Journal of Arid Environments 123 (2015) 40–46

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Natural grasslands in the Chaco. A neglected ecosystem under threat by agriculture expansion and forest-oriented conservation policies

H. Ricardo Grau [a, *], Ricardo Torres [b], N. Ignacio Gasparri [a], Pedro G. Blendinger [a], Sofía Marinaro [a], Leandro Macchi [a]

[a] CONICET – Instituto de Ecología Regional, Universidad Nacional de Tucumán, Casilla de Correo 34, 4107, Yerba Buena, Tucumán, Argentina
[b] Museo de Zoología and Cátedra de Diversidad Animal II, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 299, 5000, Córdoba, Argentina

ARTICLE INFO

Article history:
Received 13 February 2014
Received in revised form
10 September 2014
Accepted 15 December 2014
Available online 20 December 2014

Keywords:
Argentina
Biodiversity conservation
Dry Chaco
Fire suppression
Grassland distribution modeling
Land use planning
Woody encroachment

ABSTRACT

In most tropical and subtropical biomes, conservation strategies are mainly focused on the preservation of forests. However, neotropical dry forest and savanna ecoregions include open habitats that may deserve conservation attention. We analyzed the historical patterns and potential distribution of natural grasslands, as well as their biodiversity in the northern Argentina dry Chaco, which is one of the largest and yet most rapidly transforming neotropical ecoregions. Paleoecological literature, historical records, and bioclimatic modeling support the hypothesis that Chaco grasslands distribution was more extended in the past, and has been historically reduced by woody encroachment resulting from environmental changes occurred in the past century. Recent research shows that natural grasslands host distinctive components of the Chaco biodiversity, and a significant proportion of the vertebrate species have a negative association with woody biomass. Ongoing land use trends continue to threaten native grasslands both in unprotected sectors (where they are converted into agriculture and planted pastures) and inside protected areas (were fire suppression is favoring woody encroachment). Current conservation policies (Protected Areas, Argentine forest law, REDD+) neglect the importance of native grasslands for biodiversity conservation. Such forest-centered initiatives should be revised to specifically include native grasslands and their biodiversity into land use strategies that adequately balance agriculture and livestock production with biodiversity conservation.

1. Introduction

Given the costs and complexity of accurate and detailed spatial models, much biodiversity conservation planning is based on proxies. Forest distribution is paramount example. Deforestation rates and forest cover are used as key indices of national or regional ecosystem conservation (e.g. Moran et al., 1996; Gibson et al., 2011). Global conservation initiatives such as REDD + are largely based on the assumption that to some extent, biodiversity co-varies with biomass, both being maximized in well-developed forests (Phelps et al., 2012; Strassburg et al., 2012).

Forest cover and structure can be good indices of conservation in ecoregions clearly dominated by forests, but in non-forested ecoregions (e.g. grasslands, deserts), conservation should be based on other variables. By limiting the supply of potentially arable lands, forest-centered conservation initiatives could even redirect land conversion towards open ecosystems (Miles and Kapos, 2008). The dichotomy between forest or non-forest conservation schemes becomes particularly problematic in ecoregions where the natural landscape is a mosaic of forests and open areas, such as tropical and subtropical open and semi-open woodlands and savannas. Because they frequently have fertile soils in flat topographies, they are highly suitable for agriculture (Lambin et al., 2013), include some of the most active deforestation fronts (Aide et al., 2013; Hansen et al., 2013) and are among the most threatened ecoregions globally (Hoekstra et al., 2005).

Extending over north–central Argentina, western Paraguay, and Southeastern Bolivia, the dry Chaco is one of the largest remaining patches of forest/savanna ecosystems in Latin America (Portillo-Quintero and Sánchez-Azofeifa, 2010). The region currently undergoes one of the highest rates of deforestation in South America (Gasparri and Grau 2009, Clark et al., 2010; Aide et al., 2013; Gasparri et al. 2013) and such deforestation constitutes a

* Corresponding author.
E-mail address: chilograu@gmail.com (H.R. Grau).

http://dx.doi.org/10.1016/j.jaridenv.2014.12.006
0140-1963/

significant source of carbon emissions (Gasparri et al., 2008). In response to this, and considering its valuable biodiversity heritage (Bucher and Huszar, 1999), the Chaco is subject of much conservation concern. In Argentina, protected areas represent only a very small proportion of the dry Chaco (c. 1%, Izquierdo and Grau, 2009), but a more ambitious conservation initiative has been implemented since 2007: the "*Ley de Presupuestos Mínimos de protección Ambiental a los Bosques Nativos*" (law 26331). This "forest law" obligates the provinces to define maps with three categories of allowed land use (Quispe Merovich and Lottici, 2011): "protected forest" (red zones), "managed forest" (yellow zones), and areas where deforestation is allowed (green zones). Such forest-defined land-use scheme essentially ignores grasslands as a specific conservation target.

The neglect of grasslands as a valuable ecosystem in the dry Chaco may be influenced by the common perception of the ecoregion as a "forest", since present-day non-agriculture landscapes in the region are dominated by woodlands. However, the dry Chaco also includes non-forest habitats such as grasslands, scrublands and wetlands. Indeed, it has been hypothesized that the pre-European landscape had a much higher representation of fire-prone grasslands (Morello and Saravia Toledo, 1959a, 1959b; Adámoli et al., 1990). The introduction of domestic livestock in the last centuries might have removed fine fuels and favored woody encroachment over grasslands, a process globally reported across drylands and savannas (Dougill and Trodd, 1999; Eldridge et al., 2011).

