Diversity and structure of bird and mammal communities in the Semiarid Chaco Region: response to agricultural practices and landscape alterations

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Declaration of Originality

I herewith certify that the work presented in this thesis is my own and all else is referenced appropriately. I have used the first-person plural in recognition of my supervisors’ contribution. People who provided less formal advice are named in the acknowledgments.

Julieta Decarre

Copyright Declaration

“ …and we wandered for about four hours across the dense forest…Along the path I could see several footprints of wild animals, peccaries, giant anteaters, lions, and the footprint of a tiger, that is the first one I saw.”

- *Emilio Budin, 1906*[1]

I dedicate this thesis

To my mother and my father

to Virginia, Juan Martin

and Alejandro,

for being there through space and time

---

[1] Book: “Viajes de Emilio Budin: La Expedición al Chaco, 1906-1907”. Rubén M. Barquez. Lion and tiger is how local people refer, still today, to the puma and the jaguar in Northern Argentina.

Abstract

The conversion of land from natural environments to human-managed areas has been particularly pronounced in the semiarid Chaco Region. In this context, it is critical to understand the impacts that these major changes have on species diversity. The specific aims of this thesis were to understand: i) how the different human-modified environments influenced the distribution of the bird assemblages in the current agricultural matrix; ii) which local and landscape scale characteristics best explained species richness and relative abundance of mammals; and iii) what is the relationship between biodiversity and profit for both taxa, and given this relationship, to what extent can conservation and production objectives be simultaneously achieved. Bird and mammal community data was gathered in seven different habitats of an agricultural matrix and inside a National Park. Bird species richness and abundance were extremely low in highly modified environments (agriculture plots), but increased significantly in intermediate, or low modified habitats (silvopasture plots, forest outside and inside the National Park, respectively). Richness and capture frequency of mammals increased gradually across the gradient of habitat modification, from low numbers in agricultural habitats to a maximum in National Park forests. Changes in species composition with production intensification differed between birds and mammals. The bird communities were similar for low- and intermediate-intensity farming, with constant number of species, abundance and community integrity. However, further intensification led to an abrupt decline, defining a clear threshold. Mammal species richness was maintained in low-yield farming, relative abundance declined with increasing production, favoured by a wildlife-friendly farming approach. In contrast to birds, mammal community integrity decreased exponentially with increased levels of intensification, showing that only protected or well-preserved forests can support some habitat-restricted species. The results suggest that a combined strategy is the best option to achieve conservation and production targets that include both taxa.

Acknowledgments

As in all the tasks that take many years to complete, one gets to know a lot of people along the way. This project was very important to me at a personal as well as a professional level, and I want to mention each and every person that was a part of it, improved it, and helped me achieve my goal.

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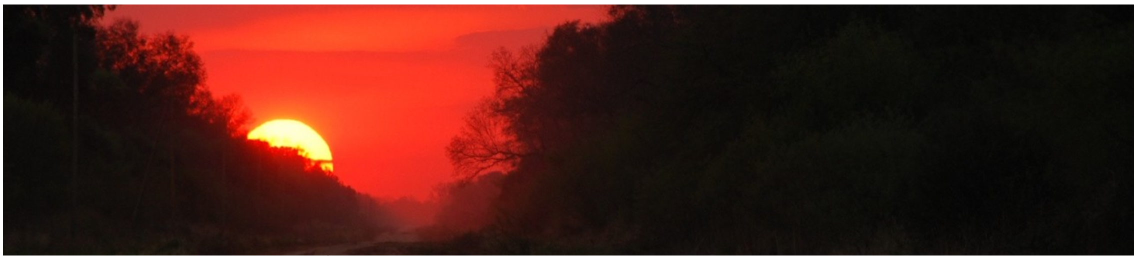

The sun sets behind the forest[2]

1 GENERAL INTRODUCTION

Environmental changes and modifications in natural ecosystem structure have attracted worldwide public concern due to the rapid loss of biodiversity. The latest publication of the global Living Planet Index (LPI) (WWF 2014), reported an alarming 52% decline in the population size of vertebrate species between 1970 and 2010. Land-use change and the resulting loss and degradation of natural vegetation cover associated with human production are considered the most important drivers of these changes (Sala 2000; Chapin III et al. 2002; Zak et al. 2004; Norris 2012). Natural ecosystems have been extensively transformed into simplified managed ecosystems with an intensification of the use of resources in order to increase the production of goods and services (Saunders et al. 1991; Tilman 1999; Boletta et al. 2006), and it is clear that the global demand for these products is going to place more pressure on land use in the future (Tilman 1999; Balmford et al. 2005; Ewers et al. 2009).

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[2] Typical sunset in Chaco. Clear skies and dusty atmosphere create amazing colours.

Changes in landscapes caused by human-induced disturbances often result in habitat loss and sub-division (i.e. fragmentation), significantly influencing the patterns of terrestrial species distribution and abundance (Saunders et al. 1991; Fahrig 2003). Based on the theory of island biogeography (MacArthur & Wilson 1967), a growing body of research has focused on the main effects of habitat loss and fragmentation on species assemblages (Ewers & Didham 2006; Fischer & Lindenmayer 2007; Tscharntke, Tylianakis, et al. 2012). Species persistence is affected mainly by the reduction of available resources, the isolation of remnant patches, and edge effects (Fahrig 2003; Fischer & Lindenmayer 2007). In general, small habitat patches can lead to population declines because resources in smaller patches may be more limited (Fischer & Lindenmayer 2007). In addition, habitat sub-division increases isolation, affecting daily movements of species, dispersion of juveniles, and even large-scale movements of species such as seasonal migration (Soulé et al. 2004). Lastly, the surrounding modified habitat influences temperature, wind action and humidity, which in turn affect vegetation structure and composition (Lopez de Casenave et al. 1995). As a consequence, the structure of animal communities is also affected (Lopez de Casenave et al. 1998; Banks-Leite et al. 2010), by what is known as “edge effects”.

The importance of maintaining heterogeneous human-modified habitats is not only limited to favour species movements across landscapes, but also to provide suitable areas available for native species (Ewers & Didham 2006; Fischer & Lindenmayer 2007). Several studies have shown that modified habitats presenting a vegetation structure similar to that of primary habitats are important for the persistence of species (Schulze et al. 2004; Barlow et al. 2007; Cozzi et al. 2007; R. Cassano et al. 2012). For example, landscape heterogeneity is recognised as beneficial for native species in European farming landscapes (Macdonald et al. 2007; Diekötter et al. 2008; Tscharntke et al. 2011), Central and South American farming landscapes (Daily et al. 2001; Gordon et al. 2007; Perfecto et al. 2003) and forestry landscapes around the world (Koh et al. 2009; Clough et al. 2011). However, the potential of modified habitats to harbour forest species varies among biological groups (Schulze et al. 2004; Harvey & González Villalobos 2007; Pardini et al. 2009). Species of a given taxonomic group differed in their response from another group in relation to its specific requirements and its ability to move throughout the landscape (Fahrig 2003;

Burel et al. 2004; Fahrig 2007). Two different groups are unlikely to react in the same way; therefore, comparisons among taxa or functional groups can highlight essential differences in their spatial dynamics and responses to spatial heterogeneity (Jeanneret et al. 2003). Additionally, the effects of land-use change are highly scale-dependent. This is partly attributable to local spill over effects across boundaries, which are higher when the proportion of undisturbed primary habitat at landscape scale also increases (Tscharntke et al. 2005; Pardini et al. 2009).

On the one hand, the identification of patterns and processes underlying species distribution and abundance at different spatial and temporal scales is a key factor for biodiversity conservation in this type of modified landscape (Saunders et al. 1991; Jeanneret et al. 2003; de Oliveira et al. 2009). Ecologists have recently started to pose fundamental questions, such as to what degree can biodiversity persist in human-modified landscapes, and which management strategies are most effective at enhancing its persistence for a given spatial and temporal scale.

On the other hand, there is mounting evidence to show that careful design and management of the matrix can help maintain not only species fluxes, but also key ecological processes. Countries in developmental transition tend to rely on agriculture for economic growth. In South America, the main driver of deforestation is agricultural expansion (Paruelo et al. 2004; Grau, Gasparri, et al. 2005; Mattison & Norris 2005) which has been particularly intense in the tropical and dry forests of the continent (Gardner et al. 2009; Portillo-Quintero & Sánchez-Azofeifa 2010). In this scenario, one of the greatest challenges is the alignment of an adequate use of the land with agricultural production (Green et al. 2005; Mattison & Norris 2005; Phalan, Onial, et al. 2011; Tscharntke, Clough, et al. 2012).

The demand for food and bioenergy crops is increasing at the expense of natural habitat, and recently, analyses have focused on whether farming and conservation land should be "spared" or set aside, thus segregating land for nature from land for production, or "shared" using integrated production and conservation practices in the same area. The land sparing vs. sharing (or wildlife-friendly farming) dichotomy is based on the argument that yields are negatively correlated to wild land biodiversity. A model by Green et al. (2005) compares the level of biodiversity obtained from intensive high-yield farming and extensive low-yield farming when biodiversity is a decreasing function of yield. For a given production target, both agricultural methods would lead to the same level of biodiversity if this were a linear function of yield. Accordingly, if the relation between yield and biodiversity is convex (function Type I Figure 1.1), species exhibit a sharp decline even with low-intensity farming practices, these species have their highest overall population when land is intensively farmed in one sector and other land is spared and left unaltered. The opposite result is obtained if the relation between biodiversity and yield is concave (function Type II, Figure 1.1). In this case, less intensive, wildlife-friendly farming may be a better strategy because the the levels of species diversity in intact natural habitat and habitat in low-intensity (low-yield) agriculture are relatively similar. The land-sparing vs. wildlife-friendly farming dichotomy is a good starting point to think about compromises, but in reality, there is a wide range of options in between, and these may differ substantially by taxon, geographic location, and spatial scale.

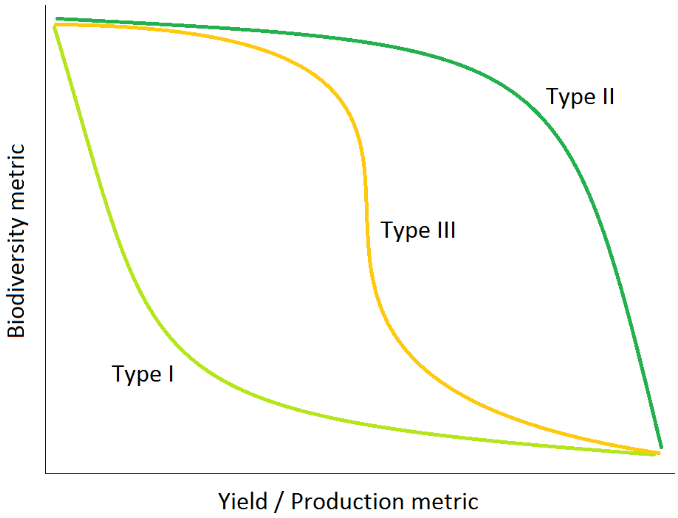

Figure 1.1. Theoretical relationships between land-use intensification and biodiversity. Systems that show an exponential decay (Type I) would be best suited for a land sparing strategy because biodiversity suffers a rapid decline as soon as intact natural habitat is converted into low-intensity agricultural production. Wildlife-friendly farming would be most appropriate in systems with a Type II curve, where biodiversity presents similar values in low-yielding farms, and in unfarmed or natural habitats. For diversity-yield functions which are neither convex nor concave (Type III), small incremental or qualitative changes in land use could lead to dramatic changes in biodiversity values, therefore a combination of strategies would be needed to achieve a sustainable production system (Green et al. 2005). *Diagram adapted from Koh et al. 2009.*

Empirical studies comparing the merits of these strategies differ in their outcome. For native vegetation in Europe and Australia (Dorrough et al. 2007; Makowski et al. 2007; Kleijn et al. 2009) extensive management proved to be the best option to maintain biodiversity and prevent further long-term degradation of the resource base. Similarly, insects, birds and mammals showed favourable responses to low-intensity farming practices (Clough et al. 2011; Gordon et al. 2007), with disproportionate ecological losses of biodiversity and ecosystem functions when greater extensions of forest were cleared for agroforestry plantations of cocoa and coffee (Steffan-Dewenter et al. 2007). Contrary to these findings, in birds and tropical forest plants, more intensively-farmed areas coupled with natural refuges appear to be better (Aratrakorn et al. 2006; Phalan, Onial, et al. 2011).

