Plant species richness in the Chaco Serrano Woodland from central Argentina: Ecological traits and habitat fragmentation effects

Luciano Cagnolo[a],*, Marcelo Cabido[b], Graciela Valladares[a]

[a]Centro de Investigaciones Entomológicas de Córdoba, F.C.E.F. y N., Universidad Nacional de Córdoba, Av. Vélez Sársfield 299, Córdoba X5000JJC, Argentina
[b]Instituto Multidisciplinario de Biología Vegetal, Universidad Nacional de Córdoba, CONICET, Argentina

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ABSTRACT

The Chaco Serrano Woodland from central Argentina has been dramatically reduced during the past 30 years, and is currently confined to several isolates of different size. In this study, we evaluated the effects of forest size, isolation and edge formation on plant species richness. Furthermore, we tested whether plants species with particular ecological traits were differentially affected by habitat fragmentation. Habitat area showed the highest explanatory value for plant species richness in stepwise multiple regressions. The effect of area was most pronounced for rare species, suggesting that large forests are necessary to preserve species with low local or regional abundance. Differences between edge and interior of Chaco Serrano were more pronounced for native and shrub species richness. The analysis of individual species cover revealed that native and biotically pollinated plants were less abundant in woodland edges. Our results showed that forest transformation into smaller remnants has lead to an impoverishment of plant communities, with particular subsets of species defined by ecological traits (rarity, origin and pollination mode) being more susceptible.

1. Introduction

Habitat fragmentation, or the transformation of a large habitat into a number of smaller isolated patches, involves a reduction of the space available for some species (Haila, 2002; Olff and Ritchie, 2002; Fahrig, 2003). Both the changes in spatial configuration and the loss of habitat could alter species number, composition and interactions (Saunders et al., 1991).

The size of a habitat is a major feature for species conservation (Saunders et al., 1991; Hill and Curran, 2001, 2003), on the basis of a positive relationship between habitat area and species richness which has been widely demonstrated through the study of species–area relationships (Holt, 1992; Rosenzweig, 1995; Connor and McCoy, 1979, 2001).

Proposed biological mechanisms leading to species–area relationships include area *per se* and habitat diversity, among others (Connor and McCoy, 1979, 2001). According to the Island Biogeography Theory (MacArthur and Wilson, 1967), area *per se* effects could result from higher extinction rates in smaller habitats, resulting from their sustaining smaller populations which tend to be more vulnerable to environmental, demographic and genetic stochasticity (Hobbs and Yates, 2003; Matthies et al., 2004). On the contrary, larger habitats

usually encompass a wider range of environmental conditions (habitat heterogeneity effects) allowing more habitat specialist species to develop (Connor and McCoy, 1979). Both area *per se* (Bastin and Thomas, 1999; Honnay et al., 1999a; Godefroid and Koedam, 2003; Hill and Curran, 2003; Krauss et al., 2004) and habitat heterogeneity (Honnay et al., 1999b; Brose, 2001) have been shown to affect plant species diversity. Sampling effects can also be important when sampling effort increases proportionally to the studied area, thus increasing the chance of finding more species. Ecological processes can therefore be obscured when non-constant areas are sampled (Hill et al., 1994; Lomolino, 2001).

Besides habitat reduction and isolation, an important feature of forest fragmentation is the increase of edges exposed to the open matrix, which can influence plant communities of forest patches (Gascon et al., 2000; Cochrane and Laurance, 2002). Edge effects could be involved in species–area relationships, since the proportion of edge habitat is inversely related to area (Connor and McCoy, 2001). In such edges, alterations of microclimatic conditions (Kapos et al., 1997; Didham and Lawton, 1999; Mesquita et al., 1999; Sizer and Tanner, 1999) and biological interactions (Bresciano et al., 1999; Bruna, 1999; Arnold and Asquith, 2002; Wahungu et al., 2002; Donoso et al., 2003) can increase plant mortality (Mesquita et al., 1999; Laurance et al., 2000) and regeneration (Sizer and Tanner, 1999), resulting in different patterns of species number and composition from those found in the interior of continuous forests (Harper et al., 2005). After edge formation, dynamic processes involving regeneration and changes in species composition can seal open spaces, reducing the extent of matrix influence into the forest (Didham and Lawton, 1999; Laurance et al., 2002; Harper et al., 2005). On the other hand, exogenous disturbance (e.g. fire, pollutants) can increase edge influence, eroding forest fragments over time (Weathers et al., 2001; Cochrane and Laurance, 2002).

