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Central Argentina vegetation characteristics linked to extinct megafauna and some implications on human populations

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Abstract

In this paper we study the relationships between plants and extinct megafauna by examining the characteristics of the vegetation in the central region of Argentina (i.e. Espinal, Monte, and Chaco phytogeographic regions). First, we study the size, shape, quantity, and characteristics of fruits and seeds. We also evaluate the presence of mechanical (spinescence and wood density) and chemical (secondary metabolic compounds) defenses against high rates of herbivory. Complementarily, we assess the importance these plants had for human populations, using archeological, ethnographic, and current data. A high percentage of the analyzed plants met the criteria proposed for fruits and seeds dispersed by megafauna, together with a high frequency of spinescence, high density woods, and secondary metabolites. We propose that these traits cannot be explained by the herbivory pressure of extant fauna in the area, but rather developed in interaction with currently extinct fauna. We suggest that Pleistocene megafaunal extinction had important consequences in the region due to their role as ecosystem engineers and to vegetation's characteristics, which were probably strongly shaped by megafauna activities. Among these consequences, we discuss the loss of certain interactions between these animals and vegetation, such as loss of seed dispersal mechanisms, shrub invasion, and increased susceptibility of vegetation to fire. Other effects for hunter-gatherer groups were the generation of highly regulated mobility patterns and the formation of barriers for the dispersal of prey. Finally, we also discuss the importance of these plants for human populations as food, construction material, medicines and firewood. Likewise, the role of humans as "heirs" of the megafauna in the propagation of tree and shrub species is highlighted.

Keywords
evolutionary anachronism, hunter-gatherers, megafaunal fruits, secondary metabolites, South America, spinescence

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Introduction

Currently, there is great concern about the loss of animal species, mainly due to human impact on terrestrial ecosystems and climate change (Ripple et al., 2014, 2015). This situation is particularly serious in the case of large animals, since their impact on ecosystems is profound (Owen-Smith, 1988). In this sense, a recent study indicates that less than 21% of the Earth's surface is home to all the extant large mammals (Morrison et al., 2007). Understandably, to a large extent, studies of the current biodiversity crisis have focused on the loss of species, the associated consequences and the identification of ways to mitigate them. A related subject has been the loss of ecological interactions, which in many cases goes along with or even precedes the extinction of species (Novaro et al., 2000; Valiente-Banuet et al., 2015). However, defaunation processes like the current ones, with the consequent loss of ecological interactions, also took place in the recent past. Appealing to a historical perspective that considers the development of these processes in time and space can help to a deeper comprehension of the intervening variables and to avoid or mitigate their effects in the present. In this context, this work explores the possible loss of ecological interactions between extinct Pleistocene megafauna and vegetation in the central region of Argentina (southern portion of South America). For this purpose, we define the following categories to be used hereafter: megafauna (animals >44 kg of adult live weight, sensu Martin and Wright, 1967), macroherbivores (animals >100 and ⩽1000 kg of adult live weight, sensu Owen-Smith, 2013), and megaherbivores (animals >1000 kg of adult live weight, sensu Owen-Smith, 1988; Teng et al., 2023).

The South American fauna was the product of a complex process that involved local evolution and contributions from other areas (Africa and North America) at different times of the Cenozoic (Supplemental Material 1, Table 1, available online). Few extinctions of this highly varied fauna occurred during the Pleistocene, but the great diversity of species came to an end 10,000 years ago (kya). In South America the severity of the extinctions was greater than in other continents: approximately 50 genera and 83 species of megafauna and megaherbivores became extinct in the period between 20 and 10 kya (Barnosky et al.,

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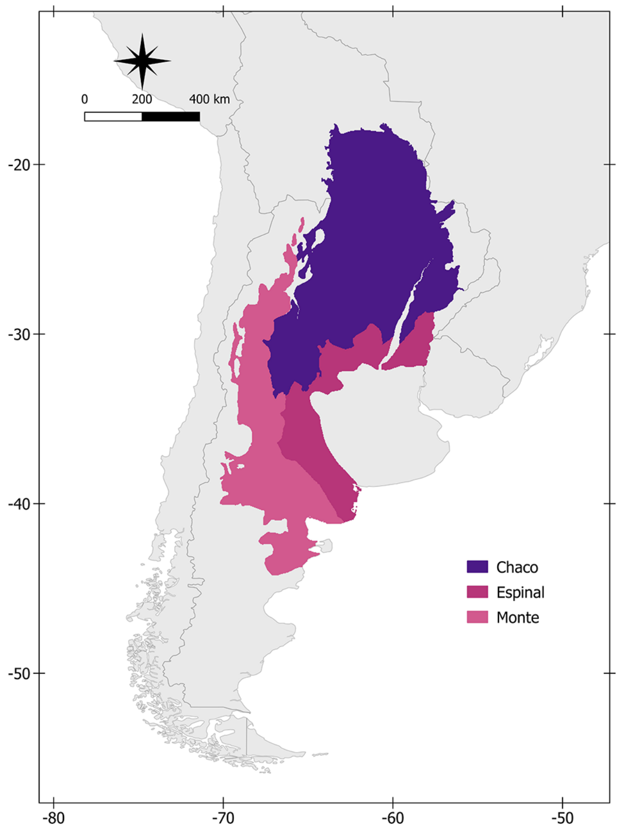

Figure 1. Chaco, Espinal, and Monte phytogeographical provinces.

2004; Cione et al., 2009; Defler, 2019; Martin and Klein, 1984). The causes of these extinctions are the subject of intense debate. Hypotheses such as extraterrestrial impacts (Firestone et al., 2007; Pino et al., 2019) and the occurrence of a hyper-disease (Lyons et al., 2004; MacPhee and Marx, 1997) have been proposed. However, most researchers favor the idea that Pleistocene megafaunal extinctions were caused by the effect of climate change, by human impacts or by a combination of these factors, although there is no consensus about the relative importance of each one (Barnosky et al., 2004; Bartlett et al., 2016; Broughton and Weitzel, 2018; Lemoine et al., 2023; Lima-Ribeiro and Felizola Diniz-Filho, 2013; Pires et al., 2020; Prates and Perez, 2021). In support of these hypotheses, it has been proposed that the disappearance of the megafauna occurred concomitantly with two events: the arrival of the first human groups to South America and the ecological changes produced by the Last Glacial Maximum and minor disturbances that followed, such as the Antarctic Cold Reversal (Prates et al., 2020; Prates and Perez, 2021; Villavicencio et al., 2016).

Beyond the causal factors of the extinctions, it is clear that over millions of years these animals established dynamic relationships with their environment, greatly impacting the development of the plant communities with which they interacted (Barlow, 2000; Janzen and Martin, 1982). In southern South America, these coevolutionary relationships were surveyed by Guimarães et al. (2008) and Donatti et al. (2007) in some areas of Brazil with high density of megafauna in the past, such as the Amazon, Cerrado, Caatinga, Atlantic Forest and Pantanal. However, the examination of vegetation characteristics to address these possible relationships between plants and extinct megafauna has not yet been systematically investigated in the central region of Argentina, which includes the phytogeographic provinces of Espinal, Monte, and Chaco (Figure 1). Particularly, these provinces comprise part of the core dispersal area of extinct megafauna (Prates and Perez, 2021; Varela and Fariña, 2016), and are ecologically similar to where the largest number of plant species with anachronistic traits was found (i.e. Pantanal area; Donatti et al., 2007; Guimarães et al., 2008). Therefore, the research of the coevolutionary relationships between extinct megafauna and vegetation in central Argentina would be useful for a deeper understanding of megafauna ecology and present environments, while allowing to examine whether the results obtained for the regions of Brazil can be generalized to other nearby areas.

