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# Land-use and land-cover effects on regional biodiversity distribution in a subtropical dry forest: a hierarchical integrative multi-taxa study

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**Abstract** Latin American subtropical dry ecosystems have experienced significant human impact for more than a century, mainly in the form of extensive livestock grazing, forest products extraction, and agriculture expansion. We assessed the regional-scale effect of land use and land cover (LULC) on patterns of richness distribution of trees, birds, amphibians, and mammals in the Northern Argentine Dry Chaco (NADC) over c. 19 million hectares. Using species distribution models in a hierarchical framework, we modeled the distributions of 138 species. First, we trained the models for the entire Argentinean Chaco with climatic and topographic variables. Second, we modeled the same species for the NADC including the biophysical variables identified as relevant in the first step plus four LULC-related variables: woody biomass, distance to crops, density of livestock-based rural settlements (*puestos*), and vegetation cover. Third, we constructed species richness

maps by adding the models of individual species and considering two situations, with and without LULC variables. Four, richness maps were used for assessing differences when LULC variables are added and for determining the main drivers of current patterns of species richness. We found a marked decrease in species richness of the four groups as a consequence of inclusion of LULC variables in distribution models. The main factors associated with current richness distribution patterns (both negatively) were woody biomass and density of livestock *puestos*. Species richness in present-day Semiarid Chaco landscapes is strongly affected by LULC patterns, even in areas not transformed to agriculture. Regional-scale biodiversity planning should consider open habitats such as grasslands and savannas in addition to woodlands.

**Keywords** Amphibians · Birds · Chaco · Hierarchical species distribution modeling · Mammals · Trees

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## Introduction

Large areas once occupied by natural ecosystems are being transformed to cropland and pastureland worldwide (Foley et al. 2005). Changes in land use/land cover (LULC), through the alteration or destruction of habitats, are considered an important factor of biodiversity loss, and, along with climate change, one of the main causes of the current high rates of extinction (Sala et al. 2000; Ceballos and Ehrlich 2002; Brook et al. 2008). The importance of LULC as a factor of species loss varies globally, with tropical and subtropical biomes being the most affected (Sala et al. 2005).

Most research and discussion on the effects of LULC on biodiversity has focused on tropical rainforests. However,

tropical and subtropical dry forests are more threatened globally (Hoekstra et al. 2005); and in Latin America, they are experiencing the second highest absolute deforestation rate after the rainforests, even though their remaining area is much smaller (Aide et al. 2013). In Latin America, the dry forests of the Chaco ecoregion constitute the largest remaining continuous forest ecoregion after the Amazon rainforest (Eva et al. 2004) and the less fragmented dry forest ecosystem (Portillo-Quintero and Sánchez-Azofeifa 2010). Consequently, it represents a major asset for continental-scale biodiversity conservation. Such biodiversity is being threatened by human land use. Since the early 1900s, the area has been extensively used for livestock ranching (Bucher and Huszar 1999), and land-use changes accelerated since the 1970s when agriculture (in particular, soybean and planted pastures) started to expand rapidly (Grau et al. 2005; Zak et al. 2008).

Despite threats posed by LULC in the Chaco are well recognized, the paucity of detailed information on species distribution has prevented progress to understand potential consequences for regional biodiversity. Up to the present, biodiversity conservation priorities in the Chaco ecoregion have been based on expert opinions without rigorous spatial analysis (e.g., The Nature Conservancy et al. 2005). To overcome this difficulty, the species distribution modeling (SDM) techniques represent an ideal approach as they offer reliable information on the environmental constraints based on a moderate number of occurrence sites, thus allowing to spatially extrapolate that environmental niche and providing robust ways to model regional patterns of species richness and its relationship with LULC (Seoane et al. 2006; Ficetola et al. 2010). Researchers aiming at simultaneously assessing the influence of both climatic variables and the land cover on species distributions must, however, consider that climate has stronger effects on species distributions at larger geographic extension and coarser grain than land cover, which become important at finer resolutions where climate has a comparatively minor importance (Pearson et al. 2002, 2004). Thus, the relative importance of different factors influencing species distribution responds to a hierarchical structure correlated with spatial scales (Collingham et al. 2000; Pearson and Dawson 2003). A hierarchical framework proposed for SDM consists of fitting a model with bioclimatic variables at larger extension and coarser grain, and then modeling at a more local extension and finer grain including the downscaled bioclimatic information obtained in the first step along with LULC variables. This results in significant improvement of models performance in comparison with non-hierarchical models (Pearson et al. 2004). Surprisingly, very few studies have addressed the SDM from a hierarchical perspective (e.g., Pearson et al. 2004; Anadón et al. 2006; Latimer et al. 2006) and the effects of LULC were only assessed in a

hierarchical integrative manner on a single species (Anadón et al. 2007). Analyzing the impact of LULC on geographic patterns of different taxonomic groups is particularly relevant, as different taxa could be affected in contrasting ways by land use (Schulze et al. 2004; Kessler et al. 2009; Dallimer et al. 2012). For instance, in evaluating the responses of plants, birds, and mammals to land use in Indonesia, Lawton et al. (1998) found that very few taxonomic groups were reliable predictors for other groups' patterns.

In this paper, we incorporated LULC variables in a multi-taxa study in the northern sector of the Argentine Dry Chaco following a hierarchical framework to model species distribution of trees, amphibians, birds, and mammals selected for their contrasting ecological requirements. Based on this, we assessed the implications of LULC variables on geographic patterns of regional biodiversity. Specifically, we contrasted the results of SDM trained in a hierarchical approach with and without LULC variables. First, we used data from museum collections, bibliography, and field observation in order to model species distributions for the entire Argentine Chaco Ecoregion based on bioclimatic and topographic variables. Second, we used the same variables plus descriptive variables of the current land use and land cover to model the same species' distributions at finer resolution in the Northern Argentine Dry Chaco. Third, we added these single-species models fitted both with and without LULC variables to obtain corresponding richness maps for each taxonomic group. Finally, we used these maps to answer two specific questions: (1) How the modeled patterns of species richness change when LULC variables are taken in account? and (2) which LULC variables are the most important drivers of the current species richness distribution patterns of different taxonomic groups, and how consistent are these drivers among taxonomic groups? We hypothesized a negative association between variables related to land-use intensity and species richness. Finally, we show how such comparisons between SDM trained in a hierarchical approach with and without LULC variables can be used to identify conservation targets. Our results highlight the drawbacks of current conservation strategies in the region, which are almost exclusively centered in forests at the expense of non-forest habitats.

