Plant Ecol (2015) 216:1499–1510
DOI 10.1007/s11258-015-0532-2

Forest fragmentation in the Argentine Chaco: recruitment and population patterns of dominant tree species

Sebastián Andrés Torrella · Rubén Ginzburg · Leonardo Galetto

Received: 28 May 2015 / Accepted: 7 October 2015 / Published online: 13 October 2015

Abstract The forest in the Central Argentine Chaco has been dramatically fragmented and persists only as isolated patches in an agricultural matrix. In this study, we evaluated the effects of fragmentation on total density, recruitment, and size-class structure of its dominant tree species, a key issue, although little explored, for forest conservation in the region. We particularly analyzed the effects of fragment size and forest cover at landscape level on seven of the most important tree species of the forest. Our results suggest that forest cover at landscape level is more important than fragment size to explain the population patterns of the main tree species. Fragment size was relevant in only one species, *Cordia americana*, whereas forest cover resulted relevant in five species. The size-class structure of *Schinopsis balansae*, one of the dominant species of the upper stratum, appeared to be affected in landscapes with less forest cover, showing lower densities of the smaller classes. Our results show that for the conservation of the forest it would be important to increase their protection degree against the expansion of agriculture, attempting to preserve as much of the forest as possible, to promote the forest cover at landscape level and give relevance even to the smallest fragments.

Keywords Size-class structure · Fragment size · Forest cover · Forest conservation · *Schinopsis*

Communicated by Kun-Fang Cao.

S. A. Torrella (✉) · R. Ginzburg
Grupo de Estudios de Sistemas Ecológicos en Ambientes Agrícolas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes 2160 4 piso #56, Pabellón II, Ciudad Universitaria (C1428EGA), Buenos Aires, Argentina
e-mail: sebast@ege.fcen.uba.ar

L. Galetto
Cátedra de Diversidad Vegetal II, Instituto Multidisciplinario de Biología Vegetal, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, CONICET, CC 495 (5000), Córdoba, Argentina

Introduction

Biodiversity includes different attributes and multiple levels of biological organization (Noss 1990). Different indicators of these attributes can vary according to the level of organization considered. The possibility of identifying both broad- and fine-scale empirically derived patterns in the recruitment and population dynamics of tree species may allow better predictions of forest succession and conservation in fragmented landscapes. A challenge in ecology of forest fragmentation is to understand how the patterns of the community and the landscape relate to those of the populations of different tree species.

Forest loss and fragmentation are some of the main threats to biodiversity conservation in the world

(Foley et al. 2005; Lindenmayer and Fischer 2006). The great agricultural expansion in the South American Chaco (Adámoli et al. 2011; Volante et al. 2012; Vallejos et al. 2014; Cáceres 2015) has converted this region in one deforestation hot spot not only at continental (Grau and Aide 2008) but also at global level (Hansen et al. 2013). In the Argentine Chaco, about four million hectares of forest were lost between 2002 and 2010 (Piquer-Rodrígez et al. 2015), causing an intense fragmentation of the remaining forest (Gasparri and Grau 2009; Ginzburg et al. 2012; Carranza et al. 2014; Torrella 2014). However, at present, little is known about the effects of forest fragmentation on the population dynamics of trees in the Chaco Region.

Forest fragmentation affects community and population processes (Hobbs and Yates 2003; Lindenmayer and Fischer 2006; Laurance 2008) and, as a consequence, responses could vary among species or functional groups (Cordeiro and Howe 2001; Laurance et al. 2006; Hernández-Stefanoni and Dupuy 2008; Montoya et al. 2008; Melo et al. 2010; Santo-Silva et al. 2013). Hence, to better understand the relationship between forest fragmentation and tree recruitment and population structure, community pattern analyses are useful, but species-specific studies are also required to better understand the patterns and processes occurring after fragmentation.

The entry of new individuals into a population or community (recruitment) can be restricted at different stage/ages according to the tree species, a fact that alters the dynamics and composition of plant communities (Ribbens et al. 1994). In fragmented forests, this critical process could be altered (e.g., Benitez-Malvido 1998; Laurance et al. 1998; Santo-Silva et al. 2013), and such alteration may operate at different spatial and temporal scales according to the fragmentation process. It has been reported that recruitment is more affected by reduction in fragment size in animal-dispersed species than in species with other dispersal strategies (Cordeiro and Howe 2001; Laurance et al. 2006; Montoya et al. 2008; Melo et al. 2010). In the long term, this could lead to a change in the population structure, with negative consequences for species conservation. In the Chaco forest, recruitment limitation may have an important impact on its structure and dynamics. Thus, identifying the recruitment patterns of the dominant tree species of this forest is critical.

