

Spatial patterns of biological diversity in a neotropical lowland savanna of northeastern Bolivia

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Received: 27 September 2010 / Accepted: 11 February 2011
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Abstract Understanding large-scale patterns of beta- and alpha diversity is essential for ecoregional conservation planning. Using the 110,000 km² shallow basin of the Beni savannas of northeastern Bolivia, we examined the spatial patterns of biological diversity of four taxonomic groups (bats, palms, reptiles, and amphibians). Since the Beni savannas are shaped by cycles of drought and flood, and farming, which, together with topography, create a mosaic of sub-ecoregions from Amazonian forests to aquatic vegetation, we hypothesize that this landscape heterogeneity results in a high turnover in species composition across sub-ecoregions. We compiled species lists for each taxon and modeled the potential distribution of each species using the algorithm MaxEnt. For those species whose modeled potential distribution produced incongruous results, we built presence-absence maps. Using the potential distribution maps, we estimated the lists of species for each sub-ecoregion. In order to establish present similarities in species composition between sub-ecoregions, we constructed dendrograms using cluster analysis of presence-absence matrices. The sub-ecoregions associated with the Moxos (southern part of the Beni savannas) were richer than the sub-ecoregions composing the Beni Cerrado (northern part of the Beni savannas). Centers of species richness were detected in the savanna-type sub-ecoregions (bats and reptiles) or associated with the Várzea forests (palms and amphibians). A south-north gradient in the pattern of distribution of four taxonomic groups was also recorded. The results suggest that the patterns of biological diversity partially respond to the mosaic arrangement of the landscape. Future exercises on conservation planning will

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point to total target areas about 5,000 km². This area seems to be sufficient to contain the biological richness of the region at least for the taxa analyzed.

Keywords Bolivia · Beni Cerrado · Llanos de Moxos · Sink-source dynamics · Várzea forests

Introduction

Tropical savannas cover 45% of the land surface in South America (Sarmiento 1983; Cole 1986). Their unique assemblages and relative abundant wildlife have been recently recognized as well as the importance of their management and conservation (Silva and Bates 2002). The Llanos of Moxos (hereafter Moxos) are among the tropical savannas. It is a hyperseasonal savanna of the Bolivian Amazon (Sarmiento 1983), shaped by cycles of drought and flood (Hanagarth and Beck 1996; Hamilton et al. 2004) and the labor of generation of farmers (Erickson 2006; Erickson and Balée 2006; Walker 2008). Its strong seasonality in rainfall and its flooded savanna ecosystems makes the Moxos a distinctive geographical region (Hanagarth 1993; Hanagarth and Beck 1996). However, the Moxos consist not only of savannas but also of other habitats. Isolated patches of different types of Amazonian tropical forests form part of this savanna-type landscape (Hanagarth 1993). The Moxos exhibit, in fact, a mosaic of forest-savanna habitats (i.e., habitat heterogeneity), that produce a relatively broad range of ecological conditions (Ibisch et al. 2003; Beck and Moraes 1997, 2004). Low-lying gallery forests along rivers and streams contrast with higher river levees and savannas (Beck and Moraes 1997, 2004). Likewise, topography and drainage influence the spatial arrangement of plant communities because soils change with drainage and differences in elevation (Hanagarth 1993; Walker 2008).

The Moxos and the Beni Cerrado (another savanna formation of the Beni department in Bolivia) make part of the so-called Beni savanna's ecoregion (10–16°S, WWF, Olson et al. 2001). Although both zones are adjacent, they have important floristic differences as well as a different susceptibility to floods (Hanagarth and Beck 1996; Bourrel and Pouilly 2004; Bourrel et al. 2009). While the Moxos are exposed to large flooded periods because of their low slope (<10 m) and soil types that characterize them, the Beni Cerrado has better drained soils and a more heterogeneous relief (>20 m), which prevent this zone from having comparable flooding levels to those that occur in the Moxos (Bourrel and Pouilly 2004; Hamilton et al. 2004). The Moxos and Beni Cerrado (84,000 and 27,000 km², respectively, Ibisch et al. 2003) cover 4% of all neotropical savannas (2,750,000 km², Cole 1986). It is evident that both savanna-type regions are high-priority sites at regional scales that require urgent conservation initiatives.

The richness and composition of biological diversity of the Moxos and Beni Cerrado is characterized by three well-known features. First, both regions allow the convergence of species belonging to three different biogeographical provinces (Amazonia, Cerrado, and Gran Chaco, *sensu* Moraes and Beck 1992; Hanagarth and Beck 1996). This creates species assemblages composed of species with different biogeographical affinities. Second, the vegetation types and their spatial distribution is closely related to microtopography (relief) in both regions. This had produced markedly differentiated plant formations (Hanagarth and Beck 1996; Beck and Moraes 1997, 2004). Broadly speaking, four types of environments are present in both regions: flooded forests, dry forests, dry savannas, and wet savannas (Walker 2008). Third, flood dynamics during the wet season likely creates cycles of range contraction and expansion, which result in natural temporal fragmentation

and isolation of populations. As a result of these processes, not only the regional diversity is relatively high (Beck and Moraes 1997, 2004), but levels of adaptation to floods are remarkable (*sensu* Lüttge 1997).

