

Do Spider Diversity and Assemblages Change in Different Contiguous Habitats? A Case Study in the Protected Habitats of the Humid Chaco Ecoregion, Northeast Argentina

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Environ. Entomol. 37(2): 419–430 (2008)

ABSTRACT Spiders are a megadiverse group that can be useful indicators of the overall species richness and health of biotic communities. The spider diversity in subtropical forests of the Neotropical region are not yet well known, especially in Argentinean subtropical forests where systematic fieldwork has not been done until recently. The Great Chaco is very important as the unique dry subtropical forest of the earth, but it is suffering increasing degradation by the advance of agriculture. Spider communities have been shown to be more directly influenced by vegetation architecture than vegetation species composition. In this study, we aim to assess whether spider diversity and assemblages change in adjacent habitats with different types of vegetation. We compare the diversity and spider assemblages in two different contiguous protected habitats (hygrophilous woodland and savannah parkland) of the Mburucuyá National Park, (Humid Chaco ecoregion). Seasonal samples were obtained using three types of sampling methods: pitfall trapping, beating, and manual litter extraction. The spider assemblages were different in the studied areas, and the abundance, diversity, evenness, and species richness were higher in the hygrophilous woodland than the savannah parkland. These differences in spider diversity and assemblages indicate that both types of habitats are important if the biodiversity is to be conserved in the Chaco ecoregion, where different types of habitat are shown as a patchy distribution.

KEY WORDS spider diversity, contiguous habitats, Humid Chaco ecoregion, Mburucuya National Park, Argentina

The protection of biodiversity is one of the most relevant issues in global conservation. Meaningful conservation, however, cannot take place if the species involved are not known (De Wet and Shoonbee 1991). In Argentina, research is needed to successfully complete this initial stage, leading to the implementation of decisions about sustainable resource management (Morrone and Coscarón 1998). A management plan to conserve the fauna can only be developed and implemented once inventories, or at least partial inventories, are completed (Whitmore et al. 2002). Quick, inexpensive, and reliable methods for estimating the species richness of taxa at particular sites (alpha diversity) could provide useful input to conservation and land management decisions (Coddington et al. 1991). Estimating local richness for a defined place at a defined time is fundamental to estimates of biodiversity at large spatial and temporal scales (Coddington et al. 1996). Accurate assessment of species rich-

ness is a basic and essential step for the effective and timely monitoring and management of biological communities (May 1988, Colwell and Coddington 1994, Boulinier et al. 1998, Shen et al. 2003).

Spiders are a typical "megadiverse" group, and they have gained a wide acceptance in ecological studies as indicators of environmental quality (Clausen 1986, Maelfait et al. 1990, Churchill 1997), because nonspecialists can be quickly trained to make remarkably accurate counts of spider morphospecies (Oliver and Beattie 1993). Spiders are useful indicators of the overall species richness and health of biotic communities (Kremen et al. 1993, Colwell and Coddington 1994, Norris 1999) because they are (1) among the most speciose animal orders (Coddington and Levi 1991), (2) generalist predators that have an important collective impact on invertebrate herbivore populations (Riechert 1974, Riechert and Bishop 1990), (3) ubiquitous and easy to collect, and (4) characterized by a high within-habitat taxonomic diversity, exhibiting taxon- and guild-specific responses to environmental change.

The Gran Chaco, located approximately between latitudes 17° and 33° S and longitudes 65° and 60° W, is a vast plain that extends through northern Argentina, southeastern Bolivia, northwestern Paraguay,

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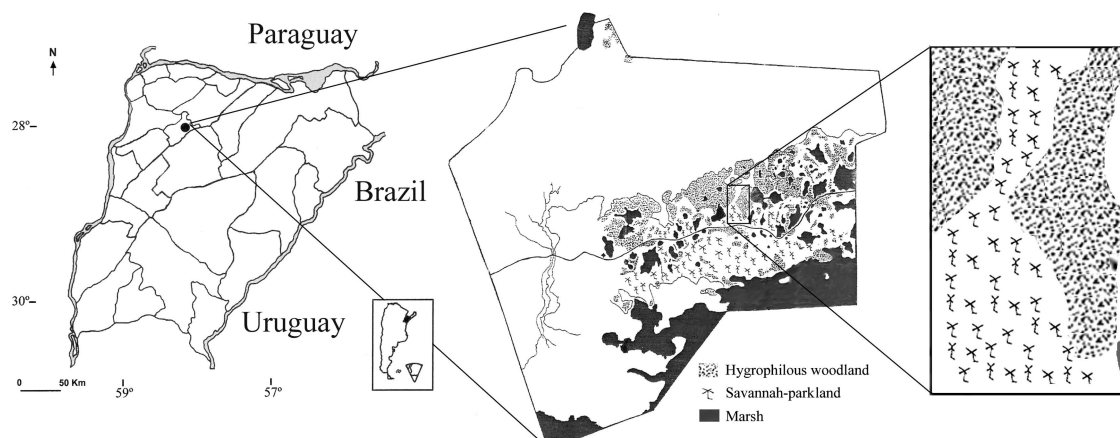


Fig. 1. Location of Mburucuyá National Park and study sites, Corrientes Province, Argentina.

and into a small area of southwestern Brazil. The Argentinean Chaco, with 655,000 km² (17% of total national territory), is very important because it is the earth's unique dry subtropical forest (Morello and Matteucci 1999). In Argentina, the Chaco can be subdivided into three ecoregions, one of which is the Humid Chaco (Chaco Húmedo), also called the Eastern Chacoan District (Cabrera 1976). This ecoregion has been classified by Dinerstein et al. (1995) as vulnerable and of importance on local and national scales, because it is suffering an increased degradation of its forests by the advance of agricultural lands (especially cotton and soybean crops) (Bertonatti and Corcuera 2000), as well as massive deforestation and overgrazing (Morello and Saravia Toledo 1959, Cabrera and Willink 1980). Only 7.93% of the Humid Chaco is protected by National Parks, Provincial Parks and Reserves, but sometimes a great amount of the land (especially the provincial ones) are "virtual protected areas," without real control or administration (Bertonatti and Corcuera 2000).