## Methods

### Study area

The Gran Chaco ecoregion in the subtropical area of South America covers ca 1.2 million km<sup>2</sup> (Dinerstein et al. 1995) in Argentina, Bolivia, and Paraguay, plus a small area in

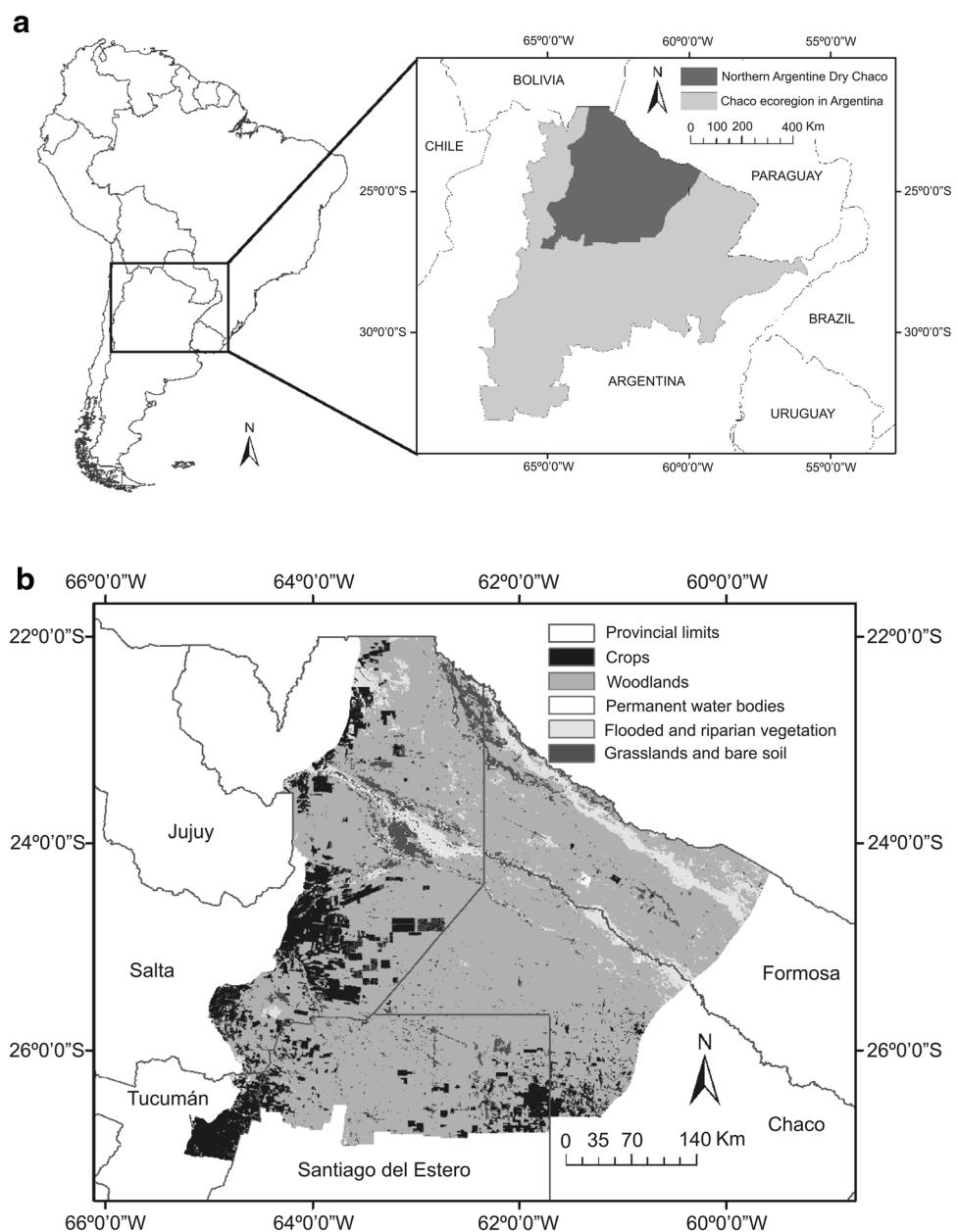


southwestern Brazil (Fig. 1). The natural vegetation is dominated by dry broad-leaf forests (Portillo-Quintero and Sánchez-Azofeifa 2010; Baldi and Jobbágy 2012), with a minor proportion covered by seasonally flooded palm and grass savannas (Bucher and Huszar 1999). Topography is predominantly flat; climate is characterized by a seasonal semiarid climate, with rainfalls concentrated in summer. The geographic rainfall pattern is characterized by a decreasing gradient from east to west. Chaco biodiversity includes ca. 145 mammal species (10 % being endemic to the ecoregion; Bucher and Huszar 1999) and over 400 species of birds (with a low number of endemisms; Short 1975). The occurrence of a variety of both seasonal and

permanent wetlands allows the existence of a rich fauna of amphibians with over 30 species (Ceí 1980; Kacolis et al. 2006). Recently, a tree diversity survey in the Argentine Dry Chaco account for 46 tree species (Giménez et al. 2011).

In this work, a hierarchical framework was adopted for model building. In consequence, we have two study area extensions. The first extension corresponds to the entire Argentine Chaco Ecoregion (ACE) used to fit models based on bioclimatic variables and topography. The second study area corresponds to the Northern Argentine Dry Chaco (NADC) for finer-scale analysis and incorporation of LULC variables (Fig. 1).

**Fig. 1** **a** Area covered by the Chaco ecoregion in Argentina (light gray) and by the study area in the Northern Argentine Dry Chaco (dark gray). **b** Detail showing vegetation classes in the study area, layer developed from interpretation of a Landsat 7TM image of 2007. The names of the Argentine provinces are provided



The ACE includes the largest proportion of the Chaco ecoregion in South America (Fig. 1), and it is divided into two zones (Cabrera 1976; Prado 1993): the western “Dry Chaco,” with precipitations between 500 and 900 mm, and the eastern “Humid Chaco” with rainfall of 900–1400 mm. In association with synoptic atmospheric patterns, annual rainfall in the Chaco increased markedly in the early 1970s, remaining relatively stable in the new higher levels during the last decades of the twentieth century (Minetti and Vargas 1999; Bucher et al. 2006).

