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Changes in forest structure and tree recruitment in Argentinean Chaco: Effects of fragment size and landscape forest cover

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ABSTRACT

Subtropical Argentinean Chaco forests have been severely deforested and fragmented due to agriculture during the last six decades. The most affected forests are located in areas that are most favorable for crops. This is the case of the semi-deciduous "bosque de tres quebrachos" ("three quebrachos forest") in southwest of Chaco Province (Argentina), where this study was carried out. The aim of this work was to analyze the fragmentation process, considering spatial (fragments and landscape levels) and temporal (land use changes) scales, studying the effects on the forest structure (density and basal area) and tree recruitment. All trees (adults and saplings) were recorded and measured in 112 plots (400 m^2) distributed in 28 forest fragments (0.9–160 ha) located at four different landscape samples (4500 ha) in one environmentally homogeneous zone (72,804 ha). The four landscape samples have different current forest cover (low/high) and different land use history (low/high). Using linear mixed models, we evaluated the effects of current and historic fragment size, landscape forest cover and land use changes on the density and basal area at stand level, and considering the two different strata (upper and middle). Results showed that fragmentation did not severely affect the structure of the older age classes of trees in the remaining fragments but affect the tree recruitment, which could influence over the ability of the forest to perpetuate itself. We found positive relationships between sapling density and fragment size for the tree species of middle stratum, and between sapling density and forest cover at landscape level for the species of upper stratum. Regarding adults, we found a negative relationship between density and historic fragment size, probably related to the past timber harvesting. We concluded that even small fragments of three quebrachos forest and those located in highly deforested landscapes have high conservation value since their structure does not differ from that of the larger fragments or landscapes with higher forest cover. Our results reveal the importance of considering landscape and fragment scales simultaneously to better understand the fragmentation process and improve the recommendations for the management of fragmented landscapes.

1. Introduction

Land use change for crop and pasture production, which inevitably leads to environment loss and fragmentation, has become one of the main threats to biodiversity conservation worldwide (Foley et al., 2005). Agriculture expansion and deforestation in Argentinean Chaco have been very intense in recent decades (Boletta et al., 2006; Carnevale et al., 2007; Gasparri and Grau, 2009; Volante et al., 2012; Zak et al., 2004), due to the application of new technologies and commodity prices (Grau et al., 2005; Hoyos et al., 2013; Zak et al., 2008). As a consequence, this region is one of the main deforestation areas of Latin America (Grau and Aide, 2008), where about 6 million ha of native forest were cleared between 1975 and 2010 (Adámoli et al., 2011).

Most of the fragmentation studies addressed the subject at fragment scale (Grez and Bustamante-Sanchez, 2006; McGarigal and Cushman, 2002), using the area as an indicator for the fragmentation process. Although this "fragment approach" has been criticized because fragmentation is fundamentally a landscape-scale process (McGarigal and Cushman, 2002), it is more appropriate to analyze and compare fragments at different landscapes. This "landscape approach" has begun to be widely used in fragmentation studies of different organisms, but few of them were applied over forest plant communities (e.g. Arroyo-Rodríguez et al., 2009; Hernández-Stefanoni and Dupuy, 2008; Lafortezza et al., 2010).

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Consequently, most studies of the effects of fragmentation on plant communities focus on particular patches (Hernández-Stefanoni and Dupuy, 2008).

Forest loss and fragmentation can impact several processes of plant communities and populations (Aguilar et al., 2006; Fahrig, 2003; Fischer and Lindenmayer, 2007; Hobbs and Yates, 2003; Lienert, 2004). However, most of the studies have been focused on seed and fruit production rather than on successful recruitment (Hobbs and Yates, 2003), and in Latin America most of the studies analyzed compositional attributes rather than structural or functional (Grez and Galetto, 2011).

There is a big amount of background about the edge effect over the forest structure and tree recruitment (Harper et al., 2005; Murcia, 1995). However we found few studies considering fragmentation and forest structure or successful recruitment at the community level, e.g. density and basal area of adult trees in different fragment sizes (Arroyo-Rodriguez and Mandujano, 2006; Echeverria et al., 2007; Santos et al., 2008). Regarding tree recruitment, some authors have found higher densities of saplings in larger fragments (Benitez-Malvido, 1998; Borges do Carmo et al., 2011), whereas others have found no effects (Echeverria et al., 2007, Sánchez-Gallen et al., 2010) and others have found both responses (Cordeiro and Howe, 2001; Melo et al., 2010). It is must be noted that all these works had been based on the fragment-approach.

