of a particular region, habitat, or geological period" or "animals that are large enough to be seen with the naked eye" (see Lexico.com). However, the ambiguity and disparity of these definitions are reflected in the vast scientific literature on megafauna, as demonstrated in a bibliographic study by Moleón *et al.* (2020). These authors reviewed and discussed the concept of megafauna and proposed a goal-oriented framework for megafaunal research.

Definitions of the megafauna concept fall into two groups, one employing an explicit body-size threshold and the other implicit body size. The former regards species as megafauna if they exceed a body-size threshold, either mass-based or length-based. Mass thresholds (*e.g.*, from ~10 kg to two tonnes) have been widely used for terrestrial contexts, whereas length thresholds (characterized by much smaller sizes) are commonly employed for benthic and epibenthic marine environments. Most vertebrate paleontologists have followed Martin's (1967) concept of animals, usually mammals (though also some birds and reptiles; see Stuart, 2021), over 100 pounds (*ca.* 45 kg), and some have used Owen-Smith's (1988, 2013) megaherbivore concept, applied to herbivores exceeding 1000 kg in adult body mass. Notably, the latter concept has been applied mainly to Pleistocene–Holocene mammals (see below), whereas it has been virtually ignored among non-avian dinosaur researchers. Implicit body size views megafauna as particular clades or groups of species that are relatively large-sized within the study group of interest and is usually applied within the context of aquatic environments. That is, for them, absolute body size per se is not a criterion for recognizing megafauna; instead, it is the large size relative to other faunal elements within a particular ecological context that is important.

Given these considerations, it is apparent that the concept of megafauna may differ based on the ecosystem studied —depending, in other words, on the ecological and biological contexts of a particular analysis. Moleón *et al.* (2020) demonstrated that application of the concept to terrestrial environments has largely been implemented in analyses of the extinction of Pleistocene megafauna, and that body mass was by far the most important species attribute associated with the concept (see below).

Moleón *et al.* (2020) noted that while there may be consensus on body size as a crucial criterion, it is not necessarily sufficient for an unambiguous definition of the term megafauna. These authors identified the lack of a conceptual definition that integrates ecological function and functional traits with a species' size (*e.g.*, body mass). They therefore proposed incorporating a functional perspective, introducing two concepts towards this end. The first concept combines a body size-based definition of megafauna with the keystone species concept (*sensu* Paine, 1969). The keystone megafauna would be the subset of the largest-sized animals that have consistently strong effects on the structure or functioning of their communities or ecosystems, both in magnitude and in the spatial and temporal heterogeneity they create (Woodward *et al.*, 2005). This concept would require deep appreciation of the functional dynamics of the ecosystem or, in the case of past ecosystems, fine-grained modeling prior to categorization; that is, categorization would be a consequence (a result) of synecological knowledge. The second functional concept is the functional megafauna, the subset of largest species of a given clade or guild with distinctive functional traits (*sensu* McGill *et al.*, 2006). A practical advantage of this concept is that the identification of megafauna is relatively straightforward as it only requires a basic ecological knowledge, mostly autoecological information. An alternative of the functional megafauna concept would be apex megafauna: animals so large that they escape most non-anthropogenic predation as adults. This concept is related to the megaherbivore and apex predator concepts (Owen-Smith, 1988, 2013, and Wallach *et al.*, 2015 respectively). As Moleón *et al.* (2020) noted, herbivores exceeding 1000 kg and carnivores above an average body mass of *ca.* 15 kg may each be considered as examples of both functional and apex megafauna. Moleón *et al.* (2020) concluded that approaching the concept of megafauna from a functional perspective would render it more broadly applicable to eco-evolutionary contexts and scientific approaches. These authors encouraged the explicit definition and contextualization of the concept of megafauna in every study as a means of achieving conceptual disambiguation. In effect, these authors suggested deemphasizing reliance on a specific absolute body mass value as a defining criterion, and encouraged focusing instead on functional ecological dynamics. Indeed, they noted that within a particular ecological context, megafauna may be considered as the subset of organisms carrying out ecological roles dictated by their size; often a size hiatus and/or particular ecological features set these organisms apart from others in the ecological setting.

