RESEARCH ARTICLE

The Chacoan bat fauna identity: Patterns of distributional congruence and conservation implications

La identidad de la fauna de murciélagos del Chaco: Patrones de congruencia distribucional e implicancias en su conservación

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ABSTRACT

The aim of this paper is to characterize the Chaco thorn-scrub savanna as a unit, biologically defined by means of its identification as a regional pattern of distributional congruence, through the evaluation of the utility of bat assemblages as biogeographical indicators of the Chaco at regional scale, and to then evaluate this characterization in terms of the conservation value of this habitat. We have considered the whole territory of Paraguay and Bolivia, and the northern of Argentina; that is the entire Chaco biogeographical province, and part of the surrounding biogeographical provinces. We conducted an exhaustive search and constructed a database consisting in 9509 geo-referenced records showing that the bat fauna of the Chaco is richer than previously reported. We used an optimality criterion to identify patterns of distributional congruence determined by the distribution of bats. We recovered several areas that correspond with the Chaco. The areas that are coincident with the Chaco were supported by eight species: *Eptesicus brasiliensis*, *E. diminutus*, *Eumops dabbenei*, *Histiotus velatus*, *Promops centralis*, *P. nasutus*, *Pygoderma bilabiatum*, and *Tonatia bidens*. These results show that bat assemblages are useful as characterizing of regional patterns of distributional congruence. These patterns provide first-step testable hypotheses of areas of endemism for future analyses of neighboring regions or analyses at more inclusive scales. Bat assemblages may be used to characterize the Chaco despite the fact that it was thought this habitat lacked an identity in relation to its bat fauna. The Chacoan nature as a biologically distinctive natural unit is clear now also in terms of regional patterns of distributional congruence of bat species, which provides further evidence for intensifying efforts to protect this endangered habitat.

Key words: Chaco, Chiroptera, optimality criterion, patterns of distributional congruence, South America.

RESUMEN

El objetivo de este trabajo es caracterizar a la provincia biogeográfica Chaqueña como una unidad, definida biológicamente por medio de su identificación como un patrón regional de congruencia distribucional, mediante la evaluación de la utilidad de los ensambles de murciélagos como indicadores biogeográficos del Chaco a escala regional, y luego evaluar esta caracterización en términos del valor de conservación de este hábitat. Se consideró el área completa de Paraguay y Bolivia y el norte de Argentina; es decir, toda la provincia biogeográfica del Chaco, y parte de las provincias biogeográficas que la rodean. Se realizó una búsqueda exhaustiva y se construyó una base de datos consistente en 9509 registros geo-referenciados mostrando que la fauna de murciélagos del Chaco es más rica de lo que se había reportado previamente. Se utilizó un criterio de optimalidad para identificar los patrones de congruencia distribucional determinados por la distribución de los murciélagos. Se recuperaron varias áreas que se corresponden con el Chaco. Las áreas que son coincidentes con el Chaco estuvieron soportadas por ocho especies: *Eptesicus brasiliensis*, *E. diminutus*, *Eumops dabbenei*, *Histiotus velatus*, *Promops centralis*, *P. nasutus*, *Pygoderma bilabiatum*, and *Tonatia bidens*. Estos resultados muestran que los ensambles de murciélagos son útiles como caracterizadores de patrones regionales de congruencia distribucional. Estos patrones proporcionan como primer paso hipótesis de áreas de endemismo que se pueden poner a prueba en análisis futuros de regiones vecinas o análisis a escalas más inclusivas. Los ensambles de murciélagos pueden ser utilizados para caracterizar el Chaco a pesar de que se pensaba que este hábitat carecía de identidad en relación con su fauna de murciélagos. La naturaleza del Chaco como una unidad natural biológicamente distintiva es clara ahora también en términos de patrones regionales de congruencia distribucional de especies de murciélagos, lo que provee de evidencia adicional para intensificar los esfuerzos para proteger este hábitat en peligro.

Palabras clave: América del Sur, Chaco, Chiroptera, criterio de optimalidad, patrones de congruencia distribucional.

INTRODUCTION

Protected areas systems should be implemented considering endemism, species richness, uniqueness of the ecosystem, and the degree of species extinction risk (Parker et al. 1993). Areas containing high concentrations of endemic taxa are important in conservation irrespective of the overall richness of the area (Mares 1992). However, geographic patterns of species richness are greatly better known than geographic patterns of endemism (Kerr 1997). Endemism means restriction of the geographic range of a taxon to a defined area (Anderson 1994, Gaston 1994). An area of endemism (AE), in turn, is defined by the coincident restrictedness of two or more taxa to a geographic area (Platnick 1991). The geographic congruence of species distributional ranges has been interpreted as the result of allopatric speciation in biological communities isolated by the appearance of a biogeographical barrier (Espinosa-Organista & Llorente-Bousquets 1993, Crisci et al. 2000). Thus, AEs reflects past, but also potentially future, speciation events (Fa & Funk 2007). Therefore, AEs are considered the fundamental units of analysis in evolutionary biogeography (Morrone 2009). Besides, because of its geographical isolation, AEs are associated with the evolution of new adaptations in species and communities (Erwin 1991, Vane-Wright et al. 1991, Spector 2002).

Several methods have been proposed over the last years to identify AEs (Morrone 1994, Linder 2001, Szumik et al. 2002, Szumik & Goloboff 2004, Deo & DeSalle 2006, Giokas & Sfenthourakis 2007, Dos Santos et al. 2008). The development of such formalized methods allow biogeographers, not only to evaluate if the traditionally proposed phyto and zoogeographical regions represent coherent units in terms of spatial overlap, but also to discover previously unrecognized regions. Purposely, Szumik et al. (2002) and Szumik & Goloboff (2004) formalized a method that explicitly evaluates the superposition between species geographic ranges by applying an optimality criterion (Szumik & Roig-Juñent 2005).

Being the ultimate goal the identification of AEs, often regional analyses have been performed as first approaches to the delineation of patterns of distributional congruence.

The amplitude of full distributional ranges of species of different taxa is highly variable. Accordingly, at regional scale, it is likely to find species with restricted ranges, which may determine AEs in strict sense (e.g., those included in the analysis of Díaz Gómez 2007), in coexistence with widespread species, whose ranges exceed that region, and which do not determine AEs in strict sense (e.g., some of those included in the analyses of Aagesen et al. 2009, Navarro et al. 2009, Sandoval et al. 2010, Nori et al. 2011, Sandoval 2012, and Szumik et al. 2012). Mammals and particularly bats are good biogeographical indicators and they are important for defining faunal regions (Koopman 1976, 1981, 1982, Proches 2005). Bat distributional records in Argentina are reasonably well documented, thus allowing meaningful biogeographical analysis. Furthermore, Barquez et al. (1999) noted that the Argentinean Chaco has the richest bat fauna when compared with other biogeographical provinces in the country. But, regionally almost all bat species are widely distributed. Bat species have mostly very wide distributional ranges, which may include records in almost entire continents. For this reason, the performing of partial analyses may serve as a first-step to establish biogeographical hypotheses. Nevertheless, although in the case of partial analysis it is possible to assess the degree of overlap between the portions included in the study area of distributional ranges of species, it is important to highlight that some of the areas resulting from the analysis constitute only regional patterns of distributional congruence and do not constitute AEs in strict sense. Yet, all of the obtained areas are equally interesting. While areas of endemism in strict sense provide strong basis for biogeographical regionalization, regional patterns of distributional congruence provide first-step testable hypotheses of areas of endemism for future analyses of neighboring regions or analyses at more inclusive scales (Szumik et al. 2012). As Aagesen et al. (2009) highlighted, we use the optimality criterion to analyze species distribution in a regional context while relaxing the criterion of endemism. Thus, as a result of our analysis, we expect to obtain characterizing species of certain areas (but not endemic to such areas). However, strictly, due to the characteristics

of the distributional ranges of these species (exceeding the limits of the study area), such species should not be considered individually as indicators of the area. But in this paper we propose to evaluate the possibility of characterizing areas that were obtained from the analysis of portions of distributional ranges of species widely distributed, not by individual species, but the by species assemblages that are characterizing these areas. That is, the identity of certain areas in regional analyzes obtained may be determined by the association of certain species, which although widely distributed, are part of a unique assemblage in that part of its range.

The Chaco, as one of the most endangered habitats of the world (Bucher & Huszar 1999, Noss et al. 2002, Zak et al. 2004) has been identified as an area of global importance for conservation (Silva & Guevara 2004). Over the last century human activities have transformed the Chaco into a dense and unproductive thorny scrubland (Bucher & Huszar 1999). The region has been particularly disturbed by severe logging and ranching, in such a way that in many areas, not only the forest has disappeared but also the herbaceous stratum, leaving only thorny bushes and cacti. The Chaco is still being impacted by uncontrolled forest exploitation (associated with timber harvesting, charcoal production, and tannin extraction), overgrazing by uncontrolled livestock, and over-exploitation of wildlife (Morello & Saravia Toledo 1959a, 1959b, Cabrera & Willink 1973, Bucher & Huszar 1999, Zak et al. 2004, The Nature Conservancy et al. 2005). The numbers are alarming: according to Zak et al. (2004), almost 85 % of the original Chacoan forest has been adversely disturbed. Additionally, the Chaco is currently being exposed to massively destructive activities such as extensive soybean crops. Conversely, only 20 % of the territory is included in any kind of reserve. The largest protected areas are in Bolivia (Kaa-Iya National Park) and Paraguay (Chaco Biosphere Reserve). Argentina, in spite of being the country with the largest portion of Chacoan territory, has protected only 9 % of this habitat (Pacheco et al. 1994, Yahnke et al. 1998, Andelman & Willig 2002, Nauman 2006). The situation of these dry forests is even more flimsy because it occurs at the limits of their

potential occurrence due to low precipitation (Hueck 1978).

Recently, in an attempt to recognize patterns of distributional congruence in northern Argentina (from 21° S to 32° S), Szumik et al. (2012) applied the optimality criterion to analyze records of more than 800 species of plants, insects, amphibians, reptiles, birds, and mammals. This analysis, the most complete made up to date, has allow the identification of the Argentinean Chaco as a pattern of distributional congruence. But so far the Chaco as a whole has not been identified as a regional pattern of distributional congruence through the use of a spatially explicit quantitative analysis.

In this paper we analyze bat distributional records from northern Argentina, Bolivia and Paraguay, in an attempt to identify the whole Chaco thorn-scrub savanna as a regional pattern of distributional congruence, through the evaluation of the utility of bat assemblages as biogeographical indicators of the Chaco at a regional scale, and to assess the importance of the Chacoan bat fauna in terms of the conservation value of this endangered habitat.

METHODS

Study area

The entire Chaco biogeographical province is included within the political limits of four countries: Paraguay, Bolivia, Brazil and Argentina (Cabrera & Willink 1973, Cabrera 1976). For the purposes of this analysis we included information from the whole territory of Bolivia and Paraguay, and from all northern Argentina provinces (Catamarca, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Jujuy, La Rioja, Misiones, Salta, San Juan, Santa Fe, Santiago del Estero, and Tucumán) containing portions of Chaco (Fig. 1). Also other vegetational units, that surround the Chaco in these Argentinean provinces, and in Bolivia and Paraguay, were considered.