The aim of this study was to evaluate the process of forest fragmentation at landscape scale and relate it to the structure of woody plants and tree recruitment of three quebrachos forest in Central Argentinean Chaco. We analyze three factors: fragment size, landscape forest cover and land use history, attempting to contemplate landscape integrity to avoid misleading interpretations as was warned by Fahrig (2003).

Our hypothesis was that if the tree regeneration was affected by fragmentation process, we can find responses in the forest structure through the use of two indicators: density and basal area for different age classes. We expected lower frequency of some age classes in landscapes which have suffered greater forest loss, and in the smaller fragments. If we found no effects on adult classes but a significative effect at juvenile classes, this would indicate an impact on tree recruitment.

2. Materials and methods

2.1. Study area

The study area occupies 72,804 ha in Central Argentinean Chaco, southwest of Chaco Province, between 61°0′ and 61°25′W, and between 27°5′ and 27°20′S (Fig. 1), within the distribution area of the three quebrachos forest (Torrella et al., 2011 and references therein). It is characterized by a fragmentation process, where remaining fragments of the three quebrachos forest were immersed in an agricultural matrix. The three quebrachos forest are located in private properties with high potential for agriculture.

Annual rainfall is 750–850 mm, mostly during the summer season, and decreasing from E to W. Mean temperature is 27 °C in summer and 15 °C in winter, with a mean maximum and minimum of 36–8 °C, respectively. The frost-free period extends during a mean of 300 days per year (Alberto and Bruniard, 1987).

2.2. Sampling design

We use forest maps elaborated with aerial photographs of 1957 and Landsat 5 TM image (scene 228/79) of 2010. Aerial photographs were scanned and georeferenced using ArcView 3.2 software by ESRI. Land cover was categorized into two classes: forest and no-forest; and polygons were digitalized directly over the computer screen at 1:50.000 scale using ArcView 3.2 software by ESRI. To assess the accuracy of the 2010 map, we conducted a ground survey for 200 GPS-located points (100 at forest sites and 100 at no-forest sites in the field) along the study area. The percentage of accuracy was high (94.5%) because of the 100 forest and no-forest points defined in the field, 91 and 98 were correctly mapped, respectively. Most of the errors are related to mismatches in the edges of the fragments. From these maps we selected four landscape samples (sub-circular polygons, approximately 4500 ha) differentiated by their current (2010) forest cover and

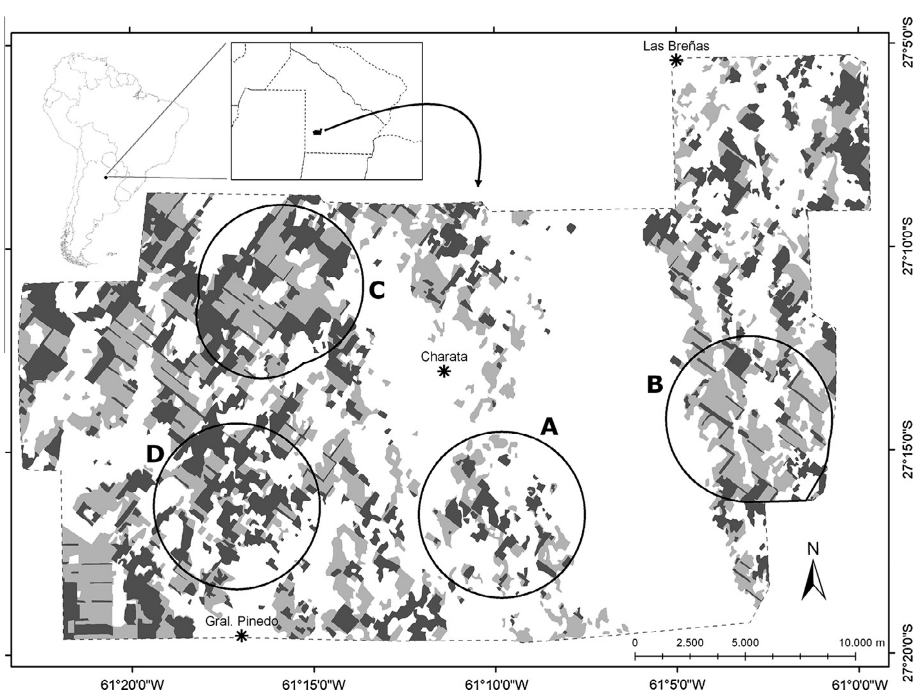

Fig. 1. Location of the study area. Polygons in black are the landscape samples (A, B, C and D). In dark gray: forest cover in 2010; in light gray: deforested areas between 1957 and 2010. Asterisks indicate cities.

their land use change history (i.e., a comparison between forest cover in 1957 and 2010). Samples A and B have low forest cover (14.5%) and samples C and D have comparatively a higher forest cover (34.5 and 34.7%, respectively); in turn, samples B and C have higher land use change between time periods (1790 and 1534 ha respectively) compared to samples A and D which have a lower land use change (659 and 715 ha, respectively) (Table 1 and Fig. 1). Forest recovery was negligible during this time period: only 2.2% of the forests identified in 2010 were not present in 1957.