In this essay, we evaluate the assertion that natural grasslands (i.e. dominated by *Elionorus adustus*, *Trichloris crinita*, *Gouinia latifolia* or *Setaria macrostachya*) are a valuable ecosystem in the dry Chaco, due to its contribution to biodiversity derived from a historically larger extension. Specific questions to be addressed here are: (1) what is the "historical" importance of the grasslands in the dry Chaco landscapes?; (2) how much Chaco grasslands contribute to the biodiversity of the ecoregion?; (3) what are the current trends on land use of grassland areas in the dry Chaco? Based on this, we discuss to which degree the current forest-oriented conservation paradigm fails to preserve the Chaco biodiversity. Most of the examples and concepts here presented are based on northern Argentina case studies, but many of the derived ideas can be also applied to the rest of the dry Chaco ecoregion, and potentially to other savanna ecoregions.

2. Past and potential extent of the Chaco grasslands

Based on the names of localities which refer to the presence of grasslands ("*pampas*" or "*simbolares*"), Morello and Saravia Toledo (1959a, 1959b) suggested that grasslands were more extensive in the past, and that their current paucity was a consequence of relatively recent environmental change mostly derived from the introduction of livestock. For the year 2006, Clark et al. (2010) estimated 12% of "grasslands" for the whole dry Chaco ecoregion, but this figure includes a substantial (and unknown) proportion of planted pastures. In the northern sector of the Argentine dry Chaco, a 2007 assessment of non-cultivated area using remote sensing indicates that the area covered by natural grasslands was approximately 7% (Gasparri and Baldi, 2013).

Paleoecological evidence shows that during the Quaternary (last million years), the Chaco region experienced periods of much drier conditions with substantial reduction in forest cover (Iriondo and García, 1993; May et al., 2008; de Vivo and Carmignotto, 2004). The records of megafauna (e.g. *Glyptodon*, *Sclerocalyptus*, *Scelidotherium*, *Megatherium*, *Macrauchenia*, *Smilodon*, *Protocyon*) from Late Pleistocene with dryer conditions than present (Hoffstetter, 1968; Marshall and Sempere, 1991; Zurita et al., 2009; Huáscar Azurduy, 2006; Prevosti and Schubert, 2013) suggest an expansion of grasslands at expenses of forests during that period (de Vivo and Carmignotto, 2004), given that most South American megamammals were associated to open grasslands (Carlini et al., 2004; Zurita et al., 2004). For instance, *Equus neogeus*, *Toxodon platensis* and *Stegomastodon platensis* fed on C_4 grasses in sites where today Chacoan dry forests (dominated by C_3 plants) thrive (McFadden et al., 1994; McFadden, 2005; Alberdi et al., 2008; Prado et al., 2011).

Humans likely arrived at the region during the early Holocene, and for thousands of years indigenous populations probably lived out of gathering and hunting based to some degree in the use of fire to drive game and generate open habitats (Coltorti et al., 2010) as occurred in other regions around the world (Kirch, 2005). Accounts from the 18th century describe extensive areas of grassland and palms, both in frequently flooded sectors near the main rivers and in extensive sectors far away from rivers, where indigenous set frequent fires (Jolis, 1972). Documents of the late 19th century also mentioned extensive grasslands and palm savannas, especially in the margins of the Bermejo and Pilcomayo rivers, the foothills of the sierra de Tartagal (northwest in Fig. 1), and in *Campo del Cielo* (southeast sector in Fig. 1) (Boedo, 1873; Fontana, 1881; Baldrich, 1889; Burmeister, 1899). For sectors of the current Formosa and Chaco provinces, Baldrich (1889) and Burmeister (1899) estimated that approximately half of the territory was covered by forest and described forest patches as east-west oriented longitudinal "islands" within a matrix of open habitats. At the beginning of the 20th century, descriptions emphasized the progressive woody encroachment and depletion of natural grasslands. Barbrooke Grubb (1919) commented: "some thirty years ago great plains of luxuriant grass extended along the banks of the upper Bermejo and in others parts. Owing, however, to overstocking and other causes, these grass plains have become to a great extent covered with low scrubs, and during the dry season, many large stretches become perfectly bare". The progressive loss of grassland due to woody encroachment (particularly by *Prosopis ruscifolia*) was postulated as a driver of human outmigration from the margins of the Bermejo river in the area near the actual limit of Salta and Formosa provinces towards central Formosa (Muello, 1926). These anecdotal observations coincide with later interpretation of the Chaco landscape by Morello and Saravia Toledo (1959a, 1959b) and Adámoli et al. (1990), who concluded that the process of natural grassland depletion continued until the 1940s and 1950s, when following a dry period of severe overgrazing, woody encroachment was accentuated and defined in part the current landscape configuration of non-cultivated areas.

To further assess the hypothesis that grasslands could be more widely distributed in the dry Chaco, we developed a consensus model (*sensu* Araújo and New, 2007) of the habitat suitability for grasslands based on climatic, soil and water-related variables. We used sites currently covered by grasslands as training points (Appendix 1) in the northern Argentina dry Chaco. Over 13% of the area showed a suitability of 50% or higher for grasslands, approximately doubling the current proportion (Fig. 1). Soil related variables, temperature seasonality and distance to water bodies were the variables more associated with grassland distribution (Appendix 2). Interestingly, 10 of 14 localities in the study area with words in their names referring to open sites covered by grasses ("*pampa*", "*aibal*", "*simbolar*" and "*tacuruzal*)" were mapped into the areas with medium to high suitability values for grasslands, despite that more than 70% of them are currently located in landscapes dominated by forests (Fig. 1).

In summary, both at the scale of millennia and of centuries, evidence suggest that dry Chaco grasslands where much more extensive in the past. Furthermore, even under present-day climatic conditions, grasslands could be much more extensive under a different land use regime.