The Chaco is a very interesting ecosystem, biogeographically and evolutionarily, because it is one of the few places in the world where the transition between the tropics and the temperate zone is not a desert, but a transition of landscapes dominated by dry forests and woodlands (Daly & Mitchell 2000).

The Chaco abuts nine ecoregions (Amazon rainforest, Chiquitano dry forests, Parana river Delta and Islands, Paranean forests, Cerrado, Pantanal, Espinal, Monte, and Yungas forests;; Nauman, 2006). Descriptions of Chacoan habitats can be found in Kerr (1950), Morello & Adámoli (1968, 1974), Ragonese & Castiglioni (1970), Adámoli et al. (1972), Cabrera & Willink (1973), Eiten (1974[1]), Cabrera (1976), Hueck (1978), and Vervoorst (1982[2]) among others.

Briefly, the Chaco lies east of the Andes in northern Argentina, southern Bolivia, and western Paraguay (plus a small portion in Mato Grosso do Sul, Brazil; Prado et
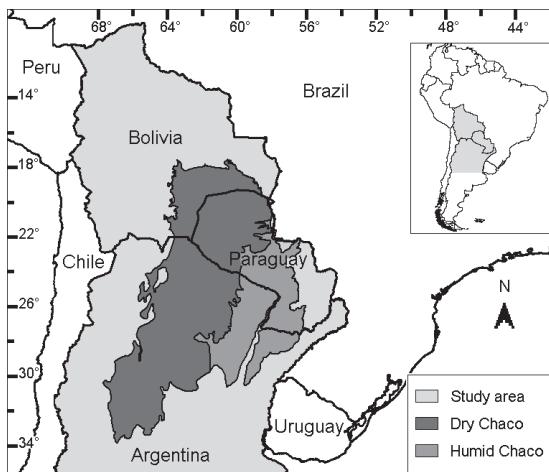
Fig. 1: Map of the study area showing the Chaco biogeographical province and its two sectors delineated in the Burkart et al. (1999)'s ecoregions scheme (see text).

Mapa de la región de estudio en el que se indica la provincia biogeográfica del Chaco y sus dos sectores delineados en el esquema de eco-regiones de Burkart et al. (1999; ver texto).

al. 1992), ranging from tropical (17° S) to subtropical environments (33° S). With a latitudinal extension of more than 1500 km, an average longitudinal extension of 750 km, and an area of over 1000000 km², the Chaco is the second largest natural biome in South America, exceeded only by the Amazon region. It is an open, xerophytic forest over a vast alluvial plain that rises gradually toward the west, with most elevations below 500 m, but reaching 1800 m in the western mountains. The climate is strongly continental. To the west, the rainfall is mainly concentrated in summer (about 350 mm per year, with more on the mountains), whereas to the east, it rains throughout the year (approximately 1200 mm per year). Temperatures decrease from north to south, and east to west. The dominant trees are species of *Schinopsis* Engl. ("quebrachos colorados"), *Prosopis* L. ("algarrobos"), as well as *Aspidosperma quebracho-blanco* Schltr. ("quebracho blanco"), *Ziziphus mistol* Griseb. ("mistol"), and others. Some cacti as *Opuntia quimilo* K. Schum. and *Stetsonia coryne* (Salm-Dick) Britton & Rose are very common, as are the "palo santo" (*Bulnesia sarmientoi* Lorentz ex Griseb.) and the palm trees *Copernicia alba* Morong and *Trithrinax campestris* (Burmeist.) Drude & Griseb.

The Chaco can be divided into longitudinal and latitudinal sectors. According to Cabrera & Willink (1973) and Hueck (1978), there are four such sectors: an eastern district or 'Chaco Oriental' (humid and with a predominance of *Schinopsis balansae* Engl.), a western district or 'Chaco Occidental' (dry and dominated by *Schinopsis lorentzii* (Griseb.) Engl.), a mountainous district or 'Chaco Serrano' (on the mountains of the western edge of the vegetal formation, Sierras Subandinas and Sierras Pampeanas, where *Schinopsis haenkeana* Engl. is predominant) and a southern district or 'Chaco Austral' (characterized by savanna grasslands and the absence of trees). Morello & Adámoli (1968) and Bucher (1982) proposed a different scheme, used by

Barquez & Ojeda (1992) in their analysis of the Chacoan bats, with three longitudinal sectors, the Eastern, the Central and the Western Chaco. Later, when defining the ecoregions, Burkart et al. (1999) divided the Chaco into only two sectors: the Humid (eastern) and the Dry (western) Chaco. We used these last two schemes to discuss our results. Latitudinally, the Chaco can be divided into a northern sector, or 'Chaco Boreal', and a southern sector or 'Chaco Austral' (Myers & Wetzel 1983, Barquez & Ojeda 1992). We also considered these sectors in our discussion.

Most of the Chacoan territory lies within Argentina, where the Chaco thorn scrub savanna extends from the border with Paraguay and Bolivia southward to San Luis province. It occupies an extension of about 675000 km², representing about 60 % of the total area of the Chaco and 25 % of the territory of Argentina. The Paraguayan and Bolivian portions, together, are slightly larger than half of the extension of the Argentinean Chaco. In Paraguay it includes approximately 260000 km² (~ 25 % of the total area of the Chaco and 60 % of the area of the country), and 153000 km² in Bolivia (representing 15 % of the total area of the Chaco, as well as of the country) (Nauman 2006).

Data source

The taxonomy used herein is in accordance to Barquez (2006) for Argentinean bats and to Gardner (2007) for
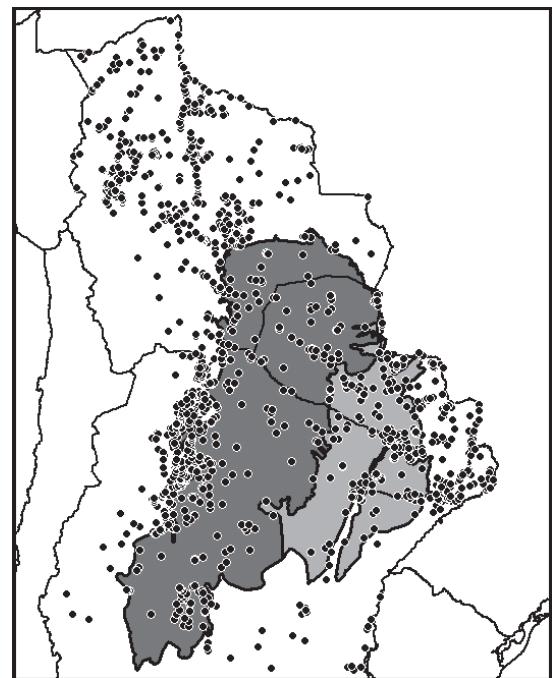
Fig. 2: Map of the study area, which includes Bolivia, Paraguay and northern Argentina, showing the distribution of the geo-referenced records of the 131 bat species that constituted the analyzed database.

Mapa de la región de estudio, que incluye Bolivia, Paraguay y el norte de Argentina, en el que se indica la distribución de los registros geo-referenciados de las 131 especies de murciélagos que constituyeron la base de datos analizada.

other bat species. We used information from records of occurrence for 131 species of bats (Appendix), this is, all bat species reported to date for Paraguay, Bolivia, and northern Argentina. The main sources of data were Anderson (1997), López-González (1998), and Barquez et al. (1999), but the distributional information has been updated taking account of other publications (Emmons 1997, López-González et al. 1998, 2001, Willig et al. 2000, Ten et al. 2001, Aguirre 2002, Siles et al. 2003, Gorresen & Willig 2004, Stevens et al. 2004, Vargas-Espinoza et al. 2004, 2008, Azurduy & Emmons 2005, Acosta & Venegas 2006, Dick et al. 2007, Flores-Saldaña 2008, Barquez et al. 2009, 2011, Díaz & Barquez 2009, Sandoval et al. 2010). Some species recently added (Acosta & Aguanta 2005, Azurduy & Emmons 2005, Emmons et al. 2006) or described from Bolivia (Pacheco et al. 2004, Solari & Baker 2006) were also considered in our analyses although they were cited from only one point of occurrence in that country, and as far as we know they are absent in Argentina and Paraguay (Gardner 2007). In total, our database consisted in 9509 geo-referenced records (Fig. 2). We agree with Tabeni et al. (2004) in the use of geo-referenced records to optimize the quality of the analysis, contrary to the use of distributional maps for the species, which tend to overestimate species diversity in the areas under study (but see Soberón et al. 2000).

Distributional analysis

The method used to identify the regional patterns of distributional congruence, determined by the distribution of bats in northern Argentina, Bolivia and Paraguay, is that proposed by Szumik et al. (2002) and Szumik & Goloboff (2004). This method implements an optimality criterion that explicitly considers the spatial position of the species in the study region. The study region is divided into cells and the groups of cells (= areas) are evaluated by means of an index which is calculated for each species and depends on the adjustment of the distribution of the species to an area. The obtained values are combined for all the species that contribute to the area to obtain the value of endemicity (score) of the area. Only the areas with the maximum endemism values (scores) are retained. This optimality criterion is implemented in the computer program NDM and its viewer VNDM (Goloboff 2005, available at http://www.zmuc.dk/public/phylogeny).

We analyzed the matrix of georeferenced data using grids with cells of different sizes (0.5, 0.75, 1, 1.25, 1.5, 1.75, and 2 degrees of latitude-longitude), and considering different values of filler for assumed and inferred presences (0 and 0, 20 and 40, 40 and 60, 60 and 80, 80 and 100, respectively; see program

TABLE 1

Search parameters (see Materials and Methods) and patterns of distributional congruence obtained that correspond with the Chaco biogeographical province (and that are discussed here). Abbreviations are as follows: CS: cell size (the side size in latitude-longitude degrees is given); A-I: values for assumed and inferred presences.

Parámetros de búsqueda (ver Materiales y Métodos) y áreas de endemismo obtenidas que corresponden con la provincia biogeográfica Chaqueña de manera más o menos precisa (y que son discutidas en el presente trabajo). Las abreviaturas son las siguientes: CS: tamaño de celda (se presenta el tamaño de lado en grados de latitud-longitud); A-I: valores para presencias asumidas e inferidas.

| Search parameters | | Chacoan regional patterns of distributional congruence | | | | | | | |
CS	A-I	*E. brasiliensis*	*E. diminutus*	*E. dabbenei*	*H. velatus*	*P. centralis*	*P. nasutus*	*P. bilabiatum*	*T. bidens*
2°	0-0	0.708	-	-	0.662	0.85	-	0.73	0.75
		-	0.82	0.82	-		0.791	-	-
1.75°	20-40	0.622	-	-	-	0.85	-	0.475	0.651
		-	0.794	0.762	-		0.707	-	
1.75°	0-20	0.676	-	-	-	0.831	-	-	0.746
1.75°	0-0	0.695	-	-	-		0.877	-	0.763
1.5°	80-100	0.667	-	-	-	0.785	-	0.454	0.653
1.5°	60-80	-	0.763	0.799	-		0.669	-	-
1.5°	40-60	0.652	-	-	-	0.644	-	0.332	0.831
		-	0.812	0.764	-	-	0.624	-	-
1.5°	20-40	-	-	-	-	-	-	-	-
1.5°	0-20	-	-	-	-	-	-	-	-
1.5°	0-0	-	-	-	-	-	-	-	-

documentation). We carried out the endemicity analysis by means of a heuristic search and default parameters: founding groups of cells by adding/eliminating one cell at a time, saving groups defined by two or more endemic species, and with scores higher or equal to 2.0. Groups of cells with more than the 50 % of species in common were ruled out, obviously retaining those with highest score, and groups of cells with a score up to 1 % inferior were stored in memory. We obtained consensus areas using 50 % of similarity in species against any of the other areas. The results were mapped using the Global Mapper v11.02 program.