Within each landscape sample, we selected seven forest fragments, attempting to use the same size range in each landscape sample, from ~1 to ⩾100 ha. Regrettably, we have not had access to fragments smaller than 4.3 ha in sample C, nor fragments larger than 50.4 ha in sample D. However, given the difficulties of the large-scales studies, we have achieved comparable ranges between landscape samples: 1.6 to 158.8 in A; 1.3 to 100.1 in B, 4.3 to 149.9 in C and 0.9 to 50.4 in D. Historic fragment size (size in 1957) range from 0.9 to 570.6 ha.

Tree assemblage was surveyed in 4× 100 m plots. We measured two plots in fragments <10 ha, four plots in fragments between 10 and 35 ha, and six plots in fragments >35 ha. A total of 112 plots arranged in the 28 fragments and four landscape samples were assessed. Within each fragment, plots were located avoiding forest edges by at least 30 m, and distanced from each other by at least 50 m. In some small fragments, this was impossible, so the minimum distances were reduced to 5 and 10 m, respectively. Plots location and orientation were randomly selected using aleatory numbers assigned to possible locations on the map, among the alternative plots allowed by the requirements explained above.

In each plot, we recorded all the individuals of the tree species previously identified in the three quebrachos forest by Torrella et al. (2011). Species were classified into two groups according to their location in the forest strata: *Schinopsis balansae*, *S. lorentzii*, *S. heterophylla* and *Aspidosperma quebracho-blanco* into the upper stratum and the remaining tree species into the middle stratum (Table 2). The lower stratum is composed of 21 species of shrubs (Torrella et al., 2011) and was not assessed in this study.

In each plot, we measured the diameter at breast height (DBH) of trees with DBH ⩾5 cm and in trees with DBH <5 cm we measured stump diameter at 10 cm height (D10). In individuals with more than one stem, each one was measured individually.

The number of individuals for all the tree species registered in the total number of plots considered per fragment was used to calculate individual density (ind/ha). We also calculated density of saplings (DBH <5 cm and D10 >1 cm) and density of "adults" (DBH >20 cm). DBH and D10 were used to calculate basal area (m^2/ha) of tree species for each forest fragment. These variables were calculated at stand level and, separately, for the upper and middle stratum. Individuals with D10 <1 cm were considered as not definitely established, and thus not taken into account.

2.3. Data analysis

We used general linear mixed models with four fixed factors: (a) fragment size in 2010, (b) fragment size in 1957, (c) forest cover in the landscape in 2010 and (d) the difference between forest cover in 2010 and 1957 (Table 1). Current and historic fragment sizes were analyzed as continuous variables, whereas forest cover in 2010 and land use change history were analyzed as discrete ones, with two levels (high and low) each. Landscape sample identity was included in models as random effect to avoid spatial pseudoreplication (i.e. fragment size) (Underwood, 1997).

Models were evaluated with information-theoretic procedures and multiple-model inference (Burnham and Anderson, 2002). A total of 16 statistical models were evaluated and compared using Akaike information criterion corrected for small samples differences (AIC_c). We calculated the AIC_c weight of each model (w_i), which indicates the relative likelihood that the each model is the best of all models. We evaluated the support for each factor summing w_i across all models that contained the parameter being considered (parameter likelihood) (Burnham and Anderson, 2002). To supplement parameter-likelihood evidence of important effects, we calculated 95% confidence interval limits (CL) of each parameter estimates. All the analyses were carried out using R 2.13.1 software (R Core Team, 2012).

Table 1
Attributes of landscape samples included in the study. Areas are in hectares.

Landscape sample	A	B	C	D
Area	4460	4608	4676	4460
Forest cover 1957	1306	2460	3148	2264
Forest cover 2010	647	670	1614	1549
Land use change 1957–2010	659	1790	1534	715

Table 2
Tree species of the three quebrachos forest in decreasing order of important value index (IVI) according to previous studies (Torrella et al. 2011).

