

REVIEW

Loss of mammalian species from the South American Gran Chaco: empty savanna syndrome?

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ABSTRACT

1. The Gran Chaco in central South America is a major savanna woodland ecosystem. Accelerated changes in land use within it have resulted in a complex matrix of areas with varying capabilities for sustaining wildlife. Furthermore, hunting and habitat loss increasingly threaten the functional diversity of mammals found there.
2. We assess the potential consequences of the loss of large and medium-sized native mammalian herbivores and frugivores on Chacoan ecosystem functioning, focusing on their role and conservation status in the Argentine Chaco.
3. Our review shows that almost 50% of the largest frugivorous mammals present in the Argentine Chaco are threatened and exhibit declining population trends. Their decline may cause changes in vegetation composition, since almost 53% of the Chacoan woody plant species display endozoochory as their seed dispersal mechanism. Moreover, 80% of the largest herbivores are threatened, which may also lead to a compositional change in savanna vegetation.
4. There is a significant void of information regarding the population status of native mammals in the Argentine Chaco and the functional roles they play in the ecosystem, and there are few studies examining the consequences of their potential loss.
5. We express our concern with the major changes taking place in this subtropical region due to significant and rapid habitat transformations and emphasize the important role of ecological functionality in restoration and conservation planning in the Gran Chaco.

INTRODUCTION

The Gran Chaco is one of the main biogeographical regions in South America and the largest ecoregion after Amazonia (Dinerstein et al. 1995). This savanna woodland ecosystem extends through the present territories of Argentina, Bolivia, Paraguay and south western Brazil, between the Paraguay and Paraná rivers and the Andean high plains (Fig. 1). The Gran Chaco is considered a vulnerable ecoregion of great importance to conservation at both local and regional scales due to the high levels of endemism and mammalian species richness it harbours (Redford et al. 1990, Mares 1992, Olson et al. 2001, Ojeda et al. 2002, Torres & Jayat 2010, Sandoval & Bárquez 2013). Chacoan vegetation ranges from dense, moist woodlands and thickets through open shrublands to extensive treeless grasslands; the composing communities form a series of floristic, faunal and environmental gradients (Bucher 1982). Herbivory, along with rain and fire, are the main agents that structure the vegetation of this ecosystem, resulting in an extensive savanna interspersed with patches of forest (Bucher 1987, van der Waal et al. 2011). The balance between woody and

herbaceous cover is regulated by a combination of these factors (Bucher 1982, Augustine & McNaughton 2004, Staver et al. 2011, Hoffmann et al. 2012), as well as the evolutionary history of the savanna (Lehman et al. 2014).

The Gran Chaco is characterized by competing or coexisting land uses produced by historical and contemporary interactions between socio-economic and intrinsic biophysical characteristics (Morello & Saravia Toledo 1959a, b, Baldi & Jobbágy 2012). The impact of human activity is linked to the introduction of domestic cattle and deforestation, which led to the elimination of fire-climax grasslands as well as to the alteration of forest composition and structure (Bucher 1982, Gasparri & Grau 2009). The replacement of grasslands by shrubs is attributed to a synergy between herbivores, climate and fire (Beerling & Osborne 2006), and the degree to which each factor regulates the dynamics of woody plants can have significant implications on the conservation and management of the savannas. More specifically, the occurrence of these three factors can exhibit positive feedbacks by removing and preventing forest encroachment and providing space for grasses that fuel more fires. In the case of herbivores, however, negative feedbacks are also observed, as they select certain grasses, thus reducing the flammability of the system and therefore promoting tree survival (Beerling & Osborne 2006).

The mammals of savanna ecosystems are key components of their dynamics due to the roles they exert (McNaughton et al. 1988, Frank et al. 1998, Odadi et al. 2011), and it is therefore essential to analyse how they cope with highly fragmented, human-influenced, unprotected landscapes. In particular, native herbivorous and frugivorous mammals are known to provide several ecosystem services to humans, including ecological (regulating ecosystem dynamics through seed dispersal of key plant species and plant recruitment), cultural (ecotourism, traditional uses and education) and provisioning (bush meat) services (du Toit & Cumming 1999, Schipper et al. 2008). However, although more than 100 species of native mammal inhabit the Gran Chaco (Anonymous 2005), there is an alarming lack of knowledge regarding their population status, the roles they play in ecosystem dynamics and the consequences of their possible demise.