Spider diversity in subtropical forests of the Neotropical region is not yet well known, especially in the Argentinean subtropical forests where systematic fieldwork were not undertaken until recently. We began to compile inventories and to conduct comparative studies of spider communities in disturbed and undisturbed areas (protected or not) of northern Argentina with the purpose of contributing to the knowledge base, taking into consideration the framework of the CBD (Convention of Biological Diversity) signed by the Argentine government. The first step in this long process was to study the spiders in Mburucuyá National Park, Corrientes Province, northeast Argentina. The hygrophilous woodland, represented by islets within savannah parkland, is a unique and interesting environmental unit of the Humid Chaco represented in this National Park. The hygrophilous woodland is characterized by an annual period of inundation, and the savannah parkland is regulated by biannual fire periods controlled by the personnel of the park. Because vegetation architecture plays an important role in spider species composition found in

a habitat (Scheidler 1990), and vegetation that is structurally more complex can sustain a higher abundance and diversity of spiders (Hatley and MacMahon 1980, Green 1999), we aimed to assess if the spider diversity and the composition of spider assemblages in two different contiguous protected habitats of the Humid Chaco ecoregion are different and change among seasons.

Materials and Methods

Study Area. The study was conducted at Mburucuyá National Park, in the midwest of Corrientes province, Argentina, from November 2003 to July 2004 (Fig. 1). This area (27°58' S, 57°59' W) consists of 15,060 ha of land of the Eastern Chacoan District (Cabrera 1976) of the Chaco Biogeographical Province (Morrone 2001). In the Mburucuyá National Park, Carnevali (1994) and Saibene and Montanelli (1997) recognized six environmental units: lakes, marshes and ravines, savannah parklands, hygrophilous woodlands, mature woodlands, and young woodland islets. The climate is subtropical humid with hot and rainy summers and cold and dry winters. The mean annual temperature and precipitation reach 21.30°C and 1,200 mm, respectively.

Data Collection. Sampling at Mburucuyá National Park was conducted in two contiguous habitats: savannah parkland and hygrophilous woodland (5.70 and 5% of the total surface of the park, respectively). The sampling period covered spring of 2003 and summer, fall, and winter of 2004. In each habitat, five quadrants 200 m apart were identified by a zigzag transect in which the beginning point was randomly chosen. This type of transect was used to cover more surface on the woodland islet. Our seasonal sampling procedure included three collecting methods of spiders in different microhabitats in these two communities: pitfall traps, beating, and manual litter extraction.

Pitfall Trapping. Three pitfall traps were placed in a 5-m triangle on each quadrant. Plastic containers (7.50 cm wide at the top, 12.00 cm deep, 5.00 cm wide

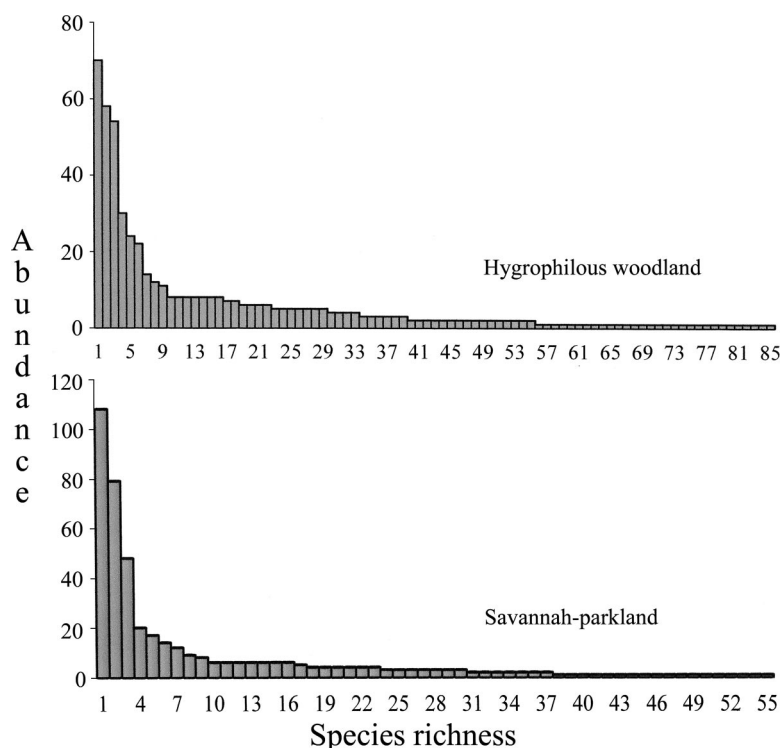


Fig. 2. Rank/abundance distribution of spider communities at Mburucuyá National Park at the studied habitats, Corrientes, Argentina (2003–2004).

at the base) were used as pitfall traps. These were buried into the soil, so the lip was flush with the soil surface and contained 100 ml of 10% aqueous solution of ethylene glycol with a few drops of unscented detergent to break the surface tension. Traps were left for 2 d, after which the contents were placed into labeled polythene bags with 70% ethanol.

Beating. Beating was done by firmly striking branches and foliage with a mallet five times each on each quadrant of both habitats. A 0.5-m square white cloth was held below the branches and foliage during the beating. Three random samples were taken in each quadrant, and a total of 15 samples from each habitat every season. The spiders were removed with forceps and soft paintbrushes and placed into labeled polythene bags with 70% ethanol.

Manual Litter Extraction. Three equal volumes of litter 0.25 by 0.25-m square and 0.05-m deep were collected on each quadrant from both habitats. The litter was placed over a white cloth and examined for 30 min, and the spiders were collected with forceps and soft paintbrushes. The collected spiders were placed into labeled polythene bags with 70% ethanol.

In the laboratory, the samples were sorted into families and morphospecies. Identification to lower taxonomic levels was made with available identification keys. The lack of taxonomic expertise in Argentina, especially in certain families, makes identification to species level impossible in some instances. Imma-

ture specimens were assigned to generic level, and in a few cases, to species level only by morphological comparison with the adults. Furthermore, we used as a reference spiders collected in 2001 from (different) woodland of Corrientes Province, identified by various Argentine spider specialists, and deposited on the Arthropod Collection of the National University of Northeast Argentina (CARTROUNNE).

