Components of woody plant diversity in semi-arid Chaco forests with heterogeneous land use and disturbance histories

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ABSTRACT

We assessed components of woody plant diversity within and between 16 sites dispersed across the nearly 200,000 ha of the Semi-arid Chaco vegetation of the Copo Conservation Unit, northern Argentina. Argentina's Semi-arid Chaco is an object of international conservation concern, as it is under pressure from conversion to agroindustry supplanting long-standing practices of logging and livestock grazing. We recorded from 16 (shrubby grassland following forest fire) to 27 (selectively logged forest) woody plant species per site and 37 species in total (gamma diversity). Additive partitioning showed that alpha diversity contributed 59% to gamma diversity and beta diversity only 41%. A separate additive partitioning of gamma diversity of the 13 forested sites alone showed that beta diversity attributable to logging history was considerably lower than remaining beta diversity and alpha diversity. Ordination analyses confirmed this finding: species composition of unlogged, selectively logged and intensively logged forest sites was quite similar. Results suggest that (1) woody vegetation, at least, of the Semi-arid Chaco is quite tolerant to traditional modes of land use and that (2) conservation of this vegetation as a whole must include not only "pristine" sites varying in edaphic conditions but also sites varying in land use and management histories.

1. Introduction

The Semi-arid Chaco of Argentina, a vast vegetation formation historically under pressure from various sources of degradation and now threatened by massive deforestation for soybean cultivation (Boletta et al., 2006; Gasparri and Grau, 2009; Zak et al., 2004), is a priority for biodiversity conservation on the regional scale (Dinerstein et al., 1995). Land use for livestock grazing and hardwood logging, along with fire, have historically been the principal sources of degradation and continue to be so outside of regions converted to soybeans (TNC et al., 2005). Despite the ubiquity of these disturbances in the Chaco ecosystem, however, to date no study has dealt with their possible consequences to species diversity and its components.

In general, human land use and associated disturbances such as fire have major impacts on local and global biodiversity (Chapin et al., 2000; Foley et al., 2005; Polasky et al., 2011). Understanding the relationship between biodiversity and land use history is crucial to management, particularly of those ecosystems already extensively modified by human activities (Halffter et al., 1999).

Species diversity is one aspect of biodiversity (Noss, 1990) and itself consists of various components. A half century ago Whittaker (1960, 1972) proposed partitioning gamma diversity (the diversity of a landscape or region) among alpha or local diversity and beta diversity (species turnover along an environmental gradient). Partitioning diversity into these two components enables ecologists and managers to better understand the interaction of local and regional processes in determining the species diversity of a landscape (Schluter and Ricklefs, 1993). In particular, the magnitude of species turnover from site to site may be critical to land use planning and management of the elements making up said landscape, for example when designing a network of protected areas (Kattan et al., 2005; Wiersma and Urban, 2005; Wu et al., 2010). Analysis of diversity components also serves as a guide for regional conservation strategies (Chandy et al., 2006; Gering et al., 2003; Jost et al., 2010; Paknia and Pfeiffer, 2011; Summerville et al., 2003).

Fewer studies have dealt with beta than with alpha diversity (Moreno et al., 2006), but the past decade has seen an increase in research on species turnover among sites at different spatial scales (Anderson et al., 2011; Colwell, 2010; Ricota, 2008). Definitions and

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terminologies for beta diversity have proliferated as well (Tuomisto, 2010a, 2010b). Recently several authors have proposed schemes for the codification and unification of approaches to measuring beta diversity (Anderson et al., 2011; Colwell, 2010; Moreno and Rodríguez, 2010; Tuomisto, 2010a, 2010b, 2011) and for the additive partitioning of gamma diversity among its alpha and beta components (Ellison, 2010; Lande, 1996; Veech and Crist, 2010; Veech et al., 2002). In additive partitioning, the different diversity components are calculated using the same units (for example, number of species) and thus can be compared directly (Wagner et al., 2000). Additive partitioning enables analysis of the hierarchical or nested structure of diversity (Gering et al., 2003). Quantified at different spatial scales, it provides insight into the processes contributing to landscape's gamma diversity and guidelines for its management (Wagner et al., 2000).

