Riparian and adjacent forests differ both in the humid mountainous ecoregion and the semiarid lowland

Edgardo J. I. Pero [ID] · Pablo A. Quiroga

Abstract Few studies have quantified changes in riparian and adjacent forest across landscape units. In this study, the composition and structure of riparian and adjacent forest were compared in a humid and a semiarid ecoregion in northwestern Argentina: the Yungas forest and the Western Chaco. We expected that differences between riparian and adjacent zones could be less marked in humid than in semiarid regions. Ten sites were surveyed with a block design. An Importance Value Index, Rank-Abundance curves, and Analysis of Similarity and multivariate analyzes (NMDS) were performed to evaluate differences between forests. Stream and floodplain widths, lateral, and longitudinal slopes of streamside were analyzed by a principal components analysis (PCA). NMDS and PCA axes were correlated to analyze the relations among physical and biological arrangements. Results revealed that riparian forest may be very different from the adjacent in both ecoregions. Marked differences in geomorphological and physical features of streamsides were found between ecoregions and they were strongly associated with assemblage distribution. In Yungas forest, dominant species were different at all sites, according to the altitudinal stratification of this region. Within Western Chaco the species *Salix humboldtiana* Willd. and *Tessaria integrifolia* Ruiz and Pav., were commonly dominant in riparian sectors. The dominance of these species in both sectors by the widest rivers could indicate that the dimensions of the riparian zone in those sites are greater than those by the smaller streams. Our study reinforced the concept of riparian zones as dynamic ecosystems and we propose considering a landscape perspective in managerial decision making.

Keywords Riparian vegetation · Riparian landscape · Yungas forest · Western Chaco · Subtropical Argentina

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Introduction

Riparian forests are considered an interface between terrestrial and aquatic ecosystems and are among the most vulnerable environments to both climate change and human impact (Capon et al. 2013). The importance of this land–water interface has been emphasized for many reasons: they are extremely dynamic environments in terms of structure, function, and diversity, and they reinforce abiotic–biotic feedbacks (Naiman et al. 1993; Corenblit et al. 2007, 2015; Pokrovsky 2016; Pinay et al. 2018). According to Naiman et al. (2005), riparian forest is defined as the vegetation directly adjacent to rivers and streams. This forest extends laterally from the active channel to the uplands, including active floodplains and the immediately adjacent terraces. Many authors have identified characteristic vegetation within riparian zones, with different compositions, structures, and functions from that of the adjacent vegetation (Gregory et al. 1991; Naiman et al. 1993; Tang and Montgomery 1995; Prach and Straskrabová 1996; Naiman and Décamps 1997). However, few studies over the last decades have quantified changes in riparian and adjacent forest relations across landscape units or ecoregions that have marked climatic or geographic differences (Pinay et al. 1990; Naiman et al. 1992; Cattaneo et al. 1995). In recent years, there has been a renewed interest in studying the relation between riparian vegetation and hydrogeomorphological processes from new conceptual frameworks (e.g., Steiger et al. 2005; Corenblit et al. 2007, 2015), although few studies have addressed this issue from a landscape perspective (Kim and Kupfer 2016; Kujanová et al. 2018).

The characteristics and dimensions of riparian zones could change according to variations in the hydrological and geomorphological features of fluvial ecosystems (Amoros and Bornette 2002; Gurnell et al. 2016). For instance, in riparian floodplains having an irregular topography, plant communities alternate between those in depressions adapted to long flooded periods and those on elevations with species also found in uplands (Salo et al. 1986; Brinson 1990; Mertes et al. 1995; Hupp and Rinaldi 2007). Furthermore, the size and position of the stream within the watershed will influence the width of the riparian zone (Décamps 1996; Junk et al. 1989; Naiman and Décamps 1990; Salo and Cundy 1987). For example,

the riparian zone may be small in the headwater streams that are surrounded by forest, while in mid-sized streams; the riparian zone is larger, composed of particular and adapted vegetation. In contrast, the riparian zones of large rivers are characterized by wider, complex, and dynamic floodplains with extended periods of seasonal flooding and a diverse vegetation (Salo et al. 1986; Malanson 1993; Naiman et al. 2005; Kujanová et al. 2018). In addition, many authors identified that "within arid and semiarid regions riparian zones act as 'ribbons' of organization for the surrounding landscape because of the concentration of water, nourishment, and habitats as compared to the uplands" (Malanson 1993 in Naiman et al. 2005, p. 101). Ecosystem processes in the riparian forest of arid and semiarid regions may be limited by moisture availability (Ellis et al. 2002), and flooding could result in an important natural disturbance that fosters strong responses in the inundated floodplain (Vallet et al. 2005). Conversely, the contrasts between riparian and adjacent upland microclimates and vegetative communities are much less dramatic in mesic regions (Naiman et al. 2005).

Historically, research on major rivers of the planet has focused on the interactions between the rivers and their floodplains in lowland fluvial landscapes (Amoros et al. 1987; Décamps et al. 1988; Junk et al. 1989; Naiman et al. 2005; Sioli 1984; Welcomme 1985). The most widely studied riparian system in northeastern Argentina is the lowland riparian forest of the Eastern Chaco region. In this region, different studies have recognized particular forest formations in the riverside of the fluvial ecosystems, distinct from the adjacent forest and principally composed of the species *Salix humboldtiana* Willd. and *Tessaria integrifolia* Ruiz and Pav. (Neiff 1986; Reboratti and Neiff 1987). On the other hand, in mountain streams of northwestern Argentina, increasing interest is evident, mainly in riparian forest quality and its influence on fluvial ecosystems (Sirombra and Mesa 2010, 2012; Mesa 2014; Fernández et al. 2016; Garcia et al. 2017). Sirombra and Mesa (2010) studied the riparian forest of the Yungas subtropical cloud forest ecoregion and concluded that the composition of riparian vegetation was not different from that of the adjacent forest and that the riparian vegetation of the Yungas forest was not influenced by hydrometric fluvial fluctuations. Nevertheless, further studies on riparian forest are necessary within

areas minimally affected by human activities to improve the knowledge of this ecosystem in such environmental conditions, and to establish reference conditions. Studies on riparian forests within an ecoregional context are important to identify differences among riparian ecosystems related to landscape features. Furthermore, characterizing riparian forests, defining their boundaries, and identifying their changes across the landscape are also of interest for decision-makers to establish riparian buffer areas (Rasmussen et al. 2011; Hunt et al. 2017) or develop and adapt riparian quality indices (Sirombra and Mesa 2012) for different riparian landscapes or ecoregions.

The Yungas forest and Western Chaco dry forest ecoregions are important components of the regional landscape, covering a great surface and including most of the urban centers and agro-industrial activities of northwestern Argentina. For this reason, many regional studies on fluvial ecosystems and water quality have focused on those ecoregions (Domínguez and Fernández 1998; Fernández et al. 2006; Molineri et al. 2009; Pero et al. 2019). The Yungas forest is characterized by mountainous and humid environments, while the Western Chaco forest is characterized by lowland semiarid environments. Accordingly, the main objective of the present study was to analyze the composition and structure of the riparian forest within and between the humid and semiarid ecoregions mentioned. Firstly, we compared the composition and structure of tree, bush, liana, and fern species between the forest zones located next to the river and those located farther away. Secondly, we analyzed the physical variables and the physiography of the streamside to compare the geomorphology among sites. Thirdly, we compared dissimilarities in forest sectors between ecoregions to analyze variations across landscapes. We expected the water availability in riparian zones in Western Chaco to allow the establishment of plant species different from those adapted to the semiarid conditions in the adjacent forest of that ecoregion. Conversely, the high levels of humidity in the Yungas forest would diminish the differences in environmental conditions between riparian and adjacent forests, allowing the establishment of common species between them (Sirombra and Mesa 2010).