Species	Family	IVI
Schinopsis balansae	Anacardiaceae	22.72
Aspidosperma quebracho-blanco	Apocynaceae	20.78
Prosopis kuntzei	Fabaceae	20.31
Ziziphus mistol	Rhamnaceae	10.34
Caesalpinia paraguariensis	Fabaceae	9.68
Schinopsis lorentzii	Anacardiaceae	9.09
Cordia americana	Boraginaceae	8.31
Schinopsis heterophylla	Anacardiaceae	2.76
Jodina rhombifolia	Santalaceae	2.37
Prosopis alba	Fabaceae	1.94
Acanthosyris falcata	Santalaceae	0.94
Sideroxylon obtusifolium	Sapotaceae	0.84
Carica quercifolia	Caricaceae	0.34
Ceiba chodatii	Bombacaceae	0.21
Geoffroea decorticans	Fabaceae	0.14
Tabebuia heptaphylla	Bignoniaceae	0.01

3. Results

A total of 3403 individuals or stems of the 16 tree species were recorded and measured in the 112 sampling plots. Results showed different relationships between the studied factors and forest structure and tree recruitment, since age classes showed different responses when the stand level and each stratum were analyzed separately (Tables 3 and 4).

3.1. Stand level

The best models that explained the variation in density of individuals include the factor "fragment size in 2010" (Table 3), where the larger the fragments, the higher the density of individuals. This pattern was also observed for the species of the middle stratum, but not for those of the upper stratum (Table 4 and Fig. 2). Although the species of the upper stratum showed no relationship between density and fragment size in 2010 (Fig. 2), they showed a trend to have higher densities in landscape samples with high forest cover ($w_i = 0.92$ although zero is included in the confidence interval, Tables 3 and 4). The historical factors considered (i.e., "past use history" and "historic fragment size") were not significant to define density variations (at stand and each stratum level).

Models for basal area were not better than the null model to explain variability at stand level and for each stratum separately (Table 5). Congruently, all the factors showed low parameters (i.e. $w_i < 0.5$) within the statistical model set that was evaluated (Table 6).

Table 3
Summary of model-selection results for models explaining variability in density of tree species in the three quebrachos forest in relation to fragment size (size10), historic fragment size (size57), forest cover at landscape level (fcover) and land use change history at landscape level (hist). Only models with $w_i > 0.1$ or $\Delta AIC_c < 2$ are shown. MS: Middle stratum; US: Upper stratum.

Response variable	Candidate models	AIC_C	ΔAIC_c	w_i
Total density	size10	400.33	0.00	0.432
	size10 size57	402.24	1.91	0.166
	size10 fcover	402.88	2.55	0.121
	size10 hist	403.14	2.81	0.106
MS total density	size10	384.77	0.00	0.338
	size10 fcover	385.71	0.95	0.211
	size10 size57	386.33	1.56	0.155
US total density	fcover	363.84	0.00	0.481
	fcover size57	366.44	2.60	0.131
	fcover hist	366.78	2.94	0.111
	fcover size10	366.83	2.99	0.108
Sapling density	size10	382.10	0.00	0.313
	size10 size57	382.20	0.05	0.305
	size10 size57 hist	384.00	1.88	0.122
MS sapling density	size10 size57 hist	370.01	0.00	0.190
	size10 size57	370.08	0.08	0.183
	size10 fcover	370.40	0.40	0.156
	size10 size57 fcover	370.53	0.52	0.146
	size10 size57 hist fcover	370.68	0.68	0.135
	size10	370.84	0.84	0.125
US sapling density	fcover	376.76	0.00	0.494
	Null model	379.41	2.65	0.132
	fcover hist	379.73	2.96	0.112
	fcover size57	379.75	2.99	0.111
DBH >20 cm density	size57	280.48	0.00	0.266
	size57 hist	280.86	0.39	0.219
	Null model	281.98	1.51	0.125
MS DBH >20 cm density	hist fcover	257.98	0.00	0.189
	fcover	258.21	0.23	0.169
	Null model	258.89	0.91	0.120
US DBH >20 cm density	size57 hist	282.86	0.00	0.235
	Null model	283.72	0.87	0.152
	size57	283.93	1.07	0.137
	hist	284.77	1.91	0.090

3.2. Saplings

Density of saplings, an indicator of forest recruitment, showed the same patterns as total density (Tables 3 and 4): the species of the middle stratum showed higher density of saplings in larger fragments (Fig. 3), while those of the upper stratum showed a trend to have higher density of saplings in landscape samples with high (ca. 34%) forest cover (Fig. 4).

3.3. Adult trees (DBH >20 cm)

The models with lower AIC_c values to explain variability in density of adults (DBH >20 cm) at the stand level, include the factor "fragment size in 1957" ($w_i = 0.73$) (Tables 3 and 4). Fragment size in 1957 and density of adults showed a negative relationship (Table 4). This pattern was also observed for the species of the upper stratum (Fig. 5), but none of the factors was relevant to explain variability in density of adults in the species of the middle stratum (Table 4). Current fragment size, land use change history and forest cover at landscape scale were not relevant to explain variability of density of trees >20 cm (DBH).