Subsistence and commercial hunting was identified as the sixth main challenge to Argentine Chacoan biodiversity conservation by the Nature Conservancy and other institutions (Anonymous 2005), after agricultural expansion, commercial forest exploitation, hydroelectric dams, livestock expansion and fire (in the dry Chaco). Wild animals have always represented important sources of food for many people in Latin America, as indicated in a thorough review regarding subsistence and commercial hunting by Robinson and Redford (1991). In particular, subsistence hunting in the Gran Chaco is a recurring activity (Ojeda & Mares 1982,

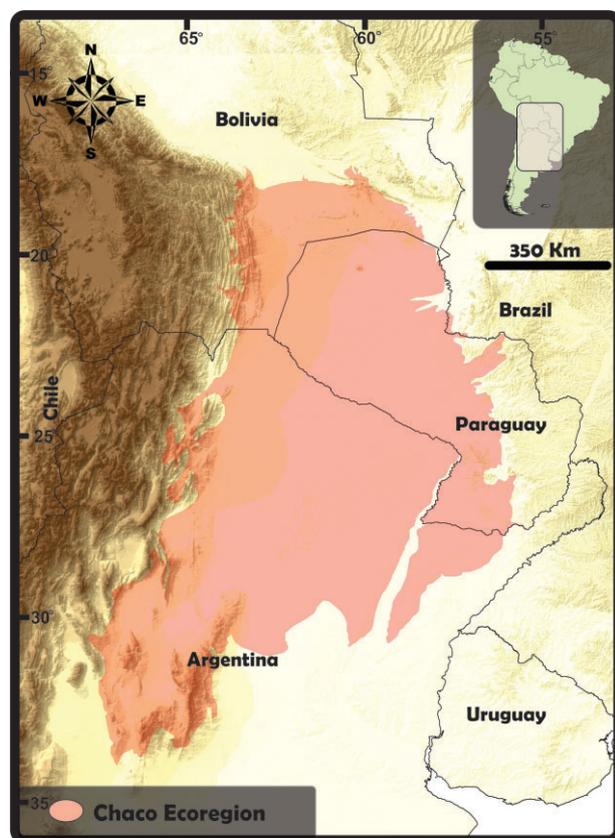


Fig. 1. Map of the South American Gran Chaco (Dinerstein et al. 1995). The Argentine Chaco is the specific focus of this review.

Altrichter 2006), though there are no records of the impact of this practice on mammalian populations. Furthermore, the high level of wildlife exploitation (that may drive change) raises a growing concern for the persistence of populations of larger (>10 kg) mammalian species and for overall species rarefaction in the richest biomes of Argentina, such as the Gran Chaco and Yungas (Mares & Ojeda 1984, Ojeda et al. 2002).

According to Bucher and Huszar (1999), the case of the Chaco can be extrapolated to all ecoregions of the developing world, and its conservation has been 'doomed to failure' for many years, unless high economic returns can be achieved from it in a sustainable manner. Moreover, the accelerated expansion of the agricultural frontier in the southern portion of the Argentine Chaco, particularly in the past 10 years, has led to the loss of remnant forest cover at an annual rate of 2.2%, one of the highest rates in recorded history for such a limited area (Eva et al. 2004, Zak et al. 2004). Thus, most of the Chaco biome has been transformed into a highly fragmented mosaic of forest patches, dense thorny scrubs, semi-natural grassland and cultivated land (Zak et al. 2004, Baxendale & Buzai 2009, Hoyos et al. 2013). As a result, the Chacoan landscapes show a complex mixture of ecological conditions, with different regeneration possibilities and varying potential to sustain populations of large and medium-sized mammalian species. In this context, understanding the roles of mammals in key ecosystem processes is crucial, as ecosystem dynamics (e.g. post-disturbance and restoration trajectories) may be affected by their abundance (Harrison et al. 2013).

The purpose of our review is to assess the potential consequences for ecosystem dynamics of the loss of native Chacoan mammalian herbivores and frugivores due to rapid and increasing habitat transformations and ongoing hunting pressures. We focus on the possible effects of losing the functional roles fulfilled by large and medium-sized mammalian species. Our working hypothesis is that the loss of locally threatened large and medium-sized mammals in the Chaco would entail the loss of their functions in the ecosystem, because each species has a particular role in the woodland savanna dynamics. To test our hypothesis, we summarize the population status and trophic ecology of native Chacoan mammals. We also suggest future directions for research, and methods for the conservation of the Gran Chaco.

METHODS

This review focuses on the southern portion of the Gran Chaco, which is located in Argentina and comprises 55% of the total 1.2 million km², encompassing both the dry and humid Chaco ecoregions (Dinerstein et al. 1995). The data used to identify the possible consequences of defaunation are derived from an extensive search of peer-reviewed litera-

ture on the role of mammals and the consequences of defaunation in different environments. We focus on 25 large and medium-sized native mammalian species (c. 1–310 kg; frugivores and herbivores), including their conservation status, population trends and diet type. We performed searches in Blackwell, Elsevier, Google Scholar, Scielo and Scopus data bases, using different combinations of the following keywords: 'mammal', 'Chaco', 'function', 'herbivore', 'frugivore', 'omnivore', 'disturbance', 'poaching', 'hunting', 'logging', 'cattle', 'defaunation' and 'fire'. We also reviewed thesis manuscripts in universities and consulted several regional and local mammal guides, as well as the Red List of Threatened Species produced by the International Union for Conservation of Nature (Anonymous 2013) and the Argentine Red List of Threatened Mammals (Ojeda et al. 2008). The complete list of articles consulted is available in the reference section and in Supporting Information Appendix S1.