In a previous work carried out at community level in the Chaco forest (Torrella et al. 2013), we found a positive relationship between fragment size and total and sapling density for the group of species of the middle stratum (most of which have zoochorous fruits). In contrast, for the group of species of the upper stratum (all of which have anemochorous fruits), we found no relationship with fragment size but a trend to higher total and sapling densities in landscapes with higher forest cover.

Despite the limitations of studies of the size-class structure based on one-year data to make inferences about population dynamics (Condit et al. 1998; Bernucci Virillo et al. 2011; Bin et al. 2012), their comparative analysis may be useful to assess the conservation status of populations when long-term data are lacking (de Souza et al. 2010) and can be the basis for management decisions (Bruna and Kress 2002). However, few studies have used the size-class structure to evaluate the effects of fragmentation on tree populations (Barbeta et al. 2011; Quitete Portela and Maes dos Santos 2014) and no clear trends have been reported. Alterations in tree recruitment and population structure in relation to edge effects in fragmented forests have also been described (e.g., Harper et al. 2005; Laurance et al. 2006; Oliveira Filho et al. 2007; Laurance et al. 2011). However, in the present study, we decided to focus on two factors whose effects over tree populations have been less explored: fragment size and forest cover.

The aim of this work was to analyze the effects of fragmentation on the structure of tree populations in the Chaco forest, a key issue, although little explored, for the conservation in the region. We studied the Three Quebrachos Forest, one of the ecosystems most affected by deforestation in the Argentine Chaco (Adámoli et al. 2011). We considered both landscape and fragment levels, an increasing approach in fragmentation research, but still scarce among studies about the effects of fragmentation on vegetation. In particular, the relationships between density, population structure and recruitment of the main tree species were analyzed considering both fragment size and forest cover in different landscapes. Results will provide the information needed to design conservation strategies in a highly threatened environment.

Taking into account the framework presented above, we predicted that: (i) species of the upper stratum (anemochorous) will present lower density of saplings in landscapes with lower forest cover and no relation with fragment size; (ii) anemochorous species of the middle stratum will present no relationships between density of saplings and fragment size or forest cover; (iii) zoochorous species of the middle stratum will present lower density of saplings in smaller fragments. For the most abundant species, we also evaluated whether these potential differences translate into alterations in the structure of the size classes, affecting not only the density of saplings but also their density in older age-classes.

Materials and methods

Study area

The study area is located in the Central Argentine Chaco, southwest of Chaco Province, between 61°0′ and 61°25′W, and between 27°5′ and 27°20′S, within the distribution area of the Three Quebrachos Forest (Morello and Adámoli 1974; Torrella et al. 2011). The area is topographically flat and homogeneous, with no rivers or surface water bodies. Unlike other zones in the region, there are no elevations formed by "levee banks" (fluvial deposits parallel to river bed), a peculiar environment that promote differences in the forest structure and composition (Adamoli et al. 1990). The original natural cover in the area used to be a mosaic of forest (70 %) and natural grasslands (30 %) (Morello and Adámoli 1974), in soils with high productive potential, mainly mollisols (63 %) and alfisols (18 %) (Morello 2012). Land-use change for agriculture has virtually eliminated grasslands and reduced the forest drastically, currently present only in fragments immersed in an agricultural matrix (Fig. 1), covering only 18 % of the area (Torrella 2014). Forests are on well-drained soils, with sandy loam texture (Morello 2012), and presents two arboreal strata (upper and middle) and a low shrub stratum (Torrella et al. 2011).

The annual rainfall is 750–850 mm, occurring mostly during the summer season and decreasing from E to W. The mean temperature is 27 °C in summer and 15 °C in winter, with a mean maximum and minimum of 36 °C and 8 °C, respectively (Alberto and Bruniard 1987).

Species

In a previous study, the composition, structure, and state of conservation of the woody plant community in