Methods

Study area

The study area is located between 26°–28°S and 66°–64°W, including most of Tucumán province and their borders with Santiago del Estero province in Northwestern Argentina (Fig. 1). The area covers a wide zone with heterogeneous landscapes containing diverse ecosystems such as deserts, mountain cloud forests, dry forests, and grasslands (Brown and Pacheco 2006). In this study, we sampled streams located in two different ecoregions: the Yungas subtropical cloud forest and the Western Chaco dry forest.

The Yungas subtropical cloud forest (Yungas forest) is a narrow belt of mountain rainforest that ranges from 400 to > 3000 m a.s.l. (Brown 2000). The Yungas forest is part of a long chain of mountain cloud forests that extends along the east side of the Andes Mountains of South America from Venezuela to northwestern Argentina. The climate is warm and humid, with mean annual temperatures ranging from 14° to 26° C and rainfall from 1000 to 2500 mm (Hueck 1978). The Yungas forest is stratified into three vegetation floors or bands. The high montane forest (1500–3000 m a.s.l.) contains monospecific tree stands that are usually either *Alnus acuminata* or *Podocarpus parlatorei*. Rainfall reaches 1000 mm. The main human activity in this area is scattered cattle and fire to maintain pastures (Brown and Pacheco 2006). The low montane forest (700–1500 m a.s.l.) has the most diverse vegetation, with many evergreen species, and is dominated by *Cinnamomum porphyrium* and *Blepharocalyx salicifolius*. The low montane forest also has the highest precipitation (2000 mm annually) and the least seasonal hydrological regime. The foothill forest (400–700 m a.s.l.) contains deciduous trees and is dominated by *Tipuana tipu* and *Enterolobium contortisiliquum*. The annual rainfall on this floor varies between 1000–1500 mm during the wet season, and the 6-month dry season (50 mm rainfall) extends from June to November (Brown et al. 2001). This area is the one, most widely modified by human activities at present, with the main urban centers and industrial activities (sugar and citrus) located in it (Brown and Pacheco 2006).

The Western Chaco ecoregion is a vast sedimentary fluvial plain formed by the streams or rivers that run
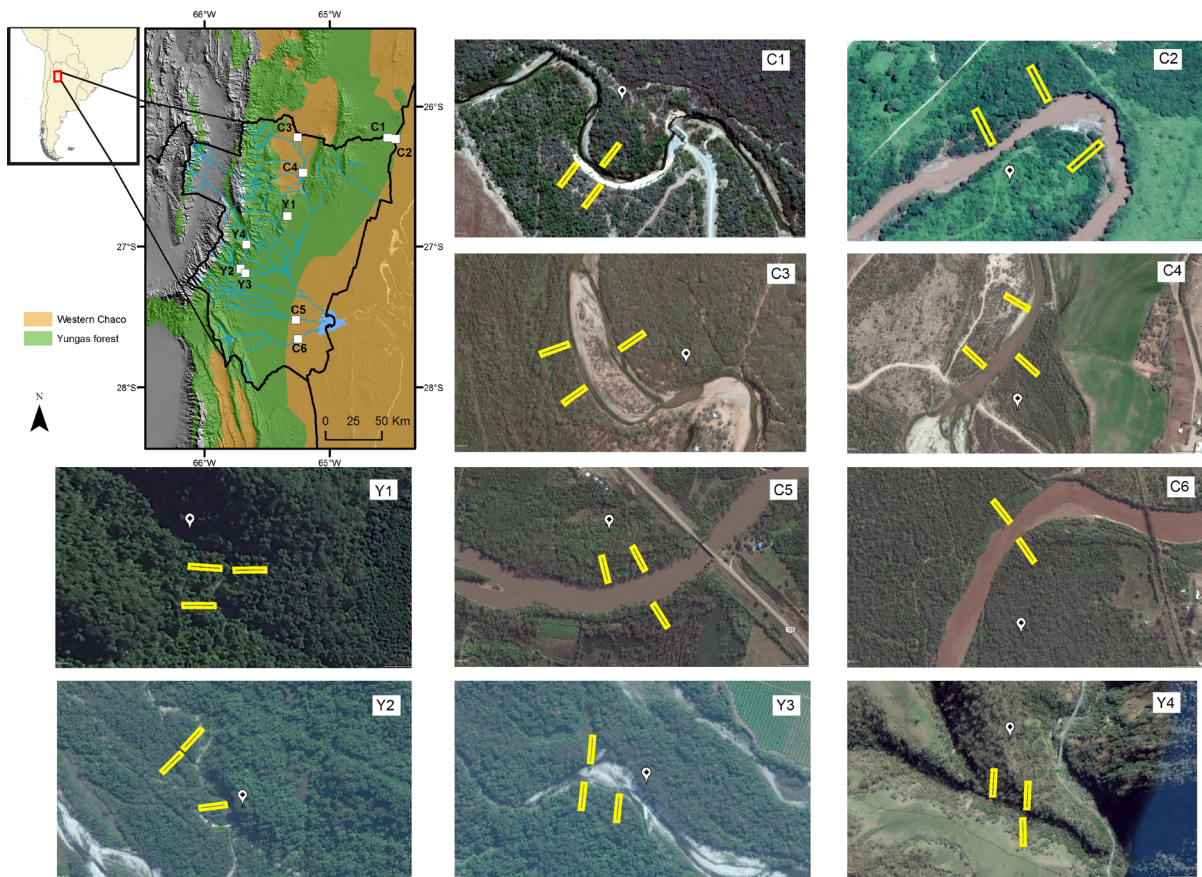
Fig. 1 Study area with location of sampling sites and a detailed image from each sampling site and the location of lateral transects (yellow lines). River water flows to the right or bottom of the image. Codes: *Y* Yungas forest, *C* Western Chaco. (Color figure online)

northwest to southeast and includes parts of northwestern Argentina, southeastern Bolivia, northwestern Paraguay, and southwestern Brazil (Great South American Chaco). The headwaters are located in the mountains, outside the region to the west, and they transport great quantities of sediments into the region. Mean annual temperatures range between 19 °C and 24 °C. Mean annual rainfall varies between 400 and 900 mm, with most precipitation falling in the summer and little falling in the winter (Minneti 1999). The vegetation is composed of dry forests and segregated grasslands. This ecoregion is classified into three sub-ecoregions: Arid Chaco, Semiarid Chaco, and Chaco Serrano (Brown and Pacheco 2006). Only the latter two are represented in the study area. The Chaco Serrano is part of the western border of the ecoregion and is characterized by low mountain topography. It is bordered in some places by the Yungas forest. The Semiarid Chaco occupies the greater portion of the

ecoregion and is a continuous xerophytic and semi-deciduous forest. A wide transition zone occurs between the Western Chaco and the Yungas forest, which includes species common in both ecoregions (Cabrera 1976), although it is currently highly modified by agricultural use (Gasparri 2016).