Not all plant species show a uniform response to habitat fragmentation nor do they have the same conservation value (Iida and Nakashizuka, 1995; Bastin and Thomas, 1999; Hill and Curran, 2001, 2005; Haila, 2002). Differential susceptibility to habitat fragmentation is expected to depend on life-history traits related to plant dispersal, establishment or persistence (Kolb and Diekmann, 2005). Evidence shows that habitat fragmentation affected plants with specific dispersal modes (Tabarelli et al., 1999; Kolb and Diekmann, 2005), low frequency of occurrence (Iida and Nakashizuka, 1995; Hill and Curran, 2001) and high habitat specificity (Iida and Nakashizuka, 1995; Lawesson et al., 1998; Hill and Curran, 2001), while non-consistent patterns were found for compatibility systems and pollination specificity (Aizen et al., 2002). It has been postulated that short-lived species like grasses and herbs should be more sensitive to edge effects (Laurance et al., 2002; Matthies et al., 2004), which would favour colonisation by ruderal, exotic (Brothers and Springarn, 1992; Bustamante and Simonetti, 2005), wind dispersed (Hovestadt et al., 1999) and wind-pollinated (Hobbs and Yates, 2003) species. Such effects could even result in a positive fragmentation influence on species richness (Tabarelli et al., 1999; Fahrig, 2003; Harper et al., 2005). The evaluation of forest sites for conservation should be based not only on species richness but also on plant species quality, which can be defined in terms of conservation value or ecological traits (Honnay et al., 1999a; Hill and Curran, 2001, 2003). Therefore, species richness patterns of native or particularly vulnerable species should be assessed in addition to variations in overall species diversity (Collins et al., 2002).

In central Argentina, a fragmented landscape, with patches of native Chaco Serrano Woodland within a predominantly agricultural matrix, is the result from human activities that have led to a 94% reduction in woodland cover in the last 30 years (Zak and Cabido, 2004). This scenario, devastating from a conservation viewpoint, offers a "ready-made experiment" of insularization effects (Saunders et al., 1991), in which the frequent application of herbicide enhances the unsuitability of the matrix for forest species. In this system, fragmentation has been shown to affect plant reproductive processes (Aguilar and Galetto, 2004) and insect herbivory rates (Valladares et al., 2006). However, plant community patterns associated with habitat fragmentation have not been studied. Here we examine plant species richness of Chaco Serrano in relation to forest area, isolation, heterogeneity related variables and edge formation. We also ask whether particular groups of plants sharing traits such as origin, rarity, life form, pollination and dispersal mode are differentially affected by habitat fragmentation.

2. Material and methods

2.1. Study area

The Chaco Serrano District, belonging to the most extensive dry forest in South America (Cabrera, 1976; Moglia and Giménez, 1998), covers in Argentina an area between 29° and 33° 30′(S), ranging in elevation from 400 to 1300 m above sea level. The annual 750 mm of rainfall is concentrated mostly in the warm season (October–April), with mean maximum and minimum temperatures of 26 °C and 10 °C respectively (Luti et al., 1979; Moglia and Giménez, 1998). The characteristic vegetation is a low and open woodland, with tree layer (8–15 m high) dominated by *Aspidosperma quebracho-blanco* Schltdl., *Prosopis* spp., *Fagara coco* Engl. and *Lithrea molleoides* (Vell.) Engl.; shrubs (1.5–3 m) dominated by *Celtis pallida* Torr. and *Acacia* spp.; herbs and grasses (0–1 m) and many vines and epiphytic bromeliads (Luti et al., 1979; Cabido et al., 1991). Native vegetation is currently restricted to isolated patches within an intensely managed matrix (Zak and Cabido, 2004).

Nineteen sites in an area between 31° 10′–31° 30′ S and 64° 00′–64° 30′ W were selected after supervised classification of digital satellite images (Landsat Thematic Mapper, 14 November 1997). The criteria for site selection were to cover a wide range of areas while keeping isolation and matrix characteristics as uniform as possible. Three of these sites represented continuous forests (>1000 ha), whereas the others covered a size gradient ranging from 117 ha to 0.13 ha (mean = 11.98 ± 7.19). All remnants had been isolated for at least 7 years, with distance to the nearest larger remnant ranging between 75 m and 200 m. The woodlands are mainly used for cattle grazing, and are embedded in an agricultural matrix

largely dominated by wheat in winter and soy or maize in summer.

Fragment shape can enhance the influence of edge effects (Cochrane and Laurance, 2002; Hill and Curran, 2003, 2005). In our study, Patton's shape index (Patton, 1975) was relatively constant across sites (2.57–1.93) and was not correlated with the variables studied (Spearman Rank-order Correlation, $P > 0.05$). Therefore, woodland shape was not included in further analyses.