The investigation of feeding processes by extant herbivores has allowed to postulate that large species are particularly effective dispersers of some fruits (Barlow, 2000; Feer, 1995; Janzen and Martin, 1982), that there is a positive relationship between body size and the capacity to damage plants (Owen-Smith, 1988, 2021), and that plants respond to high rates of herbivory by vigorously defending themselves through chemical and mechanical defenses, such as secondary metabolic compounds and spinescence (Cooper and Owen-Smith, 1986; Owen-Smith, 1993). Also, Dantas and Pausas (2022) showed that wood density is a trait that confers protection against herbivory by large animals. On the other hand, recent researches indicate that the consequences of megafauna disappearance in post-Pleistocene communities were uneven: in some places the impact was important, such as in Australia (Adeleye et al., 2023), while in others it was not (Barnosky et al., 2015). In areas where an important impact has been observed, some of the consequences of the disappearance of these animals were the loss of certain interactions between megaherbivores and vegetation (e.g. loss of seed dispersal mechanisms, shrub invasion, and increased susceptibility to fire).

Therefore, based on previous studies (Barlow, 2000; Guimarães et al., 2008; Janzen and Martin, 1982), in this article we aim to evaluate characteristics of the woody vegetation of the central Argentina to assess if they could be interpreted as a reflection of current selective pressures or as anachronisms (i.e. resulting from past relationship between megafauna and vegetation; Barlow, 2000; Janzen and Martin, 1982). For this purpose, we compiled and analyzed data on size, shape and other characteristics of fruits and seeds, as well as wood density and the presence of spines and secondary metabolic compounds. We expect that in a region with high density and diversity of megafauna in the past and similar to the previously surveyed regions of Brazil, as discussed above, there should be a large amount of vegetation showing anachronistic traits. Likewise, since it is important to consider the effect that Pleistocene extinctions and their impact on vegetation could have had in post-Pleistocene human populations, we also analyze archeological and ethnographic data to explore the probable uses of this vegetation by human populations. In this regard, we hypothesize that humans could have acted as seed dispersers after megafaunal extinctions (see also Pires et al., 2014; van Zonneveld et al., 2018). Overall, we expect that measuring the abundance of anachronistic traits in the study area will allow a better understanding of the impact of megafaunal extinctions and the functioning of past and present ecosystems.

Material and methods

Study area: Chaco, Monte and Espinal phytogeographic provinces

The Chaco-Pampean plain comprises a region of almost one and a half million square kilometers, occupying the central portion of Argentina. The area comprises three phytogeographical provinces: Chaco, Espinal, and Monte (Figure 1). The Chaco province (611,480 km^2) occupies the provinces of Chaco, Formosa and Santiago del Estero, eastern Salta, Jujuy, Tucumán, Catamarca and La Rioja, northern San Luis, Córdoba, and Santa Fe and northwest of Corrientes. Vegetationally, it is characterized by the presence of xeric deciduous forest that alternates with palm groves, savannas and grasslands (Apodaca et al., 2015; Cantero et al., 2019). The Espinal province (325,080 km^2) is distributed in a wide arc, from central Corrientes, northern Entre Rios, Santa Fe, Córdoba and San Luis, central La Pampa and southern Buenos Aires. It is characterized by the presence of dense or open low xerophilous Neltuma forests (previously referred as genus Prosopis; Hughes et al., 2022), generally occupying a single stratum, alternating with palm groves, grassy savannas, and steppes (Apodaca et al., 2015; Arturi, 2006; Cantero et al., 2019; Lewis et al., 2004, 2006, 2009; Matteucci, 2012; Sabattini et al., 2002; Torres Robles et al., 2015; Ugarteche et al., 2011). Finally, Monte province (470,408 km^2) extends from southern Salta, central Catamarca and La Rioja, east-central San Juan, Mendoza, Neuquén and Río Negro, western La Pampa and northeast Chubut. It is a phytogeographic province corresponding to a xerophilous, sammophile or halophilous shrub steppe, which alternates with scrubland and riparian forests (Apodaca et al., 2015; Cantero et al., 2019).

Data compilation and analysis

The vegetation survey was carried out from the identification of endemic species and most common vegetation assemblage based on previous works (Abraham de Noir and Bravo, 2014; Apodaca et al., 2015; Cantero et al., 2019; Demaio et al., 2015; Lewis et al., 2004, 2006, 2009; Matteucci, 2012; Sabattini et al., 2002; Torres Robles et al., 2015; Ugarteche et al., 2011). Data on fruit traits, spinescence and metabolic compounds were also surveyed from the literature (Abraham de Noir and Bravo, 2014; Apodaca et al., 2015; Cantero et al., 2019; Demaio et al., 2015). This literature was reviewed in order to have a sample of the plants that were present in the area, focusing the search on woody plants (trees, shrubs, cacti and climbing plants). From this search, lists of woody plants were made and their importance was coded by the number of citations they had. On the basis of the most mentioned plants, we created a list with those that dominate the vegetation communities in the studied provinces. For each plant, its synonymy was checked in the database of Instituto Botánico Darwinion, and the valid name provided by this institution was employed. Then, a file was created for each plant, which included: photos, taxonomic information, fruit and seed biometry data, color, fruit type, dispersal area, preferred habitat, megafauna fruit type, current, ethnographic and archeological use by humans, dispersal agent, evidence of vegetative propagation, presence of spinescence, length of spines, presence of secondary metabolites, and wood density.

An anachronism score was assigned to each plant, on the following criteria: plants that have 0–1 anachronistic trait were classified as non-anachronistic, and those with 2 (e.g. megafauna fruits and spinescence), 3 or 4 (i.e. megafauna fruits, spinescence, secondary metabolites, and dense wood) of these traits as light, medium and extreme anachronistic, respectively. In addition, online public databases were also consulted. Particularly, Seed Information Database (Society for Ecological Restoration, International Network for Seed Based Restoration and Royal Botanic Gardens Kew, 2023; ser-sid.org/), where data on weight, number of seeds and references were obtained, and the databases of Flora Argentina and the Catálogo de las Plantas Vasculares de la Flora del Cono Sur (darwin.edu.ar) of Instituto de Botánica Darwinion, for data on plants from the surveyed area. We obtained information for 191 woody plants (Supplemental Material 2, available online), which are among the most important vegetation in central Argentina. Of these, 57 species were not considered since we did not obtain for them all the data. This left a final database of 134 species of woody plants, corresponding to 37 families and 90 genera. This is approximately 16% of the 837 species of vascular plants surveyed in the total inventory of the vegetation of central Argentina (Cabido et al., 2018). In this database, we surveyed characteristics of the fruits, the presence of secondary metabolic compounds, spinescence, and wood density (see below).

Fruit traits

The main categories of plants with endozoochorous seed dispersal (i.e. dispersing through animal ingestion) are those that produce: (I) large, fleshy fruits and (II) annual herbaceous plants with small seeds (Janzen, 1984; Janzen and Martin, 1982; Spengler, 2019; Spengler et al., 2021). Therefore, plants that evolve with contrasting mutualistic systems have a particular and diagnostic morphology. Thus, many annual herbaceous plants include traits such as absence of defensive secondary metabolic compounds (toxic or unpleasant to taste) and mechanical defense structures (spines), and the presence of rapid annual growth, small indehiscent fruits on top of the plant, <2 mm seeds with hard protective coatings, rapid evolvability, high developmental plasticity, and tolerance to trampling and disturbed environments (Janzen, 1984; Kuznar, 1993; Spengler et al., 2021; Spengler and Mueller, 2019). In contrast, trees and shrubs with fleshy fruits include large fruits and seeds with high concentrations of sugars, thick pericarpal tissues, indehiscence, and other traits such as high concentrations of secondary metabolic compounds, protective structures on branches and trunk such as spines, as well as changes in plant architecture (Fuller, 2018; Purugganan and Fuller, 2009; Spengler, 2019; Spengler et al., 2021). Throughout the development of plant mutualisms studies, the realization that some trees and shrub's fruits do not have extant dispersers led to the concept of "ecological anachronisms" (Barlow, 2000; Janzen and Martin, 1982). Therefore, we chose the traits associated with fruits and seeds as a way to select those plants that showed the syndrome of "dispersal by megafauna." For the survey of fruits and seeds we follow Guimarães et al. (2008), as they introduce operational definitions based on previous analyzes of fruits consumed by current megaherbivores (Feer, 1995). These authors point out that the forest elephant (Loxodonta africana cyclotis) primarily consumed two kinds of fruits: fleshy fruits from 4–10 cm in diameter with up to five large seeds (Type I) and fleshy fruits larger than 10 cm in diameter with numerous small seeds (Type II). These observations offer formal and operative criteria for the distinction between fruits dispersed by megafauna (hereafter megafaunal fruits) and fruits dispersed by other agents (non megafaunal fruits). Although extinct megaherbivores could also have been efficient dispersers of the seeds of other plants and vice versa (Teng et al., 2023), in this work we consider the same criteria for comparative purposes. Therefore, we compiled data on fruit length (mm), fruit width (mm) and fruit mass (g), number of seeds per fruit and individual seeds mass (g) for the species included in our survey (Supplemental Material 2, available online).