In this regard as it applies to the PPM, it would be instructive to reconsider approaches on the vulnerability to and causes and timing of extinction (*e.g.*, Lessa & Fariña, 1996; Lessa *et al.*, 1997; Cione *et al.*, 2003, 2009, 2011; Prado *et al.*, 2015) in light of the keystone megafauna definition, and those on paleoecology (*e.g.*, Fariña, 1996; Prevosti & Vizcaíno, 2006; Fariña *et al.* 2014) in light of functional and apex megafauna. Paleoecology and extinction can be related topics and treated in the same article (*e.g.*, Vizcaíno *et al.*, 2012), or the research can be focused on other issues such as the fossil record (*e.g.*, Marshall *et al.*, 1984; Cione & Tonni, 1999; Prado *et al.*, 2021), biogeography or species distribution modeling (*e.g.*, Varela *et al.*, 2018; Araújo *et al.*, 2021). In these cases, clarification of the criteria on which the term megafauna is based is warranted.

For this contribution we approach the PPM (Fig. 1) from a broad functional perspective as comprising large mammals over 45 kg (Martin, 1967), including strict megaherbivores (*sensu* Owen-Smith, 1988, 2013; see above) —although some may have been more omnivorous (see Fariña, 1996; Bargo, 2001; Tejada *et al.*, 2021)— in order to include literature published prior to and thus without the benefit of suggestions in Moleón *et al.* (2020). Some of these articles have ambiguous or *ad hoc* definitions of megafauna and others contain no definition at all. In doing so, we are aware that for the specific case of the PPM or any other fauna there may be taxa that straddle this cutoff and may or may not be included depending on the calculations made (*i.e.*, the method/comparative group used to calculate body mass) or intraspecific variability (for instance males or females, in cases for which sexual dimorphism is discernable).

REFLECTIONS ON ACTUALISM

Uniformitarianism and its derivative actualism are among the more robust paradigms of the Earth sciences. Uniformitarianism refers to the constancy of physical variables and processes throughout Earth history and actualism, at least in paleontology, to the use of extant species for inferring the behavior and environmental requirements of extinct species (Gould, 1965, 1967; Harrington, 1973). However, it may be that the latter lack modern analogs; for such cases, the uncritical direct application of an actualistic approach (termed “naive actualism” by Vizcaíno *et al.*, 2017) may generate poorly supported hypotheses, with little or no heuristic value, and produce nonsensical reconstructions.

For instance, as a species’ morphology and behavior are determined by a complex interplay between phylogeny and adaptation, it cannot be assumed that an extinct animal’s morphology is solely or even largely a function of the niche and habitat occupied by its extant relatives (Vizcaíno, 2014). As Nieto-Díaz and Rodríguez (2003) claimed, the robustness of hypotheses based solely on extant relatives diminishes with time and morphological disparity, making these hypotheses highly unstable when referring to organisms very distant temporally and/or phylogenetically from modern