In the Semi-arid Chaco of the Copo Conservation Unit, north-central Argentina, we applied additive partitioning of diversity and dissimilarity analyses to data on woody vegetation across sites varying greatly in land use and disturbance history. If disturbance history affected present-day species composition to a significant extent relative to other environmental controls of diversity, we would expect variation in both alpha and in beta diversity, with considerable overturn in species composition among sites with different disturbance histories. In contrast, low beta diversity with respect to disturbance history would indicate that land use in the Chaco has had relatively little effect on the biodiversity of at least the woody plant component of this ecosystem, and that diversity is chiefly mediated by other environmental factors. Our specific objectives were to: (1) assess woody plant diversity within (alpha) and across (gamma) 16 sites with different disturbance histories, (2) assess the dissimilarity of plant species composition between pairs of sites, (3) through additive partitioning, determine the contributions of alpha and beta diversity to gamma diversity, (4)

explore the relationship between beta diversity and the logging histories of the 13 sites supporting forest, and (5) estimate the minimum number of sites required to represent gamma diversity of woody plants in this threatened landscape.

2. Materials and methods

2.1. Study area

Copo Conservation Unit (25°55′S, 62°05′W) consists of Copo National Park (114,250 ha), Copo Provincial Reserve, and Copo Multiple Use Reserve (the last two sum to 85,000 ha) in the provinces of Santiago del Estero and Chaco, Argentina (Fig. 1). Copo lies in the Semi-arid Chaco forest or Eastern Chaco Region (Prado, 1993), specifically in the Ancient Juramento Riverbeds Region (Morello and Adámoli, 1974). Rainfall and temperature are highly seasonal, with 80% of the 700 mm of annual rainfall concentrated in the spring-summer wet season.

The dominant vegetation of Copo is semi-deciduous thorn forest interrupted by belts of natural grasslands and shrubby grasslands associated with the alluvial sandy soils of ancient riverbeds (Morello and Adámoli, 1974). The tree stratum is dominated by *Schinopsis lorentzii* (Anacardiaceae), *Aspidosperma quebracho-blanco* (Apocynaceae), and *Ziziphus mistol* (Rhamnaceae), which reach heights of 18–20 m. The dense stratum of shrubs 1–6 m tall is dominated by *Capparis retusa* (Capparaceae), *Acacia praecox* (Fabaceae), *Celtis pallida* (Celtidaceae), *Achatocarpus praecox* (Achatocarpaceae) and *Schinus polygamus* (Anacardiaceae) (Tálamo, 2006; Tálamo and Caziani, 2003).

Copo includes not only primary vegetation but also vegetation subjected to a variety of anthropogenic disturbances. The most frequent disturbances are logging, livestock grazing, burning for pasture management than often leads to uncontrolled forest fires,
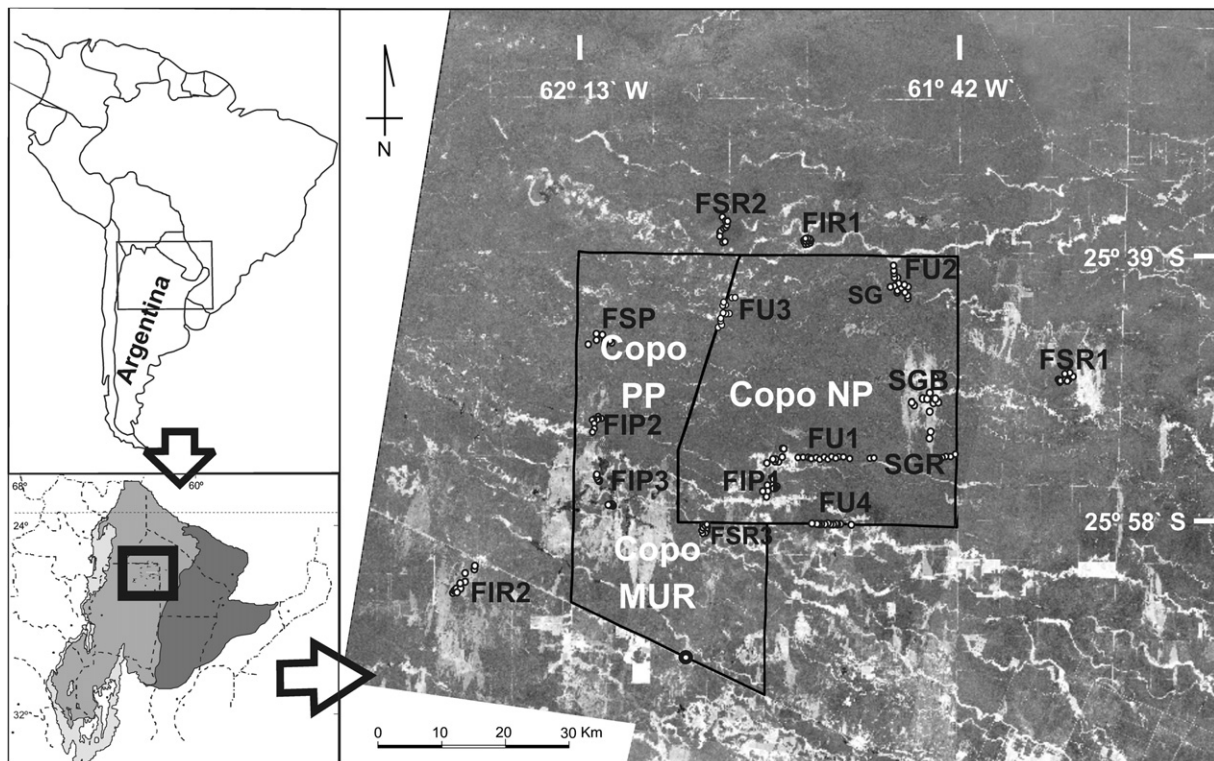