4. Discussion

Responses in total density of tree species to the fragmentation process coincided with those in sapling density, but were different from those found in adult density at the stand level and for each stratum separately. These results suggest that the overall response is determined by the variations in the sapling density. Thus, with an ecological perspective and taking our aims into account, it is more reasonable to analyze separately these results in terms of sapling density on one hand and density of adults on the other hand, rather than in terms of total densities (see discussion below).

4.1. Saplings and tree recruitment

Density of saplings is a good indicator of successful recruitment, as it includes young individuals effectively established. Hernández-Stefanoni and Dupuy, (2008) stated that the effects of fragmentation and landscape patterns on plant communities commonly focus on particular patches. There are few studies that solely considered the effect of fragment size on plant recruitment and divergent results can be pointed out: positive relationships (more recruitment in larger fragments) have been reported in tropical forests (Benitez-Malvido, 1998) and subtropical savannas (Borges do Carmo et al., 2011), whereas no relationship has been found in temperate (Echeverria et al., 2007) and tropical forests (Sánchez-Gallen et al., 2010). At the same time, Cordeiro and Howe (2001) and Melo et al. (2010) found the two kinds of responses in tree assemblages of tropical forests and that the species affected by fragment size are the most dependent on the fauna for fruit dispersal.

In the present work, we also found the two kinds of responses: greater recruitment at higher fragment size for the group of species of the middle stratum and no relationship for the species of the upper stratum. These differences could also be explained by the dispersal strategy: species of the upper stratum have samaras or winged seeds dispersed by the wind, while most of the species of the middle stratum have fleshy or sub-fleshy fruits (Torrella et al., 2011), which indicates that dispersal in this group is predominantly mediated by animals. However, there are exceptions as *Cordia americana*. This species showed the greatest abundance of saplings within the middle stratum but is considered with anemochorous fruits (Benvenutti-Ferreira and Coelho, 2009). Nevertheless, new detailed studies on dispersion of *C. americana* are required because the fruits have a fleshy pericarp that would be related to biotic dispersal.

This study, which jointly considered factors such as fragment size, landscape forest cover and historic processes (last 50 years), allowed us to detect possible effects of fragmentation additional to those related to reduction in fragment size. Recruitment of the species of the upper stratum did not vary with respect to fragment size, but seems to depend on the forest cover at landscape scale. This suggests that biological (e.g., differential herbivory or phytosanitary conditions) or anthropogenic (e.g., distance to human population) processes not considered in this study can have a decisive influence after the beginning of the regeneration and recruitment processes. In the three quebrachos forest, this impact could transcend those relative to forest structure, as it involves the most emblematic and representative plant species of the Chaco Region.

Considering biological constraints, in general terms, there are some tree recruitment differences in response to the fragmentation process in the three quebrachos forest that seem to be associated with forest strata. Thus, fragmentation could lead to future changes in the vertical structure of the forest if this trend is maintained.

4.2. Adult trees

In temperate forests, a lower basal area has been found in smaller fragments, linked with a return to early successional stages (Echeverria et al., 2007); whereas in tropical forests, a lower density of adult trees has also been found in smaller fragments, linked with a greater disturbance (Arroyo-Rodriguez and Mandujano,

Table 4
Parameter likelihoods, estimates, and 95% confidence interval limits for explanatory variables describing variation in density of individuals. Explanatory variables with confidence level excluding zero or parameter >0.7 are in bold. Size10: fragment size, size57: historic fragment size, fcover: forest cover at landscape level, hist: land use change history at landscape level.