LAND USE INTENSIFICATION IN THE ARGENTINE CHACO

The Gran Chaco has a long history of colonization, land use changes and interactions with wildlife, beginning with subsistence hunting by native people. However, over the last 200 years, land use has changed to include more intensified practices such as land fencing, livestock production, selective logging and intensive agriculture (Eva et al. 2004, Morello et al. 2006, Hoyos et al. 2013). The combination of these practices has resulted in the replacement of grasslands and woodlands with shrubs and completely eroded areas of bare soil (Morello et al. 2006, Baldi & Jobbágy 2012). In Argentina, agriculture is now expanding to almost every corner of the region; large-scale agribusinesses mainly for soybean production are taking over regions previously considered unfit for agriculture (Gasparri & Grau 2009). This expansion, coupled with climate change, technological advances (the use of genetically modified organisms, no-till farming, and pivot irrigation) and socioeconomic factors (high population density, unstable land tenure structure and high land prices) has resulted in isolated patches of forest surrounded by privately owned farms that exert daily pressures on native biodiversity (Faleiro et al. 2013, Nori et al. 2013), with little consideration for long-term sustainability (Zak et al. 2008, Dobrovolski et al. 2011, Laurance et al. 2012).

Almost 40% of the Argentine Chaco has been transformed and only approximately 2% is protected under some type of legislation (Brown et al. 2006). This is a problematic scenario for those species whose geographic ranges are constantly being constrained to protected areas, especially in those areas where protection is neither effective nor guaranteed (Brown et al. 2006). An index of mammal conservation for the different ecoregions in Argentina, taking into account endemisms,

vulnerability and taxonomic singularity, has suggested that the most urgent conservation priorities are the arid and semi-arid biomes such as the Chaco and Patagonia, and the subtropical Yungas forest (Ojeda et al. 2002).

DEFAUNATION AT A GLOBAL SCALE

Habitat loss or fragmentation threatens mammals through the loss of food (plants or prey), shelter and increased predation risk (Pimm et al. 1988, Schipper et al. 2008). Large animals at higher trophic levels are most vulnerable to habitat destruction and poaching, since they require large home ranges and more prey, and because they usually move across or use unprotected areas (Duffy 2003). Although rarity is always a risk factor, being a common species does not necessarily guarantee protection from hunting if the species is of interest (Altrichter 2006). The effects of defaunation and empty forest syndrome have been well documented in tropical forests; several consequences of vertebrate loss on ecosystem dynamics have been identified (Table 1; Dirzo & Miranda 1990, Redford 1992, Wilkie et al. 2011, Corlett 2012, Harrison et al. 2013). The main consequences of defaunation identified by Corlett (2012) include the co-extinction of parasites, a reduction in environmental heterogeneity, the release of competitors and prey (including plants) and a loss of quality and quantity in seed dispersal services.

Frugivores and ecosystem dynamics

The causes and effects of the loss of frugivores in tropical forests have been studied worldwide (Table 1). Frugivorous mammals impact ecosystem dynamics mainly by affecting plant regeneration due to seed dispersal and predation (Danell et al. 2006). For example, a decrease in populations of seed-dispersing animals can cause seed clumping close to parent trees, which can lead to an increase in seed predation by insects or an increase in seed infections, negatively affecting species recruitment. On the other hand, an increase in seedling abundance has been reported in areas with low abundance of seed predators (Table 1). Ultimately, frugivores can exert a negative effect on plant regeneration and distribution through predation, or a positive effect through seed dispersal, depending on whether the seeds consumed are destroyed or favoured after passing through the digestive tract (Willson & Traveset 2000).

A recent review on the consequences of defaunation at the community level in tropical forests showed that large-seeded species undergo reduced dispersal and increased aggregation of seedlings with the parent individuals, but also that diminished seed predation and herbivory may buffer the negative effect of reduced dispersal (Kurten 2013). Thus, the occurrence of higher or lower seedling

recruitment depends upon the life history of plant species. Nevertheless, the net effects of defaunation on the plant community were found to be a reduction in species richness and diversity and an increase in species dominance and environmental homogeneity (Corlett 2012, Kurten 2013).

Most studies on defaunation have been conducted in Neotropical rain forests (Table 1), where the percentage of vertebrate-dispersed tree species in the canopy and sub-canopy is 51–98%, and as expected, defaunation can have significant implications on forest regeneration (Stoner & Henry 2009). A decrease in seed dispersal and seedling abundance due to hunting and fragmentation has been observed in seasonal and subtropical forests (Table 1). Although these biomes are characterized by a higher percentage of mechanically dispersed species, dispersal limitations can still have significant negative effects on forest regeneration (Leithead et al. 2012).

Herbivores and ecosystem dynamics

Herbivores are responsible, in part, for determining the heterogeneity and biological diversity of a specific area, and create positive or negative feedbacks depending on the type, frequency and intensity of the disturbance (Table 1). For example, for savannas with a long evolutionary history of grazing, herbivory promotes the diversity of plant growth forms by suppressing the most vigorous species such as grasses (Danell et al. 2006). Herbivores promote shoot growth, increase light absorption by young and active tissue by removing old tissue and improve water-use efficiency and soil status (Frank et al. 1998). In particular, ungulate grazers are able to maintain permanent grazing lawns through a positive feedback loop that generates enhanced productivity from a short sward, increasing grass strength and competition for resources with woody seedlings and saplings, thereby helping to maintain the grassland state (Bardgett & Wardle 2003).