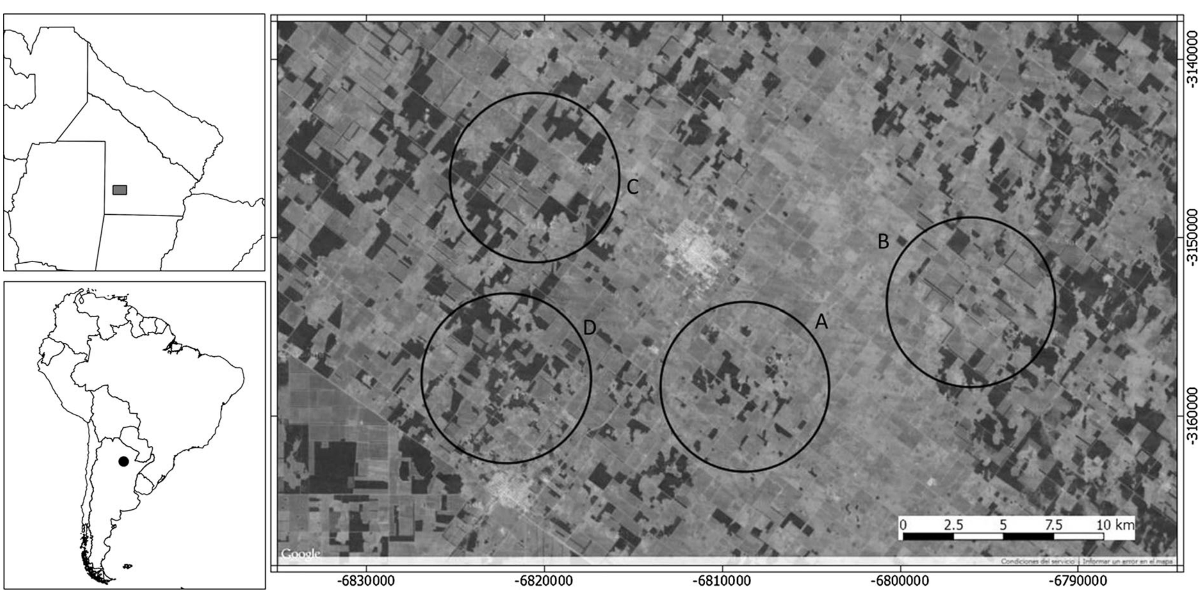

Fig. 1 Location of the study area in South America, Argentina and Chaco Province. Polygons in *black* are the landscape samples (*A*, *B*, *C* and *D*). *Dark patches* in the image are Trhee Quebrachos Forest fragments in the agricultural matrix. Urban areas are Charata, in the *center*, and General Pinedo, in the SW

remnants fragments of the Three Quebrachos Forest were studied (Torrella et al. 2011). We detected 36 species (trees and shrubs), all of them native. Considering all species together, the mean basal area for all sites was of 24.73 m^2/ha, and the density of 13,459 individuals/ha. We found a codominance between *Schinopsis balansae* and *Aspidosperma quebracho-blanco* among the species of the upper strata. The stump's analysis showed that selective extraction is limited and it does not imply a strong alteration of the forest structure (Torrella et al. 2011). In this study, we considered the seven most important tree species (*Schinopsis balansae*, *S. lorentzii, Aspidosperma quebracho-blanco*, *Prosopis kuntzei*, *Caesalpinia paraguariensis*, *Ziziphus mistol*, and *Cordia americana*), since these species account for 94 % of the arboreal basal area in this forest (Torrella et al. 2011), including species of the upper and middle stratum and with different attributes related to functional group (light-demanding or shade-tolerant) and dispersal mode (Table 1). It was not possible to include in this analysis more shade-tolerant species because they are very few in the Three Quebrachos Forest (*Sideroxylon obtusifolium*, *Tabebuia heptaphylla*) and occur in extremely low densities (Torrella et al. 2011).

Sampling design and data collection

We selected four landscape samples (circular polygons, 5574 ha): samples A and B with low forest cover ($\sim$15 %) and samples C and D with a comparatively higher forest cover ($\sim$35 %). Within each landscape sample, we selected seven forest fragments (i.e., a total of 28 fragments), attempting to use the same size range in each landscape sample, from $\sim$1 to $\geq$100 ha (Table 2).

Tree populations were surveyed in 4 $\times$ 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. The location and orientation of the plots were randomly selected.

In each plot, we recorded all the individuals of the tree species studied here. We measured the diameter at breast height (DBH) of trees with DBH $\geq$ 5 cm and the stump diameter at 10 cm height (D10) in trees with DBH < 5 cm. Individuals with D10 < 1 cm were considered as not definitely established, and thus not taken into account. In trees with more than one stem, each was measured individually.

For each species, we calculated total and sapling (DBH < 5 cm and D10 > 1 cm) density (ind/ha). For the species with higher densities, we also calculated the density of other diameter classes (for *Aspidosperma quebracho-blanco* and *Schinopsis balansae*: 5–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, and >40 cm; for *Prosopis kuntzei*: 5–10 cm, 10–20 cm, 20–30 cm and >30 cm, and for *Cordia americana*: 5–10 cm and >10 cm) and analyzed their size-class structure.