Response variable	Explanatory variable	Parameter likelihood	Parameter estimate	Confidence Lower	Level Upper
Total density	**size10**	**0.98**	**4.22**	**1.67**	**6.76**
	size57	0.30	−0.37	−1.09	0.34
	hist (low)[a]	0.22	−81.79	−861.59	698.01
	fcover (low)[b]	0.21	−68.99	−789.81	651.84
Middle stratum total density	**size10**	**1.00**	**4.23**	**2.32**	**6.15**
	size57	0.32	−0.31	−0.85	0.23
	hist (low)[a]	0.22	−64.48	−735.65	606.70
	fcover (low)[b]	0.35	101.00	−422.23	624.23
Upper stratum total density	size10	0.18	0.00	−1.35	1.34
	size57	0.21	−0.11	−0.46	0.24
	hist (low)[a]	0.19	−18.92	−721.94	684.10
	fcover (low)[b]	**0.92**	−169.35	−531.87	193.18
Sapling density	**size10**	**0.99**	**3.42**	**1.56**	**5.29**
	size57	0.51	−0.40	−0.90	0.10
	hist (low)[a]	0.23	−60.14	−602.22	481.95
	fcover (low)[b]	0.18	32.26	−478.57	543.09
Middle stratum sapling density	**size10**	**1.00**	**3.43**	**1.96**	**4.91**
	size57	0.65	−0.41	−0.84	0.02
	hist (low)[a]	0.39	−101.98	−680.70	476.73
	fcover (low)[b]	0.47	95.17	−365.58	555.91
Upper stratum sapling density	size10	0.18	0.07	−0.62	0.75
	size57	0.21	−0.04	−0.22	0.14
	hist (low)[a]	0.23	22.91	−297.24	343.05
	fcover (low)[b]	**0.73**	−65.06	−261.62	131.50
DBH >20 cm density	size10	0.18	−0.01	−0.32	0.31
	size57	**0.73**	**−0.10**	**−0.18**	**−0.01**
	hist (low)[a]	0.38	−21.12	−120.21	77.96
	fcover (low)[b]	0.21	8.24	−96.82	113.30
Middle stratum DBH >20 cm density	size10	0.24	0.08	−0.12	0.28
	size57	0.27	−0.03	−0.08	0.03
	hist (low)[a]	0.44	13.24	−74.10	100.58
	fcover (low)[b]	0.62	16.11	−56.34	88.57
Upper stratum DBH >20 cm density	size10	0.23	−0.12	−0.43	0.20
	size57	**0.58**	**−0.09**	**−0.18**	**−0.01**
	hist (low)[a]	0.51	−30.05	−135.44	75.34
	fcover (low)[b]	0.20	−7.80	−140.72	125.11

[a] Relative variable to value of land use change history (high).
[b] Relative variable to value of forest cover (high).

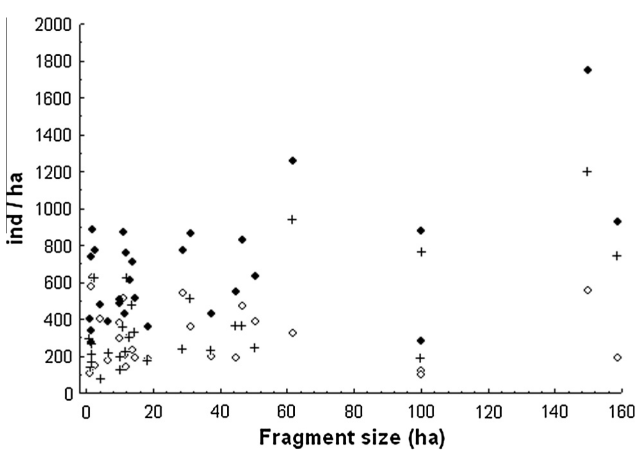

Fig. 2. Total density of the three quebrachos forest related to fragment size. Black circles: stand level ($w_i = 0.98$); crosses: middle stratum ($w_i = 1.00$); white circles: upper stratum ($w_i = 0.18$).

2006). On the other hand, fragmentation effects on indicators more complex than density and basal area, such as a change in the size structure of the tree assemblage of the Brazilian Atlantic forest, have also been reported (Oliveira et al., 2008).

Table 5
Summary of model-selection results for models explaining variability in basal area in the three quebrachos forest related to fragment size (size10), historic fragment size (size57), forest cover at landscape level (fcover) and land use change history at landscape level (hist). MS: Middle stratum; US: Upper stratum; AIC_c: Akaike information criterion corrected for small samples; ΔAIC_c : Differences in AIC_c. Only models with $w_i > 0.1$ or $\Delta AIC_c < 2$ are shown.

Response variable	Candidate models	AIC_C	ΔAIC_c	w_i
Total basal area	Null model	171.05	0.00	0.273
	size57	171.98	0.93	0.171
MS basal area	Null model	131.36	0.00	0.163
	fcover	131.72	0.36	0.136
	size10	132.04	0.68	0.116
US basal area	Null model	172.99	0.00	0.243
	fcover	174.13	1.14	0.138
	size57	174.68	1.69	0.105

In contrast, in the three quebrachos forest, we did not find differences in the basal area or adult tree density according to current fragment size, forest cover or land use changes history at the landscape scale. Echeverria et al. (2007) and Arroyo-Rodriguez and Mandujano (2006) have proposed differential harvesting as explanation for the differences found in that studies, whereas Laurance and Cochrane (2001) have suggested that many effects of fragmen-

Table 6
Parameter likelihoods, estimates, and 95% confidence interval limits for explanatory variables describing variability in basal area. Size10: fragment size, size57: historic fragment size, fcover: forest cover at landscape level, hist: land use change history at landscape level.