RESULTS

We were able to obtain patterns of distributional congruence with all the grid sizes used. With cells of 0.5º x 0.5º, 0.75° x 0.75°, 1° x 1° and 1.25° x 1.25°, we obtained only local patterns of distributional congruence, limited to Bolivian territory, which will not be presented or discussed here. With other cell sizes, we obtained remarkable results, i.e., regional patterns of distributional congruence (some of them presented in Table 1). So, for this spatial scale all grids with cells larger than 1.5º latitude-longitude are useful to obtain regional patterns of distributional congruence.

Several of the obtained patterns are very interesting because they constitute areas that are congruent with conventional vegetational units, which were not defined based either in a numerical or explicit criterion, or in their bat fauna.

We found areas that correspond to the Chaco with grids with cell sizes of 1.5°, 1.75º, and 2º latitude-longitude (Table 1). Areas corresponding to more humid forests were also recovered with grids with cell sizes of 1.5º, 1.75º, and 2º latitude-longitude, but these will be discussed elsewhere.

Chacoan patterns of distributional congruence

The areas coincident with the Chaco (Fig. 3) were recovered ten times (Table 1) and are supported by eight species, *Eptesicus brasiliensis* (Desmarest), *E. diminutus* Osgood, *Eumops dabbenei* Thomas, *Histiotus velatus* (I. Geoffroy St.-Hilaire), *Promops centralis* Thomas, *P. nasutus* (Spix), *Pygoderma bilabiatum* (Wagner), and *Tonatia bidens* (Spix). *Eptesicus brasiliensis* is an almost exclusively Chacoan species in Argentina and Paraguay, where there are few records outside the Chaco
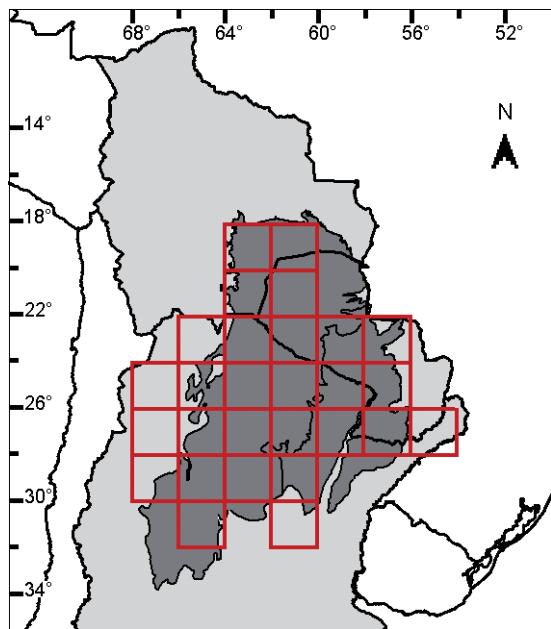
Fig. 3: Map of the study area schematizing one of the ten obtained patterns of distributional congruence that are coincident with the Chaco biogeopraphical province (cell size: 1° latitude-longitude).

Mapa de la región de estudio en el que se esquematiza uno de los diez patrones de congruencia distribucional obtenidos que son coincidentes con la provincia biogeográfica del Chaco (tamaño de celda: 1° latitud-longitud).

(Fig. 4); until now, there are no records of *E. brasiliensis* in Bolivia (Davis & Gardner 2007). *Eptesicus diminutus*, *E. dabbenei*, and *P. nasutus* have most of their occurrence points in Argentina in the Chaco, but they were also recorded in other vegetational units; however, most of their non Chacoan occurrence points are peripheral to the Chaco (Fig. 4). In Paraguay, most records of *E. diminutus* and *P. nasutus*, and all records of *E. dabbenei*, are from the Chaco (Fig. 4). Neither *E. diminutus* nor *E. dabbenei* were recorded in Bolivia (Davis & Gadner 2007, Eger 2007), although the Argentinean records of these species are very close to the political boundaries between the two countries (Fig. 4). *Promops nasutus* has most of their occurrence points in Bolivia in the Chaco, but it was also rarely recorded in other vegetational units; however, these non Chacoan records are peripheral to the Chaco (Fig. 4). In Paraguay, Bolivia, and Argentina, *H. velatus* was barely recorded and has some Chacoan records, but it was also recorded in forested natural units others than the Chaco, although
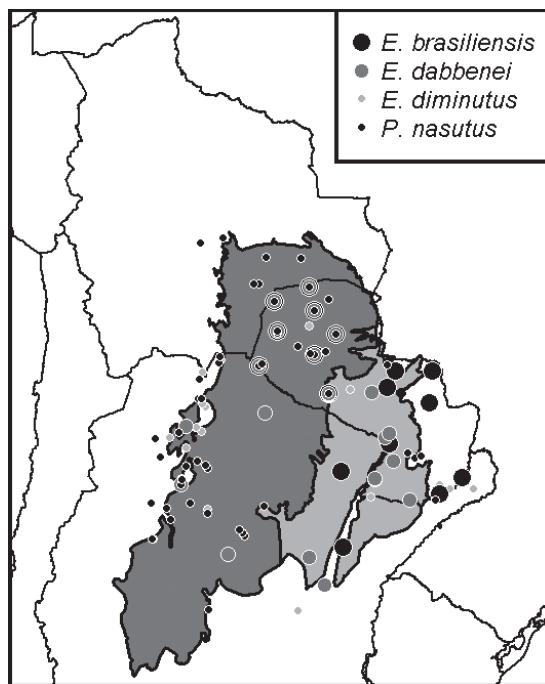
Fig. 4: Map of the study area showing the known occurrence records of four species of the eight that characterize the Chacoan pattern of distributional congruence: *E. brasiliensis*, *E. dabbenei*, *E. diminutus*, and *P. nasutus*. Distributional ranges of these four species in the study area have a remarkable fit with the Chacoan biogeographical province.

Mapa de la región de estudio en el que se indican los registros de ocurrencia conocidos de cuatro de las ocho especies que caracterizan los patrones de congruencia distribucional chaqueños: *E. brasiliensis*, *E. dabbenei*, *E. diminutus* y *P. nasutus*. Los rangos distribucionales de estas cuatro especies en la región de estudio presentan un ajuste notable con la provincia biogeográfica del Chaco.

almost all these records are peripheral to the Chaco (Fig. 5). *Promops centralis* was recorded mainly in Chacoan localities, mostly in the Paraguayan Humid and Dry Chaco and less in the Bolivian Dry and Argentinean Humid Chaco (Fig. 5). *Pygoderma bilabiatum* was recorded mostly in the Paraguayan Humid Chaco, and in the adjacent Argentinean Paranean forests, and less in the Bolivian Dry Chaco and the adjacent Bolivian and Argentinean Yungas forests; apparently, its presence in the Chaco is only marginal: all the points of occurrence in forested habitats others than the Chaco (Paranean and Yungas forests) are marginal to the Chaco (Fig. 5). In Argentina, *T. bidens*

was recorded in Chacoan localities, but also in Yungas and Paranean habitats, been all the non Chacoan records very close to the Chaco. In Paraguay, this species was recorded almost exclusively in Chacoan localities. However, in Bolivia all the known records are from the north of the country (Fig. 5).

Histiotus velatus contributes to only one of the ten equivalent recovered areas coincident with the Chaco (with an individual score of 0.662; Table 1). *Eptesicus diminutus*, *E. dabbenei* and *Pygoderma bilabiatum* contributes between 0.332 (individual score of *P bilabiatum*) and 0.82 (individual scores of *E. diminutus* and *E. dabbenei*) to the score of four of the recovered areas (Table 1). *Promops centralis* and *P. nasutus* contribute between 0.624 (*P. nasutus*)
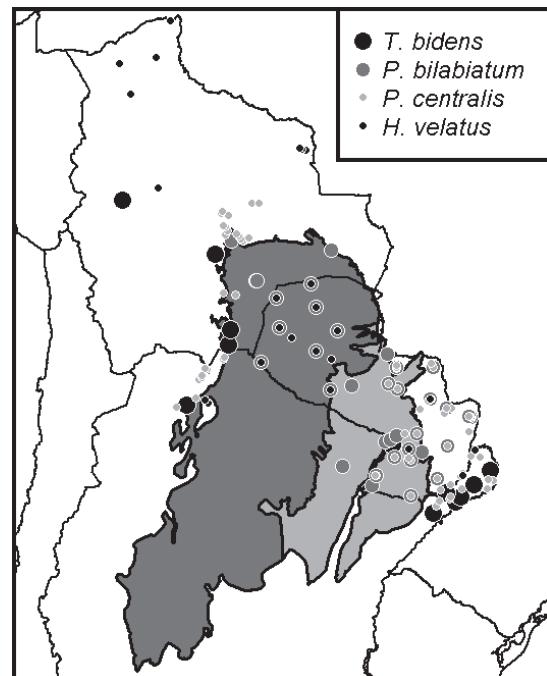

Fig. 5: Map of the study area showing the known occurrence records of four species of the eight that characterize the Chacoan pattern of distributional congruence: *T. bidens*, *P. bilabiatum*, *P. centralis*, and *H. velatus*. Distributional ranges of these four species in the study area have a number of records outside the Chacoan biogeographical province.

Mapa de la región de estudio en el que se indican los registros de presencia conocidos de cuatro de las ocho especies que caracterizan los patrones de congruencia distribucional chaqueños: *T. bidens*, *P. bilabiatum*, *P. centralis* y *H. velatus*. Los rangos distribucionales de estas cuatro especies en la región de estudio presentan un cierto número de registros por fuera de la provincia biogeográfica del Chaco.

and 0.85 (*P. centralis*) to the score of five of the recovered areas (Table 1). Finally, *E. brasiliensis* and *T. bidens* contribute between 0.622 (individual score of *E. brasiliensis*) and 0.831 (individual score of *T. bidens*) to the score of six of the recovered areas (Table 1).

DISCUSSION

Species richness

In order to build up the database that was later analyzed using the optimality criterion, it was necessary not only to review specimens deposited in museums, but also to see previously published work. As a result, information that was outdated and/or scattered was updated and compiled, contributing to the current knowledge of species richness in the whole Chaco.