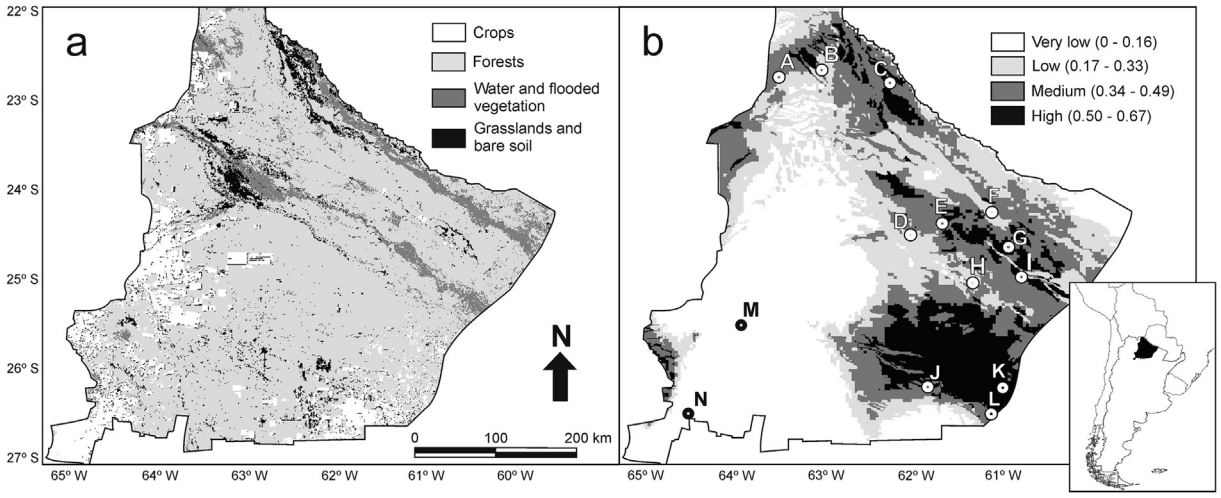

Fig. 1. Northern Argentina dry Chaco land cover maps. a) Present day (2007) vegetation classes in Northern Argentine Dry Chaco, assessed by classification of a multitemporal set of MODIS images (see Gasparri and Baldi, 2013). b) Modeled habitat suitability for grasslands based on climate, soil and water-related variables. Dots represent localities with the words "*pampa*", "*aibal*", "*simbolar*" and "*tacuruzal*" in its names (A: *El Tacuruzal*; B: *El Simbolar;* C: *El Simbolar*; D: *Simbolar;* E: *El Aibal;* F: *El Simbolar*; G: *El Tacuruzal*; H: *Tacuruzal*; I: *Laguna Pampa*; J: *Pampa de Los Guanacos*; K: *Pampa Guanaco;* L: *Pampa del Infierno*; M: *El Simbolar*; N: *Pampa Pozo*).

3. Grassland biodiversity in the argentine Chaco

If grasslands have covered a significant proportion of the dry Chaco landscape for thousands of years, is likely that a non-negligible part of its biodiversity is well adapted to, and may even depend on, this type of habitat. Our recent findings indeed support this hypothesis. Habitat suitability models based on extensive data mining from collections, specific literature and field observations, indicate that the suitability values for numerous species of vertebrates diminishes significantly with the increase in forest biomass (Table 1, Torres et al., 2014), which strongly suggests they are more commonly found in open habitats. Woody biomass was the most important predictor variable of suitability for amphibians and among the most important predictors for birds and mammals. Most amphibians and respectively a fifth and a third of bird and mammal modeled species had a negative association with it. Some examples of present day endangered fauna suggest that the scarcity of open habitats could limit their distribution. The manned wolf (*Chrysocyon brachyurus*), rarely found outside grasslands and open savannas (Dietz, 1985; Rodden et al., 2004), is currently distributed in the eastern sector of the Argentine dry Chaco, but its habitat extended further west during the drier conditions of the late Pleistocene, including large sectors of the northern Argentine dry Chaco (Torres et al., 2013). Other large vertebrates with high conservation value due to their low populations in the dry Chaco, such as rheas (*Rhea americana*), guanacos (*Lama guanicoe*) and anteaters (*Myrmecophaga tridactyla*) clearly prefer grasslands over close-canopy forests (Bellis et al., 2008; Cuéllar Soto, 2011).

Table 1
Level of association between species presence of different vertebrate taxonomic groups, and explanatory variables in northern Argentina dry Chaco (Torres et al., 2014).

	Amphibians	Birds	Mammals
Explanatory rank of biomass (in comparisons with other climatic, topographic and land use variables)	1°	2°	5°
% of species associated to biomass (both positive and negative associations)	86	65	40
% of species with negative association with biomass	86	19	36

In a comparison of habitat use by birds in the northern Argentine dry Chaco, Macchi et al. (2013) found that native grassland is the most distinctive land cover type in terms of avian composition, thus implying an original contribution to regional biodiversity. Similarity values between native grasslands and forests were less than 40%. In a similarity-based ordination analysis, native grasslands were also segregated from other non-woody land cover types (Fig. 2a). Grasslands were characterized by a combination of typical open-habitat bird species (e.g. *Melanopareia maximiliani*, *Saltatricula multicolor, Rhynchospiza strigiceps*), and species that also occur in forests (e.g. *Asthenes baeri, Poospiza melanoleuca*) which presence can be explained by scattered shrubs growing in the grassland matrix. In contrast, planted pastures presented a species composition more similar to crops, with many abundant and widely distributed species such as *Caracara plancus, Vanellus chilensis, Zenaida auriculata, Columbina picui, Myiopsitta monachus, Pitangus sulphuratus* and *Molothrus bonariensis.*

In the case of mammals, natural grasslands also have the most distinctive composition among different open-canopy land cover types (i.e. silvopastures, planted pastures and natural grasslands) (Fig. 2b). Several mammal species were more abundant in natural grasslands than in both planted pastures and silvopastures fields, including the Chacoan cavy (*Pediolagus salinicola*), the tapetí (*Sylvilagus brasiliensis*), the anteater (*M. tridactyla*), the cougar (*Puma concolor*), peccaries (*Pecari* tajacu, *Tayassu pecari*, *Catagonus wagneri*) and the gray brocket deer (*Mazama gouazoubira*) (S. Marinaro, unpublished manuscript).