All features described above indicate that biodiversity in the Moxos and Beni Cerrado may be distributed heterogeneously. The design and implementation of conservation schemes aimed at preserving a representative sample of biodiversity of both zones entails understanding the spatial patterns of biological diversity and large-scale alpha and beta diversity. If the biota is relatively homogeneous in its species composition, then a small number of areas will be enough to ensure complete representation. In contrast, if the biota is spatially heterogeneous, then more strategically located areas will be required to encompass the regional variation. Here we present results of a study of patterns of spatial diversification and geographical distribution of some taxonomic groups (bats, palms, reptiles, and amphibians), which we used as surrogate taxa of biological diversity of the Beni savanna's ecoregion. We selected these groups because they are suited for development of community ecological theory, as they represent species-rich taxa, they occupy a large variety of trophic niches (Jones et al. 2009), and have been relatively well studied in the Bolivian savannas [e.g., for bats Aguirre (2002); Loayza and Loiselle (2009), for palms Beck and Moraes (1997); Moraes (2004); Moreno and Moreno (2006); for reptiles and amphibians Embert (2007); Reichle (2006)]. Likewise, there are updated and available data for these groups.

Our primary objective was to determine the degree of similarity in species composition and patterns of geographical distribution among different sub-ecoregions composing the Moxos and Beni Cerrado. To our knowledge, this is a first time in which a sub-ecoregional approach is used in order to examine patterns of biological diversity in a neotropical savanna-type ecoregion. This information may be used in making decisions about the areas required to obtain adequate representativeness of biodiversity that contain both savanna-type regions (*sensu* Rodriguez et al. 2007).

Methods

Study site

The Llanos de Moxos cover approximately 84,000 km², which represents 8–9% of the Bolivian territory. It is a tropical savanna inside the Bolivian Amazonia, shaped by cycles of drought and flood (Hanagarth 1993; Hanagarth and Beck 1996). The Moxos and the Beni Cerrado, which encompass about 27,000 km², are locally known as the “Beni savannas” (or llanura beniana, in Spanish, Fig. 1). The Moxos consist of a complex mosaic of habitats that include continuous terra firme forest, forest islands, and open grasslands (Hanagarth, 1993), while the Beni Cerrado is characterized by the presence of wooded savannas, seasonally flooded bunch-grass community (“sartenejal”) and termite mounds (Hanagarth and Beck 1996). Moreover, both zones, together with the La Paz Cerrado (another savanna formation located in the La Paz department in northwestern of Bolivia), make part of the so-called Beni savanna's ecoregion (WWF, Olson et al. 2001), however, for Bolivia, each one of these three zones have been characterized as individual ecoregions (*sensu* Ibisch et al. 2003). A detailed description of the similarities and differences between both ecoregions may be found in Hanagarth and Beck (1996) and Beck and Moraes (2004).

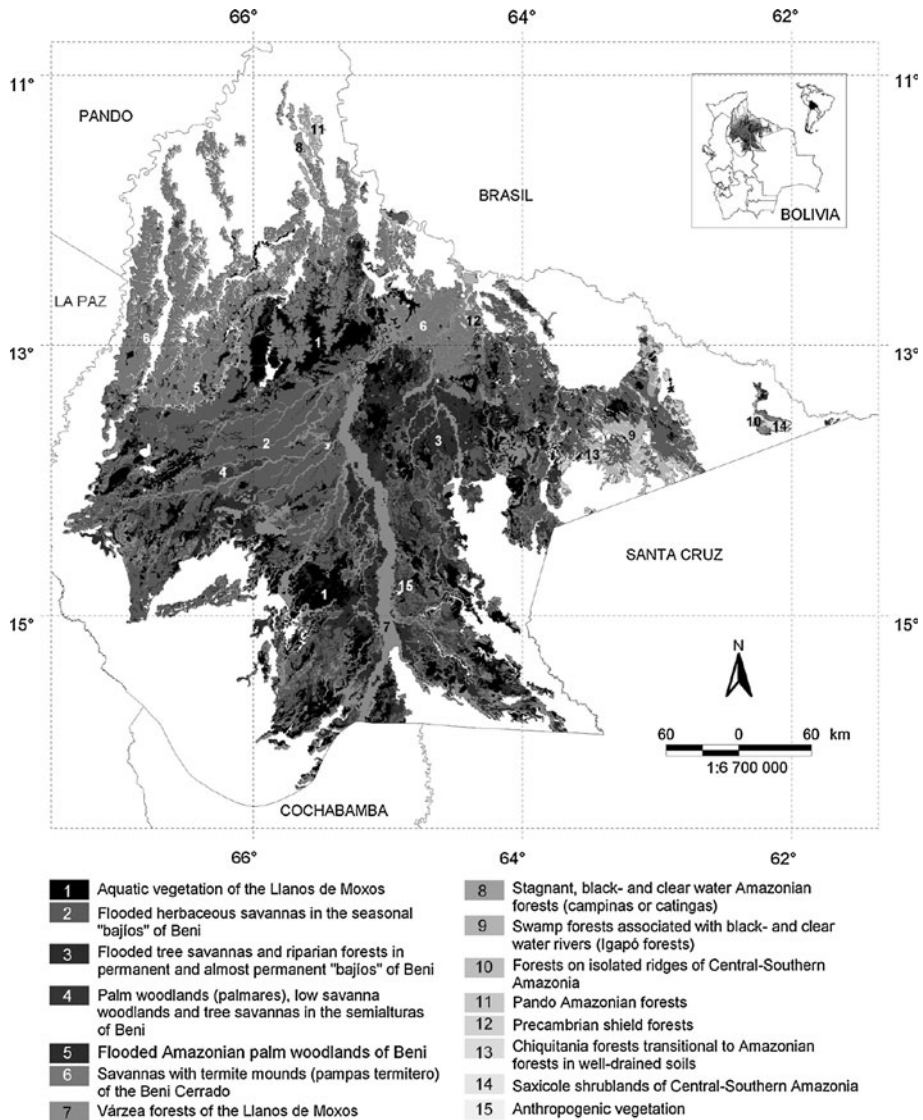


Fig. 1 Map of the Beni savannas showing the Llanos de Moxos and the Beni Cerrado. Boundaries shown are based on the Bolivia's ecoregions of Ibsich et al. (2003)

Analysis of biological diversity

To determine patterns of biological diversity, we used the sub-ecoregion's map of the Beni (Larrea-Alcázar et al. 2010), which identified eighteen sub-ecoregions for the zone (17 "natural" and one anthropogenic). Four sub-ecoregions belong to the Llanos de Moxos, two to the Beni Cerrado, and ten to Amazonian forest- and/or shrub-type formations. This vegetation map was used because the sub-ecoregions provide an appropriate resolution for a study of biological diversity at the level of the Beni savannas.