Fig. 1. Map of study sites in the Copo Conservation Unit, composed of Copo National Park (NP), Copo Provincial Park (PP), and the Copo Multiple Use Reserve (MUR). See Table 1 for definitions of acronyms.

Table 1
List of the 16 sites with different land use and disturbance histories studied in Copo Conservation Unit (northern Argentina), indicating overall physiognomy at present, disturbance history, and sampling effort (number of plots). "Selective logging" indicates extraction of quebracho colorado (*Schinopsis lorentzii*) only. "Integral logging" indicates extraction of a variety of hardwood species, not only *S. lorentzii*, for charcoal production.

Site	Physiognomy	Disturbance histories	Livestock	Years since last disturbance	No. of plots
FU1	Forest	Unlogged	Cattle	N/A	12
FU2	Forest	Unlogged	None	N/A	12
FU3	Forest	Unlogged	Cattle	N/A	12
FU4	Forest	Unlogged	Cattle	N/A	12
FSR1	Forest	Selective logging in recent past	None	2	12
FSR2	Forest	Selective logging in recent past	Cattle	1	12
FSP	Forest	Selective logging in past	Cattle	>10	12
FIP1	Forest	Integral logging in past	Cattle	>10	12
FIP2	Forest	Integral logging in past	Cattle	>10	10
FSR3	Forest	Integral logging in past and selective logging in recent past	Cattle	2	12
FIP3	Forest	Integral logging in past	Cattle	>10	12
FIR1	Forest	Integral logging long ago and again in recent past	Cattle, goats	1–2	12
FIR2	Forest	Continuous integral logging until recently	Cattle, goats	1–2	12
SG	Shrubland/Grassland	Shrubby grassland in ancient riverbed, without recent fires	None	N/A	10
SGR	Shrubland/Grassland	Shrubby grassland occupying road right-of-way cleared through forest, then abandoned	Cattle	>10	13
SGB	Shrubland/Grassland	Shrubby grassland replacing forest destroyed by intense burn	None	>10	12

and clearing to build roads for oil prospecting, roads that are later abandoned (see Tálamo and Caziani, 2003). Two forms of logging are carried out: 1) removing only *S. lorentzii* individuals for posts, railway sleepers and beams, locally referred to as selective logging, and 2) logging of all hardwood species (e.g., *S. lorentzii*, *Aspidosperma quebracho-blanco*, *Z. mistol*, *Caesalpinia paraguariensis* (Fabaceae), *Acacia furcatispina* (Fabaceae)) for charcoal production, locally referred to as integral logging.

2.2. Sampling design

In Copo, we selected 16 study sites with a variety of land use and disturbance histories (Table 1), ranging from primary forests and edaphic shrublands with little evidence of anthropogenic disturbance to forests heavily logged or burned in the past. With one exception (SGR) the areas of the sites, whether expanses of primary forest, ranches, grasslands, or logged forests, were on the order of 1000 ha. In logged forests the intensity and date of logging could be evaluated qualitatively (Table 1) but not quantitatively.

We subsampled within each site, recording woody plant species in rectangular plots, usually but not always 12 (Table 1). Each plot consisted of a 2×50 m rectangle in which we recorded all woody individuals with diameters greater than 0.5 cm DBH (trees) or 0.5 cm at 10 cm height above ground (shrubs). We used "preferential sampling" (Matteucci and Colma, 2002) to distribute the plots throughout each site so as to best represent the vegetation of the site as a whole, randomly assigning the long axis of each plot among eight orientations (N, NE, E, SE, S, SW, W, NW) in all sites but SGR, where plots had to be oriented linearly along the axis of the abandoned road. Before proceeding further with data analysis, we summed counts per species across all plots within the site.