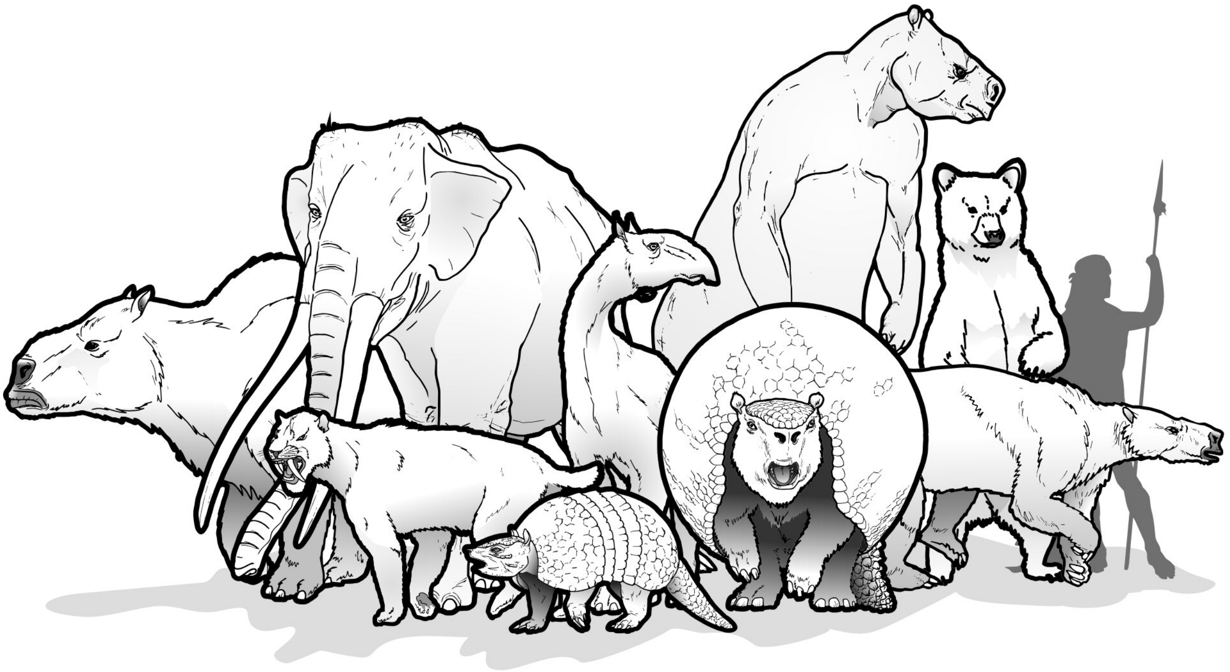

Figure 1. A cast of characters: representative genera of the main clades of the Pleistocene Pampean Megafauna (PPM). From left to right, front row: *Smilodon* (Carnivora, Felidae), *Pampatherium* (Xenarthra, Cingulata, Pampatheriidae), *Glyptodon* (Xenarthra, Cingulata, Glyptodontidae), *Glossotherium* (Xenarthra, Folivora, Mylodontidae); second row: *Toxodon* (Notoungulata, Toxodontidae), *Cuvieronius* (Proboscidea, Gomphotheriidae), *Macrauchenia* (Litopterna, Macraucheniidae), *Megatherium* (Xenarthra, Folivora, Megatheriidae), *Arctotherium* (Carnivora, Ursidae), and human silhouette for scale. *Megatherium* is depicted in a nearly hairless condition, as proposed by Fariña (2002). Illustration by Néstor Toledo.

forms. This issue is particularly relevant for many of the endemic faunal elements of the PPM —clearly, ground sloths and glyptodonts differ morphologically from their extant sloth and armadillo relatives to such a degree as to readily suggest markedly different modes of life (Fig. 2). Vizcaíno *et al.* (2018), in evaluating advantages and limitations of the use of extant xenarthrans as morphological models for paleobiological reconstructions of their extinct relatives, analyzed the overall morphometric similarity between extant and extinct xenarthrans and the accuracy of body mass estimations of extinct xenarthrans based on their close extant relatives and other mammals. These authors found that many extinct xenarthrans are more similar morphologically to extant mammals from other groups rather than to their own closest living relatives. Further, they noted that many of the equations for estimating body mass derived from extant xenarthrans predict unrealistic results due to dimensional and shape differences between most of the extinct and extant xenarthrans. They recognized that some methodological concerns related to the modeling of biological attributes of extinct xenarthrans by comparison with a phylogenetically restricted sample of extant xenarthrans involve several issues: (1) the reduced diversity of extant xenarthrans, in addition to the scarcity of detailed biological data of available specimens, introduces limitations when applying parametric modeling; (2) due to marked differences in biological design, modeling commonly extends well beyond the range of the extant sample; and (3) bias is introduced by differences in anatomical proportions—extinct taxa differ markedly in shape compared to their extant relatives, a factor that is particularly important for most glyptodonts and giant ground sloths. Vizcaíno *et al.* (2018) concluded that, for such cases, a wider comparative net must be cast to include other, more distantly related mammals and incorporate biomechanical approaches that address form-function relationships (see below). Giant sloths and glyptodonts are not, of course, the only South American clades susceptible to an overly strict application of actualism (this applies as well, for example, to notoungulates and litopterns; see McGrath *et al.*, 2018; Croft *et al.*, 2020); and neither are South American faunas unique in this regard (*e.g.*, Graham, 2005; Semken *et al.*, 2010; Faith *et al.*, 2019).

Hypotheses on paleoclimatic and paleoenvironmental conditions are also commonly based on the distribution of extant taxa that are closely related to the extinct representatives in a particular fauna. Again, however, whereas this approach is generally appropriate, its restricted and uncritical application may generate poorly supported hypotheses. For instance, Vizcaíno *et al.* (2017) pondered the case of the jaguar *Panthera onca*, a conspicuous extant species (it is the largest carnivore in South America) that is also recorded in the Pleistocene of Patagonia and the Pampean Region. Today the jaguar lives virtually exclusively in closed tropical environments; however, it is well known that in historical times it had a much wider distribution, including arid environments (*e.g.*, Povilitis, 2015; Cuyckens *et al.*, 2017). Vizcaíno *et al.* (2017) concluded that the reconstruction of paleoenvironments and paleoclimates necessitates comprehensive analyses that take into account the many interweaving threads of biotic and abiotic evidence, as the intrinsic and extrinsic factors that establish the current distribution of taxa do not necessarily reflect their maximal ranges of environmental and climatic tolerances or those of extinct taxa. Indeed, as Nieto Díaz & Rodríguez (2003) noted, the spectrum of autoecological (including the form-function dyad) and synecological possibilities we can