Herbivores may regulate the structure of vegetation communities, as well as primary productivity, through direct and indirect effects on ecosystem energy and nutrient flow (Wilkie et al. 2011). However, a plant's response to herbivory is highly dependent upon climatic constraints, herbivore diversity and biomass, and plant community (du Toit & Cumming 1999, Bardgett & Wardle 2003). For example, herbivores can cause absence of young trees in forests (Gill 2006) and damage vegetation by defoliating, trampling, depositing dung and urine, and creating wallows (Hobbs 2006). In the transition between forest and savanna, for example, herbivory is considered to reduce tree cover in an analogous manner to fire (a keystone factor), although in a less ubiquitous manner (Hoffmann et al. 2012). In this context, the balance between woody and herbaceous plants may be regulated by the selective foraging of dominant

Table 1. Functional implications of defaunation in different habitat types and for different (directly and indirectly) affected groups of mammals and trees

Habitat type*	Disturbance	Mammalian group directly affected†	Group indirectly affected	Functional implications	References‡
Neotropical forest	Hunting and local extinction	Large/medium H/F/O	Primary forest tree species, understory and animal-dispersed trees	↓ seed dispersal and dispersal distance	Wright et al. 2000, Wright & Duber 2001, Galetti et al. 2006, Forget & Jansen 2007, Vargas 2008, Holbrook & Loiselle 2009
				↓ seed predation due to low abundance of mammals or ↑ seed predation (or mortality by infections) due to clumping close to parent trees	Dirzo & Miranda 1990, Roldan & Simonetti 2001, Wright et al. 2007 Wright et al. 2000, Galetti et al. 2006, Forget & Jansen 2007
				Δ forest tree composition (↓ diversity, ↑ mechanical dispersed species) Δ spatial distribution of species	Wright et al. 2007, Nuñez-Iturri et al. 2008, Terborgh et al. 2008 Silman et al. 2003, Forget & Jansen 2007, Vargas 2008
Neotropical forest	Logging and fragmentation	Large/medium F/O	Animal-dispersed trees	↑ seed predation ↓ dispersal of seeds and distance	Galetti et al. 2006, Jorge & Howe 2009 Cramer et al. 2007, Jorge & Howe 2009, Gutierrez-Granados 2011
Neotropical forest	Hunting	Large C	Large/medium H/F/O	Δ tree distribution ↑ seed predation and seedling herbivory	Cramer et al. 2007 Asquith et al. 1997, de Steven & Putz 1984
Afro-tropical forest	Hunting and fragmentation	Large/medium H/F/O	Animal-dispersed trees	↓ seed dispersal and predation ↓ seedlings and juvenile recruitment Δ landscape configuration	Fa et al. 2005, Wang et al. 2007 Cordeiro & Howe 2001 Fa et al. 2005
Australian tropical forest	Exclusion	Large/medium H/F/O	Primary forest tree species	↑ seedling abundance and Δ composition	Theimer et al. 2011
Seasonal forest	Hunting and fragmentation	Large/medium F/O	Primary forest and animal-dispersed trees	↓ seed dispersal ↓ seedling of large-seeded trees	Brodie et al. 2009, Melo et al. 2010 Ganzhorn et al. 1999, Melo et al. 2010

* Neotropical forest = Bolivia, Peru, Brazil, Ecuador, Surinam, Panama, Costa Rica, Mexico; Afro-tropical forest = Central Africa, Cameroon, Tasmania; Seasonal forest = Thailand, Madagascar, Mexico.

† C, Carnivore; F, Frugivore; H, Herbivore; O, Omnivore.

‡ References in Supporting Information Appendix S1.

herbivores and may result in changes in ecosystem trajectory (Augustine & McNaughton 1998, du Toit & Cumming 1999, Wisdom et al. 2006).

LOSS OF CHACOAN MAMMALS AND ITS CONSEQUENCES

Species diversity has been significantly affected by the increasing land use intensification processes that have been taking place in the Gran Chaco during the past decades (Ojeda et al. 2002). This phenomenon is more marked in the Argentine Chaco, which has been highly degraded, and where optimal habitats for large and medium-sized native mammals no longer exist. Populations may begin to disappear or become less abundant in marginal areas as home ranges tend to contract, leaving deforested edge areas with fewer individuals (Ojeda et al. 2008). Moreover, these already stressed populations are still subjected to intensive poaching (Altrichter 2005, 2006). Accordingly, Chacoan mammals currently face three main threats, all of which are severe: (1) the expansion of agricultural lands to the detriment of original habitats, (2) intense hunting pressure, and (3) competition with invasive species (Ceballos & Simonetti 2002), including the European hare *Lepus europaeus*, European wild boar *Sus scrofa* and several species of deer introduced for sport hunting.