More than a quarter of the South American bat fauna occurs in the "Gran Chaco" biogeographical province (Barquez & Ojeda 1992). Myers & Wetzel (1983) have mentioned 38 species inhabiting the Chaco Boreal, and Barquez & Ojeda (1992) have mentioned 44 inhabiting the Chaco Austral (they mentioned 43 species, but the treatment of *Histiotus laephotis* as a full species increases the number to 44). After Barquez & Ojeda (1992), Barquez (2006) added *Myotis rubber* (É. Geoffroy St.-Hilaire), *Cynomops abrasus* (Temminck), and *C. planirostris* (Peters) to the Argentinean Chaco, but did not include *Diaemus youngi* (Jentink), *Glossophaga soricina* (Pallas) and *Eumops auripendulus* (Shaw), therefore considering that there are 44 species of bats in the Argentinean Chaco (Table 2). For the Paraguayan Chaco, Barquez & Ojeda (1992) mentioned 34 species, but later López-González (1998) mentioned 48. For the Bolivian Chaco, Barquez & Ojeda (1992) mentioned 10 species, and Anderson (1997) 32, suggesting other 11 species as probable (Table 2). In summary, almost 60 species are present in the Chaco thorn-scrub savanna; this is, as stated by Barquez & Ojeda (1992), more than a quarter of the almost 250 bat species recorded for South

TABLE 2

Bat species recorded by different authors in the latitudinal sectors of the Chaco. X indicates that reliable records of the species exist; X* indicates that the author has mentioned that unconfirmed data make the species presence probable; P indicates that the species would be present according with the area considered by the author, but there are no punctual records confirming its presence. A 1997: Anderson (1997); B 2006: Barquez (2006); B&O 1992: Barquez & Ojeda (1992); L-G 1998: López-González (1998); M&W 1983: Myers & Wetzel (1983).

Especies de murciélagos registradas por diferentes autores en los sectores latitudinales del Chaco. X indica que existen registros fehacientes de la especie; X* indica que el autor ha mencionado que datos no confirmados hacen la presencia de la especie probable; P indica que la especie estaría presente de acuerdo al área considerada por el autor, pero no hay registros puntuales que confirmen su presencia. A 1997: Anderson (1997); B 2006: Barquez (2006); B&O 1992: Barquez & Ojeda (1992); L-G 1998: López-González (1998); M&W 1983: Myers & Wetzel (1983).

Portions of the Chaco	Argentina = Chaco Austral		Chaco Boreal	Paraguay (part of Chaco Boreal)		Bolivia (part of Chaco Boreal)	
Species	B&O 1992	B 2006	M&W 1983	B&O 1992	L-G 1998	B&O 1992	A 1997
P. macrotis	-	-	X	X	X	X	X
N. albiventris	X	X	X	X	X	-	P
N. leporinus	X	X	X	X	X	X	X
A. caudifer	-	-	-	-	X	-	X
A. fimbriatus	X	X	-	-	X	-	-
A. lituratus	X	X	X	X	X	-	P
A. planirostris	X	X	X	X	X	X	X
A. obscurus	-	-	-	-	-	-	P
C. perspicillata	X	X*	X	X	X	X	X

TABLE 2. Continuation

Portions of the Chaco	Argentina = Chaco Austral		Chaco Boreal	Paraguay (part of Chaco Boreal)		Bolivia (part of Chaco Boreal)	
Species	B&O 1992	B 2006	M&W 1983	B&O 1992	L-G 1998	B&O 1992	A 1997
C. auritus	X	X	X	X	X	-	X
D. rotundus	X	X	X	X	X	-	X
D. youngi	X	-	-	-	X	-	P
G. soricina	X	-	X	X	X	X	X
L. brasiliense	-	-	-	-	X	-	-
L. sylvicolum	-	-	-	-	X	-	P
P. discolor	-	-	X	X	X	-	X
P. hastatus	-	-	X	-	-	X	P
P. dorsalis	-	-	X	-	-	X	X
P. lineatus	X	X	X	-	X	X	X
P. bilabiatum	-	-	-	-	X	-	X
S. erythromos	X	X	-	-	-	-	X
S. lilium	X	X	X	X	X	X	X
T. bidens	X	X	X	X	X	-	-
D. ega	X	X	X	X	X	-	X
E. brasiliensis	X	X	-	-	-	-	-
E. diminutus	X	X*	-	-	X	-	-
E. furinalis	X	X	X	X	X	-	X
H. laephotis	X	X	-	-	X	-	-
H. macrotus	X	X	-	-	-	-	-
H. montanus	X	X	-	-	-	-	-
H. velatus	-	-	-	-	X	-	X
L. blossevillii	X	X	X	X	X	-	X
L. cinereus	X	X	X	X	X	-	X
M. albescens	X	X	X	X	X	-	X
M. dinellii	X	X	-	-	-	-	P
M. keaysi	X	X	-	-	-	-	X
M. nigricans	X	X	X	X	X	X	X
M. riparius	X	X	X	X	X	-	P
M. ruber	-	X	-	-	X	-	-
M. simus	X	X	X	X	X	-	P
C. abrasus	-	X	X	X	X	-	-
C. paranus	X	X	-	-	-	-	-
C. planirostris	-	X*	X	X	X	-	X
E. auripendulus	X	-	X	X	X	-	P
E. bonariensis	X	X	X	-	X	-	X
E. dabbenei	X	X	X	X	X	-	-
E. glaucinus	X	X	X	X	X	-	X
E. patagonicus	X	X	-	X	X	-	-
E. perotis	X	X	X	X	X	-	-
M. temminckii	X	X	X	X	X	-	X

TABLE 2. Continuation

Portions of the Chaco	Argentina = Chaco Austral		Chaco Boreal	Paraguay (part of Chaco Boreal)		Bolivia (part of Chaco Boreal)	
Species	B&O 1992	B 2006	M&W 1983	B&O 1992	L-G 1998	B&O 1992	A 1997
M. c. bondae	-	-	-	-	X	-	-
M. molossus	X	X	X	X	X	-	X
M. rufus	X	X	X	X	X	-	P
N. aurispinosus	-	-	-	-	-	-	X
N. laticaudatus	X	X	X	X	X	-	X
N. macrotis	X	X	X	X	X	-	X
P. centralis	X	X	X	X	X	-	X
P. nasutus	X	X	X	X	X	-	X
T. brasiliensis	X	X	X	-	X	-	-
TOTAL = 59 SPP	44	44	38	34	48	10	43
PERCENT	74.6	74.6	64.4	57.6	81.4	16.9	72.9

America (Gardner 2007). The Argentinean Chaco contains 44 species of bats, making this the most diverse region of Argentina with regard to bats (Barquez et al. 1999, Barquez 2006). Twenty four of these species were also recorded in the Bolivian Chaco (not considering eight of probable presence) and 37 in the Paraguayan Chaco (Anderson 1997, López-González 1998).

In their study, Barquez & Ojeda (1992) established that the Western and Eastern Chaco holds the largest number of species of the whole Chaco in Argentina. They have pointed out that 31 species are present in each portion, whereas the Central Chaco contains only 14 (Barquez & Ojeda 1992). They assumed that differences in richness are likely related to the contact of the Chaco with the humid and transitional habitats that occur adjacent to the Western and Eastern sectors and to the contributions of these habitats to the bats assemblages of those portions. They conclude that 11 species (*Artibeus planirostris* (Spix), *Diaemus youngi*, *Eumops bonariensis* (Peters), *E. glaucinus* (Wagner), *Histiotus macrotus* (Poeppig), *H. montanus* (Philippi & Landbeck), *Myotis keaysi* J. A. Allen, *M. dinellii* Thomas (cited as *M. levis* I. Geoffroy St.-Hilaire), *Nyctinomops macrotis* (Gray), *Sturnira erythromos* (Tschudi), and *Tonatia bidens*) are restricted to the western portion (which is in close proximity with

the Yungas rainforests), and that 12 species (*Artibeus fimbriatus* Gray, *A. lituratus* (Olfers), *Carollia perspicillata* (Linnaeus), *Cynomops paranus* (Thomas), *Eptesicus brasiliensis*, *Eumops auripendulus*, *Glossophaga soricina*, *Myotis simus* Thomas, *Noctilio albiventris* Desmarest, *Nyctinomops laticaudatus* (É. Geoffroy St.-Hilaire), *Promops centralis*, and *Platyrrhinus lineatus* (É. Geoffroy St.-Hilaire) occur exclusively in the eastern portion, next to the southern limits of the Paranean and gallery forests. They have also listed species that are present both in the western and eastern portions, but that are not recorded in the central portion (*Chrotopterus auritus* (Peters), *Dasypterus ega* (Gervais), *Eptesicus diminutus*, *Lasiurus blossevillii* (Lesson & Garnot), *Lasiurus cinereus* (Beauvois), and *Molossus rufus* (É. Geoffroy St.-Hilaire)) (Barquez & Ojeda 1992). Today, with the new subdivision of the Chaco into two ecoregions, the Dry Chaco (roughly equivalent to the Western Chaco), holds 35 species, whereas the Humid Chaco (roughly equivalent to the Eastern Chaco), holds 29 species (Table 3).

Distributional analysis

Koopman (1982) delimited nine biogeographical areas for South America based on distribution of bats and vegetation

TABLE 3

Bat species recorded in the sectors of the Chaco as ecoregion according with updated records. X indicates that reliable records of the species exist; X* indicates that the author has mentioned that unconfirmed data make the species presence probable; P indicates that the species would be present according with the area considered by the author, but there are no punctual records confirming its presence.

Especies de murciélagos registradas en los sectores del Chaco como eco-región de acuerdo a registros actualizados. X indica que existen registros fehacientes de la especie; X* indica que el autor ha mencionado que datos no confirmados hacen la presencia de la especie probable; P indica que la especie estaría presente de acuerdo al área considerada por el autor, pero no hay registros puntuales que confirmen su presencia.

Sectors of the Chaco	Dry Chaco			Humid Chaco	
Species	Argentina	Paraguay	Bolivia	Argentina	Paraguay
N. albiventris	-	-	P	X	X
N. leporinus	X	X	X	X	X
A. caudifer	-	-	X	-	X
A. fimbriatus	-	-	-	X	X
A. lituratus	-	-	P	X	X
A. planirostris	X	-	X	X	X
C. perspicillata	-	-	X	X*	X
C. auritus	X	X	X	X	X
D. rotundus	X	X	X	X	X
D. youngi	-	X	P	-	X
G. soricina	-	-	X	-	X
P. lineatus	-			X	X
P. bilabiatum	-	-	X	-	X
S. erythromos	X	-	X	-	-
S. lilium	X	X	X	X	X
T. bidens	X	X	-	-	X
D. ega	X	X	X	X	X
E. brasiliensis	X	X	X	X	X
E. diminutus	X*	X	-	-	X
E. furinalis	X	X	X	X	X
H. laephotis	X	X	-	-	-
H. macrotus	X	-	-	-	-
H. montanus	X	-	-	-	-
H. velatus	-	-	X	-	X
L. blossevillii	X	X	X	X	X
L. cinereus	X	X	X	-	X
M. albescens	X	X	X	X	X
M. dinellii	X	-	P	-	-
M. keaysi	X	-	X	-	-
M. nigricans	X	X	X	X	X
M. riparius	X	X	P	X	X
M. ruber	-	-	-	X	X

TABLE 3. Continuation

Sectors of the Chaco	Dry Chaco			Humid Chaco	
Species	Argentina	Paraguay	Bolivia	Argentina	Paraguay
M. simus	-	-	P	X	X
C. abrasus	X	-	-	-	X
C. paranus	-	-	-	X	-
C. planirostris	X*	X	X	-	X
E. auripendulus	-	X	P	-	X
E. bonariensis	X	-	X	-	X
E. dabbenei	X	X	-	X	X
E. glaucinus	X	X	X	-	X
E. patagonicus	X	X	-	X	X
E. perotis	X	X	-	X	X
M. temminckii	X	X	X	X	X
M. molossus	X	X	X	X	X
M. rufus	X	X	P	X	X
N. laticaudatus	X	X	X	X	X
N. macrotis	X	X	X	-	-
P. centralis	-	-	X	X	X
P. nasutus	X	X	X	X*	X
T. brasiliensis	X	-	X	X	X
TOTAL = 50 SPP	35	28	37	29	41
PERCENT	70.0	56.0	74.0	58.0	82.0

patterns. He sustained that the Argentinean bat fauna could be almost all included within the zoogeographic "Patagonian subregion", and just a little part would be included in the Eastern Brazilian Highlands and Coast subregions, in northeastern Argentina. Barquez et al. (1999) considered that Koopman's division is no longer plausible, and pointed out that the Chacoan element is pronounced and forms a great faunal ecotone between the subtropical forests, being distinctive from the Patagonian subregion of Koopman (Barquez et al. 1999). According to their analysis, however, at that time Barquez et al. (1999) maintained the idea that bats are not of great utility to delineate faunal regions. They considered that the Argentinean Chaco cannot be considered as a faunal region for bats, and treated it as an ecotonal, southern, semiarid extension of the Yungas rainforests to the west and the Paranean forests to the east (Barquez et al. 1999).

