A contribution to the understanding of the woody encroachment of grasslands/savannahs from South American Semiarid Chaco

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ABSTRACT. The grasslands/savannahs in South American Semiarid Chaco have been massively transformed into shrublands. However, the ecology of this phenomenon is little known and restoration initiatives almost non-existent. Information is provided regarding 1) the differences in plant structure and diversity along a woody encroachment gradient, and 2) the association of plant structural and functional attributes with environmental factors. Using 38 sample units, we obtained tree and shrub cover, herbaceous biomass, species richness and composition of grasses and woody plants, and several herbaceous functional types (mainly grasses). The environmental factors were historical grazing intensity and fire frequency. Related to item 1, it was found that: a) shrub cover was significantly and progressively greater along the woody encroachment gradient and largely exceeded tree cover, b) herbaceous biomass was significantly smaller, with a high woody cover ($\bar{x}$=89.7%), c) grass species richness was maximum at intermediate levels of woody cover ($\bar{x}$=39.3% and 64%), d) dissimilarity in grass species composition was maximum between very low and high levels of woody cover ($\bar{x}$=15.8% and 89.7%), and e) woody species richness and composition were uniform along the woody encroachment gradient. Regarding item 2, it was observed that: 1) the increase in historical grazing intensity was significant and strongly associated with the reduction of fire frequency, which, in turn, was significantly associated with the increase in tree and shrub cover and the decrease in herbaceous biomass, suggesting that overgrazing reduces or eliminates grassland fires and promotes woody encroachment; and 2) several grass functional types were significantly associated with the historical grazing intensity and fire frequency. Our results are useful for both, anticipating grassland/savannah responses to woody encroachment processes and planning restoration and management strategies.

[Keywords: woody cover, shrub cover, herbaceous biomass, plant functional types, plant diversity, restoration, grazing intensity, fire frequency]

Running title: Woody encroachment of grasslands/savannahs of Semiarid Chaco

INTRODUCTION

In the last 150 years, many arid and semiarid grasslands/savannahs have suffered a process of woody encroachment as a consequence of woody plants establishment and spreading (D'Odorico et al. 2012). This phenomenon, called *lignificación* in Spanish literature, is defined as an increase in density, coverage and biomass of woody plants (Van Auken 2009). Shrub cover usually increases in a substantial way, while tree cover shows variable responses (Eldridge et al. 2011). This situation has a negative impact on pastoral production and alters biodiversity, hydrological cycles and carbon balance of ecosystems (Archer et al. 2017). At broad scales and over long time periods, the balance between woody and herbaceous cover is affected by global warming and the increase of CO_2 concentrations in the atmosphere (Archer et al. 2017). At a local scale, this balance varies according to geomorphology, topography, soil types and natural and anthropic disturbances (Archer et al. 2017).

Historically, fire could have contributed to control woody plants and keep herbaceous plants prevalence in grasslands/savannahs (Morello and Adamoli 1974; Allen 2008; D'Odorico et al. 2012). Grazing intensity interacts with fire frequency by regulating the production of herbaceous biomass (i.e., fine fuel), which spreads fire in grasslands (Allen 2008; Scott et al. 2013). Chronic overgrazing drastically decreases herbaceous biomass production that, at the same time, reduces fire events and promotes woody plant spreading and soil erosion (Morello and Adamoli 1974; Van Auken 2009; D'Odorico et al. 2012). The mentioned mechanism is called "the overgrazing hypothesis", and at a local scale it would be the main cause of woody encroachment in different arid and semiarid regions (Van Auken 2009).

Woody encroachment strongly influences in diversity and functional types of plants (Bestelmeyer et al. 2003; Archer et al. 2017). While woody encroachment progresses, the adapted species to grasslands/savannahs decrease in time and are replaced by others adapted to shrubs/forests (Archer et al. 2017), suggesting that most of the differences in species compositions would occur between low and high levels of woody encroachment. Frequently, maximum species richness occurs when both, the herbaceous and the woody components are well represented, that is to say at intermediate woody encroachment levels (Archer et al. 2017). Overgrazing can cause the prevalence of non-palatable woody plants and the replacement of perennial palatable grasses by annual herbs or grasses (Vetlter 2005; Evans et al. 2017). Frequent fires in grasslands create habitats with a great sunlight availability benefiting shade-intolerant species and excluding fire-intolerant ones (Ripley et al. 2015).

Semiarid Chaco is a vast sedimentary flatland that in South Aerica occupies parts of Argentina, Bolivia and Paraguay (Iriondo 1993). Until early 20th century, historical references indicate that the native landscape was dominated by forests, grasslands and savannahs (Bucher 1982; Morello et al. 2013). In general, at a local scale (i.e., 500 m - few kilometers), these vegetation types were distributed along a light topographic gradient: 1) forests in highlands, 2) grasslands/savannahs in lowlands, and 3) open woodlands (i.e., ecotones between the formers) in intermediate lands (Morello and Saravia Toledo 1959; Morello and Adamoli 1968; Iriondo 1993; Kunst et al. 2006) (Figure 1a). This relationship between topographic position and vegetation types has been classified as three different ecological sites defined by Kunst et al. (2006) as highlands, midlands and lowlands. Since early 20th century, the original landscape physiognomy started being modified by a progressive increase of low height woody cover, happening in both forests and in grasslands/savannahs. This derived in a massive homogenization of the landscape (Figure 1b) (Adamoli et al. 1972; Kunst et al. 2006). The main causes mentioned of this process in forests are tree logging and overgrazing, and in grasslands/savannahs are overgrazing and fire suppression; in all cases they are intensified by droughts (Adamoli et al. 1972; Kunst et al. 2006).

Massive woody encroachment in this region had a severe impact in ecological and productive aspects. Colonizer woody plants are usually *Geoffroea decorticans*, *Aspidosperma quebracbo-blanco*, *Vachellia aroma* and other species belonging to *Prosopis* and *Acacia* genera (Morello and Saravia Toledo 1959; Morello and Adamoli 1974). Many shade-intolerant fodder grasses, which are typical of grasslands/savannahs (e.g., genera like *Paspalum, Pappophorum, Cenchrus,* etc.), have almost disappeared in shrublands (Morello and Saravia Toledo 1959; Morello and Adamoli 1974; Kunst et al. 2006). Different bird and mammal species adapted to grasslands/savannahs have decreased in their population by woody encroachment of their habitats, changes in land use and illegal hunting (Chebez 2008; Grau et al. 2014; Torres et al. 2014). In extreme degradation context, the reduction of livestock receptivity exceeds 90% (Kunst et al. 2006). In this region, ecological restoration activities of grasslands/savannahs are almost non-existent. On the other hand, the main management paradigm focuses on solving the pastoral problems by reducing or eliminating woody cover by means of mechanical disturbances (e.g. rolling chopping) and implantation of African fodder grasses. The effects of these practices on native vegetation are little known.

In Semiarid Chaco, knowledge about the ecology of woody encroachment in grasslands/savannahs is mainly qualitative and descriptive. In consequence, new studies are required to better understand the phenomenon and to improve restoration and sustainable use of these ecosystems by quantitative approaches. Two questions are addressed. 1) What differences are observed in vegetation structure and in woody and grass plant diversity along a woody encroachment gradient? 2) How structural and functional attributes of vegetation are associated with environmental factors such as historical grazing intensity and fire frequency? Our general hypothesis proposed that woody encroachment is promoted by overgrazing and consequent reduction/suppression of fire occurrence (i.e., overgrazing hypothesis). Regarding the first question, it was predicted that 1) the main structural changes take place by an increase in shrub cover (i.e., not in tree cover) and a decrease in herbaceous biomass, 2) maximum richness of grass and woody species occurs at intermediate levels of a woody encroachment gradient, and 3) most dissimilarities in grass and woody composition are registered between the higher and lower sides of the gradient. In relation to the second question, it was predicted that 4) the structural and functional attributes of vegetation are consistently associated with the historical grazing intensity and fire frequency. Besides, we provide information to guide the ecological restoration and the sustainable management of grasslands/savannahs.