Chemical defenses: Secondary metabolic compounds

Plants generate various secondary metabolic products, compounds that are necessary for their interaction with the environment and that are produced in response to stress—for example, terpenes, phenolic compounds, polyketides, and alkaloids, among others (Crozier et al., 2006; Iason et al., 2012). Among its functions are inter and intra-specific communication and the defense against factors such as solar radiation, freezing, pathogens and parasites. One of the most important roles is to discourage or prevent the consumption of plants by herbivores, especially on leaves and other vegetative structures (Owen-Smith, 1993). There is evidence that mammal body size is related directly to the palatability of certain plants, with megafauna having more tolerance to high concentrations of secondary metabolites than smaller mammals (Kistler et al., 2015). In environments with the presence of extant megafauna, plants show high concentrations of these compounds in reaction to high rates of herbivory (Owen-Smith, 1993; Owen-Smith et al., 2019). Taking this into account, we compiled data on the presence of secondary metabolic compounds from the specific bibliography (Supplemental Material 2, available online).

Mechanical defenses: Spinescence and wood density

A typical response of vegetation to herbivores presence and to high rates of herbivory is the occurrence of plants heavily armed with spines (Cooper and Owen-Smith, 1986). These observations have generally been made in the Paleotropical domain, but the presence of spinescence has also been recorded in the Neotropics (Owen-Smith, 2021). In order to analyze the presence of these traits in those plants that also met the operational characteristics of fruits dispersed by megafauna outlined by Guimarães et al. (2008), we compiled data on the presence of spinescence in our database, as well as the size of the thorns (Supplemental Material 2, available online). On the other hand, it has been observed that current Paleotropical megafauna, especially the African (Loxodonta africana) and Asian (Elephas maximus) elephants can exert heavy damage on the trees during the feeding process (Charles-Dominique et al., 2019; Owen-Smith et al., 2019; Pradhan et al., 2007). We think that a similar but even more extreme situation could occur in South America, given the high number of megabrowser species, which included two species of gomphotherids, one species of megatheriid, three species of mylodons, one species of megalonychid, and two species of glyptodonts weighing more than 1000 kg (Owen-Smith, 2013). By comparison, Africa has two, Australia one, North America two and Eurasia three species of browsers over 1000 kg (Owen-Smith, 2013). In this context, we propose that an evolutionary trait that confers resistance to mechanical destruction, such as the density of wood, could possibly have been quickly selected (Berzaghi et al., 2023; Read and Stokes, 2006; Swenson and Enquist, 2007). Therefore, as a way of evaluating the general architecture of woody plants, we use wood density values compiled by Chave et al. (2006, 2009), and the differences between the wood density of the study area of Central Argentina and the regions analyzed by these authors were explored through an ANOVA analysis.

Evidence of consumption: Fruit size and size of the masticatory apparatus of pleistocene megafauna species

In order to detect large herbivores consumption of megafaunal fruits, we compiled published information about estimates of the megaherbivores's masticatory apparatus size, under the premise that there would be correspondence between the sizes of the fruits and the oral cavity of the megafauna. We obtained data for the following species: E*quus neogenus, Lestodon armatus, Toxodon platensis, Scelidotherium leptocephalum, Doedicurus clavicaudatus, Megatherium americanum, Glossotherium robustum*, and *Notiomastodon platensis*. We chose these species, which are a subset of all those in the area, because they represent the main extinct orders and families. In addition, they are representative of all animal body size categories that we defined. Also, these species are characterized by different dietary adaptations: equids, toxodonts, and armadillos had diets with high grass content and a component of mixed diets, and prosbocids, megatherids and some mylodons were browsers. Values were compared with seed-dispersing mammals and birds currently inhabiting the study area (Supplemental Material 1, Table 2, available online).

Human use of possible megafaunal dispersal syndrome plants

In order to detect probable human use of plants with possible megafaunal dispersal syndrome, discuss the importance it acquired for human populations, and the impact its use had on its dispersal after the extinction of megafauna, we reviewed the ethnographic and archeological literature of central Argentina and surrounding areas. The variables considered were dietary consumption, their use for construction, medicine, poison, insecticide, firewood, trade (when there was evidence of alien or transported plants), and to manufacture artifacts. To accommodate the archeological cases in which the presence of a certain plant species was recorded but data about its use was not provided, the N/D category was included. The archeological site of provenance of the data and the region in the case of ethnographic observation were recorded (Supplemental Material 3, Tables 1 and 2, available online). Finally, following Guimarães et al. (2008), we coded the current use of plants by humans with category 0 (no use by humans), 1 when there was local consumption, 2 when consumption occurred in plantations in a region and 4 when it exceeded regional use and was cultivated commercially.

Table 1. Number of species per family exhibiting traits that suggest possible interactions with megafauna.

Family	Megafruits	Spinescence	Secondary metabolites
Achatocarpaceae		1	1
Anacardiaceae		5	9
Annonacea	2		2
Apocinaceae	2	1	3
Araceae	2		2
Arecaceae	3	5	2
Asteracea			1
Bignoniaceae	5		4
Boraginaceae			1
Bromeliacea	3	3	3
Cactaceae	5	5	5
Cannabaceae		1	1
Capparaceae	2	1	4
Caricaceae	1		1
Celastracea		1	2
Euphorbiaceae		1	3
Fabaceae	51	30	42
Malvaceae	1	1	1
Meliaceae	1		1
Myrtaceae			2
Nyctaginaceae		1	1
Olacaceae		1	1
Passifloraceae	1		1
Poligonaceae			3
Ranunculaceae			1
Rhamnaceae		4	4
Rosacea			2
Rutaceae		1	1
Salicaceae			1
Santalacea	1	2	2
Sapindaceae			2
Sapotaceae		1	1
Simaroubaceae		1	1
Solanaceae	1		1
Ulmaceae	1		
Zygophyllaceae	4	1	4
Subtotal	86	67	116
Total plants	134	134	134

Results

We compared the size (width and length) of fruits in our database. Under the previously indicated operational definitions of Type I and II of fruit plants in Guimarães et al. (2008), 64% of the woody vegetation for which we obtained data present characteristics of fruits possibly dispersed by megafauna (Table 1). They correspond to 17 families and 52 genera (Supplemental Material 2, Table 1, available online). Of this total, most of the species with fruits with anachronistic features belong to the Fabaceae family,

Figure 2. Photographs of some plants considered in this study, showing fruits: (a) Ceiba chodatii, (b) Vachellia caven, (c) Pseudananas sagenarius, (d) Passiflora caerulea, (e) Aspidosperma quebracho-blanco, (f) Cereus forbesii, (g) Vachellia aroma, (h) Geoffroea decorticans, (i) Senna aphylla, (j) Chloroleucon tenuiflorum, (k) Vachellia astrigens, (l) Neltuma alpataco; and spines: (m) Gleditzia amorphoides, (n) Acrocomia aculeata, (o) Ceiba chodatii. Images modified from Darwinion Botanical Institute (http://www.darwin.edu.ar/).

followed by Cactaceae, Bigognaceas, Zygophyllaceas, Capparaceas, and Arecaceae families.