2.3. Data analysis

Objective 1. We calculated within-site diversity as species richness (S) per site (across all plots in that site), and gamma diversity (S_g) as the cumulative number of species across all 16 sites.

Objective 2. We assessed dissimilarity in species composition between pairs of sites in three ways. First, we calculated the complementarity index (C) between sites (Colwell and Coddington, 1994):

$$C = \left(S_j + S_k - 2V_{jk} \right) \big/ \left(S_j + S_k - V_{jk} \right),$$

where S_j and S_k are the numbers of species recorded for sites j and k respectively and V_{jk} is the number of species common to both sites. The presence-absence index C varies between 0 (sites identical in species composition) and 1 (no species in common). Next, we incorporated relative abundance of species by calculating proportional dissimilarity (PD), or $(1 - PS)$ where $PS =$ proportional similarity (Whittaker, 1975):

$$PD = 1 - \sum \min\left(p_{i,A};\ p_{i,B}\right),$$

where $p_{i,A}$ is the proportional abundance of species i in site A, and $p_{i,B}$ is its proportional abundance in site B. PD varies between 0, when both samples are identical not only in composition of species but also in their proportional abundances, and 1, when no species are shared between samples. Finally, using the metaMDS function of the "Vegan" statistics package of the R programme (R Development Core Team, 2010) we performed non-metric multidimensional scaling (NMDS) analyses, using first the values for C and then the values for PD as distance measures.

Objective 3. Following the additive partitioning approach of Lande (1996), we partitioned gamma diversity across all 16 sites into the components of within-site (alpha) diversity and between site (beta) diversity. That is, for this analysis:

$$\gamma = \alpha + \beta$$

where the components α and β are expressed as number of species $S_{\text{component}}$ out of the total of $S_{\text{landscape}}$ (γ). We compared observed values of α and β with the distributions of 4999 sets of values for α and β produced by a null model (Crist et al., 2003) that randomized the data base by means of the PARTITION programme (Veech and Crist, 2007). The p value generated by this procedure for a given diversity component represent the proportion of randomly generated values of $S_{\text{component}}$ (that is, α or β, respectively) that are greater than the observed value.

Objective 4. To assess the extent to which land use history, specifically logging history (none, selective, or integral logging), contributed to gamma diversity we partitioned diversity as for *Objective 3* but this time analyzing only the 13 forested sites and a different partitioning model:

$$\gamma = \alpha + \beta_1 + \beta_2$$

where α is the component of γ associated with within-site diversity (but with different values for both α and γ, as the three sites with shrubby grassland did not enter in the analysis), β_1 is the component of among-site diversity and β_2 is the additive component associated with the three classes of logging history. We compared observed values of α, β_1 and β_2 with those generated by a new randomization, now of the data from the 13 forested sites, with 4999 repetitions as before. In addition, we ran a new NMDS analysis (see above, Objective 2), using values of PD for the 13 forested sites alone. Here, we graphed the 95% confidence ellipses of the centroids of each of the three classes of logging history. Using the R programme, we then applied an analysis of similarity (ANOSIM, Clarke, 1993) to evaluate the null hypothesis of no difference between the magnitude of dissimilarity among sites with different forestry histories.

Objective 5. To estimate the minimum number of sites necessary to achieve 100% of gamma diversity we used a macro in Excel developed by H. Arita (Universidad Autónoma de México). The procedure first selects the site richest in species and successively adds the sites contributing the greatest number of new species to the cumulative list until the asymptote of γ is reached.

3. Results

3.1. Alpha and gamma diversity

Across the 16 sites (Table 1) we recorded a total of 37 species of woody plants pertaining to 17 families (Electronic Appendix 1). Families with the greatest number of species were Fabaceae (13 species) and Capparidaceae (five species). Average species richness ($\pm$SE) per site was 21.94 $\pm$ 0.59 species. SGB had the lowest richness of all sites (16 species, 43% of gamma diversity) and FSP the highest (27 species, 73% of gamma) (Electronic Appendix 1).

3.2. Dissimilarity in species composition

Complementarity (*C*) between pairs of sites varied between 0.13 (FU1 vs FSR2 and FU1 vs FIP2) and 0.52 (SGB vs FU3 and SGB vs FSP). Average complementarity across all possible pairs of sites was 0.31. The site with the greatest average complementarity with the remaining 15—in other words, the most unique site based on

pairwise comparisons—was SGB (0.44), followed by SG (0.39) (Electronic Appendix 2).