We compiled information from institutions and published data on geographic distribution for bats [Programa de Conservación de Murciélagos de Bolivia (PCMB)], palms [Moraes (2004); Moreno and Moreno (2006) and Tropicos specimen database, www.tropicos.org], and amphibian and reptile species [Museo de Historia Natural Noel Kempff Mercado (MHNNKM); Museo de Historia Natural Alcide D'Orbigny; Centro de Investigación y Preservación de la Amazonia (CIPA)] reported for the Beni department. Species with no accurate records or taxonomic problems were excluded. The final data bases were composed by a total of 379 species [79 species of bats (887 records), 54 species of palms (239 records), 156 species of reptiles (1,109 records), and 90 species of amphibians (705 records)]. Species of each taxon were grouped in two sub-groups. The first sub-group was composed of species with equal or more than five records. By using the algorithm MaxEnt (Maximun Entropy Modelling, <http://maxent.sourceforge.net>, Phillips and Dudík 2008), we modeled the potential distribution of each species (“Inductive method”). In all cases, we used climatic layers proposed by WorldClim (Hijmans et al. 2005) as predictor variables and a 90 m² digital elevation model (DEM). Depending on the taxa, we used other environmental variables, such as floods and water bodies (MDS 2004), ecoregions (WWF, Olson et al. 2001; Ibsch et al. 2003) and *complexes of ecological systems* (CES, Josse et al. 2007). The potential distribution for each species was produced resampling of individual records using 80% of the points to generate the potential distribution and 20% of the points to validate the results (e.g., Phillips and Dudík 2008). By using Arc View 3.2, we converted the MaxEnt models to binary presence (1)–absence (0) maps using equal training sensitivity–specificity threshold values. The maps were adjusted using the majority filter tool in order to clean the small isolated zones. All the species distribution maps modeled were revised and validated by specialists of each taxa. The second sub-group included species with less than five records. The presence–absence maps were built by specialists of each taxonomic group assigning the presence of each species to vegetation units that correspond to the known distribution of each species (“deductive method”). Data on vegetation varied from series of plant communities (Navarro and Ferreira 2004, 2007) to ecoregions (Ibsch et al. 2003). All the distribution maps were created at a resolution of 30 arc s (900 × 900 m). Using the potential distribution maps, we estimated the list of species for each sub-ecoregion (*sensu* potential species richness). A species was assigned as present in a sub-ecoregion if it had a potential distribution in at least one 900 × 900 grid.

We compiled data on endemism (species with geographical ranges restricted to <50,000 km²), conservation status [for bats Tarifa and Aguirre (2009), for palms Moraes 2004, for reptiles Cortez (2009), for amphibians Aguayo (2009)] and rarity of species studied. For bats, the rarity was defined as a function of four criteria: (a) geographical range, (b) habitat specificity, (c) local abundance, and (d) habitat use (based on Rabinowitz et al. 1986). For palms, reptiles and amphibians, rarity was determined in relation to the total number of records. Species with at least of three records were considered “rare” (for palms Moraes 2004; Moreno and Moreno 2006, for reptiles Embert 2007, for amphibians Reichle 2006). In all cases, the lists produced were again revised and validated by specialists of each taxonomic group. Although the lists were produced with two different methods, we assumed that the species composing each taxon belong to the target flagship group. These lists were used in order to build maps of areas of concentration of flagship species. For each case, the individual maps were joined to generate maps of endemic, threatened, and rare species. The final maps were compared with the sub-ecoregion map in order to assign the presence of each species to each sub-ecoregion type.

In order to establish present similarities in species composition among sub-ecoregions, we constructed dendrograms using cluster analysis of presence–absence matrices with the pc-ord statistical package (version 4.0). We used Jaccard's coefficient of similarity (J) as a distance measure, and centroid clustering. Jaccard's coefficient is defined as $J = c(a + b - c)$, where a is a number of species in site A, b the number of species in site B, and c the number of shared species. This index equals one in cases of complete similarity and zero if the sites have no species in common. Finally, we used Spearman rank correlations to test for cross-taxon species richness correlations.

Results

In general, the sub-ecoregions associated with the Moxos (southern part of the Beni savannas) were the richest (391 species \pm 5.7; mean \pm SD) compared with the sub-ecoregions composing the Beni Cerrado (333 species \pm 42.4) (northern part of the Beni savannas). Occurrence of bats and amphibians species were detected in sub-ecoregions in which, to date, do not exist species recorded (Table 1). The highest numbers of species richness were found in the flooded herbaceous savanna (396 species in total) or in the aquatic vegetation (394 species) of the Moxos. The lowest numbers of species richness were found in the forests on isolated ridges (123 species) and *saxicole* shrublands (149 species) of central-southern Amazonia. The species/genus ratio varied among the taxa examined (bats = 1.76, palms = 2.62, reptiles = 1.96, amphibians = 3.63) showing that most genera have one to four species present in the study area. The most diverse genera were *Artibeus* (7 spp.) and *Eumops* (6 spp.) for bats, *Bactris* (10 spp.) and *Geonoma* (9 spp.) for palms, *Liophis* (10 spp.) and *Chironius* (8 spp.) for reptiles, and *Leptodactylus* (20 spp.) and *Dendropsophus* (13 spp.) for amphibians.

