ECOLOGY, BEHAVIOR AND BIONOMICS

Orb-Weaving Spider Diversity in the Iberá Marshlands, Argentina

Gonzalo D Rubio[1], Claudia E Moreno[2]

[1]CONICET, Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Univ Nacional de Córdoba, Av Vélez Sarsfield 299, X5000JJC Cba, Argentina; grubio@conicet.gov.ar
[2] Centro de Investigaciones Biológicas, Univ Autónoma del Estado de Hidalgo, Apartado Postal 69 plaza Juárez, 42001 Pachuca, Hgo., Mexico; cmoreno@uaeh.edu.mx

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ABSTRACT - The Iberá Marshlands RAMSAR reserve, in the northeast of Argentina, is one of the largest and most important wetlands of America. In this study we assess orb-weaving spider (Araneae: Orbiculariae) diversity in this reserve, analyzing different facets of local diversity (species richness, diversity, evenness and taxonomic distinctness), and the contribution of species differentiation (beta diversity) among localities and habitat types to the composition of regional diversity. We found 1657 individuals of 59 orb-weaving spider species/morphospecies. Local diversity differs among the three sampled localities. At the habitat level, the different facets of biodiversity followed a clear pattern, where woodlands have higher species richness, diversity, evenness and taxonomic distinctness than savannas. Savanna sites shared a common spider species composition, while woodland communities have high values of complementarity. Thus, beta diversity has a very high contribution to the regional diversity of the orb-weaving spiders in the Iberá Marshlands. We suggest that conservation management in the reserve should be directed towards promoting natural spatial heterogeneity, giving special protection to habitat mosaics in different localities.

KEY WORDS: Spider inventory, species richness, ecological diversity, taxonomic distinctness, beta diversity

The Iberá system comprises a macro functional unit of terrestrial, aquatic and interface environments with a surface of 12300 km^2. It is located in the northeast of Argentina and is considered one of the largest and most important marshlands of America (Neiff & Poi de Neiff 2006). Due to its geographical location, inaccessibility and low human population density, this ecosystem has remained relatively unaltered compared with other Neotropical marshlands (Neiff 2004). The Iberá Reserve was designated a RAMSAR site in January 2002 (Giraudo 2003). This reserve is one of the few protected areas without anthropic modifications, and thus it represents a valuable scenario for studying the structure, distribution, organization and function of biological communities in native environments.

One of the most diverse groups within the Order Araneae is Orbiculariae, which is represented by the families Araneidae, Tetragnathidae, Theridiosomatidae, Anapidae, Nephilidae, Symphytognathidae, Mysmenidae, Uloboridae, and Deinopidae. The common characteristic of all them is that they build orbicular webs in strict sense (Coddington 1986). Orb-weaving spiders are strongly influenced by habitat type (Uetz 1991, Hurd & Fagan 1992). Their abundance and species composition are affected by the structural complexity of vegetation, giving their site preferences for building their webs (Hatley & MacMahon 1980, New 1999, Whitmore *et al* 2002, Tews *et al* 2004, Tsai *et al* 2006, Jiménez-Valverde & Lobo 2007). Also, orb-weaving spiders are easily located due to the conspicuousness of their webs and their high abundance in ecosystems (Blanco-Vargas *et al* 2003). These features lead to consider this group as an appropriate model for biodiversity studies (Coddington & Levi 1991, Blanco-Vargas *et al* 2003).

Spider diversity in subtropical forests of the Neotropical region is not well known, especially in Argentina where systematic fieldwork has not been carried out until recently. Only few aspects of species composition, diversity and distribution patterns are known so far (Corronca & Abdala 1994, Avalos *et al* 2006, 2007, Rubio *et al* 2008). Considering the framework of the Convention of Biological Diversity signed by the Argentine government (CBD 1992), species inventories and comparative studies of spider assemblages in areas of northern Argentina are needed. An accurate species inventory with quick, inexpensive and reliable methods is a basic and essential step for effectively managing and monitoring biological communities (May 1988, Coddington *et al* 1991, Colwell & Coddington 1994, Boulinier *et al* 1998, Shen *et al* 2003). Furthermore, the assessment of species diversity should ideally incorporate a set of measures in order to capture different facets of biodiversity.

Besides species richness, the analysis of differences in species composition (beta diversity) provides an overview of the degree of resemblance between communities and its importance to the composition of regional richness (gamma diversity). In this sense, distinctness in species composition over sites of a region can be assessed using a measure of complementarity (Colwell & Coddington 1994) in order to capture the idea that complementary communities form parts of a whole. Also, from an ecological point of view, species diversity incorporates information on the community structure in terms of species abundances (number of individuals) assuming that a community with a more even distribution of abundances among the species is more diverse than a community that is clearly dominated by a few species and has many rare.

From another point of view, the degree of species phylogenetic relatedness is an additional feature that can be used in the analysis of species diversity and has great potential in setting conservation priorities and for environmental monitoring (Vane-Wright *et al* 1991, Williams *et al* 1991, Warwick & Clarke 1995, 1998, Clarke & Warwick 1999). This facet of biodiversity can be easily assessed with Clarke & Warwick's taxonomic diversity indices, which take into account the taxonomical arrangement of species as a crude approximation to their evolutionary diversity (Warwick & Clarke 1995, Clarke & Warwick 1998), and is based on the idea that a community with closely related species is less biodiverse than a community with low relatedness among species.

The purpose of this study is to assess orb-weaving spider assemblages in the Iberá marshlands, analyzing different facets of local diversity, and the contribution of species differentiation (beta diversity) among localities and habitat types to the composition of regional diversity. The three studied localities are separated along 150 km in a NE-SW trajectory and they have particular conditions as the environmental units are arranged as groups of islands among lentic systems of great extension in the Paranaense-Espinal gradient. This implies a gradual difference in the vegetation between localities (Cabrera & Willink 1973).