4. Natural grasslands and current land use trends in the Chaco

Natural grasslands are not reliably discriminated from planted pastures in the available remote sensing analyses (Clark et al., 2010), and there are no government statistics on the actual area of native grasslands in the dry Chaco. However, is clear that natural grasslands currently cover a very limited proportion of the landscape, and observations of the ongoing processes clearly suggest this proportion is further shrinking (Fig. 3). In addition to the historical trend of woody encroachment (Adámoli et al., 1990), conversion into agriculture and planted pastures in sectors without soil limitation contribute to such reduction. Given the sustained

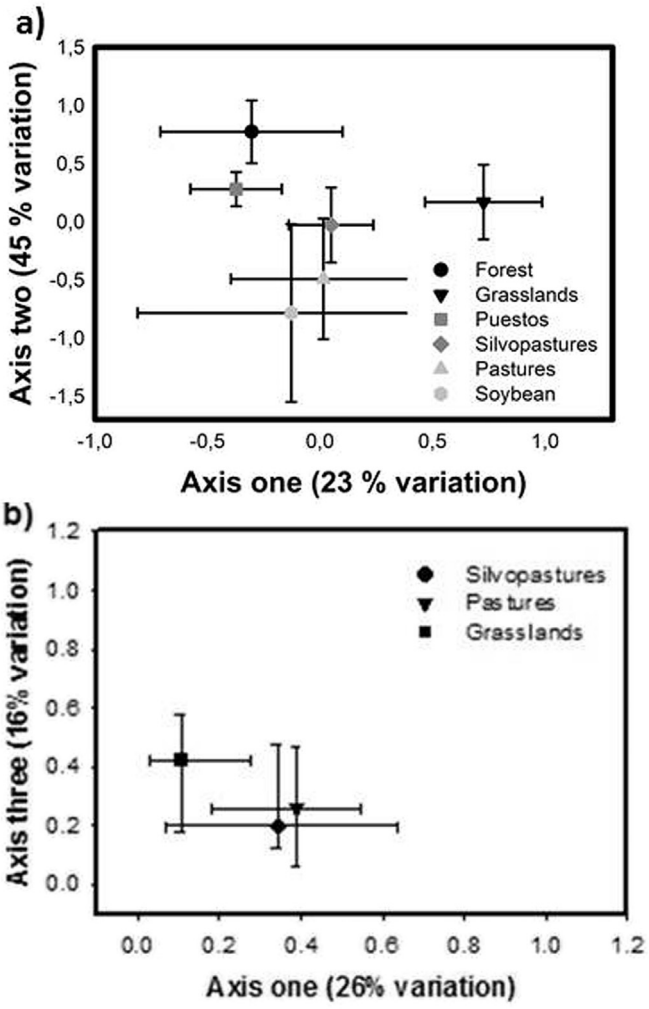

Fig. 2. Ordination diagrams showing the discrimination between natural grasslands and other land cover categories in terms of community composition (a) Non-Metric Multidimensional analysis of avian composition in different land cover types (Macchi et al., 2013); (b) Principal components analysis (axes 1 and 3) based on mammals composition of different "open canopy" landscapes (S. Marinaro unpublished manuscript).

demand for both meat and agriculture products such as soybean, and the suitability of the region for agriculture development (Lambin et al., 2013), conversion of grasslands (specially pyrogenic grasslands in loessic soils) into pastures (with higher productivity) and agriculture (with higher production value) is likely to continue in the near future.

Another land use/cover category expanding in the dry Chaco is silvopasture systems ("*desbajerados*"), in which shrubby understory is mechanically removed allowing grasses to grown underneath a relatively sparse tree canopy. In contrast to complete deforestation, conversion of forests into silvopasture system is allowed in the extensively managed forest (yellow) zones of the Argentine "forest law" (Quispe Merovich and Lottici, 2011). Since they have some management advantages over completely open grasslands (trees provide shade and shelter to livestock and extend the growing season for grasses), this type of land cover is expanding in the region. But, they tend to be planted with the same exotic grasses (e.g. Buffell grass, Gaton Panic); and when tree cover deteriorates, these plots tend to transition to a composition of planted pastures rather than to native grasslands (Fig. 3).

It is difficult to have an actual "natural" reference for Chaco grasslands. Native grasslands grazed exclusively by native grazers such as guanacos and rheas could potentially occur in protected areas, but given current management policies, this is not the case in the dry Chaco. The few grasslands occurring inside protected areas, such as Copo National Park in Argentina, are either managed with domestic grazers with very low density of native grazers (the guanacos are locally extinct) or are subject to fire suppression, with the resulting woody encroachment (Cardozo et al., 2011). Outside protected areas, when native grasslands are not converted into agriculture or planted pastures, fire is the main factor preventing woody encroachment. Fire prevents woody encroachment and favors grassland resprout (Casillo et al., 2012) and enhances herbaceous species diversity (Kuntz et al., 2003). However, since almost all the native grasslands outside protected areas are heavily grazed by domestic livestock, is difficult to assess if they are representative of grasslands growing under "natural" conditions.