The Gran Chaco is rapidly being transformed into a place where the 'big things that run the world' are in jeopardy; the larger mammals that play key roles in regulating the savanna woodland ecosystem are disappearing (Terborgh 1988). Almost 70% of the large and medium-sized native mammals the geographical ranges of which include the Argentine Chaco have decreasing or unknown population trends at the global level: 36% of the species are considered endangered, vulnerable or near threatened (Table 2; Anonymous 2013). However, the scenario at a national level is even worse (Ojeda et al. 2012): 52% of large and medium-sized mammalian species native to Argentina are considered to be endangered, vulnerable or near threatened (Table 2). Discrepancies between global and national status occur in 10 species, and national categories are always more severe (Table 2).

Chacoan plant strategies

The Chaco is a seasonal woodland that ranges from subtropical to temperate regions; the harshest environmental conditions (water deficit stress) occur in the southernmost portion (dry Chaco). Although both of the dominant canopy tree species, quebracho colorado *Schinopsis balansae* and quebracho blanco *Aspidosperma quebracho-blanco*, have anemochory as their seed dispersal strategy, the Chaco is characterized by a high diversity of woody species (trees and

tall shrubs), of which approximately 53% are dispersed by endozoochory (Abraham de Noir et al. 2002). Thus, the local extinction of mammals may lead to changes in vegetation composition and landscape structure. Among the most abundant woody species of the Argentine Chaco, 70% disperse their fruits rather than their seeds. Of those, 31% are fleshy fruits (e.g. *Celtis ehrenbergiana*, *Condalia microphylla* and *Zizyphus mistol*) and 36% are dry-indehiscent fruits (e.g. *Acacia aroma*, *Prosopis alba* and *Prosopis nigra*) that are mainly dispersed by mammals (Abraham de Noir et al. 2002).

Fleshy fruits are also dispersed by ants and birds, which may potentially buffer the negative effects of frugivorous mammal loss on the dispersal of these seeds. However, the larger mammals that consume large quantities of seeds and are able to disperse them further are among the most threatened (e.g. *Chrysocyon brachyurus*, Table 2). Thus, the compensatory capacity of this ecological function may only occur (if it is even possible) with an increase in the abundance of the remaining fauna, but very few mammals are increasing in abundance (Table 2). The potential redundancy of frugivorous mammals in the dispersal of the woody species with dry-indehiscent fruits is not easy to evaluate. For example, how many of these species disperse the fruits of a keystone tree such as *Prosopis sp.*? Is a mammalian species responsible for most of the dispersal and seedling recruitment? Campos et al. (2008) showed that the passage of *Prosopis* seeds through the digestive tract of a mammal can modify germination capacity and speed, with great variability among species. This variability limits our capacity to analyse potential redundancy in dispersal and the role of non-threatened mammals in compensating for a given function. In light of this, and as stated by Wotton and Kelly (2011), conserving the full range of dispersers within an ecosystem ensures that ecological redundancy is retained and provides a buffer to plant extinction.

Chacoan frugivores

The Argentine Chaco is inhabited by 17 native large and medium-sized mammalian frugivores and omnivores, of which nine are near threatened, vulnerable or endangered at the Argentine national level (Table 2). Threatened species include several emblematic species, such as the large *Catagonus wagneri*, *Chrysocyon brachyurus*, *Mazama americana*, *Pecari tajacu*, *Tapirus terrestris* and *Tayassu pecari* (Table 2). For these species, the Argentine Chaco is the southernmost part of their geographical range, where most of them show a reduction in population size and range occupancy (Table 2).

In particular, the tagua *Catagonus wagneri* has disappeared from approximately 40% of its original geographic range in the Argentine Chaco, and the remaining very fragmented populations are in decline, mostly due to an intense

Table 2. Large and medium-sized herbivorous and frugivorous native mammals of the Argentine Chaco, showing their diet type, conservation status and population trends; species are listed alphabetically within each order