MATERIALS AND METHODS

Study area

The study area is located in the southwest of Santiago del Estero province, Semiarid Chaco, Argentina (north= 28°04'15.60'' S, south = 28°30'50.02'' S, west= 65°05'42.53' O and east= 64°33'27.09'' O) (Figure 2). The climate is subtropical semiarid, with cold dry winters and warm rainy summers (Boletta 1998). The average annual precipitations vary between 500-600 mm (Noe et al. 2012) and the water balances are quite homogeneous (e.g., mostly droughts and water excesses affect all area equally) (Ravelo et al. 2014). At a 1:500000 cartographic scale, the study area is a plain (i.e., general slopes between 0.5 and 2%) covered by loess sediments and subdivided in three geomorphologic units (i.e., Rolling Northern Plain, Southern Plain and Foothills) (Angueira and Vargas Gil 1993; Kunst et al. 2006) (Figure 2). The soils belong to the Great Groups of Haplustolls and Natrusolls, being the first the dominant one (Angueira et al. 2007).

In each mentioned geomorphologic unit, at a 1:20000 cartographic scale, the ecological site gradient (i.e., highland, midland and lowland) (Figure 1) is mainly developed between a distance of 1-2 km (Kunst et al. 2006). At a local scale, these ecological sites are well correlated with the spatial variations of plant communities and these are the ecosystem units used for research and management purposes (Kunst et al. 2006). Highland ecological sites were originally occupied by hardwood forests with a superior tree layer integrated by *A. quebracho-blanco* and *Schinopsis lorentzii*, although most of these forests became secondary forests and shrublands. Midland ecological sites were originally occupied by ecotones between forests and grasslands/savannahs. Currently, these ecotones are mostly encroached by woody plants with abundance of *A. quebracho-blanco* and *P. nigra* trees and shrubs such as *V. aroma* and *Celtis ehrenbergiana.* Lowland ecological sites, where this study was focused on, were originally occupied by grasslands/savannahs, with scattered trees such as *S. lorentzii* and *A. quebracho-blanco,* shrubs like *V. aroma*, *G. decorticans* and *Aloysia* sp., and shade-intolerant grasses as *Elionurus muticus*, *Schizachyrium tenerum*, *Paspalum* sp., *Pappophorum* sp. and *Bothriochloa* sp., among others. When these grasslands/savannahs are encroached by shrubs, *V. aroma*, *P. nigra*, *Geoffroea decorticans* and *Schinus* sp. abound. Apart from receiving direct water from precipitations, low topographic positions receive runoffs from the highest ones and, due to their gentle slopes (i.e., <3%), often they become temporarily flooded (Angueira 2007). This provides more humid and favorable environments for native grasses productivity (Morello and Adamoli 1974).

Sampling units

Sampling units of this study belong to a wider database created by INTA EEA Santiago del Estero in the '90s.

<u>Complete database characteristics.</u> It was obtained by dividing homogeneous ecosystems by means of a progressive and hierarchic disaggregation method (Gastó et al.1990, 1993), which is similar to the balance model of woody-grass plants of Archer et al. (2017). In this method, the first determinant factor of the ecosystem is the climate that acts at the top of the hierarchy. Then, geomorphology, local topography, soil type and natural and anthropic

disturbances act at a local scale in the hierarchic order. The complete database has 110 sampling units distributed among the three geomorphologic units previously mentioned (38 in Southern Plain, 46 in Rolling Northern Plain and 26 in Foothills). At the same time, in each geomorphologic unit, the sampling units were distributed among the three ecological sites. The sampling system is explained below. 1) Each sampling unit was a plot (surface=1 ha) located in a deferred and fenced paddock. The deferment technique consists in suppressing grazing during the growing season to let the grassland rest or to create a standing hay for winter and early spring (Díaz 2015). In consequence, selected plots did not have grazing during the growing season before field measurements. 2) In each geomorphologic unit, different locations were selected in ranches dedicated to cow-calf operations by means of remote image interpretation. Within each location, at least two independent samples were sampled. 3) In the local landscape context, relative topographic positions (i.e., high, middle and low) were visually determined by evaluating the orientation of slopes, direction of superficial movement of rainwater and litter acumulation. Complete database was previously used in two studies: the first one, related to homogenous ecosystems definition (Kunst et al. 2006); the second one, regarding grasses as indicators of range conditions for grazing purposes (Kunst et al. 2007).

Sampling units used in this study. From the complete data base previously mentioned, only the sampling units located in lowland ecological sites were reused. Altogether, there were 38 sampling units (16 in the Rolling Northern Plain, 19 in the Southern Plain and 3 in the Foothills) and field work was conducted between 1992 and 1994. Unfortunately, original paper cartography is lost and there is not a geographic coordinate record (i.e., at the time this field work took place, GPS system was not allowed for worldwide civil use). Therefore, it is impossible to show precise locations of these sampling units.

Three-month Standard Precipitation Index (SPI) reliably shows short- and long-term humidity conditions, and gives a seasonal estimate of precipitation (Svoboda et al. 2012; Ravelo et al. 2014). In the study area, the three-month SPI, during the study time (i.e., from the beginning of the growing season 1991-1992 until the end of the growing season 1993-1994, that is to say from October 1991 to March 1994) indicates incipient drought events during some periods in 1993 (three-month SPI in April, June, July, August, September and December) and in 1994 (three-month SPI in January and March), precipitations being normal or above during the rest of the periods (Ravelo et al. 2014) (see methodology of estimation in Additional Material A). Therefore, during this study, there were not strong water restrictions for herbaceous productivity.

Vegetation sampling and attributes

Herbaceous layer. By species and total herbaceous biomass (kg DM/ha) was estimated by using the BOTANAL method (Tothill et al. 1978). This method was applied at the end of the growing season (i.e., autumn) in order to get the maximum expression of the herbaceous layer productivity and diversity. The nomenclature of species was updated according to the Instituto de Botánica Darwinion (2017). This technique has two parts. 1) Herbaceous biomass estimate. Each sampling unit was visually estimated by means of 52 random subsamples (i.e., quadrat=0.25 m^2). Every subsample was rated from 1 to 5, in which 1 represented the lowest amount of herbaceous biomass and 5 the highest one. Rates from 2 to 4 represented a progression between the previous ones. As a reference, five patterns previously selected and properly identified were used. They represented a scale from 1 to 5 containing the herbaceous biomass variations earlier described. Once the visual estimates were done, patterns (i.e., two per each rate from 1 to 5) were cut and oven-dried (i.e., 60 °C during 48 h) in order to obtain dry weights. A linear regression was built by using the biomass values from the 5 patterns (y=a+bx). This allowed estimating herbaceous biomass availability (y) from the average of visual estimates (x). 2) Estimate of by especies herbaceous biomass. The method was based in visually estimating which species occupy the first, second and third place, in terms of dry weight, from the same subsamples of the previous step. Dry biomass of species i (y), was estimated as

$$yi = (p1i * 70.19 + p2i * 21.08 + p3i * 8.73)* y/ 100$$

where $p1_i$, $p2_i$ and $p3_i$ represent the subsample proportion in which species i was registered in the first, second and third place, respectively, and y represents total herbaceous biomass obtained from the previous step.