Centers of species richness were detected in the savanna-type sub-ecoregions (bats and reptiles) or associated with the Várzea forest along the north and south of the Mamoré river (palms and amphibians, Fig. 2). A south-north gradient in the pattern of distribution of two taxonomic groups was recorded. This pattern was positive (for palms), negative (for reptiles) or relatively neutral (for amphibians and partially for bats, Fig. 2). For bats, an east–west gradient in the central part of the Moxos was recorded, in which an accumulation of species was detected in the flooded tree savannas located in the eastern part of the region. For reptiles, accumulations of species were detected in the aquatic vegetation and flooded tree savannas located in the eastern Moxos and scarcely in the Várzea forests located up-river. In contrast, palms and amphibians showed strong accumulation of species along the Mamoré river (Fig. 2).

Centers of species richness in four taxonomic groups correlated with area of the sub-ecoregions. In all cases, the maximum number of species was recorded about the 5,000 km² (Fig. 3). This area is larger than the individual cover of ten sub-ecoregions composing the Beni savanna (Table 1) and corresponds to between 27 and 87% of the cover of the sub-ecoregions with greater cover (flooded herbaceous savannas and flooded tree savannas, respectively). These results suggest that the majority of the species pool would be found in 5,000 km² areas in each sub-ecoregion.

Dendrograms showing the clustering of sub-ecoregions for the different taxa are shown in Fig. 4. The species composition similarity in bats across the Beni savannas' sub-ecoregions was higher ($J \leq 0.86$) compared with other taxa (palms $J \leq 0.56$; amphibians $J \leq 0.66$). Two large sets were clustered. A first group, in which, for all taxa the assemblages of the *saxicole* shrublands and the Chiquitania forests clustered together. These

Table 1 Potential species richness (number of species recorded in parenthesis) for four taxa in different sub-ecoregions of two savanna-type ecoregions

Sub-ecoregions	Area (km ²)	Bats	Palms	Reptiles	Amphibians
Aquatic vegetation of the Llanos de Moxos	18,814.3	89 (24)	47 (9)	164 (10)	94(10)
Flooded herbaceous savannas in the seasonal “bajíos” of Beni	36,411.7	89 (44)	49 (15)	163 (66)	95 (32)
Flooded tree savannas and riparian forests in permanent and almost permanent “bajíos” of Beni	11,508.4	88 (18)	46 (3)	164 (24)	93 (29)
Palm woodlands (palmares), low savanna woodlands and tree savannas in the semi alturas of Beni	6,368.7	87 (24)	47 (2)	159 (13)	90 (28)
Flooded Amazonian palm woodlands of Beni	1,173.9	79 (0)	31 (0)	131 (2)	62 (7)
Savannas with termite mounds (pampas termitero) of the Beni Cerrado	18,377.6	84 (15)	45 (4)	147 (19)	87 (4)
Várzea forests of the Llanos de Moxos	16,271.3	88 (30)	44 (10)	162 (49)	97 (30)
Stagnant, black- and clear water Amazonian forests (campinas or catingas)	633.4	84 (0)	43 (0)	144 (0)	64 (0)
Swamp forests associated with black- and clear water rivers (Igapó forests)	4,045.1	85 (9)	46 (4)	150 (20)	89 (0)
Forests on isolated ridges of central-southern Amazonia	18.9	51 (0)	6 (0)	42 (0)	24 (0)
Pando Amazonian forests	1,740.2	85 (0)	44 (2)	142 (0)	84 (0)
Precambrian shield forests	1,337.5	78 (6)	30 (0)	130 (2)	76 (0)
Chiquitania forests transitional to Amazonian forests in well-drained soils	900.5	75 (0)	27 (1)	116 (0)	67 (0)
Saxicole shrublands of central-southern Amazonia	156.5	57 (0)	7 (0)	49 (0)	36 (0)
Anthropogenic vegetation	277.9	86 (0)	40 (3)	148 (22)	84 (18)
Mean of potential species richness (min–max)	7,879.1 (18.9–36,411.7)	80.3 (0–44)	36.8 (6–49)	134.1 (42–164)	76.1 (24–97)

sub-ecoregions are located towards the eastern side of the Beni savannas. The proportion of species shared between both sub-regions was high ($J = 0.80\text{--}0.98$). The second group can be divided in three sub-groups: (a) a first sub-group composed by the black- and clear water Amazonian forests, which may be clustered to the Precambrian shield forests (palms $J = 0.84$) or to the flooded palm woodlands (amphibians $J = 0.87$); (b) a second sub-group where the Igapó, Pando Amazonian and Chiquitania Forests tended to be grouped together [the dendrograms for bats and reptiles include in this set the savannas with termite