The hypothesis is that the presence of contrasting habitats (savanna and woodland) and the variation between localities might be reflected in orb-weaving spider diversity, causing an important contribution of differentiation between communities to the regional diversity in the reserve. If this occurs, 1) there would be clear differences between habitats and localities considering as response variables species richness, diversity, evenness and taxonomic diversity; 2) there would be high complementarity and a clear differentiation in species composition between the habitat types of each locality, and among localities; and 3) regional richness would depend on the values of local alpha diversity, but would also have a strong contribution of beta diversity (between habitats and localities). In this scenario, management for conservation should be directed towards promoting spatial heterogeneity, giving special emphasis to natural habitat mosaics in different localities. Alternatively, if we found a single spider assemblage in the reserve without spatial variation, we would suggest focusing management efforts in protecting only those habitats or localities that result more biodiverse.

Material and Methods

Study area. The study was conducted at the Iberá Marshlands Reserve (Corrientes, Argentina). In this area, three localities were selected: Colonia Pellegrini (CP) (28°32'S - 57°11'W) in San Martin department; Paraje Galarza (PG) (28°05'S - 56°41'W) in Santo Tomé department; and Estancia Rincón (ER) (28º44'S - 57º40'W) in Mercedes department (Fig. 1). This area consists of 12300 km^2 of wetlands of the Paranaense (CP, PG) and Espinal (ER) Biogeographical Provinces (Cabrera & Willink 1973).

Two predominant habitat types are observed in all three localities: woodlands and savannas, which are distributed along the wetland system. The hygrophilous woodlands are found as "forest islands", where the herbaceous stratum is characterized by the presence of *Oplismenus hirtellus* (pasto bezerro; Poaceae) and *Chaptalia nutans* (cerraja; Asteraceae). The shrub stratum shows a variable density, dominated by *Brunfelsia australis* (jasmín paraguayo; Solanaceae), *Byttneria urticifolia* (Sterculiaceae) and *Ephedra tweediana* (tramontana; Ephedraceae). The arboreal stratum, for medium to low height (between 8 m and 15 m), is represented mainly by *Handroanthus heptaphyllus* (lapacho; Bignoniaceae), *Peltophorum dubium* (ibirá pitá; Fabaceae), *Cordia americana* (guayaibí; Boraginaceae), *Enterolobium contortisiliquum* (timbó; Fabaceae), *Nectandra angustifolia* (laurel negro; Lauraceae) and some undergrowths of *Guadua chacoensis* (tacuara; Poaceae); *Zanthoxylum fagara* (tembetarí; Rutaceae) and *Chloroleucon tenuiflorum* (tatané; Fabaceae) are also present but less frequent. The savanna is characterized by the dominance of *Andropogon laterales* (paja colorada; Poaceae), two marked strata are identified by the presence of *Paspalum notatum* (pasto horqueta; Poaceae) and abundant small grasses such as *Cuphea* sp. (Lythraceae), *Tibouchina gracilis* (Melastomataceae), *Angelonia integerrima* (Plantaginaceae) and *Desmodium incanum* (pega pega; Fabaceae).

The climate of this region is subtropical humid with warm rainy summers and cold and dry winters, the annual temperature and precipitation averages are 21.30 ºC and 1700 mm respectively (Neiff & Poi de Neiff 2006); however, the studied localities show less bioclimatic variations (Carnevali 1994).

Data collection. Field work was carried out during the dry (August) and rainy (December) seasons of 2005. At the three localities, samples were collected in the two main habitat types: woodland and savanna. In order to achieve a better representation, we used three different sampling techniques: 1) Sweeping. A sweeping net was used to collect spiders from the vegetation of the savanna in 10 randomly located transects each season, for a total of 20 samples per locality. A sample consisted of 50 alternate strokes of the sweeping net along each transect. 2) Beating. Beating was used to collect spiders from 10 randomly selected sites in woodlands each season (20 samples per locality). Each sample consisted of five strong knocks with a bar on the branches and foliage. A white cloth quadrant (50 x 50 cm) was held below the foliage during the beating to collect spiders. 3) Manual extraction. Samples were taken in five randomly located sites in woodlands (one sample per site), where we collected spiders from the vegetation each

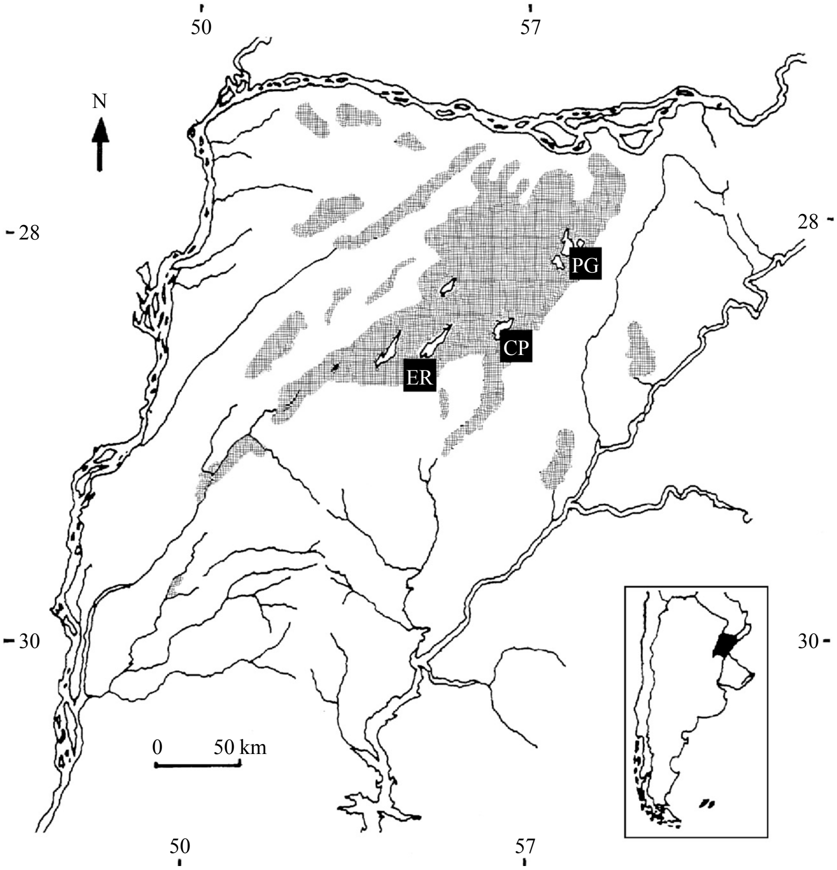

Fig 1 Location of Iberá marshlands system (shaded area) and study localities (squares), Corrientes Province, Argentina. CP: Colonia Carlos Pellegrini; ER: Estancia Rincón; PG: Paraje Galarza.