Gallardo (1979) demonstrated that amphibian and snakes show a high level of endemism in the Chaco. For birds, as for individual species of bats, it seems that there is a low level of endemicity (Straube & Di Giacomo 2007). The species of birds that inhabit the Chaco tend to be widely distributed over South America (Short 1975), as well as the bats from the Chaco. Most species of bats from the Chaco biogeographical province have broad distributions in South America and occur in diverse habitats (Koopman 1982, Myers & Wetzel 1983). As noted by Myers & Wetzel (1983), this apparently common pattern of low endemicity rates between birds and bats may be the result of the increased vagility of volant vs. non volant vertebrates and the absence of barriers (Straube & Di Giacomo 2007), or more precisely, the inefficiency of barriers that may isolate populations of species of other taxa less vagile. Several authors (Koopman 1982,

Myers & Wetzel 1983, Barquez & Ojeda 1992) have mentioned that the Chaco seems to have a lack of endemic species of bats. Barquez et al. (1999) pointed out that three species are restricted to the Chaco in Argentina: *Eptesicus brasiliensis*, *Cynomops paranus*, and *Promops centralis*, but later Barquez (2006) included the distribution of the former two to other regions in the country. *Promops centralis* remains as endemic, but only for the eastern portion of the Chaco in Argentina, and not for the entire region (Barquez et al. 1999) and is not exclusive of the Chaco in Paraguay or Bolivia (Anderson 1997, López-González 1998). Briefly, as mentioned by Myers & Wetzel (1983), the unique composition of the Chacoan bat fauna seemed to result from the deletion of species from neighboring areas, rather than from the differentiation or inclusions of new elements.

However, according to our analysis, bat assemblages are good indicators of regional patterns of distributional congruence that are coincident with the Chaco biogeographical province. We have been able to identify the Chaco as a regional pattern of distributional congruence analyzing bat records. Although this biogeographical province seems not to have exclusive species, it does have a set of typical species allowing defining it as a natural unit. This faunal assemblage, although not as rich in species as its tropical rainforest counterparts, is distinctive in species composition and has its own identity.

The reasons for this apparent contradiction between exclusive and typical species may be those pointed out by Barquez & Ojeda (1992) and Willig et al. (2000). Although there are not exclusive species in the Chaco, Barquez & Ojeda (1992) found a group of species whose optimum abundance seems to correspond well with this region in Argentina. According to them, the central portion of the Argentinean Chaco reflects the optimum occurrence for 11 species, which can be rated as common or abundant. We have identified regional patterns of distributional congruence that are coincident with the Chaco and these areas are supported by eight species (Table 1). These species are not the same as listed by Barquez & Ojeda (1992), but, like those, all are widely distributed species. According to Barquez & Ojeda (1992), the important thing for species being considered as characteristic of the Chaco would

be their relative abundance. The eight species that are indicators of Chacoan regional patterns have records outside the Chacoan habitat, but these are mostly marginal records at the limits of the main distributional area resulting in high values of individual endemicity scores. Thus, we could refer to this group of species as "Chacoan species", despite its presence in surrounding areas. In turn, Willig et al. (2000) found that strong differences exist in the Paraguayan chiropteran fauna between sites East (mesic) and West (xeric) of the Rio Paraguay. They argued that these differences are related to dominance by molossids and vespertilionids in dry regions, versus phyllostomids in mesic regions. Three of our eight Chacoan indicator species are molossids (*Eumops dabbenei*, *Promops centralis*, and *P. nasutus*), three are vespertilionids (*Eptesicus brasiliensis*, *E. diminutus*, and *Histiotus velatus*), and there are only two phyllostomids (*Pygoderma bilabiatum* and *Tonatia bidens*). Of our eight indicator species, molossids plus vespertilionids represent 75 % of the species.

Although in our study region the identified characterizing species have a distributional area more or less restricted to the Chacoan biographic province, in a larger spatial context this is not so. Because distributional ranges of most bat species included in this analysis continue outside the study region (i.e., extending over other American countries), it seems reasonable to criticize the present study arguing that the study region is inadequate or not natural, or that the selected taxon (bats) is not appropriate for this kind of analysis. However, as stated by Szumik et al. (2012), this would be equivalent to criticize phylogenetic analyses for dealing with possibly incomplete monophyletic groups. Our analysis aims to hypothesize relationships between cells in the study area and "nothing is stated or implied about cells that would occupy an extended grid" (Szumik et al. 2012, p. 319) Besides, although all the eight species that characterize areas tightly related to the Chaco (*Eptesicus brasiliensis*, *E. diminutus*, *Eumops dabbenei*, *Histiotus velatus*, *Promops centralis*, *P. nasutus*, *Pygoderma bilabiatum*, and *Tonatia bidens*), have ranges that exceed to lesser or greater extent the Chacoan biogeographical province when the entire South American continent is considered the complete assemblage

of species is characteristic only of areas closely related to the Chaco. Undoubtedly, inclusion of other biomes will led to obtain other results, but will no necessarily affect the ability to delineate the Chaco as a pattern of distributional congruence or most probably as part of a composite area of endemism (e.g., the recently proposed new biogeographical province known as "Seasonally Dry Tropical Forests" of South America, which currently would include the Eastern Chaco, among other forest formations; Prado 2000). Thus, a priori, we think that the results are robust despite the selection of outlier areas. Nevertheless, it would be very interesting to include all biomes in South America and to formally test the robustness of these results.

Therefore, it is important to note that the species that determine the patterns of distributional congruence identified through the analysis are characterizing species and not necessarily endemic species of those areas. A characterizing species may or may not be endemic to an area. Therefore, although there are not bat species endemic to the Chaco, it is possible to consider some bat species assemblages as characterizing of the Chaco. An endemic species means that the species is native to a region and occurs there and only there. A species that is endemic to an area is found nowhere else. According to this, it is well known that the Chaco lacks endemic bat species. On the other hand, the term "characterizing species" is not equivalent in the sense that it is not expected that these species to be endemic to the area they define. The method chosen to test the hypothesis of bat assemblages as indicators of regional patterns of distributional congruence was developed within the context of areas of endemism. We used this method because it allows assessing, through an optimality criterion, the degree of overlap between the distributional areas of species, but it is important to note that the areas resulting from the analysis constitute only regional patterns of distributional congruence and not areas of endemism in strict sense, but possibly patches of a bigger area of endemism. Only those areas determined by the distributional areas of species of restricted ranges would constitute areas of endemism in strict sense. The NDM/VNDM program, actually widely

used for biogeographical regionalization (e.g., Carine et al. 2009, Casagranda et al. 2009), has consistent theoretical basis and is well grounded in a valid and mostly accepted concept of areas of endemism, and can be used not only to identify areas of endemism in strict sense but also to identify regional patterns of distributional congruence determined by widespread species whose ranges exceed the study region (Aagesen et al. 2009).

Conservation priorities

Conservation assessment is a rapidly evolving discipline whose goal is the design of networks of protected areas that represent and ensure the persistence of nature (i.e., species, habitats, and environmental processes) by separating priority areas from the activities that degrade or destroy them (Knight et al. 2008). The number of species at risk of extinction continues to increase every year, and the extinction rates have increased to mass extinction proportions (Hughes et al. 1997, May & Tregonning 1998, Chapin et al. 2000, Kerr & Deguise 2004).

Species extinctions in tropical South America in general, and in the Amazon rainforest in particular, have attracted almost all the attention and efforts of the conservationists (Mann 1991). However, Redford et al. (1990), Mares (1992), and Willig et al. (2000) have suggested that others areas than tropical rainforests deserve the same allocation of time and resources. In fact, as Mares (1992) has shown, for mammals the drylands of South America support more endemic species, genera, and families than the Amazon rainforest. So, conservation of mammalian diversity requires increasing the number of protected areas in the extensive drylands of South America. Unfortunately, there is an inadequate number of protected areas in Northwestern Argentina. Ojeda et al. (2003) noted that while the Puna and Yungas biomes are rather well protected, the arid and semiarid Monte and Chaco are not. Besides, Ojeda et al. (2003) pointed out that large areas in the Chaco have never been sampled. Therefore, additional faunal surverys are badly needed in this biome, which is under strong pressure by humans (Ojeda & Mares 1984, Ojeda 1999, Ojeda et al. 2002, 2003).

Conservation strategies that consider biogeographical units at the scale of ecoregions are ideal for protecting a full range of representative areas, conserving special elements, and ensuring the persistence of populations and ecological processes, particularly those that require the largest areas or are most sensitive to anthropogenic alterations (Olson et al. 2001). Although conservation efforts should focus on maximizing the protection of as many species as possible (Andelman & Willig 2002), the conservation of adaptive variation of species may be as important as the conservation of particular species (Araújo 2002). Thus, protection should not only maximize the number of protected species but should maximize variation in the attributes of species as well (Stevens et al. 2004). In this sense, even though bat species that determine the patterns of distributional congruence that are equivalent to the Chaco are mostly widespread species, it is important to note that identified species assemblages could be and should even be considered a conservation priority. The identification of species assemblages that characterize those patterns is important in a regional context and to protect these assemblages would imply the protection of particular attributes associated with particular ecological and evolutionary processes in which bats are involved. At regional level, Paraguay, Bolivia, and Argentina should ensure the protection of representative areas of all different landscapes, even those that apparently do not have their own specific identity, and apparently are nothing more than impoverished versions of neighboring habitats, as the Chaco was regarded in relation to its chiropteran fauna.