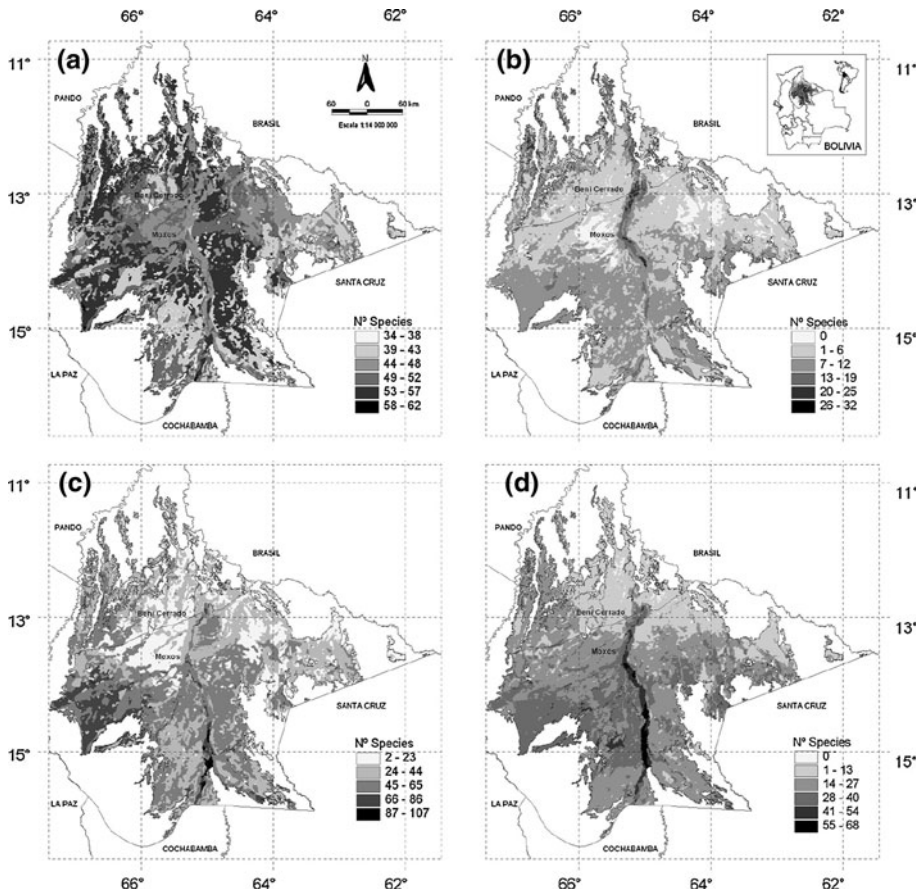


Fig. 2 Centers of species richness for **a** bats, **b** palms, **c** reptiles, and **d** amphibians for the Beni savannas. The map shows the potential number of species for each taxonomic group occurring at a resolution of 30 arc s (900×900 m)

mounds (or pampas termitero of the Beni Cerrado); this sub-group was not found in the amphibians dendrogram], and (c) a third sub-group that clustered to assemblages the four savanna's sub-ecoregions of the Moxos (aquatic vegetation, flooded herbaceous savannas, flooded tree savannas, and palm woodlands) and the Várzea forests; the assemblages of this sub-group shared a higher proportion of species (in all cases $J \geq 0.96$). This result supports the hypothesis that the Várzea forests are a component of the forest-flooded savanna landscape of the Moxos (Navarro and Ferreira 2004, 2007). Finally, the assemblages associated with the anthropogenic vegetation reveal to this “sub-ecoregion” as a transitional floristic formation between the forest and savanna's sub-ecoregions; this may reflect to some degree the levels of disturbance to which they are exposed.

Similarity in composition among sub-ecoregions was evaluated by examining in how many sub-ecoregions each species occurs. Seventy-nine % of the species in the four taxonomic groups occurred in eleven or more sub-ecoregions (i.e., 317 of 397 species) and about 5.5% (i.e., 22 of 397 species) occurred in five or less sub-ecoregions. Bats and reptiles were the groups with the most widely distributed species.

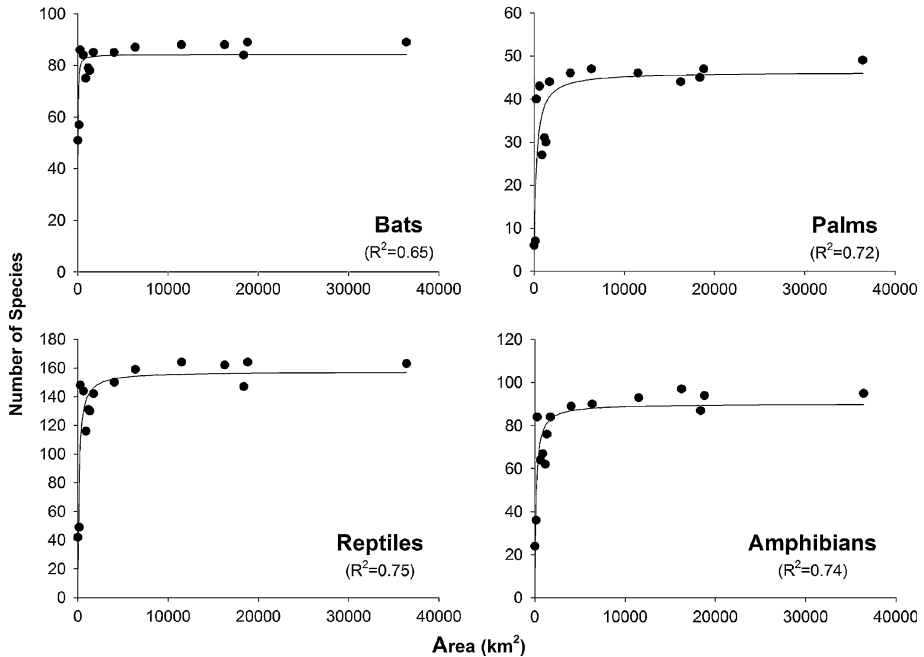


Fig. 3 Species-area relationships for four taxonomic groups in different sub-ecoregions of the Beni savannas. In all cases, non-linear regressions on untransformed axes produced higher R^2 values than log–log regressions

Patterns of distribution of flagship species (conservation status, species rarity, and endemism) show that the Beni savannas contain many rare species (Fig. 5). Reptiles were noteworthy for the dominance of the rare species category in all sub-regions. Anyway, the forests on isolated ridges of central-southern Amazonia contained lower numbers of flagship species compared to other sub-ecoregions (15 species in total). Except for the flooded palm woodlands, all sub-ecoregions associated to the Moxos and Beni Cerrado, including the *Várzea* forests, showed a high potential presence of flagship species (63–66 species depending of the sub-ecoregions).