Statistical analysis

We used generalized linear mixed models (GLMM) with two fixed factors: Log (fragment size) and forest cover. Fragment size was analyzed as a continuous variable, whereas forest cover was analyzed as a discrete one, with two levels (high and low). Landscape sample identity was included in the models as random effect to avoid spatial pseudoreplication (i.e., fragment size) (Underwood 1997). The interaction term (fragment size $\times$ landscape forest cover) was tested but its inclusion did not improve the model significantly in any case. The total and sapling densities of each species were used as response variables. In four of the species analyzed, we also used the density of other size classes. The statistical significance of individual fixed factors was tested with the z statistics for GLMMs. As these data derived from counts and are over-dispersed with respect to Poisson distribution, models were fitted with negative binomial distribution and negative binomial "zero inflated" using glmmADMB package (Fournier et al. 2012; Skaug et al. 2013) in R v.3.1.1 (R Development Core Team 2010).

Results

Total and sapling density

Schinopsis balansae, *Schinopsis lorentzii* and *Caesalpinia paraguariensis* showed higher total density in landscapes with high forest cover, whereas *Cordia*

Table 1 Taxonomic and ecological characteristics of the species studied. Information based on own observations and on observations made by (1) Tortorelli (2009), (2) Gómez and Hampel (2005), (3) Lorenzi (1992), (4) Scarpa (1996), Abraham de Noir and Bravo (2014) and Torrella et al. (2011)

Species	Family	Stratum	Functional group	Dispersal mode	Distribution	Fruit size	Seed size	Relative basal area
Aspidosperma quebracho-blanco Schltdl.	Apocynaceae	Upper	Heliophilous (2)	Anemochorus	Whole Chaco	7–13 × 4–6 × 1–2.5 cm	30–60 mm diam	20.8
Caesalpinia paraguariensis (D. Parodi) Burkart	Fabaceae (Caesalpinoideae)	Middle	Heliophilous (1)	Zoochorus	Whole Chaco	2–6 × 2 × 1 cm	7–10 × 5–7 × 3–4 mm	6.7
Cordia americana (L.) Gottschling and J.S. Mill	Boraginaceae	Middle	Umbrophilous (2)/Helio-philous	Anemochorus	East	3.5–7 × 2.5–4 mm	2.5–6 × 1.5–4 mm	4.6
Prosopis kuntzei Harms	Fabaceae (Mimosoideae)	Middle	Heliophilous (1)	Zoochorus	Whole Chaco	10–30 × 2 × 1 cm	8–13 × 5–6 mm	21.6
Schinopsis balansae Engl.	Anacardiaceae	Upper	Heliophilous (1)	Anemochorus	East	10 × 4 mm	5–6 × 2 mm	24.5
Schinopsis lorenzi (Griseb.) Engl.	Anacardiaceae	Upper	Heliophilous (1)	Anemochorus	West	2.3–3 × 0.7–1 cm	7 × 5 mm	8.7
Ziziphus mistol Griseb	Rhamnaceae	Middle	Heliophilous (1)	Zoochorus	Whole Chaco	15 mm diam	6–7 mm long	7.4

Table 2 Attributes of landscape samples and fragments included in the study

Landscape sample	A	B	C	D
Total area (ha)	5574	5574	5574	5574
Forest cover (ha)	673	831	1850	1712
Forest cover (%)	12.1	14.9	33.2	30.7
Sampled fragments				
n	7	7	7	7
Mean size	51.4	34.4	52.9	18.8
Size range	(1.6–158.8)	(1.3–100.1)	(4.3–149.9)	(0.9–50.4)