Sampling design and methods

Ten sites were surveyed, each consisting of a stream or river reach of around 100 m in length (Fig. 1). Four sites were located in the Yungas forest ecoregion (Apeadero Muñoz [High montane forest], Las Conchas [Low montane forest], and El Sonador streams and Pueblo Viejo river [Foothill forest]) and the other six in the Western Chaco ecoregion (Tala and Salí [Chaco Serrano] and Chico, Marapa, and two sites in Urueña river [Semiarid Chaco]) (geographic coordinates in Online Resource 1). All the sites selected were

minimally impacted by human activities. Neverthe-less, the sites located in Western Chaco were closer to human settlements and had some sign of cattle presence in the area, such as dung. A block design was performed to minimize the differences among sites in the analyzes (Feinsinger 2001). Three longi-tudinal transects randomly distributed (left or right riparian margin) and situated in a perpendicular direction from the stream or river channel were surveyed in each sampling site (Fig. 1). Each transect was divided into sampling units (SU) of 5 m in length and 1 m in width, totaling 10 SU per transect. The first four SU (0 to 20 m) were considered a priori as the "riparian forest" sectors closest to the water course and the last four (30 to 50 m) were considered the "adjacent forest" sectors distant from the water course. The middle SU (20 to 30 m) were considered a buffer area between forest sectors and were therefore not included in the analyzes (Feinsinger 2001). The composition and structure of riparian and adjacent forests were surveyed through transects, totaling 120 m^2 surveyed in each site (60 m^2 per forest sector). In each transect, the identity, basal area (calculated using diameter at breast height, DBH) and height of each tree, bush, liana, and fern individual were registered. Only specimens with more than 50 cm in height and 1 cm in DBH were considered. Specimens were identified to species level following the South American catalog for vascular plants (Zuloaga et al. 1994; Zuloaga and Morrone 1996; Zuloaga and Morrone 1999). All species found were listed in a table ("Appendix"). In addition, at each transect, the lateral slope of the river margins was measured using a clinometer, which was aligned between two distant objects (1-m-high sticks) every 10 m to produce a physiographic lateral view of the margins. A longitu-dinal slope was obtained from a digital elevation map (ASTER DEM 30 × 30 m resolution) and calculated using Geographic Information Systems (GIS) soft-ware (QGIS, 2014). The widths of the wet channel and floodplain (the area between the wet channel banks and the base of the enclosing valley walls, Naiman et al. 2005) were measured with metric ruler in each site. Site C6 was not completed and only two transects were surveyed in it due to climatic conditions during the sampling work. Site Y4 had a canyon-constrained reach and it was therefore very difficult to survey the adjacent forest sectors completely. Sampling was carried out during October 2015 and May 2016.

Data analyzes

The Importance Value Index (IVI, Lamprecht 1990) was calculated for each species in each sample site, both for the riparian forest sector and for the adjacent forest sector. The IVI was formulated using three main variables of the species (x_i) in the community: density (d), dominance (D), and frequency (f), IVI $x_i = d\, x_i + D\, x_i + f\, x_i$. First, d was calculated as the number of individuals of the species (n_i) over the area surveyed in each forest sector per site (60 m^2), $d = n_i/60$ m^2. Second, D was calculated as the sum of normal section area (X_i) of all stems at DBH level, $D = \sum_{i=1}^{n} X_i$. Third, the f was calculated as the number of SU in which the species was present (n_i) over the total number of SU for the corresponding forest sector in each site (N), $f = n_i/N$. Data from the total transects in each site were added up to calculate the IVI. A ranking list of IVI value for each species was obtained for both the riparian forest sector and the adjacent forest sector in each site.

We used rank-abundance (RA) curves (dominance–diversity curves) to compare how forest structure (species abundance as basal area) varied across the different sectors and ecoregions (Feinsinger 2001). For the comparison among sites, the species abun-dance matrix had a datum (the sum of abundance from the three transects) for each species (columns) at each forest sector from each ecoregion (rows). For the comparison between ecoregions, we analyzed average abundance from each species by sector. RA curves, in combination with species identity, can provide insight into specific patterns of species diversity, dominance, rarity, and composition (e.g., Andresen 2005; Cultid-Medina and Escobar 2016; Vidaurre et al. 2006). We used these analyzes to complement the IVI and multivariate analyzes and allow more detailed obser-vations of compositional and structural differences among forests.

We used the species abundance matrix to calculate a dissimilarity value by applying Bray–Curtis index (BC, Bray and Curtis 1957) to evaluate and compare the composition and structure among riparian and adjacent forest sectors of the two ecoregions. As defined by Bray and Curtis, the index of dissimilarity is $BC_{ij} = 1 - \frac{2C_{ij}}{S_i + S_j}$, where C_{ij} is the sum of the lesser values of only those species in common between both sites. S_i and S_j are the total number of specimens

counted at both sites. The BC is bounded between 0 and 1, where 0 means that the two sites have the same composition, and 1 means that the two sites do not share any species. We used ANOSIM (Legendre and Legendre 1998) to determine if forest composition based on abundance data differed statistically between sectors regardless of ecoregion (riparian or adjacent) and among sectors within each ecoregion. We also used multivariate analyzes to determine if differences in forest composition among sites were associated with sectors and ecoregions. We used Non-metric Multidimensional Scaling (NMDS) based on dissimilarity values obtained from abundance data to visualize if the positions of sites in species space were concordant with sectors and ecoregions. Average dissimilarity was also compared at ecoregional level to evaluate the degree of difference between forest sectors at this scale using confidence interval (CI) 95%. Non-overlapping CIs were considered to indicate statistically significant differences among treatments (Cumming et al. 2007; MacGregor-Fors and Payton 2013).

Physical variables were analyzed by a Principal Components Analysis (PCA) using the function "dudi.pca" in the ade4 R package (version 1.7–8/ Dray et al. 2017). The lateral slope for each site was calculated by averaging the lateral slopes from both streamsides. In addition, we determined if forest assemblage positions along the NMDS axes were correlated (Pearson correlation coefficients) with environmental PCA axes, and then we accounted for multiple comparisons with a Bonferroni correction (Scheiner and Gurevitch 1993). Bray–Curtis, NMDS, PCA, and Pearson Correlation analyzes were produced via the R platform (version 3.3.0 2012, R Foundation for Statistical Computing, Vienna), and IVI index and RA curves via Microsoft Office Excel 2007.

Results

Importance Value Index

Variations were registered between the IVI ranking of riparian and adjacent sectors in most of the Western Chaco sites (Fig. 2 and Online Resource 1). Within the Yungas forest, variations in IVI ranking between

riparian and adjacent sectors were not evident in all sites (Fig. 3 and Online Resource 1).
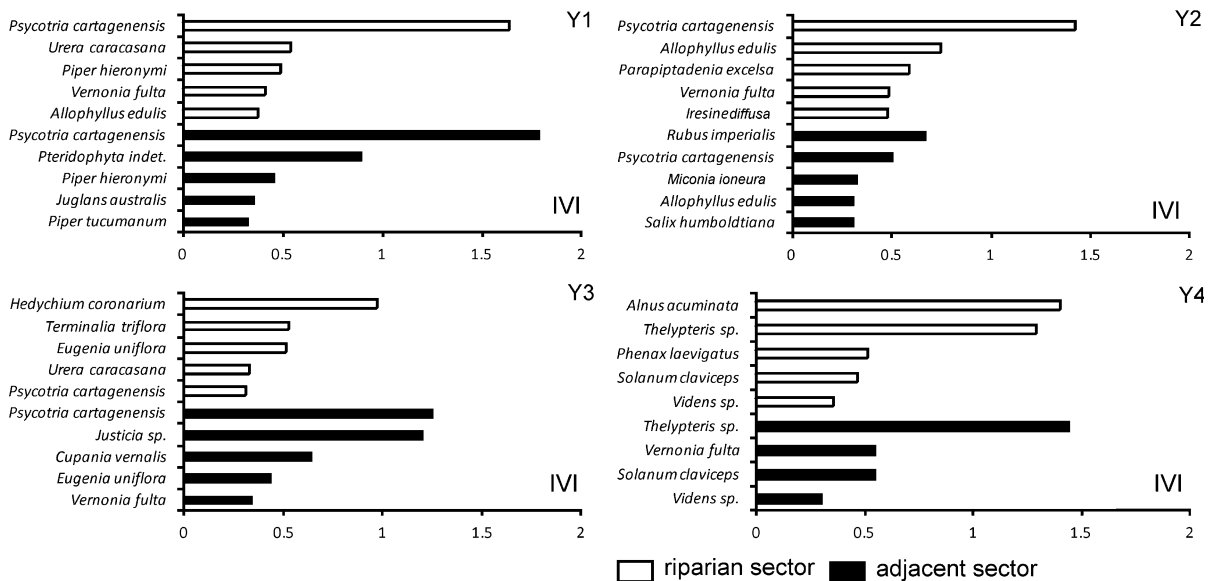
Rank-Abundance curves