Species	Common name	Body mass (kg)*	Diet type†	IUCN Red List Status‡§	Argentine Red List Status¶	Population Trend IUCN	References for diet type**
Cingulata							
<i>Chaetophractus vellerosus</i>	Screaming hairy armadillo	0.7–1.2	IO	LC	LC	=	Bruno & Cuellar 2000, Abba & Cassini 2010
<i>Chaetophractus villosus</i>	Large hairy armadillo	1.5–3.6	FG	LC	LC	↑	Bruno & Cuellar 2000
<i>Dasyurus hybridus</i>	Southern long-nosed armadillo	1.1–2	IO	NT	NT	↓	Abba & Cassini 2010
<i>Euphractus sexinctus</i>	Yellow armadillo	3.2–6.5	FG	LC	LC	=	Bruno & Cuellar 2000
<i>Tolypeutes matacus</i>	Southern three-banded armadillo	0.9–1.6	IO	NT	NT	↓	Bolkovic et al. 1995, Bruno & Cuellar 2000
Primates							
<i>Alouatta caraya</i>	Howler monkey	4–9.5	FH	LC	VU	↓	Bazzalo 2001, Bravo & Sallenave 2003, Ludwig et al. 2008
<i>Aotus azarae</i>	Azara's night monkey	0.6–1.4	FO	LC	LC	↓	Ganzhorn & Wright 1994, Giménez & Fernandez-Duque 2003
Carnivora							
<i>Cerdocyon thous</i>	Crab-eating fox	4.5–8.5	FO	LC	LC	=	Juarez & Marinho-Filho 2002, Gatti et al. 2006, Rocha et al. 2008
<i>Chrysocyon brachyurus</i>	Maned wolf	20.5–26	FO	NT	EN	?	Carvalho & Vasconcelos 1995, Motta Jr. et al. 1996, Azevedo & Gastal 1997, Juarez & Marinho-Filho 2002, Santos et al. 2003, Rodrigues et al. 2007
<i>Lycalopex gymnocercus</i>	Pampas fox	3–8.2	FG	LC	LC	↑	García & Kittlein 2005, Varela et al. 2008
<i>Nasua nasua</i>	Coati	4–8	IO	LC	LC	↓	Alves-Costa et al. 2004, Beisiegel & Mantovani 2006, Alves-Costa & Eterovick 2007, Hirsch 2009
Perissodactyla							
<i>Tapirus terrestris</i>	Tapir	190–310	FH	VU	EN	↓	Salas & Fuller 1996, Henry et al. 2000, Chalukian et al. 2013
Artiodactyla							
<i>Blastocerus dichotomus</i>	Marsh deer	80–125	HG	VU	EN	↓	Becaccci 1996, Thomas & Salis 2000, Costa et al. 2006
<i>Catagonus wagneri</i>	Chacoan peccary	30–40	FH	EN	EN	↓	Mayer & Brandt 1982, Taber et al. 1993
<i>Lama guanicoe</i>	Guanaco	100–140	HG	LC	LC	=	Bahamonde et al. 1986, Bonino & Sbriller 1991, Candia & Dalmaso 1995, Puig et al. 2001, Baldi et al. 2004
<i>Mazama americana</i>	Red brocket deer	18.5–65	FH	DD	NT	?	Bodmer 1997, Gayot et al. 2004
<i>Mazama gouazoubira</i>	Gray brocket deer	8–25	FH	LC	LC	↓	Gayot et al. 2004, Kufner et al. 2008, Serbent et al. 2011
<i>Ozotoceros bezoarticus</i>	Pampas deer	25–40	HG	NT	EN	↓	Jackson & Giulietti 1988, Costa et al. 2006
<i>Pecari tajacu</i>	Collared peccary	17–35	FH	LC	VU	=	Kiltie 1981, Olmos 1993, Beck 2005, 2006, Keuroghlian & Eaton 2008, Desbiez et al. 2009
<i>Tayassu pecari</i>	White-lipped peccary	25–45	FH	VU	EN	↓	Kiltie 1981, Olmos 1993, Altrichter et al. 2001, Beck 2005, 2006, Keuroghlian & Eaton 2008, Desbiez et al. 2009
Rodentia							
<i>Dolichotis patagonum</i>	Patagonian cavy	8–16	HG	NT	VU	↓	Bonino et al. 1997, Campos 1997, Rodriguez & Dacar 1992, Chillo et al. 2010
<i>Hydrochoerus hydrochaeris</i>	Capybara	35–73.5	HG	LC	NT	?	Quintana et al. 1998, Borges & Gonçalves Colares 2007, Corriale et al. 2011
<i>Lagostomus maximus</i>	Plains viscacha	3.5–5	HG	LC	LC	?	Campos 1997, Branch et al. 1994, Kufner & Monge 1998, Pereira et al. 2003
<i>Pediolagus salinicola</i>	Chacoan mara	1.5–2.7	HB	LC	LC	=	Rosati & Bucher 1995, Chillo et al. 2010
Lagomorpha							
<i>Sywilagus brasiliensis</i>	Tapeti	0.7–1.3	HG	LC	LC	?	Valero & Durant 2001

*Canevari & Vaccaro, 2007.

†Diet type: HG, Herbivore-grazer; FH, Frugivore-herbivore; FG, Frugivore-granivore; FO, Frugivore-omnivore; IO, Insectivore-omnivore; HB, herbivore-browser.

‡IUCN Red List Categories: LC, Least concern; NT, Near threatened; VU, Vulnerable; EN, Endangered; DD, Data deficient.

§Anonymous (2013) The IUCN Red List of Threatened Species. Version 2013.2. <http://www.iucnredlist.org>.

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**References in Supporting Information Appendix 51.

increase in deforestation (Altrichter & Boaglio 2004). The current estimate of the maned wolf *Chrysocyon brachyurus* population in Argentina is around 660 individuals (Paula et al. 2008). This seed disperser is the largest canid in South America (Motta-Junior & Martins 2002); its primary threats result from, among other things, conflicts with humans, drastic reduction in habitat, and hunting for fur and for parts used in alternative medicine (Anonymous 2013). The lowland tapir *Tapirus terrestris*, although common in the Amazon and even in some areas of Argentina, 'seems unlikely to persist anywhere humans occur at densities any greater than 1 individual per km²' due to ongoing population reductions attributed to deforestation, hunting and competition with livestock (Naveda et al. 2008). The peccaries *Pecari tajacu* and *Tayassu pecari* are considered seed predators and dispersers via endozoochory of small seeds, excretion of large seeds and epizoochory (Beck 2005, Lazure et al. 2010). The original range of the peccaries in the so-called impenetrable portion of the Argentine Chaco, an area of 4 million hectares in the semiarid Chaco, has been reduced by 68% (Altrichter & Boaglio 2004). The white-lipped peccary *Tayassu pecari* currently exists in only 21% of its historical global geographic range (Keuroghlian et al. 2013). The species is heavily hunted in its entire range; subsistence hunting is considered sustainable in some areas of Peru, where it is abundant, and not sustainable at all in other regions, such as the Argentine Chaco (Altrichter 2005).