The NADC encompasses 189,150 km<sup>2</sup>, covering 17 departments (administrative units) in the east of the province of Salta, northeast of Tucumán, north of Santiago del Estero, and west of Chaco and Formosa. The study area boundaries coincide in the north and south with those of such departments; the eastern boundary was demarcated along the 900 mm year<sup>-1</sup> isoline, which is roughly considered the limit between the Dry Chaco from the Humid Chaco, while the western boundary was set at the limit between the Chaco and Yungas ecoregions as defined by the National Forest Inventory (SAyDS 2004). Mean annual temperature is 20–22 °C (24–27 °C for the hottest month—January and 14.5–15.5 °C for the coldest month—July). The lowest rainfall occurs in the center of study area (ca. 500 mm), increasing west-, south-, and eastward to 700–900 mm, and is markedly seasonal, with rainy summers and dry winters and early springs (Minetti 1999). Natural vegetation is characterized by dry forests (Fig. 1) with *Aspidosperma quebracho-blanco*, *Schinopsis lorentzii*, *Ceiba chodatti*, *Caesalpinia paraguariensis*, and *Prosopis* spp. being the most important trees (Cabrera 1976) and (in smaller extension) natural grassland and flooded savannas with *Copernicia alba* palms (Cabrera 1976).

Pre-European landscape in the NADC was probably a mosaic of patches of forests and periodically burnt grasslands, and the current dominance of woody vegetation is likely a consequence of fine biomass removal, and the resulting decrease in fire frequency resulting from the introduction of the domestic livestock in the early twentieth century (Morello and Saravia Toledo 1959a, b; Adámoli et al. 1990). Salient features of the current landscape in the NADC are the livestock “*puestos*,” rural settlements consisting on a main house, a water reservoir, and corrals (Grau et al. 2008). *Puestos* are typically surrounded by bare soil as a result of the overexploitation of woody vegetation and overgrazing. Modern agriculture fields expanded rapidly without interruption until the present since the 1970s (Grau et al. 2005; Gasparri et al. 2013), as a consequence of the increase in rainfall, growing prices of the main agriculture products (particularly soybean), and technological changes (no-tillage agriculture associated with genetically modified soybean cultivars). Thus, the main changes in LULC occurred after 1970 in the study area.

## Species distribution modeling

As we stated above, we modeled at two spatial scales. First, we build species distribution models for the ACE fitted with bioclimatic and topographic variables. Later, we modeled the distribution of the same species for the NADC, including those biophysical variables highlighted as relevant in the previous step, plus four LULC variables (woody biomass, density of *puestos*, vegetation classes, and distance to crops). The species selection, environmental variables, and modeling procedures are fully described in Supplementary Material 1. The final number of species considered was 108 (18 trees, 25 amphibians, 48 birds, and 17 mammals).

## Richness patterns

To quantify the effects of LULC on the patterns of species richness, two sets of richness maps in the NADC were made separately for trees, amphibians, birds, and mammals. (1) Adding final models of individual species fitted for the ACE only with bioclimatic and topographic variables downscaled at the extension and resolution of the NADC. (2) Adding final models of individual species fitted in the NADC with bioclimatic, topographic, and LULC variables.

Richness maps (in which for each cell, richness is computed as the summation of species with the presence data on it) with and without the inclusion of LULC variables were compared under the assumption that models fitted only with bioclimatic and topographic variables represent the potential distributions of the species without LULC variables in the ACE. A second assumption is that modeled species reached the equilibrium with the environment after the main LULC changes in the NADC (i.e., the location of occurrence points recorded in field really represent distributions constrained by LULC variables). Therefore, the models for the NADC should be good representations of current species distributions according to LULC patterns of the last decades.

We tested whether richness maps of the four groups, constructed by adding individual species models, are a good representation of their richness distribution patterns both in the ACE and in the NADC. The Sørensen similarity index was used to compare the modeled richness and species composition with the observed values in “well-surveyed cells” (see below). Similarity values range from 0 to 1; values over 0.75 were considered to reflect very high similarity, values between 0.51 and 0.75 describe high similarity, between 0.25 and 0.50 moderate similarity, and below 0.25 low similarity (Ratcliff 1993; Faggi et al. 2006). Well-surveyed cells were identified following the

procedures delineated in Pineda and Lobo (2009), who calculated a completeness index as

$$100 \times \text{observed/predicted}$$

where “observed” are the true observed richness values, and “predicted” are the maximum species richness predicted by any of three richness estimators (Chao 2, Jackknife 1, and species number predicted at the 95 % upper confidence interval of accumulation curves produced with Mao Tau function). Richness estimators and similarity values were obtained with ESTIMATES 8.2 (Colwell 2006). We considered a cell with a completeness value of 50 % as “well-surveyed”; selecting higher values prevented comparisons given the very low number of cells that reached these levels (a consequence of the scarcity of biodiversity inventories in the Chaco).

Differences in richness between maps with and without LULC variables were assessed throughout a repeated-measures ANOVA for each group and for all groups together, comparing 479 cells selected at random from richness maps. Additionally, considering all the pixels sharing the same richness value as a “richness category,” we calculated the “percentage of like adjacencies” of each richness category in each group, using FRAGSTATS version 3.3 (McGarigal et al. 2002). The “percentage of like adjacencies” is a widely used (e.g., Cushman et al. 2008; Ramjohn et al. 2012; Schlinder et al. 2013) metric of aggregation of a given category that equals the number of like adjacencies (or joins) between cells, divided by the total number of cell adjacencies, and multiplied by 100 (McGarigal et al. 2002). The percentage of like adjacencies equals zero when the corresponding category is maximally disaggregated, and increasing values indicate increasing aggregation of the category in question. The relative importance of the more relevant variables in models fitted with LULC variables was visually evaluated by plotting the number of species which models selected each variable in each group. The importance and effect of multiple LULC variables (woody biomass, distance to crops, and density of *puestos*) on species richness per cell was evaluated in a general linear model (GLM) with a multivariate design, conducted with the same 479 randomly selected cells used in the ANOVA, taking as dependent variable the difference in richness values between assemblies of models trained with and without LULC variables. The effect of vegetation, a categorical variable, on species richness changes was analyzed separately by means of Kruskal–Wallis nonparametric tests, given we found a lack of homoscedasticity between classes within the four taxonomic groups, which precludes the use of a parametric test. Vegetation classes that differed significantly were detected with a post hoc multiple comparison test.