The results of these different transitions are illustrated in Fig. 4. In the more fertile sites outside protected areas, native grasslands tend to be replaced by soybean fields or planted pastures (C in Fig. 4a). They can persist as grasslands, heavily grazed by cattle and sheep, in marginal areas for agriculture due to low rainfall, poor soils or very small patch size (A in Fig. 4a). Inside protected areas, when traditional use is not allowed, they tend to experience woody encroachment, due to current policies of fire suppression (B in Figs. 4a and b).

5. Discussion

For over half a century, it has been hypothesized that the pre-20th century landscape of the dry Chaco was characterized by a much larger extension of natural grasslands (Morello and Saravia Toledo, 1959a, 1959b). Based on an updated review of paleoecological and historical literature, as well as on bioclimatic models, we find strong support for this hypothesis (Fig. 1). In addition, recent research provides quantitative evidence that the biodiversity of vertebrates is favored by the existence of natural grasslands (Table 1, Fig. 2), which continues to be reduced as a result of woody encroachment and present-day management practices (both outside and inside protected areas) (Figs. 3 and 4).

When compared to agricultural places, forests could contribute to the conservation of species which prefer open habitats, by reducing the chances of hunting. But the maintenance of native grasslands would certainly favor the persistence of a wider range of species in higher densities, including several ones with conservation concerns. In consequence, we argue that natural grasslands need to be specifically targeted by biodiversity conservation planning, which is not the case of current forest-based initiatives. Current provincial zonation resulting from the Argentine forest law in the Chaco ecoregion simply ignores natural grasslands as a conservation target. Under a persistent demand of agriculture products, conservation policies solely based on forest protection may even result in an increased pressure over non forested landscapes, such as natural grasslands (Miles and Kapos, 2008). Protected areas in the ecoregion, such as National and Provincial Parks, do not ensure grassland conservation; rather, a fire suppression policy is applied which favor woody encroachment, potentially leading to the disappearance of some grasslands with the highest conservation value (Cardozo et al., 2011). International initiatives with potential impact in the region such as REDD+, target the preservation of biomass stocks, but above-ground biomass is maximized by woody biomass, which in turn has a negative association with significant components of the dry Chaco biodiversity (Torres et al., 2014, Table 1).

Some measures (and research needed) to revert these trends should include: (1) Specific inclusion of natural grasslands in the

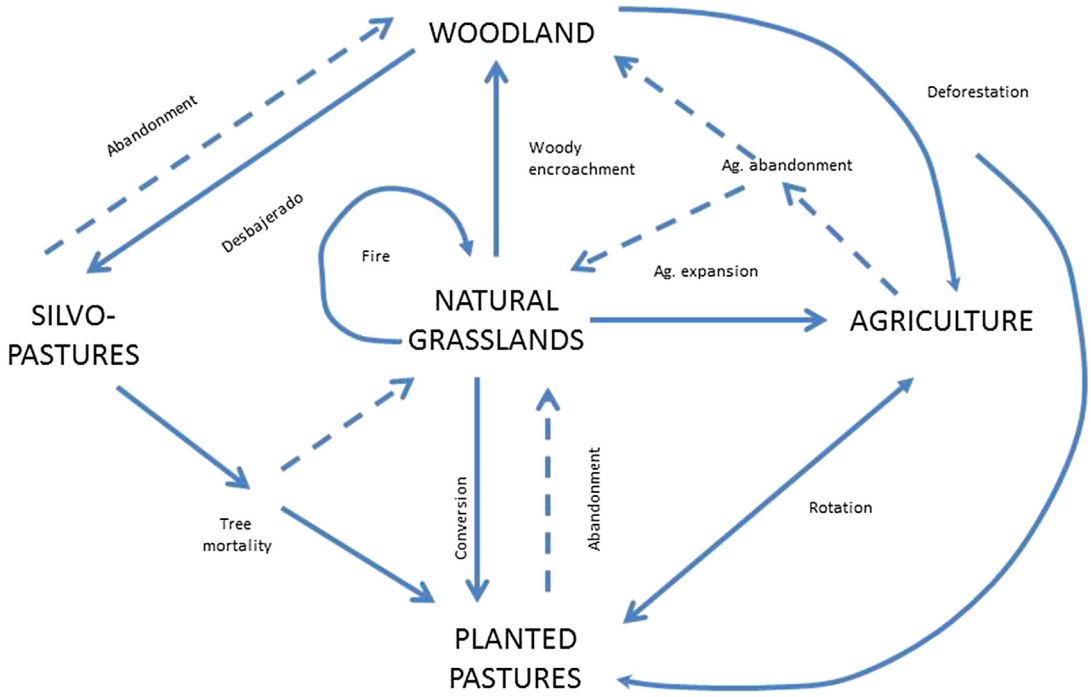

Fig. 3. Diagram of main transitions between land cover/use categories (capital letters) in the dry Chaco. Thick lines represent common transitions, while dashed lines represent unusual transitions. Processes are depicted in lower case.

Argentine dry Chaco zonation categories resulting from the "forest law". This would require a mapping and monitoring system of natural grasslands, which represents a challenging methodological goal since they are not easily discriminated from crops and in particular from planted pastures in remote sensing analyses. In addition, ecological and agronomic research is needed to compromise livestock production with fire management and biodiversity conservation, and to identify production practices and pressures associated with the cultivated land that limits the suitability for species with affinity to open habitats. (2) Developing policies of fire prescription and native grazers' management in protected areas, in order to have samples of dynamically stable natural grasslands without exotic livestock. This would require developing or adapting models of fire behavior in relation to grazing, climate variability, ignition sources and fuel dynamics associated to grazers foraging. (3) Acknowledging that carbon sequestration may not be a concomitant goal with biodiversity conservation. The associations, synergisms and antagonisms between biodiversity conservation and carbon storage should be a priority, including currently unavailable research on below-ground carbon stocks and dynamics.