Proportional dissimilarity (PD) between sites varied between 0.13 (FU1 vs RSL2) and 0.73 (SG vs FIR2) (Electronic Appendix 2). Average PD across all possible pairs of sites was 0.29 and the sites with the greatest average PD with the remaining 15 were, in decreasing order, SG (0.64), SGB (0.38) and SGR (0.37), with all other having average PD of <0.35 (Electronic Appendix 2).

The two NMDS analysis likewise displayed sites SG, SGB and SGR as the most dissimilar to the remainder (Fig. 2a, b). In these analyses, the 13 forested sites clustered together independently of logging histories.

3.3. Additive partitioning of woody plant diversity across all 16 sites

Gamma diversity across all 16 study sites (Table 1) was 37 species, partitioned between alpha or within-site diversity of 21.94 species (59%) and beta or between-site diversity of 15.06 species (41%). The null model analysis showed that it was extremely unlikely that these values arose randomly: the average expected value for the alpha component was 27.20 species (73.5%) and for the beta component, 9.80 species (26.5%). That is, observed alpha diversity was considerably lower ($p = 1$) and observed beta diversity significantly higher ($p = 0$) than any of the values expected if woody plants were to be distributed randomly across the 16 sites.

3.4. Additive partitioning and ordination among the 13 forested sites with different logging histories

The gamma diversity of woody plants across the 13 forested sites, 35 species, likewise partitioned into an alpha diversity component substantially lower, and beta diversity components substantially higher, than those expected by chance (Table 2). The observed absolute value of beta diversity attributable to logging histories, though, was low compared to observed beta diversity among sites (Table 2). That is, logging history contributed far less than expected to differences in species composition among forested sites. The NMDS analysis confirmed this result (Fig. 3). The ellipses of the 95% confidence limits of the centroids for unlogged forest sites, sites with selective logging and sites with integral logging overlapped greatly. Likewise, in the ANOSIM analysis dissimilarity among forested sites with different histories was not substantially different from dissimilarity among sites with similar histories (R statistic = −0.17, $p = 0.915$). Instead, the NMDS results

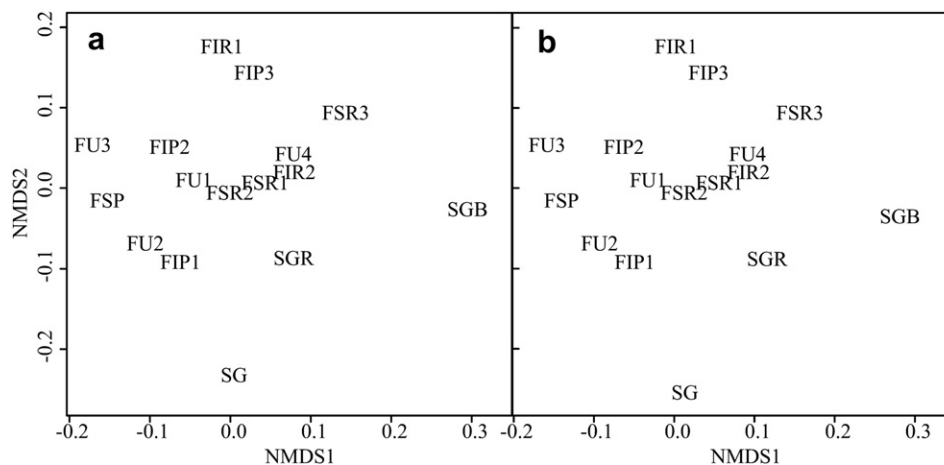

Fig. 2. Two-dimensional NMDS ordination of all 16 sites with respect to composition of woody plant species. Distance measures used are (a) Complementary (*C*) and (b) Proportional Dissimilarity (PD). See Table 1 for definitions of acronyms.

Table 2
Additive partitioning of woody plant diversity in 13 sites with different logging histories. S_{obs} is observed value of the diversity component, S_{exp} is the expected value, % is percent contribution of the observed component to gamma diversity and p is the proportion of randomly generated values greater than the observed value. See text for explanation.

Diversity component	Scale	S_{obs}	S_{exp}	%	p
α	Within sites	22.46	26.10	64.18	1.000
β_1	Among sites	8.21	4.93	23.44	0.000
β_2	Among logging histories	4.33	3.97	12.38	0.002
γ	Entire landscape	35			

(Fig. 3) show that recently logged sites (FSR, FIR in Table 2) tend to cluster apart from sites logged in the past (FSP, FIP in Table 2) and unlogged sites (FU in Table 2).