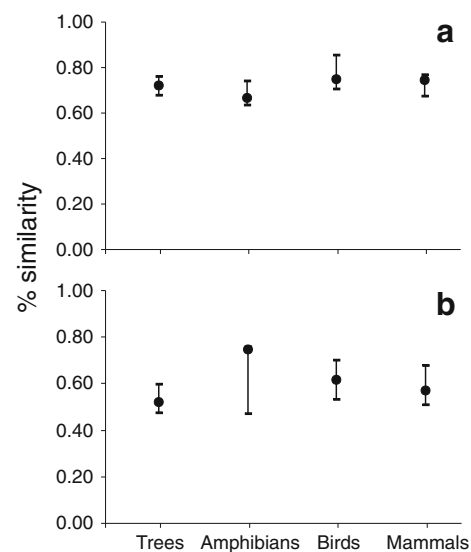
## Results

A total of 108 species (18 trees, 25 amphibians, 48 birds, and 17 mammals) met the criteria for the analysis of richness distribution patterns in the NADC. Well-surveyed cells showed similarity values high to very high when comparing the observed richness and species composition with the values obtained from richness maps constructed by superimposing species distribution models (Fig. 2).

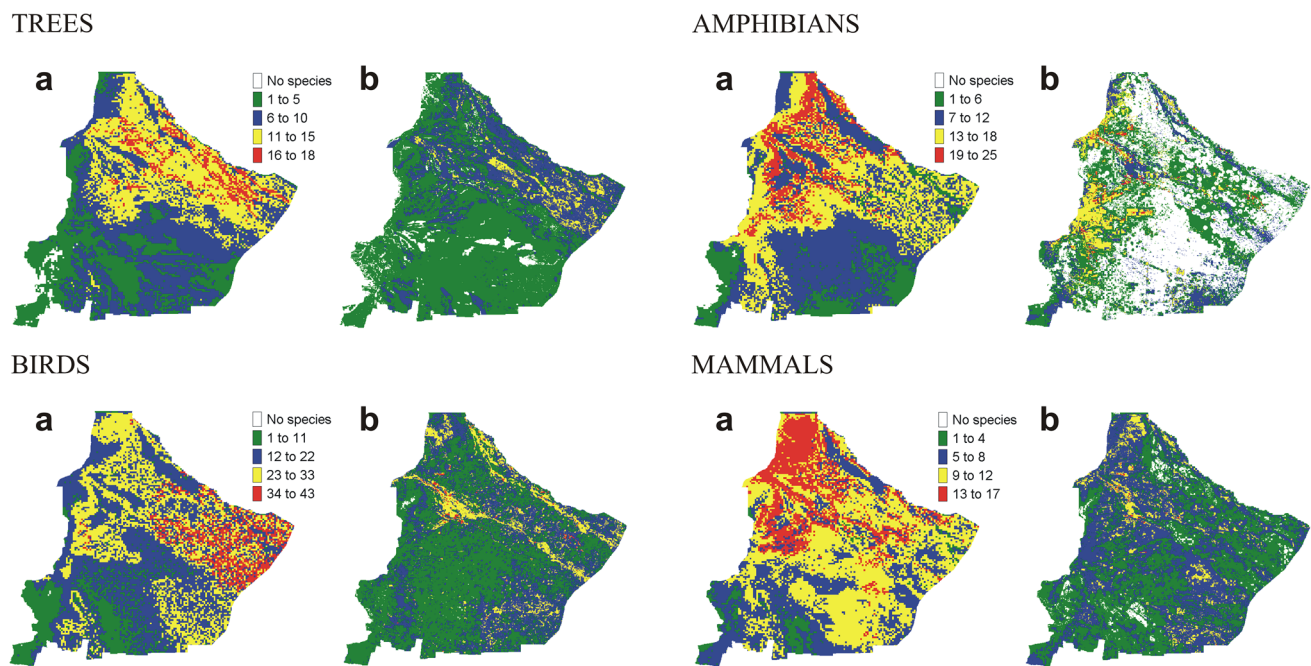
### LULC effects on species richness

In the models fitted only with biophysical variables, low richness areas roughly coincided for all groups in the south of NADC, while the richest areas were located in the north of the NADC for trees, in the northwest for amphibians and mammals, and in the northeast for birds (Fig. 3a). The inclusion of LULC variables in the models (Fig. 3b) caused a drastic reduction in the modeled mean richness values ( $F_{1, 1,912} = 2458.9$ ,  $n = 479$ ,  $P < 0.001$ , repeated-measures ANOVA; Table 1); with an average decrease in species richness per pixel ranging from 16.4 % in mammals to 59.9 % in amphibians (Figs. 3, 4).

In general, intermediate values predominated in richness maps derived from models fitted with only biophysical variables. Maps from models including LULC variables showed a leftward displacement in the figure with most area covered by low richness values (Fig. 4). This reduction was stronger in amphibians, where the category zero species became the most spatially extended.



**Fig. 2** Similarity between observed richness values and those obtained by superimposing species distribution models in: **a** the Argentine Chaco ecoregion; and **b** the Northern Argentine Dry Chaco. Plots show the median and the 25th and 75th percentiles



**Fig. 3** Patterns of species richness distribution in tree species, amphibians, birds, and mammals in the Northern Argentine Dry Chaco, comparing between maps obtained from **a** models fitted for

the entire Argentine Chaco without LULC variables and resampled to extension and resolution of the study area and **b** maps corresponding to models fitted in the study area with LULC variables

**Table 1** Within-group contrasts between richness models fitted with and without LULC variables ( $n = 479$  cells in all cases)

	Mean richness without LULC variables $\pm$ SD	Mean richness with LULC variables $\pm$ SD	$t$	$p$
Trees	8.49 $\pm$ 4.28	4.19 $\pm$ 3.05	15.64	<0.0001*
Amphibians	11.87 $\pm$ 5.10	3.08 $\pm$ 5.06	31.96	<0.0001*
Birds	20.50 $\pm$ 8.29	11.46 $\pm$ 7.17	32.87	<0.0001*
Mammals	9.62 $\pm$ 2.99	4.48 $\pm$ 2.50	18.70	<0.0001*

\* Significant value at  $\alpha = 0.05$

Aggregation (depicted by the percentage of like adjacencies) was high across all richness categories and taxa (Fig. 4). Spatial aggregation of richness was approximately constant across the richness gradient in maps from models with biophysical variables only, while in the richness maps from models with LULC variables, the adjacency values were more diverse across categories, showing a decrease from approximately 80 % to 40 % or less in the different groups in comparison with richness maps from models fitted without LULC variables (Fig. 4). The steepest drop in these maps occurred in the highest richness classes, implying that high diversity pixels became more isolated in the landscape (Figs. 3, 4).