Phalan, Balmford, et al. 2011 concluded that incrementing yield through agricultural intensification would decrease human requirement for land. This idea has been heavily criticized (Vandermeer & Perfecto 2005; Fischer et al. 2011; Tscharntke, Clough, et al. 2012; Perfecto & Vandermeer 2012) as it does not incorporate the complexity and variety of productions systems around the world (Kleijn et al. 2009; Koh et al. 2009; Tscharntke, Clough, et al. 2012), and overlooks the beneficial effects of ecosystem services that could be provided by the biodiversity associated to this kind of environments (Tscharntke et al. 2005; Norris 2012). There are several objections against this approach: first, as Clough et al. 2011 showed in their study, wildlife friendly farming can reach yield levels as good as those of conventional agriculture. There is evidence to support that wildlife friendly productions generate positive effects both in their biodiversity content as in the quality of the matrix they create, besides producing reliable yields (Perfecto et al. 2005). The high variability in yield-biodiversity relationships is due to differences in land-use intensity (mainly between temperate and tropical regions, i.e. developed and developing countries). This generates a wide range of management options that allow to balance human and ecological needs (Mattison & Norris 2005; Steffan-Dewenter et al. 2007; Kleijn et al. 2009). Secondly, increasing yield can either increase or decrease deforestation rates depending on local conditions. As such, allowing intensification would not necessarily spare land for nature (Ewers et al. 2009). Thirdly, agricultural production is highly dependent on ecosystem services such as pest control, pollination and soil fertility, among others (Tscharntke et al. 2005; Flynn et al. 2009; Norris 2012). Conventional intensification, frequently relying on the use of pesticides and agrochemicals, tends to disrupt beneficial functions of the biodiversity at different spatial and temporal scales (i.e. inside and outside farmed areas, and in the short and long term) (Tscharntke et al. 2005). Lastly, the environmental quality of the matrix is often overlooked in the land sparing vs sharing debate. Almost all landscapes are currently fragmented, with patches of more or less native vegetation interspersed among a matrix of different land-use systems, including agriculture. In this scenario, metapopulation and metacommunity dynamics exist among patches and organisms through the use of corridors and remnants of natural vegetation (Gehring & Swihart 2003; León & Harvey 2006; R. Cassano et al. 2009; Barlow, Gardner, et al. 2010). If the land-sparing strategy includes the implementation of monocultures and the elimination of small remnants of natural habitats, that may severely affect organisms with broad home ranges (e.g. large carnivores) or those attempting to migrate between patches.

Regardless of the attempts to frame research within land-sparing vs. land-sharing, biodiversity-yield functions for most taxa remains unknown in the majority of systems. Therefore it is possible that some groups exhibit “unstable” and less predictable responses to intensification resulting on dramatic changes in composition with only small changes in the production system (function Type III, Figure 1.1) (Koh et al. 2009; Hodgson et al. 2010).

In this thesis, we address some of these topics as they represent interesting theoretical issues as well as critical practical conservation challenges linking the development of human activities in increasingly threatened natural environments. We carried out the field research in the semiarid Chaco Region in Argentina, an important yet understudied ecosystem that is being rapidly degraded by agricultural expansion and intensification (Zak et al. 2004; Piquer-Rodriguez et al. 2015). Recent ecological studies have started to address the complex relationships between wildlife and human activities given the growing importance of the region for both conservation and productive uses (Macchi & Grau 2012; Mastrangelo & Gavin 2012; Quiroga et al. 2013; Macchi et al. 2013; Mastrangelo & Gavin 2014; Torres et al. 2014; Piquer-Rodriguez et al. 2015). It is well known that the effects of land use on community diversity and composition varies among animal groups (Schulze et al. 2004; Tscharntke, Clough, et al. 2012). This work adds to the knowledge of previous research: firstly, by considering changes in bird and mammal community assemblages inhabiting a gradient of agricultural and natural habitats. This will be the first study addressing the issue of land use change and intensification on more than one taxa at the same time for the study area, facilitating the comparison of their requirements and the evaluation of differential responses to habitat loss and modification. Second, the study area encompassed approximately 720,000 hectares of the semiarid Chaco Region, including a National Park that holds one of the best preserved remaining stands of forest and an extensive agricultural mosaic representing the most important land-use types and livelihoods developed in the area. Lastly, the range of land-use types incorporated not only include productive systems, but also small natural elements in the landscape (i.e. forest strips or windbreaks consisting of narrow strips of native forest in the edges of agricultural fields) that may play an important role in the dispersion and subsistence of animal populations.

1.1. Objectives

In this thesis we aim to provide sound scientific evidence to inform policy and decision-making processes, and to influence management and planning towards the sustainable development of productive systems together with wildlife conservation. Following further discussion of the main topics, the thesis is composed of three data-based chapters focusing on variation in bird species assemblages (Chapter 2); mammal species assemblages (Chapter 3); and responses in both taxa to changes in agricultural yield (Chapter 4). An overview and summary of the main findings is presented in Chapter 5 including discussions on future lines of research to improve our understanding of agriculture-biodiversity relationships in the region. The following paragraphs outline the main objectives for Chapter 2 to 4.

1.1.1. Chapter 2: *Bird assemblages and habitat relationships in agricultural landscapes of the semiarid Chaco*

The specific objective was to analyse species diversity and composition of bird community in response to land use. We used bird species richness, abundance and composition of bird assemblages to characterize a gradient from natural protected forest to intermediate-intensity agroforestry system (i.e. shaded cattle ranching), and annual crops. A community with a large number of species might be restricted to a few functional roles depending on the species arrangement. In order to analyse this aspect, we examined the differences in bird assemblages between habitats at trophic guild level.

1.1.2. Chapter 3: *Mammal community response to a gradient of land use intensification*

In this chapter, we studied how mammalian communities change in response to anthropogenic management, and also investigated the influence of the surrounding landscape on the assemblage diversity. We assessed the effect of five land-use types present in the agricultural landscape and we compared them with non-production ecosystems. Additionally, we evaluated mammal community structure and composition using variables from local and landscape scales. This research represents the first landscape scale study for the mammal community inhabiting the agricultural mosaic in the semiarid Chaco.

1.1.3. Chapter 4: *Balancing biodiversity and agricultural production: conservation of bird and mammal communities in the agricultural frontier*

Here, we attempted to combine information on economic output and biodiversity for each site and each animal group studied in the previous chapters. We assessed the responses of community measures (species richness, abundance and community similarity) for birds and mammals along the gradient of production profit. We also aimed at analysing the economic differences in profit among the farming systems in the region, and most importantly, at evaluating a potential unified strategy that incorporates the ecological requirements of birds and mammals.

1.2. Study area

The Gran Chaco Americano is a vast region shared by Paraguay, Bolivia, Argentina, and a small portion of Brazil (Figure 1.2). It constitutes one of the few areas in the world where the transition between the tropics and the temperate belt does not occur in the form of a desert, but as semiarid forests and woodlands. The Chaco Region is one of the largest forests in South America, only after Amazonia (Cabrera 1971; Bucher & Huszar 1999; Grau, Aide, et al. 2005) extending from the foothills of the Andes range in the West to the Paraná and Paraguay rivers in the East. It holds an exceptional biological and cultural diversity that includes 25 indigenous groups and hundreds of communities of European immigrants who live across the region. It is a highly threatened and poorly studied ecosystem of great importance as a conservation "hotspot" (The Nature Conservancy (TNC) et al. 2005), although much of its species have suffered a strong reduction in population numbers (Short 1975; Aizen & Feisinger 1994; Bucher & Huszar 1999). In the last 30 years, the area has suffered a widespread and strongly-accelerated deforestation process that resulted in a substantial increase in forest fragmentation and loss of potential connectivity (Piquer-Rodriguez et al. 2015).

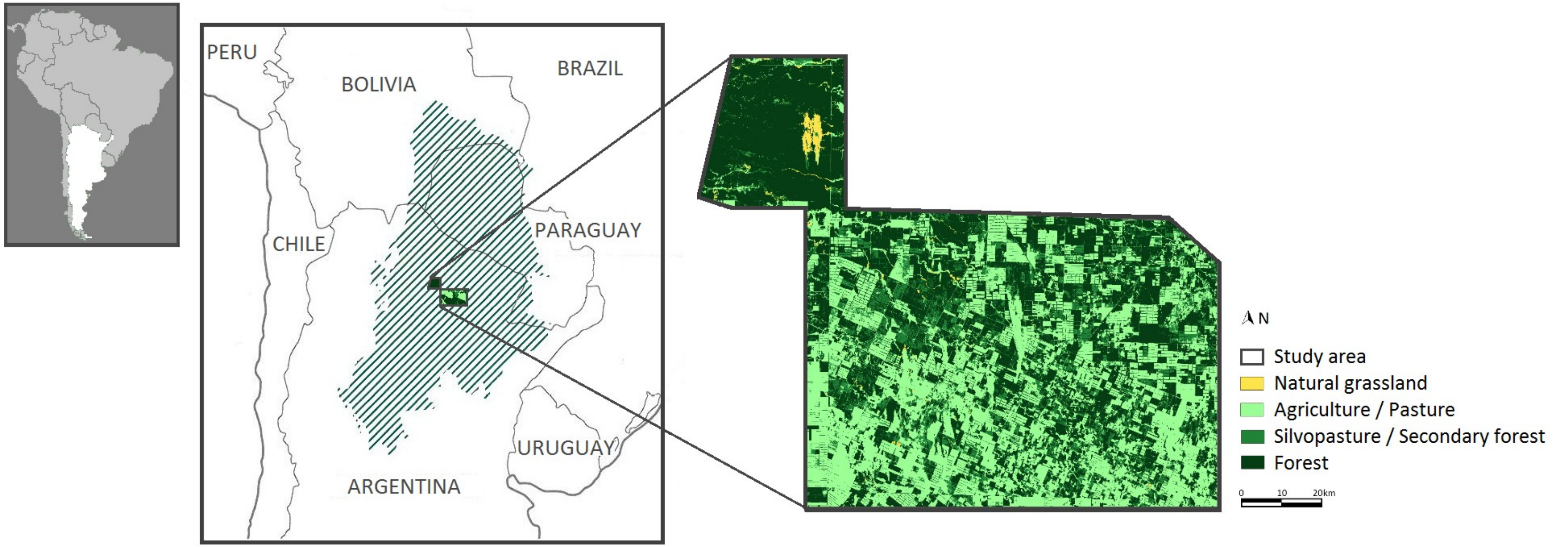

Figure 1.2. Location of the study area in the Argentine Chaco in the context of Chaco Region in South America. The top left rectangle shows the location of Argentina in South America. The map in the middle shows the distribution of the Gran Chaco Region in South America (green lines area), and the study area (agricultural landscape shown as a small rectangle in green and light green, and Copo National Park shown as a small polygon in dark green in the North-West corner of the agricultural landscape). The figure to the right is a detailed land cover map of the study area. The different shades of green indicate the presence of forest, secondary forest, and agriculture land covers (from dark green to light green, respectively). Natural grassland is shown in yellow. The lower rectangle represents the agricultural landscape encompassing an area of c. 600,000.00 ha, and the upper polygon (dark green with a yellow patch) represents Copo National Park (c. 118,120.00 ha). Only a big patch of natural grassland is evident in the study area given the coarse-grain scale of the map.

Use of the natural resources in the Chaco Region

The Gran Chaco, extending more than one million square kilometres, is a remarkable biodiversity repository not only of animal and plant species, ecosystems and landscapes, but also of cultural knowledge and traditions of its native ethnic groups (The Nature Conservancy (TNC) et al. 2005). Along with the historic development, this biome has suffered profound changes and extinctions of wildlife, inhabitants, traditions, and production practices extending across multiple spatial scales (Morello & Saravia-Toledo 1959).