Functional plant types are defined as plant groups, usually polyphyletic, presenting similar responses to environmental factors and producing similar effects in the main ecosystem processes (Walker 1992). From herbaceous biomass by species, different functional types were obtained. The *a priori* method was used, generally based on only one functional character that is fixed before typification (Díaz et al. 2002) (Additional Material B). a) Herbaceous plants according to their life form, two classes: grasses and herbs (Instituto de Botánica Darwinion (2017). b) Grasses according to their life cycle, perennial and annual (Instituto de Botánica Darwinion 2017). c) Grasses according to their shade tolerance, two types: tolerant and intolerant (Morello and Saravia Toledo 1959; Kunst et al. 1998, 2006, 2007; Molina and Rúgolo de Agrasar 2006). d) Grasses according to their fire tolerance, two types, high and middle-low tolerants (Kunst et al. 1998). In this case, there was not enough information to classify every grass species according to their fire tolerance; in consequence, high tolerance class grouped only six species and middle-low tolerance class grouped only five species. e) Grasses according to their palatability, two types: palatable (i.e., fodder species) and low palatable (i.e., little or no consumed species) (Morello and Saravia Toledo 1959; Kunst et al. 1986, 1998; Díaz 2015; Ledesma et al. 2017).

Woody cover. The modified *Point transect* method was used (Passera et al. 1983). In each sampling unit, along a transect, 52 sampling points separated 50 cm from each other were evaluated. In each sampling point, a telescopic pole was placed in a vertical position and the contacts between the pole and the woody plant organs were counted, distinguishing species and cover types (i.e., tree >3m and shrub ≤3 m). Based on these measures, the following variables were obtained: 1) total woody cover, tree cover and shrub cover (%) from the percentage of sampling points where there was contact with each type of cover, and 2) woody cover by species (contact/transect), counting the respective contacts.

Environmental factors

The following environmental factors were also estimated.

Fire frequency. Defined by how many times each sampling unit was totally burned during the ten years before the sampling took place, taking as an initial reference (i.e., time 0) the year in which the sampling was done (i.e., it must be taken into account that the sampling was held between 1992/94). The variable was estimated through rancher's interviews, complemented by field indicators such as fire scars in tree trunks and branches and the presence of pyrophytic species. Each sampling unit was classified according to the following fire frequency categories. Category 3, High (a fire per year). Category 2, Middle (a fire every 3-4 years). Category 1, Low (a fire at least once in the last 10 years). Category 0, Non-existent (no fires in more than ten years).

Historical grazing intensity. The most used direct measure of grazing intensity in long-term studies has been the percentage of herbaceous fodder plants consumed or destroyed by herbivores (Holechek et al. 1999). However, there are many indirect measures that can be used, like the number and biomass of dung (i.e., short-term estimates), width and depth of herbivores tracks (i.e., long-term estimates) (Eldridge et al. 2017), distance to the watering points (i.e., short- and long-term estimates) (Díaz 2015) and range conditions (i.e., long-term estimates) (van Oudenhoven et al. 2015). In this study, for each sampling unit, historical grazing intensity (i.e., more than 20 years of use) was indirectly estimated (Eldridge et al. 2017) from the percentage of the eroded soil area. This estimation strategy is based on the fact that in arid and semiarid regions around the world, the maintenance of plant cover is the key to reduce erosion; and that excessive defoliation of herbaceous layer, caused by intense grazing, accelerates the erosion and loss of soil organic matter and nutrients (Abril and Bucher 1999; Van Auken 2000; Bestelmeyer et al. 2003; Zhao et al. 2007; Siffredi et al. 2011; D'Odorico et al. 2012; Díaz 2015;van Oudenhoven et al. 2015;Archer et al. 2017; Eldridge et al. 2017; Zhou et al. 2017).

The employed database presents a classification of sampling units taking into account the following categories of soil erosion. Category 3, Severe (more than 50% of the area affected by erosion). Category 2, Moderate (between 50-30% of the area affected by erosion). Category 1, Low (less than 30% of the area affected by erosion). Category 0, Nill (abundant litter or no signs of soil loss).

Soil erosion was evaluated in field by observing litter accumulation, the presence of pedestals and gullies, and superficial losses of soil. Percentages of the eroded area were visually estimated in metallic frames of 0.25 m^2, with 52 subsamples per sampling unit.

In this study, the nill and severe erosion classes were respectively used as estimators of low/nill and very high historical grazing intensity (i.e., disturbance extremes). On the other hand, low and moderate erosion classes respectively estimated intermediate levels of historical grazing intensity between the previous ones.

Data analysis

Classification of sampling units. In order to analyze the modifications in structural attributes and grass and woody plant diversity (i.e., predictions 1, 2 and 3), the sampling units were arbitrarily grouped in four levels of woody encroachment (i.e., percentage of total woody cover): very low (0-25%), low (25.1-50%), moderate (50.1-75%) and high (75.1-100%).

Structural attributes. Significant differences in tree cover, shrub cover and herbaceous biomass were evaluated using single-factor ANOVA (woody encroachment level) and LSD test of Fisher, α=0.05. Before the analysis, in order to keep normality and homogeneity of residual variances, tree and shrub covers (%) were transformed using the arcsine method (i.e., suitable when the variable is a proportion), while herbaceous biomass was transformed by the square root method (Fowler and Cohen 1990). The analysis was done using the INFOSTAT Software 2013 version (Di Rienzo et al. 2013).

Species diversity. Grass biomass by species (kg DM/ha) and woody cover by species (contact/transect), were transformed to presence/absence by species in order to carry out the following analysis (Colwell 2013): a) to get the non-parametric estimator Chao2 of grass and woody plant richness for each woody encroachment level; b) to compare statistically grass and woody plant richness between woody encroachment levels by means of rarefaction method based on samples and extrapolation. The procedure equates the smaller sample sizes to the biggest one and generates an estimation of accumulated species richness with the respective confidence intervals at 95%. The non-superposition of confidence intervals indicates significant differences in species richness at a level α=0.05; and c) to obtain the non-parametric Chao-Sorensen similarity index of grass and woody plant species composition between pairs of woody encroachment levels. Values were multiplied by 100 to obtain the similarity percentage. The classes of similarities were: 0-39.9% (low), 40-69,9% (moderate) and 70-100% (high). The analysis was done using the EstimateS 9.10.0 Software (Colwell 2013).

Associations between structural and functional attributes with environmental factors. To evaluate these associations (i.e., prediction 4), the Spearman rank correlation coefficient was used This coefficient is used when one or both variables to be correlated are on an ordinal scale (i.e., in this study, fire frequency and historical grazing intensity) and the number of sample pairs is equal or greater than 7 (i.e., this study had 38 sample pairs) (Fowler and Cohen 1990; Di Rienzo et al. 2013). Correlation intensity (positive or negative), was categorized as the following: 0-0.19 (very weak), 0.2-0.39 (weak), 0.4-0.69 (moderate), 0.7-0.89 (strong) and 0.9-1(very strong) (Fowler and Cohen 1990). Correlation significances were evaluated at level α=0.05. The analysis was done using the INFOSTAT Software 2013 version (Di Rienzo et al. 2013).

RESULTS

Classification of sampling units

For each woody encroachment level, averages ($\bar{x}$) and standard deviations (S.D.) of total woody cover, as well as sample sizes (n), had the following results: very low woody encroachment level ($\bar{x}$=15.8%, S.D.= 11.9%, n=4), low woody encroachment level ($\bar{x}$=39.3%, S.D.=6.7%, n=10), moderate encroachment level ($\bar{x}$=64.0%, S.D.=9.3%, n=13) and high woody encroachment level ($\bar{x}$=89.7%, S.D.= 9.1%, n=11).

Structural attributes

Figure 3 presents average and standard deviations of plant structural attributes plus the results of variance analysis. It is consistent with prediction 1, a) shrub cover was significantly higher while woody encroachment gradient progressed (Figure 3a); b) although a tree cover significantly greater was observed in the higher level of woody encroachment than in the lower ones (Figure 3b), it is observed that shrub cover widely predominated over tree cover along the woody encroachment gradient (Figure 3a, 3b); and c) herbaceous biomass was significantly lower in the high woody encroachment level than in the very low and low ones (Figure 3c).