2.2. Floristic data

Data were collected from April to May 2003. At each site, complete floristic composition was recorded in two 500 m^2 plots, assigning each plant species to one of the following cover-abundance categories: <1%, 1–5%, 6–25%, 26–50%, 51–75%, and >75% (Braun-Blanquet, 1950). In order to evaluate edge effects, one plot was set at the edge (5 m inside the woodland) and the other at the interior (50 m from the edge; at the geometric centre in remnants <4 ha) of each site. Although edge effects have been shown to reach up to 400 m into the forest (Harper et al., 2005), the distance here selected has frequently proved adequate to detect edge-related floristic changes (Murcia, 1995; Williams-Linera et al., 1998; Meiners and Pickett, 1999; Sizer and Tanner, 1999; Honnay et al., 2002; Laurance et al., 2002; Harper et al., 2005).

Since sampling effort and number of species recorded are usually related (Magurran, 1988; Hill et al., 1994; Lomolino, 2001), the area sampled was kept constant in all sites in order to avoid sampling artefacts on the effects of habitat fragmentation (Hill et al., 1994). The size of sampling plots was established following previous phytosociological studies in which the minimal area needed to include almost all the species present was determined using species accumulation curves (Cabido et al., 1991; Zak and Cabido, 2002).

The abundance of species can be described in terms of geographic range, use of habitats and population density (Thomas and Mallorie, 1985; Hartley and Kunin, 2003). We classified plant species as rare or common, following two criteria: (1) rarity within sites, considering plant cover (average midpoint of the corresponding cover category from the two 500 m^2 plots) in each site where the species was present (rare: cover per site ⩽0.1%; common: cover per site ⩾1%); (2) rarity among sites, estimated from the species frequency of occurrence among the 19 forest remnants (rare: found in ⩽3 sites; common: found in ⩾10 sites). Cut-off points were decided on the basis of allocating a sufficient number of species in each category to perform the proposed analyses. This classification refers only to the 19 sites included in this study and does not mean an absolute attribute of the species involved.

Plant species were also classified according to their life form (trees, shrubs, herbs, grasses, vines, epiphytes, ferns and Cactaceae) and to their origin (native and exotics) after consulting the Flora Argentina Catalogue (Instituto Darwinion, 1997). Pollination and dispersal mode were derived from literature (Abraham de Noir et al., 2002; Aizen et al., 2002; Marco and Páez, 2002) and the observation of flower and fruit structures that represent an attraction or reward to animals. Data from the two sampling plots from each site were pooled in order to estimate remnant species richness (total and for each category).

2.3. Habitat variables

In addition to area and isolation, remnants were characterised in terms of habitat heterogeneity by recording altitude and number of cattle excrements in each of the two plots used for vegetation surveys. Grazing intensity and altitude range within a remnant could relate to habitat diversity through generation of hyperdisturbed habitat patches (Lawesson et al., 1998) or higher topographic complexity (Kerr and Packer, 1997; Lawesson et al., 1998) respectively.

In order to explore the relative effects of area per se and indicators of habitat diversity on species richness, we performed partial correlation analyses and multiple regression models with stepwise selection of the following independent variables:

1. Remnant area (in hectares).
2. Remnant isolation distance to the nearest larger remnant (in metres).
3. Grazing intensity: number of cattle excrements.
4. Altitude range: difference in altitude between the two sampling plots of each site (in metres).

Landscape variables are usually correlated (Fahrig, 2003). Because high levels of collinearity between explanatory variables can bias the significance of parameters estimates (Philippi, 1993), the extent of multicollinearity was determined for every multiple regression. Acceptable collinearity values (variance inflation factor < $1/(1 - R^2)$) as proposed by Freund and Littell (1991) were found in all cases. All variables were $\log_{10}$ transformed to achieve residuals normality or homoscedasticity.

2.4. Data analysis

Sensitivity to habitat area was compared among plants with different ecological traits (origin, rarity, and life forms) by an ANCOVA design with species richness as the response variable, plant category as the fixed factor and remnant area as the continuous independent variable; interaction terms were left in the model, as tests for homogeneity of slopes. A significant interaction indicates that the slopes of the groups considered are different (Zar, 1996; Johnson et al., 2003).

Species richness in woodland edge and interior location was compared by means of a paired-samples t test (or Wilcoxon paired rank test when data did not fulfil parametric statistics requirements). The same tests were used to compare edge vs. interior abundance (% cover) of the most frequent species (present in at least four sites), after arcsine square root transformation to achieve normality. Plant species were thus classified as having: (1) significant ($p < 0.05$) or marginal ($p < 0.1$) bias to the interior of the forest, (2) significant ($p < 0.05$) or marginal ($p < 0.1$) bias to the edge of the forest, (3) non-significant bias ($p > 0.1$). Chi-square tests were used to determine whether species bias to either edge or interior was independent of plant origin (native or exotic) and

dispersal and pollination mechanisms (biotic i.e. involving mutualisms, or abiotic). For edge-interior comparisons, three sites (in which the sampling plots could not be placed to at least 10 m from each other) were excluded. Species richness of epiphytes, Cactaceae and ferns was not included in the statistical analyses due to the low number of species recorded and to their absence in a large number of sites.