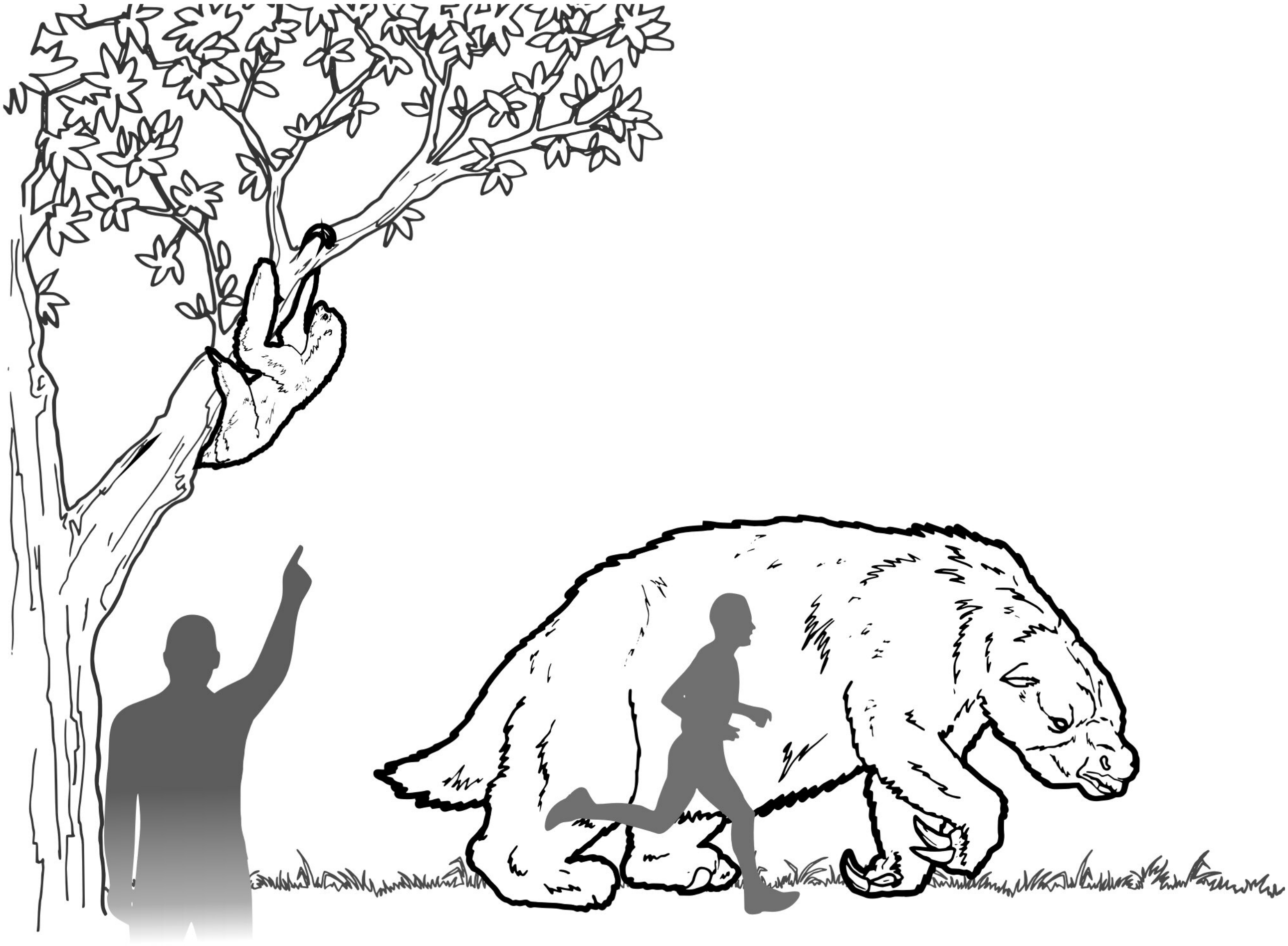

Figure 2. Illustrations, by Néstor Toledo, of the ~ four kilogram extant tree sloth *Bradypus* in the foreground and the four tonne (or more) Pleistocene giant ground sloth *Megatherium* in the background, with two human silhouettes for scale. The size and general morphology of the postcranial skeleton readily indicate markedly different modes of life despite their phylogenetic affinity. *Megatherium* is depicted in a more traditional quadrupedal and furred condition (based on an old illustration exhibited in the División Paleontología Vertebrados of the Museo de La Plata, Argentina).

observe nowadays should not be taken as representative of that of extinct biota and past environments. We wish to be clear that we do not consider that such caveats invalidate actualism. Rather, we maintain that it need not necessarily be phylogenetically restricted and should be applied with critical judgment. Additional consideration of these topics may be found in Catena & Croft (2020).