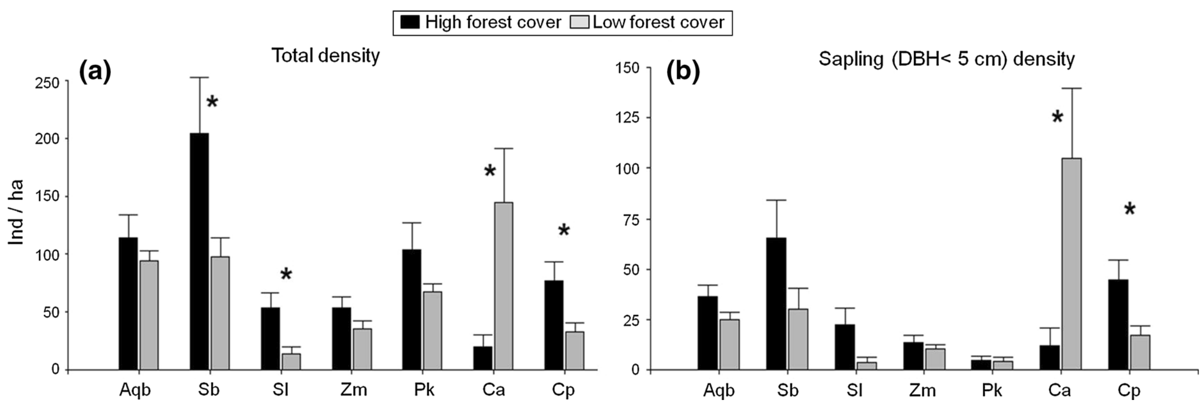

Fig. 2 Total and sapling density of the main tree species of the Three Quebrachos Forest in landscapes with high (*black bars*) and low (*gray bars*) forest cover. Mean and SE; $^*p < 0.05$. Aqb: *Aspidosperma quebracho-blanco*; Sb: *Schinopsis balansae*; Sl: *Schinopsis lorentzii*; Zm: *Ziziphus mistol*; Pk: *Prosopis kuntzei*; Ca: *Cordia americana*; Cp: *Caesalpinia paraguariensis*

americana showed the inverse pattern (Fig. 2a; Table 3). The same tendencies were observed in sapling (DBH < 5 cm) density: higher values in the landscapes with higher forest cover in *S. balansae*, *S. lorentzii*, and *C. paraguariensis*, and the opposite in *C. americana* but with statistical significance only in the last two species (Fig. 2b; Table 3).

Fragment size showed a significant relation only with total and sapling density of *C. americana*, with higher density in the larger fragments (Fig. 3; Table 3).

Size-class structure

For *Aspidosperma quebracho-blanco*, we found no significant effects of landscape forest cover or fragment size on the density of any size class. However, we observed a trend to higher densities in landscapes with high forest cover for the classes with DBH < 20 cm (Fig. 4a; Table 3). In *Schinopsis balansae*, we observed the same pattern, with statistically significant differences in the classes with DBH 5–10 and 10–20 cm (Fig. 4b; Table 3). In *Prosopis kuntzei*, we found notable differences in the classes 5–10 and 10–20 cm, with higher densities in landscapes with higher forest cover, although statistically significant only in the first case (Fig. 4c; Table 3).

Cordia americana showed higher densities in the landscapes with low forest cover, statistically significant in DBH <5 and >10 cm (Fig. 4d; Table 3).

Discussion

Our general results suggest that forest cover at landscape level is more important than fragment size to explain the density and population structure of the main tree species in the Three Quebrachos Forest. We found significant effects of the fragment size only in one of the seven species analyzed, whereas forest

Table 3 GLMM outputs of stem density for different size-classes in seven tree species of the Three Quebrachos Forest in relation to fragment size and landscape forest cover

Species	DBH	Factor	Estimate	SE	z	*p*
Schinopsis balansae	<5	Log area	0.0817	0.4172	0.2	0.84
		Forest cover	−0.792	0.5804	−1.37	0.17
	5–10	Log area	0.204	0.496	0.41	0.681
		Forest cover	−1.396	0.593	−2.35	**0.019**
	10–20	Log area	0.234	0.501	0.47	0.641
		Forest cover	−1.341	0.589	−2.28	**0.023**
	20–30	Log area	−0.0708	0.5282	−0.13	0.89
		Forest cover	−0.3352	0.641	−0.52	0.6
	30–40	Log area	0.24	0.497	0.48	0.63
		Forest cover	0.428	0.529	0.81	0.419
	>40	Log area	0.127	0.543	0.23	0.8158
		Forest cover	0.306	0.571	0.53	0.5928
	Total	Log area	0.0981	0.2874	0.34	0.733
		Forest cover	−0.74	0.3657	−2.02	**0.043**
Aspidosperma quebracho-blanco	<5	Log area	0.228	0.236	0.97	0.33
		Forest cover	−0.358	0.333	−1.07	0.28
	5–10	Log area	−0.067	0.501	−0.13	0.89
		Forest cover	−0.319	0.509	−0.63	0.53
	10–20	Log area	0.187	0.262	0.71	0.48
		Forest cover	−0.351	0.349	−1.01	0.31
	20–30	Log area	−0.3318	0.4069	−0.82	0.41
		Forest cover	0.0421	0.5169	0.08	0.94
	30–40	Log area	−0.0611	0.3529	−0.17	0.86
		Forest cover	0.2745	0.4352	0.63	0.53
	>40	Log area	0.939	0.5407	0.17	0.862
		Forest cover	0.5641	0.6174	0.91	0.361
	Total	Log area	0.022	0.163	0.13	0.89
		Forest cover	−0.194	0.19	−1.02	0.31
Cordia americana	<5	Log area	1.346	0.278	4.85	**<0.00001**
		Forest cover	1.507	0.413	3.65	**0.00026**
	5–10	Log area	0.391	0.791	0.49	0.62
		Forest cover	0.938	1.281	0.73	0.46
	>10	Log area	0.474	0.27	1.76	0.079
		Forest cover	1.635	0.393	4.16	**<0.0001**
	Total	Log area	0.969	0.403	2.4	**0.0162**
		Forest cover	1.671	0.625	2.67	**0.0075**
Prosopis kuntzei	<5	Log area	−0.0766	0.4091	−0.19	0.85
		Forest cover	−0.1852	0.3166	−0.58	0.56
	5–10	Log area	0.619	0.386	1.6	0.10945
		Forest cover	−1.186	0.497	−2.39	**0.01702**
	10–20	Log area	0.144	0.425	0.34	0.73
		Forest cover	−0.958	0.565	−1.7	0.09
	20–30	Log area	−0.2337	0.2123	−1.1	0.27
		Forest cover	−0.0273	0.2786	−0.1	0.92