The original vegetation in our study area was parkland or savannah with patches of hardwood intermingled with grasslands (Morello & Saravia-Toledo 1959). This mosaic of vegetation was kept stable by periodic fires until the arrival of the colonists and their introduction of domestic cattle, which led to a period of overgrazing and extinction of the fauna in the natural grasslands. Consequently, the woody vegetation rapidly encroached upon the open areas replacing the grasses by opportunistic shrub species (Morello et al. 2006; Bucher & Huszar 1999). A second stage in the process of landscape alteration started in the 1880's when the demand of forest products such as wood for railway sleepers, fence posts, charcoal and firewood, increased the harvest of timber. In addition, the incursion of the cattle into the forest, severely affected the regeneration of some of the most charismatic and important plant species of the region (Torrella & Adamoli 2006; Morello et al. 2006). In this period, the expansion of the railway network also favoured the arrival of peasants to previously unoccupied areas establishing new settlements and small agricultural plots by clearing forest patches (Bucher & Huszar 1999; Morello et al. 2006). Since the beginning of 1900, and for more than sixty years, the British "Forest Land, Timber and Railways Company" exploited millions of hectares of forest to extract tannin and oils mainly from two species of trees, the "quebracho colorado santiagueño" (*Schinopsis quebracho-colorado*), and the "palo santo" (*Bulnesia sarmientoi*), almost exhausting the resource (Morello et al. 2006; Torrella & Adamoli 2006). By the 1970's another large-scale extracting activity arrived to the Chaco Region. The lengthening of trails and roads for oil and water explorations, and to establish federal limits facilitated the access of people to pristine areas. Hunters, peasants, wildlife collectors, pet traders, lumbermen and smugglers took advantage of a new set of resources that would otherwise be inaccessible (Bucher & Huszar

1999; Morello et al. 2006). The agricultural expansion process started around 1975 and brought technologic changes that shaped the landscape. The “Green Revolution” came with the possibility of significantly increasing crop yields through the use of new cultivars, machinery and potent agrochemicals (Morello et al. 2006; Grau, Gasparri, et al. 2005; Grau, Aide, et al. 2005). The expansion of conventional agriculture involved the complete replacement of the native ecosystem for extensive cropping areas. By 1996, the introduction of transgenic soybean cultivars with resistance to a powerful herbicide (glyphosate) allowed a more intensive use of the land by cropping it all year round (Grau, Aide, et al. 2005; Aizen et al. 2009). Soybean cultivation pushed cattle pastures further into the agricultural frontier and imposed an industrialized-agriculture model leading to one of the most radical and intensive processes of land conversion and landscape transformation (Morello et al. 2006; Grau, Gasparri, et al. 2005; Grau, Aide, et al. 2005; Gasparri & Grau 2006).

The history of natural resources use in the semiarid Chaco region has led to a landscape consisting of a mosaic of primary forest remnants, agroecosystems, and secondary growth forest. Nowadays, the area is mostly rural with people living in several towns along a National road or in small settlements spread throughout the forest, and in agricultural fields.

Characteristics of the region

The Chaco Region in Argentina occupies approximately 675,000 km^2 that can be divided in sub-regions based on an East-West rainfall gradient (Cabrera 1971; Bucher & Huszar 1999). Rainfall occurs mainly in the summer months (December to March), and range from 800 mm in the East to 400 mm in the West. The mean temperatures are 26.9° C for the hottest month (January) and 12.4° C for the coolest month (July). Extreme temperatures range between 42° C and 45° C in summer and -7° C to -8° C in winter (Cabrera 1971; Boletta et al. 2006). The humid sub-region is the most productive one, and it has been intensively transformed for agricultural production over the last four decades (Bucher & Huszar 1999). This region possesses the highest human density and the landscape is a heterogeneous mosaic of semi deciduous tall forest, wetlands, gallery forests and agriculture. The semiarid sub-region is the driest and most markedly seasonal, but increasing deforestation over the last decade suggests a change in conditions for cropping. Soybean expansion into forest areas has been attributed to an increase in rainfall, economic changes in the international market, and technological improvements (i.e. new crop varieties that override environmental constraints, Grau, Gasparri, et al. 2005; Grau, Aide, et al. 2005). This current trend of deforestation and habitat loss represents a serious threat for biodiversity conservation (Torrella & Adamoli 2006).

There are five protected areas within this territory, but only two of them hold a National Park category: Copo National Park (c. 118,120.00 ha) in the semiarid sub-region, and Chaco National Park (c. 15,000 ha), in the humid sub-region (Altrichter & Boaglio 2004; Torrella & Adamoli 2006). Habitat loss and fragmentation, together with hunting pressure, have altered the population of several species of vertebrates (IUCN 2014). Chaco is a wooded region of exceptional biodiversity with unique ecological processes. It presents one of the highest faunal diversity in Argentina, with approximately 500 bird species, 150 species of mammals, 120 species of reptiles, and 100 species of amphibians (The Nature Conservancy (TNC) et al. 2005). Redford et al. 1990 attributed a high conservation value to this region because of the presence of large mammal species, including characteristic species, such as, the jaguar (*Panthera onca*); the rare giant armadillo (*Priodontes maximus*); three species of peccaries (*Tayassu tajacu; Tayassu pecari,* and *Catagonus wagneri*) coexisting only in this region, with the the last species being endemic and previously know only from fossil records and rediscovered in 1974; the giant anteater (*Myrmecophaga tridactyla*) and the South American tapir (*Tapirus terrestris)* (Parera 2002; Barquez et al. 2007; Canevari & Vaccaro 2007). A particularly diverse community of birds is present as well, including the Crowned Eagle (*Harpyhaliaetus coronatus); and the* Black-bodied Woodpecker (*Dryocopus schulzi*); the Black-legged Seriema (*Chunga burmeisteri*); the Quebracho Crested Tinamou (*Eudromia formosa*), and the Cinereous Tyrant (*Knipolegus striaticeps*) (Olrog 1963; Short 1975; Narosky & Yzurieta 2003). Despite harbouring a high diversity, the Chaco hosts only one endemic bird species (i.e. the Quebracho Crested Tinamou, *Eudromia formosa*) (Short et al. 1974). Its central location and accessibility within South America may explain its low avian endemicity. The Chaco region neighbours other xeric regions along the “dry diagonal” comprising Chaco, Cerrado and Caatinga regions, and also highly diverse mesic regions such as the Yungas, Atlantic and Amazon rainforests, with which it shares many bird species (Short 1975).

The most frequent production systems are agriculture and cattle ranching. Agricultural fields usually produce two types of crops per year: soybean, cotton, sunflower and corn during summer, and wheat, oats and pastures during winter. Farmed plots vary in size and proportion of natural vegetation in the borders or inside the plot. Areas of highest intensification, cleared up more than 10 years ago, consist of big extensions of mechanized cropland with no remnant of forest cover, and practically no hedgerows or live fences separating the plots. More recent agricultural systems are enclosed by forest strips and are of smaller size (Ginzburg et al. 2012) . Silvopasture is common practice for livestock production. It is a type of agroforestry that integrates cattle husbandry under the shade of native trees. Some species of trees within a pre-determined plot are selectively harvested and the woody understory is then removed, leaving an approximate density of 100 trees per hectare in the paddock. Afterwards, non-native grasses (e.g. *Panicum maximun*) are implanted in the lower stratum to feed the cattle (Figure 1.3).

Throughout this thesis the term “management intensification”, “agricultural intensification” or “land use intensification” are used to indicate the transition from ecosystems with high diversity associated to agricultural or production practices (i.e. the collection of plants and animals that are part of the managed system) and low external inputs, to ecosystems with low diversity and increased use of external inputs that facilitates the maintenance of high productivity (i.e. use of agrochemicals and heavy machinery). In the case of the semiarid Chaco, the gradient in land use intensification refers to (i) low levels of habitat alteration in forest patches outside protected areas, caused by selective timber harvesting, and extensive cattle raising. Forest patches included in this study were bigger than 500 ha and had a canopy cover >70%; (ii) downsized and re-shaped forest patches inserted in a highly modified environment (i.e. forest strips surrounding arable fields and linking bigger patches of forest); (iii) reduction or intensive elimination of forest cover accompanied by clearance of the bushy understorey, and introduction of exotic pastures and cattle (i.e. silvopasture plots with an average size between 50 and 80 ha.); (iv) complete elimination of forest cover and its replacement by cash crops in relatively small management units with the preservation of well maintained forest strips separating and/or surrounding each arable plot (i.e. agricultural plots of c.75-150 ha. with forest strips); (v) complete elimination of forest cover in extensive areas (bigger than 200 ha.) and its replacement by cash crops. These final stages in the intensification gradient include the use of products (i.e. agrochemicals) to increase yield (Figure 1.3).

Figure 1.3. Examples of the seven land cover / land-use types surveyed in the semiarid Chaco Region, with diagrams representing the change in management intensification and its consequent impact on the biodiversity value. Pictures (from left to right): grassland areas of native species are scarce in the study region; these environments have been used since the beginning of colonization for human settlements and production. Nowadays, only small remnant patches are scattered across the agricultural matrix, and only relatively undisturbed natural grasslands persist inside Copo National Park. In this study, surveyed sites for this land cover presented the lowest level of land-use intensification (intensification= zero), and therefore, it has one of the highest biodiversity values. Contrarily, the intensification level is highest in arable fields (second picture from the left), where vast areas of forest are cleared to produce cash-crops, while significantly reducing habitat available for biodiversity. In agriculture plots with forest strips (third picture from the left) the intensification inside the plot equals the one in the last-mentioned land use. However, the presence of native forest windbreaks surrounding each plot introduces heterogeneity and provides habitat for wildlife, thus increasing biodiversity per unit area. Silvopasture (middle picture) is a type of agroforestry system where native trees are used to provide shade for cattle. This environment provides good opportunities for wildlife, while an intermediate to high human disturbance regime and modification level is maintained. Forest strips (fifth picture from the left) represent narrow patches of native forest alongside agricultural fields. Intensification is high in the surrounding areas (agriculture), thus affecting the environment inside the strip (i.e. occasional wood extraction, cattle invasion, burning). Yet, the conservation value of these environments has been proved in several studies (Lopez de Casenave et al. 1998; Barlow, Louzada, et al. 2010). Forest remnants in private lands (sixth picture from the left) differ in size, shape and preservation status. In general, land-use intensification is low but different from zero, as extensive livestock production and wood harvesting are still common practices in the region. However, most patches present good vegetation structure (secondary forest) and those big enough to keep a relatively undisturbed interior could offer habitat for forest-dependant species. The last picture in the row (from left to right) shows the South limit of Copo National Park. Forest vegetation inside the park is relatively well preserved with only its central area being used for livestock production (cows and goats) by previous settlers of the region. However, the samples for this study were taken only from areas were livestock is excluded. *Diagram adapted from Phalan, Balmford, et al. 2011.*

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Bird species of the Chaco Region [3]

2 BIRD ASSEMBLAGES AND HABITAT RELATIONSHIPS IN AGRICULTURAL LANDSCAPES OF THE SEMIARID CHACO

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[3] Some characteristic bird species found in the study area. Pictures by the author, otherwise stated in brackets. From left to right: *Milvago chimachima; Myrmorchilus strigilatus; Campephilus leucopogon* (Jeremías Mancini)*; a pair of Phacellodomus sibilatrix building their nest* (José M. Segovia)*; Spiziapteryx circumcincta.*

Summary

The semiarid Chaco Region in Argentina is undergoing an important process of change and habitat degradation since extensive areas of natural vegetation are being converted to human productive systems. We evaluated the distribution and diversity of bird species, and the associated response of the trophic guilds, across a gradient of land use intensification. Abundance data for birds was collected during 2011 and 2012, in six different habitats ranging from highly human-modified agricultural plots, to slightly altered habitats, including forest inside a National Park. Response variables included bird species richness, abundance, and Berger-Parker dominance index. A Bray-Curtis dissimilarity matrix was also calculated to compare bird assemblages among land-use types. Results indicate a decline in bird species richness and abundance of individuals in relation to the degree of intensification, with an abrupt change between two main land uses (agricultural and forested habitats). This pattern is also reflected in the composition of the assemblages with more similar communities present in less intensively-managed environments. Insectivores and granivores are present at higher densities than omnivores and predators in all habitats. Insectivores was the most diverse and abundant guild overall, and was also best represented in forested land uses. Proportional richness of granivore species did not vary along the intensification gradient and its proportional abundance was higher in medium-intensified systems, whereas predators preferred sites where high and medium habitat alterations resulted in more open environments. Our study concurs with studies showing that medium and low modified land uses maintain a diverse and abundant community of birds, contrarily to highly altered habitats. However, this response is likely to be correlated with the composition and configuration in the surrounding landscape that still preserves a high proportion of native forest.