Rank-Abundance curves revealed changes in composition and structure between riparian and adjacent forest sectors within (Fig. 4) and between ecoregions (Fig. 5). Within Western Chaco, most of the riparian sectors were dominated mainly by two species, *S. humboldtiana* and *T. integrifolia* (Fig. 4a). These species were also dominant in some adjacent sectors. Different species were dominant in the rest of the adjacent sectors (Fig. 4b). Consequently, these species had the highest average abundance in riparian sectors of Western Chaco (Fig. 5a, b). The slope of the curves (species evenness) was similar between sectors in Western Chaco. In addition, in the Yungas forest, variations in species dominance and composition were also evidenced between riparian and adjacent sectors (Fig. 4c, d), although the dominant species were different at all the sites. Two species were present in all riparian sectors in the Yungas forest, *Urera caracasana* (Jacq.) Gaudich. ex Griseb. and *Vernonia fulta* Griseb. The slope of the curves was less steep (higher species evenness) in adjacent than in riparian sectors in most of the Yungas sites (Fig. 4d). Some species that were more commonly found in Yungas were also found in the riparian forest in Western Chaco: *Heimia montana* (Griseb.) Lillo, *Terminalia triflora* (Griseb.) Lillo, *U. caracasana*, and *V. fulta*. The slope of Western Chaco curves was steeper (lower species evenness) than that of Yungas curves. Variations were noted in the community composition and structure between transects of the same sampling site. Some species commonly found in riparian transects were less abundant or even absent in some transects. On the contrary, other species more typically present in adjacent sectors were dominant in the riparian sectors of those transects. In addition, exotic invasive species were found in riparian sectors, such as *Hedychium coronarium* J. König in the Yungas forest, as well as *Arundo donax* L., *Ricinus communis* L., *Morus* sp. L., and *Tamarix ramosissima* Ledeb. in Western Chaco.

Dissimilarity

ANOSIM results ($p = 0.001$) showed that assemblages were significantly associated with sectors
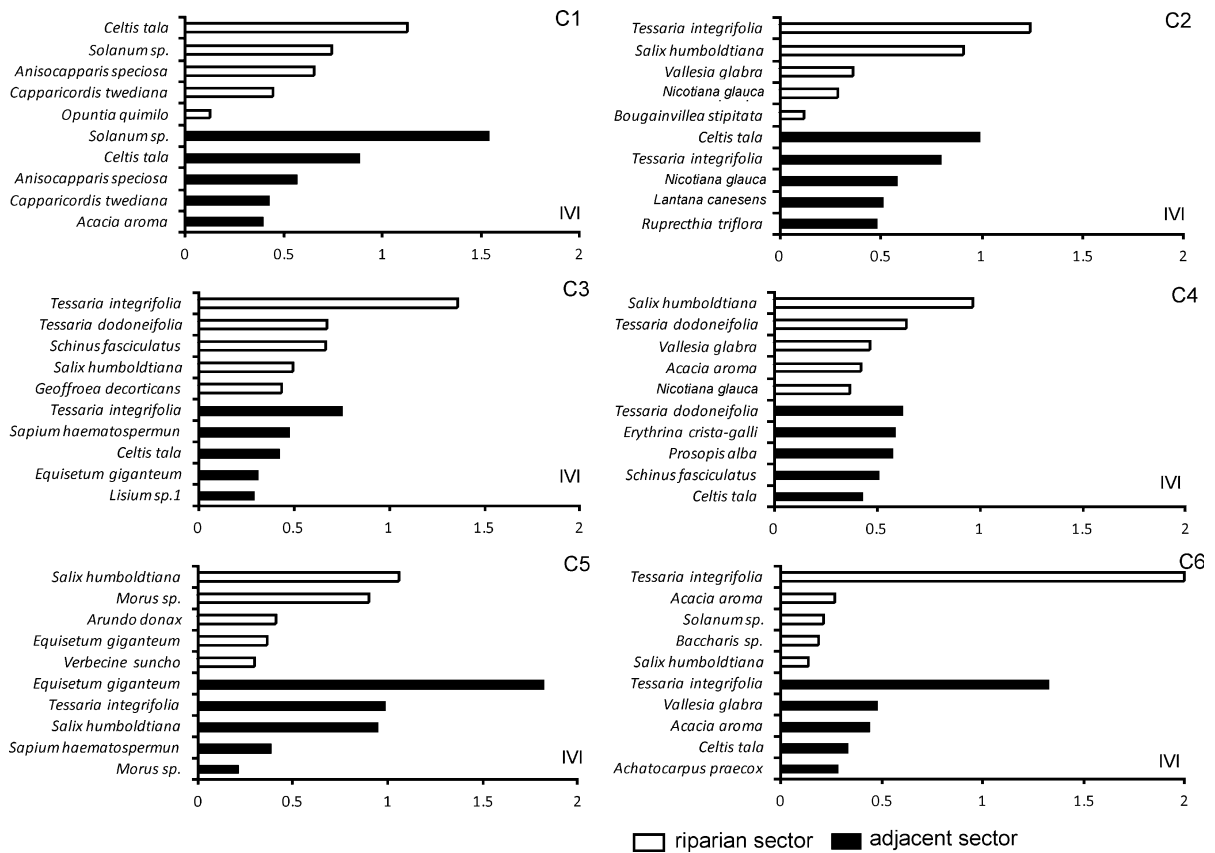
Fig. 2 IVI ranking list with the first five species with the highest values from riparian and adjacent forests of each sampling site within Western Chaco (C). Ordinate axis: IVI value, Abscissa axis: species

Fig. 3 IVI ranking list with the first five species with the highest values from riparian and adjacent forests of each sampling site within Yungas forest (Y). Ordinate axis: IVI value, Abscissa axis: species