A FORM-FUNCTION APPROACH FOR PALEOBIOLOGICAL RECONSTRUCTION

In vertebrate paleontology, most information is derived from fossilized skeletal material, principally of bones and teeth. Therefore, a logical method of approaching different aspects of paleobiology is to apply the principle of form-function correlation, which holds that there is a close relationship between the two, such that the latter can be inferred from the former. Without doubt, the PPM is an unusually abundant source for such studies, yielding nearly complete skeletons of the more representative taxa of all main lineages (*i.e.*, xenarthrans, notoungulates, litopterns; proboscideans, and carnivorans), either of a single individual or as composites assembled from several individuals.

Once again, seeking a suitable analog should not be restricted to a phylogenetically based search. According to Currie (2013), homoplasic (*e.g.*, convergent) traits, though uninformative from a phylogenetic perspective, may instead be highly significant in a functional and adaptive framework. Currie (2013) defined analogy as a similarity between two lineages that meets two conditions: (1) the trait must be present in the two lineages, but not in their common ancestor (it must be homoplasic); and (2) the trait must have evolved in the two lineages non-accidentally. This author focused on “analogous inferences”, *i.e.*, inferences that take a trait-environment dyad from one lineage and project it onto another. This author concluded that analogy plays a central role in the confirmation of adaptive hypotheses, providing important “evidence for the construction and testing of historical hypotheses about biological form and function” (Currie, 2013, p.771). In this sense, the PPM poses particular challenges for reconstruction given that larger taxa lack comparable modern representatives. Hence, as mentioned above for the Pleistocene ground sloths and glyptodonts, if there are no comparable extant relatives of the animal of interest, analysis of its design may proceed based on analogous forms that are not close kin.

Several of the caveats noted for xenarthrans (see above) also apply to representatives of other lineages of the PPM with wider extant diversity or closely similar extant analogs and for which considerably more biological information is available—*e.g.*, extant artiodactyls and perissodactyls for the extinct toxodonts and macrauchenians, and extant carnivorans and proboscideans for the extinct machairodontines and mastodonts. This is so due in some cases to marked differences in certain particular biological features (*e.g.*, narial anatomy of macrauchenians—Forasiepi *et al.*, 2021—and extreme development of canines in machairodontines—Chimento *et al.*, 2019) or because body size fell well beyond the range of the extant sample (body mass of machairodontines may have been twice that of tigers and lions, the largest extant felids; Fariña *et al.*, 1998; Christiansen & Harris, 2005).

Investigations on the South American Native Ungulates (SANUs) are particularly telling in this regard. Modern hoofed herbivores can and have been used as ecological and functional models (see for example Croft, 2000). However, in many respects overall resemblance declines upon broader comparisons, due largely to the wide degree of diversity among SANUs, particularly notoungulates. For example, for some notoungulates, such as the small typotherians and proterotheriids, rodents instead serve as reliable extant analogues (see Elissamburu, 2004; Cassini *et al.*, 2012; Muñoz *et al.*, 2017). In addition, many notoungulates possessed euhypsodont teeth, not only among rodent-sized paedotherians and medium-sized mesotheriids but also among the larger toxodontians. The peculiar facial anatomy of macrauchenians defies comparison to any living terrestrial mammal, and their narial anatomy remains uncertain (Forasiepi *et al.*, 2016, 2021; Moyano & Giannini, 2018). Regarding body mass, some of the clades with the largest representative among native ungulates (astrapotheres and pyrotheres) had become extinct by the Pliocene, leaving only the notoungulates and litopterns to survive into the Pleistocene. Both of the last two lineages showed a trend toward increased body size from the Miocene until the Late Pleistocene (Vizcaíno *et al.*, 2012), *Macrauchenia* nearly reaching and *Toxodon* surpassing a mass of one tonne

(Fariña *et al.*, 1998). This trend included, on the one hand, increased maximum body mass with respect to the Miocene toxodontians and macrauchenians (110 kg *Adinotherium* and 640 kg *Nesodon*, and about 140 kg *Theosodon* respectively; see Cassini *et al.*, 2012). On the other hand, the formerly abundant and diverse typotherians and proterotheriids experienced a remarkable reduction in diversity, being represented in the Pleistocene mainly by the 1.9 kg *Paedotherium* and 20–40 kg *Neolicaphrium*, respectively (see Elissamburu, 2004; Ghizzoni *et al.*, 2020).