Table 3 continued

Species	DBH	Factor	Estimate	SE	z	*p*
	>30	Log area	−0.331	0.207	−1.59	0.111
		Forest cover	0.506	0.275	1.84	0.066
	Total	Log area	0.0881	0.1895	0.47	0.642
		Forest cover	−0.4181	0.2455	−1.7	0.089
Caesalpinia paraguariensis	<5	Log area	0.208	0.476	0.44	0.663
		Forest cover	−0.978	0.484	−2.02	**0.043**
	Total	Log area	0.406	0.42	0.97	0.333
		Forest cover	−0.843	0.423	−2	**0.046**
Ziziphus mistol	<5	Log area	−0.0143	0.4367	−0.03	0.97
		Forest cover	−0.2608	0.5567	−0.47	0.64
	Total	Log area	0.0772	0.298	0.26	0.8
		Forest cover	−0.3439	0.4349	−0.79	0.43
Schinopsis lorentzii	<5	Log area	0.417	1.176	0.35	0.723
		Forest cover	−2.002	1.112	−1.8	0.072
	Total	Log area	−0.0926	0.4921	−0.19	0.851
		Forest cover	−1.341	0.5681	−2.36	**0.018**

Significant values are highlighted in bold

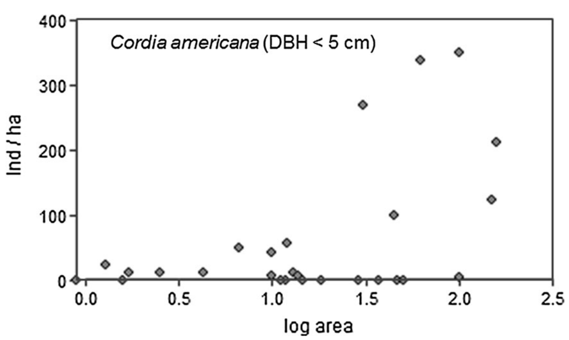

Fig. 3 *Cordia americana* sapling (DBH < 5 cm) density in relation to forest fragment area. Total density showed the same pattern (not displayed)

cover in the landscape was a relevant factor in five of them. The same trends have been observed in tropical forests, when evaluating fragmentation effects on tree diversity (Arroyo-Rodríguez et al. 2009; Hernández-Ruedas et al. 2014).

As the analyzed species are light-demanding, it might seem that they may benefit from disturbances in the environment, such as forest fragmentation. However, it is worth to note that this is neither an assembly of secondary forest nor an early stage in a succession; instead, with the exceptions of *Prosopis kuntzei* and *Cordia americana*, these trees are the typical species in mature and well preserved Chaco forests (Morello and Adámoli 1974; Prado 1993; Tálamo and Caziani 2003; Morello 2012). *Prosopis kuntzei* is not very abundant in other areas and have been mentioned that is benefited by fire (Morello and Adámoli 1974), a disturbance not analyzed here. However, our results do not suggest that *P. kuntzei* (nor the others light-demanding species) may have been benefited by forest fragmentation. *C. Americana*, on the other hand, was the only species that showed higher densities in the landscapes with lower forest cover. This species has been described as pioneer and "harmful" (Lorenzi 1992), and we can thus not rule out that it is expanding in the area as a consequence of the changes in landscape configuration (Tabarelli et al. 2012). The other result obtained for *C. americana*, i.e., the fact that it presented higher densities in the larger fragments, would seem to contradict this possibility. However, these changes in landscape and fragment scale should not necessarily have consequences "in the same sense" in a given population.