Patterns of cross-taxon species richness were highly variable among taxa. Incongruence of species richness was recorded for bats. Bats and palms and bats and amphibians richness were significantly negatively correlated ($r_s = -0.86$ and -0.80 , respectively, $P < 0.01$ in both cases). The relationship between bats and reptiles was marginally negatively correlated ($r_s = -0.63$, $P = 0.06$). Other comparisons between taxa were significantly positively correlated showing a high congruence among these taxa (palms vs. reptiles: $r_s = 0.66$, $P < 0.05$; palms vs. amphibians $r_s = 0.89$, $P < 0.01$; reptiles vs. amphibians $r_s = 0.85$, $P < 0.01$).

Discussion

The Beni savannas are generally recognized by their distinctive assemblages of wildlife (Aguirre et al. 1996; Hanagarth and Beck 1996; Beck and Moraes 1997, 2004) and the flood dynamics that characterize it (Hanagarth 1993; Hamilton et al. 2004), however, they

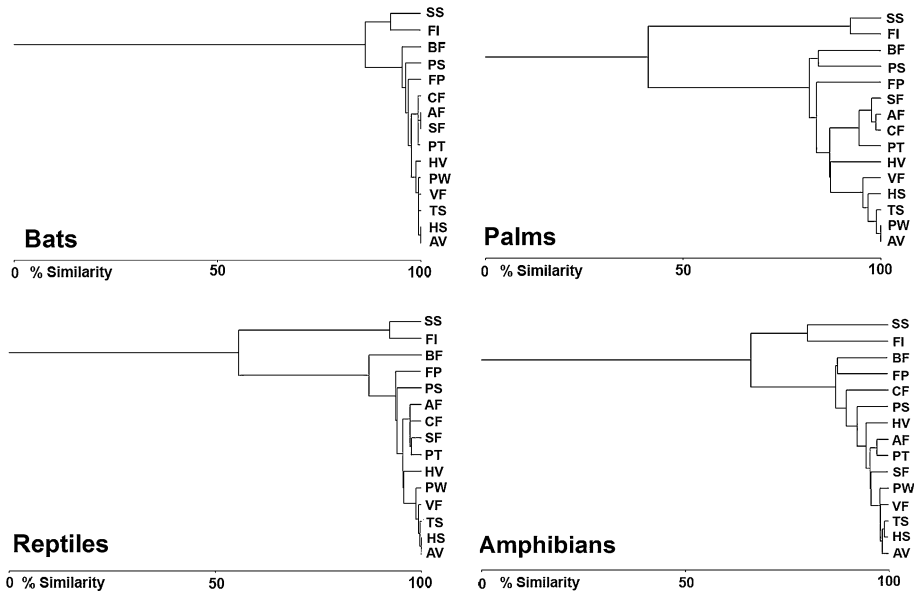


Fig. 4 Dendrograms showing similarity in species composition among sub-ecoregions composing the Beni savannas. Aquatic vegetation of the Llanos de Moxos (AV); flooded herbaceous savannas in the seasonal “bajíos” of Beni (HS); flooded tree savannas and riparian forests in permanent and almost permanent “bajíos” of Beni (TS); palm woodlands (*palmares*), low savanna woodlands and tree savannas in the semialturas of Beni (PW); flooded Amazonian palm woodlands of Beni; savannas with termite mounds (pampas termitero) of the Beni Cerrado (PT); Várzea forests of the Llanos de Moxos (VF); stagnant, black- and clear water Amazonian forests (campinas or catingas) (BF); swamp forests associated with black- and clear water rivers (Igapó forests) (SF); forests on isolated ridges of central-southern Amazonia (FI); Pando Amazonian forests (AF); Precambrian shield forests (PS); chiquitania forests transitional to Amazonian forests in well-drained soils (CF); saxicole shrublands of central-southern Amazonia (SS); anthropogenic vegetation (HV)

have only recently begun to receive the kind of attention from a conservation viewpoint that has been given to Amazonian Bolivian forests (Araujo et al. 2010). Although the Beni savannas (especially the Moxos) have been recognized as an important area of endemism and species richness in South America (Beck and Moraes 1997, 2004), its biogeographical history remains still poorly known. Our results suggest that the species of all four taxonomic groups may be semi-dependent on the savanna-type landscape. However, the present data support the hypothesis that the Várzea forests associated with the Mamoré river are necessary to maintain the regional diversity (*sensu* Ibsich et al. 2003). In fact, high concentrations of potential species richness were found in this zone; thus, these forests could maintain viable populations within the savannas, likely favoring a source-sink dynamic between the gallery-riverine forests (the source) and savannas (the sink). The high values of species turnover found between the Várzea forests and savannas sub-ecoregions (mainly in bats, reptiles, and amphibians) support also this notion. This high concentration of potential species in a given region could be explained also by high local turnover rates that some components of the biota (e.g., bats) exhibit within particular habitats, such as forest islands (Aguirre et al. 2003). The high importance of the Várzea forests for the maintenance of the biota in the region makes to this sub-ecoregion a key spatial priority for biodiversity conservation in the Moxos. These results add to priorities detected in previous