season (10 samples per locality). Manual samples were taken at night by two people over 30 min by looking up and down (Coddington *et al* 1991). Overall, we took 150 samples (50 per locality). All samples were preserved in polyethylene bags (20 x 30 cm) with a small amount of 70% ethanol.

In the laboratory, spiders were sorted into families and morphospecies. Identification to lower taxonomic levels was made with the available bibliography. Species nomenclature follows Platnick (2009). Immature specimens were assigned to generic level and in a few cases to species level only by morphological comparison with the adults, and their inclusion was necessary to obtain reliable estimates of species richness (Jiménez-Valverde & Lobo 2007). Furthermore, we used a reference collection made by various Argentine spider specialists (Avalos *et al* 2006, 2007) including spiders from different environments of Corrientes province. All the collected specimens were deposited in the Arthropod Collection of the Universidad Nacional del Nordeste, Argentina (CARTROUNNE).

Data analysis. The information collected using different techniques and sampling through the year allowed us to get more comprehensive species inventories by broadening the sampling universe. But in order to simplify this manuscript with a clear focus on our objectives, we do not pretend to analyze here the variation of spider assemblages between seasons or among sampling techniques. So, in this paper we restrict our analysis to the patterns of spider diversity between habitats and localities.

As a first step, we calculated the ratio between total number of individuals and total number of species (individuals: species) as a measure of sampling effort. As the number of individuals to capture one species increases, the inventory becomes more comprehensive assuming that less species remain to be capture. Then, we assessed the completeness of the spider inventories in each locality as the proportion of observed species richness relative to maximum expected richness. Expected richness was calculated using the Abundance-based Coverage Estimator (ACE), a non-parametric richness estimator, which was calculated with EstimateS 8 (Colwell 2006).

Species richness is a natural measure (May 1988); it is the simplest way to describe community and regional diversity (Magurran 2004), and it is fundamental for comparisons among sites. To test for differences in cumulative species richness between habitats and localities, we used rarefaction to standardize samples given that total number of individuals collected in each habitat and locality was markedly different (Gotelli & Colwell 2001, Colwell *et al* 2004, Magurran 2004). Rarefaction curves based on the number of individuals collected, with standard errors, were calculated with the software Species Diversity and Richness ver.3.0.2 (Henderson & Seaby 2002). The Shannon diversity and Pielou evenness indexes (Magurran 2004) were calculated with 95% confidence intervals obtained by bootstrap resampling using the Species Diversity and Richness software (Henderson & Seaby 2002).

In addition, we used two taxonomic measures called Average Taxonomic Distinctness (Δ+) and Variation in Taxonomic Distinctness (Λ+) (*sensu* Clarke & Warwick 1998, 2001). On one hand, Δ+ takes into account the taxonomic level at which any two species are related and can be thought of as the average length –in the taxonomic tree– between any two randomly chosen species present in the sample (Warwick & Clarke 1995, Magurran 2004). Thus, Δ+ is a direct measure of taxonomic diversity: a high value of Δ+ reflects high taxonomic diversity (low relatedness among species). On the other hand, Λ+ reflects the degree to which certain taxa are over- or under-represented in samples. Therefore, Λ+ measures the unevenness in the taxonomic tree, and is thus contrary to the concept of taxonomic biodiversity: high taxonomic diversity would be expected for a community with an even distribution of species among the taxonomic levels and units, a situation that would result in a low value of Λ+.

We used a simple linear scaling whereby the largest number of steps in the tree is set to $\omega = 100$. We also performed a randomization test (1000 random samples) to detect differences in the taxonomic distinctness at each observed sample transect, from the expected values derived from the species pool, taking into account the number of species of the samples (Clarke & Warwick 1998). The null hypothesis assumes that each sample contains species randomly selected from the pool and that it should therefore fall within the 95% confidence intervals. All the analyses of taxonomic diversity measures and randomization tests were performed using PRIMER (Clarke & Gorley 2001).

The degree of distinctness among pairs of localities was measured using the complementarity index suggested by Colwell and Coddington (1994). The value of this index, expressed as a percentage, ranges from 0% for identical species composition to 100% when species composition is completely different. This measure of complementarity is therefore a direct measure of beta diversity. Also, we used detrended correspondence analysis (DCA) to explore patterns in community composition across habitats and localities. DCA is a multivariate technique that orders samples based on the number of individuals of each species. Our ordination used the total number of each spider species recorded at each habitat type in each locality. Samples closer to one another in ordination space are more similar in species composition than samples that are further apart. We performed the DCA in CANOCO (ter Braak & Smilauer 2006).

Finally, in order to analyze the percentage contribution of point species richness (alpha diversity) and of dissimilarity in species composition (beta diversity) to the total spider richness, we used a model of additive partitioning of species richness (Lande 1996, Veech *et al* 2002, Crist *et al* 2003). According to this model, total spider richness in the Iberá Marshlands (gamma diversity) is considered as a result of summing mean species richness within habitats (alpha diversity), species change between the habitats of each locality (beta habitats), and species change among localities (beta localities):

$$\gamma = \bar{\alpha} + \beta_{habitats} + \beta_{localities}$$

Using a completely randomized null model, we tested if the observed percentages of contribution of alpha and the two levels of beta diversity were statistically different from the expected values (1000 randomizations), assuming a random distribution of the individuals (Crist *et al* 2003). We used the PARTITION software (Veech & Crist 2007) to compute these values.