Fig. 4 Rank-Abundance curves for riparian and adjacent forest sectors in each sampling site. Western Chaco: A = Riparian sectors and B = Adjacent sectors; Yungas forest: C = Riparian sectors and D = Adjacent sectors. See species code in "Appendix"
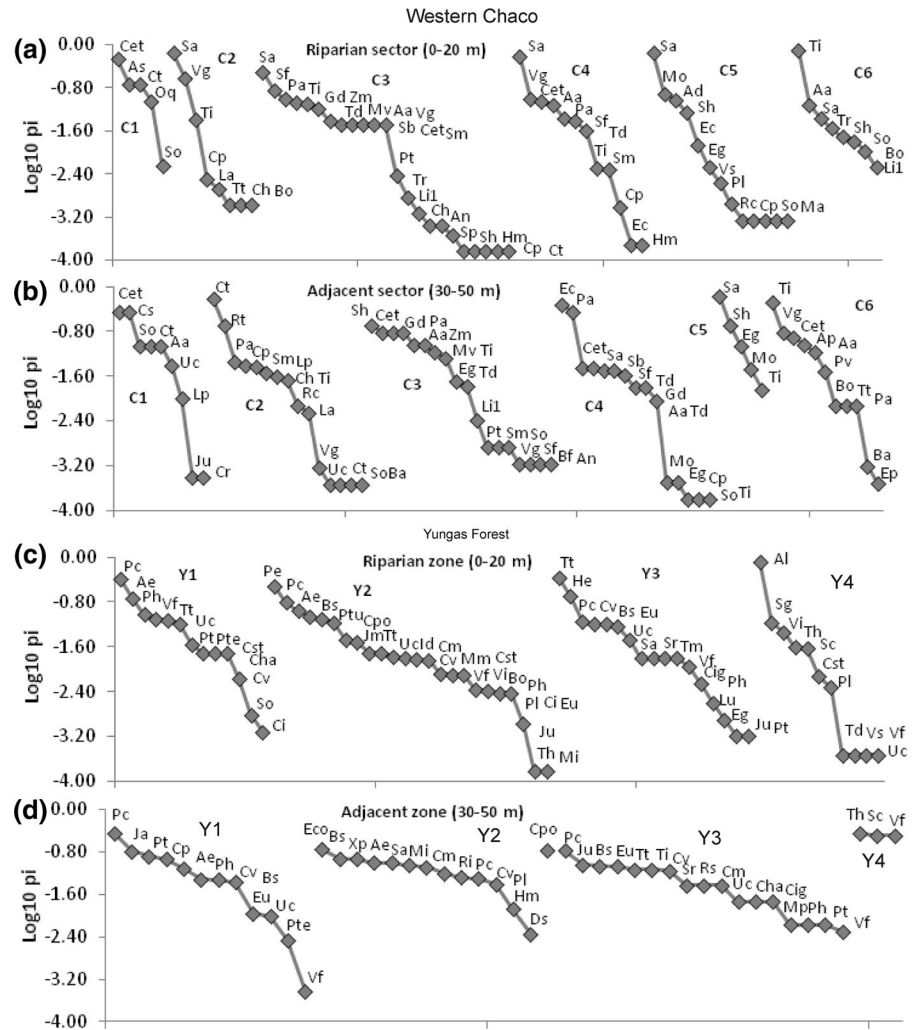

(riparian or adjacent) within each ecoregion ($R = 0.50$), but not with sectors in general ($R = -0.08$). The overall structure of the forest assemblages was concordant with ecoregions. NMDS axis 1 segregated two groups: one composed of the Yungas assemblages and the other composed of those in Western Chaco. Within each group, an association between forest assemblages according to sectors (riparian or adjacent) was evidenced, although discrete groups were not clearly visualized (Fig. 6). Most of the sites showed high dissimilarity values between riparian and adjacent sectors (dissimilarity coefficient > 0.5), while only two sites had dissimilarity values lower than 0.5 (Table 1). In addition, at the ecoregional level, the difference between the average sector dissimilarities was slightly significant.

Physical variables and streamside physiography

Wet channel and floodplain widths were broader in Western Chaco than in Yungas forest, whereas lateral and longitudinal slopes were higher in Yungas forest than in Western Chaco (Table 2). PCA ordination of the sites using the physical variables (wet channel width, floodplain width, lateral, and longitudinal slopes) showed that sites clearly grouped following an ecoregional scheme (Fig. 7). PCA revealed that two main factors (PC-1 and PC-2) accounted for most ($\sim 93\%$) of the variation in the dataset. PC-1 ($\sim 76\%$ of total variation) was negatively correlated with floodplain and wet channel widths and positively with lateral and longitudinal slopes. Western Chaco sites were located on the negative side of axis 1 (higher wet

Fig. 5 Rank-Abundance curves with average abundance for riparian and adjacent forests in each ecoregion. Western Chaco: A = Riparian sectors and B = Adjacent sectors; Yungas forest: C = Riparian sectors and D = Adjacent sectors. See species code in "Appendix"
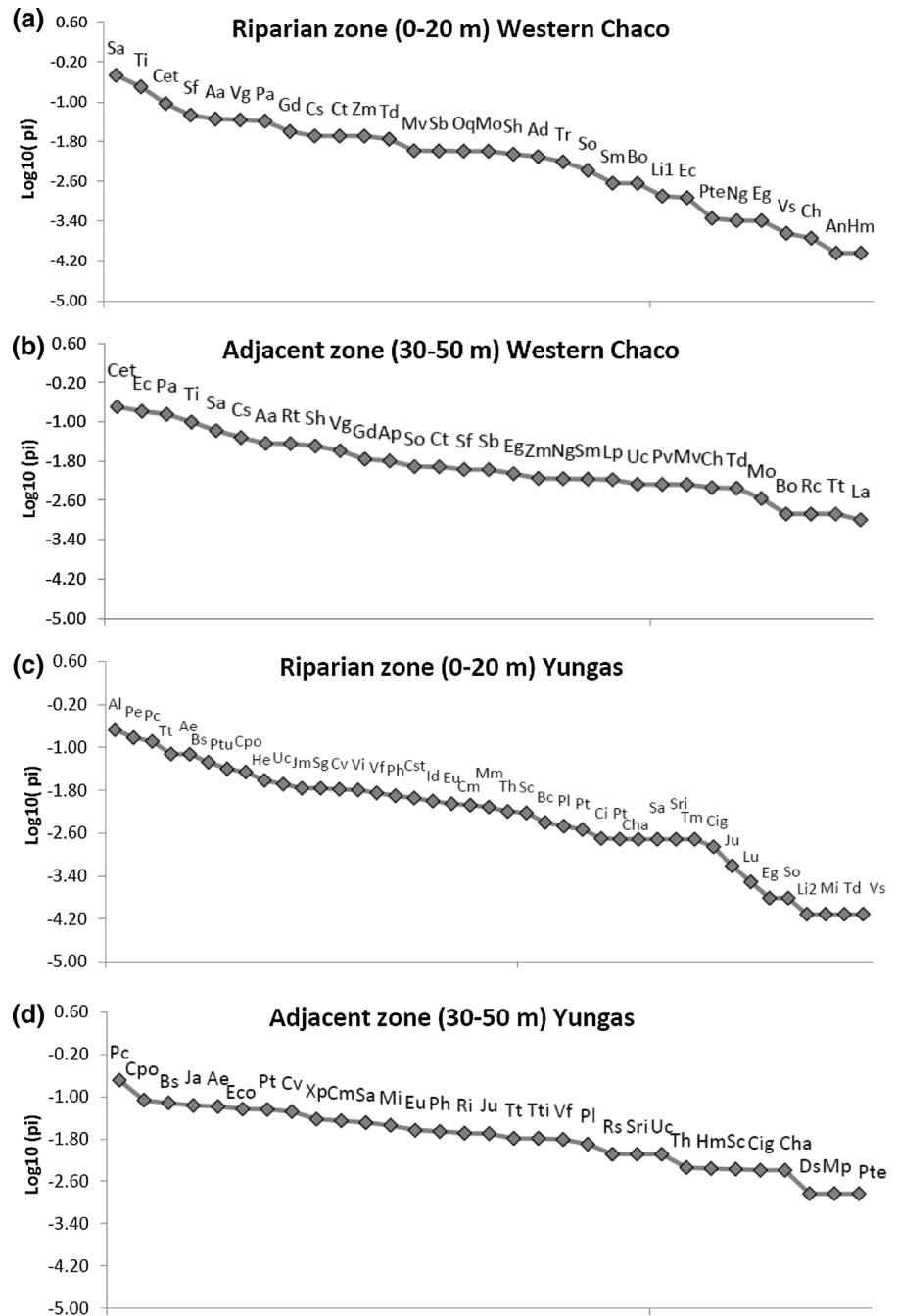
channel and floodplain widths and lower lateral and longitudinal slopes), while Yungas forest sites were situated on the positive side of the axis 1 (higher lateral and longitudinal slopes and lower wet channel and floodplain widths). These characteristics were observed and they coincided with the physiographic draft from each site (Fig. 8).