The comparison of richness maps derived from biophysical and biophysical plus LULC variables showed a drastic decrease in richness across most of the study area

when LULC were added (Fig. 5; Table 2). Cells with little or no changes (from 10 % of species lost to 10 % of species gained) and cells with gains represent a minor fraction (between 8 and 20 %) of the study area, and were generally located at the south and southwest of the NADC, although birds showed two important clusters of these cells in the northwest (Fig. 5). In the four groups, the most frequent cell category was that of a reduction of more than 50 % in species richness.

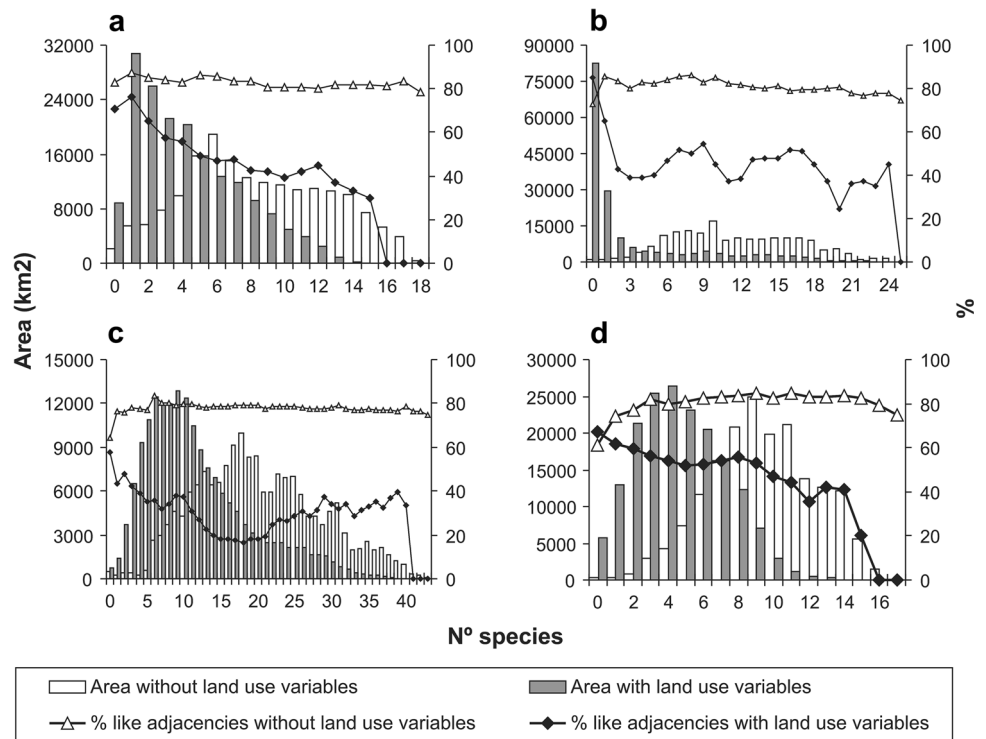
#### Drivers of the current species richness distribution patterns

The importance of the variables determining single-species distribution in the NADC models varied across taxonomic groups (Fig. 6). Soil texture was the most frequently selected variable in models of trees, while, unsurprisingly, woody biomass and vegetation classes were the most important LULC variables. Woody biomass showed a positive response in 62.5 % of the individual species models that selected this variable as relevant (28 % of all tree species; Fig. 6).

In amphibians, birds, and mammals, slope and the four LULC variables were always among the variables more frequently selected (Fig. 6b–d). Woody biomass was the most frequently selected LULC variable in models of amphibians and birds. The response of the probability of presence to the woody biomass was negative for all



**Fig. 4** Area covered by each richness category, and percentages of like adjacencies with and without LULC variables for **a** trees; **b** amphibians; **c** birds; and **d** mammals, in the Northern Argentine Dry Chaco



amphibians species, for 25 % of bird species and for 50 % of mammal species which models included woody biomass (17 and 18 % of all bird and mammal species, respectively; Fig. 6). In birds, notwithstanding, the more frequent response to woody biomass (44 % of species models selecting this variable; 30 % of all bird species) was positive. The density of *puestos* was the most relevant LULC variable in mammals (Fig. 6), with a negative association in 75 % of species models that selected this variable (35 % of all mammal species; Fig. 6).

Woody biomass was the continuous land-use variable more closely related to the differences in species richness between maps with and without LULC variables, in all taxonomic groups (Multivariate GLM: Wilks' lambda = 0.52,  $F_{4,472} = 110.60$ ,  $P < 0.0001$ ) followed by the density of *puestos* (Wilks' lambda = 0.86,  $F_{4,472} = 18.58$ ,  $P < 0.0001$ ), while the distance to crops had no significant effect (Wilks' lambda = 0.99,  $F_{4,472} = 1.09$ ,  $P = 0.36$ ). Percentage difference in the species richness of amphibians ( $R^2 = 0.51$ ,  $P < 0.0001$ ), birds ( $R^2 = 0.15$ ,  $P < 0.0001$ ), and mammals ( $R^2 = 0.27$ ,  $P < 0.0001$ ) was negatively related to woody biomass and to the density of *puestos* (Table 3). The difference in the richness of tree species ( $R^2 = 0.01$ ,  $P = 0.38$ ) was not related to any of the above variables of land use (Table 3).