Thus, the ecosystem function of frugivory may be under threat in the Argentine Chaco, since the mammals that guarantee this function are all under threat and have decreasing populations. As we hypothesized, the uniqueness of the function that these species perform makes it difficult to identify other non-threatened species that may compensate for its loss; there are only a few appropriate species with increasing population trends, and they are much smaller in size (e.g. *Chaetophractus villosus* and *Lycalopex gymnocercus*, Table 2). This raises concerns regarding the potential changes in vegetation composition and structure, since a decrease in seed dispersal and tree seedlings has been found in seasonal forests where large and medium-sized frugivores are missing (Table 1).

Chacoan herbivores

Fifteen large and medium-sized mammals that inhabit the Argentine Chaco have herbivory as a primary or secondary feeding strategy; 10 of them are near threatened, vulnerable or endangered at the Argentine national level (Table 2). Of the 15 species, eight are mainly herbivorous and 50% of them are threatened. Moreover, the Chaco ecoregion is the southernmost part of the geographical range of 74% of the herbivorous species. Medium-sized species are the most

diverse in their dietary strategies, and it is possible to identify certain degrees of functional complementarities in main food categories between species of similar body size (Table 2). For example, the Patagonian mara *Dolichotis patagonum* and the Chacoan cavy *Pediolagus salinicola* are two medium-sized herbivorous rodents with very similar ecological characteristics. However, they differ in their feeding strategy: the mara is mainly a grazer and the cavy is mainly a browser (Chillo et al. 2010). The plains vizcacha *Lagostomus maximus*, another medium-sized rodent, presents different ecological characteristics with regard to habitat use but has dietary similarities with the Patagonian mara (Table 2).

The largest (8–140 kg) herbivores are ungulates, of which 78% have decreasing or unknown population trends (Table 2). The four largest herbivores in the Gran Chaco region are also the most threatened and least abundant of the Chacoan mammalian species (*Blastocerus dichotomus*, *Lama guanicoe*, *Tapirus terrestris* and *Ozotocerus bezoarticus*). In particular, the Pampas deer *Ozotocerus bezoarticus* has suffered a 98% reduction in its historical global geographical range (Ojeda & Mares 1982, González et al. 1998) and is considered endangered at the national level (Table 2); its declining populations are currently at high risk of extinction in the wild (Ojeda et al. 2012). The main causes of population decline are habitat loss and hunting. Current estimates in Argentina suggest that approximately 1200–1400 individuals exist in four isolated populations, including one in the Argentine Chaco with about 170 individuals (Gonzalez & Merino 2008). The current range of the guanaco *Lama guanicoe*, once the most widespread ungulate of the continent, has retracted by about 58% in Argentina, 75% in Chile and Peru, almost completely in Bolivia and Paraguay, and completely in Ecuador, where the species is considered extinct (Baigún et al. 2008). The Andean and Patagonian populations in Argentina and Chile are recovering thanks to conservation efforts and are classified as being of least concern (Ojeda et al. 2012), however the remnant populations in the Chaco were already heading towards extinction 20 years ago (Cunazza et al. 1995). These Chacoan populations, which are spread between Bolivia, Paraguay and Argentina, still face intense hunting pressure and habitat loss, and there is a clear need for trilateral conservation efforts (Baldi et al. 2008).

The densities of domestic ungulates are often higher than those of their wild counterparts in the Argentine Chaco, and the movement of herbivores has changed due to fencing, artificial water provision and nutrient supplementation, which has limited the ability of plants to recover from defoliation (Staver et al. 2011). Grassland responses to grazing differ between native and domestic (livestock) grazing, and the positive feedbacks that help maintain grasslands under wildlife herbivory may change to those that may maintain degradation in livestock production systems (du Toit &

Cumming 1999, Wisdom et al. 2006). The replacement of native with exotic herbivores eliminates the ecosystem service the native species provide and may also promote invasions, which may even lead to exotic species facilitating additional invasions (Parker et al. 2006). In the Chaco, a changing land mosaic is rapidly emerging where domestic and wild herbivores share a limited resource. A long-term enclosure experiment in the semi-arid savanna of Kenya has shown that cattle can reduce the intensity of use of shared habitats by native herbivores because of competition for a common resource (Riginos et al. 2012). Taken together, these findings show that the role performed by large native herbivores may not be compensated for by livestock, but rather that livestock may lead to a different trajectory of the system. Here, as with frugivory, the function of herbivory of helping maintain the savanna woodland dynamics may be under threat, since there may not be a compensatory alternative in medium-sized native herbivores or in domestic cattle.