Data Analysis. The range/abundance distribution was drawn to show the distribution of our data in both communities. We used estimators of species richness to determine whether the communities had been sufficiently sampled and diversity indices to evaluate and compare the spider communities in both studied habitats. Species richness is a natural measure (May 1988), it is the simplest way to describe community and regional diversity (Magurran 1988), and it is fundamental to comparisons among sites. We generated sample-based rarefaction curves for both sites using EstimateS 7.0 (Colwell 2004). For species richness, the same computer program was used to evaluate the performance of different nonparametric species-richness estimators with our datasets. Percentage complementarity (Colwell and Coddington 1994), inventory completeness index (Toti et al. 2000), Bray-Curtis index (Bray and Curtis 1957), Sorensen's index, and Morisita-Horn's index of similarity (Magurran 1988) were used to compare the taxonomic composition of the two communities.

To compare the diversity in the studied habitats, we used indices that incorporate both species richness and evenness in a single value (Magurran 1988). The diversity and evenness indices of the spider communities were calculated using the Bio-DAP program (Gordon and Douglas 1988). The indices used were the Shannon index (H'), evenness (E), and the Berger-Parker dominance index, because they are simple and commonly used. Ecologists and other biologists have long recognized that there are undiscovered species in almost every survey or species inventory (Chao et al. 2000). Our dataset was run through the program SPADE (Chao and Shen 2003–2005) to obtain estimated shared-species richness and to generate a prediction of the number of species remaining to be discovered in both communities if we make further surveys in the future. This prediction provides an objective basis on which to assess the effectiveness of further surveys so that sampling efforts and funding can be allocated among sites for effective and timely management of biological communities, and it can also be used to estimate the minimum effort needed to reach a certain level of completeness (Chao and Shen 2004).

Results

Community Composition. A total of 959 spiders representing 28 families and 104 species/morphospecies were present in the 120 samples collected in this study; juveniles represented 75.08% of the total. The abundance and the observed richness were higher in the hygrophilous woodland ($N = 520$; $S = 85$) than in the savannah parkland ($N = 439$; $S = 55$; Fig. 2; Appendix 1).

The inventory completeness index (the percentage of species that are not singletons), another indication of how well a community has been sampled (Toti et al. 2000), was slightly lower for the hygrophilous woodland (64.29%) than for the savannah parkland (66.67%; Table 1).

Seventy-seven percent of the spiders in the hygrophilous woodland are represented by Lycosidae, Araneidae, Theridiidae, Thomisidae, and Salticidae, whereas in the savannah parkland, the same value corresponds to Lycosidae, Philodromidae, Araneidae, Salticidae, and Anyphaenidae (Fig. 3). In both communities, Lycosidae was always the most abundant family (Appendix 1).

Spiders were divided into three main functional groups (guilds) in accordance with Dippenaar-Schoeman et al. (1999): plant wanderers, ground wanderers, and web builders. The guild composition was different in both habitats and in sampling periods (Appendix 1). The ground-wanderer guild was very abundant in the two habitats, but it was higher in the savannah parkland (46.33%). The web-builder group in the hygrophilous woodland was almost double (29.63%) that in the savannah parkland, and the plant-wanderers were more abundant in the latter habitat (36.01%) than in the hygrophilous woodland (29.63%).

Table 1. Richness estimates and other summary values for each community

	Hygrophilous woodland	Savannah parkland
Observed richness	85	55
Richness estimates		
Chao 1	112.13 $\pm$ 13.53	77.14 $\pm$ 14.79
Chao 2	131.12 $\pm$ 21.72	78.50 $\pm$ 14.34
ACE	112.90	68.76
ICE	121.24	72.06
First-order jackknife	118.42 $\pm$ 7.05	74.65 $\pm$ 5.02
Second-order jackknife	139.90	86.04
Bootstrap	99.01	63.20
MM runs	120.54	70.60
MM mean	115.01	70.62
No. of samples	60	60
No. of individuals	520	439
No. of singletons	30	18
No. of doubletons	16	7
No. of uniques	35	21
No. of duplicates	13	9
Inventory completeness index	64.29	66.67
H' (Shannon index)	3.57	2.90
E (evenness)	0.80	0.72
Var H'	0.00326	0.00480
Berger-Parker index	0.135	0.246
C_J (Jaccard index)		0.333
C_S (Sørensen qualitative index)		0.500
C_N (Sørensen quantitative index)		0.473
C_{MH} (Morisita Horn index)		0.698
C_{jk} (complementarity)		67.92%

Each richness estimate represents the mean (and, for some estimators, the SD) for 100 randomizations of sample order. Sampling intensity is the ratio of individuals to species. Inventory completeness is the percentage of species that are not singletons.

Values of the complementary and similarities indices show that these two communities differ greatly in spider species composition: only 34 species were common to both communities (Table 1). Complementary indices by season showed that winter is the season with more complementarity between both communities ($C-I = 0.8966$; Appendix 2). In the hygrophilous woodland, the three most abundant species represent 35% (Lycosid 1, Lycosid 3, and *Tmarus* sp. 1) of all specimens collected, and in the savannah parkland, the three most abundant species represent >53% (Lycosid 1, Lycosid 3, and *Paracleonemys* sp.; Appendix 1). Because of this, the Morisita-Horn index is moderate (Table 1); this index is strongly influenced by the most abundant species (Magurran 1988).

In the hygrophilous woodland, singletons represent >35% of all specimens, and in the savannah parkland, they reach 33%.

Species Richness Estimates. For none of the three samples sets do the mean, randomized, observed species accumulation curves reach an asymptote (Fig. 4). The Michaelis-Menten, ICE, and Chao2 estimator curves approach an asymptote more rapidly as the sample number increases than do the other estimator curves (Fig. 5). In both cases, the Michaelis-Menten estimate seems to approach an asymptote more closely than do the other estimates, especially in the hygrophilous woodland data-