3. Results

From a total of 253 plant species recorded, species richness at each site ranged from 131 in the largest forest to 57 species in the third smallest patch (0.7 ha). Exotics comprised 15.3% of all the species recorded. There were more rare than common species, according to our two classifications of relative rarity: we found 135 species restricted to three or fewer sites (mean = 1.53 ± 0.06) while only 67 species were present in at least 10 sites (mean = 14.37 ± 0.35); moreover, a low plant cover (0.1% or less; mean = 0.06 ± 0.001) was recorded for 149 species whereas only 51 species showed an average cover of 1% or more (mean = 5.22 ± 0.58).

Multiple regression models accounted for two thirds of the variation in total and native species richness, and for around half of the variation in species richness of rare plants (both in terms of occurrence and abundance) and those with relatively high plant cover. Grazing was included in all models, and isolation contributed to explain plant diversity of common plants (Table 1), but in all cases only woodland area remained as a significant factor after controlling for the effect of the other variables. Only the number of species relatively abundant among sites (recorded in more than 10 sites) was unrelated to any of the studied variables (Table 1).

When plant life form was considered, woodland area was again the most important factor, being included in all models and significantly affecting species richness of trees, shrubs, herbs and grasses (Table 2). Isolation also showed significant negative effects for tree and vine species richness, even after controlling for other factors. Grazing intensity showed a weak, negative effect in the models explaining tree and grass species richness. Elevation range did not show significant effects on species richness of any of the plant groups considered.

A comparison of slopes from simple linear regressions of species richness on forest area revealed that plants were not all equally affected by habitat size ($F_{2,51} = 10.12$, $p < 0.001$). As woodlands became smaller, loss of rare species (particularly those restricted to few remnants, i.e. rare among sites), was more pronounced than that of total, native or common species (Fig. 1). Moreover, there were marginally significant differences in this regard when comparing species richness of plants differing in their life form ($F_{4,85} = 2.16$, $p = 0.08$). This result actually reflected the lack of area effects on vine species richness, which set this group apart from the rest (Fig. 2).

A general trend of higher species richness in the interior than at the edge of the woodlands was observed (Fig. 3), though differences were significant only for native plants ($t = 2.112$, df = 15, $p = 0.05$), all other categories being statistically similar on both locations (t test, $p > 0.1$).

When life forms were considered, shrubs were better represented in the woodland interior ($t = 2.192$, df = 15, $p = 0.04$) and, although non-significant differences between woodland edge and interior were found for trees, grasses, herbs (t test, $p > 0.1$, in all cases) or vines (Wilcoxon test, $p > 0.1$), plants

Table 1 – Stepwise multiple regression and partial correlation results of total, native, common and rare (by occurrence and cover) plant species richness (S) on habitat area, isolation, grazing intensity and altitude range in 19 Chaco Serrano Woodland remnants from central Argentina

Response variables	Multiple regression coefficients (R^2)	Model	Partial correlation coefficients
Total species richness	0.67***	$\log_{10}(S) = 1.83 + 0.07^{*}\log_{10}$ (area) $- 0.03^{*}\log_{10}$ (grazing)	Area: $r = 0.79$*** Grazing: $r = -0.28$ns
Native plant species richness	0.66**	$\log_{10}(S) = 1.74 + 0.08^{*}\log_{10}$ (area) $- 0.03^{*}\log_{10}$ (grazing)	Area: $r = 0.53$* Grazing: $r = -0.23$ns
Common plant species richness (present in $\geqslant$ 10 sites)	0.10ns	–	–
Rare plants species richness (present in $\leqslant$ 3 sites)	0.51***	$\log_{10}(S) = 0.71 + 0.30^{*}\log_{10}$ (area) $- 0.17^{*}$ (grazing)	Area: $r = 0.71$*** Grazing: $r = -0.32$ns
Common plant species richness (cover per site $\geqslant$ 1%)	0.47**	$\log_{10}(S) = 1.31 + 0.08^{*}\log_{10}$ (area) $+ 0.05^{*}\log_{10}$ (isolation) $- 0.04^{*}$ $\log_{10}$ (grazing)	Area: $r = 0.71$** Isolation: $r = 0.46$ms Grazing: $r = -0.43$ms
Rare plant species richness (cover per site $\leqslant$ 0.1%)	0.60***	$\log_{10}(S) = 1.36 + 0.12^{*}\log_{10}$ (area) $- 0.05^{*}\log_{10}$ (grazing)	Area: $r = 0.75$*** Grazing: $r = -0.43$ns

ns: $p \geqslant 0.1$; ms: $0.1 < p > 0.05$; $n = 19$.
* $p \leqslant 0.05$.
** $p \leqslant 0.01$.
*** $p \leqslant 0.001$.