Species diversity

The species richness estimator Chao2, on average, estimated 17.6 grass species in the very low woody encroachment level, 60.0 in the low level, 71.0 in the moderate level and 23.7 in the high level. Also, on average, it estimated 19.2 woody species in the very low woody encroachment level, 25.3 in the low level, 25.2 in the moderate level and 36.1 in the high level. The abundance of the complete species list is presented in the additional materials B and C.

In rarefaction and extrapolation analysis (Figure 4), taking into account that the lack of superposition of confidence intervals indicates significant differences in species richness, it is observed that: a) consistent with prediction 2, there was a significant peak of grass richness at intermediate levels of woody encroachment (i.e., low and moderate) (Figure 4a); and b) there were not significant differences in woody richness between levels of woody encroachment (i.e., all confidence intervals were superposed) (Figure 4b), which is not consistent with prediction 2.

Table 1 presents similarity percentages of grass and woody compositions between woody encroachment levels (i.e., Chao-Sorensen index). Consistent with prediction 3 for grasses, the lower similarity was registered between very low and high woody encroachment levels (i.e., moderate similarity), while among the rest of pairs of woody encroachment levels, similarities were high in all cases. For woody plants, although the lower similarity was also registered between the very low and high woody encroachment levels, all pairs of woody encroachment level showed high similarities, which did not agree with prediction 3

Associations between structural and functional attributes with environmental factors

Table 2 represents the complete correlations matrix in table format. Now, only the correlations of our interest are highlighted. Consistent with prediction 4, structural and diverse functional attributes were significantly associated with environmental factors. A very important fact is that correlations indicated in items 1 and 2 were coherent with the overgrazing hypothesis and they are detailed as follows. 1) Fire frequency and historical grazing intensity: there was a strong and negative significant association. 2) Structural factors with environmental factors. Fire frequency showed the following significant associations: a) negative and moderate with tree and shrub covers, and b) positive and moderate with herbaceous biomass. 3) Herbs and grasses with environmental factors. Fire frequency showed a positive and moderate significant asocciation with grasses. Historical grazing intensity had a negative and strong significant association with grasses. 4) Perennial and annual grasses with environmental factors. Fire frequency had a positive and moderate signficant association with perennial grasses. Historical grazing intensity showed a negative and strong significant association with perennial grasses. 5) Grasses according to their palatability with environmental factors. Fire frequency had a positive and moderate significant association with palatable grasses. Historical grazing intensity showed a negative and strong significant association with palatable grasses. 6) Grasses according to their shade tolerance with environmental factors. Fire frequency had a positive and moderate significant association, with shade-intolerant grasses. Historical grazing intensity showed the following significant associations: a) negative and strong with shade-tolerant grasses and b) negative and moderate with shade-intolerant grasses. 7) Grasses according to their fire tolerance with environmental factors. Fire frequency showed a positive and moderate significant association with high fire tolerant grasses. Historical grazing intensity had a negative and moderate significant association with middle-low and high fire tolerant grasses.

In Additional Material D, a complementary descriptive statistic of the different plant functional types is presented.

DISCUSSION

Woody encroachment gradient and plant structure

A worldwide analysis of cases showed that, consistently, woody encroachment increases shrub cover and decreases herbaceous cover, while tree cover shows variable responses (Eldridge et al.2011). According to prediction 1, our results suggested that woody encroachment would be mainly explained by substantial increases of shrub cover (i.e., on average, shrub cover went from 15.8% in the very low woody encroachment level to 88.9% in the high level), while tree cover would be minimum and have a minor role (i.e., on average, tree cover represented 0%, 4.7%, 2.3% and 5.4% of the total woody cover in very low, low, moderate and high woody encroachment levels, respectively). The observed shrub dominance coincides with a study carried out in low ecological sites in the Experimental Ranch F. Cantos (INTA Santiago del Estero), where woody encroached grasslands/savannahs had a very high shrub cover (91.5%, on average) and a low tree cover (23.9% on average) (Coria et al. 2016). In Semiarid Chaco in Salta province, common colonizer woody plants, such as *A. quebracho-blanco*, *P. nigra* and *S. mistol*, in time (approximately more than 50 years), become trees and transform the shrubland physiognomy in a low forest one (Morello and Saravia Toledo 1959). In our study, on average between all the sampling units, *P. nigra* occupied the second place (55.8 contact/transect), *A. quebracho-blanco*, the seventh (20.0 contact/transect) and *S. mistol*, the tenth (9.1 contact/transect). This indicates that they were common species, and if anthropic or natural disturbances do not limit the growth of individuals (i.e., mechanic, fire, diseases), there would be potential for older shrublands evolving to low height forests.

Consistent also with prediction 1, smaller significant herbaceous biomass observed in high woody encroachment level (57.7% lesser regarding the very low woody encroachment level) would be related to the combined effect of overgrazing and competence exerted by woody plant high density, that limits herbaceous vegetation development (Bestelmeyer et al. 2003; Kunst et al. 2012; Díaz 2015) (reflected in the fact that historical grazing intensity was significantly and positively associated with tree and shrub cover, and significantly and negatively associated with herbaceous biomass). Our results suggest that places with woody cover smaller than 75% still have potential to produce high levels of herbaceous biomass (i.e., >3000 kg DM/ha).

Woody encroachment gradient and grass and woody diversity

At any spatial scale, habitat variety promotes a greater biodiversity (Fischer et al. 2006). Consistent with prediction 2, the observed significant peak of grass richness in low and moderate woody encroachment levels would be related to its intermediate woody cover (on average, 39.3% and 64%, respectively) and its abundant herbaceous biomass (on average, 4053.1 and 3279.7 kg DM/ha, respectively). This would determine that both woody and herbaceous habitats were well represented (Archer et al. 2017).

Consistent with prediction 3, the lowest similarity in grass composition between very low and high woody encroachment levels would be a consequence as woody encroachment increases grassland/savannah adapted species decrease and shrubland/forest adapted species increase (Archer et al. 2017). This would have maximized dissimilarities in species composition between these two extremes of the woody encroachment gradient. Regarding this, our results suggest that a) in very low woody encroachment level, grassland/savannah adapted grasses (i.e., shade intolerant) tended to dominate shrubland/forest adapted grasses (i.e., shade tolerant) due to their contribution of 68.8% of species (11) and the 70.4% of biomass (2952.4 kg DM/ha); and b) in high woody encroachment level, taking into account the previous situation, grassland/savannah adapted grasses tended to contribute with less species (60.9%, 14) and biomass (41.8%. 631.4 kg DM/ha). Within shrublands, grassland/savannah adapted grasses usually survive in microhabitats without woody cover (small clearings).

Along the woody encroachment gradient, woody richness was even, which is consistent with a worldwide analysis of cases that showed shrub and tree richness tending to not being significantly modified by woody encroachment (Eldridge et al. 2011). Moreover, similarities in woody plant composition between each pair of woody encroachment level were interpreted as high in all cases (Chao-Sorensen index≥83.3%) (Table 1). Therefore, woody plant composition was quite uniform along the woody encroachment gradient. Our results suggest that both woody plant richness and composition would be attributes little affected by woody encroachment, which is not consistent with predictions 2 and 3.