Response variable	Explanatory variable	Parameter likelihood	Parameter estimate	Confidence Level	
				Lower	Upper
Total basal area	size10	0.21	0.01	−0.035	0.055
	size57	0.44	−0.01	−0.020	0.004
	hist (low)[a]	0.27	−1.82	−15.683	12.046
	fcover (low)[b]	0.22	−1.09	−14.208	12.036
Middle stratum basal area	size10	0.45	0.016	−0.005	0.036
	size57	0.26	−0.002	−0.008	0.003
	hist (low)[a]	0.29	0.907	−6.813	8.627
	fcover (low)[b]	0.43	1.254	−5.111	7.618
Upper stratum basal area	size10	0.19	−0.007	−0.053	0.038
	size57	0.36	−0.008	−0.021	0.004
	hist (low)[a]	0.32	−2.496	−19.321	14.330
	fcover (low)[b]	0.36	−2.325	−16.767	12.117

[a] Relative variable to value of land use change history (high).
[b] Relative variable to value of forest cover (high).

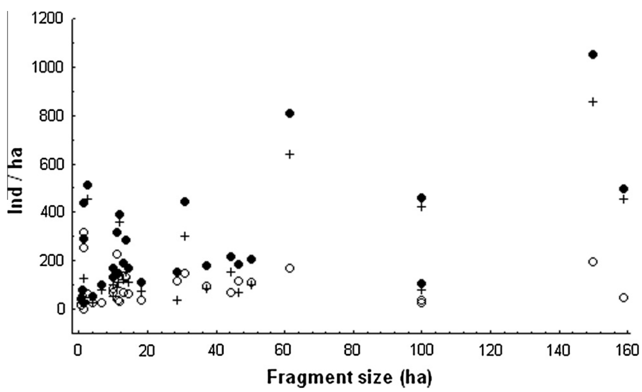

Fig. 3. Density of saplings of the three quebrachos forest in relation to fragment size. Black circles: stand level (w_i = 0.99); crosses: middle stratum (w_i = 1.00); white circles: upper stratum (w_i = 0.18).

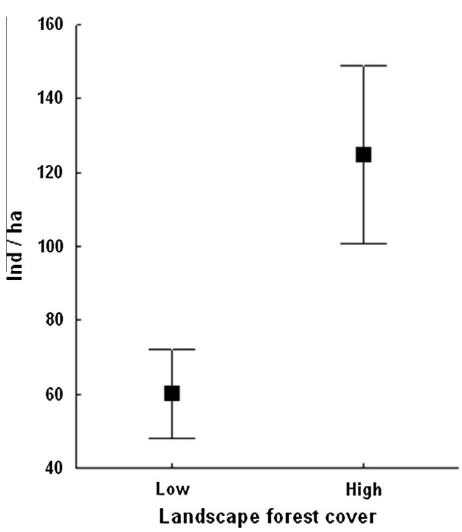

Fig. 4. Density of saplings (DBH <5 cm) of species of the upper stratum in landscapes with high and low forest cover. Mean ± SE.

tation are related to human uses. We attempted to control this factor (human use) in the present study, aiming to detect "purely biological effects", and this must be taken into account in interpreting our results. Although there are no "pristine forests" in the study

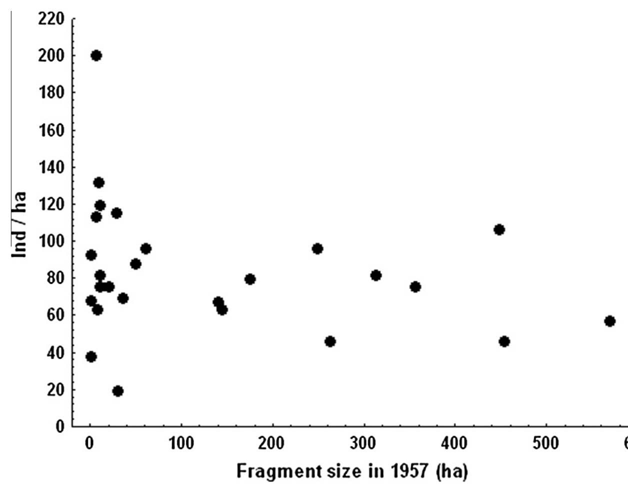

Fig. 5. Density of adult trees (DBH >20 cm) of the upper stratum of the three quebrachos forest in relation to the historic fragment size (w_i = 0.58).