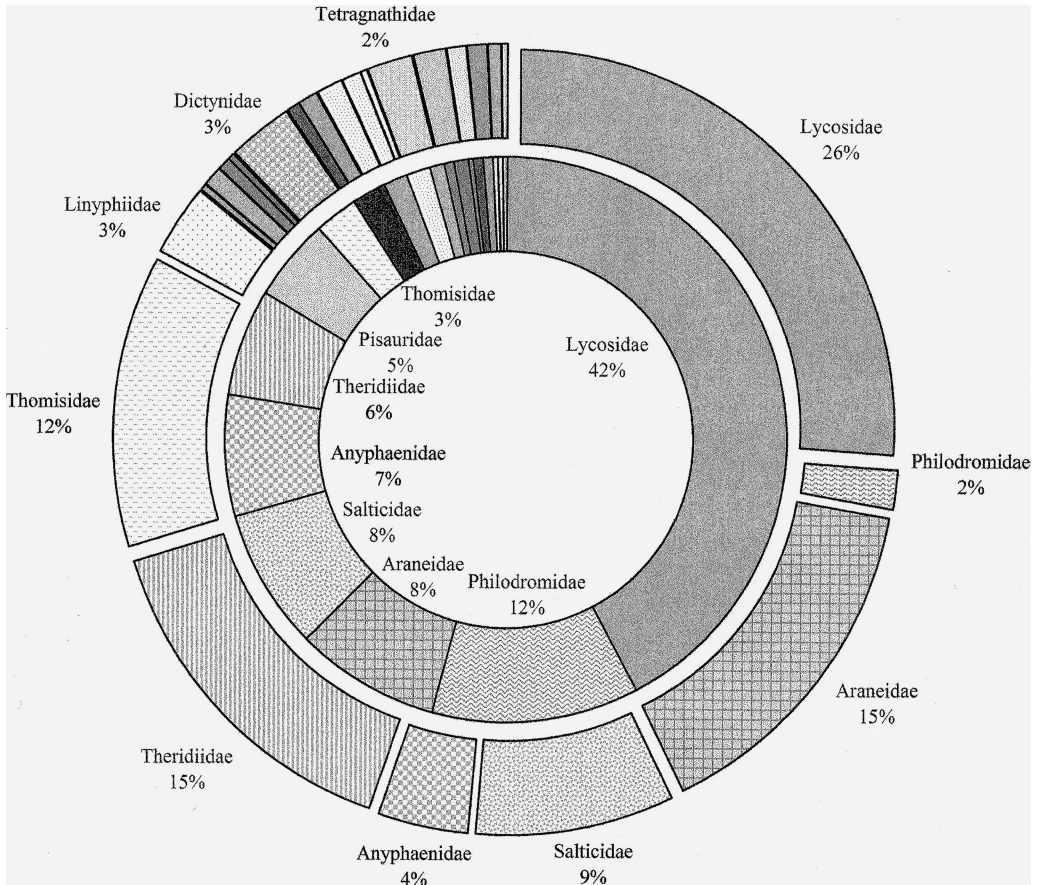


Fig. 3. Spider family composition in percentages in both habitats of Mburucuyá National Park, Corrientes, Argentina (2003–2004). Inner circle represents savannah parkland.

set, where few samples reach the same value of the observed species richness. The second-order jackknife estimate climbs more steeply for every dataset than does the first-order jackknife estimate (Fig. 5). The shape of the bootstrap estimator curve departs relatively little

from the observed species accumulation curve. In both cases, plots of singletons and uniques rise quickly, level off, and do not decline. There are more uniques than singletons. Plots of doubletons and duplicates rise more slowly, level off, and begin to fall in the savannah park-

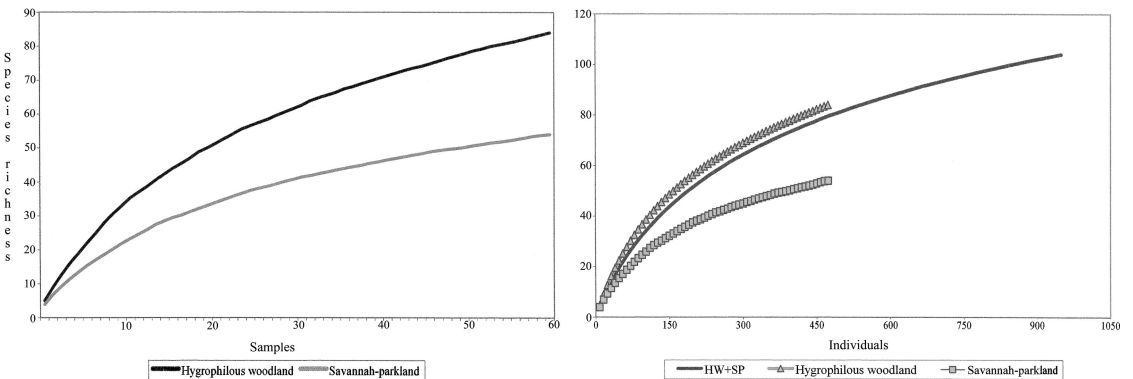


Fig. 4. Mean species accumulation curve and mean individuals accumulation curves for spiders sampled at Mburucuyá National Park, Corrientes, Argentina (2003–2004). The species accumulation curve plots the observed number of species as a function of the number of pooled samples/individuals calculated from 100 iterations of random samples/individuals of the raw data using EstimateS 7.5.0 (Colwell 2004). HW, Hygrophilous woodland; SP, Savannah parkland.