Table 2 – Stepwise multiple regression and partial correlation results of tree, shrub, vine, herb, and grass species richness (S) on habitat area, isolation, grazing intensity and altitude range in 19 Chaco Serrano Woodland remnants from central Argentina

Response variable (species richness)	Multiple regression coefficients (R^2)	Model	Partial correlation coefficients
Trees	0.59[***]	$\log_{10}(S) = 0.87 + 0.12^* \log_{10}(\text{area}) + 0.09^* \log_{10}(\text{isolation}) - 0.04 \log_{10}(\text{grazing})$	Area: $r = 0.77$[***] Isolation: $r = 0.59^*$ Grazing: $r = -0.35$[ns]
Shrubs	0.68[***]	$\log_{10}(S) = 1.02 + 0.09^* \log_{10}(\text{area})$	Area: $r = 0.84$[***]
Vines	0.21[ms]	$\log_{10}(S) = 1.18 - 0.08^* \log_{10}(\text{isolation}) - 0.03^* \log_{10}(\text{area})$	Isolation: $r = -0.51^*$ Area: $r = -0.35$[ns]
Herbs	0.38[**]	$\log_{10}(S) = 1.38 + 0.06^* \log_{10}(\text{area})$	Area: $r = 0.64$[***]
Grasses	0.31[*]	$\log_{10}(S) = 0.9 + 0.12^* \log_{10}(\text{area}) - 0.13^* \log_{10}(\text{grazing})$	Area: $r = 0.62^*$ Grazing: $r = -0.45$[ms]

ns: $p \geqslant 0.1$; ms: $0.1 < p > 0.05$; $n = 19$.
* $p \leqslant 0.05$.
** $p \leqslant 0.01$.
*** $p \leqslant 0.001$.
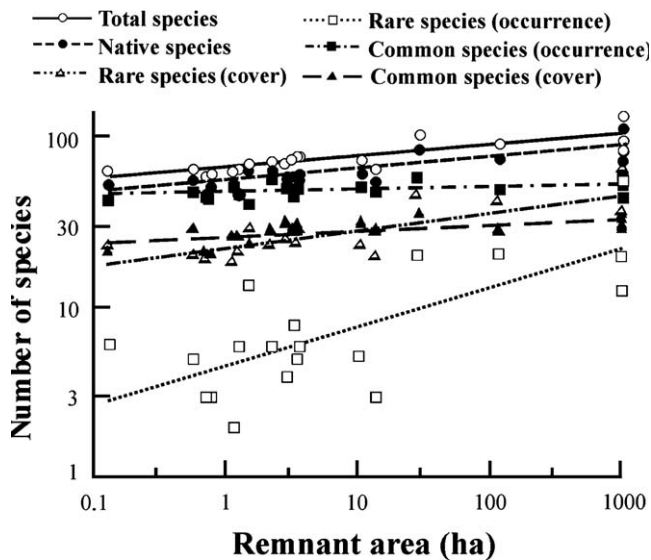
Fig. 1 – Species–area relationship for total, native, rare and common (by occurrence and cover) species in 19 Chaco Serrano Woodland remnants from central Argentina. Total species: z = 0.06, p < 0.001; native species: z = 0.07, p < 0.001; rare species (occurrence): z = 0.27, p < 0.001; common species (occurrence): z = 0.01, p = 0.20; rare species (cover): z = 0.10, p < 0.001; common species (cover): z = 0.035, p = 0.006.

in most life forms (except grasses) tended to be more diverse in the forest interior (Fig. 4).

By analysing relative plant cover, we detected nine species being significantly more abundant (higher percentage cover) at the woodland edge, whereas 12 species showed a positive association with the woodland interior (Table 3). Plant association with the edge or the interior of Chaco Serrano woodland was independent of seed dispersal mechanism ($\chi^2 = 0.15$, df = 1, $p = 0.69$), but was affected by whether pollination involved biotic or abiotic agents ($\chi^2 = 7.88$, df = 1, $p = 0.005$) and

by plant origin ($\chi^2 = 3.70$, df = 1, $p = 0.05$). Edges seem to favour species with abiotic pollination (60% of edge-biased species) and exotic origin (56%), whereas species interacting with animals for pollination (91% of interior-biased species) and those native to the region (92%) were more abundant in the woodland interior (Table 3). More than half of the species favoured by edge conditions were grasses, but only two out of 12 interior related plants belonged to this group.