In any event, testing form-function correlations in extant forms should be addressed as a prerequisite for developing hypotheses on adaptation. In doing so, data on extant species must be carefully and rigorously gathered to establish form-function relationships—*i.e.*, that the behaviors or functions do indeed correlate with a particular anatomical form (Radinsky, 1987; Vizcaíno & Bargo, 2021). Finally, if there are no biological analogs available at all, mechanical analogies can be employed (Paradigmatic Analysis; Rudwick, 1964). Understanding an animal's biological design (that is, how an animal's specific biological attributes functioned) may allow interpretation of the roles it played in particular ecosystems of the geological past.

METABOLISM IN PALEOECOLOGY

Despite the obvious advantages and theoretical or conceptual possibilities of a form-function approach, an ecological understanding of the PPM would not be complete without considering other features (*e.g.*, metabolism, population density, reproduction rate, lifespan) that cannot be measured directly from bones and teeth. One of the central goals of ecology is to understand how energy and material flows govern ecosystem function and stability (Humphries & McCann, 2014), establishing metabolism as probably the most relevant among these other features. Metabolism is the biological processing of energy and materials and determines the rates of almost all biological activities, and the demands that organisms place on their environment for all resources (Brown *et al.*, 2004). Over the past several decades considerable attention has been focused on a metabolic unification of ecology, centered around a Metabolic Theory of Ecology (MTE; Brown *et al.*, 2004). Currently, metabolic ecologists are involved in the search for varied metabolic models to be applied to a wide diversity of animal ecology research (Humphries & McCann, 2014).

Some efforts have considered metabolism in paleoecological reconstructions of the PPM. For example, Fariña (1996) addressed the trophic relationships of the Late Pleistocene Lujanian megafauna based on the general ecological relationships between population density, body size, and basal metabolic rate. This author calculated the energy requirements for each species (as a product of standing biomass and basal metabolic rate) and, with the incorporation of several assumptions, estimated consumption of the habitat's primary productivity, concluding that there was an excess of herbivores in relation to the plant resources available and in relation to estimates of carnivore biomass. A competing hypothesis by Prevosti & Vizcaíno (2006) proposed that if high herbivore biomass occurred during the Lujanian, then a higher density of carnivores could be supported, although Fariña *et al.* (2014) were critical of the evidence advanced by Prevosti & Vizcaíno (2006).

In our view, this remains unresolved. The PPM herbivore guild was clearly dominated in terms of taxonomic richness by xenarthrans (Vizcaíno *et al.*, 2012), a clade characterized by significantly lower metabolism than other placental mammals of similar body masses (McNab, 1985). The lower energetic requirements compared to other placental mammals and, therefore, consumption of a specific type of food imply that Lujanian xenarthrans may have required lower intake than other placental mammals of similar body masses. In this sense, the PPM has no counterpart among extant faunas, and paleoecological reconstructions for the PPM thus lack strict analogs; therefore, alternatives to purely comparative actualistic approaches must be used (Vizcaíno *et al.*, 2012).

There remain, however, critical operational limitations in the generation of reliable estimates of basal metabolism, given uncertainty in how basal metabolism scales with body size in animals that are so much larger than and morphologically different from their extant relatives, as is the case for ground sloths and glyptodonts. In contrast to our thoughts above, on guarding against an overly strict imposition of phylogeny in the reconstruction of paleobiology, it seems clear that within the conceptual framework of metabolic ecology there may be no way of avoiding consideration of phylogenetic signal in the estimation of basal metabolism of these animals.

We hope that the development of newer methods based either on biotic or abiotic factors could provide more evidence to generate reliable estimates of basal metabolism in these animals. Among those based on the former factor, one discipline that has grown recently is paleohistology. In relation to estimating metabolism, Legendre *et al.* (2016) performed statistical predictive modeling using the method of phylogenetic eigenvector maps on a set of histological bony features for a sample of extant and extinct vertebrates, to estimate metabolic rates of fossil archosauromorphs. Among abiotic factors, isotopic paleontology can also contribute. For instance, oxygen isotope values of bone phosphate have been used to determine the relative temperature variations experienced by skeletal regions during bone deposition (Barrick & Showers, 1999). Temperature variations relate to an animal's thermal physiology and can be used to estimate their metabolic physiology. To our knowledge, none of these approaches has so far been applied to estimate metabolism among the PPM. However, isotopes have been used to interpret diet (*e.g.*, Czerwonogora *et al.*, 2011) and, hence, could provide information on metabolism.