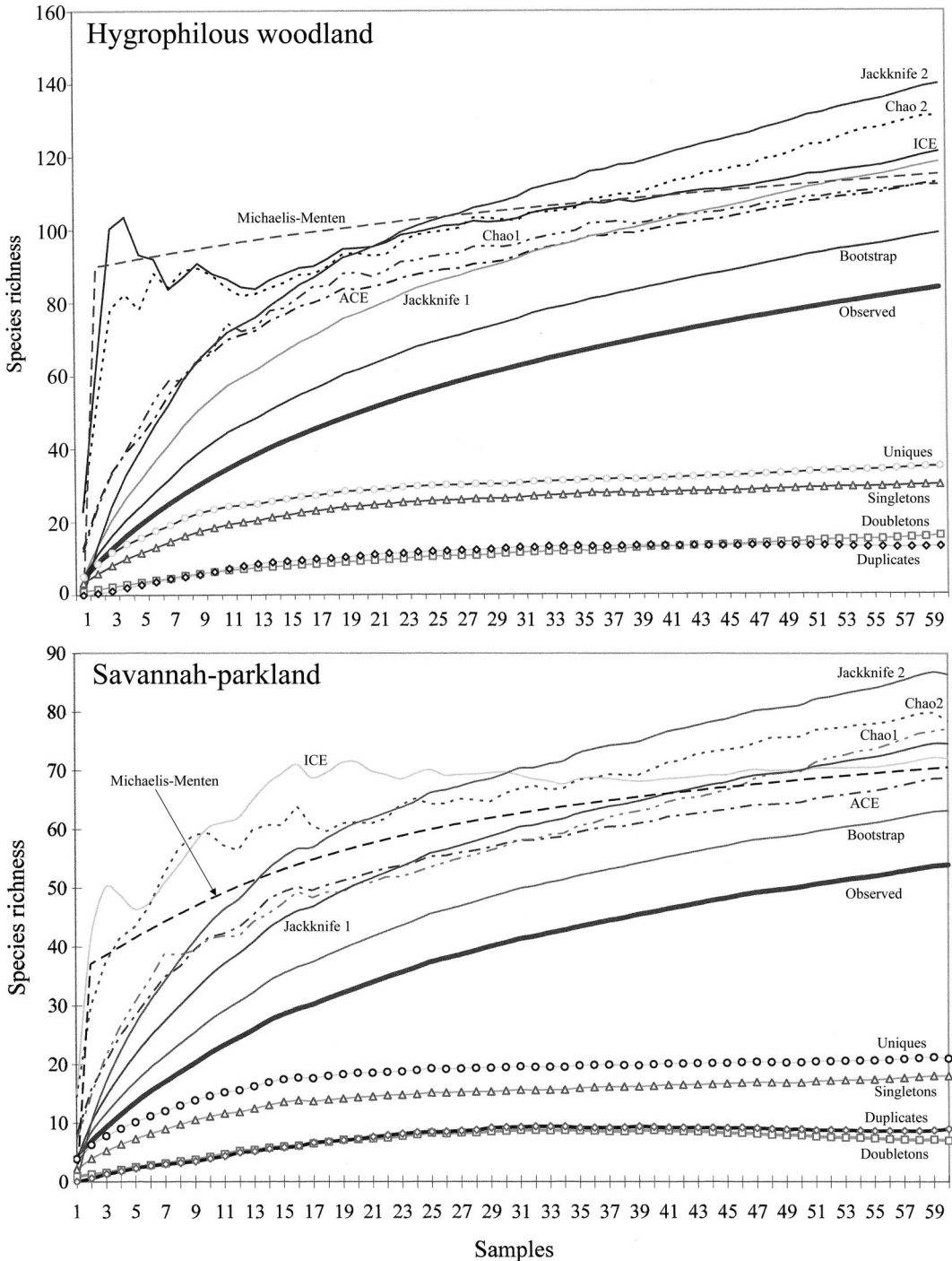


Fig. 5. Plots comparing the performance of eight estimators of species richness with the observed species accumulation curve, using data from the sets of spider samples at Mburucuyá National Park, Corrientes, Argentina (2003–2004). The four curves at the bottom of the graphs plot mean numbers of singletons, doubletons, uniques, and duplicates as a function of cumulative number of samples. For all 13 curves, each point is the mean of 100 values based on 100 randomizations of sample accumulation using order.

land, but in the hygrophilous woodland, the doubletons plot increases and the duplicates plot reach an asymptote.

The second-order jackknife and Chao2 produce the highest estimates for both habitats (Table 1). The other estimators, except the bootstrap, tended to clus-

Table 2. Diversity, evenness, and dominance index for the both communities at Mburucuyá National Park, Corrientes, Argentina (2003–2004) by seasons

	HW-spring	HW-summer	HW-fall	HW-winter	SP-spring	SP-summer	SP-fall	SP-winter
H' (Shannon index)	2.78	3.10	3.28	3.15	2.97	2.12	2.38	2.49
E (evenness)	0.78	0.85	0.87	0.84	0.83	0.72	0.75	0.82
Var H' (variance Shannon)	0.01035	0.00781	0.00850	0.00930	0.00966	0.01241	0.00891	0.01600
S (species richness)	35	38	44	43	35	19	24	21
No. of individuals	138	125	124	133	117	106	140	76
Most abundant (Nmax)	33	20	23	27	25	34	35	26
Berger-Parker index	0.239	0.160	0.185	0.203	0.214	0.321	0.250	0.342
1/Berger-Parker index	4.182	6.250	5.391	4.926	4.680	3.118	4.000	2.923

ter in very similar values, but the ranges spanned by these estimators are smaller for the savannah parkland dataset than for the corresponding hygrophilous woodland dataset (Fig. 5).

According to the species richness estimators (140–100 for the hygrophilous woodland and 86–63 for the savannah parkland), the observed richness (85 and 55, respectively) indicates that more spider species live in the hygrophilous woodland community than in the savannah parkland community. This result is also supported by the observation that the savannah parkland dataset produced a smaller adjusted estimate range, which suggests that the savannah parkland inventory is more nearly complete than the hygrophilous woodland inventory. We found the same pattern when we plotted species accumulations curves using the number of specimens for the independent variable instead of the number of samples (Fig. 4). The hygrophilous woodland curve is steeper than the savannah parkland curve.

According to results from the SPADE program, there are still 11 shared species not discovered in the survey; the 95% confidence interval for the true number of shared species is (35, 66). For the hygrophilous woodland, the method of Chao and Shen (2004) indicates that, if an additional survey with double the size of the original sample is to be conducted, the predicted number of new species would be 28, with a 95% confidence interval between 99 and 144, and would be 14 with a 95% confidence interval of 61–92 for the savannah parkland community.

Indices of Diversity, Evenness, and Dominance. The Shannon diversity and evenness indices showed consistently higher values in the hygrophilous woodland than in the savannah parkland except to spring (Table 2). This higher diversity index also is supported by higher estimated diversity calculated from different nonparametric estimators (Table 1). The Berger-Parker dominance index (Table 2) is higher in the savannah parkland where three lycosid species were abundant in all sampled periods. There was a significant difference between the overall diversity ($t = 7.457$; $P < 0.05$) and when compared by seasons in both communities, with the exception of the spring comparison, when a nonsignificant difference ($t = 1.333$; $P < 0.10$) was detected (Table 2).