2.1. Introduction

The current widespread and rapid conversion of land to provide human goods and services is regarded as one of the major threats to the conservation of biological diversity (Tilman 1999; Sala 2000; Hausner et al. 2003). The way in which land is managed has profound effects on the distribution and abundance of many animal and plant species, and in turn, on ecosystem functions (Saunders et al. 1991; McLaughlin & Mineau 1995; Freemark & Kirk 2001; Henle et al. 2004; Norris 2012). In this context, the alignment of the demands for crop production and the need for biodiversity conservation is a key factor to identify the processes driving patterns of species distribution and abundance in this type of agricultural landscapes (Saunders et al. 1991; Jeanneret et al. 2003; de Oliveira et al. 2009).

Decreasing patterns of biodiversity with increasing habitat modification have been documented in previous studies in several geographical regions, and at different spatial scales (Perfecto et al. 2003; Schulze et al. 2004; Mattison & Norris 2005; Barlow et al. 2007; Harvey & González Villalobos 2007; Schrag et al. 2009). Farina (1997) found that for birds, the main factor explaining species richness in sub-Mediterranean landscapes is the heterogeneity of uses where species diversity increases with the number of land cover types, while other factors, such as the specific composition of habitats, play a secondary role (Atauri & de Lucio 2001; Benton et al. 2003). Studies addressing this spatial scale refer to a certain threshold for coverage of suitable habitats that would allow the coexistence of different communities of birds, resulting in greater richness values (Pardini et al. 2009; Andrén 1994). However, in regions where habitat loss and modification have been operating since long ago, the decline of many agricultural bird species is explained by attributes at local scale. For example, in North America (McLaughlin & Mineau 1995; Freemark & Kirk 2001), as in Europe (Siriwardena et al. 2000; Tscharntke et al. 2005; Geiger et al. 2010), the presence of non-crop habitats, the implementation of organic practices, in opposition to conventional farming regimes, or the permanence of soil cover were highly correlated with species-rich and more abundant bird assemblages. In turn, countries in developmental transition tend to rely increasingly on agriculture, and although they possess large areas of natural vegetation, deforestation in these regions cause significant declines in suitable habitat and shifts in environmental niche space for globally threatened taxa (Mattison &

Norris 2005; Ewers et al. 2009). Several studies have reported a significant decrease of forest bird species as a result of the rapid expansion and intensification of staple crops, like palm oil within Southeast Asia (Foley et al. 2005; Aratrakorn et al. 2006; Maas et al. 2009) or soybean in South America (Perfecto & Vandermeer 2008; Gardner et al. 2009; Schrag et al. 2009; Piquer-Rodriguez et al. 2015).

Land use intensification usually triggers deforestation to create grazing plots or arable fields, and this process has been particularly strong in the Chaco Region (Short 1975; Grau et al. 2005; Aizen et al. 2009; Torres et al. 2014). The southern distribution of this biome in Argentina is facing an accelerated degradation process, where farming has been increasing, not only in areas previously used for other forms of agricultural and livestock production, but also in extensive newly-cleared areas of forest (Adamoli et al. 1990; Tálamo & Caziani 2003; Tálamo et al. 2009).

The increasing human activity in the semiarid Chaco results in a variety of habitats with different amount and arrangement of vegetation cover. Land-use types can be categorized along a gradient of environmental change, from protected forests, to highly intensive and completely cropped land. Copo National Park is the nearest and one of the most important protected areas within this territory; it holds not only primary dry forest, but also vegetation that has been subjected to a variety of disturbances (logging and clearing in the past, and livestock grazing in the present). In spite of alterations occurring in a small section of the park, overall, it can be considered as a low intensity exploitation area (Tálamo et al. 2012; Tálamo & Caziani 2003). Outside the park, the landscape consists of a complex mosaic of agricultural plots and agroforestry systems (livestock production under shade) interspersed with forest patches of varying ages and degrees of intervention. These land uses differ markedly in their structural and floristic composition, as well as in their management practices. The size and use of the forest remnants vary from small and fragmented patches to considerably big fragments (more than 500 ha), and from well-preserved primary forest to heavily-degraded or open forest with predominance of scrubland. Silvopasture is a type of agroforestry that combines beef production with forest management and presents a medium to high degree of transformation, where some of the trees and the woody understory in the forest is removed to grow pastures to feed the cattle (Mastrangelo & Gavin 2012). Lastly, on the extreme of habitat alteration, cultivated land can differ in extent and heterogeneity. The oldest plots are extensive crop fields established in completely cleared areas. On the other hand, recently established plots are of smaller size and they are surrounded by forest strips that constitute linear elements of native vegetation connecting patches of forest.

The semiarid Chaco Region has been defined as a conservation "hotspot" (The Nature Conservancy (TNC) et al. 2005). More than 200 species of birds were cited in this region in the past (Olrog 1963; Short 1975) including several Neotropical migrants (18 species reported by Codesido & Bilenca 2004). The best-represented families are Furnariidae, Tyrannidae, Icteridae and Emberizidae. Distinctive elements of the Chaco avifauna include, for instance, the Turquoise-fronted Amazon (*Amazona aestiva*), a heavily exploited species whose populations have progressively decreased due to pet trading (Berkunsky et al. 2012); the Quebracho Crested Tinamou (*Eudromia formosa*) that is the only endemic bird species in the Chaco Region; the Black-bodied Woodpecker (*Dryocopus schulzi*), and the Crowned Eagle (*Harpyhaliaetus coronatus*), which are classified as near threatened and endangered respectively (IUCN 2014); together with several other highly-valued species that play an important role as food items (e.g. the Chaco chachalaca, *Ortallis canicollis*; the Black-legged Seriema, *Chunga burmeisteri*) or are closely associated with local folklore (Short 1975). Despite the fact that most of these species extend well beyond the Chaco Region, a significant part of its populations have suffered strong reductions mainly due to habitat loss and fragmentation (Tálamo & Caziani 2003; Altrichter & Boaglio 2004; Boletta et al. 2006; Torrella & Adamoli 2006). For bird assemblages, food availability, courtship and nesting sites, protection from predators and environmental conditions are closely related with habitat structure (Rotenberry & Weins 1980; Wiens 1992). In this chapter we used birds to measure the effects of land use intensification and disturbance, not only because they have diverse and well-known habitat preferences, exhibiting a broad range of inter-specific responses to human impact, but also because they are relatively easy to identify, cost-effective to survey, and represent an important conservation target (Sekercioglu et al. 2007; Tscharntke et al. 2008).

Although the status and distribution of Chaco avifauna have been studied in the past (Short 1975; Codesido & Bilenca 2004; Codesido et al. 2009; Lopez de Casenave et al. 1995; Lopez de Casenave et al. 1998), it was not until recently that researchers have started to investigate the effects of habitat modification on the bird community. Mastrangelo and Gavin (2012, and 2014) studied the response of bird assemblages to intensification in cattle production in the Dry Chaco Region. They found that local structural attributes explained most of the variation in the distribution of birds among habitats, and that intermediate levels of intensification can maintain a highly diverse avian assemblage. Macchi and Grau (2012) analyzed the impact of traditional livestock management ("puestos") on the bird community and found that the abundance of trophic guilds decreased with increasing distance from the puestos, showing a positive effect of the resources and the heterogeneity generated around human-modified habitats. On the other hand, both studies concluded that rare forest species had their highest densities in primary forest, highlighting the importance of the different range of requirements that can be present within the same taxonomic group. In this study, forests and silvopasture systems were sampled, and we add to the knowledge of previous studies by incorporating new landscape elements that were not considered before, and that constitute three distinctive land uses in the intensification gradient: (1) extensive and highly modified arable fields where mechanized agriculture is used to generate the highest possible yield; (2) arable fields of smaller size with the same management but surrounded by forest strips; and (3) we considered the forest strips themselves as an important feature since they are wide enough to preserve a well structured vegetation and may represent a suitable habitat for biodiversity (Barlow et al. 2010).

We characterized species diversity and composition of bird community in response to land use. We investigate the specific changes in diversity occurring between different human-modified and natural habitats and which land-use type holds the most diverse bird assemblage. Functional diversity is as important as compositional diversity. Function involves important ecological and evolutionary processes as pollination, nutrient cycling, and biological control, among others. Hence, a community with a large number of species might be restricted to a few functional roles depending on the species arrangement. To analyse this aspect we examined the differences in bird assemblages between habitats at trophic guild level. Our predictions are that biodiversity should decrease in intensively cropped areas due to a decrease in habitat quality and availability. Given that each land-use type has an associated value in terms of resources provision, a change in the characteristics of land uses or the intensity of its management should result in an equivalent change in the availability of those resources, and hence the abundance and diversity of the species should be modified. Changing to more intensively managed systems, or increasing the area under crop that provide fewer key ecological requirements, is likely to lead to an impoverished community in that system. We expect a gradual change in bird community composition in response to human management intensification, varying from very poor assemblages with low species richness and abundance of birds for highly modified environments (i.e. agriculture plots), to highly diverse communities for the native forest. A gradual increase in bird community diversity is predicted to match the gradient in habitat modification; hence agriculture under agro-ecological schemes and silvopasture should present intermediate degrees of bird community diversity.

2.2. Methods

Study site

The study area is located in the semiarid part of the Chaco Region, and encompasses a rectangle of 600,000.00 ha (centered at 26° 24’ S, 61° 09’ W) in the southern portion of Almirante Brown Department, Chaco Province, and an adjacent portion of protected forest inside Copo National Park, Santiago del Estero Province (Figure 1.2, see Chapter 1). The area is characterized by a flat topography (approximately 160m above sea level) with no surface water bodies, except for the reservoirs made for livestock. The landscape is a mosaic of agricultural fields and interspersed fragments of subtropical semi deciduous dry forest. The farming land is periodically covered by different crops, depending on the time of the year. Winter crops include mainly wheat and oats, whereas alfalfa and other grasses are used in grazing areas. During this study, agricultural plots presented cotton or soy bean stubble remnants from the summer season, with a high percentage of bare soil. Strips of natural grassland occurred along ancient river beds, but over the last few decades, these have been replaced by crops (Adamoli et al. 1990; Tálamo et al. 2009).

The Copo National Park (25° 46’ S, 61° 47’ W) represents one of the best-preserved and most extensive portions of Chaco woodland in Argentina, characterized by quebracho colorado santiagueño (*Schinopsis lorentzii.*), quebracho blanco (*Aspidosperma quebracho-blanco*) and mistol (*Ziziphus mistol*), as dominant tree species (Cabrera 1971; Bucher & Huszar 1999; Tálamo & Caziani 2003; Zak et al. 2004; Tálamo et al. 2009). The understory layer is formed by dense thorny shrubs, grasses, and exposed bare soil. Settlers reside inside the park where they also keep cattle that wander foraging in the west-central and northern part of the park. Therefore, sampling sites for birds in this study were located near the East border, where an extensive stand of old-growth forest persists, to avoid areas with high levels of human and livestock interference. The climate in this region is markedly seasonal, with rain (400 to 900mm) falling during November and March. The average annual temperature is around 22° C, with absolute maximum temperatures above 45° C in summer, and below zero during winter (Cabrera 1971; Grau et al. 2005).

Sampling design

Five land uses represented the most common elements in the agricultural landscape: forest, forest strips, silvopasture, and agriculture. Forest (F) is the characteristic natural habitat. However, almost all of the forest fragments in the area have been used for selective logging in the past, as well as for traditional ranching; therefore, it is second growth forest (Cabrera 1971; Adamoli et al. 1990; Bucher & Huszar 1999; Tálamo & Caziani 2003). Silvopasture (S) is an agroforestry system for livestock production in which some trees and the woody understory are selectively removed, leaving an approximate density of 100 trees per hectare in the paddock; non-native grasses (e.g. *Panicum maximun*) are then sowed to feed the cattle. Following a gradient of intensification, two types of agricultural systems are present. Areas of highest intensification, cleared up more than 10 years ago, and consisting in big extensions of mechanized cropland with no remnant patches of forest nearby, and practically no hedgerows or live fences separating land uses represented agriculture plots (A). More recent agricultural systems of smaller size and enclosed by forest strips represented lower intensity agriculture with forest strips (AFS). Finally, forest strips (FS) consisting in long sections of forest, usually ranging between 80 to 100-meters-wide, that surround agriculture plots were considered the fifth land-use type. In addition, forest control sites were located inside Copo National Park to represent a habitat that has not been modified by logging or ranching, hence the sixth category was forest inside National

Park (FNP) (Tálamo & Caziani 2003; Tálamo et al. 2009). Several kilometres of abandoned roads inside the park, only accessible on foot, were used to reach sites deep in the forest.