RESEARCH NEEDS AND CONCLUSION

Redford et al. (2011) urge researchers to try to understand species' recent historic distribution, abundance, genetic diversity and ecological roles and to ensure that these attributes are maintained over time. In this review, we have identified native mammals that inhabit the Argentine Chaco, whose feeding strategies include the consumption of plants and whose populations are under ever-increasing threats. Most of the species currently show declining populations or are in danger of being vulnerable to threats in the near future (Table 2). More importantly, we show that the functions they carry out in the ecosystem may be at risk as well. Changes in vegetation structure and composition caused by human-induced disturbances, particularly in drylands worldwide, can result in a significant loss of mammalian functional diversity (Chillo & Ojeda 2012). Important knowledge gaps exist regarding not only the population status of these large and medium-sized native mammals, but also their functional roles and how, if at all, they are adapting to the rapid land use changes. In particular, we have scant knowledge of whether these roles will or even can be carried out by other species (Wright et al. 2007).

Understanding the role of large and medium-sized mammalian herbivores and frugivores in an ecosystem can shed light on its evolutionary and ecological history and, more importantly, on the potential consequences of native mammal loss on ecosystem functioning. There is no doubt that the South American Gran Chaco is undergoing accelerated land use changes and that its ensemble of large native mammals continues to suffer from hunting pressure. Therefore, the potential losses of functionally unique species could lead to changes that severely undermine the dynamics of this

savanna woodland ecosystem (O'Gorman et al. 2011). Uncertainties in the consequences of losing functionally unique species demand urgent attention, and therefore we list the major challenges and future research needs for the conservation of mammal functional diversity in the Gran Chaco.

First, there continues to be a void in baseline information for many of the species (occurrence, relative abundance and habitat use). Research on biodiversity loss should include species-based and population-based approaches, as well as research on service-providing units grouping species that perform similar ecosystem functions (Luck et al. 2003). We also need to have a clear understanding of the nature and strength of the interactions between functionally unique species in the food web (O'Gorman et al. 2011). In particular, we must consider the potential effects of the loss of functionally unique species in any restoration attempt, as this loss may lead to a different restoration trajectory, as well as strategies that favour the recolonization of large species (Anand & Desrochers 2004).

Second, hunting is a current threat to medium-sized and large mammals, and therefore, for conservation projects to be successful, they must include the knowledge of local people when assessing the distribution and abundances of the principal mammalian species included in their diet (e.g. brocket deer, edentates, peccaries and tapir). Third, local and regional forums must be established to enhance a fluid and continuous multidisciplinary and multisectoral dialogue among different Chaco stakeholders, in order to produce stronger bases for long-term management and conservation (Díaz et al. 2011). Fourth, any restoration attempt must include consideration of the importance of woody plants and the ecological services they provide, such as shade, forage, soil stability, habitats for wildlife, and as a source of biodiversity and carbon storage (Kunst et al. 2012).

Lastly, protected areas in the Argentine Chaco are insufficient and inefficient (Ojeda et al. 2002), especially because the degradation of matrix habitats surrounding protected areas reduces their conservation capacity, even if habitat is maintained within their administrative boundaries (Hansen et al. 2005). Unprotected areas are crucial to the overall conservation strategy, and developing strategies for those areas is essential since, according to conservative predictions, more than 80% of the world's land will remain outside protected areas (Primack 2012). Although large-scale conservation strategies, such as the identification of priority ecoregions and biodiversity hotspots, have been effective responses in the right direction (Loyola et al. 2009), conservation management is still failing to protect functionally unique species and the ecosystem processes needed to maintain the system (Eken et al. 2004, McConkey et al. 2012). Also, the Chaco region is commonly left out of many of these prioritization schemes, including Conservation International's 'Biodiversity Hotspots'. Therefore, we

consider it necessary not only to create new protected areas and conservation corridors, but also to improve the effectiveness of established areas and privately owned surrounding areas, for the protection of functionally diverse species. There is a particular need for the establishment of conservation priorities aimed at minimizing population and species extinctions, reducing conservation conflicts, and preserving ecosystem services (Ceballos et al. 2005).

In the South American Gran Chaco, we are losing species faster than we learn how important they are, the roles they play or how their disappearance would affect the entire ecosystem. We are currently experiencing a disruption in the equilibrium between mammalian herbivores, frugivores and their plant resources, and we probably already face 'the irreversible erosion of diversity at all levels' (Terborgh 1988). Biodiversity is undergoing a global crisis in which defaunation and deforestation are commonly accepted consequences of human sprawl, and ecologists are already discussing the need for reforestation and refaunation (Oliveira-Santos & Fernandez 2011). It is with this in mind that we urge governments with stakes in this vast area not to stand idle while destruction of this unique savanna woodland ecosystem continues without regard for its biodiversity and conservation value. We consider that any efforts to prevent the disappearance of the South American Gran Chaco and to restore the savanna woodland dynamics must take into account the ecological roles played by its native mammals. We must concentrate future conservation efforts on the native mammals and ecosystem dynamics of the Chaco before it is too late.

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SUPPORTING INFORMATION

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Appendix S1. Additional references cited only in the Tables