Results

Representativeness of spider inventories. We found 1657 individuals from 59 species/morphospecies, representing 25 genera and four families of orb-weaving spiders (*Online Supplementary Material*). The highest abundance and richness values were accounted by family Araneidae, which represented more than 72% of the individuals and 83% of the species. Contrary, family Nephilidae was represented by only two individuals and only one species [*Nephila clavipes* (L)]. The four families of orb-weaving spiders found in the region (Araneidae, Nephilidae, Tetragnathidae and Uloboridae) were collected in CP, while in ER and PG only Araneidae and Tetragnathidae families were observed. Genera with more species were *Alpaida* (five spp.), *Eustala* (five spp.), *Larinia* (four spp.), *Micrathena* (four spp.) and *Parawixia* (four spp.). In CP *Metazygia gregalis* (O. P.-Cambridge), *Leucauge venusta* (Walckenaer) and *Eustala* sp.1 were the most abundant taxa, accounting for 35.25% of the number of individuals. In ER the dominant taxa were *Eustala* sp.2, *Alpaida veniliae* (Keyserling) and *Alpaida nonoai* Levi (39.26% of total abundance), whereas *Ocrepeira hirsuta* (Mello-Leitão), *A. veniliae* and *Parawixia bistriata* (Rengger) were dominant in PG (49.64% of total abundance).

Total sampling effort represents an individuals:species ratio of 28:1. In CP we captured 776 individuals of 42 taxa (18.48:1 individuals:species ratio, 16.29:1 in woodland and 11.44:1 in savanna). In ER we found 307 individuals of 22 species/morphospecies (13.95:1 individuals:species ratio, 10.73:1 in woodland and 11.23:1 in savanna). And in PG we captured a total of 574 individuals of 37 species/morphospecies (15.51:1 individuals:species ratio, 3.93:1 in woodland and 25.33:1 in savanna).

Richness comparison between habitats and localities. The rarefaction curves showed clear differences in species richness between habitats in the three localities. Even after standardizing sampling effort to a total of 206 individuals per habitat, in CP rarefaction curves show a significantly higher cumulative richness in woodland (25.6 species) than in savanna (18 species, Fig 2a). In ER, with a standard value of 146 individuals, the species richness was 14.8 species for woodland and 13 species for savanna (Fig 2b). Finally, in PG the difference is even clearer: standardizing sampling effort to a total of 118 individuals per habitat, we found significantly higher cumulative richness in woodland (30 species) than in savanna (13 species, Fig 2c). Among localities, comparison of species richness at the level of 307 individuals showed a clearly lower number of species en ER (22 species) than in

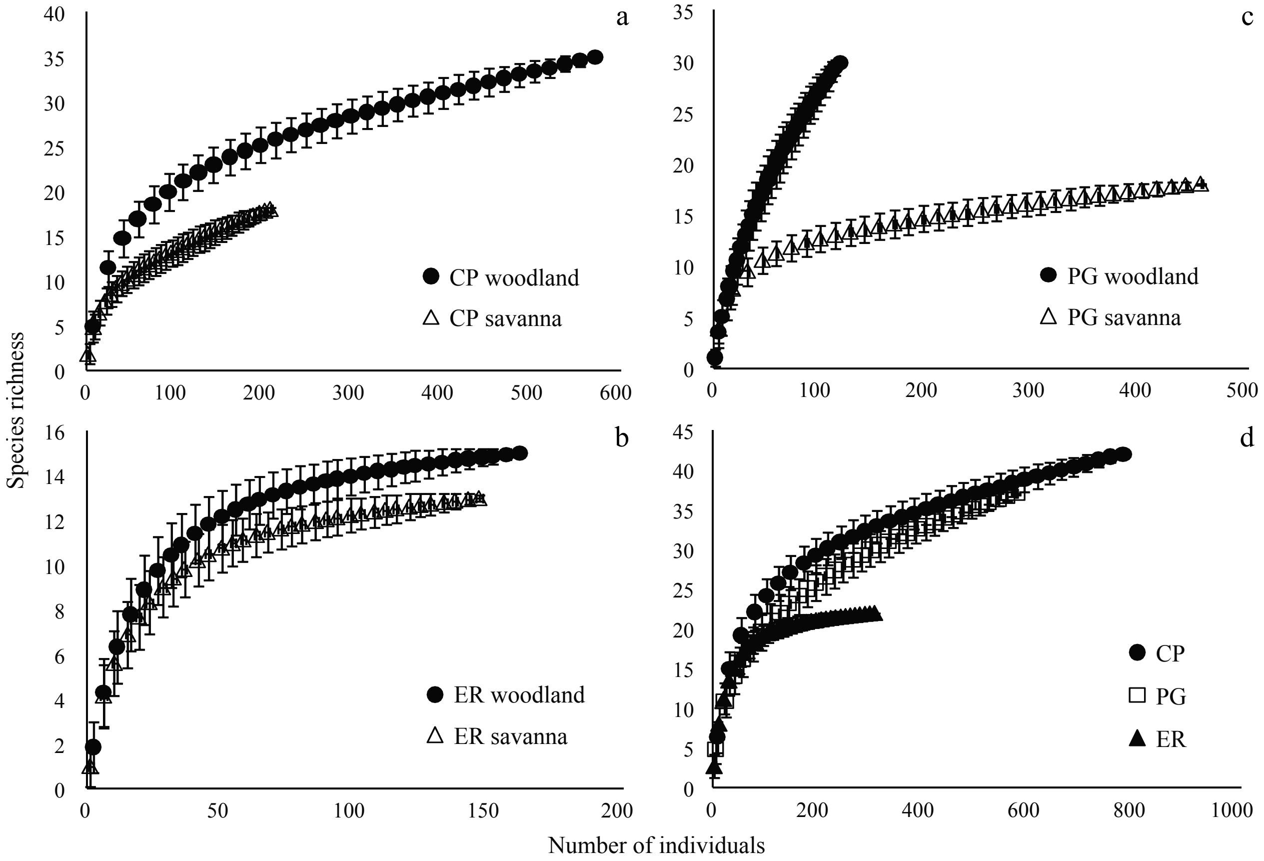

Fig 2 Rarefaction curves for woodland and savanna communities of orb-weabing spiders in the three localities studied: a) Colonia Pellegrini; b) Estancia Rincón; c) Paraje Galarza; and d) a comparison among the three localities. The bars are standard errors.

the other two localities, while no statistical difference was found in the species richness between CP and PG (Fig 2d).