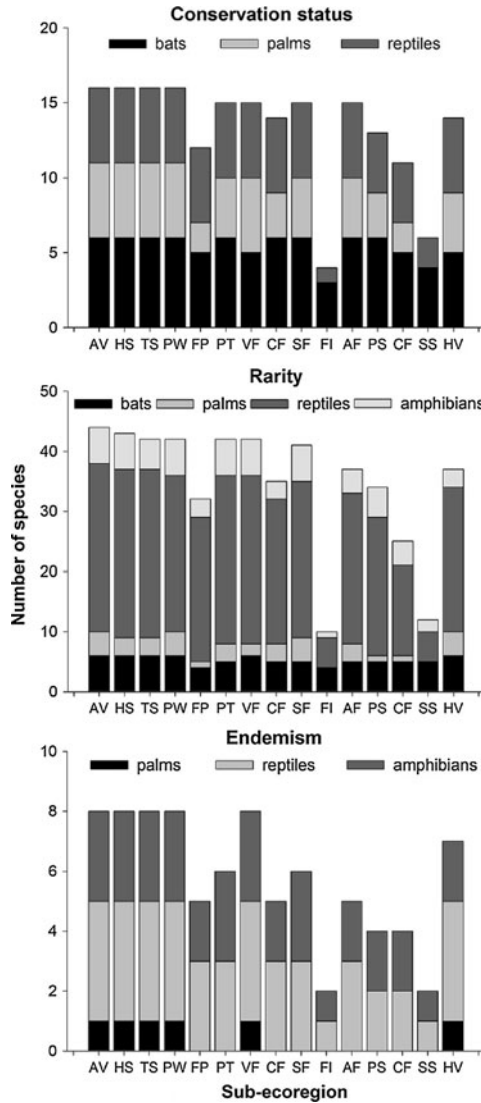


Fig. 5 Patterns of geographical distribution of flagship species along the sub-ecoregions composing the Beni savannas. Information about the conservation status, rarity, and endemism are shown. See Fig. 4 for details of the names of all the sub-ecoregions

studies where mostly regions of flooded tree savannas and aquatic vegetation were highlighted (Araujo et al. 2010). Clustering patterns of sub-ecoregions suggest also a latitudinal gradient of differentiation of the Beni savannas biota from north to south, evidenced by the differentiation of the biota associated with the Moxos (south side) compared with the biota of the Beni Cerrado (north side). The potential assemblages found in the small patches of *saxicole* shrublands and forests on isolated ridges of central-southern Amazonia seem to be markedly different from all the rest of the Beni savannas. Both sub-ecoregions are associated with the southwestern Amazonian moist forests ecoregion and have been highlighted

by their geology and floristic composition (Navarro and Ferreira 2004, 2007; Josse et al. 2007), and form, together with the precambrian shield forests, a peculiar forest-type landscape in the eastern Bolivia.

Among the groups analyzed, the effect of vegetation (sub-ecoregion) seems to be more important in the patterns of biological diversity in palms and amphibians. In palms, this diversification resulted in a relatively high diversity associated with the *Várzea* forests (mainly in the north region). In amphibians, the values of species turnover between the *Várzea* forests and savannas sub-ecoregions were high. The high biological diversity in palms contrasts with the low level of endemism of the group (only one endemic species is present in the Moxos, *Bactris faucium*). The percentage of endemic species varies across different taxa and is generally low (see Beck and Moraes 2004), however, because large areas of the Beni savannas remain unknown, these numbers will likely change when additional biological inventories are conducted. These new data would also affect the patterns of potential species richness found here.

In some cases the use of new sampling techniques and surveys might help to strengthen the trends found in this article. For the last years, records of bats have been obtained only by using mist nets set at ground level, thus leaving a large portion of the species assemblage out of the inventories, including aerial insectivores that are common in open areas. Currently, new acoustic detection methods are being used and soon will clarify patterns of distribution of species seldom captured with conventional techniques (e.g., species belonging to Molossididae and Vespertilionidae; Estrada et al. 2010).

The patterns of biological diversity described here have important implications for conserving the peculiar and unique biota of the Beni savannas. The medium to high species richness that characterize the area is an outcome of the high beta diversity, i.e., the spatial turnover in species composition that may occur over short distances. Our results support as well the notion that biological communities associated with the *Várzea* forests form part of the widespread savanna-type landscape that characterizes this area. The data on bats, reptiles, and amphibians sustain this hypothesis, suggesting also that most of their species will occur in both forests (closed vegetation) and savannas (open vegetation) (*sensu* semi-dependent species, Silva 1995; Silva and Bates 2002). This pattern is less noticeable in palms, where the species turnover between *Várzea* forests and savannas is relatively lower than in the other taxa. The results suggest also that in 5,000 km² areas (ca. 4.5% of the total area) the majority of the species pool would be found. This is a key data in order to discuss and define future strategies of conservation of the zone. At present, the protected natural areas (PAs) existing in the Beni savannas cover from 1,237 (III, IUCN category) to 12,472 km² (IV, IUCN category) of the area (Larrea-Alcázar et al. 2010). Our data suggest that small PAs (<5,000 km²) would be insufficient to harbour the potential species richness of the zone.