To select the sites inside the agricultural landscape, a LANDSAT 5TM image was overlaid with a 100 x 60km grid of 10 x 10km side, and 10 grid squares were randomly selected (Figure 2.1). Inside each grid square, all potential sites consisting of a patch or plot of homogeneous land use were identified. When the grid square selected did not contain the required sites, the nearest available site outside the grid square was used. Sites were identified, and visited to verify the dimension and configuration of the vegetation cover. Subsequently, five sites (one for each land use) inside each of the ten grid squares were selected randomly. Inside the National Park, all potential sites were restricted to the existing trails located along the East border, avoiding in this way, to survey in disturbed areas where cattle of local settlers are used to wander. We identified old and abandoned trails inside the forest and randomly selected five sites.

Bird survey

The bird community was sampled during spring season (mid-September), in 2011 and 2012 at four randomly established points per site for the agricultural mosaic. As a result, each of the ten grid squares contained five sites (i.e. one for each land-use type) with four points each (40 points per land-use type, 200 points in total, Figure 2.1). Points inside sites were at least 200m apart, encompassing a homogeneous habitat, and in the case of agriculture with forest strips, points were inside the plot, 150 metres apart from the edge to specifically account for the forest strip effect (Hill 1973; Hutto et al. 1986; Bibby et al. 1992; Codesido & Bilenca 2000; Derlindati & Caziani 2005; Sutherland 2006). For the protected forest inside Copo National Park, five sites were surveyed during the same season, and the same years.

Two teams of observers visited all the sites once each year. When possible, the same observers were maintained in order to minimize the variation resulting from differences in detection and identification skills. Each point was surveyed for 10 minutes using the fixed-radius point count method and all the species, heard or seen within a radius of 100 meters, were registered (Hill 1973; Hutto et al. 1986; Bibby et al. 1992; Codesido & Bilenca 2000; Sutherland 2006). Surveys were carried out between 07:00 – 11:00 and 16:30 – 19:00, and were not undertaken in extreme weather conditions (windy and/or rainy days).

Data analysis

Species accumulation curves were constructed to visually verify that the sampling effort adequately represented the true species richness of each habitat. Species were accumulated by point-count for all sites (sample-based using 10,000 random iterations without replacement, Soberon & Llorente 1993; Flather 1996; Gotelli & Colwell 2001; Thompson & Thompson 2007).

To characterize alpha diversity in each site, two components of diversity were measured: species richness and dominance (Magurran 1988; McCune & Grace 2002; Magurran & McGill 2011). For the first component, the total number of bird species (hereafter species richness) was calculated. Species richness equals the total number of observed species and provides a great deal of information about the community, comparable across habitats. However, this index can be biased by sample size: as more individuals are sampled, more species will be recorded. Hence, differences in sample size between land-use types were incorporated using rarefied species richness. Rarefaction represented the interpolation of species richness to a smaller number of individuals. We rarefied species richness per site to the average number of individuals registered in the two land uses with the lowest mean number of individuals (i.e. approximately 20 individuals for A and AFS) (Magurran & McGill 2011; Gotelli & Chao 2013). For the second component of diversity we used the Berger-Parker dominance index that expresses the proportional importance of the most abundant species in the assemblage. Low values indicate low dominance by any one species and it is generally accompanied by an increase in evenness. Absolute number of individuals (hereafter abundance) was also measured.

All indices were computed by grouping the data for the four points inside each site, and considering both years together, controlling for spatial and temporal pseudoreplication respectively (Hill 1973; Magurran & McGill 2011). In order to describe patterns and characteristics of bird assemblages we investigated the relationship between the response variables and land use followed by factor level reduction until reaching the minimum adequate model. We used model selection based on Akaike Information Criterion corrected for small samples (AICc) to identify the models that were best supported by the data. A set of biological meaningful models, established *a priori*, varied in the way that land uses (factor levels) were collapsed together (Table 2.1). An inspection of models residuals showed that

Poisson errors and log link provided the best fit for species richness, whereas residuals for models with Berger-Parker (square root transformed) and abundance of individuals as response followed normal distribution of errors. Generalized and General linear Mixed Models (GLMM and LMM, respectively) were used considering the hierarchical design of the study where sites are nested inside grid squares; therefore, grid square was the random variable in a random intercept model (Crawley 2007; Zuur et al. 2009).

To assess variation in species composition of the bird assembly across land uses a Bray Curtis dissimilarity matrix was submitted to a Principal Coordinates Analysis (PCoA) (Faith et al. 1987; Quinn & Keough 2002). The dissimilarity matrix was first double standardized: along species range (to avoid a strong weighting by a few highly abundant species and to balance the contribution of rare ones) and along sites (to control for differences in sampling effort). The results of the ordination were assessed by inspecting the diagrams and the scores (Quinn & Keough 2002). We then performed single regressions (LMM) between the scores of PCoA axis 1 and land use (predictor variable) followed by factor level reduction.

Functional diversity is another important measure for community characterization. Bird species were originally classified into seven feeding guilds: (1) insectivores, (2) granivores, (3) omnivores, (4) nectarivores, (5) frugivores, (6) carnivores, and (7) scavengers (Supplementary information Table 2.S1). The assignment of species was made based on known feeding habits described in ornithological literature (Kratter et al. 1993; del Hoyo et al. 1996; Lopez de Casenave et al. 1998; Narosky & Yzurieta 2003; del Hoyo et al. 2003; Codesido & Bilenca 2004; de la Peña 2011). Because of low sample sizes, bird species of nectarivores, frugivores, and scavengers (i.e. guilds that represented less than 5% of all captures) were included within omnivores, granivores, and carnivores respectively. To better understand the distribution of functional groups inside each habitat, we subsequently re-classified the granivore and insectivore species considering not only their diet composition, but also, their foraging behaviour. As a result, we obtained seven new groups: (1) TG: terrestrial granivores, (2) AG: arboreal granivores, (3) TI: terrestrial insectivores, (4) LFI: long-flight insectivores, (5) SFI: short-flight insectivores, (6) BI: bark insectivores, and (7) FI: foliage insectivores (Lopez de Casenave et al. 1998; del Hoyo et al. 2003; Codesido & Bilenca 2004; de la Peña 2011; Macchi et al. 2013). We measured diversity in each land-use type using proportional species richness (number of species of a given guild in a given site in relation to total number of species for that site) and proportional abundance (number of individuals of a given guild in a given site in relation to total number of individuals for that site) for each guild.

For each response variable and guild we fitted a GLMM with Binomial distribution and logit link using land-use type as predictor variable (Zar 1996; Quinn & Keough 2002; Crawley 2007). We then assessed differences among the levels of land use using Tukey's Honest Significant Difference tests (Tukey HSD).

All the calculations and statistical analysis were carried out using software R v.3.1.1 (R Core Team 2014). Species accumulation curves, the dissimilarity matrix, and the PCoA were calculated using package "vegan" (Oksanen et al. 2012). LMM and GLMMs were run using package "lme4" (Bates et al. 2014).

2.3. Results

Species richness

We recorded a total of 5067 individuals of 126 bird species during the study (plus 29 species observed in the study area but not registered during the point-count sampling, Supplementary information Table 2.S1). Silvopasture plots had the highest absolute species richness (97 species, 77 % of the total); followed by forest strips, forest, and forest inside National Park (86, 82 and 66 species respectively; accounting for the 84% of the total species richness among all types of forests), while a much lower richness was found in agriculture (19 species) and agriculture with forest strips (18 species) (Table 2.2). This marked difference between arable fields and the other four land uses is also reflected in the species accumulation curves (Figure 2.2). The curves for A and AFS behave differently than the rest of the curves. The number of cumulative species rises uniformly with the addition of sites, and reaches an asymptote at considerably low values. For the forest-type habitats (i.e. forest inside and outside National Park, forest strips, and silvopasture), accumulation curves indicate a rapid increase in the initial number of species registered (Figure 2.2). The curve has almost plateaued for F and FS, and both curves have similar shape. Although the curve for S could yet reach a higher number of species, it is close to the asymptote. This indicates that the sampling effort was large enough to accurately assess species richness in those habitats. For the FNP, the sampling effort resulted in half the number of points as compared to that of the rest of the land uses. It is clear that the species accumulation curve could be extrapolated to different numbers of species, and eventually species richness could exceed that of F or FS with additional sampling effort.

Differences at habitat level

We found that semiarid Chaco bird assemblages in multiple-use agricultural landscapes change markedly along the gradient of human impacts and land-use intensity. Species richness responded to habitat type with a clear pattern. As previously shown in the species accumulation curve, there were two similar land-use types with significantly lower species richness.

Both agriculture and AFS showed a low number of bird species, and this characteristic differentiated them from the rest of the habitats (mean species richness, A= 4.6±3.8; AFS= 3.5±1.3, Figure 2.3 A). A sharp increment in species richness is evident for land uses with trees, which remained grouped together in the best minimum adequate model (Table 2.3). Bird species richness was similar in S, FS, F and FNP (mean species richness= 41.4±7.8; 39.3±5.3; 42.3±6.7; 37.8±8.5, respectively). Results for rarefied species richness were similar to the former, showing that differences in the number of individuals sampled do not change the pattern in the distribution of species among the land uses (Table 2.2 and 2.3, Figure 2.3 B). The mean Berger-Parker index values showed an inverse result that corresponds with a significant decrease in dominance from A and AFS to the four other land uses (Figure 2.3 D). Both types of agriculture had the highest values in dominance, mainly represented by high numbers of the Eared Dove (*Zenaida auriculata*, Columbidae, BP index= 0.6±0.3 for A, Supplementary information Table 2.S1) and the Southern Lapwing (*Vanellus chilensis*, Charadriidae, BP index= 0.5±0.1 for AFS), species commonly found in open and modified human environments (Kratter et al. 1993; del Hoyo et al. 1996; del Hoyo et al. 2003). Silvopasture comes next with 0.16±0.14 dominance, followed by FS with 0.11±0.03, also for the Eared Dove. Whereas species more related with forest as the White-tipped Dove (*Leptotila verreauxi*, Columbidae) and the Masked Gnatcatcher (*Polioptila dumicola*, Polioptilidae) were dominant in lower numbers in F and FNP (BP index= 0.08±0.01, and BP index=0.10±0.02 respectively).

Only three bird species were registered in all land uses, the Eared Dove, the Picazuro Pigeon *Patagioenas picazuro* and the Rufous-collared sparrow *Zonotrichia capensis*, all of them considered species adapted to open habitats. In contrast, 28 bird species were reported in only a single habitat type: of these, thirteen were sighted in forested land-use types (four in FNPF, five in F, and four in FS), ten only in silvopasture and five only in A and AFS. The Principal Coordinates Analysis was performed on the Bray-Curtis dissimilarities for all 55 sites and 126 species. The first two axis of the ordination explained 47% of the variation in community composition. The inspection of the ordination graph provided useful information to understand the changes in the assemblages among the land-use types (Figure 2.4). The data showed a strong division between two main groups of habitats, as reflected by the previous analysis. Along the first axis, positive scores correspond to a packed group of sites (green characters in Figure 2.4) that showed similar community composition corresponding to S, FS, F and FNP. This first group clearly separates from the rest of the sites that belong to A and AFS. Community composition (PcoA axis 1) showed only significant differences between A+AFS and the rest of the land-use types, whereas the distribution along the second axis was not related with the characteristics of the habitats.