This essay has focused on the effects of land use drivers and threats to native grasslands and their biodiversity. In the coming decades, the forcing of these trends are likely to persist (e.g. Gasparri et al., 2009, 2013; Lambin et al., 2013) and in consequence land use of the region needs to search for spatially explicit models of land use aimed to balance agriculture production, carbon

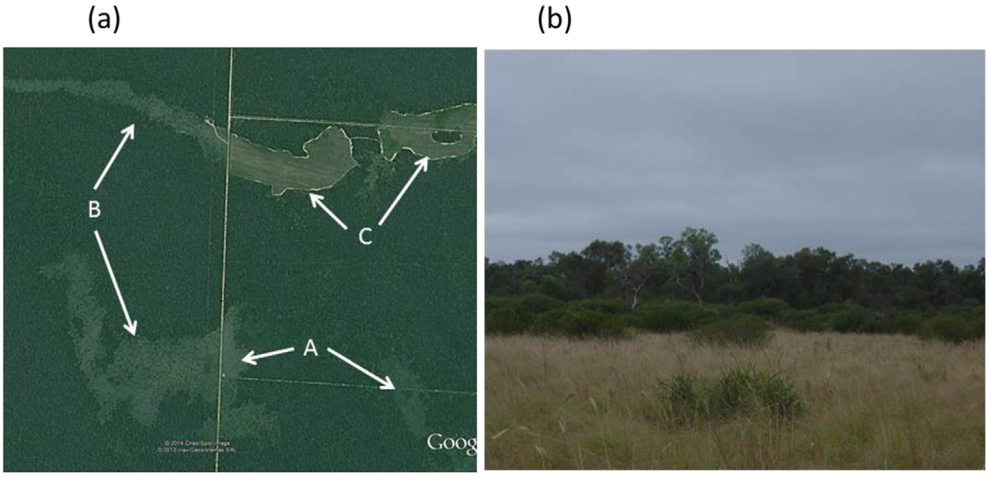

Fig. 4. (a) Google Earth® scene of the western boundary of Copo National Park (located west of the road). The vertical (north-south) line is the road representing the park limit. (A) are natural grasslands, preserved as such outside the park. (B) are natural grasslands undergoing woody encroachment (inside the park). (C) are zones of grasslands now replaced by agriculture plots. (b) Picture of the natural grassland inside the park (upper left of the (a) figure), undergoing woody encroachment.

sequestration and biodiversity conservation (Grau et al., 2008, 2013), specifically including natural grasslands as a component of the natural heritage (Macchi et al., 2013). In addition, semiarid grasslands across the world can experience accelerated changes (e.g. intensification of woody encroachment) due to climatic change and CO_2 atmospheric "fertilization" (Adámoli et al., 1990; Archer et al., 1995; Brunelle et al., 2014; Fensholt et al., 2012; Redo et al., 2013); and merit specific conservation strategies (Parr et al., 2014). The complex interactions between biophysical and socioeconomic processes driving trends of Chaco natural grasslands represent a major scientific challenge to preserve this shrinking environment and its valuable biodiversity.

Acknowledgments

This research was supported by funds from FONCYT (Argentina Research and Technology Agency) projects PICT 2009 #1693 and PICT 2011 #2524, CONICET PIP 0968 (Argentine Research Council), and PIUNT 26 G 420 (Research Council of the National University of Tucumán). Veronica Piriz Carrillo collaborated with training sites collection.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2014.12.006.