Our predictions were fulfilled only partially. For the species of the upper stratum, the trend to higher densities in landscapes with higher forest cover was found only for two of them, *S. balansae* and *S. lorentzii*, without statistically significant differences in the saplings. In addition, although we had previously

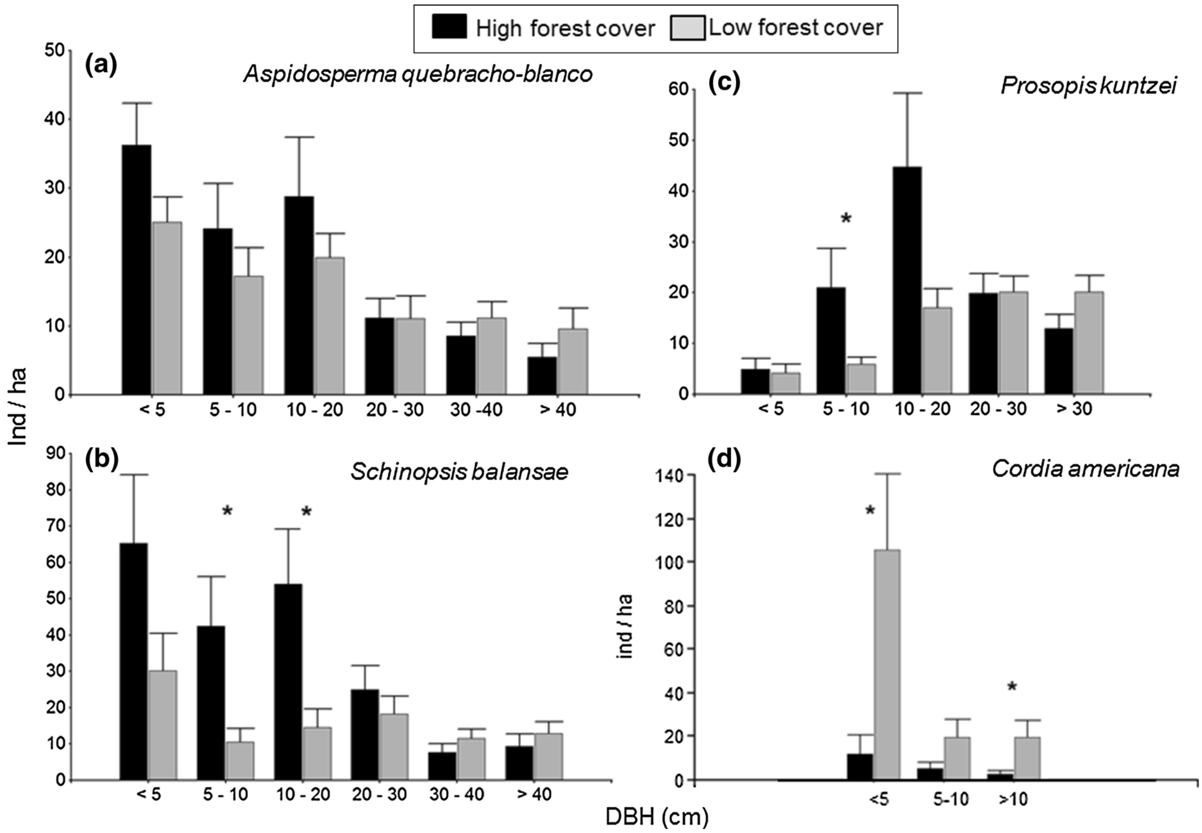

Fig. 4 Size-class structure of four tree species of the Three Quebrachos Forest in landscapes with high (*black bars*) and low (*gray bars*) forest cover. Mean and SE; *$p < 0.05$

found that this factor had no significant effects on the whole group of species of this stratum (Torrella et al. 2013), in the present study we found unexpected effects—with opposite patterns—in two species of the middle stratum: *C. americana* and *C. paraguariensis*.