4.   Discussion

Our results show that forest transformation into smaller remnants, a classical consequence of habitat fragmentation (Fahrig, 2003), has lead to an impoverishment of plant communities in the Chaco Serrano of central Argentina, whether total or native species are considered.

Habitat area could affect species richness through stochastic area-dependent extinction or as a surrogate for habitat diversity (Connor and McCoy, 1979). In the present study, besides considering habitat area and isolation, we incorporated variables related to habitat heterogeneity, in particular intensity of cattle grazing and altitudinal variations within the sampling sites. Remnant area showed the highest explanatory value for plant species richness in the studied system, as found in many other studies involving different taxa and regions (Fahrig, 2003).

Although we cannot completely discard habitat heterogeneity or isolation effects, we found strong evidence of the area *per se* effect. This evidence is reinforced by the constancy of sampling effort across sites belonging to the same biogeographic region and under similar landscape management. Considering that species–area models frequently explain less than half of the variation in species number (Godefroid and Koedam, 2003), the high correlation coefficients obtained in this work suggest that area effects on plant species richness in the Chaco Serrano are remarkably strong, hence the contribution of other factors might be limited. However, it must be noticed that predicting the loss of species accompanying a certain amount of area reduction is not a straightforward
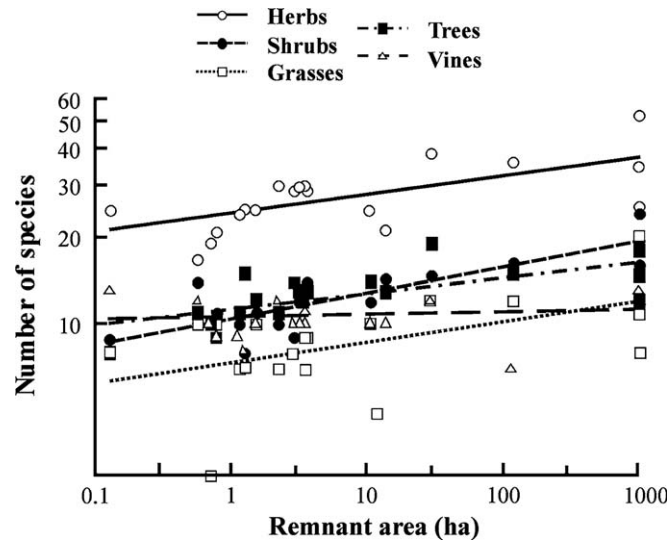
Fig. 2 – Species–area relationship for herb, shrub, grass, tree, and vine species in 19 Chaco Serrano Woodland remnants from central Argentina. Grasses: $z = 0.07$, $p < 0.05$; herbs: $z = 0.06$, $p < 0.01$; vines: $z = 0.01$, $p > 0.05$; shrubs: $z = 0.09$, $p < 0.001$; trees: $z = 0.05$, $p < 0.01$.
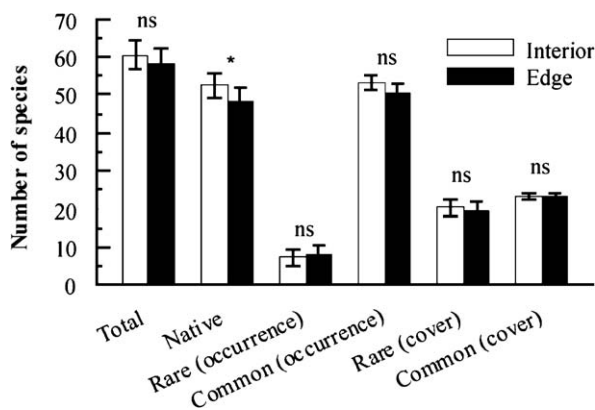

Fig. 3 – Number of total, native, rare and common (by occurrence and cover) species in edge and interior plots of 19 Chaco Serrano Woodland remnants from central Argentina. ns: $p \geqslant 0.1$; ms: $0.1 < p > 0.05$; *: $p \leqslant 0.05$; **: $p \leqslant 0.01$; ***: $p \leqslant 0.001$.
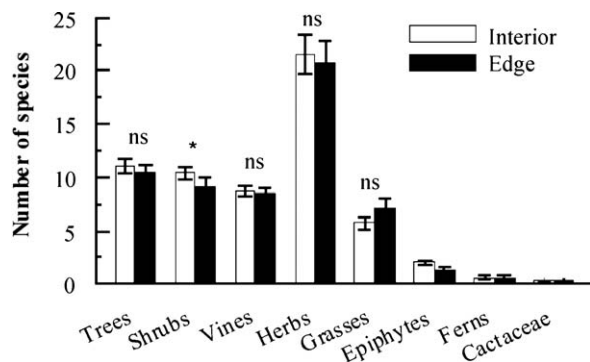

Fig. 4 – Number of species according to their life form, in edge and interior plots of 19 Chaco Serrano Woodland remnants from central Argentina. ns: $p \geqslant 0.1$; ms: $0.1 < p > 0.05$; *: $p \leqslant 0.05$; **: $p \leqslant 0.01$; ***: $p \leqslant 0.001$.

application of species–area curves, since much more information is needed, such as the degree of overlap in the species composition of the fragments (Connor and McCoy, 2001; Wilsey et al., 2005).