Here, we want to emphasize the conservation value of the Chaco in terms of patterns of distributional congruence of its bats, and to highlight its nature of being a biologically defined unit with its own assemblages of species and ecological and evolutionary processes that it is necessary to protect. Studies like this one are useful in defining priority conservation areas, which may consider not only endemism in their determination and their definition (Myers 1988, 1990, Bibby 1994, Baquero & Tellería 2001, Kerr & Burkey 2002, Silva & Guevara 2004; but

see Dinerstein & Wikramanayake 1993, Pressey et al. 1993, Ceballos & Brown 1995).

LITERATURE CITED

AAGESEN L, CA SZUMIK, FO ZULOAGA & O MORRONE (2009) Quantitative biogeography in the South America highlands -recognizing the Altoandina, Puna and Prepuna through the study of Poaceae. Cladistics 25: 295-310.

ACOSTA L & F AGUANTA (2005) Nota sobre un nuevo registro de murciélago (*Lampronycteris brachyotis)* para Bolivia. Kempffiana (Bolivia) 1: 65-69.

ACOSTA L & C VENEGAS (2006) Algunas consideraciones taxonómicas de *Histiotus laephotis* e *H. macrotus*, en Bolivia. Kempffiana (Bolivia) 2: 109-115.

ADÁMOLI J, R NEUMAN, AD RATIER DE COLINA & J MORELLO (1972) El Chaco aluvional Salteño. Convenio Instituto Nacional de Tecnología Agropecuaria - Provincia de Salta. Revista de Investigaciones Agropecuarias, INTA, Serie 3, Clima y Suelo (Argentina) 9: 165-237.

AGUIRRE LF (2002) Structure of a Neotropical savanna bat community. Journal of Mammalogy 83: 775-784.

ANDELMAN SJ & MR WILLIG (2002) Alternative configurations of conservation reserves for Paraguayan bats: considerations of spatial scale. Conservation Biology 16: 1352-1363.

ANDERSON S (1994) Area and endemism. The Quarterly Review of Biology 69: 451-471.

ANDERSON S (1997) Mammals of Bolivia, taxonomy and distribution. Bulletin of the American Museum of Natural History 231: 1-652.

ARAÚJO MB (2002) Biodiversity hotspots and zones of ecological transition. Conservation Biology 16: 1662-1663.

AZURDUY H & L EMMONS (2005) Nota sobre dos nuevas especies de murciélagos para Bolivia. Ecología en Bolivia (Bolivia) 40: 53-57.

BAQUERO RA & JL TELLERÍA (2001) Species richness, rarity and endemicity of European mammals: a biogeographical approach. Biodiversity and Conservation 10: 29–44.

BARQUEZ RM (2006) Orden Chiroptera Blumenbach, 1779. In: Barquez RM, MM Díaz & RA Ojeda (eds) Mamíferos de Argentina, sistemática y distribución: 56-86. Sociedad Argentina para el Estudio de los Mamíferos, Mendoza, Argentina.

BARQUEZ RM & RA OJEDA (1992) The bats (Mammalia: Chiroptera) of the Argentine Chaco. Annals of the Carnegie Museum 61: 239-261.

BARQUEZ RM, MA MARES & JK BRAUN (1999) The bats of Argentina. Special Publications, the Museum, Texas Tech University (United States of America) 42: 1-275.

BARQUEZ RM, MS SÁNCHEZ & JC BRACAMONTE (2009) Nueva especie de *Eptesicus* (Chiroptera, Vespertilionidae) para Argentina. Mastozoología Neotropical (Argentina) 16: 199-203.

BARQUEZ RM, MS SÁNCHEZ & ML SANDOVAL (2011) Nuevos registros de murciélagos (Chiroptera) en el norte de Argentina. Mastozoología Neotropical (Argentina) 18: 11-24.

BIBBY C (1994) A global view of priorities for bird conservation: a summary. Ibis 137: S247-S248.

BUCHER EH (1982) Chaco and Caatinga: South American arid savannas, woodlands and thickets. In: Huntley B & B Walker (eds.) Ecology of tropical savannas: 48-79. Ecological Studies: 42, Springer Verlag, Berlin.

BUCHER EH & PC HUSZAR (1999) Sustainable management of the Gran Chaco of South America: Ecological promise and economic constraints. Journal of Environmental Management 57: 94-108.

BURKART R, NO BÁRBARO, RO SÁNCHEZ & DA GÓMEZ (1999) Ecoregiones de la Argentina. Administración de Parques Nacionales, Buenos Aires.

CABRERA AL (1976) Regiones fitogeográficas argentinas. Enciclopedia Argentina de Agricultura y Jardinería, Second edition, Volume II. Editorial ACME, Buenos Aires.

CABRERA AL & A WILLINK (1973) Biogeografía de América Latina. Secretaría General de la OEA, Monografía Científica Serie Biología: 13, Washington, Washington.

CARINE MA, CJ HUMPHRIES, R GUMA, JA REYES-BETANCORT & A SANTOS GUERRA (2009) Area and algorithms: evaluating numerical approaches for the delimitation of areas of endemism in the Cabary Islands archipelago. Journal of Biogeography 36: 593-611.

CASAGRANDA MD, S ROIG-JUŇENT & C SZUMIK (2009) Endemismo a diferentes escalas espaciales: un ejemplo con Carabidae (Coleoptera: Insecta) de América del Sur austral. Revista Chilena de Historia Natural 82: 17-42.

CEBALLOS G & JH BROWN (1995) Global patterns of mammalian diversity, endemism, and endangerment. Conservation Biology 9: 559-568.

CHAPIN FS III, ES ZAVALETA, VT EVINER, RL NAYLOR, PM VITOUSEK et al. (2000) Consequences of changing biodiversity. Nature 105: 234–242.

CRISCI JV, L KATINAS & P POSADAS (2000) Introducción a la teoría y práctica de la biogeografía histórica. Sociedad Argentina de Botánica, Buenos Aires, Argentina.

DALY DC & JD MITCHELL (2000) Lowland vegetation of tropical South America - an overview. In: Lenz D (ed) Imperfect balance: landscape transformations in the pre-Columbian Americas: 391-454. Columbia University Press, New York.

DAVIS WB & AL GARDNER (2007) Genus *Eptesicus* Rafinesque, 1820. In: AL Gardner (ed) Mammals of South America. Volume 1. Marsupials, xenarthrans, shrews, and bats: 440-450. The University Chicago Press, Chicago.

DEO AJ & R DESALLE (2006) Nested areas of endemism analysis. Journal of Biogeography 33: 1511-1526.

DÍAZ MM & RM BARQUEZ (2009) Primer registro de *Micronycteris microtis* (Phyllostomidae, Phyllostominae) para la Argentina. Chiroptera Neotropical 15: 461-465.

DÍAZ GÓMEZ JM (2007) Endemism in *Liolaemus* (Iguania: Liolaemidae) from the Argentinian Puna. South American Journal of Herpetology (Brazil) 2: 59-68.

DICK CW, D GETTINGER & SL GARDNER (2007) Bolivian ectoparasites: a survey of bats (Mammalia: Chiroptera). Comparative Parasitology 74: 372-377.

DINERSTEIN E & ED WIKRAMANAYAKE (1993) Beyond "hotspots": how to prioritize investments in biodiversity in the Indo-Pacific region. Conservation Biology 7: 53-65.

DOS SANTOS DA, HR FERNÁNDEZ, MG CUEZZO & E DOMÍNGUEZ (2008) Sympatry inference and network analysis in biogeography. Systematic Biology 57: 432-448.

EGER JL (2007) Family Molossidae P. Gervais, 1856. In: Gardner AL (ed) Mammals of South America. Volume 1. Marsupials, xenarthrans, shrews, and bats: 399-440. The University Chicago Press, Chicago.

EMMONS LH (1997) Mammals of the Río Urucuti Basin, South Central Chuquisaca, Bolivia. In: Schulenberg TS & K Awbrey (eds) A rapid assessment of the humid forests of South Central Chuquisaca, Bolivia: 30-33. Conservation International, Washington.

EMMONS LH, M SWARNER, A VARGAS-ESPINOZA, M TSCHAPKA, H AZURDUY et al. (2006) The forest and savanna bat communities of Noel Kempff Mercado National Park (Bolivia). Revista Boliviana de Ecología y Conservación Ambiental (Bolivia) 15: 47-57.

ERWIN TL (1991) An evolutionary basis for conservation strategies. Science 253: 750–752.

ESPINOSA-ORGANISTA D & J LLORENTE-BOUSQUETS (1993) Fundamentos de biogeografías filogenéticas. Universidad Nacional Autónoma de México - Comisión Nacional para el Conocimiento y Uso de la Biodiversidad), México D.F., México.

FA JE & SM FUNK (2007) Global endemicity centres for terrestrial vertebrates: an ecoregions approach. Endangered Species Research 3: 31-42.

FLORES-SALDAÑA MG (2008) Estructura de las comunidades de murciélagos en un gradiente ambiental en la Reserva de la Biósfera y tierra comunitaria de origen Pilón Lajas, Bolivia. Mastozoología Neotropical (Argentina) 15: 309-322.

GALLARDO JM (1979) Composición, distribución y origen de la herpetofauna chaqueña. In: Duellman WE (ed) The South American herpetofauna: its origin, evolution, and dispersal: 299-307. Monograph N° 7, Museum of Natural History University of Kansas, Kansas.

GARDNER AL (2007) Order Chiroptera. In: Gardner AL (ed) Mammals of South America. Volume 1. Marsupials, xenarthrans, shrews, and bats: 187-188. University of Chicago Press, Chicago.

GASTON KJ (1994) Rarity. Chapman & Hall, London, United Kingdom.

GIOKAS S & S SFENTHOURAKIS (2007) An improved method for the identification of areas of endemism using species co-ocurrences. Journal of Biogeography 35: 892–902.

GOLOBOFF P (2005) NDM/VNDM v.2.5. Programs for identification of areas of endemism. Programs and documentation avalaible at www.zmuc.dk/public/phylogeny/endemism.

GORRESEN PM & MR WILLIG (2004) Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. Journal of Mammalogy 85: 688-697.

HUECK K (1978) Los bosques de Sudamérica. Ecología, composición e importancia económica. Agencia Alemana de Cooperación Técnica (GTZ), Berlín.

HUGHES JB, GC DAILY & PR EHRLICH (1997) Population diversity: its extent and extinction. Science 278: 689–692.

KERR JG (1950) A naturalist in the Gran Chaco. Cambridge University Press, Cambridge.

KERR JT (1997) Species richness, endemism, and the choice of areas for conservation. Conservation Biology 11: 1094-1100.

KERR JT & TV BURKEY (2002) Endemism, diversity, and the threat of tropical moist forest extinctions. Biodiversity and Conservation 11: 695–704.

KERR JT & I DEGUISE (2004) Habitat loss and the limits to endangered species recovery. Ecology Letters 7: 1163–1169.

KNIGHT AT, RM COWLING, M ROUGET, A BALMFORD, AT LOMBARD et al. (2008) Knowing but not doing: Selecting priority conservation areas and the research-implementation gap. Conservation Biology 22: 610-617.

KOOPMAN KF (1976) Zoogeography. In: Baker RJ, JK Jones, Jr. & DC Carter (eds) Biology of bats of the New World family Phyllostomidae: Part 1: 39-47. Special Publications, the Museum, Texas Tech University (United States of America) 10: 1-218.