A relevant interpretation derived from the previous results states that woody encroachment would be mainly a consequence of increase of abundance of woody species already present and not a cause of new species arrival from other places, exposing the importance of species dispersal mechanisms. In this study, most of woody species disperse their seeds through dispersal agents: birds (*C. atamisquea*, *C. ehrenbergiana*, *C. microphylla* and *Schinus* sp.), birds and ants (*J. rhombifolia*), ants (*P. sericantha*), domestic and wild mammals (*V. aroma*, *C. coccinea*, *G. decorticans*, *M. carinatus*, *O. quimilo*, *P. alba*, *P. nigra*, *S. mistol*y *X. Americana*), and wind (*A. quebrachoblanco*, *C. praecox*, *L. divaricata*, *S. lorentzii* and *A. gratissima*) (Morello and Saravia Toledo 1959; Abraham de Noir and Bravo 2014). A reduced group of species disperse their seeds without agents (i.e., autochory) such as *S. praecox*, *M. Detinens* and *S. Aphylla* (Morello and Saravia Toledo 1959; Abraham de Noir and Bravo 2014), and only one species mainly in an asexual way (*L. turbinata*). The dispersal strategy of *J. Xylosteoides* remains unknown.

Associations between structural and functional attributes with environmental factors

Consistent with prediction 4, structural and diverse functional attributes were associated in a significant way with considered environmental factors. In first place, there was a series of significant correlations coherent with the overgrazing hypothesis. Historical grazing intensity was strongly associated with the reduction of fire frequency, which, at the same time, was associated with the increase of tree and shrub cover and a decrease in herbaceous biomass (i.e., this statistical evidence represents an original contribution of our study). In worldwide arid and semiarid regions, woody encroachment causes usually mentioned are climate change, high CO_2 levels, overgrazing, changes in fire frequency, changes in competitive abilities of grasses, seed dispersal by cattle, small animal activities and a combination of all of them (Van Auken 2009; D'Odorico et al. 2012; Archer et al. 2017). However, overgrazing and the consequent reduction of grassland fires seem to be the main reasons of woody encroachment in arid and semiarid regions of Southwestern North America and other places (Van Auken 2009), including Semiarid Chaco (intensified by droughts) (Morello and Saravia Toledo 1959; Morello 1970; Adamoli et al. 1972, 1990; Morello and Adamoli 1974). Finally, in Semiarid Chaco, floods in specific places a cause of regular river overflows (e.g., Bañados del Río Dulce) represent another mechanism with great influence in woody/grass plant balance in favor of grasses (Morello 1970; Morello and Adamoli 1974), although this is not the case in our study area.

Significant decrease of grasses in general and other specific grass types (i.e., perennial, palatable, shade tolerant and intolerant and middle-low and high fire tolerant) with the increase in historical grazing intensity suggest that overgranzing would decline the abundance of these plants. On the other hand, the association between historical grazing intensity with the increase of shrub and tree cover and the decrease of palatable grasses agrees with the well-known fact that overgrazing promotes dominance of woody plants communities with poor fodder value over fodder grass communities (Evans et al. 2017), being a traditional problem for pastoral systems connected to woody encroachment (Archer et al. 2017).

Overgrazing can also induce herbs to be dominant over grasses (with variable impacts on soil processes depending on the species) or, in other cases, it induces annual grasses dominance over perennial ones (linked to problems like few or non-existent herbaceous cover during droughts, erosion increase, elimination of fertility islands created by perennial species, etc.) (Vetter 2005; Evans et al. 2017). In our study, annual herbs and grasses did not show significant associations with historical grazing intensity (i.e., a positive association was expected). Besides, along the woody encroachment gradient, perennial grasses dominated annual herbs and grasses (i.e., perennial grasses represented 89.8%, 87.6%, 82.1% and 77% of total herbaceous biomass in very low, low, moderate and high woody encroachment levels, respectively). These results match with the information about native grassland in Arid Chaco; where, despite overgrazing, perennial grasses prevailed (Díaz 2015). However, in both Arid and Semiarid Chaco, the complete replacement of perennial grasses communities by pure communities of herbs or annual grasses without fodder value and very low productivity (e.g., 0- 100 kg DM/ha) was reported in extreme degradation situations (e.g., A soil horizon eliminated) (Morello and Saravia Toledo 1959; Díaz 2015). In our study, the prevalence of perennial grasses along the woody encroachment gradient indicates that in general, our sampling units were not deeply altered.

Significant increase of grasses in general and other grass specific types (i.e., perennial, palatable, shade intolerant and high fire tolerant) with the increase of fire frequency is probably related to the fact that periodic grassland fires reduce competence of woody plants and stimulate grass flowering (of certain species), germination and growth (Allen 2008; Scott et al. 2013), which was also observed in Semiarid Chaco (Kunst et al. 2003a). Besides, shade-intolerant and high fire tolerant grasses could have been favored by frequent fires that created open habitats with high sunlight availability and decreased the abundance of fire-intolerant species (Ellis et al. 1980; Everson et al. 1988; Bond et al. 2003; Foster et al. 2004). In our study, five of the six evaluated shade-intolerant grasses were at the same time highly tolerant to fire (Additional Material B), which suggests that, at least for these species, shade intolerance and high fire tolerance could be the linked functional traits.

Towards restoration and sustainable use of grasslands/savannahs

Woody encroachment along with transformation of native ecosystems in crop lands (including exotic grasses) were identified as the main causes of grassland/savannah disappearance in Chaco Region (Grau et al. 2014; Fernández et al. 2020). Nowadays, there are not important activities in restoration and sustainable use of these ecosystems. This would be majorly a cause of Argentinian preservation policies prioritizing forests and ignoring grasslands/savannahs (Grau et al. 2014). In the scientific community, there is a growing interest in this problem (Grau et al. 2014; Torres et al. 2014; Kunst et al. 2015; Fernández et al. 2020), but it is insufficient due to the seriousness of the matter. Therefore, it is essential to stimulate politicians in including grasslands/savannahs in preservation and sustainable use of native ecosystems policies, and also encourage the scientific community in contributing the necessary knowledge for an effective decision making (Grau et al. 2014; Fernández et al. 2020).

In areas under cow-calf operations, restoration of grasslands/savannahs would have greater success possibilities if it also constitutes a profitable alternative. The challenge would be returning from a shrubland state to a grassland/savannah productive state and then keep it in time. Our study suggests that would be appropiate a management oriented to restore or keep natural fire regimes (i.e., they regulate woody cover and favor palatable grasses) and rationally graze the environments. However, this suggestion is not new for the region and it was expressed in several occasions (Morello 1970; Morello and Adamoli 1974; Kunst et al. 2003b). Rational grazing is achieved by adjusting stocking rate (e.g., ha/animal unit) to the standing herbaceous forage available in the paddocks, by using "forage balance method" (Kunst et al. 2015).

Fires constitute a vegetation management tool in several parts around the world where they are considered as ecological events with great influence on landscape dynamics. To exert an efficient control over shrub cover, grassland fires must have high intensity, which requires a fine fuel load greater than 3000 kg DM/ha (Kunst et al. 2003b). Our results suggest that in the study area, woody cover smaller than 75% would have potential to produce herbaceous biomass beyond this threshold. In these cases, rational gazing and application of precribed fires each 3-4 years would allow the proggresive restitution or maintenance of grasslands/savannahs as habitats for cattle and native flora and fauna, keeping palatable grasses (Kunst et al. 2003b, 2003a). However, woody cover over 75% would not produce herbaceous biomass beyond the threshold of 3000 kg DM/ha and, in consequence, intense grassland fires could not occur. In these cases, grassland/savannah restoration could be accelerated by means of disturbance regimes using them in sequence 1) low intensity rolling chopping (i.e., mechanic disturbance) to decrease shrub competence, minimizing course woody debris generation that increase severe fire risk; 2) grazing suppression during one or two growing seasons causing herbaceous biomass accumulation; and 3) prescribed grassland fires to decrease even more the shrub competence and favor again herbaceous vegetation (Kunst et al. 2003b, 2008). Finally, when degradation is extreme, there is a high probability of native perennial palatable grass disappearance and loss of soil seed bank viability. Therefore, treatments like rolling chopping and grazing suppresion would not produce satisfactory increases in grass biomass, being necessary to sow them (Kunst et al. 2008; Díaz 2015; Puthod et al. 2020).