Diversity and evenness. Variation of species diversity (Shannon index) and evenness (Pieolou index) follow the same trend than species richness only at the habitat level. Woodland has significantly higher values of diversity (Fig 3a) and evenness (Fig 3b) only in CP, whereas in the other two localities woodland communities were also slightly more diverse and even than savanna communities, but we did not found statistically different values between these habitat types (Fig 3a, b). Among localities, CP has higher values of diversity (Fig 4a) and evenness (Fig 4b) than the other two localities, while no statistical difference was found in the values of these indices between ER and PG (Fig 4a, b).

Taxonomic diversity. The Average Taxonomic Distinctness (Δ+) index had higher values of taxonomic spider diversity in woodlands than in savannas in the three localities (Table 1). However, only the value of woodland in CP was statistically higher from the value calculated with the randomization test, taking into account the species richness of each habitat. CP also has the higher value of Δ+ at the locality level, although not significantly different from the expected by random.

A similar pattern was found with the index of Variation in Taxonomic Distinctness (Λ+), for which woodlands also had higher values than savanna, but only the value of woodland in CP was statistically higher from the value calculated with the randomization test. CP was the locality with the higher value of Λ+, and this value was significantly different from the expected by random (Table 1).

Beta diversity. The value of the complementarity index was very similar for pairs of localities: 60.87% between CP and ER, 61.40% between CP and PG, and 62.79% between ER and PG (mean complementarity among localities: 61.69%). We also found slightly higher complementarity values when comparing the two habitat types (woodland and savanna) within each locality: 73.81% in CP, 72.73% in ER, and 70.27% in PG (mean = 72.27%). Interestingly, when comparing pairs of the same habitat type but found at different localities, we found higher beta diversity among woodlands (72.45% mean complementarity) than among savannas (63.82% mean complementarity).

This trend is better visualized in the DCA plot (Fig 5), where sites of savanna are clumped very closely while woodland sites are more disperse. Axe 1 has an eigenvalue of 0.772, and a total length of gradient of 3.437 standard deviations. This first Axe clearly separates sites according to their habitat type, without any influence of the locality. The Axe 2 has an eigenvalue of 0.411, and a total length of gradient of 2.373 standard deviations. This second Axe

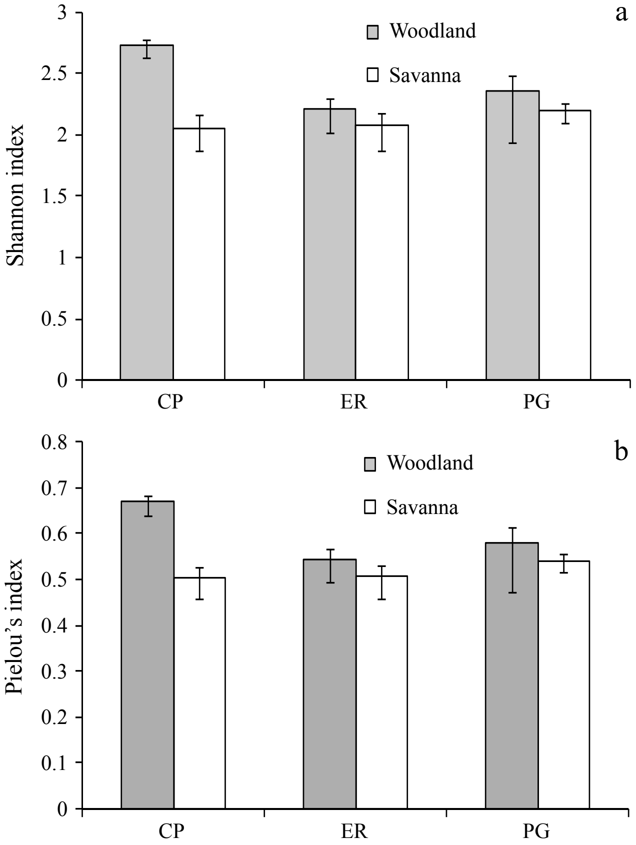

Fig 3 Diversity (a) and evenness (b) of orb-weaving spider communities between woodland and savanna habitats in the three localities studied. CP: Colonia Carlos Pellegrini; ER: Estancia Rincón; PG: Paraje Galarza. The bars are 95% confidence intervals.

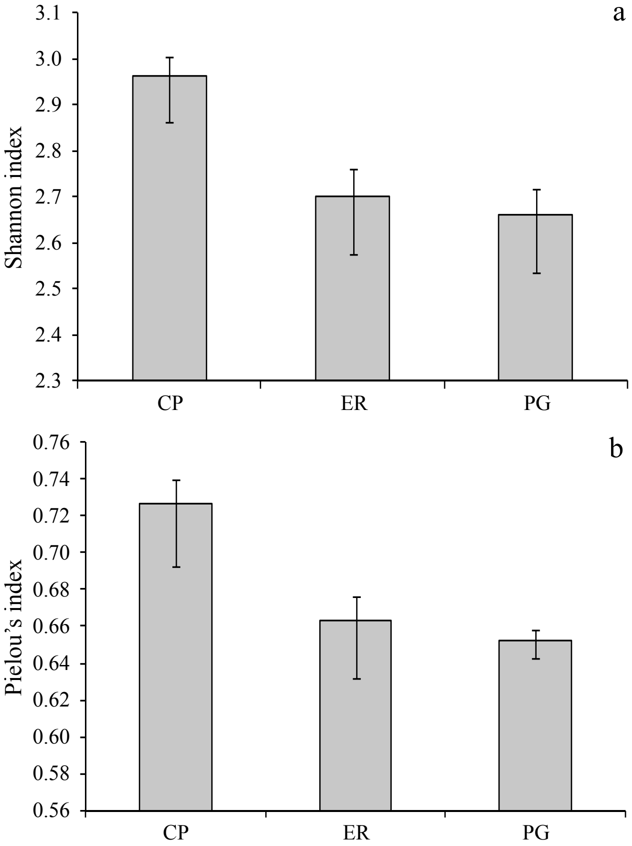

Fig 4 Diversity (a) and evenness (b) of orb-weaving spider communities in the three localities studied. CP: Colonia Carlos Pellegrini; ER: Estancia Rincón; PG: Paraje Galarza. The bars are 95% confidence intervals.