In general terms, zoochorous tree species are more sensitive to reduction in fragment size than species with other dispersal strategies in other fragmented forests (Cordeiro and Howe 2001; Laurance et al. 2006; Montoya et al. 2008; Melo et al. 2010; Jesus et al. 2012; Freitas et al. 2013); which can be explained by the local extinction of medium and large vertebrates, or defaunation (Galetti and Dirzo 2013), in landscapes or fragments that lose habitat quality after fragmentation. However, we did not find this trend because we observed this relationship only in *C. americana*, which has anemochorous dispersion. Among the zoochorous species that we analyzed, only *C. paraguariensis* showed lower density of seedlings in landscapes with less forest cover. This species is dispersed by mammals (Abraham de Noir et al. 2002), so the observed pattern could be a consequence of defaunation in the landscape. To date there are no information over mammals in the Three Quebrachos Forest, so further research is needed to find if defaunation is the process that explains the pattern observed here. It is worth noting how the species-specific analysis revealed relations that were masked in the community assessment, even within the same structural and/or functional group.

The analysis of the size-class structure for *S. balansae* in relation to forest cover at landscape level showed no differences in the upper classes (DBH > 20 cm) but a marked decrease in the density of the lower classes in the landscapes with lower forest cover. This difference could be due to a decrease in the recruitment of this species in the landscapes with lower forest cover, which could have negative implications for its conservation. In fact, other authors have characterized populations with this type of size-class structure as "in risk" (Kohira and Ninomiya 2003). Being *S. balansae* one of the dominant species of the Three Quebrachos Forest (Torrella et al. 2011) and a key forest resource in the region (Barberis et al. 2012), these results deserve to be taken into particular account when assessing conservation strategies in the Chaco.

Aspidosperma quebracho-blanco and *P. kuntzei* could represent similar situations because their patterns were notably concordant, with differences in the classes <20 cm. However, these differences were of lesser magnitude in the former species, and statistically significant only in the 5–10-cm class in the latter species. The <5 cm class of *P. kuntzei* presented no differences but individuals of this class in Chaco forest are very scarce.

There are contradictory data about the characterization of *C. americana*, since this species has been described as light-demanding (Lorenzi 1992), shade-tolerant (Gómez and Hampel 2005), hemi-esciophyte (Scarpa 1996) and hemi-heliophilous (Tortorelli 2009). Our results showed a size-class structure with an "inverse J" shape, characteristic of shade-tolerant species (Newton 2007). Among light-demanding species, only *P. kuntzei* in landscapes with higher forest cover showed the expected "bell shaped" size-class structure (Newton 2007). While there is consensus in the characterization of *S. balansae* and *A. quebracho-blanco* as light-demanding species (Gómez and Hampel 2005; Tortorelli 2009; Barberis et al. 2012), our results allow us to state that these species are also able to recruit juveniles under the forest canopy.

Implications for management and conservation

In the study area, between 1957 and 2010, more than half the forest area was lost at the expense of a process of agricultural expansion that is still in force. Therefore, today, forest cover is below 18 % (Torrella 2014). The results of the present study show that changes in the degree of forest cover in the landscape could be causing changes in the population density of several of the dominant tree species of the Three Quebrachos Forest, threatening their conservation. At the same time, our results suggest that small fragments have a high functional value, since the density and size-class structure of the tree populations did not change with fragment size, with the exception of *C. americana*. On the other hand, it has been highlighted that the remaining fragments in the area have a key role in regional connectivity, acting as stepping stones (Piquer-Rodrígez et al. 2015).

Regrettably, the prospects for the conservation of the Three Quebrachos Forest are uncertain. In the area, the agricultural production has been politically prioritized, since under the local law, which allows a deforestation of up to 90 % of the area in most properties (Chaco Province law no 6409), this forest belongs to the lowest protection category. As shown in the present study, this high percentage of deforestation could be, at the landscape level, endangering the conservation of some of the dominant tree species of the forest.

Since it is no longer possible to create natural reserves in the Three Quebrachos Forest with large forest areas, it would be necessary to establish an integrated landscape management (Fischer et al. 2006; Döbert et al. 2014), aiming to achieve functional landscapes, as it has been proposed for tropical areas where the natural vegetation cover coexists with agriculture productions (Melo et al. 2013). It would be important to increase the protection degree of the Three Quebrachos Forest against the agriculture expansion, attempting to preserve as much of the forest as possible, to promote the forest cover at landscape level and to give relevance even to the smallest fragments.

Acknowledgments Special thanks are given to two anonymous reviewers for useful suggestions on early version of this paper, to Serge Listello and Angel Langellotti for their collaboration in the logistics during fieldwork and to the local owners and farmers who provided access to their properties. We thank L. Oakley, V. Mogni, J. Bonanata, A. Palmerio, and F. Massa for their collaboration in the fieldwork. LG is a researcher from Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina and thanks CONICET and SECyT (UNC) for financial support. This study was funded by The Rufford Small Grants Foundation (grant number 74.06.09).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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