Figure 2 shows some examples of these fruits. When we compare the sizes of these fruits with those of the phytogeographical provinces of Brazil, they are similar, although the fruits of these last regions are wider, while those of our study region present higher values in fruit length. This is possibly linked to the importance of Fabaceae in the database, which have long and narrow fruits in diameter. Another portion of the plants included in the database has smaller sizes and possibly depends on other dispersing agents. Figure 3 also shows the muzzle and beak width of extinct and extant seed dispersing animals in the study area. The measurements considered were palatal width (PAW) and muzzle width (MZW) for current and extinct mammals and mouth width or rectal commissure and culmen or beak length for birds (sensu Caziani, 1996; Fariña et al., 1998; Janis and Ehrhardt, 1988; Mendoza et al., 2002; Montaldo, 2000; Supplemental Material 2, Table 2, available online). Muzzle sizes of extinct animals almost do not overlap with measures of extant mammals and birds, being the extinct fauna an order of magnitude wider. When possible megafaunal dispersed fruit size and non-megafaunal fruit size are compared (Figure 3), together with palatal size of extinct and extant seed-dispersing animals, it is evident that allegedly megafaunal fruits are found mostly in the range of muzzle sizes of extinct fauna, while non-megafaunal fruit falls within muzzle sizes of extant mammalian and avian dispersers. These results do not imply that extant mammals and birds cannot be involved in the movement and dispersal of plants with possible megafaunal dispersal syndrome, but it can be pointed out that they may not be as optimal for long-distance endozoochory as extinct megafauna possibly were.

Figure 4 provides descriptive measurements of megafaunal and non-megafaunal fruits and seeds. The megafruits—that is, fruits possibly dispersed by megafauna—have an average diameter of 22.65 mm (Figure 4a) and a high average mass of 30.42 g (Figure 4b). Moreover, the number of seeds per fruit is 45.41 (Figure 4c), while each individual seed has an average mass of 0.90 g (Figure 4d). It is worth mentioning that the dispersion of the dimensions and traits values selected to describe the fruits and their seeds analyzed in this work is manifestly greater in those from plants possibly dispersed by megafauna. Likewise, within this set, the larger measurements are constituted by outliers that visibly deviate from the mean values for all the variables selected. On the contrary, the dispersions of the fruits dispersed by other agents are smaller, constituting a more clearly delimited assemblage.

Of the total ($N=134$), 50% of plants show spinescence (Table 1 and Figure 5). The average length of the spines is 52.83 ± 9.55 mm. Regarding the presence of secondary metabolites, 86.57% of the plants in our database also have those compounds (Table 1 and Figure 5).

Most of the surveyed trees and shrubs present heavy and very heavy density woods. The average wood density in the database is

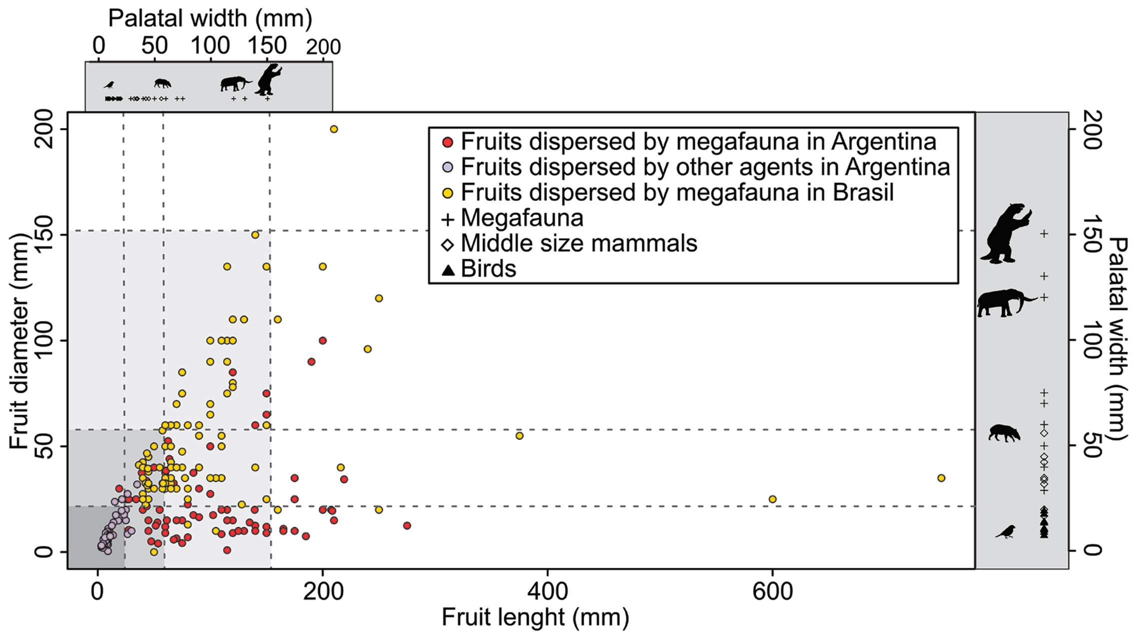

Figure 3. Dimensions (diameter and length in mm) of possible megafaunal dispersed fruits from Argentina and Brazil versus non-megafaunal fruits from Argentina and muzzle and beak size of extant and extinct mammals and birds. Extinct mammals: Glyptodon reticulatus, Panochtus tuberculatus, Doedicurus clavicaudatus, Megatherium americanum, Lestodon armatus, Glossotherium robustum, Scelidotherium leptocephalum, Macrauchenia patachonica, Toxodon platensis, Hippidion principale, Stegomastodon superbus; Extant mammals: Lama guanicoe, Vicugna vicugna, Blastoceros dichotomus, Hippocamelus bisulcus, Mazama americana, Ozotocerus bezoarticus, Tapirus terrestris, Dicotyles tajacu, Tayassu pecari; Birds: Leptotila verrauxi, Columba picazuro, Pitangus sulphuratus, Elaienia parvirostris, Turdus rufiventris, Turdus amaurochalinus, Thraupis sayaca, Stephanophorus diadematus, Ortalis canicollis, Elaienia albiceps.