area and all fragments have been harvested in the past to some extent for more or less time, we did not select fragments with more intense or recent harvesting. However, our knowledge of the study area allows us to state that there is no obvious relationship between fragment size and forest harvesting degree (Torrella et al., 2011). Instead, larger fragments could have been more attractive for timber harvesting than smaller ones. This differential harvesting could explain the lower density of adults of the upper stratum found in fragments historically larger, since the species of the upper stratum are the most important as timber resource. Our general results for adult trees may indicate that either the forest structure has not been – at least so far- severely affected by fragmentation or that it has been homogeneously affected with respect to fragment size and the other factors considered here. We think that the first alternative is more likely (a) because the sampling design covered a wide range of fragment sizes and forest covers at landscape level, and (b) because we have compared the basal area of the three quebrachos forest in the study area with those of other Chaco forests in protected areas and they showed similar values (Torrella et al., 2011). In this regard, we have previously highlighted the almost complete absence of exotic woody species (Torrella et al., 2011), although we cannot discard a process of homogenization of communities by the expansion of native species, as described by Tabarelli et al. (2012) for Amazonia and the Atlantic forest.

4.3. Implications for management and conservation

The sampling design linked to the current conceptual framework of the fragmentation process allowed us to evaluate effects both at fragment and landscape scales, making explicit the fact that fragmentation is a landscape-scale process (McGarigal and Cushman, 2002), but also recognizing the possibility that both scales may be interdependent (Didham et al., 2012). Although we did not find this interdependence, we found that while a group of species respond to factors acting at the fragment scale, another group responds to factors acting at landscape scale.

The structure of the older age tree class in the remaining fragments of the three quebrachos forest seems not be linked with the three studied factors of the fragmentation process (fragment size, landscape forest cover and deforestation history). However, the recruitment of young individuals appeared to be affected, which could in turn affect the ability of the forest to conserve the same structure and richness along the time.

In the study area we have previously recorded a loss of 50% of the three quebrachos forest area between 1957 and 2010 (from 26,000 to 13,000 ha respectively) and a twofold increase in the number of fragments (Torrella et al., 2007; Torrella, unpublished data); land use changes are still taking place nowadays. The legal regulation of the provincial state set limits to land use changes depending on the size of properties. Most of the properties are 100 ha, and their owners can deforest up to 90% surface, i.e. at least 10 ha of forest must remain standing. Then in an extreme (but possible) scenario, the study area could have only 10% of forest cover. This would mean the loss of about 50% of the current forest area and lead fragmentation to an extreme level.

Beyond that, we think that the current legal regulation for the Chaco region, which is crucial to generate practices to mitigate the impacts of fragmentation on the three quebrachos forest, is liberal and permissive, thus promoting deforestation.

Current laws regulate only the forest area that must be standing, but not its spatial distribution, its position with respect to neighbor fragments, the number of fragments in which the remaining surface will be scattered, or the forest cover in the landscape. In addition, the control of those regulations is weak and deficient.

Our results show that the size of the remnant fragments should be maximized for an accurate recruitment of the tree species of the middle stratum of the forest. An option would be that the remaining area after legal land use change must stay in a single large fragment; in addition, neighbor properties could be oriented to maintain adjacent fragments, to increase the chances of functional connectivity.

However, considering that these guidelines are complex and their implementation would not be easy, we think that the most advisable in the short term is to simply reduce the percentage of land use change allowed in this region, and determine that the remaining forest must stay in a single fragment. This guideline, which coincides with those proposed in general terms for conservation in agricultural (Fischer et al., 2006) and fragmented landscapes (Tabarelli and Gascon, 2005), would necessarily mitigate the fragmentation effects, would help to preserve the remaining fragments as functional conservation units, and could be determining in the conservation of the three quebrachos forest in the Argentinean Chaco.

5. Conclusions

The main messages based on our results are: (A) Recruitment of the species of the middle stratum could be affected by fragment size, while recruitment of the species of the upper stratum appears to be affected by forest cover at landscape level. Thus, if this trend is maintained, fragmentation could lead to future changes in composition and vertical structure of the forest. (B) The three quebrachos forest would be seriously threatened if a recruitment threshold is exceeded. (C) Data on biological interactions are needed to better understand some of the trends evidenced here. (D) Future research on animal-plant interactions of tree species in the three quebrachos forest is needed to provide information about periodic measurement of tree saplings, recruitment, extant fauna in forest fragments, and seed dispersal in the current condition of fragmented landscape. (E) Small fragments of three quebrachos forest have high conservation value in the study area, mainly for adult trees, even those located in highly deforested landscapes, since their structure does not differ from that of the larger fragments not either from those fragments located within landscapes with lower forest loss.

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