There were significant differences in richness among vegetation classes in the four taxonomic groups: trees (Kruskal–Wallis test:  $H_{3,479} = 15.64$ ,  $P = 0.013$ ), amphibians ( $H_{3,479} = 196.28$ ,  $P < 0.001$ ), birds ( $H_{3,479} = 91.51$ ,

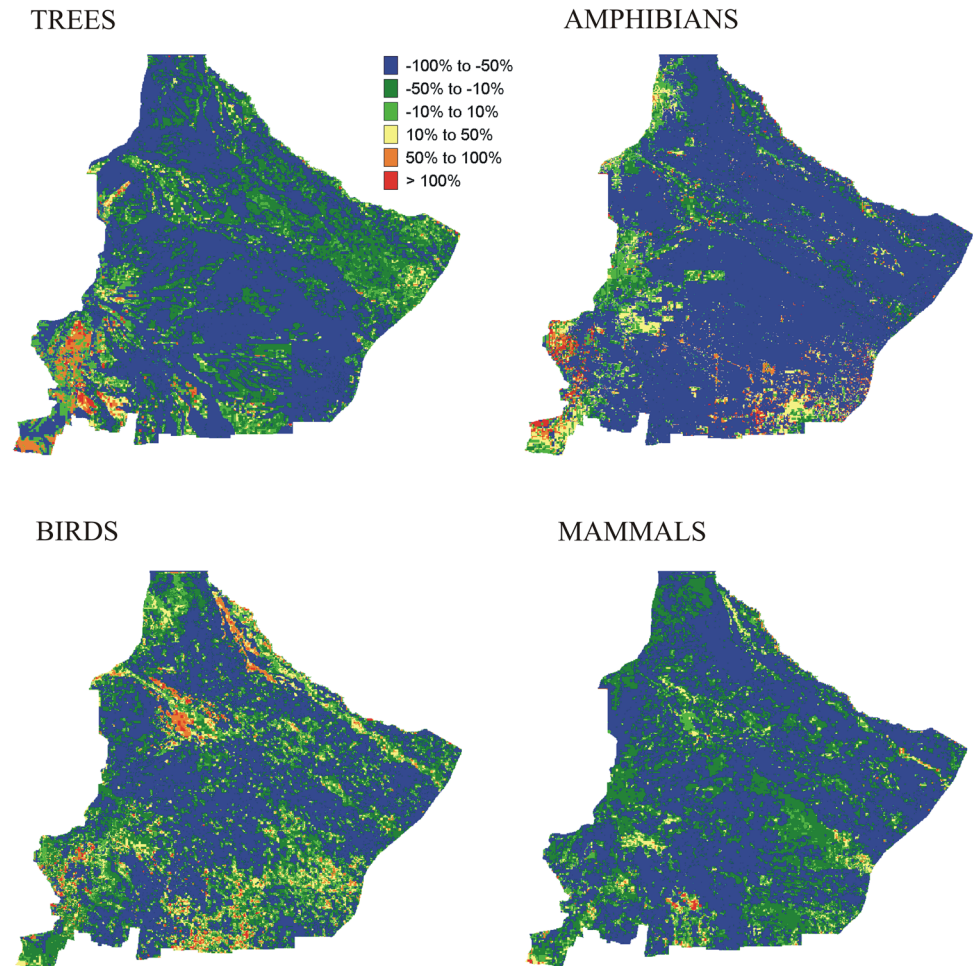
$P < 0.001$ ), and mammals ( $H_{3,479} = 83.80$ ,  $P < 0.001$ ). In general, change in species richness was greater in woodlands (high negative mean values) and lower in the grassland/bare soil category (mean values of positive sign or close to zero), while crops and riparian and flooded vegetation had intermediate values (Fig. 7).

## Discussion

The hierarchical modeling approach allowed us to compare situations with and without LULC variables. We found strong evidences of major effects of land use and land cover on species richness patterns of trees, amphibians, birds, and mammals in the Dry Chaco (Figs. 3, 4, 5). Our results indicate that current LULC operate as a local restriction for many species despite being in a favorable bioclimatic situation. The vast majority of the study area shows a significant lower richness when LULC is taken into account, even in extensive areas of seminatural woodland vegetation (Fig. 5). Unexpectedly, results showed an overall negative effect of landscapes dominated by woodlands on a main portion of Dry Chaco species (Fig. 7), which suggest a major change is needed in the dominant forest-centered conservation paradigms in the region.

The woody biomass is the more frequently selected LULC variable by models, although the unexpected negative relationship between the woody biomass and both the

**Fig. 5** Changes per  $30 \times 30$  arc-seconds cell in richness values between assemblies of models trained without LULC variables and those of models that incorporate LULC variables in the Northern Argentine Dry Chaco



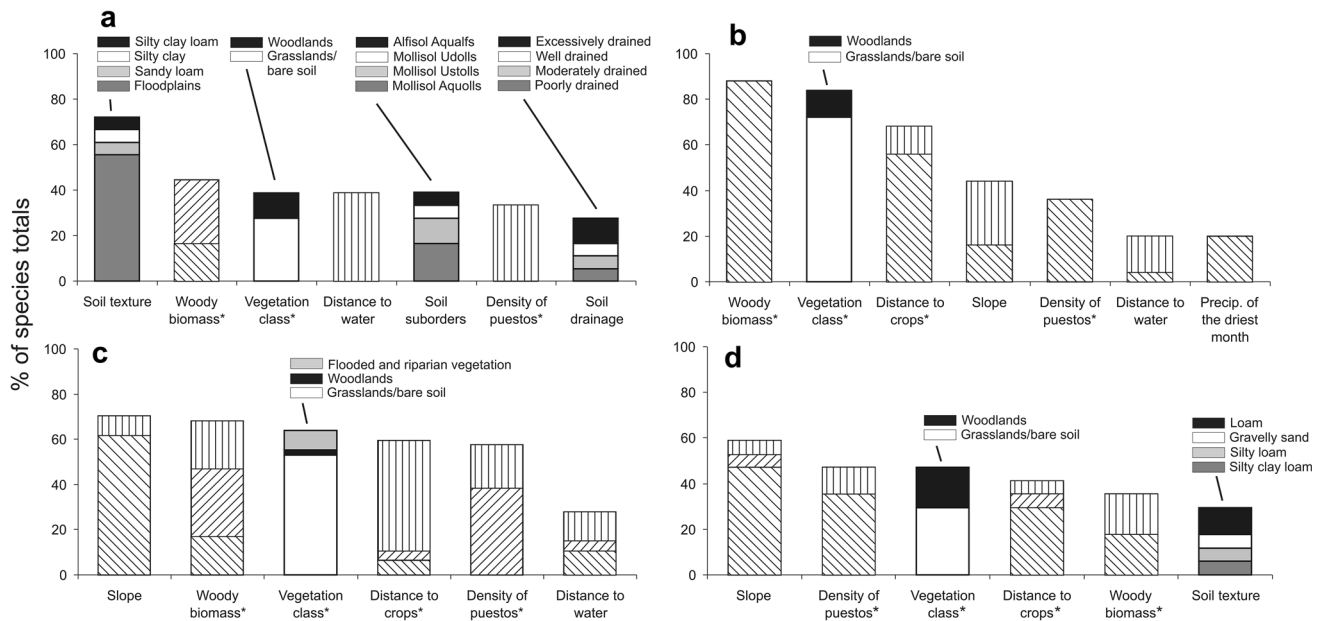
**Table 2** Area ( $\text{km}^2$ ) covered by each category of species richness difference by loss or gain of species