Loss of habitat has been shown to affect biotic interactions in the Chaco Serrano system, and such alterations could be involved in the species–area relationships here documented. For example, pollination becomes less efficient as woodland area decreases, which could affect plant reproductive success (Aizen and Feisinger, 1994a,b; Aguilar and Galetto, 2004), whereas negative interactions such as seed predation (Chacoff et al., 2004) and herbivory (Valladares et al., 2006), also decreasing with habitat reduction, could alter the competitive balance among species (Carson and Root, 2000).

Isolation is expected to be another major factor determining the number of species in an island or habitat patch (MacArthur and Wilson, 1967; Fahrig, 2003) but, coinciding with other authors (Hill and Curran, 2003), we did not find significant effects of this variable. This result should be cautiously considered, since the isolation range included in our study may have been too narrow for effects to be detected. Besides, distance between fragments provides only a part of the information needed to assess habitat isolation (Brose, 2001) and the simple unidirectional measure used here may be limited compared with more complex isolation indexes (e.g. Hansky, 1999). Moreover, important effects of isolation can be missed when focusing on species richness, since each species has its own individual pattern of habitat and dispersal (Bastin and Thomas, 1999). Isolation effects could also be masked by matrix species being present in the woodlands, hence reducing the separation distance between populations (Godefroid and Koedam, 2003; Martínez-Garza and Howe, 2003), but this explanation is not likely to apply to our system given the intensive use of herbicides in the fields surrounding these remnants.

When different ecological traits were considered, species loss due to habitat fragmentation in the Chaco Serrano appeared to follow a predictable pattern rather than being a

Table 3 – Preferential location and ecological traits of plant species showing significant bias in their percentage cover between edge and interior plots of 16 Chaco Serrano Woodland remnants from central Argentina

Species	p value (Wilcoxon test)	Life form	Pollination mode	Dispersal mode	Origin
Interior-related					
Aloysia gratissima (Gillies and Hook.) Tronc.	0.04	Shrub	Biotic	Abiotic	Native
Condalia buxifolia Reiss.	0.07	Tree	Biotic	Biotic	Native
Dolichandra cynanchoides Cham.	0.07	Vine	Biotic	Abiotic	Native
Eupatorium argentinum Ariza	0.09	Herb	Biotic	Biotic	Native
Ligustrum lucidum Aiton	0.04	Tree	Biotic	Biotic	Exotic
Mandevilla pentlandiana Woodson	0.07	Vine	Biotic	Abiotic	Native
Oplismenus hirtellus (L.) P. Beauv	0.02	Grass	Abiotic	Abiotic	Native
Passiflora coerulea Auct.	0.09	Vine	Biotic	Biotic	Native
Salpichroa origanifolia (Lam.) Baill.	0.09	Herb	Biotic	Biotic	Native
Setaria hunzikeri Anton	0.04	Grass	Abiotic	Abiotic	Native
Solanum sp.1	0.07	Herb	Biotic	Biotic	Native
Tillandsia hieronymi Mez.	0.07	Epiphyte	Biotic	Abiotic	Native
Edge-related					
Capsicum chacoense A.T. Hunziker	0.07	Herb	Biotic	Biotic	Native
Cynodon dactylon Steud.	0.07	Grass	Abiotic	Abiotic	Exotic
Digitaria sanguinalis (L.) Scop.	0.04	Grass	Abiotic	Abiotic	Exotic
Geoffroea decorticans (Gillies ex Hook. and Arn.) Burkart	0.003	Tree	Biotic	Biotic	Native
Janusia guaranitica A. Juss.	0.04	Vine	Biotic	Abiotic	Native
Eleusine tristachya (Lam.) Lam.	0.07	Grass	Abiotic	Abiotic	Exotic
Schinus longifolius Speg.	0.04	Tree	Biotic	Biotic	Native
Setaria geniculata P. Beauv.	0.08	Grass	Abiotic	Abiotic	Exotic
Sorghum halepense (L.) Pers.	0.02	Grass	Abiotic	Abiotic	Exotic

random process, with rare species being the most negatively affected. Our results support the idea that larger habitats should be particularly rich in species with small population size (Hill and Curran, 2001; Matthies et al., 2004) or low frequency of occurrence (Iida and Nakashizuka, 1995; Godefroid and Koedam, 2003). This finding is relevant from a conservation perspective and suggests that large refuges would be necessary to increase the chances of survival of such rare species. Rarity can be related to life-history traits such as smaller plant size or lower reproductive output, which may confer a higher sensitivity to fragmentation (Kolb and Diekmann, 2005), although the relationship between population size and extinction probability is still not clear (Honnay et al., 1999a).