From the beginning, cow-calf operations in Semiarid Chaco were sustained by native grasses, which are still used. However, nowadays African fodder grasses are very used which seeds are easily acquired in the market. The most used cultivars belong to *Megathyrsus maximus*, *Cenchrus ciliaris* and *Chloris gayana* sp. (Díaz 2015) Commonly, mechanic diturbances to woody vegetation are applicated and exotic grasses are sowed simultaneously; in this way, herbaceous forage productivity increases up to 400-500% (Fumagalli and Kunst 2002). The challenge would be finding the way in which grassland/savannah restoration is complementary and coexists with these highly productive management alternatives. It has been emphasized that the exotic grass employment must be restricted in the most degraded areas of the productive lands; this means that well managed natural grasslands are profitable (Díaz 2015). Another way to satisfactorily increase herbaceous fodder supply, but in an environmentally friendly way, would be the use of commercial cultivars of native herbaceous fodder (i.e., grasses, legumes and other broadleaf plants) adapted to the environmental heterogeneity of Chaco ecosystems (Díaz 2015; Pensiero et al. 2017). However, this aspect still cannot be consolidated in the region and the way to gather native herbaceous seeds is haverting in the field (Díaz 2015; Pensiero et al. 2017). Today, there is only one developed native fodder grass cultivar named Chamical INTA and belongs to *T. crinita* species (present in our study and common in Arid and Semiarid Chaco), which is valued because its great fodder potential, its saline and clay soil adaptation and its drought and cold tolerance (Ledesma et al. 2017); although aspects linked to seed production still remain in the technological development phase.

CONCLUSIONS

Regarding the first question, our results suggested that: a) woody encroachment would be basically a cause of substantial increases in shrub cover, while tree cover would have a minor role, b) significant decreases in herbaceous biomass productivity would occur with high levels of woody encroachment, c) maximum grass richness would occur at intermediate levels of woody encroachment, d) maximum dissimilarity in grass composition would happen between very low and high levels of woody encroachment, and e) woody plant richness and composition would be little affected by woody encroachment.

Regarding our second question, we obtained statistical evidence in favor of overgrazing hypothesis, based on the increase in historical grazing intensity being significantly and strongly associated with the reduction of fire frequency, which at the same time, was significantly associated to the increase of tree and shrub cover and the decrease of herbaceous biomass. Results also suggested that 1) the increase in historical grazing intensity would be associated with a decrease of grasses in general and other specific types of grasses (i.e., perennial, palatable, shade tolerant and intolerant and a middle-low and high fire tolerant), 2) the lack of association between historical grazing intensity with herbs and annual grasses would be due to these functional types dominating in extreme degradation conditions (it would not be the case of our study), and 3) the increase in fire frequency would be associated to the increase of grasses in general and other specific types of grasses (i.e., perennial, palatable, shade intolerant and high fire tolerance)

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Table 1. Similarity percentage of species composition (Chao-Sorensen index) among pairs of woody encroachment levels. The similarity classes are indicated in parentheses: 0-39.9% (low), 40-69.9% (medium) and 70-100% (high).

Chao-Sorensen similarity index (%)			
Woody encroachment level	Woody encroachment level	Woody plants	Grasses
Very low	Low	94 (high)	83.6 (high)
Very low	Moderate	92.7 (high)	79.5 (high)
Very low	High	83.3 (high)	63.6 (moderate)
Low	Moderate	94.4 (high)	100 (high)
Low	High	96.7 (high)	84.5 (high)
Moderate	High	98.3 (high)	92.6 (high)

Table 2. Correlation matrix among structural and functional attributes and environmental factors, in table format.

Variable (1)	Variable (2)	Coef. Sperman	P-value	Strength
Fire frequency	Historical grazing intensity	-0.71	0.000	Strong
Fire frequency	Shrub cover	-0.67	0.001	Moderate
Fire frequency	Tree cover	-0.59	0.003	Moderate
Fire frequency	Herbaceous biomass	0.63	0.001	Moderate
Fire frequency	Grasses	0.60	0.003	Moderate
Fire frequency	Herbs (broadleaf)	0.15	0.485	Very weak
Fire frequency	Annual grasses	0.21	0.339	Weak
Fire frequency	Perennial grasses	0.60	0.003	Moderate
Fire frequency	Palatable grasses	0.60	0.003	Moderate
Fire frequency	Low palatable grasses	-0.16	0.463	Very weak
Fire frequency	Shade tolerant grasses	0.34	0.108	Weak
Fire frequency	Shade intolerant grasses	0.51	0.012	Moderate
Fire frequency	High fire tolerant grasses	0.64	0.001	Moderate
Fire frequency	Middle-low fire tolerant grasses	0.04	0.854	Very weak
Historical grazing intensity	Shrub cover	0.43	0.044	Moderate
Historical grazing intensity	Tree cover	0.43	0.048	Moderate
Historical grazing intensity	Herbaceous biomass	-0.71	0.000	Strong
Historical grazing intensity	Grasses	-0.71	0.000	Strong
Historical grazing intensity	Herbs (broadleaf)	-0.30	0.175	Weak
Historical grazing intensity	Annual grasses	-0.01	0.959	Very weak
Historical grazing intensity	Perennial grasses	-0.71	0.000	Strong
Historical grazing intensity	Palatable grasses	-0.71	0.000	Strong
Historical grazing intensity	Low palatable grasses	0.39	0.074	Weak
Historical grazing intensity	Shade tolerant grasses	-0.72	0.000	Strong
Historical grazing intensity	Shade intolerant grasses	-0.54	0.009	Moderate
Historical grazing intensity	High fire tolerant grasses	-0.61	0.002	Moderate
Historical grazing intensity	Middle-low fire tolerant grasses	-0.50	0.018	Moderate
Shrub cover	Tree cover	0.31	0.148	Weak
Shrub cover	Herbaceous biomass	-0.42	0.045	Moderate
Shrub cover	Grasses	-0.42	0.046	Moderate
Shrub cover	Herbs (broadleaf)	0.08	0.725	Very weak
Shrub cover	Annual grasses	-0.17	0.440	Very weak
Shrub cover	Perennial grasses	-0.42	0.046	Moderate
Shrub cover	Palatable grasses	-0.42	0.045	Moderate
Shrub cover	Low palatable grasses	-0.15	0.490	Very weak
Shrub cover	Shade tolerant grasses	-0.13	0.551	Very weak
Shrub cover	Shade intolerant grasses	-0.4	0.055	Moderate
Shrub cover	High fire tolerant grasses	-0.54	0.007	Moderate
Shrub cover	Middle-low fire tolerant grasses	0.04	0.849	Very weak
Tree cover	Herbaceous biomass	-0.36	0.096	Weak
Tree cover	Grasses	-0.39	0.067	Weak
Tree cover	Herbs (broadleaf)	0.08	0.706	Very weak
Tree cover	Annual grasses	-0.37	0.082	Weak
Tree cover	Perennial grasses	-0.39	0.067	Weak
Tree cover	Palatable grasses	-0.39	0.066	Weak
Tree cover	Low palatable grasses	0.05	0.806	Very weak
Tree cover	Shade tolerant grasses	-0.45	0.033	Moderate
Tree cover	Shade intolerant grasses	-0.25	0.253	Weak
Tree cover	High fire tolerant grasses	-0.55	0.007	Moderate
Tree cover	Middle-low fire tolerant grasses	-0.15	0.480	Very weak
Herbaceous biomass	Grasses	0.94	0.000	Very strong
Herbaceous biomass	Herbs (broadleaf)	0.38	0.072	Weak
Herbaceous biomass	Annual grasses	0.22	0.304	Weak
Herbaceous biomass	Perennial grasses	0.94	0.000	Very strong
Herbaceous biomass	Palatable grasses	0.95	0.000	Very strong
Herbaceous biomass	Low palatable grasses	0.07	0.753	Very weak
Herbaceous biomass	Shade tolerant grasses	0.64	0.003	Moderate
Herbaceous biomass	Shade intolerant grasses	0.92	0.000	Very strong