Correlations

Correlations among axes (Table 3) showed that NMDS-1 was significant and most strongly correlated with PC-1 (−) after they were adjusted for multiple comparisons (adjusted significance: $p < 0.001$). Thus, the segregation between the Yungas forest and
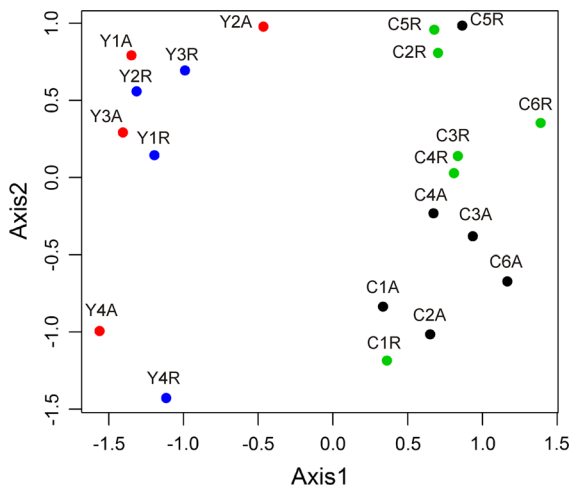
Fig. 6 Non-metric multidimensional scaling (NMDS) analyzes of dissimilarity of forest sectors of the two ecoregions: Yungas = Y, Western Chaco = C. Stress = 15.9

Western Chaco assemblages was most strongly related to PC-1.

Discussion

Our results revealed that the riparian forest may be very different from the adjacent, mainly in species dominance. Our hypothesis that differences between riparian and adjacent zones would be less marked in humid than semiarid regions was not supported by the obtained results. However, marked differences in geomorphological and physical streamside features were found between ecoregions, and they were strongly associated with assemblage distribution. In the Yungas forest, dominant species were different at all sites, according to the altitudinal stratification of

Table 1 Dissimilarity between forest sectors (riparian and adjacent) in each sampling site and average dissimilarity between forest sectors in each ecoregion (Yungas and Western Chaco) with their confidence interval (CI) 95%

	Dissimilarity (Bray–Curtis) between forest sectors
Y1	0.5216
Y2	0.8200
Y3	0.6001
Y4	0.9681
Average for Yungas	0.7275 (± 0.0069)
C1	0.3742
C2	0.9794
C	0.7222
C	0.8206
C5	0.2959
C6	0.5140
Average for Western Chaco	0.6664(± 0.0080)

Table 2 Physical variables of the sampling sites

	Wet channel width (m)	Floodplain width (m)	Lateral slope (°)	Longitudinal slope (°)
Y1	0.23	1.74	22.5	17.3
Y2	5.00	9.00	21.5	7.60
Y3	20.1	10.0	14.7	2.14
Y4	2.05	3.15	25.2	10.2
C1	2.90	10.0	4.85	0.82
C2	4.80	6.00	4.80	0.86
C3	10.7	17.0	2.90	0.75
C4	21.4	13.6	2.00	0.79
C5	79.0	19.0	1.40	0.61
C6	29.9	14.1	0.90	0.32

Fig. 7 Principal Components Analysis (PCA) ordination of physical variables measured from the ten sampling sites. *D* = 1 corresponds to the grid size. PCA biplot of physical variables and sampling sites, with the barplot of eigenvalues added at the upper left corner
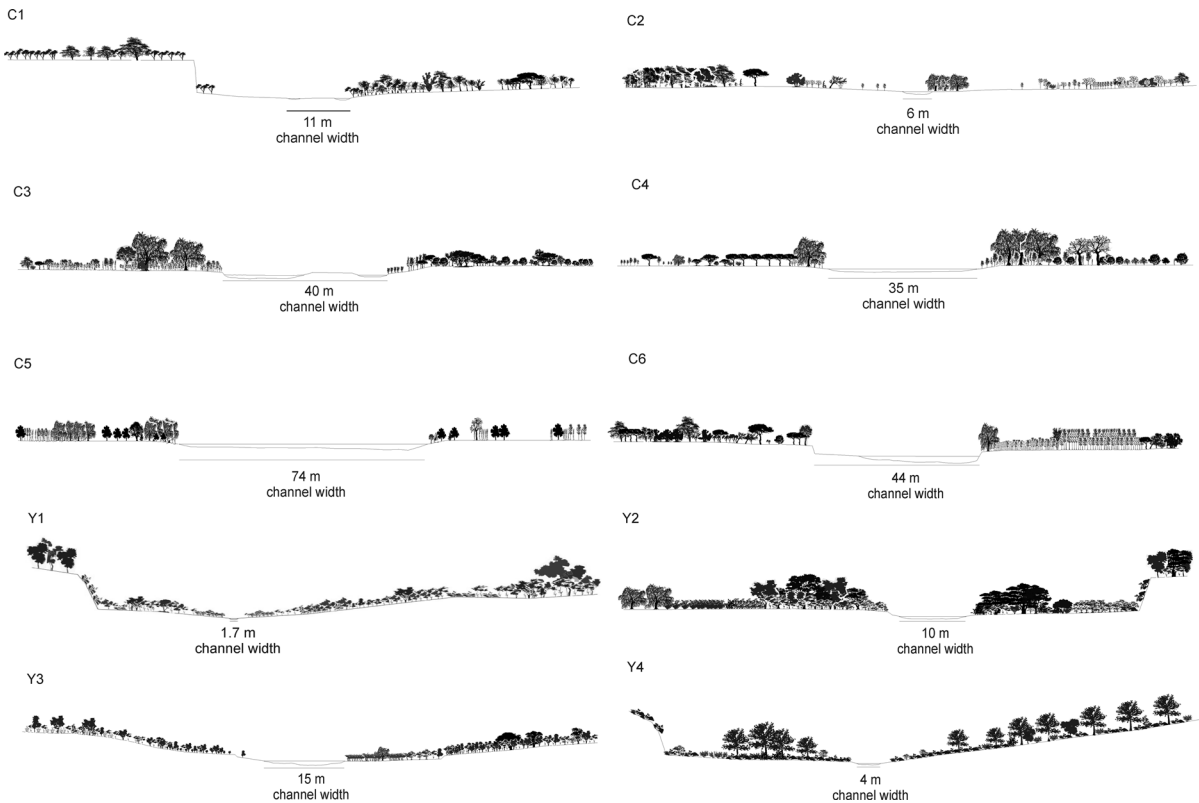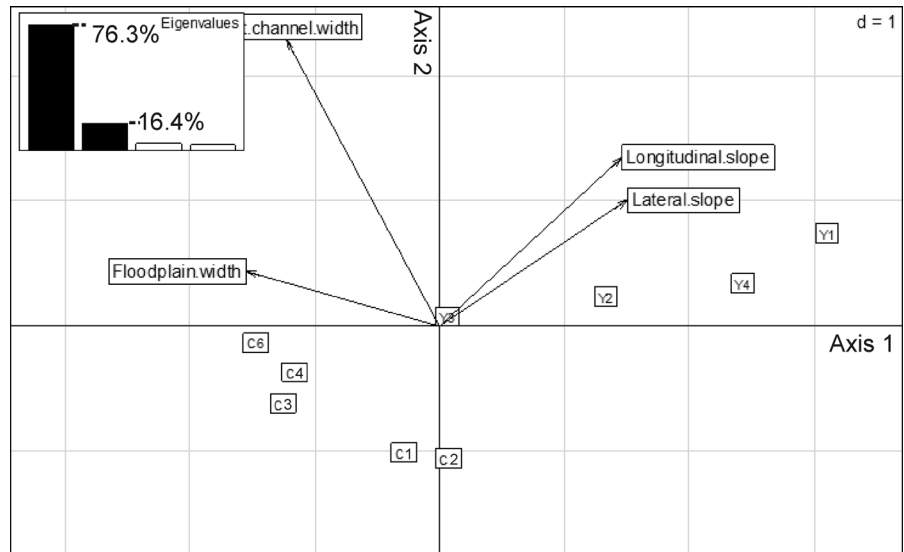
Fig. 8 Lateral view of river channel and sideways including 50 m to the left and right margin. C: Western Chaco sites and Y: Yungas forest sites