3.5. Minimum number of sites (out of 16) needed to reach gamma diversity

A minimum of six of the 16 sites is needed to reach the recorded gamma diversity of 37 woody plant species. This set begins with the most diverse site (27 species), a forest selectively logged long ago (FSP). The shrubby grassland (SG) adds four species, an unlogged forest (FU4) three more, and any one of three other sites with different land uses histories adds the final species: another unlogged forest (FU3), a recently selectively logged forest (FSR2), or a forest that recently experienced integral logging (FIR2).

4. Discussion and conclusions

In contrast with semi-arid forests studied by other authors, for example fragmented forests near Xalapa, México (Williams-Linera, 2002) or the Chamela-Cuixmala Biosphere Reserve in Jalisco, México (Balvanera et al., 2002), the Chaco forest has very little topographical relief. In the absence of that source of heterogeneity in vegetation, at first glance the most likely sources of vegetation heterogeneity would seem to be edaphic variation associated with ancient riverbeds vs interfluvial areas, and disturbance history (Table 1). Indeed, results show significant between-site heterogeneity in woody plant species: beta diversity was considerably
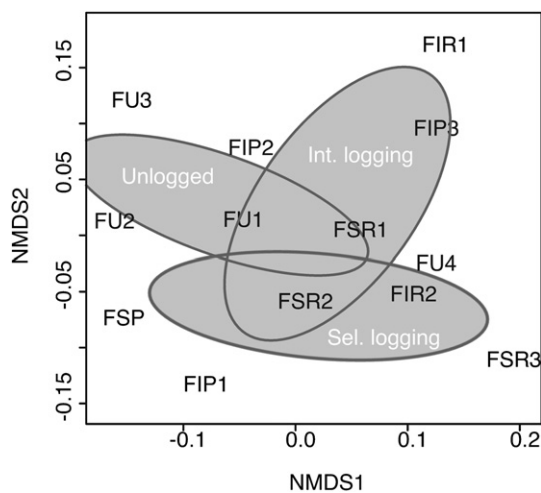

Fig. 3. Two-dimensional NMDS ordination of the 13 forested sites using Proportional Dissimilarity (PD) as the distance measure and with 95% confidence ellipses for the centroids of the clusters of sites according to logging history (unlogged, selective logging and integral logging). See Table 1 for definitions of acronyms.

higher than that projected by the null model of species distributed randomly across sites. Nevertheless, in absolute numbers beta diversity contributed considerably less than alpha diversity to landscape (gamma) diversity.

High intensity disturbances (road construction, fire) contributed substantially to beta diversity (Fig. 2) but logging history, from none to quite intense, contributed little (Table 2, Fig. 3). Indeed, the site most unique in species composition (SG) was not substantially disturbed. Instead, this shrubby grassland was the only site located in the sandy soil of an ancient riverbed. All remaining sites, including the two grassy shrublands associated with earlier disturbances (SGR, SGB) and following SG in terms of uniqueness in species composition, were located on interfluviae. The perturbations in those two grassy shrublands had been severe: SGR had been razed for road construction and then abandoned, and SGB occupied the site of an intense forest fire (Tálamo and Caziani, 2003). Composition of woody vegetation varied relatively little among the 13 sites that were still forested.

Nevertheless, the average value for C (complementarity) across the 16 study sites (0.31) was considerably lower than that found for shrubs and trees in the fragmented forests that Williams-Linera (2002) studied (0.84 and 0.80) and for the trees that Balvanera et al. (2002) studied (0.58). Most likely this contrast is due to the contrast in topographical relief and edaphic variability (Balvanera et al., 2002) between the Mexican sites and the Chaco forest, as mentioned above. Apart from the contrast between ancient riverbeds and interfluvial regions, soil types and even chemical composition in the Chaco varied little across the 16 study sites (Tálamo, 2006; T. Chafatinos, pers. com.).

Additive partitioning of woody plant diversity among its alpha and beta components, following the approach of Lande (1996), enabled us to assess the possible influence of different process on the overall gamma diversity of the woody vegetation of the Chaco landscape, following the reasoning of Gering et al. (2003). Here we did not define beta diversity relative to Whittaker's (1960, 1972) original concept—the magnitude of species turnover along an environmental gradient—because the Semi-arid Chaco is not characterized by any notable large-scale physical gradient. Rather, we used the approach of "resemblance" (Moreno and Rodríguez, 2010) or "turnover" (Tuomisto, 2011), that is, the degree of differentiation in species composition between sites across a landscape with or without notable physical gradients. Although this degree of differentiation was greater than that expected by the null model applied to our entire data set, its magnitude relative to alpha diversity was considerably lower than in other studies applying additive partitioning to woody vegetation, in which beta diversity contributes on average 50% to gamma diversity (Chandy et al., 2006; Dodson and Peterson, 2010).