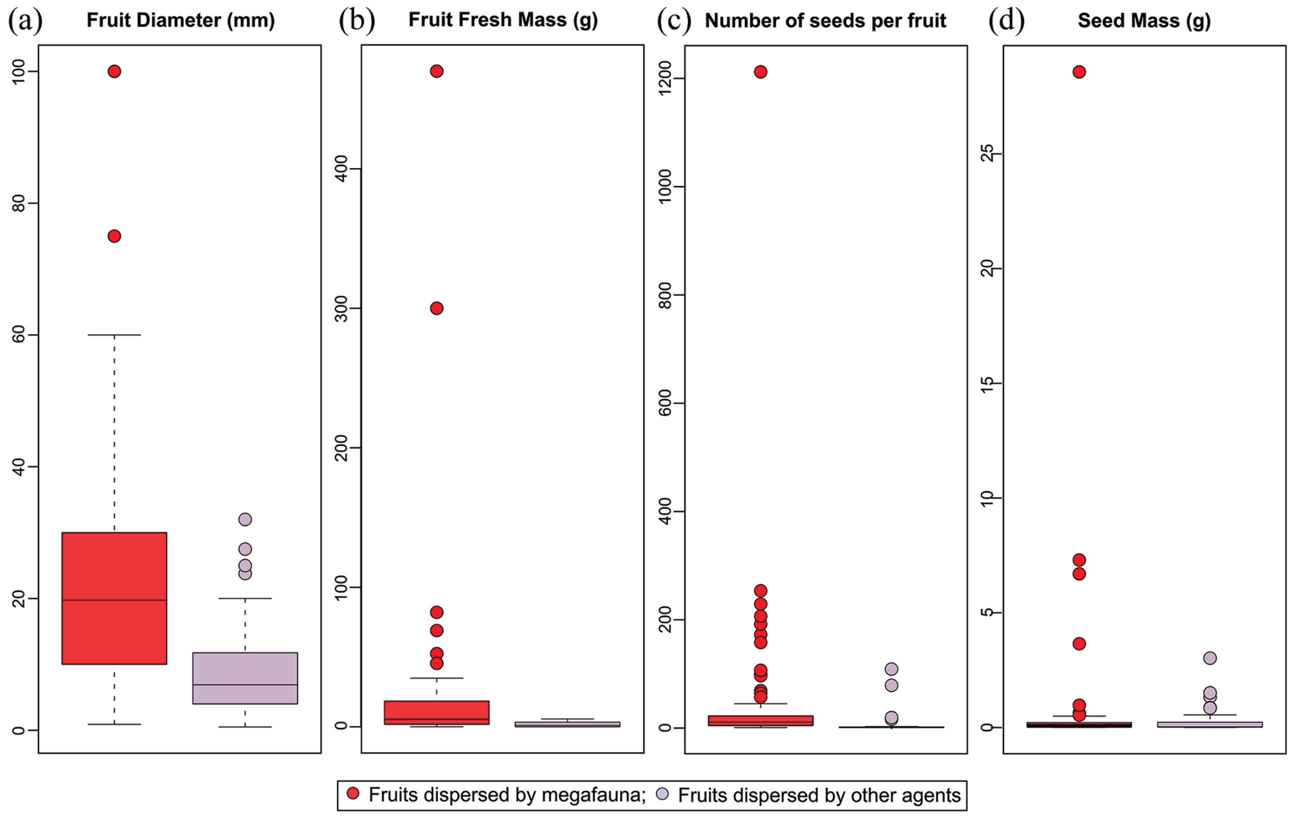

Figure 4. Boxplots of most diagnostic dimensions of the fruits analyzed and their seeds. (a) Fruit diameter. (b) Fruit fresh mass. (c) Number of seeds per fruit. (d) Seed mass.

0.686 g/m^3. To put these results in proper context, the mean wood density of megafauna plants is higher than the South, Central, and North American mean (Figure 5). It is also higher than the world average (Chave et al., 2006, 2009). To explore these differences, we perform an ANOVA using data from Chave et al. (2009) and compared Central Argentina versus North America ($F=27.23$, $p=0.000000375$), Central America ($F=12.68$, $p=0.000408$), South America (tropical, excluding our study area) ($F=3.036$, $p=0.0815$), and the world average wood density ($F=5.943$, $p=0.0148$). All results are statistically significant with the

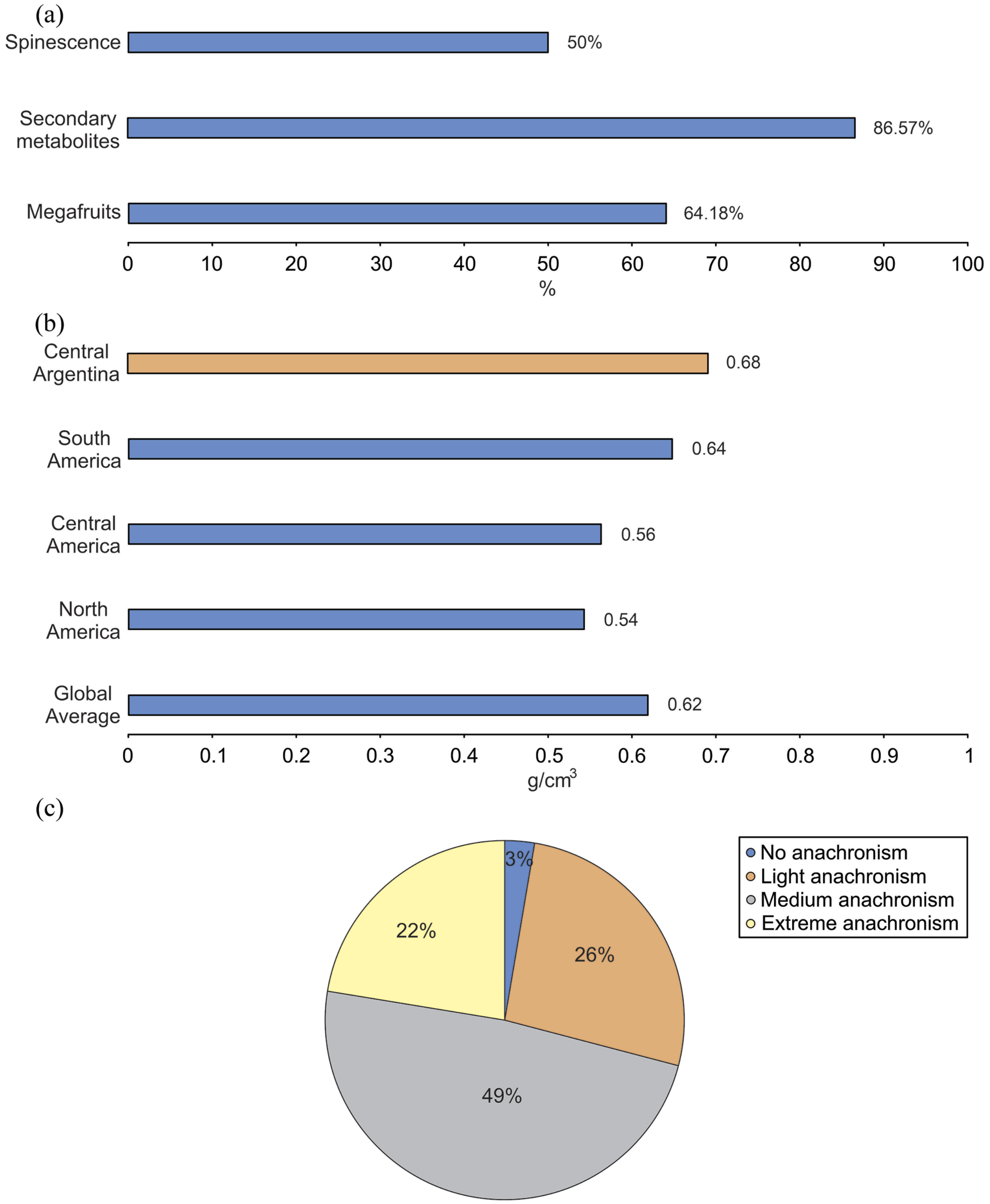

Figure 5. (a) Percentage of plants with spinescence, secondary metabolites and megafaunal dispersed fruits (*N* = 134). (b) Mean wood density value of megafaunal plants compared with South, Central, and North American and global wood density mean (data from Chave et al., 2009). (c) Anachronism scoring (*N* = 76).

exception of the comparison with the rest of South America, which makes sense since it includes our group of woods within a similar and smaller sample size.