CONSEQUENCES OF MEGAFAUNAL EXTINCTION

The PPM has been treated extensively in the literature (including many articles cited above). One general conclusion that may be drawn from these research efforts is that large size, compared to other factors (*e.g.*, South American versus North American origin of the lineages and dietary habits; Lessa & Fariña, 1996), explains most of the vulnerability to extinction. Another is the multifactorial nature of the causes of extinction, including a web of environmental and human based reasons (*e.g.*, climatic change, hunting, accompanying fauna and diseases; Cione *et al.*, 2003, 2009; Grayson, 2015; Prates & Pérez, 2021; and references therein). A third one is that the PPM extinction was not an "instantaneous" phenomenon, but a process that may be still occurring, or at least that its consequences continue to have a lingering impact on natural environments even today. Croft (2012) distinguished the Late Pleistocene extinctions more broadly as a particular episode, termed the Hypoamerican phase, in the evolution of South America's mammals.

Johnson (2009) evaluated possible ecological consequences of Pleistocene–Holocene transition megafaunal extinctions worldwide, finding that there were significant changes in plant communities following megafaunal extinctions, and that the ecological aftershocks of those extinctions persist to the present day. According to this author, habitat biodiversity and complexity in some dry, lowland, wooded landscapes became impoverished as a result of large herbivore extinctions, while others contain anachronistic plants that may be in long-term decline. Most extant species evolved coevally with and ecologically connected to megafauna. Therefore, many are likely to be adapted either to megafauna themselves or to the environmental conditions that they created; and consequently, loss of these animals may have had large impacts on the abundance, life history, and survival of many other species (Swift *et al.*, 2019). According to Malhi *et al.* (2016), understanding the consequences of past extinctions is valuable for several reasons. Among them is that the loss of megafauna may have an enduring but little-recognized legacy on the functioning of the contemporary biosphere and that our current understanding of ecosystem ecology and biogeochemistry has been developed in a world depleted of giants. For instance, it is known that modern-day grassland herbivores play a role in limiting wildfires by consuming potentially flammable material. Karp *et al.* (2021) present evidence that herbivore-fire interactions affected fire on a global scale in the past. These authors found that fire activity of grassy ecosystems increased to a larger extent in response to herbivore extinction on continents that suffered the largest losses of grazers, as is the case in South America, although it has not been fully evaluated for the Pampean region.

Vizcaíno *et al.* (2012) claimed that the PPM extinction produced an enormous ecological gap in the herbivorous guild during the Holocene that persisted for about 6000 years, until it was filled, at least in part, by herds of cattle introduced since the second half of the sixteenth century. By the end of that century, these cattle had become so numerous that the trade in cow hides became one of the main economic colonial activities for the next two centuries. But it also affected the economy of the native people, who shifted away from hunting camelids (*Lama guanicoe*), deer (*Ozotoceros bezoarticus*), and rheas (*Rhea americana*) (*e.g.*, Ramos *et al.*, 2008). Two analyses provide different views on the impact of the megafaunal extinction in South America. Doughty *et al.* (2016) estimated how savanna woody biomass may have changed by creating an empirical model. This model combined a large dataset of savanna woody cover with estimates of mammal ranges and weights and abiotic variables (*e.g.*, temperature and precipitation). Their results indicate that South America's land surface cover may have been drastically transformed following the megafauna extinctions. Indeed, these authors suggested that had the megafauna not gone extinct, total savanna woody cover in South America could possibly have decreased by ~ 29% and that savannas would likely have been more open, similar to current African savannas. Barnosky *et al.* (2016), searched for biotic transitions recognizable in the fossil record for the Pampas and southwestern Patagonia in South America, and the northeastern and northwestern United States and the Alaska/Yukon area in North America. They found that major shifts in ecological states were consistent with expectations of defaunation in North American, but not South American, sites. These authors viewed climate change, rather than defaunation, as the primary cause of the transition from C3 to C4 grasses in the Pampean Region. They reasoned that the increase in C4 grasses and other vegetational changes in the pampas are consistent with late Quaternary climatic warming driving a transition to warmer, more humid conditions, as also indicated by sedimentological, malacological, and paleobotanical data. Barnosky *et al.* (2016) also held that xenarthrans were not ecosystem engineers and likely became extinct only well after the vegetation transition began, and there is no evidence that loss of the proboscidean *Notiomastodon* (extant proboscideans are acknowledged as important ecosystem engineers in Africa) significantly impacted the amount of shrubby vegetation in the dry southern pampas.