References

Adámoli, J., Senhauser, E., Acero, J.M., Rescia, A., 1990. *Stress and disturbance*: vegetation dynamics in the dry chaco region of Argentina. J. Biogeogr. 17, 491–500.
Aide, T.M., Clark, D., Grau, H.R., Levy, M., Carr, D., Redo, D., Andrade, M., 2013. Deforestation and forest expansion in Latin America: 2001–2010. Biotropica 45, 262–271.
Alberdi, M.T., Cerdeño, E., Prado, J.L., 2008. *Stegomastodon platensis* (Proboscidea, Gomphoteridae) en el Pleistoceno de Santiago del Estero, Argentina. Ameghiniana 45, 257–271.
Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22, 42–47.
Archer, S., Schimel, D., Holland, E., 1995. Mechanisms of shrubland expansion: land use, climate or CO2? Clim. Change 29, 91–99.
Baldrich, J.A., 1889. El Chaco central norte. In: Peuser (Ed.) (Buenos Aires).
Barbrooke, Grubb, W., 1919. The paraguayan chaco and its possible future. Geogr. J. 54, 157–171.
Bellis, L.M., Pidgeon, A.M., Radeloff, V.C., St-Louis, V., Navarro, N.I., Martella, M.B., 2008. Modeling habitat suitability for greater rheas based on satellite image texture. Ecol. Appl. 18, 1956–1966.
Boedo, E.C., 1873. Estudios sobre la navegación del Bermejo y la colonización del Chaco. In: Libro cuarto: riquezas naturales. Imprenta, litografías y fundición de la sociedad anónima (Buenos Aires).
Brunelle, A., Minckley, T.A., Delgadillo, J., Blissett, S., 2014. A long-term perspective on woody plant encroachment in the desert southwest, New Mexico, USA. J. Veg. Sci. 25, 829–838.
Bucher, E.H., Huszar, P.C., 1999. Sustainable management of the gran chaco of South America: ecological promise and economic constraints. J. Environ. Manag. 57, 99–108.
Burmeister, C., 1899. El campo del cielo (territorio del chaco). Ministerios de Agricultura de la República, Argentina. Buenos Aires.
Cardozo, S., Tálamo, A., Mohr, F., 2011. Composición, diversidad y estructura del ensamble de plantas leñosas en dos paleocauces con diferente intervención antrópica del Chaco semiárido, Argentina. Bosque 32, 279–286.
Carlini, A.A., Zurita, A.E., Gasparini, G., Noriega, J.I., 2004. Los Mamíferos del Pleistoceno de la Mesopotamia argentina y su relación con los del Centro Norte de la Argentina, Paraguay y Sur de Bolivia, y los del Sur de Brasil y Oeste de Uruguay: *Paleobiogeografía y Paleoambientes*. INSUGEO (Tucumán, Argentina). Miscelánea 12, 83–90.
Casillo, J., Kuntz, C., Semmartin, M., 2012. Effects of fire availability on the emergence and recruitment of grasses, forbs and woody species in a semiarid chaco savanna. Austral. Ecol. 37, 452–459.
Clark, M., Aide, T.M., Grau, H.R., Rinner, G., 2010. A scalable approach to mapping annual land cover at 250m using MODIS time series data: a case study in the dry chaco ecoregion of South America. Remote Sens. Environ. 114, 2816–2832.
Coltorti, M., Della Fazia, J., Paredes Ríos, F., Tito, G., 2010. The Ñuagapua alluvial fan sequence: early and late holocene human-induced changes in the bolivian Chaco? Proc. Geol. Assoc. 121, 210–228.
Cuéllar Soto, E., 2011. Ecology and Conservation of the Guanaco Lama Guanicoe in the Bolivian Gran Chaco: Habitat Selection within a Vegetation Succession (PhD thesis). University of Oxford.
de Vivo, M., Carmignotto, A.P., 2004. Holocene vegetation change and the mammal faunas of South America and Africa. J. Biogeogr. 31, 943–957.
Dietz, J.M., 1985. Chrysocyon brachyurus. Mamm. Species 234, 1–4.
Dougill, A., Trodd, M., 1999. Monitoring and modeling open savannas using multi-source information: analyses of kalahari studies. Glob. Ecol. Biogeogr. 8, 211–221.
Eldridge, D.J., Bowkerb, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol. Lett. 14, 709–722.
Fensholt, R., Langanke, T., Rasmussen, K., Reenberg, A., Prince, S., Tucker, C., Scholes, R., Le, Q.B., Bondeau, A., Eastman, R., Gaughan, A., Hellden, U., Mbow, C., Olsson, L., Paruelo, J., Schweitzer, C., Seaquist, J., Wessels, K., 2012. Greeness in semiarid areas across the globe - 1981-2007- an earth observing satellite-based analysis of trends and drivers. Remote Sens. Environ. 121, 144–158.
Fontana, L.J., 1881. El Gran Chaco. Imprenta Ostwald y Martínez, Buenos Aires.
Gasparri, N.I., Baldi, G., 2013. Regional patterns and controls of biomass in semiarid woodlands: lessons from the Northern Argentina dry chaco. Reg. Environ. Change 6, 1131–1144.
Gasparri, N.I., Grau, H.R., 2009. Deforestation and fragmentation of chaco dry forest in NW Argentina (1972–2007). For. Ecol. Manag. 258, 913–921.
Gasparri, N.I., Grau, H.R., Manghi, E., 2008. Carbon pools and emissions from deforestation in extra-tropical forests of northern Argentina between 1900 and 2005. Ecosystems 11, 1247–1261.
Gasparri, N.I., Grau, H.R., Gutierrez-Angonese, J., 2013. Linkages between soybean and neotropical deforestation: coupling and transient decoupling dynamics in a multidecadal analysis. Glob. Environ. Change 23, 1605–1614.
Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Corey, J., Bradshaw, A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.
Grau, H.R., Gasparri, N.I., Aide, T.M., 2008. Balancing food production and nature conservation in the neotropical dry forests of northern Argentina. Glob. Change Biol. 14, 985–997.
Grau, H.R., Kuemmerle, T., Macchi, L., 2013. Beyond land sparing and land sharing. Globalization, environmental gradients and the allocation of land for agriculture production and nature conservation. Curr. Opin. Environ. Sustain. 5, 477–483.
Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–853.
Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecol. Lett. 8, 23–29.
Hoffstetter, R., 1968. Ñuapua, un gisement de vertebres pleistocenes dans le chaco bolivien. Bull. Du. Mus. Natl. d'Hist. Nat. 40, 823–836.
Huáscar Azurduy, F., 2006. Primer registro de tigre dientes de sable (*Smilodon*) en la llanura chacobeniana, Parque Nacional Kaa-Iyá, Bolivia. Kempffiana 2, 150–153.
Iriondo, M.H., García, N.O., 1993. Climatic variations in the Argentine plains during the last 18,000 years. Palaeogeography, Palaeoclimatology. Palaeoecology 101, 209–220.
Izquierdo, A.E., Grau, H.R., 2009. Agriculture adjustment, land use transition, and protected areas in northwestern Argentina. J. Environ. Manag. 90, 858–865.
Jolis, S.J.J. (Ed.), 1972. Ensayo sobre la historia natural del Gran Chaco. Universidad Nacional del Nordeste (Instituto de Historia), Resistencia, Chaco.
Kirch, P.V., 2005. Archaeology and global change: the holocene record. Annu. Rev. Environ. Resour. 30, 409–440.
Kuntz, C., Bravo, S., Moscovich, F., Herrera, J., Godoy, J., Vélez, S., 2003. Fecha de aplicación de fuego y diversidad de herbáceas en una sabana de *Elionorus muticus* (Spreng) O. Kuntze. Rev. Chil. Hist. Nat. 76, 105–115.
Lambin, E.F., Gibbs, H.K., Ferreira, L., Grau, H.R., Mayaux, P., Meyfroidt, P., Morton, D., Rudel, T.K., Gasparri, I., Munger, J., 2013. Estimating the world's potentially available cropland using a bottom-up approach. Glob. Environ. Change 23, 892–901.
Macchi, L., Grau, H.R., Zelaya, P., Marinaro, S., 2013. Trade-offs between land use intensity and avian biodiversity in the dry chaco of Argentina: a tale of two gradients. Agric. Ecosyst. Environ. 174, 11–20.
Marshall, L.G., Sempere, T., 1991. The eocene to pleistocene vertebrates of Bolivia and their stratigraphic context: a review. Fósiles y facies de Bolivia – vol. 1 Vertebrados. Rev. Téc. YPFB 12, 631–652.
May, J.H., Argollo, J., Veit, H., 2008. Holocene landscape evolution along the andean piedmont, bolivian chaco. Palaeogeogr. Palaeoclimatol. Palaeoecol. 260, 505–520.
McFadden, B.J., 2005. Diet and habitat of toxodont megaherbivores (Mammalia, Notoungulata) from the late quaternary of South and Central America. Quat. Res. 64, 113–124.
McFadden, B.J., Wang, Y., Cerling, T.E., Anaya, F., 1994. South American fossil mammals and carbon isotopes: a 25 million-year sequence from the bolivian Andes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 107, 257–268.
Miles, L., Kapos, V., 2008. Reducing greenhouse gas emissions from deforestation and forest degradation: global land-use implications. Science 320, 1454–1455.
Moran, D., Pearce, D., Wendelaar, A., 1996. Global biodiversity priorities. A cost-effectiveness index for investments. Glob. Environ. Change 6, 103–119.