Bird assemblages

Significant variations were observed only for insectivores and granivores. These two groups resulted in the most diverse and abundant trophic guilds along the land-use gradient. Insectivores was the most abundant group (Supplementary information Table 2.S2), almost 50% of all species registered belonged to this guild (71 species and 2507 individuals); followed by granivores (30 species and 2211 individuals, including frugivores), carnivores (16 species and 106 individuals, including scavengers), and omnivores (9 species and 243 individuals, including nectarivores).

The insectivore guild was best represented in F and FNP with the highest proportional richness and number of individuals among all land uses (Table 2.4, Figure 2.5). The diversity of insectivore species was second-highest in S and FS; and smallest in both types of arable fields. Carnivores showed the opposite pattern with the lowest proportional diversity in forested habitats, increasing with land use intensification (FS=F=FNP < S < AFS=A; χ^2=47.1, df= 3, p<0.001). Granivores and omnivores presented similar proportion of species across all land uses. The abundance of granivores and insectivores was evenly distributed in AFS, S and FS, whereas in A, F and FNP, insectivores were predominant. Omnivores represented a small proportion of individuals in all the environments. Carnivores were also scarce in most of the land uses apart from AFS, where they presented the highest proportion in species richness and abundance of individuals.

Almost a quarter of the species considered in the subdivision belonged to foliage insectivore species, that resulted in the most diverse guild with 23 out of 94 species, followed by terrestrial granivores (17 species), terrestrial insectivores (16 species), short-flight insectivores and bark insectivores (12 species), long-flight insectivores (8 species), and arboreal granivores with only 6 different species. When considering the number of individuals, terrestrial granivores was the most abundant guild (1659 individuals), followed by foliage insectivores (909 individuals), terrestrial insectivores (603), short-flight insectivores (480), arboreal granivores (406), bark insectivores (386), and the least abundant, long-flight insectivores (129).

In arable plots (A and AFS) we only found species that feed on the ground (terrestrial granivores and insectivores), and insectivores with long attack distances (long-flight insectivores, mean attack distance over 1 metre). In the rest of the land uses (S, FS, F and FNP) all the guilds were present (Figure 2.6, Table 2.5 and Supplementary information Table 2.S3). Differences in the proportional number of species among habitats were significant only for three guilds (Table 2.5), with terrestrial granivores, and terrestrial insectivores showing the highest proportion of species richness in A and AFS, and long-flight insectivores presenting the lowest proportional richness in S and FS (Table 2.5). The proportion of individuals of terrestrial granivores was highest in S and FS, and lowest in F and FNP, whereas terrestrial insectivores had the highest proportional abundance in A and AFS. Forest and forest inside the National Park showed similar proportion of individuals of long-flight insectivores and foliage insectivores, both being the highest among the rest of the land-use types (Figure 2.6, Table 2.5).

2.4. Discussion

Diversity and composition of bird assemblages in agricultural landscapes of the semiarid Chaco showed a clear segregation along the intensification gradient. This pattern reflected a substantial change in community structure with a sharp decline in diversity from low- to highly-modified habitats. Coincidentally with several studies assessing changes in bird diversity in production areas (Perfecto et al. 2003; Mastrangelo & Gavin 2012; Moura et al. 2013), our results indicate that intensified land uses hold only a small portion of the regional avifauna; and, as we predicted, a reduced offer of relevant ecological resources is likely to be the cause of the low species richness and abundance of birds in these sites. During the sampling season, almost all the sites presented a high percentage of bare soil (80-90%), or remaining soybean or cotton stubble. In this conditions, only a few bird species were registered (e.g.: *Zenaida auriculata,* Ear Dove; *Columbina picu,* Picui Ground-Dove; *Patagioaenas picazuro*, Picazuro Pigeon; *Nothura maculosa,* Spotted Nothura). And unlike most of the forest-specialists, the species present in highly intensified arable fields were generalist, with terrestrial habits, usually foraging on the ground in open areas, where the lack of roosting or perching sites does not represent a major drawback. In that sense, when that important resource was available, it did not have the expected influence on the bird diversity; otherwise, differences should have arisen between A and AFS. We predicted that birds may be responsive to the location of less intensively managed habitats (like forest strips) in the surroundings of arable fields, and this would be translated into higher bird diversity in AFS. Many studies have highlighted the importance of non-cropped habitat in maintaining farmland biodiversity, where birds often use field edges more than areas further into the field, enabling them to forage close to cover (Benton et al. 2003; Perfecto et al. 2003; Tscharntke et al. 2008). This was the case for several ground dwelling species commonly found in edge-like environments (e.g.: *Ortalis canicollis,* Chaco Chachalaca; *Crypturellus tataupa,* Tataupa Tinamou; *Guira guira* Guira Cuckoo) that were frequently seen inside the plot and in the surroundings of forest strips. However, these events must have been too scarce or infrequent to be detected during the study. On the other hand, to correctly assess the use of the agricultural plot by birds inhabiting forest strips, a different sampling design should be employed, such as line transects along the border (Barlow et al.

2010), or possibly the sampling should be carried out in a different period when crop fields have vegetation cover (i.e. October-November).

Bird species richness was similar among human-modified forested land uses (S and FS), including forest patches in and outside protected areas (F and FNP). This general conclusion is supported by results from similar studies of land-use intensity gradients elsewhere in the Chaco Region (Mastrangelo & Gavin 2012; Macchi & Grau 2012), in the Atlantic Forest (Moura et al. 2013), and Central America (Perfecto et al. 2003; Harvey & González Villalobos 2007). The number of species did not differ greatly for intermediate to low intensification land uses at the same time that the dissimilarity analysis showed high correspondence between the assemblages. Silvopasture is a type of agroforestry with an intermediate-intensity production level where human-caused alterations frequently occur due to livestock occupation and movements, periodical removal of the shrubby understory, and fire events. Avian community composition in this land use did not appear to be the result of a simple combination of grassland and forest assemblages (i.e. ecotone). Whilst 81% of the species present in forested habitats (FS, F and FNP) were also found in silvopasture, no primarily grassland bird was found to be abundant. All the grassland dwelling species recorded in our samples (e.g. White-browed Blackbird *Sturnella supercilliaris*; Great Pampa-Finch *Embernagra platensis;* Southern Lapwing *Vanellus chilensis*) were registered solely in agricultural plots. The relatively high diversity present in silvopastures is likely to be related to the combined characteristics of this system that, although structurally simpler, retains some of the most representative native tree species in the canopy layer; and, on the other hand, introduces an open understorey with a novel set of resources (Nair 1985).

The result obtained from the analysis of rarefied species richness showed the same trend obtained for species richness alone, and the best model remained significant, even when the sampling effort was reduced to 20 individuals (AICc=248.7, Table 2.3). Although the effect is non-significant, when the number of species is shown relative to the number of individuals in the sample (Figure 2.3 B), the silvopasture land-use type declined below the rest of the habitats (FS, F and FNP). As in our study, high abundance of most birds' guilds was recorded in low intensity cattle management systems by Macchi & Grau 2012, whilst Mastrangelo & Gavin 2012 found that silvopastoral systems provided habitat for 70% of the bird species also registered in forests. Despite that agroforestry land uses or secondary forests had relatively high diversity and abundance of bird species, these environments should not be consider as adequate replacements of primary forests, since their capacity to support forest interior or forest-dependent species has not been tested in this study and may depend on context-specific characteristics (Lopez de Casenave et al. 1998; Tscharntke et al. 2008).

An important factor that could be influencing our results is the difference in the detectability of a species or a group of species (e.g. trophic guild) when we consider the range of land-use types sampled (MacKenzie et al. 2002). The vegetation structure, and the species behaviour associated with it, among other factors, could be facilitating the detection of individuals in the more open forested habitats (i.e. S and FS). We did not adjust for potential differences in detectability among land-use types because the requirements in the number of repeated surveys per location could have been almost impossible to meet in such a large-scale study. Additionally, in this type of subtropical biome, communities are composed of many naturally rare species that could have been left aside because of their extremely low recapture rate (Banks-Leite et al. 2014). However, some measures were taken in order to minimize this bias: (1) the same observer, or observers with similar knowledge and experience, performed the sampling; (2) training sessions and sampling drills were carried out in advance to standardize counting techniques and criteria; (3) special attention was paid to follow the movements of each individual bird when in S, FS, F and FNP, to avoid counting the same individual twice.

Strips of forest also presented highly diverse assemblages. This reveals its importance as a distinctive feature in the farming landscapes. The width of this habitat ranged from 80 to 100 metres, and given the relatively small proximity of its borders, they could be considered as an edge environment altogether. High species richness and abundance of individuals could be related with the vegetation in these edges, which enhances the availability of cover and nesting sites. Lopez de Casenave et al. (1998) found that edges also hold a great number of insects, seeds and fruits promoting increased bird densities because food abundance is an important factor that influences the distribution of these birds. Therefore, the similarity in bird community structure obtained between forest strips and forest could be indicating the role of the former as a refuge during the period between crops or the important role as a corridor connecting forest fragments and allowing the movement of individuals from one place to another (Barlow et al. 2010). Lopez de Casenave et al. 1998 found 10 avian species to be present exclusively in the forest interior, and 17 species, solely in edge environments. All but one of the species from the first group were registered in our study, all in forested habitats, not only in those with a good status of conservation (F and FNP), but also in land uses with "edge" characteristics (S, and FS). From the second group of birds (i.e. "edge species"), we registered 13 species, and 10 of them were found in different combinations of land-use types including at least one record in F or FNP (forest interior). Patterns of high species diversity in disturbed or modified forest patches have been reported for several regions elsewhere (Harvey & González Villalobos 2007; Fischer et al. 2011; Cáceres et al. 2014) and are most likely to be related with the maintenance of forest cover at higher spatial scales that may provide the appropriate conditions for the persistence of bird communities in agricultural landscapes (Andrén 1994; Cushman & McGarigal 2002; Martensen et al. 2012; Banks-Leite et al. 2013).

Differences in bird communities between forest and forest inside National Park were not evident in this study. We expected to find a higher diversity in Copo National Park than in forest fragments within the agricultural matrix, mainly due to the higher level of disturbance and history of use in the latter area. There are several possible factors to explain this result. Tálamo et al. 2012 described unlogged and livestock free areas inside the park as presenting similar diversity of woody vegetation to areas with previous disturbance history; therefore the composition and status of the forest can be considered as fairly undisturbed. This information was taken into account and, consequently, point-counts were located in the interior of the forest in an attempt to represent the best preserved conditions. However, the region surrounding the park might have had an effect in the bird assemblage composition given the proximity of the East limit (approximately between 300 and 600 metres). In the neighbouring area, private land is currently under production, and deforestation and clearing, including the use of fire can be frequent. Therefore, the bird community sampled might not have been one of unique forest interior species. An alternative explanation could be that forests patches in unprotected areas have been increasingly reduced, modified and fragmented by exploitation and poorly developed management strategies resulting in degraded remnants of forests (Aizen & Feisinger 1994).

This process may have increased the heterogeneity in the forest, with the eventual colonization of new generalist species incorporated to the existing assemblage, hence increasing the species richness of the community. Interestingly, the only bird species under near-threatened category with distribution in the area (i. e. the Black-bodied Woodpecker, *Dryocopus schulzi*) was present in S, F and FNP. Yet, being registered only four times in total, it could be showing that available resources and conditions in these habitats are not profoundly different, given that the Black-bodied Woodpecker is a species considered to be restricted to Chaco woodland.

The study of functional composition through the analysis of trophic guilds is an important contribution to the knowledge of community structure. Feeding habits of birds are linked to functional roles in ecosystems. Therefore, the absence of a trophic guild in a community can affect essential processes like seed dispersal, pollination, and biological control (Tscharntke et al. 2008). Analysing proportional diversity and abundance of birds instead of total numbers allowed us to detect differences in the functional roles present in each land-use type. Previous studies suggest that the replacement of forests with simplified agricultural systems results in shifts toward less specialized bird communities, with altered proportions of functional groups (Tscharntke et al. 2008). Our results show that all the trophic guilds were represented in each of the land-use types, therefore the differences in the provision of functional services would be more related with low numbers of individuals in more intensified land uses (Supplementary information Table 2.S2), rather than with the number of trophic guilds in these environments.