Table 1 Orb-weaving spider taxonomic diversity values for habitat types and localities at the Ibera Marshlands Reserve, Corrientes, Argentina, according to the indices proposed by Clarke and Warwick (1998).

Habitats	Average Taxonomic Distinctness (Δ+)	Variation in Taxonomic Distinctness (Λ+)
CP woodland	79.33*	366.31*
CP savanna	74.95	338.14
ER woodland	75.87	370.27
ER savanna	74.79	290.2
PG woodland	76.7	300.25
PG savanna	71.68	272.64
Localities		
CP	77.51	339.33*
ER	73.16	289.72
PG	74.77	284.61

*: statistically significant different from the predicted value by a randomization test ($P < 0.05$). CP: Carlos Pellegrini; ER: Estancia Rincón; PG: Paraje Galarza.

separates the three sites of woodlands, but has no influence on savannas. These two first Axes explain a 59.20% of the variance in species data.

Partitioning of regional spider diversity. Mean observed alpha diversity (21.5 species) was significantly lower ($P < 0.001$) than the value expected by random according to the null model (36.7 species). This observed alpha diversity contributes with only 36.44% to the gamma diversity of the orb-weaving spiders in the Iberá Marshlands (Fig 6). Consequently, beta diversity between habitats and beta diversity among localities have significantly greater contributions than those expected by random.

Discussion

The number of orb-weaving spider species found in the Iberá Marshlands Reserve was higher than the number of species found in other investigations carried out in the Corrientes province, Argentina. For example, Rubio and collaborators (2008) found 29 species in two different protected habitats (hygrophilous woodland and savannah parkland) of the Mburucuyá National Park; and Avalos and collaborators (2007) reported 41 species in degraded forests

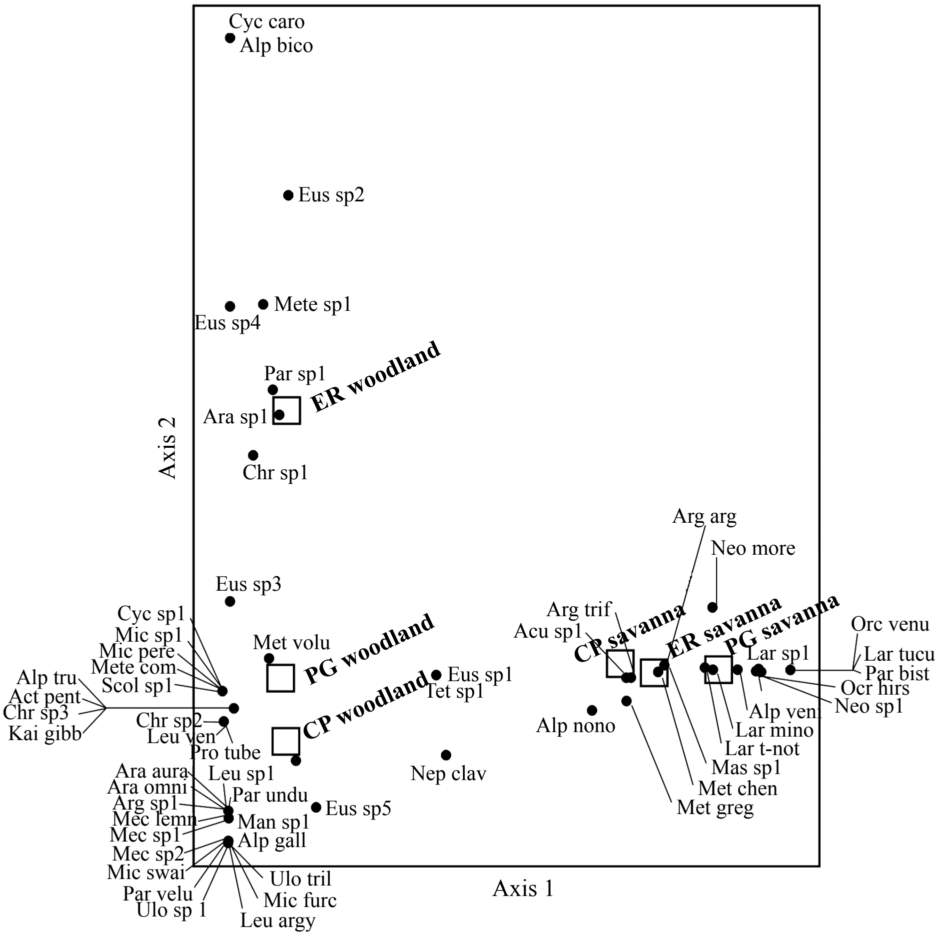

Fig 5 Biplot of the DCA ordination for the orb-weaving spider communities in two habitat types at the three localities studied. CP: Colonia Carlos Pellegrini; ER: Estancia Rincón; PG: Paraje Galarza. The species names are abbreviated according to the key listed in the Online Supplementary Material.