The studied plants make a rapid appearance (late Pleistocene-early Holocene) in the archeological record—for example, Cueva Huenul, Los Morrillos, Gruta del Indio (Llano and Barberena, 2013; Roig, 1993; Semper and Lagiglia, 1962; Figure 6a). The most conspicuous archeological uses were as fuel material, food, manufacturing material for artifacts and, probably, as medicine. The ethnographic record provides a richer description of the importance of these plants for human populations. In this regard, multiple uses have been reported ethnographically. To the main uses recorded in the archeological record is added the observation of their use as construction materials, poisons, insecticides, as well as a variety of uses related to magic (Agra et al., 2007; Arenas, 2003, 2016; Karlin, 2016; Noelli, 1993; Saur Palmieri et al., 2018; Figure 6b). These species are of economic importance even today, and Figure 6c shows the degree of the current use by humans. The review of the specific literature allows us to infer that the choice by humans seems to be linked to the characteristics that this vegetation acquired in co-evolution with the megafauna. In this sense, it is observed that the large fruits are especially used

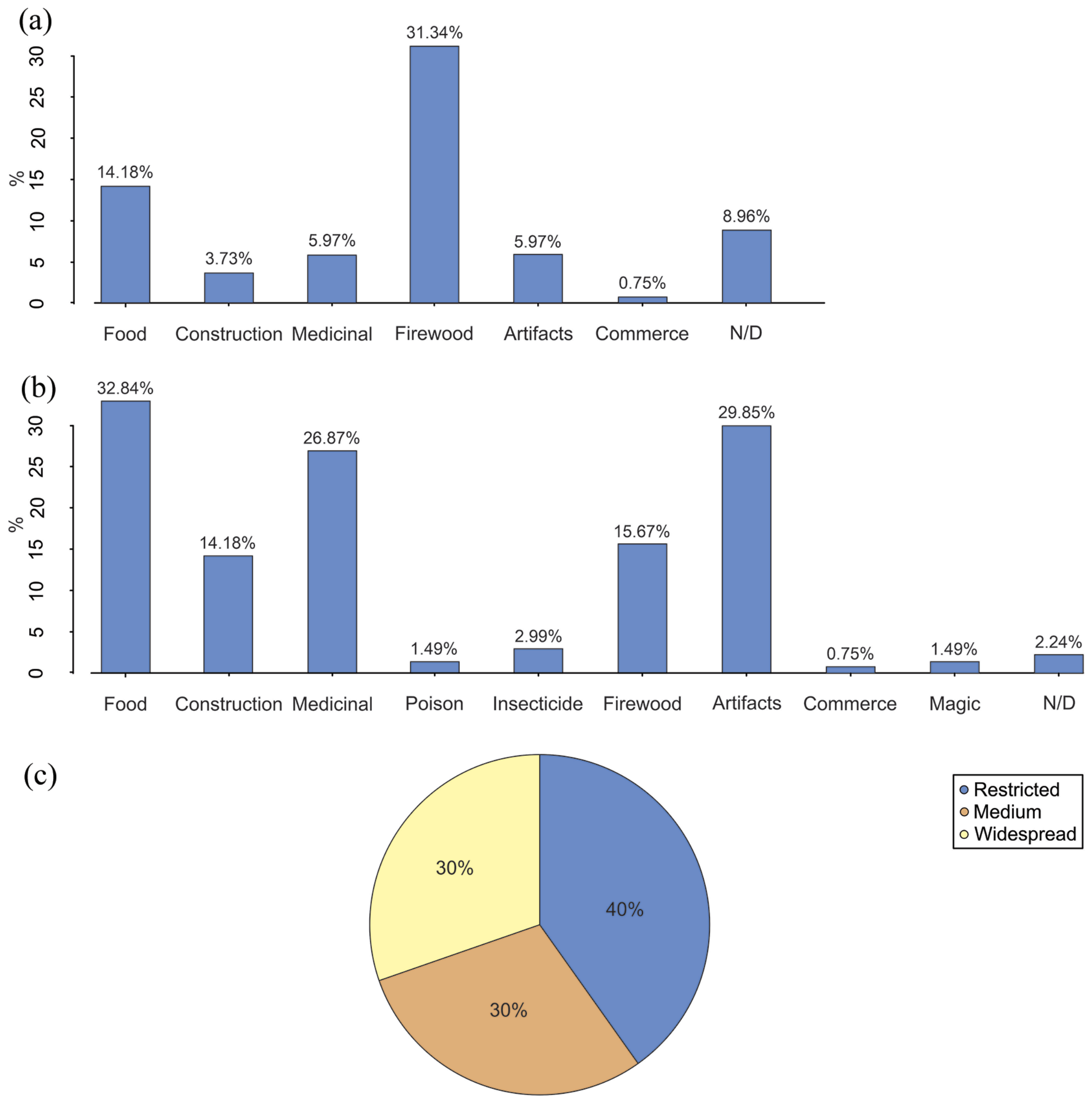

Figure 6. (a) Percentage of megafaunal plants with archeological use ($N = 134$). (b) Percentage of megafaunal plants with ethnographic use ($N = 134$). (c) Current human use of megafaunal plants ($N = 132$); restricted: local use, medium: regional use, and widespread: extra-regional commercial use (e.g. plantations).

for food (e.g. Geoffroea, Cereus, Opuntia, several species of Neltuma, Celtis, Annisocapparis, Vachellia), that hardwoods have been systematically selected as construction material (e.g. several species of Neltuma, Vachellia, Anadanthera), firewood (Litrhraea, Schinopsis, Schinus, Aspidoderma, Celtis, Tecoma, Neltuma) and utensils manufacturing (Enterolobium, Cereus, Erythrina, Neltuma, Vachellia, Schinus, Geoffroea). In addition, the use of secondary metabolites has been reported as substances for medicinal use (Enterolobium, Erythrina, Neltuma, Vachellia, Passiflora, Schinus, Aspidoderma, Jacaranda, Tecoma, Opuntia, Senegalia, Anadanthera, Geoffroea), as insecticides (Synandrospadix, Thaumatophyllum, Stetsonia, Bulnesia) and as poisons (Anadanthera, Enterolobium) (see Supplemental Material 3, available online).

Discussion

The pattern: Anachronistic traits on vegetation in the study area

Our results indicate that a high proportion of the vegetation in central Argentina has fruits whose characteristics are compatible with those consumed by megafauna in Asia and Africa. Likewise, these plants show a high frequency of spinescence, secondary metabolic compounds and high-density wood. Some arguments have been put forward to explain the vegetation traits we analyzed. Typically, for example, spinescence has been associated with a strategy to reduce radiation flux (Nobel, 1988) or assist a plant to climb (Grubb, 1992). On the other hand, one possibility is that megafruits seeds were dispersed by extant species. For example, Teng et al. (2023) observed that in Southeast Asia plants with megafruits are also dispersed by small to medium terrestrial mammals. Likewise, the density of wood has been related to abiotic variables such as height above sea level, temperature and precipitation (Chave et al., 2006, 2009). Lastly, secondary metabolites fulfill multiple functions in plants, so their presence may not necessarily be related to conditions of high herbivory (Crozier et al., 2006; Iason et al., 2012). Although these are possibilities to consider and may be factors that act synergistically with the impact of extinct megaherbivores, they do not fully explain the presence of these traits together. In this regard, the current vegetation of Chaco, Monte and Espinal shows characteristics that are not easily explained from the interactions with extant native herbivores. Several authors have pointed out the scarcity of herbivore species, especially macro and megaherbivores. The current species also have low densities (Borghetti et al., 2019; Bucher, 1987), and the most important herbivore niches are occupied by ants and termites (Costa et al., 2008; Owen-Smith, 2021). However, many of the investigated plant species show adaptations for seed dispersal by macro and megaherbivores. Additionally, the woody vegetation of the surveyed phytogeographic provinces shows an important presence of adaptations against herbivory, particularly against predation by vertebrates.

A possible explanation for the presence of these paradoxical features in the woody vegetation is that they co-evolved with a currently extinct faunal group (i.e. Pleistocene megafauna). In the first place, this vegetation overlaps with the core dispersion of extinct megafauna (Prates and Perez, 2021; Varela and Fariña, 2016). In this regard, the reconstructed distribution of megafauna species during the Pleistocene using species distribution models underscores the open and closed vegetation mosaics in which most of these species lived (Fariña et al., 2013). These environments have no modern analogs in the area (Bucher, 1987), and it is probable that the physiognomy of the current vegetation is very different from that which occurred up to 10,000 years ago.

Likewise, a very important factor is the number of extinct species and their diets. Browsers had more species than grazers in the Pleistocene (Owen-Smith, 2013), which highlights the importance of woody vegetation for megafauna. South America had more than twice as many species (~16) of megaherbivores (over 1000 kg) than any other continent, and fewer small herbivores. Most of the extinct South American mammals exceeded 100 kg (Faurby and Svenning, 2016; Smith et al., 2003). Furthermore, South America had the largest and most diverse browser megafauna in the world (Catena and Croft, 2020; Owen-Smith, 2021; Owen-Smith, 2013). Almost 60% of South American mammals were browsers, and only 36% were grazers (Archibald et al., 2019; Owen-Smith, 2013). One implication of this is that present-day South American fauna is very different from that which inhabited the region throughout its evolutionary development (Catena and Croft, 2020).