Insectivores responded positively to low intensity land-use types, and both, species diversity and number of individuals, were the highest inside the forest. The structural and floristic diversity of these habitats is likely to provide excellent opportunities for species that feed on insects in several different ways. Accordingly, when the insectivore guild was subdivided based on the stratum and the way in which species forage, we observed that forest and forest inside National Park had the highest proportion of individuals feeding on insects from twigs, branches and leaves (i.e. foliage insectivores) and harboured species only present in well-preserved forest like the Short-billed Canastero *Asthenes baeri*, the Striped-crowned Spintail *Cranioleuca pyrrhophia*, the Greater Thornbird *Phacellodomus ruber*, and the Freckle-breasted Thornbird *Phacellodomus striaticollis*) (Lopez de Casenave et al. 2008; Codesido et al. 2009; Macchi & Grau 2012). Also, with the highest proportion in F and FNP, we found insectivores like the Little Nightjar *Caprimulgus parvulus*, the Rufous Nightjar *C. rufus*, and the Crowned Slaty Flycatcher *Empidonomus aurantioatrocristatus* that feed mainly while flying (i.e. long-flight insectivores). Bark insectivores (woodpeckers and woodcreepers) rely heavily on the availability of trees as their diet consists primarily of insects and larvae that they probe from under the bark. Contrarily to Macchi et al. 2013 , that found an exponential decrease in the abundance of this guild for silvopastures, our results show that bark insectivore species were present in similar numbers in all the forested land-use types (S, FS, F and FNP), indicating that an adequate density of trees standing in the silvopasture paddocks could preserve these species. Fischer & Lindenmayer (2002) found that many birds commonly detected in woodland patches, in a pastoral landscape of Australia, were also common in paddock trees. However, some birds with special habitat requirements were absent from paddock trees. Surprisingly in our study, almost all the bark insectivore species (10 out of 12 species) were found in all the forested habitats, even the Black-bodied Woodpecker *Dryocopus schulzi,* as mentioned before. Inside the arable fields, the most abundant species had terrestrial habits (i.e. terrestrial granivores and insectivores) as expected, derived from the limitations in vegetation cover, both natural and cultivated (Lopez de Casenave et al. 1998; Harvey & González Villalobos 2007; Tscharntke et al. 2008; Macchi & Grau 2012; Mastrangelo & Gavin 2012). Carnivores preferred more open habitats where the absence of the understorey stratum facilitates hunting and visualization of prey. This guild was most abundant in agriculture with forest strips where the availability of sites to perch, might be related with the high numbers found for this land-use type.

In general, our results shed light on the distribution and composition of bird communities in different land-use types related to human activities in the semiarid Chaco Region, where the degree of intensification in the agricultural practices generates a variety of habitats for the avian community. Our results support a nonlinear relation between land-use type and patterns of species richness and abundance with very poor communities present in the most intensified land uses, and similar assemblages of birds shared among intermediate to low intensification environments. However, the composition of the assemblages should be analysed in detail taking into account habitat affiliations and species of conservation concern as the use of species richness does not reflects shifts between habitat specialists and habitat generalists species. Additionally, ecological processes are often simultaneously influenced by factors acting across a range of scales, or at several organizational levels. For these reasons, in the next chapters we incorporate into the analysis a taxonomic group with different habitat requirements, and we also consider landscape configuration variables that could be influencing animal movements between managed and natural habitats.

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Table2.1. List and description of models for the categorical variable “land use”. Name refers to the name and number given to the explanatory variables with different factor level arrangement. Factor level arrangements were based on a set of *a priori* hypothesis that ensured biological interpretation of the results. Each particular model (hypothesis) was described by GLMM or LMM (depending on the response variable). We used model selection based on the Akaike Information Criterion corrected for small samples to compare the set of candidate models, with deletion tests (Wald’s chi-square test for species richness and F-test for abundance) to assess the significance of the increase in deviance that resulted when a given term was removed from the current model.

Name	**Factor level arrangement**	**Particular hypothesis justification**
Land use 1	A, AFS, S, FS, F, FNP	Each land use has a particular effect at local scale, mainly given their specific vegetation cover and management regime.
Land use 2	A + AFS, S, FS, F, FNP	Intensive arable systems (A and AFS) are not different from each other in their bird community, mainly because habitat availability in these land uses is very low despite local differences in forest strips surrounding AFS plots. The rest of the land uses present a distinctive bird community.
Land use 3	A + AFS, S, FS, F + FNP	Intensive arable systems (A and AFS) are not different from each other. Land-use types presenting a well-preserved forest cover (F and FNP) are not different from each other.
Land use 4	A + AFS, S + FS, F + FNP	Intensive arable systems (A and AFS) do not differ. Intermediate intensity land uses (S and FS) are grouped accordingly to their habitat alteration level and disturbance regime. Land uses with a well-preserved forest cover (F and FNP) are not different from each other.
Land use 5	A + AFS, S, FS + F + FNP	High-intensity land uses (A and AFS) do not differ. Intermediate intensity land uses, where forest cover has been significantly reduced (S) hold a distinctive bird community. Land uses presenting a well-preserved and structured forest cover, regardless of size (FS, F and FNP) are not different from each other.
Land use 6	A + AFS, S + FS + F, FNP	High-intensity land uses (A and AFS) do not differ. Sites inside protected areas (FNP) hold a different bird community than the rest of forested land-use types (with reduced or slightly altered vegetation cover) outside the National Park.
Land use 7	A + AFS, S + FS + F + FNP	Intensive arable systems (A and AFS) are not different from each other. The category of protection does not affect bird community assemblages: land-use types presenting a range of intermediate forest cover (S), good forest cover outside protected areas (FS and F) and well-preserved forest cover inside National Park (FNP) do not differ.

Abbreviations: A: agriculture; AFS: agriculture with forest strips; S: silvopasture; FS: forest strip; F: forest; FNP: forest inside Copo National Park

Table 2.2. Summary statistics for the bird community data surveyed in the semiarid Chaco Region during 2011 and 2012. Land-use types included the most common land uses present in the study area and a reference land use (forest control) inside Copo National Park. Number of sites sampled in each land use are shown. Absolute values express the total number of individuals and total number of species registered in each land-use type. Mean values represent averaged abundance, species richness, rarefied species richness, and Berger-Parker dominance index per land use (± standard error). Species richness was rarefied using 20 individuals (minimum mean number registered in agriculture and agriculture with forest strips). Berger-Parker dominance index represents the mean proportion of the most abundant species for each land use.

Land-use type	**Number of sites**	**Absolute values**		**Mean values (± se)**			
		Abundance	**Species richness**	**Abundance**	**Species richness**	**Rarefied sp.richness**	**Berger-Parker**
Agriculture	10	173	19	17.3 ± 18.1	4.6 ± 3.8	3.7 ± 2.4	0.6 ± 0.3
Agriculture with forest strips	10	103	18	10.3 ± 10.0	3.5 ± 1.3	3.3 ± 1.2	0.5 ± 0.1
Silvopasture	10	1834	97	183.4 ± 66.8	41.4 ± 7.8	13.4 ± 2.1	0.16 ± 0.14
Forest strip	10	1156	86	115.6 ± 22.8	39.3 ± 5.3	14.9 ± 0.7	0.11 ± 0.03
Forest	10	1233	82	123.3 ± 28.3	42.3 ± 6.7	15.1 ± 0.7	0.08 ± 0.01
Forest inside National Park	5	568	66	113.6 ± 36.2	37.8 ± 8.5	15.0 ± 0.7	0.1 ± 0.02
Total	55	5067	126	-	-	-	-

Table 2.3. Summary of statistical analysis and models tested. For each response variable tested, the table lists: the explanatory variables (a factor variable with 6 levels corresponding to each land-use type grouped in different ways, accordingly to *a priori* hypothesis, see Table 2.1); the number of parameters estimated in the model (k); the Akaike's Information Criterion value corrected for small samples (AICc); the delta AICc (as a measure of each model relative to the best model), and the Akaike's weight (w, indicating the probability of a model as the best among the whole set of models). Models are sorted in descending order of importance with the first model for each response variable being the best model. The best model selected is shown in bold.

Response variable	Explanatory variable	k	AICc	∆AICc	w
Species richness	**Land use 7**	**3**	**333.5**	**0.0**	**0.40**
	Land use 6	4	334.7	1.2	0.22
	Land use 5	4	335.5	2.0	0.15
	Land use 4	4	335.7	2.2	0.13
	Land use 3	5	337.6	4.1	0.05
	Land use 2	6	338.5	5.0	0.03
	Land use 1	7	339.6	6.1	0.02
	intercept	2	1140.0	806.5	0.00
Rarefied species richness	**Land use 7**	**3**	**248.7**	**0.0**	**0.39**
	Land use 5	4	249.7	1.0	0.24
	Land use 4	4	250.5	1.8	0.16
	Land use 6	4	251.0	2.3	0.12
	Land use 3	5	252.2	3.5	0.07
	Land use 2	6	254.7	6.0	0.02
	Land use 1	7	257.1	8.4	0.01
	intercept	2	421.0	172.3	0.00
Abundance	**Land use 5**	**5**	**553.7**	**0.0**	**0.70**
	Land use 3	6	556.1	2.4	0.21
	Land use 2	7	558.4	4.7	0.07
	Land use 1	8	561.0	7.3	0.02
	Land use 4	5	571.0	17.3	0.00
	Land use 7	4	573.2	19.5	0.00
	Land use 6	5	573.7	20.0	0.00
	intercept	3	632.9	79.2	0.00
Berger-Parker dominance (squared root)	**Land use 5**	**5**	**-84.4**	**0.0**	**0.34**
	Land use 4	5	-83.5	0.9	0.22
	Land use 7	4	-83.1	1.3	0.18
	Land use 3	6	-82.5	1.9	0.13
	Land use 6	5	-81.0	3.4	0.06
	Land use 2	7	-80.1	4.3	0.04
	Land use 1	8	-78.7	5.7	0.02
	intercept	3	-5.2	79.2	0.00

Table 2.4. Summary statistics for the analysis of trophic guilds. Values represent the mean proportion of species richness and abundance of birds per trophic guild (± standard error) in each land-use. We report χ^2: chi-square statistic and E.D: explained deviance as a measure of statistical significance. Mean proportions were calculated as: number of species of a given guild in a given site in relation to total number of species for that site (averaged by sites inside the same land use); and, number of individuals of a given guild in a given site in relation to total number of individuals for that site (averaged by sites inside the same land use). Superscript letters indicate the outcome of multiple comparisons using Tukey HSD (statistically different results at alpha=0.05 are those whose combination present at least one different letter). Significant comparisons among land uses with p<0.001 are in bold.

	A	**AFS**	**S**	**FS**	**F**	**FNP**	χ^2	***E.D***
Richness								
Granivores	0.27 + 0.21	0.37 + 0.39	0.33 + 0.05	0.35 + 0.04	0.29 + 0.05	0.280 + 0.007	6.01	0.03
Insectivores	0.49 + 0.33 ^{a}	0.24 + 0.22 ^{a}	0.55 + 0.07 ^{b}	0.53 + 0.05 ^{b}	0.61 + 0.05 ^{c}	0.64 + 0.03 ^{c}	**30.29**	0.13
Omnivores	0.13 + 0.14	0.06 + 0.13	0.06 + 0.04	0.09 + 0.03	0.07 + 0.02	0.05 + 0.02	9.03	0.06
Carnivores	0.10 + 0.14 ^{a,b,c}	0.33 + 0.31 ^{a,b}	0.06 + 0.03 ^{a,c}	0.02 + 0.02 ^{d,e}	0.02 + 0.02 ^{d,e}	0.03 + 0.01 ^{d,e}	**47.1**	0.26
Abundance								
Granivores	0.28 + 0.29 ^{a}	0.32 + 0.41 ^{a}	0.48 + 0.15 ^{b}	0.49 + 0.06 ^{b}	0.40 + 0.03 ^{c}	0.27 + 0.02 ^{c}	**76.92**	0.14
Insectivores	0.60 + 0.34 ^{a}	0.33 + 0.26 ^{b}	0.46 + 0.16 ^{b}	0.43 + 0.06 ^{b}	0.53 + 0.03 ^{a}	0.68 + 0.03 ^{a}	**56.93**	0.11
Omnivores	0.06 + 0.08 ^{a}	0.06 + 0.17 ^{a}	0.02 + 0.01 ^{b,c}	0.07 + 0.04 ^{a,c}	0.06 + 0.02 ^{a,c}	0.03 + 0.02 ^{a,c}	**74.5**	0.23
Carnivores	0.05 + 0.08 ^{a}	0.27 + 0.31 ^{b}	0.03 + 0.02 ^{a,c}	0.006 + 0.008 ^{e}	0.007 + 0.007 ^{e}	0.011 + 0.007 ^{e}	**80.4**	0.30

Abbreviations: A: agriculture; AFS: agriculture with forest strips; S: silvopasture; FS: forest strip; F: forest; FNP: forest inside Copo National Park. E.D: explained deviance.