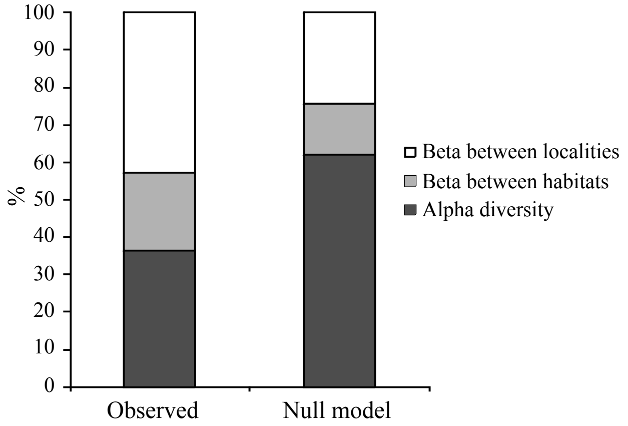

Fig 6 The percentage of total orb-weaving species richness in the Iberá Marshlands explained by alpha- and beta-components of observed diversity. Three levels are represented in this analysis: within a habitat type in one locality (alpha), between habitat types (woodland and savanna) in each locality, and among localities. Values are expressed as the percent of the total species richness explained by each hierarchical level. The observed partitions are compared to expected values from a individual-based randomization null model.

from the humid Chaco, although these authors also reported the families Deinopidae and Theridiosomatidae. These two families inhabit mainly in cosmotropical environments, so their presence may be exceptional and dependent of their casual dispersion by means of the lotic floating vegetation (Rubio *et al* 2004, Avalos *et al* 2007). The number of species recorded in this study area is also larger to that observed by Blanco-Vargas and collaborators (2003) and Cepeda-Valencia & Florez-Daza (2006), both in the woodlands of the Colombian Andes. However, the number of species in this study in the Iberá marshlands was lower than that found by Silva (1996) in the Peruvian rainforest, if the same sampling techniques are considered. In our study Araneidae was the most abundant and species rich family of the orb-weaving spiders, a dominance that has also been reported by other authors (Silva 1996, Whitmore *et al* 2002, Benavides & Florez 2006).

Despite of the sampling effort, spider inventories are not complete yet. For the three localities studied, species inventories have recorded more than 70% of the expected species richness. But when assessing the completeness of inventories at the habitat level within each locality, only in ER we found a good representation of the expected richness (94%). Similar values have been obtained by other researchers: 68-89% (Coddington *et al* 1996), 86% (Blanco-Vargas *et al* 2003), 61-87% (Rubio *et al* 2008), 78-88% (Cardoso *et al* 2008). In the other two localities it seems that more sampling effort is needed in order to get a good representation of the expected species richness, particularly in the woodland of PG and in the savanna of CP. We did not found a clear trend between the percentage of inventory completeness according to the ACE estimator and the individuals:species ratio, so we propose that at least in this system sampling effort and inventory efficiency are more intuitively evaluated considering the proportion of observed species richness relative to the expected richness using a non-parametric estimator. Nevertheless, this method estimates only the portion of the Iberá system orb-weaving spider fauna present in the sampled area, during the time of sampling and with the used, accessible methods. Expected values of richness are, therefore, estimates of the "instantaneous" species richness of studied localities, and they probably underestimate richness over larger scales (Coddington *et al* 1996).

The assessment of different facets of biodiversity at the locality and habitat levels offers a broad perspective on the orb-weaving spider communities. At the locality level, ER –located at southwest of the studied area– has the lower number of species and the lower taxonomic distinctness. CP –located at northeast of the studied area– was the locality with higher number of species, significantly higher diversity and evenness, and also higher values of taxonomic distinctness. However, this locality had also the higher value of variation in taxonomic distinctness, indicating an over- or under-representation of some taxa. This possible uneven representation of taxa in the community structure, and its implications for ecological functioning, is an issue that should be studied in deep.

At the habitat level, the different facets of biodiversity showed a clear trend where woodlands have higher species richness, diversity, evenness and taxonomic distinctness than savannas. This may be explained by the complexity in vegetation structure in woodlands, giving that orb web building spiders rely on vegetation for their life cycle, either for finding food, building retreats or for web building. The structure of the vegetation is therefore expected to influence the diversity of spiders found in the habitat (Whitmore *et al* 2002). This indicates that structural diversity of the vegetation may, in some way, influence the spider diversity in the study area. Studies have demonstrated that a correlation exists between the structural complexity of habitats and species diversity (MacArthur 1964, Uetz 1979, Hatley & MacMahon 1980, Tews *et al* 2004, Pinkus-Rendón *et al* 2006, Jiménez-Valverde & Lobo 2007). Diversity generally increases when a greater variety of habitat types are present (MacArthur 1964). Uetz (1991) suggests that structurally more complex shrubs can support a more diverse spider community. Downie *et al* (1999) and New (1999) have demonstrated that spiders are extremely sensitive to small changes in the habitat structure; including habitat complexity, litter depth and microclimate characteristics. Thus, the physical structure of environments has an important influence on the habitat preferences of spider species, especially web-building species (Uetz 1991, Hurd & Fagan 1992, Tsai *et al* 2006). This could explain the larger spider richness and diversity observed in woodlands, and particularly in CP, where vegetation seems more diverse. Also, grazing in the savannas could be a factor decreasing orb-weaving spider diversity, given that in general, as disturbance increases the spider species richness decreases (Shochat *et al* 2004, Pinkus-Rendón *et al* 2006).

When assessing beta diversity among localities, we observed that the proportion of shared species was low, thus the complementarity between localities is ca. 60%. This relatively high percentage is an indication that these localities are sufficiently apart, showing a variation in their vegetation structure and/or bioclimatic characteristics (Coddington *et al* 1996). Distance does not seem to influence the complementarity between localities. Spider composition in ER is more different when compared with the two other localities. These results are also supported by its location in the Espinal Biogeographical Region, where the environment is slightly drier and the vegetation is sparser and lower than in the Paranaense Region (Cabrera & Willink 1973).