Morello, J., Saravia Toledo, C., 1959a. El bosque chaqueño I. Paisaje primitivo, paisaje natural y paisaje cultural en el oriente de Salta. Rev. Agron. Noroeste Argent. 3, 5–81.
Morello, J., Saravia Toledo, C., 1959b. El bosque chaqueño II. La ganadería y el bosque en el oriente de Salta. Paisaje primitivo, paisaje natural y paisaje cultural en el oriente de Salta. Rev. Agron. Noroeste Argent. 3, 209–258.
Muello, A.C. (Ed.), 1926. Geografía económica del Chaco y Formosa. Oceana, Buenos Aires.
Parr, C.L., Lehmann, C.E.R., Bond, W.J., Hoffmann, W.A., Andersen, A.N., 2014. Tropical grassy biomes: misunderstood, neglected and under threat. Trends Ecol. Evol. 29, 205–213.
Phelps, J., Webb, E.L., Adams, W.M., 2012. Biodiversity co-benefits of policies to reduce forest-carbon emissions. Nat. Clim. Change 2, 497–503.
Portillo-Quintero, C.A., Sánchez-Azofeifa, G.A., 2010. Extent and conservation of tropical dry forests in the Americas. Biol. Conserv. 143, 144–155.
Prado, J.L., Sánchez, B., Alberdi, M.T., 2011. Ancient feeding ecology inferred from stable isotopic evidence from fossil horses in South America over the past 3 Ma. BMC Ecol. 11, 15.
Prevosti, F.J., Schubert, B.W., 2013. First taxon date and stable isotopes (δ13C, δ15N) for the large hypercarnivorous South American canid *Protocyon troglodytes* (Canidae, Carnivora). Quat. Int. 305, 67–73.
Quispe Merovich, C., Lottici, M.V., 2011. Los desafíos del ordenamiento ambiental del territorio y los servicios ecosistémicos. In: Laterra, P., Jobbágy, E.G., Paruelo, J.M. (Eds.), Valoración de Servicios Ecosistémicos. Conceptos, Herramientas y Aplicaciones para el Ordenamiento Territorial. INTA, Buenos Aires, pp. 315–331.
Redo, D., Aide, T.M., Clark, M., 2013. Vegetation change in Brazil's dryland ecoregions and the relationship to crop production and environmental factors: Cerrado, Caatinga, and Mato Grosso, 2001–2009. J. Land Use Sci. 8, 123–153.
Rodden, M., Rodrigues, F., Bestelmeyer, S., 2004. Maned wolf (*Chrysocyon brachyurus*). In: Sillero-Zubiri, C., Hoffmann, M., Macdonald, D.W. (Eds.), Canids: Foxes, Wolves, Jackals and Dogs. IUCN/SSC Canid Specialist Group, Gland, Switzerland and Cambridge, U.K, pp. 38–43.
Strassburg, B.B.N., Rodrigues, A.S.L., Gusti, M., Balmford, A., Fritz, S., Obersteiner, M., Kerry Turner, R., Brooks, T.M., 2012. Impacts of incentives to reduce emissions from deforestation on global species extinctions. Nat. Clim. Change 2, 350–355.
Torres, R., Jayat, J.P., Pacheco, S., 2013. Modelling potential impacts of climate change on the bioclimatic envelope and conservation of the maned wolf (*Chrysocyon brachyurus*). Mamm. Biol. 78, 41–49.
Torres, R., Gasparri, N.I., Blendinger, P.G., Grau, H.R., 2014. Land use and land cover effects on regional biodiversity distribution in a subtropical dry forest: a hierarchical integrative multi-taxa study. Reg. Environ. Change 14, 1549–1561.
Zurita, A.E., Carlini, A.A., Scillato-Yané, G.J., Tonni, E.P., 2004. Mamíferos extintos del Cuaternario de la Provincia del Chaco (Argentina) y su relación con aquéllos del este de la región pampeana y de Chile. Rev. Geol. Chile 31, 65–87.
Zurita, A.E., Miño-Boilini, A.R., Carlini, A.A., Iriondo, M., Alcaraz, M.A., 2009. Paleontología del Chaco Oriental. Una nueva localidad con mamíferos fósiles pleistocenos en el río Bermejo (Formosa, Argentina). Rev. Mex. Cienc. Geol. 2, 277–288.