Herbaceous biomass	High fire tolerant grasses	0.66	0.001	Moderate
Herbaceous biomass	Middle-low fire tolerant grasses	0.10	0.662	Very weak
Grasses	Herbs (broadleaf)	0.19	0.376	Very weak
Grasses	Annual grasses	0.09	0.677	Very weak
Grasses	Perennial grasses	1.00	0.000	Very strong
Grasses	Palatable grasses	1.00	0.000	Very strong
Grasses	Low palatable grasses	0.04	0.849	Very weak
Grasses	Shade tolerant grasses	0.72	0.000	Strong
Grasses	Shade intolerant grasses	0.86	0.000	Strong
Grasses	High fire tolerant grasses	0.77	0.000	Strong
Grasses	Middle-low fire tolerant grasses	0.27	0.213	Weak
Herbs (broadleaf)	Annual grasses	-0.13	0.544	Very weak
Herbs (broadleaf)	Perennial grasses	0.19	0.376	Very weak
Herbs (broadleaf)	Palatable grasses	0.20	0.352	Weak
Herbs (broadleaf)	Low palatable grasses	-0.24	0.266	Weak
Herbs (broadleaf)	Shade tolerant grasses	0.05	0.813	Very weak
Herbs (broadleaf)	Shade intolerant grasses	0.35	0.100	Weak
Herbs (broadleaf)	High fire tolerant grasses	0.00	0.986	Very weak
Herbs (broadleaf)	Middle-low fire tolerant grasses	-0.01	0.961	Very weak
Annual grasses	Perennial grasses	0.09	0.677	Very weak
Annual grasses	Palatable grasses	0.09	0.677	Very weak
Annual grasses	Low palatable grasses	0.56	0.005	Moderate
Annual grasses	Shade tolerant grasses	0.07	0.739	Very weak
Annual grasses	Shade intolerant grasses	0.26	0.238	Weak
Annual grasses	High fire tolerant grasses	0.05	0.837	Very weak
Annual grasses	Middle-low fire tolerant grasses	-0.45	0.030	Moderate
Perennial grasses	Palatable grasses	1.00	0.000	Very strong
Perennial grasses	Low palatable grasses	0.04	0.849	Very weak
Perennial grasses	Shade tolerant grasses	0.72	0.000	Strong
Perennial grasses	Shade intolerant grasses	0.86	0.000	Strong
Perennial grasses	High fire tolerant grasses	0.77	0.000	Strong
Perennial grasses	Middle-low fire tolerant grasses	0.27	0.213	Weak
Palatable grasses	Low palatable grasses	0.04	0.868	Very weak
Palatable grasses	Shade tolerant grasses	0.72	0.000	Strong
Palatable grasses	Shade intolerant grasses	0.86	0.000	Strong
Palatable grasses	High fire tolerant grasses	0.77	0.000	Strong
Palatable grasses	Middle-low fire tolerant grasses	0.27	0.219	Weak
Low palatable grasses	Shade tolerant grasses	-0.19	0.397	Very weak
Low palatable grasses	Shade intolerant grasses	0.15	0.504	Very weak
Low palatable grasses	High fire tolerant grasses	-0.01	0.963	Very weak
Low palatable grasses	Middle-low fire tolerant grasses	-0.53	0.009	Moderate
Shade tolerant grasses	Shade intolerant grasses	0.42	0.047	Moderate
Shade tolerant grasses	High tolerance to fire grasses	0.46	0.026	Moderate
Shade tolerant grasses	Middle-low fire tolerant grasses	0.58	0.003	Moderate
Shade intolerant grasses	High fire tolerant grasses	0.62	0.001	Moderate
Shade intolerant grasses	Middle-low fire tolerant grasses	-0.01	0.980	Very weak
High fire tolerant grasses	Middle-low fire tolerant grasses	0.17	0.436	Very weak

Figure 1. General model of the landscape at local scale in Semiarid Chaco.

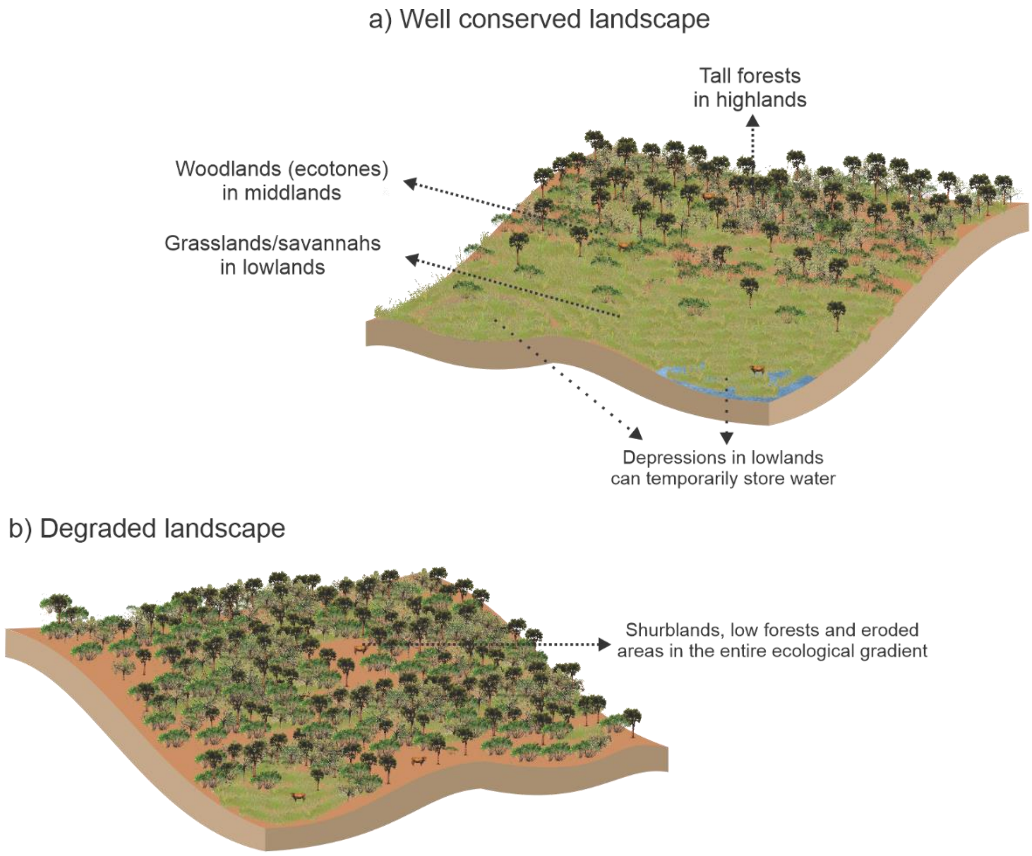

Figure 2. a) Localization of the study area in South American Semiarid Chaco. b) View of the study area, with geomorphologic units delimited and Lavalle, Choya and Villa la Punta towns as geographic references. The remote image corresponds to December 1994. c) View of the relief of the study area, elaborated through a Digital Elevation Model (SRTM; resolution: 30x30 m). The Ovanta-Lavalle fault separates the Southern Plain from the Rolling Northern Plain. Subfigures 'a' and 'c' were elaborated using the software GRASS GIS 7.8. Subfigure 'b' was elaborated using the Google Earth Pro 7.3.3.7786(64-bit) application.