Beta diversity is higher between habitat types within localities (>70%). Also, complementarity shows higher values among woodlands than among savannas. This is corroborated in the DCA where savanna sites are found in a compact group because of their common species composition, while woodland sites are found more distant in the ordination space. Particularly, the woodland in ER is differentiated from the other woodlands because of its particular spider fauna (e.g. *Alpaida bicornuta* and *Cyclosa* cf *caroli*). These clear differences in species composition among habitats and localities explain the significant contribution of beta diversity to the regional orb-weaving spider richness in the Iberá Marshlands (Fig 6).

To preserve spider biodiversity, land management strategy design requires an understanding of the patterns of spider diversity on an appropriate regional scale (New 1999) and it is feasible starting from the local knowledge of the diversity considering that this has a high correlation with the vegetation complexity that appears as a powerful predictor of the local spiders species richness on a regional scale (Jiménez-Valverde & Lobo 2007). In the Iberá Marshlands we found that the presence of contrasting habitats and the variation between localities have a great influence in orb-weaving spider communities, leading to an important contribution of beta diversity to the regional spider species richness. Thus, we suggest that besides reinforcing protection in CP (the most diverse locality for orb-weaving spiders) management for conservation in the reserve should be directed towards promoting natural spatial heterogeneity, giving special emphasis to habitat mosaics in different localities. However, to provide a better framework for conservation managing, other biological groups should be studied. Moreover, microhabitat variables and/or disturbance effects should also be investigated because they may represent important factors influencing diversity, especially in order to assess the potential anthropic activities in this type of RAMSAR areas.

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Online Supplementary Material

Rubio G D, Moreno C E (2010) Orb-weaving spider diversity in the Iberá Marshlands, Argentina. Neotrop Entomol 39(4): 496-505.

List of spider species/morphospecies and number of individuals from the Iberá marshlands, Corrientes, Argentina. Ar: Araneidae; Te: Tetragnathidae; Ne: Nephilidae; Ul: Uloboridae

Family	Species/morphospecies	Key	Total
Ar	*Actinosoma pentacanthum* (Walckenaer)	Act pent	1
Ar	*Aculepeira* sp1	Acu sp1	6
Ar	*Alpaida bicornuta* (Taczanowski)	Alp bico	7
Ar	*Alpaida gallardoi* Levi	Alp gall	66
Ar	*Alpaida nonoai* Levi	Alp nono	42
Ar	*Alpaida truncata* (Keyserling)	Alp trun	2
Ar	*Alpaida veniliae* (Keyserling)	Alp veni	165
Ar	*Araneus aurantiifemuris* (Mello-Leitão)	Ara aura	1
Ar	*Araneus omnicolor* (Keyserling)	Ara omni	9
Ar	*Araneus* sp1	Ara sp1	20
Ar	*Argiope argentata* (Fabricius)	Arg arg	2
Ar	*Argiope* sp.	Arg sp1	1
Ar	*Argiope trifasciata* (Forsskål)	Arg trif	21
Te	*Chrysometa* sp1	Chr sp1	17
Te	*Chrysometa* sp2	Chr sp2	5
Te	*Chrysometa* sp3	Chr sp3	1
Ar	*Cyclosa* cf *caroli* (Hentz)	Cyc caro	1
Ar	*Cyclosa* sp1	Cyc sp1	1
Ar	*Eustala* sp1	Eus sp1	105
Ar	*Eustala* sp2	Eus sp2	67
Ar	*Eustala* sp3	Eus sp3	10
Ar	*Eustala* sp4	Eus sp4	3
Ar	*Eustala* sp5	Eus sp5	10
Ar	*Kaira gibberosa* O. P.-Cambridge	Kai gibb	1
Ar	*Larinia minor* (Bryant)	Lar mino	33
Ar	*Larinia* sp1	Lar sp1	4
Ar	*Larinia t-notata* (Tullgren)	Lar t-not	60
Ar	*Larinia tucuman* Harrod, Levi & Leibensperger	Lar tucu	1
Te	*Leucauge argyra* (Walckenaer)	Leu argüí	25
Te	*Leucauge* sp.	Leu sp1	20
Te	*Leucauge venusta* (Walckenaer)	Leu ven	166
Ar	*Mangora* sp1	Man sp1	6
Ar	*Mastophora* sp1	Mas sp1	1
Ar	*Mecynogea lemniscata* (Walckenaer)	Mec lemn	1
Ar	*Mecynogea* sp1	Mec sp1	7
Ar	*Mecynogea* sp2	Mec sp2	30
Ar	*Metazygia chenevo* Levi	Met chen	18
Ar	*Metazygia gregalis* (O. P.-Cambridge)	Met greg	163
Ar	*Metazygia voluptifica* (Keyserling)	Met volu	98
Ar	*Metepeira compsa* (Chamberlin)	Mete com	1
Ar	*Metepeira* sp1	Mete sp1	28

Continue

Continuation

Family	Species/morphospecies	Key	Total
Ar	*Micrathena furcata* (Hahn)	Mic furc	1
Ar	*Micrathena peregrinatorum* (Holmberg)	Mic pere	1
Ar	*Micrathena* sp1	Mic sp1	2
Ar	*Micrathena swainsoni* (Perty)	Mic swai	1
Ar	*Neoscona moreli* (Vinson)	Neo more	40
Ar	*Neoscona* sp1	Neo sp1	16
Ne	*Nephila clavipes* (L)	Nep clav	2
Ar	*Ocrepeira hirsuta* (Mello-Leitão)	Ocr hirs	114
Ar	*Ocrepeira venustula* (Keyserling)	Ocr venu	34
Ar	*Parawixia bistriata* (Rengger)	Par bist	79
Ar	*Parawixia* sp1	Par sp1	11
Ar	*Parawixia undulata* (Keyserling)	Par undu	40
Ar	*Parawixia velutina* (Taczanowski)	Par velu	1
Ar	*Pronous tuberculifer* Keyserling	Pro tube	5
Ar	*Scoloderus* sp1	Scol sp1	5
Te	*Tetragnatha* sp1	Tet sp1	57
Ul	*Uloborus* sp1	Ulo sp1	1
Ul	*Uloborus trilineatus* Keyserling	Ulo tril	21
Total	Number of species = 59		1657