Discussion

The spider diversity observed in these two protected habitats of the Eastern Chacoan District of Argentina is rich in spider diversity, with records of 46.67 (Platnick 2007) and 63.64% (Avalos et al. 2006) of all spider families recorded in Argentina and in the Corrientes province, respectively. The high number of immature spiders collected can be explained by the greater seasonality of temperate communities, which fosters narrower species-specific breeding seasons and thus may cause a sample of adults collected in a short period (a few weeks or less) to mimic the dominance of low diversity early successional stages (Coddington et al. 1996).

The habitat type and land use have been shown to have a significant influence on the spider communities (Weeks and Holtzer 2000). The vegetation architecture plays an important role in the species composition found in a habitat (Scheidler 1990), and vegetation that is structurally more complex can sustain a higher abundance and diversity of spiders (Hatley and MacMahon 1980, Green 1999). These statements can be applied to our study, where the overall spider diversity showed a significant difference between both types of habitats over a very short distance. The same difference was observed when we compared spider species diversity by season between studied habitats, with the exception of spring, where there was a lower difference. These findings indicate that the structural diversity of the vegetation may, in some way, influence the spider diversity, as was also shown in the different percentages of the functional groups between the hygrophilous woodland and the savannah parkland. In the hygrophilous woodland, the overall percentage of the three functional groups was more homogeneous than in the savannah parkland, where the ground wanderers were more important and the less-represented were web builders. According to Uetz (1991), Hurd and Fagan (1992), and Withmore et al. (2002), the physical structure of environments has an important influence on the habitat preferences of spider species, especially the web-builder species that need more structural complexity to build their webs. This statement is true in our data because the web builders were more abundant and diverse in the hygrophilous woodland than the savannah parkland. It is possible that ground wanderers were most abundant because

pit falls were active for longer time periods than the other capture methods. The study might be enhanced by improving the protocol of the other sampling techniques.

The difference observed in the spider assemblages between the hygrophilous woodland and surrounding savannah parkland at Mburucuya National Park introduced the possibility that adjacent assemblages can differ, even when there are minor differences in nearest habitat (Underwood and Chapman 1996, Ferrier et al. 1999, Gibb and Hochuli 2002).

The large number of singletons found should not to be confused with rarity, because it may be a result of the patchy distributions. Perhaps these species are cryptic or our sample protocol was not good enough to record them adequately. A high proportion of singletons has also been observed in other spider inventories and studies made by different researchers in tropical and temperate forests and savannahs (Coddington et al. 1996, Toti et al. 2000, Sørensen et al. 2002, Whitmore et al. 2002).

The similarity among the estimators suggest either they were measuring the true species richness or were affected similarly specially in the savannah, as was pointed out in other research (Coddington et al. 1996).

As suggested by the nonparametric species richness estimators and because no species accumulation curves plateaued for the studied habitats, we concluded that, despite our efforts, a significant number of species have not yet been collected. Because the inventory completeness index was higher for the grassland, the rank between the lowest and highest richness estimates was smaller, the observed and estimated richness curves most closely approached an asymptote and small gaps existed among these curves; the grassland was the less diverse and better collected habitat.

The habitats studied are characterized by both natural and intentional disturbance: inundation in the hygrophilous woodland and fire in the savannah parkland. Both habitats may exert control on the communities living there and help to maintain their biodiversity. In fire ecosystems, resident communities (spiders and other arthropod communities) are sometimes significantly different from those in surrounding unburned areas, and studies have shown that sites with recurring fires tend to have a larger number of species and a characteristic species composition that differs from that of unburned and single-fire sites (Moretti 2000). This is another explanation for the fact that the studied habitats differ in spider diversity, have unique families and species, and may also maintain diversity. It indicates that both habitats are important if biodiversity is to be conserved, especially in this Chaco ecoregion where different types of habitats show a patchy distribution, sometimes in very small islets. Because the habitats of Mburucuyá National Park considered in this study did not suffer human alteration more than the biannual intentional fire period controlled by the personnel of the park, the spider community data obtained in this study provide a good

framework for which to compare subsequent systematic studies in the Chaco region, both in disturbed and nondisturbed areas.

Acknowledgments

J.A.C. and G.D.R. thank P. Selden and M. Lindgrin for help and suggestions about the final English version of the manuscript and CONICET for support; G.D.R. and M.P.D. thank Lic. Gilberto Avalos and Universidad Nacional del Nordeste. This study was supported by a scholarship given to G.D.R. by the Secretaría de Ciencia y Técnica de la UNNE.

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Received 4 May 2007; accepted 8 November 2007.

Appendix 1. Total numbers of spider guild, families, genera, species, and individuals sampled from Mburucuyá National Park, Corrientes, Argentina (2003–2004)