this region. On the other hand, Western Chaco showed lower slopes and the species *S. humboldtiana* and *T. integrifolia* were commonly dominant in riparian sectors, and could be considered a gallery forming corridors across the dry Chaco forest, which is similar to the gallery forest in savannas and grassland

Table 3 Pearson correlations between NMDS axis values and PCA axis values

	PC-Axis1	PC-Axis2
NMDS-Axis1	− 0.79*	− 0.32[NS]
NMDS-Axis2	− 0.11[NS]	0.44[NS]

NS not significant

*$p < 0.001$

environments (Malanson 1993) or the Eastern Chaco floodplains (Neiff 1986; Reboratti and Neiff 1987). Furthermore, the dominance of these species in both riparian and adjacent sectors by the widest rivers could indicate that the dimensions of the riparian zone in those sites are greater than 50 m.

Our findings help us to understand how the relation between riparian and adjacent vegetation could vary when rivers flow through different ecoregional land-scapes. Our result contrasted with a previous study of Sirombra and Mesa (2010), where only presence–absence data were used. These authors concluded that riparian vegetation in Yungas was not different from that in the adjacent forest because all species from the riparian zone had already been cited as typical of the ecoregion. Beyond this fact, the use of abundance data in our study allowed us to detect structural differences between riparian and adjacent sectors in Yungas. These results indicated that riparian vegetation could be influenced by environmental conditions near streams or rivers both in humid and semiarid regions. Therefore, riparian communities could be expected to share a set of functional traits among ecoregions regardless of their species identities. Consequently, according to Naiman et al. (2005) several studies suggested that closer to the wet channel it is common to find plants with a set of characteristics related with early successional stages, such as adaptation to low nutrient availability, and tolerance to high light levels, whereas at higher elevations, distant to the channel, vegetation communities are commonly composed of woody vascular plants with traits such as, long-lived, tolerance to shade, and usually low tolerance to long flooded periods. It would be interesting to evaluate if the differences between riparian and adjacent forests found could be related to functional aspects of the vegetation associated with the frequent occurrence of

natural disturbance within riparian zones such as floods and sediment removal.

Our results reinforce the idea that geomorphology and hydrology are important factors influencing riparian characteristics. For example, the variation in species dominance and composition within Yungas is probably related to the typical altitudinal stratification of its vegetation. Altitudinal gradients also influence the geomorphic structure of riparian zones, as described by Ward et al. (2002), who observed that streams in high montane forest had typically con-strained reaches, whereas streams and rivers in lowland forest had increasingly large floodplain reaches. These geomorphological and hydrological patterns could explain the presence and abundance of some hydrophilic plants in both riparian and some adjacent sectors of the Yungas foothill floor and Chaco Serrano. The presence of these species in adjacent sectors could indicate the location of old floodplains or water channels and the development of oxbows, which are water bodies typical of the braided to meandering transition zone of a river corridor, as proposed by Ward et al. (2002). Thus, riparian ecosystems in foothill forest and Chaco Serrano could be considered a transitional area, similar to that proposed by Naiman et al. (2005), who described mid-order streams as transitional areas between small streams and large rivers. In addition, rivers in Western Chaco had increasingly larger floodplain reaches, and the species that dominated their riparian forests were adapted to flooded soil conditions and survive with a long-lasting inundation phase in similar ecosystems, such as the Eastern Chaco (Casco et al. 2010). Lateral hydrologic exchange is concentrated near the river in constrained reaches, whereas it extends laterally in larger flood-plains (Naiman et al. 2005). Hence, it would be important to evaluate the flooded soil/dry soil time ratio across the different ecoregions to check if this variable is related to the observed vegetation distribution.

The local site heterogeneity noted in physical and biological features between streamsides could influ-ence the composition of the riparian biota. Some streamsides were located in a floodplain area and others in a more elevated surface or terrace. These types of streamsides could be very different in soil composition and flood conditions. Accordingly, other studies observed that variations in soil composition and flood conditions within riparian zones influenced

species establishment and survival (Casco et al. 2010; Corenblit et al. 2015). Several authors have recognized the importance of geomorphic processes in shaping distributional patterns of vegetation and soil (e.g., Rot et al. 2000; Corenblit et al. 2007) and included related variables in the classification of riparian vegetation (van Coller et al. 1997). Furthermore, many authors suggested that this habitat heterogeneity within riparian forest probably influences the high biodiversity and production noted in these environments (Naiman and Décamps 1997; McClain et al. 2003). A number of studies in the Brazilian Cerrado forest, which has floristic and environmental similarities with Western Chaco, revealed a greater diversity of tree and shrub species in the riparian forest than in the adjacent Cerrado itself (Ramos 1995; Pereira et al. 1993). Thus similar diversity patterns could be found between the riparian and inner forest of the Western Chaco if a larger distance to the river is considered. On the other hand, Oliveira and Marquis (2002) proposed that this diversity pattern observed in the Brazilian Cerrado could be associated with the diverse floristic elements from which the communities of the riparian forest are derived. Consequently, we could hypothesize that the riparian forest allows some species, more commonly found in Yungas, to extend their distribution through the semiarid conditions of Western Chaco. These results also support the concept of riparian zones as biological corridors that permit the movement of species between habitats (Naiman et al. 1993; Paolino et al. 2018).

Other observations are considered important in terms of ecosystem management, such as the record of exotic invasive species in some riparian sectors, mostly in Western Chaco, some of them recently recorded for the first time in this ecoregion (Pero 2017). These findings must raise an alert, and further studies should be done on the ecological behavior of these alien species within riparian ecosystems. In addition, the knowledge obtained here about the composition of species inhabiting minimally impacted riparian forests could be useful in developing restoration programs for modified riparian ecosystems, and mainly in selecting which species to reintroduce.

The variations observed between riparian and adjacent sectors reinforced the concept of riparian zones as dynamic and diverse ecosystems (Naiman et al. 2005; Pokrovsky 2016). Furthermore, the changes across ecoregions supported that landscape features could influence the composition and structure of riparian forests. The dimensions and boundaries considered as defining these ecosystems could vary between ecoregions. These differences must be taken into account for the development and implementation of protection laws or riparian buffers. Finally, we propose that riparian forests must be studied also from a landscape perspective to improve their study, conservation, and management.