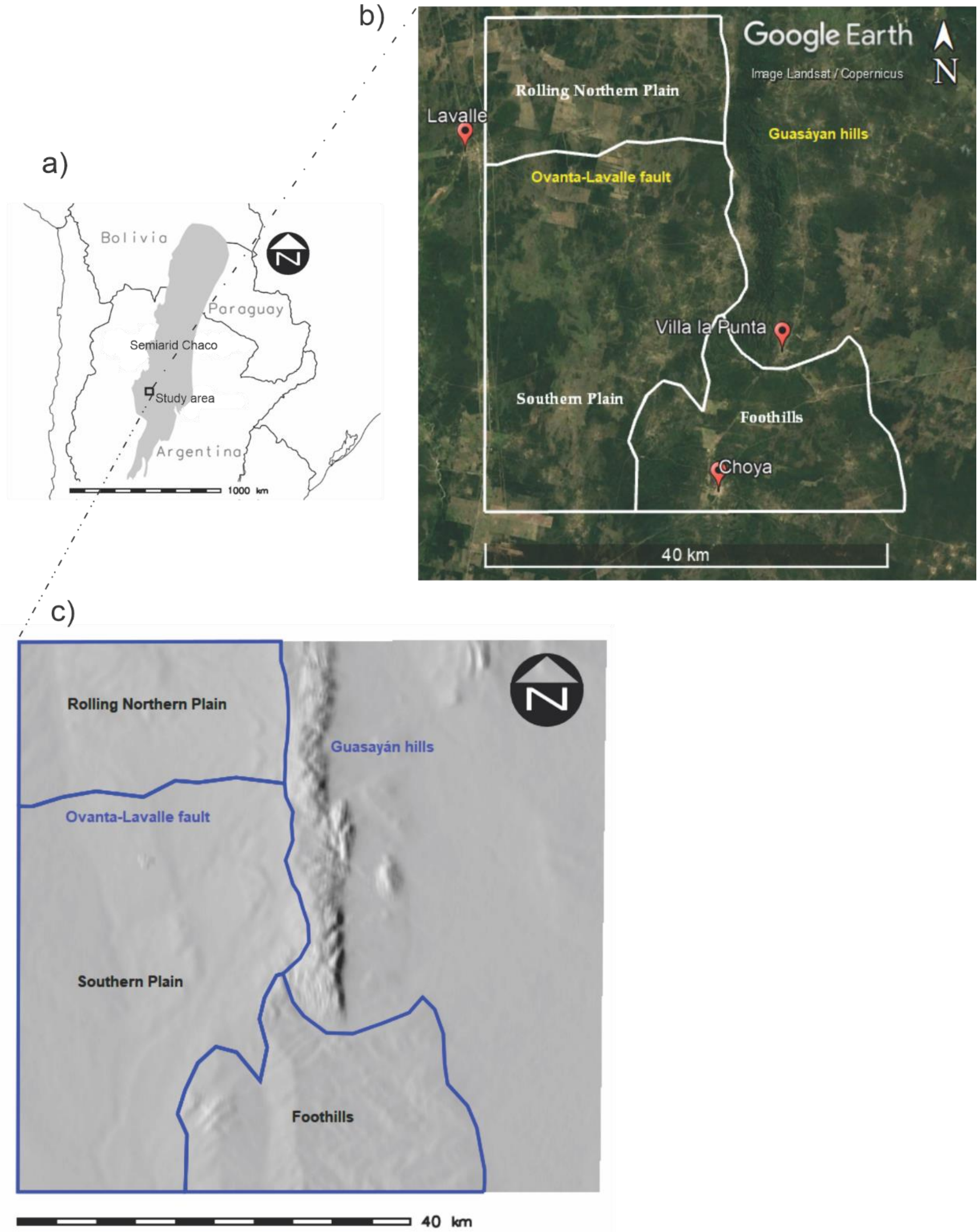

Figure 3. Bar graphics (average + S.E.) for the variables a) shrub cover, b) tree cover and c) herbaceous biomass. Per each variable, the results of analysis of variances are presented. Df=degrees of freedom, F=F statistical, α=0.05. Averages with common letters are not significantly different (LSD Fisher test).

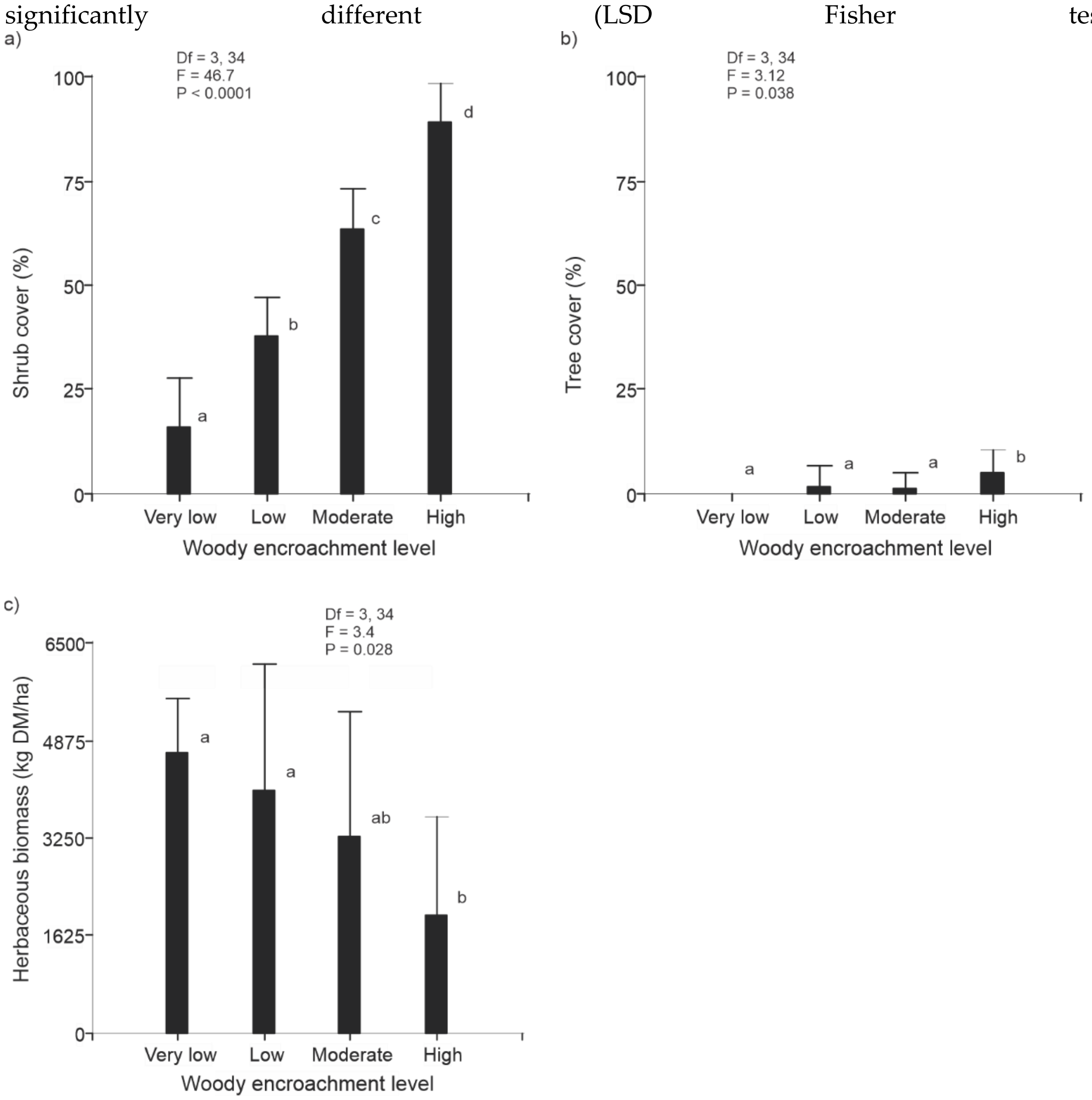

Figure 4. Estimation of species accumulated richness and confidence intervals through the rarefaction and extrapolation method. a) Grass species; b) Woody species.