Guild/family	Species/morphospecies	HW- spring	HW- summer	HW- fall	HW- winter	HW relative abundance (%)	SP- spring	SP- summer	SP- fall	SP- winter	SP relative abundance (%)
Ground wanderers											
Lycosidae	Lycosid 1	33	12	1	12	11.15	8	34	30	7	17.99
	Lycosid 2	16	4	2	2	4.61	0	0	0	0	0
	Lycosid 3	0	20	23	27	13.46	25	22	35	26	24.60
Gnaphosidae	Gnaphosid 1	1	0	2	1	0.76	1	0	0	1	0.45
Coriniidae	<i>Castianeira</i> sp.	1	1	0	0	0.38	0	0	0	0	0
	Coriniid 1	1	0	0	0	0.19	0	0	0	0	0
	Coriniid 2	0	0	0	0	0	0	0	0	2	0.45
Ctenidae	<i>Trachelas</i> sp.	0	1	0	0	0.19	0	0	0	0	0
	Ctenid 1	1	0	0	0	0.19	0	0	0	0	0
	Ctenid 2	0	0	0	0	0	3	0	0	0	0.68
Zodariidae	<i>Cybaeodamus</i> sp.	0	0	1	2	0.57	1	1	1	0	0.68
Oonopidae	<i>Gamasomorpha</i> sp.	1	0	0	0	0.19	0	0	0	0	0
	<i>Oonopid</i> 1	0	0	0	1	0.19	0	0	0	0	0
	<i>Oonops</i> sp.	0	0	1	1	0.38	0	0	1	0	0.22
Scytodidae	<i>Scytodes</i> sp.	0	0	0	0	0	1	0	2	3	1.36
Palpimanidae	<i>Ottothops payak</i> Grismado & Ramírez, 2002	0	0	1	1	0.38	0	0	0	0	0
Selenopidae	<i>Selenops</i> sp.	0	0	0	0	0	1	0	0	0	0.22
	Total	54	38	31	47	32.69	40	57	69	39	46.69
Plant wanderers											
Salticidae	Salticid 1	5	0	1	2	1.53	1	0	0	5	1.36
	Salticid 2	7	2	2	1	2.30	1	0	0	0	0.22
	Salticid 3	4	2	0	0	1.15	1	0	0	0	0.22
	Salticid 4	1	0	0	1	0.38	1	4	3	1	2.05
	Salticid 5	2	1	0	0	0.57	0	0	1	1	0.45
	Salticid 6	0	0	0	0	0	4	0	0	0	0.91
	Salticid 7	0	4	7	0	2.11	3	3	0	0	1.36
	Salticid 8	0	0	0	0	0	1	0	0	0	0.22
	Salticid 9	0	1	0	0	0.19	0	1	0	0	0.22
	Salticid 10	0	1	0	0	0.19	0	0	0	0	0
	Salticid 11	0	0	0	0	0	0	0	4	0	0.91
	<i>Sarinda marcosi</i> Piza, 1937	0	0	0	1	0.19	0	0	0	0	0
	<i>Aphantochilus</i> sp.	0	0	1	0	0.19	0	0	0	0	0
	<i>Platylarachne</i> sp.	0	0	0	0	0	1	0	3	0	0.91
Thomisidae	<i>Misumenops</i> sp.	1	0	1	0	0.38	0	0	1	0	0.22
	Thomisid 1	0	0	0	0	0	2	0	3	0	1.13
	Thomisid 2	0	0	0	1	0.19	0	0	0	0	0
	<i>Tmarus</i> sp. 1	21	15	11	7	10.38	0	1	0	0	0.22
Pisauridae	<i>Tmarus</i> sp. 2	0	1	2	2	0.96	0	0	0	0	0
	Pisaurid 1	1	0	0	0	0.19	14	2	1	3	4.55
	Pisaurid 2	0	0	0	0	0	1	0	0	0	0.22
Oxyopidae	<i>Oxyopid</i> 1	1	3	1	1	1.15	0	1	0	0	0.22
Sparassidae	<i>Polybetes</i> sp.	0	1	0	0	0.19	0	0	1	0	0.22
Miturgidae	Miturgid 1	0	1	0	0	0.19	1	5	0	0	1.36
Mimetidae	<i>Gelanor</i> sp.	0	2	1	4	1.34	0	0	0	0	0
Philodromidae	<i>Paracleonemis</i> sp.	2	2	3	1	1.53	9	19	15	5	10.93
Anyphaenidae	Anyphaenid 1	1	7	0	0	1.53	6	2	0	0	1.82
	Anypahenid 2	0	0	0	0	0	2	1	0	0	0.68
	Anyphaenid 3	0	0	3	4	1.34	0	0	0	2	0.45
	Anyphaeninae	0	0	0	0	0	0	0	0	3	0.68
	<i>Jessica</i> sp.	1	0	3	0	0.76	7	2	5	0	3.18
	<i>Otoniela quadrivittata</i> (Simon, 1897)	0	0	0	1	0.19	0	0	0	0	0
	Total	47	43	36	26	29.23	55	41	37	20	34.85
Web-builders											
Araneidae	<i>Acacesia</i> sp.	0	1	0	1	0.38	0	0	0	0	0
	<i>Aculepeira</i> sp.	1	4	0	0	0.96	0	0	0	0	0
	<i>Aculepeira travassosi</i> (Soares & Camargo, 1948)	0	0	0	1	0.19	0	0	0	0	0
	<i>Alpaida bicomuta</i> Taczanowski, 1878	0	0	1	0	0.19	0	0	0	0	0
	<i>Alpaida</i> sp.	3	0	0	3	1.15	0	0	0	0	0
	Araneid 1	0	1	0	0	0.19	1	0	0	0	0.22
	Araneid 2	0	6	0	2	1.53	0	1	16	0	3.87
	Araneid 3	0	0	8	14	4.23	2	1	0	0	0.68
	Araneid 4	0	0	5	0	0.96	0	0	0	0	0