KOOPMAN KF (1981) The distributional patterns of new world nectar-feeding bats. Annals of the Missouri Botanical Garden 48: 352-369.

KOOPMAN KF (1982) Biogeography of the bats of South America. In: Mares MA & HH Genoways (eds) Mammalian biology in South America: 273-302. Special Publication Series, Pymatuning Laboratory of Ecology, University of Pittsburgh, Pennsylvania.

LINDER HP (2001) On Areas of Endemism, with an example from the African Restionaceae. Systematic Biology 50: 892–912.

LÓPEZ-GONZÁLEZ C (1998) Systematics and zoogeography of the bats of Paraguay. Ph.D. Thesis, Texas Tech University, Lubbock, USA.

LÓPEZ-GONZÁLEZ C, SJ PRESLEY, RD OWEN, MR WILLIG & I GAMARRA DE FOX (1998) Noteworthy records of bats (Chiroptera) from Paraguay. Mastozoología Neotropical (Argentina) 5: 41-45.

LÓPEZ-GONZÁLEZ C, SJ PRESLEY, RD OWEN & MR WILLIG (2001) The taxonomic status of *Myotis* (Chiroptera: Vespertilionidae) in Paraguay. Journal of Mammalogy 82: 138-160.

MANN CC (1991) Extinction: are ecologists crying wolf? Science 253: 736-738.

MARES MA (1992) Neotropical mammals and the myth of the Amazonian biodiversity. Science 255: 976-979.

MAY RM & K TREGONNING (1998) Global conservation and UK government policy. In Mace GM A Balmford & JR Ginsberg (eds) Conservation in a changing world: 287-301. Cambridge University Press, Cambridge, United Kingdom.

MORELLO J & J ADÁMOLI (1968) Las grandes unidades de vegetación y ambiente del Chaco argentino. Primera parte: Objetivos y Metodología. Instituto Nacional de Tecnología Agropecuaria (Argentina), Serie Fitogeográfica 10: 1-125.

MORELLO J & J ADÁMOLI (1974) Las grandes unidades de vegetación y ambiente del Chaco argentino. Segunda parte: Vegetación y ambiente de la provincia del Chaco. Instituto Nacional de Tecnología Agropecuaria (Argentina), Serie Fitogeográfica 13: 1-130.

MORELLO J & C SARAVIA TOLEDO (1959a) El bosque chaqueño I. Paisaje primitivo, paisaje natural y paisaje cultural en el oriente de Salta. Revista Agronómica del Noroeste Argentino (Argentina) 3: 5-81.

MORELLO J & C SARAVIA TOLEDO (1959b) El bosque chaqueño II. La ganadería y el bosque en el oriente de Salta. Paisaje primitivo, paisaje natural y paisaje cultural en el oriente de Salta. Revista Agronómica del Noroeste Argentino (Argentina) 3: 209-258.

MORRONE JJ (1994) On the identification of areas of endemism. Systematic Biology 43: 438-441.

MORRONE JJ (2009) Evolutionary biogeography: an integrative approach with case studies. Columbia University Press, New York.

MYERS N (1988) Threatened biotas: 'hotspots' in tropical forests. The Environmentalist (Netherlands) 8: 1-20.

MYERS N (1990) The biodiversity challenge: expanded hot-spots analysis. The Environmentalist (Netherlands) 10: 243-255.

MYERS P & RM WETZEL (1983) Systematics and zoogeography of the bats of the Chaco Boreal. Miscellaneous Publications, Museum of Zoology, University of Michigan (United States of America) 165: 1-59.

NAUMANN M (2006) Atlas del Gran Chaco Sudamericano. Sociedad Alemana de Cooperación Técnica (GTZ), ErreGé & Asoc., Buenos Aires, Argentina.

NAVARRO FR, F CUEZZO, PA GOLOBOFF, C SZUMIK, M LIZARRALDE DE GROSSO et al. (2009) Can insect data be used to infer areas of endemism? An example from the Yungas of Argentina. Revista Chilena de Historia Natural 82: 507-522.

NORI J, JM DÍAZ GÓMEZ & GC LEYNAUD (2011) Biogeographic regions of Central Argentina based on snake distribution: evaluating two different methodological approaches. Journal of Natural History 45: 1005-1020.

NOSS A, MA MARES & MM DÍAZ (2002) El Chaco/ The Chaco. In: Mittermeier RA, CG Mittermeier, P Robles Gil, J Pilgrim, GAB da Foseca, T Brooks & WR Konstant (eds) Áreas silvestres: las últimas regiones vírgenes del mundo/Wilderness Earth's last wild places: 165-172. CEMEX (Monterrey), Conservation International (Washington D. C.) and Agrupación Sierra Madre (México D. F.), Washington and México.

OJEDA RA (1999) Biodiversidad y conservación de mamíferos de la interfase tropical-templada de la Argentina. In: Matteucci SD, OT Solbrig, J Morillo & G Halffter (eds) Biodiversidad y uso de la tierra: conceptos y ejemplos de Latinoamérica: 443-462. Editorial Universitaria de Buenos Aires, Universidad de Buenos Aires, Buenos Aires.

OJEDA RA & MA MARES (1984) La degradación de los recursos naturales y la fauna silvestre en Argentina. Interciencia (Venezuela) 9: 21-26.

OJEDA RA, CE BORGHI & VG ROIG (2002) Mamíferos de Argentina. In: Ceballos G & JA Simonetti (eds) Diversidad y conservación de los mamíferos neotropicales: 23-63. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad - Universidad Nacional Autónoma de México, México D.F.

OJEDA RA, J STADLER & R BRANDL (2003) Diversity of mammals in the tropical–temperate Neotropics:

hotspots on a regional scale. Biodiversity and Conservation 12: 1431–1444.

OLSON DM, E DINERSTEIN, ED WIKRAMANAYAKE, ND BURGESS, GVN POWELL et al. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. BioScience 51: 933-938.

PACHECO LF, JA SIMONETTI & M MORAES (1994) Conservation of Bolivian flora: representation of phytogeographic zones in the national system of protected areas. Biodiversity and Conservation 3: 751-756.

PARKER TA, AH GENTRY, RB FOSTER, LH EMMONS & JV REMSEN (eds) (1993) The lowland dry forest of Santa Cruz, Bolivia: a global conservation priority. Rapid Assessment Program Working Paper 4, Conservation International, Washington DC.

PLATNICK N (1991) On areas of endemism. Australian Systematic Botany 4: 11-12.

PRADO DE (2000) Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phytogeographic unit. Edinburgh Journal of Botany 57: 437-461.

PRADO DE, PE GIBBS, A POTT & VJ POTT (1992) The Chaco - Pantanal transition in southern Mato Grosso, Brazil. In: Furley PA & JA Proctor (eds) Nature and dynamics of forest savanna boundaries: 451-470. Chapman & Hill, London, England.

PRESSEY RL, CJ HUMPHRIES, CR MARGULES, RY VANE-WRIGHT & PH WILLIAMS (1993) Beyond oportunism: key principles for systematic reserve selection. Trends in Ecology and Evolution 8: 124-128.

PROCHES S (2005) The world's biogeographical regions: cluster analyses based on bat distributions. Journal of Biogeography 32: 607-614.

RAGONESE AE & JA CASTIGLIONI (1970) La vegetación del Parque chaqueño. Boletín de la Sociedad Argentina de Botánica 11 (Argentina): 133-136.

REDFORD K, AB TABER & JA SIMONETTI (1990) There is more to biodiversity than the tropical rain forests. Conservation Biology 3: 328-330.

SANDOVAL ML (2012) Diversidad y distribución de micromamíferos en las Yungas de Argentina. Tesis Doctoral, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina.

SANDOVAL ML, MS SÁNCHEZ & RM BARQUEZ (2010) Mammalia, Chiroptera Blumenbach, 1779: new locality records, filling gaps, and geographic distribution maps from Northern Argentina. Check List (Brazil) 6: 64-70.

SANDOVAL ML, CA SZUMIK & RM BARQUEZ (2010) Bats and marsupials as indicators of endemism in the Yungas forest of Argentina. Zoological Research 31: 633-644.

SHORT LL (1975) A zoogeographic analysis of the South American Chaco avifauna. Bulletin of the American Museum of Natural History 154: 167-352.

SILES L, N ROCHA, A SELAYA & L ACOSTA (2003) Estructura de la comunidad, monitoreo y conservación de los murciélagos del PN-ANMI Kaa Iya del Gran Chaco (Bolivia). Revista Electrónica Manejo de Fauna Silvestre en Latinoamérica (Perú) 1:101-110

SILVA X & M GUEVARA (2004) Priority conservation areas and management alternatives for the five ecoregions of Latin America. Lyonia (United States of America) 6: 35-45.

SOBERÓN JM, JB LLORENTE & L OÑATE (2000) The use of specimen-label databases for conservation purposes: An example using Mexican Papilionid and Pierid butterflies. Biodiversity and Conservation 9: 1441–1466.

SOLARI S & RJ BAKER (2006) Mitochondrial DNA sequence, karyotypic, and morphological variation in the *Carollia castanea* species complex (Chiroptera: Phyllostomidae) with description of a new species. Occasional Papers, the Museum, Texas Tech University (United States of America) 254: 1-16.

SPECTOR S (2002) Biogeographic crossroads as priority areas for biodiversity conservation. Conservation Biology 16: 1480–1487.

STEVENS RD, MR WILLIG & I GAMARRA DE FOX (2004) Comparative community ecology of bats from eastern Paraguay: taxonomic, ecological, and biogeographic perspectives. Journal of Mammalogy 85: 698–707.

STRAUBE FC & A DI GIACOMO (2007) A avifauna das Regiões Subtropical e Temperada do Neotrópico: desafios biogeográficos. Ciência & Ambiente (Brazil) 35: 137-166.

SZUMIK C & P GOLOBOFF (2004) Areas of endemism: an improved optimality criterion. Systematic Biology 53: 968-977.

SZUMIK C & S ROIG-JUÑENT (2005) Criterio de optimalidad para áreas de endemismo: el caso de América del Sur Austral. In: Morrone JJ & J Llorente Bousquets (eds) Regionalización biogeográfica en Iberoamérica y tópicos afines: 495-508. Universidad Nacional Autónoma de México, México D.F.

SZUMIK C, F CUEZZO, P GOLOBOFF & A CHALUP (2002) An optimality criterion to determine areas of endemism. Systematic Biology 51: 806-816.

SZUMIK C, L AAGESEN, D CASAGRANDA, V ARZAMENDIA, D BALDO et al. (2012) Detecting areas of endemism with a taxonomically diverse data set: plants, mammals, reptiles, amphibians, birds, and insects from Argentina. Cladistics 28: 317-329.

TABENI MS, JB BENDER & RA OJEDA (2004) Puntos calientes para la conservación de mamíferos en la provincia de Tucumán, Argentina. Mastozoología Neotropical 11: 55-67.

TEN S, I LICEAGA, M GONZÁLEZ, J JIMÉNEZ, L TORRES et al. (2001) Reserva Inmovilizada Iténez: primer listado de vertebrados. Revista Boliviana de Ecología y Conservación Ambiental (Bolivia) 10: 81-110.