Functional groups usually have different life spans, migration tendencies and may require home ranges of different size (Kattan and Murcia, 2003). Accordingly, different responses to habitat fragmentation could be expected. However, similar rates of species loss were observed for plants in all the life forms here considered. Only vines appeared unaffected by habitat loss or any of the studied fragmentation variables, showing only a weak negative response to habitat isolation.

Besides area loss and isolation, habitat fragmentation entails an increase in the proportion of edge habitat (Saunders et al., 1991; Fahrig, 2003). Edges disrupt ecological continuity and generate environmental contrasts, which can alter diversity patterns (Murcia, 1995; Meiners and Pickett, 1999). Edges resulting from fragmentation of the Chaco Serrano in central Argentina were slightly poorer in most plant groups than the woodland interior, only grasses showing the opposite trend, although significant differences were restricted to native species and shrubs. Since trees have much longer life spans than herbs, vines or grasses, we expected edge-interior differences

in species richness to be more pronounced for short lived groups (Laurance et al., 2002; Matthies et al., 2004), but such differences might have been blurred by the variable time since isolation of these remnants. These results contrast with the higher plant diversity found on edges as compared to the interior, in another Chaco forest system (López de Casenave et al., 1995). Edge origin (edaphic in the latter system, deforestation in ours) and age (long *vs.* short time of formation) may explain such different results since edge influence can change over time decreasing or increasing plant diversity (Harper et al., 2005). The weak edge effects here observed seem to support the idea that such effects would be stronger in dense tropical forests than in more open temperate systems like central Argentina woodlands, mainly due to weaker microclimatic contrasts between edges and forest interior in the latter (Harper et al., 2005).

The analysis of individual species revealed that species showing higher cover in woodland edges compared to the interior were predominantly wind-pollinated whereas interior-biased species were mostly pollinated by animals, suggesting an edge-related disruption of mutualistic interactions. Edges usually favour the establishment of pioneer, shade-intolerant and invaders, disturbance-adapted species that may modify the floristic composition of the original forest by dispersing from edges into the forest (Janzen, 1983; Brothers and Springarn, 1992; Meiners and Pickett, 1999; Harper et al., 2005). In our study, plants that responded positively to the woodland interior were predominantly native, contrasting with the higher representation of exotics (more than half of species) in the edge-favouring group. However, it must be noticed that *Ligustrum lucidum*, one of the most aggressive invaders in central Argentina (Aragón and Morales, 2003), responded positively to the interior condition.

Such changes in the interaction scenario and in native/exotic species rate could generate time-delayed extinctions that may became evident in the future (Tilman et al., 1994). The lack of relationship between dispersal mode and edge/interior location could be linked to the lack of isolation effects in this system, since dispersal is mainly affected by patch isolation (Kolb and Diekmann, 2005).

4.1. Implications for conservation

Fragmentation of the Chaco Serrano woodland has recently reached a dramatic scale in central Argentina (Zak and Cabido, 2004), affecting plant reproduction and impairing the regeneration of various species (Aizen and Feisinger, 1994a,b; Aguilar and Galetto, 2004; Chacoff et al., 2004). We have now demonstrated that two aspects of habitat fragmentation (remnant area and edge effects) strongly affect diversity of the overall plant community, with particular subsets defined by ecological traits (mainly relative rarity, origin and pollination mechanism) being most susceptible. These results are particularly important considering the relatively short time span of the fragmentation process here studied, which has taken place mainly during the last 30 years. Although in comparison with other studies (Lawesson et al., 1998; Honnay et al., 1999a), ours can be considered a relatively short-term, post-excision fragmentation system, we found a remarkable loss of plant species – particularly rare ones – with habitat loss, as well as edge effects suggesting a negative impact on native and animal-pollinated plants. Such changes could have a cascading effect on higher trophic levels, affecting vertebrate and invertebrate diversity, multitrophic interactions, and ultimately ecosystem functioning (Saunders et al., 1991; Martínez-Garza and Howe, 2003).

Our results suggest that conservation management of the Chaco Serrano should give priority to large area remnants. Nevertheless, since among-site rarity appears as the most significant trait in relation to habitat loss, conservation efforts should also focus on ensuring a regionally spread remnant net, thus allowing rescue effects (Wilsey et al., 2005) to preserve viable regional populations of those rare species.

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