In addition, the evidence recovered from stable isotopes analysis (De Melo França et al., 2015; Domingo et al., 2012, 2020; Tomassini et al., 2020), micro and meso-wear (Asevedo et al., 2012; Corona et al., 2018) as well as plant macroremains recovered in coprolites (Marcolino et al., 2012; Martinez Carretero et al., 2013) indicate that the Pleistocene megafauna consumed a high component of woody plants. These animals were mostly predominantly mixed-feeder and fed on both C3 and C4 plants (Tomassini et al., 2020). This again indicates the "ecotonal" character of these species (see Fariña et al., 2013) and is consistent with the premise that species with larger body sizes have greater dietary flexibility. Likewise, the importance of woody vegetation for megafauna is also evidenced by the presence of South American grasses less adapted to supporting high rates of herbivory (Owen-Smith, 2021; Visser et al., 2016).

Coevolution with extinct fauna: A plausible explanation

Some characteristics of the woody vegetation of this part of South America allow us to glimpse dynamic mutualistic relationships with extinct fauna. In South America the dominant tree clades are legumes Papillonoideae and Detariodeae, with contributions from the subfamily Vochysiaceae (Archibald et al., 2019). This is reflected quantitatively by the clear dominance of Fabaceae among the plants that present megafaunal dispersal syndrome.

In Africa and Asia, with extant populations of large browsers, the vegetation presents defenses such as spines and secondary metabolites, that may help counteract the high rates of herbivory (Scogings and Sankaran, 2019). Two traits of ecosystems with macro and megaherbivores are replicated in Central Argentina dry forest: the presence of physical (i.e. spinescence and high wood density), and chemical (i.e. secondary metabolic compounds) defenses. In our study area, as in a good part of Tropical America (Cooper and Owen-Smith, 1986), plants are heavily armed with spines, thorns, and prickles. Observations in extant species indicate that the basic function of spinescence in woody vegetation is not to prevent herbivory, but to delay it by forcing the consumer to take small bites (Cooper and Owen-Smith, 1986). Besides, it is not clear that the plant incurs high costs by producing spines (Charles-Dominique et al., 2019), but theoretically plants could present them only if their costs are lower than those that would result from losses due to herbivory (Gowda, 1996). This does not seem to be the case in the study area, where the herbivorous ecological niche is mostly occupied by insects such as leaf-cutter ants (Bucher, 1987; Costa et al., 2008), which are not affected by the presence of structural defenses such as spines. (Owen-Smith, 2021). We also present the idea that tree wood density was linked to selective pressures imposed by megafauna (Dantas and Pausas, 2022), as megaherbivores, particularly elephants, are capable of causing intense physical damage to the trees, even killing it (Asner and Levick, 2012; Chafota and Owen-Smith, 2009; Morrison et al., 2016; Owen-Smith, 2021; Owen-Smith et al., 2019). This constitutes a powerful selective force to generate tissues resistant to mechanical stress, which would be reflected in the density of the wood. This is corroborated in our area since many trees have hard or very hard wood, above the world and South American average (Chave et al., 2006, 2009). It is interesting to note that the presence of hardwood forests is currently recorded in Africa and Southeast Asia (Den Outer and Van Veenendaal, 1976; Dudley et al., 1992; Habel et al., 2017; Pradhan et al., 2007), in addition to South America and eastern North America (Perrotti et al., 2022; Weber, 2011). In the first two places there are still populations of elephants, while in South America there were at least two species of gomphotherids. Moreover, in this region the presence of extinct giant ground sloths and glyptodonts was registered (Cione et al., 2009). Even when there are no modern analogs for these taxa, we expect a heavy damage on vegetation by these animals, based in body size and the fact that there were mostly browsers (Supplemental Material 1, Table 2, available online). Also, in eastern North America the presence of mastodons was recorded (Haynes, 1993).

The available evidence on defenses against herbivory topic suggests an evolutionary pattern in which plants developed various strategies that prevent the loss of their foliage at the hands of herbivores. A characteristic way of inhibiting its consumption is by incorporating secondary metabolites. In woody vegetation, these compounds generally take the form of tannins or other phenolic compounds, such as terpenes, polyketides, and alkaloids (Crozier et al., 2006; Iason et al., 2012; Scogings and Sankaran, 2019). In the case of macro and megaherbivores, these compounds have been observed to act by interfering with digestion, affecting microbes that degrade cellulose in the stomach (Owen-Smith, 1993, 2021). As in the case of spines, the metabolites that serve to stop insects do not work on large mammals and vice versa, and do not stop herbivory completely, but instead restrict rates of leaf loss and impose physiological costs on their consumers. Species with evidence of dispersal syndrome by megafauna such as Tecoma stans, Sesbania virgata, Enterolobium contortisiliquum, Vachellia astrigens, Synandrospadix vermitoxicum, Vachellia aroma, Sesbania virgata, Caesalpina paraguariensis, Cynophalla retusa, Anisocaparis speciosa, Opuntia quimilo, and Aspidoderma quebracho-blanco show concentrations of secondary metabolic compounds that cause cattle to avoid them or in the case of being consumed, even causing death (Arenas, 2016; Braggio et al., 2002; Roger, 2020; Seigler et al., 1983; Slanis, 2018). As previously pointed out, this is not an isolated characteristic of some species in the area: more than half of the studied plants present some of these compounds.

Nascimento et al. (2020) suggested that some characteristics are associated with each other. These authors, for example, propose an association between megafauna fruit size and color and spinescence in neotropical palm species. In our case, we found similar trade-offs, such as the presence of megafauna fruits and spinescence. In some species this can be expanded to include secondary metabolites and wood density. As Janzen (1979) and Barlow (2000) pointed out, the presence of anachronistic traits in an organism is not a matter of all or nothing, but of degrees of anachronism: every organism is anachronistic in some sense, that is, it presents adaptations to past environments. (Barlow, 2000; Janzen, 1979). Barlow (2000) has suggested that we should abandon the binary concept of anachronist or non-anachronist trait or organism and think of anachronisms as a continuum. In our case, it allowed us to categorize our vegetation sample in terms of a simple scale that could classify the species as moderate, substantial and extreme anachronisms according to the characteristics presented. Besides, variables such as fruit size, spinescence and presence of secondary metabolites were derived from the observation of the herbivory patterns of current macro and megaherbivores in Africa and Asia (Feer, 1995). However, there are no modern analogs for many of the extinct South American megafauna, particularly megatheriids, mylodons, armadillos, and notoungulates. It is necessary to combine different lines of evidence to account for the adaptations of these animals. For example, from functional analysis it is evident that many of the South American megafauna were burrowers (Bargo et al., 2000; Vizcaíno et al., 2011). It would be interesting to explore in the future whether plant species with underground storage organs have adaptations to interact with these species. In this sense, it is possible that there are syndromes not yet described, such as those that would occur among burrowing megafauna, plants with underground storage organs/geophytes, spinescence, secondary metabolites, and epizoochory, as manifested by several plant species in Pampa and Patagonia.

Ecological and evolutionary changes after the extinction of the megafauna: The role of humans in the dispersal of megafaunal plants

The megafauna extinction must have had profound consequences for the Holocene ecosystems in the study area. This occurred on three scales, physiological/behavioral, ecological, and evolutionary (sensu Galetti and Dirzo, 2013). On a physiological/behavioral scale, the extinction of megafauna disproportionately impacted the megaherbivorous niche and within it, the browser niche. Among the main implications we find that after megafauna extinctions, Central Argentine environments went from being regulated by herbivores (Top-Down) to being regulated by physical factors that mediate the availability of nutrients (Botton-Up), such as fire, precipitation and soil chemistry (Mistry, 1998; Ruggiero et al., 2002).