TNC (THE NATURE CONSERVANCY), FVSA (FUNDACIÓN VIDA SILVESTRE ARGENTINA), DESDEL CHACO (FUNDACIÓN PARA EL DESARROLLO SUSTENTABLE DEL CHACO) & WCS (WILDIFE CONSERVATION SOCIETY BOLIVIA) (2005) Evaluación Ecorregional del Gran Chaco Americano / Gran Chaco Americano Ecoregional Assessment. Fundación Vida Silvestre Argentina, Buenos Aires, Argentina.

VANE-WRIGHT R, CJ HUMPHRIES & PH WILLIAMS (1991) What to protect? - Systematics and the agony of choice. Conservation Biology 55: 235-254.

VARGAS-ESPINOZA A, LF AGUIRRE, M SWARNER, L EMMONS & M TERAN (2004) Distribución de *Vampyrum spectrum* en Bolivia y comentarios sobre su estado de conservación. Ecología en Bolivia (Bolivia) 39: 46-51.

VARGAS-ESPINOZA A, LF AGUIRRE, M GALARZA & E GARECA (2008) Ensamble de murciélagos en sitios con diferente grado de perturbación en un bosque montano del Parque Nacional Carrasco, Bolivia. Mastozoología Neotropical (Argentina) 15: 297-308.

WILLIG ML, SJ PRESLEY, RD OWEN & C LÓPEZ-GONZÁLEZ (2000) Composition and structure of bat assemblages in Paraguay: a subtropical-temperate interface. Journal of Mammalogy 81: 386-401.

YAHNKE CJ, I GAMARRA DE FOX & F COLMAN (1998) Mammalian species richness in Paraguay: the effectiveness of national parks in preserving biodiversity. Biological Conservation 84: 263-268.

ZAK MR, M CABIDO & JG HODGSON (2004) Do subtropical seasonal forests in the Gran Chaco, Argentina, have a future? Biological Conservation 120: 589-598.

FOOTNOTES

[1] EITEN G (1974) An outline of the vegetation of South America. Proceedings of the 5th Congress of the International Primatological Society, Nagoya, 21-24 Aug 1974.

[2] VERVOORST F (1982) Noroeste. Simposio Conservación de la vegetación natural en la República Argentina, XVIII Jornadas Argentinas de Botánica, Ministerio de Cultura y Educación, Fundación Miguel Lillo, Sociedad Argentina de Botánica 4-7 May 1981.

APPENDIX

Bat species included in the analysis. The taxonomy used herein is in accordance to Barquez (2006) for Argentinean bats and to Gardner (2007) for the other bat species.

Especies de murciélagos incluidas en el análisis. La taxonomía adoptada es la propuesta por Barquez (2006) para los murciélagos de Argentina y por Gardner (2007) para las otras especies de murciélagos.

Family Emballonuridae
  Subfamily Emballonurinae
  1. *Diclidurus albus* Wied-Neuwied 1820
  2. *Peropteryx kappleri* Peters 1867
  3. *Peropteryx macrotis* (Wagner 1843)
  4. *Rhynchonycteris naso* (Wied-Neuwied 1820)
  5. *Saccopteryx bilineata* (Temminck 1838)
  6. *Saccopteryx canescens* Thomas 1901
  7. *Saccopteryx leptura* (Schreber 1774)
Family Molossidae
  Subfamily Molossinae
  8. *Cynomops abrasus* (Temminck 1826)
  9. *Cynomops paranus* (Thomas 1901)
  10. *Cynomops planirostris* (Peters 1866)
  11. *Eumops auripendulus* (Shaw 1800)
  12. *Eumops bonariensis* (Peters 1874)
  13. *Eumops dabbenei* Thomas 1914
  14. *Eumops glaucinus* (Wagner 1843)
  15. *Eumops hansae* Sanborn 1932
  16. *Eumops patagonicus* Thomas 1924
  17. *Eumops perotis* (Schinz 1821)
  18. *Eumops trumbulli* (Thomas 1901)
  19. *Neoplatymops mattogrossensis* (Vieira 1942)
  20. *Molossops neglectus* Williams & Genoways 1980
  21. *Molossops temminckii* (Burmeister 1854)
  22. *Molossus molossus* (Pallas 1766)
  23. *Molossus rufus* É. Geoffroy St.-Hilaire 1805
  24. *Nyctinomops aurispinosus* (Peale 1848)
  25. *Nyctinomops laticaudatus* (É. Geoffroy St.-Hilaire 1805)
  26. *Nyctinomops macrotis* (Gray 1839)
  27. *Promops centralis* Thomas 1915
  28. *Promops nasutus* (Spix 1823)
  29. *Tadarida brasiliensis* (I. Geoffroy St.-Hilaire 1824)
Family Mormoopidae
  30. *Pteronotus gymnonotus* (Wagner 1843)
  31. *Pteronotus parnellii* (Gray 1843)
  32. *Pteronotus personatus* (Wagner 1843)
Family Natalidae
  33. *Natalus stramineus* Gray 1838
Family Noctilionidae
  34. *Noctilio albiventris* Desmarest 1818
  35. *Noctilio leporinus* (Linnaeus 1758)
Family Phyllostomidae
  Subfamily Carolliinae
  36. *Carollia benkeithi* Solari & Baker 2006
  37. *Carollia brevicauda* (Schinz 1821)
  38. *Carollia manu* Pacheco, Solari & Velazco 2004
  39. *Carollia perspicillata* (Linnaeus 1758)
  40. *Rhinophylla pumilio* Peters 1865
  Subfamily Desmodontinae
  41. *Desmodus rotundus* (É. Geoffroy St.-Hilaire 1810)
  42. *Diaemus youngi* (Jentink 1893)
  Subfamily Glossophaginae
  43. *Anoura caudifer* (É. Geoffroy St.-Hilaire 1818)
  44. *Anoura cultrata* Handley 1960
  45. *Anoura geoffroyi* Gray 1838
  46. *Choeroniscus minor* (Peters 1868)
  47. *Glossophaga soricina* (Pallas 1766)
  48. *Lichonycteris obscura* Thomas 1895
  49. *Lionycteris spurrelli* Thomas 1913
  50. *Lonchophylla dekeyseri* Taddei, Vizotto & Sazima 1983
  51. *Lonchophylla thomasi* Allen 1904
  Subfamily Phyllostominae
  52. *Chrotopterus auritus* (Peters 1856)
  53. *Glyphonycteris daviesi* (Hill 1965)
  54. *Lampronycteris brachyotis* (Dobson 1879)
  55. *Lonchorhina aurita* Tomes 1863
  56. *Lophostoma brasiliense* Peters 1866
  57. *Lophostoma carrikeri* (Allen 1910)
  58. *Lophostoma silvicolum* D'Orbigny 1836
  59. *Macrophyllum macrophyllum* (Schinz 1821)
  60. *Micronycteris hirsuta* (Peters 1869)
  61. *Micronycteris megalotis* (Gray 1842)
  62. *Micronycteris microtis* Miller 1898
  63. *Micronycteris minuta* (Gervais 1856)
  64. *Micronycteris sanborni* Simmons 1996
  65. *Mimon crenulatum* (É. Geoffroy St.-Hilaire 1803)

66. *Phylloderma stenops* Peters 1865
67. *Phyllostomus discolor* (Wagner 1843)
68. *Phyllostomus elongatus* (É. Geoffroy St.-Hilaire 1810)
69. *Phyllostomus hastatus* (Pallas 1767)
70. *Tonatia bidens* (Spix 1823)
71. *Tonatia saurophila* Koopman & Williams 1951
72. *Trachops cirrhosus* (Spix 1823)
73. *Trinycteris nicefori* Sanborn 1949
74. *Vampyrum spectrum* (Linnaeus 1758)
Subfamily Stenodermatinae
75. *Artibeus anderseni* Osgood 1916
76. *Artibeus fimbriatus* Gray 1838
77. *Artibeus glaucus* Thomas 1893
78. *Artibeus gnomus* Handley 1987
79. *Artibeus lituratus* (Olfers 1818)
80. *Artibeus planirostris* (Spix 1823)
81. *Artibeus obscurus* (Schinz 1821)
82. *Chiroderma doriae* Thomas 1891
83. *Chiroderma salvini* Dobson 1878
84. *Chiroderma trinitatum* Goodwin 1958
85. *Chiroderma villosum* Peters 1860
86. *Enchisthenes hartii* (Thomas 1892)
87. *Mesophylla macconnelli* (Thomas 1901)
88. *Platyrrhinus albericoi* Velazco 2005
89. *Platyrrhinus brachycephalus* (Rouk & Carter 1972)
90. *Platyrrhinus helleri* (Peters 1866)
91. *Platyrrhinus infuscus* (Peters 1880)
92. *Platyrrhinus lineatus* (É. Geoffroy St.-Hilaire 1810)
93. *Platyrrhinus masu* Velazco 2005
94. *Platyrrhinus nigellus* (Gardner & Carter 1972)
95. *Pygoderma bilabiatum* (Wagner 1843)
96. *Sphaeronycteris toxophyllum* Peters 1882
97. *Sturnira erythromos* (Tschudi 1844)
98. *Sturnira lilium* (É. Geoffroy St.-Hilaire 1810)
99. *Sturnira magna* de la Torre 1966

100. *Sturnira oporaphilum* (Tschudi 1844)
101. *Sturnira sorianoi* Sánchez-Hernández, Romero-Almaraz & Schnell 2005
102. *Sturnira tildae* de la Torre 1959
103. *Uroderma bilobatum* Peters 1866
104. *Uroderma magnirostrum* Davis 1968
105. *Vampyressa pusilla* (Wagner 1843)
106. *Vampyressa thyone* Thomas 1909
107. *Vampyriscus bidens* (Dobson 1878)
108. *Vampyrodes caraccioli* Thomas 1889
Family Thyropteridae
109. *Thyroptera discifera* (Lichtenstein & Peters 1854)
110. *Thyroptera tricolor* Spix 1823
Family Vespertilionidae
Subfamily Vespertilioninae
111. *Eptesicus andinus* Allen 1914
112. *Eptesicus brasiliensis* (Desmarest 1819)
113. *Eptesicus chiriquinus* Thomas 1920
114. *Eptesicus diminutus* Osgood 1915
115. *Eptesicus furinalis* (d'Orbigny & Gervais 1847)
116. *Lasiurus blossevillii* (Lesson & Garnot 1826)
117. *Lasiurus cinereus* (Beauvois 1796)
118. *Dasypterus ega* (Gervais 1856)
119. *Histiotus laephotis* Thomas 1916
120. *Histiotus macrotus* (Poeppig 1835)
121. *Histiotus montanus* (Philippi & Landbeck 1861)
122. *Histiotus velatus* (I. Geoffroy St.-Hilaire 1824)
123. *Myotis albescens* (É. Geoffroy St.-Hilaire 1806)
124. *Myotis dinellii* Thomas 1902
125. *Myotis keaysi* Allen 1914
126. *Myotis nigricans* (Schinz 1821)
127. *Myotis oxyotus* (Peters 1866)
128. *Myotis riparius* Handley 1960
129. *Myotis ruber* (É. Geoffroy St.-Hilaire 1806)
130. *Myotis simus* Thomas 1901
131. *Rhogeessa io* Thomas 1903