Continued on following page

Appendix 1. Continued

Guild/family	Species/morphospecies	HW- spring	HW- summer	HW- fall	HW- winter	HW relative abundance (%)	SP- spring	SP- summer	SP- fall	SP- winter	SP relative abundance (%)
Theridiidae	<i>Araneus</i> sp.	3	1	0	1	0.96	0	3	1	0	0.91
	<i>Argiope argentata</i> (F., 1775)	0	0	0	0	0	0	0	0	2	0.45
	<i>Argiope</i> sp.	0	0	0	0	0	0	0	0	1	0.22
	<i>Cyclosa caroli</i> (Hentz, 1850)	0	1	0	1	0.38	0	0	0	0	0
	<i>Eustala</i> sp.	0	0	0	0	0	0	1	0	0	0.22
	<i>Larinia</i> sp.	0	0	0	0	0	0	2	2	2	1.36
	<i>Metazygia chenevo</i> Levi, 1995	0	0	0	0	0	0	0	1	0	0.22
	<i>Metazygia</i> sp.	0	0	0	0	0	0	0	1	0	0.22
	<i>Metepeira</i> sp.	0	0	1	0	0.19	0	0	0	0	0
	<i>Micrathena</i> sp. 1	6	0	0	0	1.15	0	0	0	0	0
	<i>Micrathena swuainsoni</i>	0	0	2	0	0.38	0	0	0	0	0
	<i>Paravixia audax</i> (Blackwall, 1863)	0	0	1	0	0.19	0	0	0	0	0
	<i>Paravixia</i> sp.	0	1	0	0	0.19	0	0	0	0	0
	<i>Paravixia velutina</i> (Taczanowski, 1878)	1	1	1	0	0.57	0	0	0	0	0
	<i>Pronous</i> sp.	1	2	2	0	0.96	0	0	0	0	0
	<i>Euryopsis spinifera</i> (Mello-Leitão, 1944)	0	3	0	0	0.57	1	0	2	1	0.91
	<i>Faiditus cf. laraensis</i> (González, 1996)	0	0	2	0	0.38	0	0	0	0	0
	<i>Anelosimus</i> sp.	8	9	8	5	5.76	0	0	0	0	0
	<i>Ariannes longissimus</i> Keyserling, 1891	1	0	4	0	0.96	0	0	0	0	0
	<i>Argyrodes</i> sp. 1	0	1	0	0	0.19	0	0	0	0	0
	<i>Argyrodes</i> sp. 2	0	0	1	1	0.38	0	0	0	0	0
	<i>Dipoena</i> sp.	0	0	1	0	0.19	0	0	0	0	0
	Theridiid 1	1	0	0	0	0.19	0	0	0	0	0
	Theridiid 2	0	0	0	0	0	2	0	0	4	1.36
	Theridiid 3	0	0	1	0	0.19	1	0	0	0	0.22
	Theridiid 4	1	1	0	0	0.38	0	0	0	0	0
	Theridiid 5	0	0	0	0	0	2	0	0	0	0.45
	Theridiid 6	0	2	0	0	0.38	1	0	0	0	0.22
	Theridiid 7	0	0	4	4	1.53	1	0	9	2	2.73
	Theridiid 8	0	0	1	0	0.19	0	0	0	0	0
	<i>Theridion</i> sp.	1	0	0	0	0.19	0	0	0	0	0
Hersiliidae	<i>Tama</i> sp.	0	0	0	1	0.19	0	0	0	0	0
Linyphiidae	Erigoninae	0	0	2	1	0.57	0	0	0	0	0
	Linyphiid 1	3	0	0	5	1.53	5	0	1	0	1.36
	Linyphiid 2	0	2	0	0	0.38	1	0	0	2	0.68
	Linyphiid 3	1	0	0	1	0.38	0	0	0	0	0
	Linyphiid 4	0	0	1	1	0.38	0	0	0	0	0
Pholcidae	Pholcid 1	0	1	1	2	0.76	0	0	0	0	0
Tetragnathidae	<i>Chrysometa</i> sp.	0	0	0	1	0.19	0	0	0	0	0
	<i>Leucauge</i> sp.	0	1	3	4	1.53	0	0	0	0	0
	Tetragnathid 1	0	0	1	0	0.19	0	0	0	0	0
Uloboridae	<i>Conifaber guarani</i> Grismado, 2004	0	1	1	1	0.57	0	0	0	0	0
	<i>Uloborus</i> sp.	0	0	1	1	0.38	0	0	0	0	0
Amaurobiidae	Amaurobid 1	4	0	0	0	0.76	0	0	1	2	0.68
Filistatidae	<i>Misionella mendensis</i> (Mello-Leitão, 1920)	0	0	0	1	0.19	0	0	0	0	0
Dictynidae	Dictynid 1	1	5	2	6	2.69	2	0	0	0	0.45
	Total	36	44	55	58	37.11	19	8	34	16	17.53
Unidentified		1	0	2	2	0.96	3	0	0	1	0.91
S (no. of species)		35	38	44	43		35	19	24	21	
N (no. of individuals)		138	125	124	133	100	117	106	140	76	100

HW, hygrophilous woodland; SP, savannah parkland.

Appendix 2. Values of complementarity and similarity indices for the two communities at Mburucuyá National Park, Corrientes, Argentina (2003–2004)

	HW-spring	HW-summer	HW-fall	HW-winter	SP-spring	SP-summer	SP-fall	SP-winter
HW-spring	100% (0) C_J = C_N = C_MH =							
HW-summer	71.93% (16) C_J = 0.304 C_N = 0.418 C_MH = 0.593	100% (0)						
HW-fall	74.60% (16) C_J = 0.254 C_N = 0.275 C_MH = 0.275	73.85% (17) C_J = 0.262 C_N = 0.490 C_MH = 0.761	100% (0)					
HW-winter	74.19% (6) C_J = 0.258 C_N = 0.317 C_MH = 0.401	73.44% (17) C_J = 0.286 C_N = 0.504 C_MH = 0.762	57.38% (26) C_J = 0.450 C_N = 0.599 C_MH = 0.831	100% (0)				
SP-spring	81.36% (11) C_J = 0.228 C_N = 0.180 C_MH = 0.223	78.33% (13) C_J = 0.217 C_N = 0.397 C_MH = 0.616	78.46 (14) C_J = 0.215 C_N = 0.373 C_MH = 0.639	81.82% (12) C_J = 0.200 C_N = 0.408 C_MH = 0.693	100% (0)			
SP-summer	82.61% (8) C_J = 0.200 C_N = 0.361 C_MH = 0.560	76.09% (11) C_J = 0.239 C_N = 0.390 C_MH = 0.561	83.33% (9) C_J = 0.167 C_N = 0.304 C_MH = 0.394	80.77% (10) C_J = 0.192 C_N = 0.351 C_MH = 0.574	68.29% (13) C_J = 0.286 C_N = 0.475 C_MH = 0.638	100% (0)		
SP-fall	79.59% (10) C_J = 0.204 C_N = 0.288 C_MH = 0.433	85.19% (8) C_J = 0.148 C_N = 0.340 C_MH = 0.649	84.75% (9) C_J = 0.133 C_N = 0.280 C_MH = 0.523	82.46% (10) C_J = 0.175 C_N = 0.374 C_MH = 0.693	71.74% (13) C_J = 0.283 C_N = 0.444 C_MH = 0.717	69.70% (10) C_J = 0.303 C_N = 0.634 C_MH = 0.874	100% (0)	
SP-winter	80.85% (10) C_J = 0.191 C_N = 0.196 C_MH = 0.211	88.68% (6) C_J = 0.113 C_N = 0.328 C_MH = 0.606	85.93% (8) C_J = 0.140 C_N = 0.340 C_MH = 0.646	89.66% (21) C_J = 0.164 C_N = 0.411 C_MH = 0.730	69.77% (13) C_J = 0.302 C_N = 0.518 C_MH = 0.793	82.35% (6) C_J = 0.300 C_N = 0.429 C_MH = 0.685	67.65% (11) C_J = 0.324 C_N = 0.454 C_MH = 0.802	100% (0)

See text for definitions of the indices. Index values in parentheses were generated after deleting all singletons found in only one community. C_J, Jaccard index; C_N, Sørensen quantitative index; C_MH, Morisita Horn index.