% Change	Trees	Amphibians	Birds	Mammals
–100 to –50	99,704	134,712	83,112	102,984
–50 to –10	52,990	15,350	57,002	58,645
–10 to 10	12,893	10,151	14,307	7,484
10 to 50	5,328	10,094	14,243	5,553
50 to 100	4,073	3,780	5,876	1,084
>100	1,063	1,963	1,509	300

The percentages of change are relative to values in richness maps made with models fitted without LULC variables, in each  $30 \times 30$  arc-seconds cell

probability of presence of many species and accordingly in the increase in species richness indicates that open habitats are important for a significant fraction of the regional pool of species. The preference for landscapes dominated by open habitats was also observed for species traditionally known as forest dwellers. These unexpected results may be related with the concept of the original Chaco landscape ecoregion proposed by several authors (Morello and

Saravia Toledo 1959a, b; Adámoli et al. 1972; Bucher and Huszar 1999; Adámoli et al. 1990). These authors proposed that the pre-European vegetation physiognomy of the Chaco was a mixed landscape of woodlands and open savannas, which experienced substantial woodland encroachment as a result of overgrazing by domestic livestock. The region also experienced successive fluctuations between dry and humid periods during the Late Pleistocene and Holocene (Iriando and García 1993), with dry periods associated with reductions in the forest cover and expansion of open areas (May et al. 2008). Thus, a considerable proportion of the biota in the Chaco ecoregion could have evolved in landscapes more similar to savannas rather than woodlands; for instance, many Chaco bird species have derived largely from forms of the arid scrubs, semiopen habitats, and forest edges situated to north and east of the Chaco (Short 1975). An analytical bias favoring to the grasslands/bare soil class should not be discarded, given that current landscapes dominated by the grasslands/bare soil class represent a minor proportion of the Chaco, and maximum entropy models assign the greatest importance to less represented categories even with few



**Fig. 6** Importance of biophysical (*without asterisks*) and LULC (*with asterisks*) variables according to the percent of species in which these variables were selected as relevant by niche models, in **a** trees, **b** amphibians, **c** birds, and **d** mammals, in the Northern Argentine Semiarid Chaco. The response of the probability of presence to continuous variables (inverse: descending oblique stripes; direct:

ascending oblique stripes; threshold-divided vertical stripes) and the main selected class of categorical variables are specified. Variables selected by models in less than five species were not plotted. Threshold variables are characterized by a positive (or negative) response in part of the range, and the inverse response in the rest

**Table 3** Effects of LULC variables on the percentage of species richness difference between maps built with models fitted with and without LULC variables, in four taxonomic groups

	Log woody biomass			Density of <i>puestos</i>			Distance to crops		
	Beta ( $\beta$ )	$F_{1,475}$	$p$	Beta ( $\beta$ )	$p_{1,475}$	$p$	Beta ( $\beta$ )	$F_{1,475}$	$p$
Trees	-0.06	1.80	0.18	-0.04	0.70	0.40	0.00	0.003	0.96
Amphibians	-0.68	436.14	<0.0001*	-0.10	9.05	0.0027	-0.06	3.14	0.08
Birds	-0.20	20.51	<0.0001*	-0.30	48.59	<0.0001*	0.01	0.11	0.74
Mammals	-0.37	83.54	<0.0001*	-0.30	55.59	<0.0001*	-0.04	0.91	0.34

The data were analyzed by means of a multivariate general linear model ( $n = 479$  randomly selected cells in the NADC)

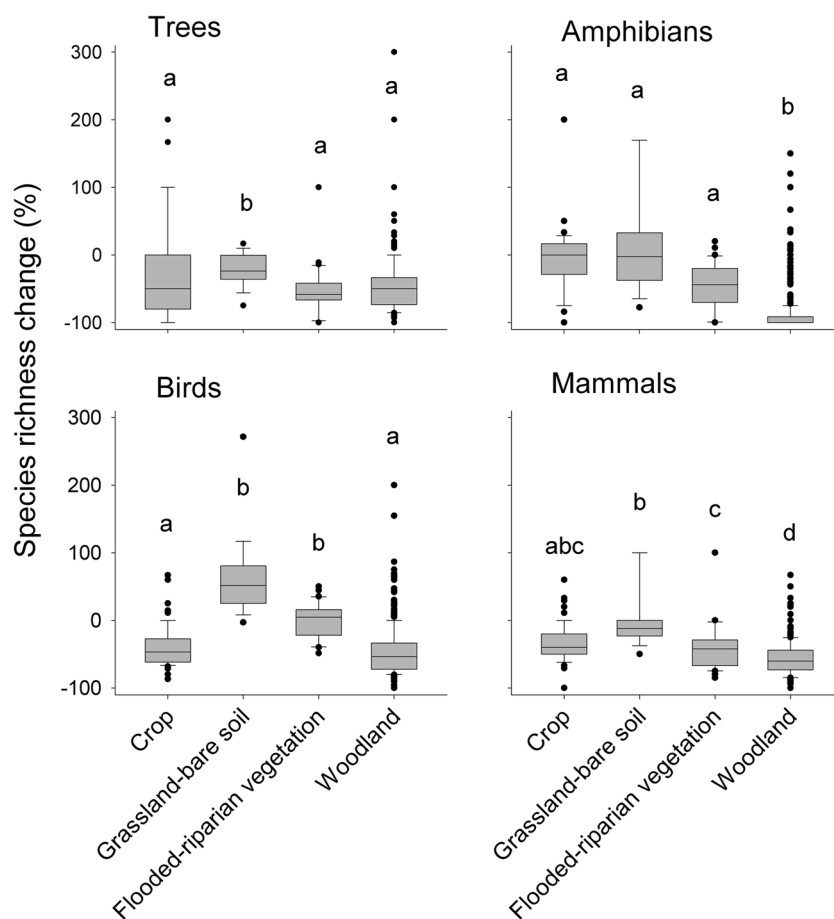
\* Significant value at  $\alpha = 0.05$