On an ecological scale, among the main effects we find the loss of seed dispersal mechanisms. This absence often results in assemblages of closed vegetation dominated by shrubs, and monospecific sets of plants (“quebrachales,” “caldenares,” “talares,” “babacuais”) (Chapman and Chapman, 1995; Donatti et al., 2007). In certain plant species (i.e. Neltuma spp.) this has led to problems such as shrub encroachment (Cabral et al., 2003). Another change in vegetation associated with the extinction of megafauna was the increase in woody cover (Doughty et al., 2016). This, in turn, produce a reduced density of some species such as the guanaco, which avoid areas of closed and thorny vegetation such as those that dominate most of the region today (Alzogaray, 2008; Cuéllar Soto et al., 2017; Segundo et al., 2004; Sosa and Sarasola, 2005). The more closed and monospecific vegetation, in turn, is important when considering changes in fire regimes. The disappearance of megafauna and the increase in tree cover could facilitate the increase in flammability of the central zone of South America (Karp et al., 2021; Pinter et al., 2011). Also, abundant ethnographic information indicates that humans used fire extensively to create vegetation patches suitable for game species and to create corridors that facilitated mobility (Arenas, 1981, 2003; Arenas and Porini, 2009; Métraux, 1946; Scarpa and Arenas, 2004), controlling for the effects of the disappearance of megaherbivores (Pinter et al., 2011).

The megafaunal extinction also has had a direct impact on mammalian diversity, leaving post-Pleistocene communities composed mainly of mesoherbivores and mesopredators (Pires et al., 2020). This is reflected in the structure of the current fauna, which presents a low variety and density of herbivores and whose largest representative is the tapir (Supplemental Material 1, available online). Regarding the consequences of megafauna extinction for humans, our results indicate that the relationship between humans and megafaunal dispersed plants is long-standing and operated at multiple levels. These plants appear abundantly in the archeological record, show multiple uses in the ethnographic record, and continue to be used today. It is important to note that the selection of megafaunal plants by humans is directly linked to the characteristics that this vegetation acquired in possible coevolution processes with the megafauna: large fruits (food uses), hardwoods (construction, firewood and utensils) and the presence of secondary metabolites (medicines, insecticides and poisons). This long-standing familiarity suggests an important role in the dispersal of megafaunal plants by humans after their extinction 10,000 years ago. Humans were not strictly redundant with megaherbivores in their dispersal role, as they modify long-distance dispersal patterns, change dispersal routes, and favor certain plants over others (Bullock et al., 2018). However, for many species humans became even better dispersers by expanding the geographic range of plants that would have suffered range contractions after the disappearance of megafauna (van Zonneveld et al., 2018). Furthermore, the dispersal and management of plants initially dispersed by megafauna by humans may have played a very important role in the domestication process (Spengler, 2020; Spengler et al., 2021; van Zonneveld et al., 2018). On the other hand, certain traits of megafauna plants, such the ability to fix nitrogen in Mimosidae and Papillonoidae, is only beneficial with a high phosphorus intake. In soils deficient in this element, the disappearance of the input provided by the excrement and urine of megafauna species has been calculated to result in a 98% reduction in phosphorus flux (Doughty et al., 2013). Poor soils such as the ones present in the study area (Rozas et al., 2012) combined with the absence of megafauna and the presence of few and solitary mesoherbivores proves that the only compensatory source of phosphorus for these species are human populations. The spatial redundancy observed between monospecific assemblages of some of these plants with prehistoric human settlements (e.g. Neltuma spp.; Roig, 1993) is possibly due to the high nutrient conditions that characterize human occupied areas. Humans inherited originally constructed mutualistic relationships between plants and megafauna, voluntarily or involuntarily offering dispersal services and conducive environments to some species that possibly would have reduced their distribution and density in their absence.

Anachronistic adaptations: An emerging pattern

Finally, on an evolutionary scale, the effects of megafaunal extinction on plants are subtle, but extend over thousands of years. Firstly, some of the plants that were dispersed by the megafauna have discontinuous distributions or are in danger of extinction (Butia yatay, Butia paraguayensis, Caesalpina paraguayensis, Ramorinoa girolae, Amburana cearensis, Bulnesia retama, Bulnesia sarmientoi, Tabebuia nodosa, Vasconcellea quercifolia). Others have azonal distributions, such as near watercourses (hydrozoochory) (Erythrina crista-galli, Ramorinoa girolae, Inga saltensis, and Inga uraguensis). More than 50% of the plants dispersed by megafauna show evidence of vegetative growth and/or are dispersed by domestic livestock (Supplemental Material 2, available online). In addition, several species do not have problems surviving without dispersers or with sub-optimal dispersers (Chapman and Chapman, 1995), forming dense groups of monospecific vegetation. Also, as noted above, many species have a long history of mutualism with past and present humans. In other words, there is a whole range of possible responses in plants regarding the loss of legitimate dispersers that explains their survival to this day. This points to the different evolutionary tempo between plants and animals (Traverse, 1988). The South American megafauna became extinct in a short period of time (Prates and Perez, 2021; Villavicencio et al., 2016), but to date there have not been plant extinctions associated with this process (Guimarães et al., 2008). However, the loss of dispersers in the long term translates into loss of genetic diversity and inbreeding, which can cause extinction processes in the future. Likewise, the forests of the study area present one of the highest deforestation rates in the world (Piquer-Rodríguez et al., 2015). This is due in the first place to the advance of the agricultural frontier. The reconversion of forest to agricultural land are the main threats to the conservation of those important ecosystems. Less discussed, however, is the possibility that there are other contributing factors, such as the loss of seed dispersal mechanisms and the concomitant loss of genetic diversity. Likewise, the role that humans traditionally played in the area, as plant dispersal agents and key players in the use of fire in the area, is lost as the groups settle down and knowledge of the plant species is forgotten (Rosso and Scarpa, 2017). We believe that these should be factors to take into account when planning conservation strategies for these highly threatened ecosystems (Teng et al., 2023).

The case of megafauna-dispersed fruiting plants illustrates most convincingly the point that some characteristics of organisms are not adapted to current conditions, but rather to previous ones. Finally, it is important to note that several of these anachronistic characteristics occur together in a high percentage of species. This is a notion to be explored in the future, since similar trade-offs between spinescence, large fruits, hard wood, and high concentrations of secondary metabolic compounds occur in a good number of the surveyed species. This suggests a genetically based link. Likewise, this raises the possibility of an interplay between antagonistic (spininess plus secondary metabolites) and mutualistic (fruit size) interactions in plant-animal relationships in the past.

Conclusions

In this work we study the relationships between plants and extinct megafauna in the central region of Argentina, in the phytogeographic provinces of Espinal, Monte, and Chaco. We propose that several characteristics of the vegetation, such as the presence of large fruits, spinescence, secondary metabolic compounds and high wood density, respond to selective pressures generated by the extinct Pleistocene megafauna, which disappeared around 10,000 years ago. Consequently, the loss of megafauna, in turn, probably had dramatic consequences on this vegetation, including demography, long-distance dispersal capacity, distribution in the landscape, and fire susceptibility of these post-pleistocene communities. Several characteristics of these species, such as vegetative reproduction, dispersal by sub-optimal mechanisms, and dispersal by introduced herbivores, were factors that ensured their long-term survival. An additional factor was the presence of humans, who colonized the area just before the extinction, and who have a long history of using these vegetable species for various purposes. By colonizing the area, humans not only adapted to the particular environmental conditions and constructed a particular niche, but also inherited mutualistic relationships that the vegetation had established with the megafauna for millions of years. It is possible that this type of relationship has occurred many times in different parts of the world, and that unraveling this history may be an important factor in explaining processes such as plant domestication.

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Supplemental material

Supplemental material for this article is available online.

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