Together with the Cerrado, Pantanal and patches of savannas located close to transition between Amazonia and Cerrado, the Beni savannas compose the southern block of the South American tropical savannas region, while the northern block is composed of the Llanos de Orinoco, Roraima, Paru, Monte Alegre, Amapá, and Marajó (Silva and Bates 2002). A phytogeographical analysis (Sarmiento 1983) and geological evidence (Mayle et al. 2000, 2009) suggest that these regions were probably connected in the recent past. Three northern-southern savanna corridor hypotheses have been proposed in the past (Haftner 1967, 1974; Webb 1991; Silva and Bates 2002): (a) an Andean corridor, (b) a central Amazonian corridor, and (c) a coastal corridor. The Beni savannas are a key biogeographical element to support the first hypothesis (Silva and Bates 2002). If this corridor did exist (likely during the quaternary climatic cycles, Mayle et al. 2000, 2009),

the patterns of distribution of the “savanna-adapted” biota might show evidence of their legacy. Our results showed that biotas associated with the sub-ecoregions of the Beni savannas (mainly the Moxos) are distinct from those linked to forest-type sub-ecoregions (with the exception of the Várzea forests). This partially supports the hypothesis of this Andean Corridor, however, we still need comparable studies in other savanna regions, such as the Llanos de Orinoco and Grã-Sabana, which may support this suggestion. In contrast, the relative high levels of precipitation that characterize the Beni savannas (1800–2000 mm/year, Hanagarth 1993) highlight this region composing the northern block. Therefore, a widespread savanna corridor following a chain of low precipitation across the Andes (or a belt in the Amazonian basin) may not have existed (*sensu* Silva and Bates 2002).

The floods in the Beni savannas result from two relatively well known processes: the exogenous (or “water from below”) and endogenous (or “water from above”) process (Bourrel and Pouilly 2004; Walker 2008; Bourrel et al. 2009). The first kind is caused by the arrival of the flood wave from the Mamore river and its tributaries, while the second is induced by increased groundwater levels caused by local precipitation (Bourrel et al. 2009). This interaction between two processes and local topography causes a mosaic (or water gradient) of environments from aquatic vegetation to Amazonian terra firme forests. Our results suggest that the patterns of biological diversity partially respond to this arrangement of landscape. Likewise, our study strongly supports the notion that the cross-taxon congruence of species richness between pairs of taxa may be variable both geographically and taxonomically (Su et al. 2004; Pawar et al. 2007). This pattern had been suggested both at regional (Sætersdal et al. 2004; Lamoreux et al. 2006) and global scales (Gaston 1996; Orme et al. 2005); however, our study is the first attempt to study the patterns of spatial diversity for a neotropical savanna from a set of living organism from vertebrates (bats, reptiles, and amphibians) to vascular plants (palms). Although patterns of species richness were relatively variable, we found that the flooded forests (or Várzea forests) and wet savannas (herbaceous and palm savanna sub-ecoregions) correspond to potentially high-priority sites for all taxa studied. Both sites are also fundamental to allow and maintain the dynamic of flood both in the up-river as well as in the down-river zones (Hamilton et al. 2004; Bourrel et al. 2009). These results can help to develop the most appropriate conservation strategies for these often-neglected sites.

A topic usually excluded from analysis of patterns of biological diversity is the historic effect of human population density. There is growing evidence supporting the theory of dense populations in the Amazonian regions in the past, which are sparsely populated today (Lehmann et al. 2003; Glaser 2007). The archaeological evidence from the Beni savannas (mostly in the Moxos; e.g., Denevan 2001; Erickson 2000), support the hypothesis that Amazonia likely maintained dense and complex societies, which had perhaps a major impact on the composition and arrangement of the savanna-type landscape that today characterize this region. In fact, the Moxos is usually cited as an example of a landscape with intensive use by indigenous Amazonians in the pre-columbian period (Walker 2001, 2008; Erickson 2006; Erickson and Baleé 2006).

In summary, our study suggests that the patterns of biological diversity of the Beni savannas, a high-priority ecoregion at neotropical scale (Mayle et al. 2009), respond to the mosaic-like arrangement of its landscape. Future research analyzing the patterns of diversification of grasses, birds, and fishes may be decisive in order to support the results presented here. It is also important to assess the impact of their main threats (logging degradation, burning, and livestock). Here, we propose that future strategies on conservation, planning, and species management should point to total target areas of at least

5,000 km². This area seems to be sufficient to include the biological distinctiveness of the Moxos at least in terms of bats, palms, reptiles, and amphibians. Large-scale modeling surveys may be critical for understanding and predicting species responses to anthropogenic change and habitat alteration, and ultimately for long-term biodiversity conservation.

Acknowledgments We thank the researchers who provided data for our analysis: (1) For bats A. Vargas, C. Zambrana-Torrelío, D. Peñaranda, I. Moya, J.C. Perez-Zubieta, L. Siles, and M. Terán; (2) For reptiles and amphibians D. Embert, S. Reichle, A. Muñoz, R. Aguayo, C. Cortez, E. Domic, M. Maldonado, J. Padiál, L. Gonzales, R. Montaña, M. Jansen and M. Guerrero; (3) For palms L.R. Moreno and S. Altamirano. We also thank the Programa para la Conservación de Murciélagos de Bolivia (PCMB) and the Museo de Historia Natural Noel Kempff Mercado (MHNNKM) for their support in the compiling and systemizing of the comprehensive data base used in this study. P. Caballero and G. Huanca helped in the gathered and systematized the data base as well as in the spatial analysis modeling. The study was supported by funds provided by The John D. and Catherine T. MacArthur Foundation (Grant 08-91570-000-GSS, Project: Linking socioeconomic and environments agenda to conserve the Moxos Plains) and the Netherlands Embassy to Fundación Amigos de la Naturaleza (FAN). LFA would like to acknowledge Wildlife Trust Alliance and Whitley Fund for Nature for research funding. Ramiro P. López and two anonymous reviewers made valuable comments and criticisms on early versions of this manuscript.

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