occurrences in it (in an analogous way to a selectivity index, e.g., Neu et al. 1974). However, the protocol here followed control such bias by smoothing classes in the land-cover layer and by the inclusion of a bias grid in the modeling process.

The density of *puestos* and the woody biomass shows a negative effect on the probability of presence in almost all amphibian and mammal species and a half of bird species in which both variables are important. Thus, the direct disturbance due to human presence, instead the forest degradation around rural settlements, seems to be the main cause of deleterious effects of *puestos* on these species. This is particularly likely for mammals, which include several species hunted either for bushmeat (e.g., *Pecari*

*tajacu*; Altrichter and Boaglio 2004) or livestock protection from predation (e.g., *Leopardus pardalis*, *Panthera onca*; Zimmermann et al. 2005; Altrichter et al. 2006). Several birds (e.g., *Harpyhaliaetus coronatus*, *Campephilus leucopogon*, *Melanerpes cactorum*, and *Pachyramphus viridis*) for which our models show a lower probability of presence at decreasing woody biomass and increasing density of *puestos*, appear to be affected by the habitat degradation close to rural settlements. For these forest species, habitat loss more than direct human activity may be the main negative effect of *puestos*, where both the vegetation degradation and the bare soil cover increase by overexploitation and overgrazing. Although local conditions (e.g., water and food resources) nearby *puestos* clearly favor

**Fig. 7** Differences between species richness of maps built with models fitted with and without LULC variables, associated with vegetation classes with characteristic differences in their main land uses in the Northern Argentine Semiarid Chaco. *Plots* show the median, quartiles, 10th and 90th percentiles, and extreme values; means with *different letters* were significantly different in a post hoc test of Kruskal–Wallis analyses



some bird species and guilds (Macchi and Grau 2012), as also expected to occur in other taxa, on a regional scale, the effects of *puestos* on species richness are mostly negative and, given the low productivity of these management systems, imply they are a rather inefficient way to balance biodiversity conservation with meat production (Grau et al. 2008).

The species richness of vascular plants, amphibians, birds, and mammals covary globally across geographic regions (Qian and Ricklefs 2008). These diverse set of taxa also showed congruent patterns species richness in the Dry Chaco when biophysical attributes were considered alone (Fig. 3a), but not when LULC variables were included. Our results are consistent with a non-causal congruence in species richness patterns because of shared responses of plants and vertebrates to regional environmental determinants (Hawkins and Pausas 2004; Qian and Ricklefs 2008). LULC appears to disrupt this strong spatial relationship, mainly between trees and terrestrial vertebrate classes. Predicted species richness was not similarly influenced by LULC variables (Fig. 3b) across vertebrate classes and trees, suggesting idiosyncratic responses to human disturbances such as agriculture, livestock, logging, firewood and

charcoal harvesting, and hunting pressure. These idiosyncratic responses may be relevant for ecological and conservation issues. For example, Kissling et al. (2008) found that regional congruence in bird and woody plant species richness in Kenya was mostly explained by functional relationships, and Egoh et al. (2009) found a positive, although moderate, correlation between species richness and ecosystem services hotspots in South Africa. Therefore, changes in richness patterns of plants could profoundly alter the regional diversity of terrestrial vertebrates and the ecosystem services they provide.

Moreover, forces determining the current richness distribution patterns in the Dry Chaco have different effects on distinct species even belonging to the same group. Consequently, conservation actions should implement the proper management in extensive areas more than focus in protecting areas for specific groups. For instance, a low-intensity management for the Dry Chaco forest was proposed as an option to combine cattle production and provision of habitat for native species (Bucher and Huszar 1999). However, the Chacoan bird species richness decreases across a gradient of cattle ranch production in relation to forest degradation despite the creation of open



habitats (Mastrángelo and Gavin 2012). Thus, while open habitats would be important in the landscape of the Dry Chaco, the novel open habitats created by cattle ranch production and agriculture would not provide adequate habitats for bird species. Thus, identifying production practices and pressures associated with the cultivated land that limit the suitability for species with affinity to open habitats, represents an emerging challenge for conservation in the Dry Chaco.

Both the current Argentine “forest law” of land-use ordination and international conservation initiatives (e.g., REDD+) are based on the assumption that forests should be the main target of conservation, restoration, and sustainable management, but is not supported by our results. A conservation strategy centered in woody areas may be incomplete and even misleading since continuous forests alone seem to be a suboptimal habitat for many species. Instead, much more attention should be directed to the conservation of native grasslands and open savannas, which according to our’s and other recently published results (Macchi et al. 2013) represent a favorable habitat for an important part of the regional biodiversity. Moreover, the under-appreciation of grasslands and open habitats for conservation should be seriously considered for other dry woodlands regions of the world that faced encroachment process promoted by extensive cattle ranching.

This study represents a first step to understand how LULC could have profound effects on the biodiversity patterns of the Dry Chaco, the largest remaining continuous patch of subtropical semiarid woodlands in South America, and how hierarchical niche modeling approaches can contribute to land-use planning. The incorporation of LULC variables into modeling in a hierarchical approach depicts not only a decoupling between geographic richness patterns across taxonomic groups but also a change from a spatially smooth richness pattern to a highly patchy and heterogeneous, with major consequences for planning biodiversity conservation at regional scale.

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