The result that not only observed beta diversity but also observed alpha diversity differed substantially from the values generated by the null model, coupled with the results that logging history had relatively little influence on species composition (Fig. 3) and contributed relatively little beta diversity (Table 2), tends to support classical models of environmental control over forest diversity (Legendre et al., 2009). That is, the data suggest that site to site variation in species composition appears to be associated more strongly with local environmental conditions than with disturbance history, unless the disturbance is so intense as to alter physiognomy from forest to shrubby grassland (Table 1, Fig. 2). The relatively low importance of logging history—other than time since logging—on composition and diversity of woody vegetation suggests that the Chaco forest studied here is quite resilient with respect to the disturbance caused by traditional land uses (logging and extensive livestock grazing).

Even though species turnover between sites (beta diversity) was lower than that in comparable forests with greater topographical

variation, though, beta diversity was not inconsiderable (Table 2). Conserving only primary forests would be an inadequate strategy for conserving gamma diversity of the Semi-arid Chaco vegetation as a whole. At least for the 16 sites studied, the minimum number necessary to reach total gamma diversity, six, included shrubby grassland in ancient riverbeds and secondary vegetation resulting from different categories of land use and other disturbance (fire). As Castillo-Campos et al. (2008) suggested for tropical semi-deciduous forests in Mexico, we propose that secondary forests contribute significantly to gamma diversity of vegetation in the semi-arid Chaco forest. Therefore, management strategies involving networks of protected areas should include not only "pristine" sites but also sites with varied land use histories. As a cautionary note, though, we add that we have analyzed only one attribute of the Chaco ecosystem (species composition of woody plants) and that other components of this landscape might show very different patterns. Exhaustive field studies should be conducted on other elements of the Chaco biota. Additive partitioning of diversity across a broader range of taxa would help greatly to decide on conservation strategies on those tracts of the Semi-arid Chaco that survive the ongoing process of conversion to soybean production.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found online at http://dx.doi.org/10.1016/j.jaridenv.2012.05.008.

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Electronic Appendix 1. List of woody plant species present in the 16 sites with different land use and disturbance histories studied in Copo Conservation Unit (northern Argentina). See table 1 for site acronyms and descriptions.

Scientific name	FU1	FU2	FU3	FU4	FSR1	FSR2	FSP	FIP1	FIP2	FSR3	FIP3	FIR1	FIR2	SG	SGR	SGB
Acacia aroma (Fabaceae)								X			X			X	X	
Acacia furcatispina (Fabaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X		X	
Acacia praecox (Fabaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Achatocarpus praecox (Achatocarpaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Aloysia scorodonioides (Verbenaceae)														X		
Aloysia sp. (Verbenaceae)														X		X
Aspidosperma quebracho-blanco (Apocynaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Bougainvillea praecox (Nyctaginaceae)	X	X	X	X	X	X	X	X	X		X	X	X	X		
Caesalpinia paraguariensis (Fabaceae)			X				X		X		X					
Capparis atamisquea (Capparaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
Capparis retusa (Capparaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Capparis saliscifolia (Capparaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Capparis speciosa (Capparaceae)	X	X	X	X	X	X	X	X		X	X		X	X	X	X
Capparis tweediana (Capparaceae)	X	X	X	X	X	X	X	X	X		X		X	X	X	X
Castela coccinea (Simaroubaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Celtis pallida (Celtidaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Cercidium praecox (Fabaceae)				X	X	X				X	X	X	X		X	
Condalia sp. (Rhamnaceae)				X												
Geoffroea decorticans (Fabaceae)														X		
Jodina rhombifolia (Santalaceae)	X		X	X	X	X	X		X	X	X		X	X		X
Lycium sp. (Solanaceae)	X	X		X	X	X	X	X	X	X		X	X	X	X	X
Maytenus spinosa (Celastraceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Mimozyganthus carinatus (Fabaceae)	X	X	X			X	X	X	X	X						
Mimosa detinens (Fabaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X
No determined (Fabaceae)			X													
Porliera microphyllia (Zygophyllaceae)		X	X		X								X			
Prosopis kuntzei (Fabaceae)						X										
Prosopis nigra (Fabaceae)				X		X	X	X			X		X			
Prosopis sericantha (Fabaceae)		X	X			X	X									
Prosopis sp. (Fabaceae)				X						X	X	X	X			X
Ruprechtia triflora (Polygonaceae)	X		X				X		X	X		X				
Schinus polygamus (Anacardiaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Schinopsis lorentzii (Anacardiaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Senna aphila (Fabaceae)		X					X								X	
Tabebuia nodosa (Bignoniaceae)							X									
Ximenia americana (Ximeniaceae)	X				X	X	X						X	X		
Ziziphus mistol (Rhamnaceae)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Alpha diversity	22	22	24	23	21	23	27	23	21	22	22	19	23	23	20	16