Appendix: Species list

Species	Family	Ecoregion	Abbreviation
Abutilon niveum Griseb.	Malvaceae	C	An
Acacia aroma Gillies ex Hook. and Arn	Fabaceae	C	Aa
Achatocarpus praecox Griseb.	Achatocarpaceae	C	Ap
Allophylus edulis (A. St.-Hil., A. Juss. and Cambess.) Hieron. ex Niederl.	Sapindaceae	Y	Ae
Alnus acuminata Kunth	Betulaceae	Y	Al
Anisocapparis speciosa (Griseb.) X. Cornejo and H.H. Iltis	Capparaceae	C	As
Arundo donax L.	Poaceae	C	Ad
Baccharis sp.	Asteraceae	C	Ba
Bidens sp.	Asteraceae	Y	Bi
Blepharocalyx salicifolius (Kunth) O. Berg	Myrtaceae	Y	Bs
Bougainvillea stipitata Griseb.	Nyctaginaceae	C	Bo
Bulnesia foliosa Griseb.	Zygophylaceae	C	Bf
Caesalpinia paraguariensis (D. Parodi) Burkart	Fabaceae	C	Ce
Capparicordis tweediana (Eichler) H.H. Iltis and X. Cornejo	Capparaceae	C	Ct
Celtis iguanaea (Jacq.) Sarg.	Celtidaceae	Y	Cg
Celtis tala Gillies ex Planch. = *Celtis ehrenbergiana* (Klotzsch) Liebm. var. ehrenbergiana	Celtidaceae	C	Cet
Cestrum strigilatum Ruiz and Pav.	Solanaceae	Y	Cst
Chamissoa altissima (Jacq.) Kunth	Amaranthaceae	Y	Cha
Chenopodium sp.	Chenopodiaceae	C	Ch
Chrysophyllum marginatum (Hook. and Arn.) Radlk.	Sapotaceae	Y	Cm
Cinnamomun porphyrium (Griseb.) Kosterm. = *Ocotea porphyria* (Griseb.) van der Werff	Lauraceae	Y	Cpo
Citrus aurantium L.	Rutaceae	Y	Ci
Croton sp.	Euphorbiaceae	C	Cr
Cupania vernalis Cambess.	Sapindaceae	Y	Cv
Duranta serratifolia (Griseb.) Kuntze	Verbenaceae		Ds
Enterolobium contortisiliquum (Vell.) Morong	Fabaceae	Y	Eco
Ephedra sp.	Ephedraceae	C	Ep
Equisetum giganteum L.	Equisetaceae	C, Y	Eg
Erythrina crista-galli L.	Fabaceae	C	Ec
Eugenia uniflora L.	Myrtaceae	Y	Eu
Geoffroea decorticans (Gillies ex Hook. and Arn.) Burkart	Fabaceae	C	Gd
Hedychium coronarium J. König	Zingiberaceae	Y	He
Heimia montana (Griseb.) Lillo	Lythraceae	C, Y	Hm
Iresine diffusa Humb. and Bonpl. ex Willd.	Asteraceae	Y	Id
Jacaranda mimosifolia D. Don	Bignoniaceae	Y	Jm
Juglans australis Griseb.	Juglandaceae	Y	Ja
Justicia sp.	Acanthaceae	C, Y	Ju
Lantana canescens Kunth	Verbenaceae	C	La
Lippia sp.	Verbenaceae	C	Li
Ludwigia sp.	Onagraceae	Y	Lu
Lycium sp.1	Solanaceae	C	Ls
Lycium sp.2	Solanaceae	C	LsII
Malva sp.	Malvaceae	C	Ma

continued

Species	Family	Ecoregion	Abbreviation
Maytenus vitis-idaea Griseb.	Celastraceae	C	Mv
Melia azedarach L.	Meliaceae	C	Me
Miconia ioneura Griseb.	Melastomataceae	Y	Mi
Morus sp. L.	Moraceae	C	Mo
Myrcianthes mato (Griseb.) McVaugh	Myrtaceae	Y	Mm
Myrcianthes pungens (O. Berg) D. Legrand	Myrtaceae	Y	Mp
Nicotiana glauca Graham	Solanaceae	C	Ng
Opuntia quimilo K. Schum.	Cactaceae	C	Oq
Parapiptadenia excelsa (Griseb.) Burkart	Fabaceae	Y	Pe
Phenax laevigatus Wedd.	Urticaceae	Y	Pl
Piper hieronymi C. DC. var. hieronymi	Piperaceae	Y	Ph
Piper tucumanum C. DC.	Piperaceae	Y	Pt
Prosopis alba Griseb.	Fabaceae	C	Pa
Prosopis ruscifolia Griseb.	Fabaceae	C	Pv
Prunus tucumanensis Lillo	Rosaceae	Y	Ptu
Psycotria carthagenensis Jacq.	Rubiaceae	Y	Pc
Pteridophyta indet.	–	C	Pte
Randia micracantha (Lillo) Bacigalupo	Rubiaceae	Y	Rs
Ricinus communis L.	Euphorbiaceae	C	Rc
Rubus imperialis Cham. and Schltdl.	Rosaceae	Y	Ri
Ruprechtia apetala Wedd.	Polygonaceae	C	Rt
Salix humboldtiana Willd.	Salicaceae	C	Sa
Sapium haematospermum Müll. Arg.	Euphorbiaceae	C	Sh
Schinus bumelioides I.M. Johnst.	Anacardiaceae	C	Sb
Schinus fasciculatus (Griseb.) I.M. Johnst.	Anacardiaceae	C	Sf
Schinus gracilipes I.M. Johnst.	Anacardiaceae	Y	Sg
Senna morongii (Britton) H.S. Irwin and Barneby	Fabaceae	C	Se
Serjania marginata Casar.	Sapindaceae	C	Sm
Sida rhombifolia L.	Asteraceae	C	Sr
Solanum sp.	Solanaceae	C, Y	So
Solanum palinacanthum Dunal = *S. claviceps*	Solanaceae	Y	Sc
Solanum hieronymi Kuntze	Solanaceae	C	Sp
Solanum riparium Pers.	Solanaceae	Y	Sri
Tamarix ramosissima Ledeb.	Tamaricaceae	C	Tr
Terminalia triflora (Griseb.) Lillo	Combretaceae	C, Y	Tt
Tessaria dodoneifolia (Hook. and Arn.) Cabrera	Asteraceae	C	Td
Tessaria integrifolia Ruiz and Pav.	Asteraceae	C, Y	Ti
Thelypteris sp.	Thelypteridaceae	Y	Th
Tipuana tipu (Benth.) Kuntze	Fabaceae	Y	Tti
Trema micranta (L.) Blume	Urticaceae	Y	Tm
Urera baccifera (L.) Gaudich.	Urticaceae	Y	Ub
Urera caracasana (Jacq.) Gaudich. ex Griseb.	Urticaceae	C, Y	Uc
Vallesia glabra (Cav.) Link	Apocynaceae	C	Vg
Verbesina suncho (Griseb.) S.F. Blake	Asteraceae	C, Y	Vs
Vernonia fulta Griseb. = *Quechualia fulta* (Griseb.) H. Rob.	Asteraceae	C, Y	Vf

continued

Species	Family	Ecoregion	Abbreviation
Xylosma pubescens Griseb.	Salicaceae	Y	Xp
Ziziphus mistol Griseb. = *Sarcomphalus mistol* (Griseb.) Hauenschild	Ramnaceae	C	Zm

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