With regard to the statement of Barnosky *et al.* (2016) on xenarthrans not being ecosystem engineers, we note that large sloths have been implicated as builders of several large Plio–Pleistocene burrows in deposits along the Atlantic coast of Argentina (see Vizcaíno *et al.*, 2001). While only a few of these structures have been investigated as to their cause of origin, it is highly likely that most, and possibly all, similar structures not yet investigated were also excavated by large sloths. If further research does indeed confirm this to be the case, then xenarthans' status as ecosystem engineers may warrant further consideration (see also Desbiez & Kluyber, 2013). It is worth noting that similar structures, suggested as likely having been formed by xenarthrans, have been reported from other South American localities. For example, Frank *et al.* (2015; see also references therein) suggested that ground sloths probably excavated caves in the southern Brazilian state of Rio Grande do Sul.

FINAL CONSIDERATIONS

As mentioned above, we did not set out to present an exhaustive review on the paleoecology of the PPM and its extinction. Rather, we wished to share our thoughts on some of the issues that have impacted our individual and collective mindset in approaching the study of this unique biotic assemblage. We modestly propose that these issues be incorporated in research protocols for the study of the PPM.

We began with the concept of megafauna and early on drew attention to one of the most important initial aspects of the communication process in science, that of clear and unambiguous expression of the cognitive constructs or images produced during the investigation of objects of study, given that any researcher carries conceptual baggage (Vizcaíno *et al.*, 2016). Different researchers operate in slightly or markedly different conceptual frameworks, and this influences the final configuration of the mental construct about a particular event or concept. Both the determined methodology applied and the conclusions drawn from them are shaped by their specific epistemological framework. Thus, we emphasize the need of clearly defining what we mean when we talk about megafauna.

In the subsequent two sections we called attention to the risks of falling too readily for a simplistic approach in assuming that extinct taxa had virtually the same biological requirements as those of their extant counterparts or, as has been so aptly remarked (though we cannot give credit for its pronouncement, as we cannot recall its source), condemning the past to be just like the present. This is so for even apparently disparate approaches such as those implied in the dyad distribution patterns/environmental conditions, and form/function. We reiterate that these caveats do not invalidate actualism; we claim only that it need not be rigidly phylogenetically restricted and should be applied after critical review. Within the PPM, the abundance of taxa distantly related to or morphologically very different from their living counterparts (especially xenarthrans) raises serious problems in understanding their paleobiology.

As noted in the subsequent section, avoiding such "naive actualism" applies also, to a certain degree, when considering the paleoecology of the PPM from a metabolic perspective: as the PPM was clearly dominated by allegedly hypometabolic megaherbivores (xenarthrans), there is no clear counterpart in living faunas. However, the estimation of how basal metabolism scales with body size in these animals requires a critical consideration of phylogenetic signal.

Lastly, we dealt with the extinction of the PPM. According to Malhi *et al.* (2016, p. 844–845).

More philosophically, the Pleistocene and early Holocene megafaunal extinctions can stimulate us to reevaluate what is natural in the world and what sort of nature we seek to conserve or restore. If we accept the increasing evidence for a strong human role in these early extinctions, it forces a look inwards and recognition of the deep prehistoric entanglement between humans and environmental change, a realization that some of the most dramatic human-induced changes to the nature of life on Earth and the functioning of the biosphere may have occurred even before the dawn of agriculture." In our view, from the perspective of current human actions, the question of what caused the extinction is somewhat beside the point. The Pleistocene megafauna is gone. Undoubtedly, human activity is responsible for the current extinction (of the megafauna and many more biological entities). Therefore, if we are going to "manage" or "administer" any part of nature, it seems relevant to ask in what state we received it. To these ends, we think it is important to realize that the environment that we "received" and generally view as a static, balanced system was in reality dynamic and undergoing continued change, and that it is crucial to determine which phenomena were occurring even before we became aware that we were altering it.

In summary, we still have much more to learn about the PPM or, rather, the PPM still has much to teach us about evolutionary biology. Certainly, the need for much further fieldwork and fossil collection and the applications of other approaches like taphonomy, ichnology and biogeochemistry is warranted. As the philosopher Adrian Currie (2015) claimed, earth scientists, as well as other historical scientists, are methodological omnivores who construct specially designed epistemic tools to generate evidence on highly specific research topics. This allows them to gather multiple lines of independent evidence and thus maximize their epistemic reach. Their approach resembles a research scaffolding: investigation proceeds piecemeal and information only becomes relevant as evidence once certain hypotheses are well supported.

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