Electronic Appendix 2. Dissimilarity values among the 16 sites with different land use histories studied in Copo Conservation Unit (northern Argentina). Values for the Proportional Dissimilarity Index (PD) appear in italics below the diagonal and values of the Complementarity Index (C) appear above the diagonal. The two columns at the right present averages of each statistic per site. See table 1 for site acronyms and description.

	FU1	FU2	FU3	FU4	FSR1	FSR2	FSP	FIP1	FIP2	FSR3	FIP3	FIR1	FIR2	SG	SGR	SGB	Average PD	Average C
FU1		0.24	0.23	0.27	0.21	0.13	0.19	0.2	0.13	0.37	0.24	0.29	0.2	0.33	0.32	0.42	**0.24**	**0.25**
FU2	*0.17*		0.23	0.33	0.21	0.27	0.25	0.2	0.28	0.43	0.37	0.36	0.33	0.39	0.25	0.48	**0.27**	**0.31**
FU3	*0.27*	*0.2*		0.38	0.27	0.32	0.24	0.32	0.27	0.36	0.3	0.41	0.38	0.43	0.43	0.52	**0.29**	**0.34**
FU4	*0.14*	*0.22*	*0.25*		0.17	0.23	0.33	0.3	0.24	0.2	0.27	0.25	0.16	0.36	0.28	0.38	**0.25**	**0.28**
FSR1	*0.17*	*0.18*	*0.23*	*0.19*		0.17	0.34	0.31	0.25	0.28	0.28	0.26	0.17	0.31	0.22	0.39	**0.28**	**0.26**
FSR2	*0.13*	*0.24*	*0.29*	*0.16*	*0.23*		0.28	0.23	0.24	0.33	0.27	0.32	0.16	0.36	0.28	0.44	**0.27**	**0.27**
FSP	*0.2*	*0.16*	*0.16*	*0.2*	*0.2*	*0.19*		0.21	0.22	0.37	0.31	0.41	0.33	0.39	0.38	0.52	**0.27**	**0.32**
FIP1	*0.19*	*0.22*	*0.28*	*0.21*	*0.25*	*0.2*	*0.24*		0.24	0.33	0.39	0.38	0.3	0.3	0.28	0.5	**0.3**	**0.3**
FIP2	*0.19*	*0.16*	*0.21*	*0.17*	*0.2*	*0.19*	*0.16*	*0.2*		0.35	0.28	0.26	0.31	0.37	0.36	0.46	**0.26**	**0.28**
FSR3	*0.29*	*0.32*	*0.34*	*0.19*	*0.32*	*0.32*	*0.34*	*0.27*	*0.24*		0.24	0.36	0.27	0.39	0.32	0.42	**0.33**	**0.33**
FIP3	*0.27*	*0.38*	*0.36*	*0.23*	*0.3*	*0.27*	*0.36*	*0.38*	*0.3*	*0.27*		0.22	0.27	0.5	0.38	0.42	**0.34**	**0.32**
FIR1	*0.33*	*0.35*	*0.27*	*0.24*	*0.3*	*0.32*	*0.3*	*0.37*	*0.25*	*0.29*	*0.19*		0.25	0.5	0.3	0.48	**0.33**	**0.34**
FIR2	*0.24*	*0.32*	*0.26*	*0.25*	*0.27*	*0.22*	*0.24*	*0.33*	*0.27*	*0.38*	*0.27*	*0.3*		0.36	0.28	0.38	**0.32**	**0.28**
SG	*0.59*	*0.61*	*0.69*	*0.58*	*0.65*	*0.63*	*0.66*	*0.6*	*0.62*	*0.59*	*0.65*	*0.67*	*0.73*		0.41	0.44	**0.64**	**0.39**
SGR	*0.33*	*0.24*	*0.22*	*0.36*	*0.32*	*0.38*	*0.29*	*0.34*	*0.33*	*0.43*	*0.42*	*0.37*	*0.36*	*0.7*		0.43	**0.37**	**0.33**
SGB	*0.3*	*0.36*	*0.39*	*0.31*	*0.34*	*0.34*	*0.34*	*0.37*	*0.38*	*0.44*	*0.4*	*0.39*	*0.3*	*0.61*	*0.4*		**0.38**	**0.44**