Table 2.5. Summary statistics for the trophic guilds reclassified. Values represent the mean proportion of species richness and abundance of birds per trophic guild (± standard error) in each land-use. We report χ^2: chi-square statistic and E.D: explained deviance as a measure of statistical significance. Mean proportions were calculated as: number of species of a given guild in a given site in relation to total number of species of granivores and insectivores for that site(averaged by sites inside the same land use); and, number of individuals of a given guild in a given site in relation to total number of individuals of granivores and insectivores for that site (averaged by sites inside the same land use). Numbers were averaged by sites inside the same land use. Superscript letters indicate the outcome of multiple comparisons using Tukey HSD (statistically different results at alpha=0.05 are those whose combination present at least one different letter). Significant comparisons among land uses with p<0.001 are in bold.

	A	**AFS**	**S**	**FS**	**F**	**FNP**	χ^2	***E. D***
Richness								
Terrestrial granivores	0.41 ± 0.33 ^{a}	0.51 ± 0.41 ^{a}	0.28 ± 0.05 ^{b}	0.27 ± 0.05 ^{b}	0.19 ± 0.03 ^{c}	0.19 ± 0.02 ^{c}	**33.8**	0.16
Arboreal granivores	0.00 ± 0.00	0.00 ± 0.00	0.07 ± 0.04	0.10 ± 0.03	0.08 ± 0.04	0.07 ± 0.02	0.89	0.01
Terrestrial insectivores	0.55 ± 0.35 ^{a}	0.43 ± 0.37 ^{a}	0.11 ± 0.03 ^{b}	0.11 ± 0.04 ^{b}	0.08 ± 0.04 ^{b}	0.08 ± 0.02 ^{b}	**32.28**	0.17
Long-flight insectivores	0.04 ± 0.08 ^{a,b}	0.05 ± 0.17 ^{a,b}	0.01 ± 0.01 ^{a,b,c}	0.03 ± 0.02 ^{a,b,c}	0.04 ± 0.03 ^{a,b}	0.09 ± 0.04 ^{a,b,d}	**17.34**	0.15
Short-flight insectivores	0.00 ± 0.00	0.00 ± 0.00	0.12 ± 0.04	0.13 ± 0.04	0.16 ± 0.04	0.16 ± 0.08	2.83	0.02
Bark insectivores	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.04	0.14 ± 0.05	0.17 ± 0.03	0.13 ± 0.01	0.76	0.00
Foliage insectivores	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.03	0.23 ± 0.03	0.27 ± 0.05	0.28 ± 0.06	2.23	0.01
Abundance								
Terrestrial granivores	0.33± 0.35 ^{a}	0.39 ± 0.41 ^{a}	0.42 ± 0.15 ^{b}	0.38 ± 0.05 ^{b}	0.32 ± 0.05 ^{c}	0.21 ± 0.02 ^{c}	**54.9**	0.11
Arboreal granivores	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.06 ^{a}	0.13 ± 0.05 ^{b}	0.09 ± 0.03 ^{a}	0.04 ± 0.01 ^{a}	**14.69**	0.06
Terrestrial insectivores	0.65 ± 0.33 ^{a}	0.37 ± 0.40 ^{a}	0.11 ± 0.06 ^{b}	0.08 ± 0.03 ^{c}	0.09 ± 0.05 ^{c}	0.09 ± 0.03 ^{c}	**331.06**	0.48
Long-flight insectivores	0.02 ± 0.05 ^{a}	0.02 ± 0.08 ^{a}	0.01 ± 0.02 ^{a}	0.02 ± 0.02 ^{a}	0.04 ± 0.03 ^{b}	0.08 ± 0.05 ^{b}	**20.68**	0.10
Short-flight insectivores	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.07 ^{a}	0.12 ± 0.06 ^{b}	0.12 ± 0.03 ^{b}	0.14 ± 0.06 ^{b}	**6.25**	0.02
Bark insectivores	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.03	0.09 ± 0.05	0.10 ± 0.04	0.07 ± 0.03	1.49	0.01
Foliage insectivores	0.00 ± 0.00	0.00 ± 0.00	0.18 ± 0.09 ^{a}	0.17 ± 0.05 ^{a}	0.24 ± 0.06 ^{b}	0.36 ± 0.05 ^{b}	**31.8**	0.10

Abbreviations: A: agriculture; AFS: agriculture with forest strips; S: silvopasture; FS: forest strip; F: forest; FNP: forest inside Copo National Park. E.D: explained deviance.

Figure legends

Figure 2.1. Land cover map showing (A) the 100 x 60 km grid overlaid across the study area. Light grey shaded squares indicate each of the ten randomly selected grid squares for the survey, (B) detail of one of the grid squares selected, red dots represent the location of the site for each of the five land-use types, (C) detail of several sites located nearby, red dots indicate the layout of point-count stations. Different vegetation cover is represented by different colours.

Figure 2.2. Bird species accumulation curves for each land use. Curves represent the total number of species recorded with increasing number of point-counts sampled. Different colours indicate different land-use types. A, agriculture; AFS, agriculture with forest strip; S, silvopasture; FS, forest strip; F, forest; FNP, forest inside National Park. The dashed vertical line illustrates a species richness comparison standardized to 20 point-count stations, which was the smallest number of points sampled in FNP.

Figure 2.3. Bird diversity measures for each land-use type. (A) Species richness; (B) Species richness rarefied; (C) Abundance of individuals; (D) Berger-Parker dominance index. Thick lines represent the median, boxes represent the interquartile range and whiskers represent minimum and maximum values, points represent sites (replicates). On the horizontal axis, land-use types are sorted from the most intensified agricultural practices to the least modified habitats. A, agriculture; AFS, agriculture with forest strip; S, silvopasture; FS, forest strip; F, forest; and FNP, forest inside National Park. Land uses with different letters differ significantly in the diversity measure (Tukey’s Honestly Significant Difference test: $P < 0.05$).

Figure 2.4. Principal Coordinates Analysis (PCoA) plot based on a Bray Curtis dissimilarity matrix for all 55 sites and 126 bird species. The first two axis of the ordination explained 47% of the variation in community composition. A marked division is appreciated along the first axis, between positive scores corresponding to sites in forested land uses and negative scores corresponding to sites in A and AFS. Sites are shown in coloured symbols, with each

character indicating a different land use. A, agriculture; AFS, agriculture with forest strip; S, silvopasture; FS, forest strip; F, forest; FNP, forest inside National Park.

Figure 2.5. Trophic guild distribution in each land-use type. (A) Proportional species richness per guild, per land use. Proportions in each bar represent the number of species of a given guild in relation to the total number of species in that land-use type. (B) Proportional abundance per guild per land use. Proportions in each bar represent the number of individuals of a given guild in relation to total abundance in that land-use type. Different colours represent different trophic guilds: Carn: carnivores; Omni: omnivores; Inse: insectivores; Gran: granivores. A: agriculture; AFS, agriculture with forest strip; S, silvopasture; FS, forest strip; F, forest; FNP, forest inside National Park.

Figure 2.6. Subdivision of main trophic guilds and their distribution per land-use type. Only species belonging to major trophic guilds (granivores and insectivores) were reclassified into seven new groups defined by diet and foraging behaviour. (A) Proportion of species per guild, per land use. Proportions in each bar represent the number of species of a given guild in relation to the total number of species in that land-use type. (B) Proportional abundance per group per land use. Proportions in each bar represent the number of individuals of a given guild in relation to total abundance in that land-use type. Different colours represent different guilds: FI: foliage insectivores; BI: bark insectivores; SFI: short-flight insectivores; LFI: long-flight insectivores; TI: terrestrial insectivores; AG: arboreal granivores; TG: terrestrial granivores. A: agriculture; AFS, agriculture with forest strip; S, silvopasture; FS, forest strip; F, forest; FNP, forest inside National Park.

Figure 2.1.

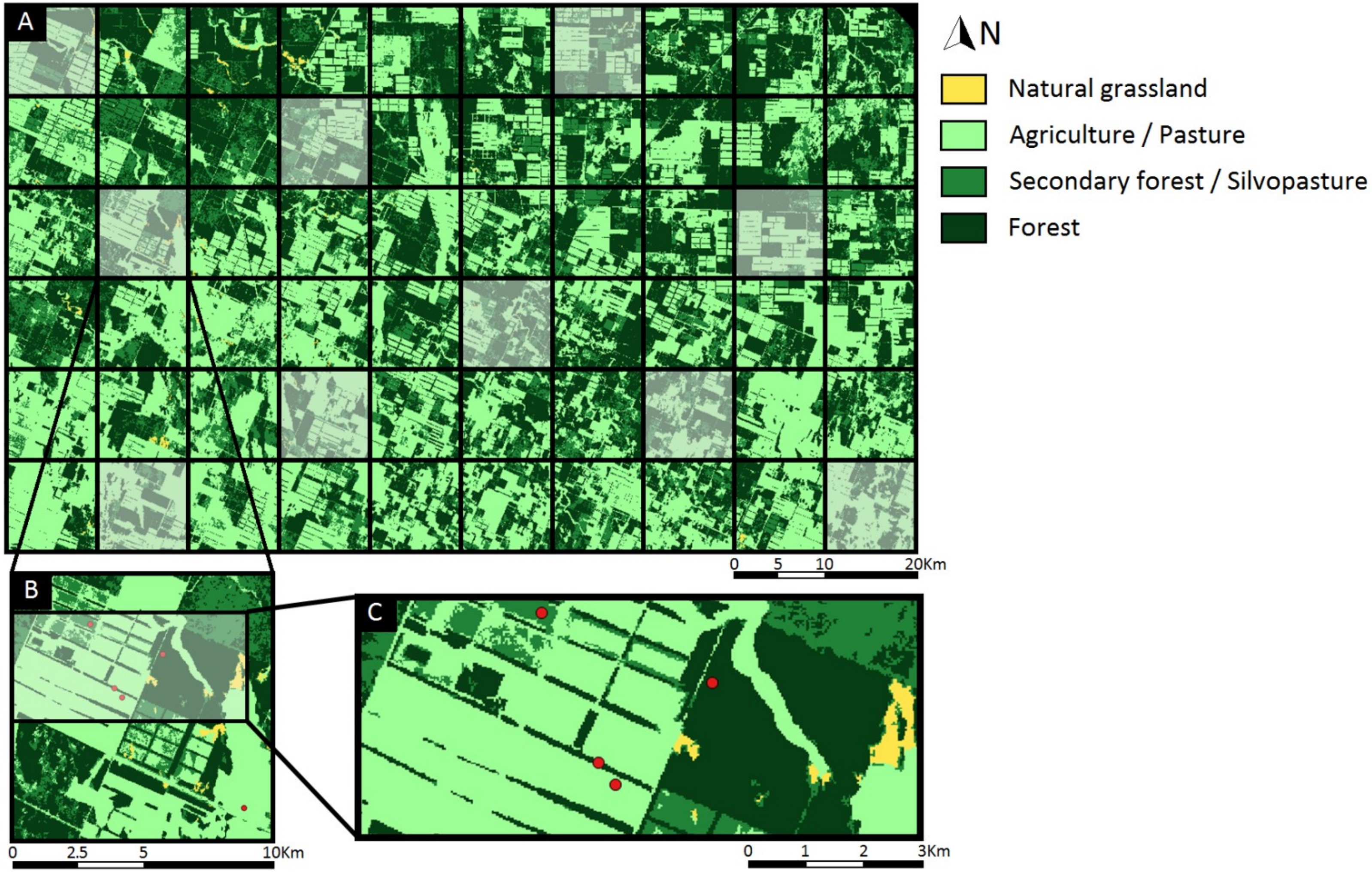

A
N
Natural grassland
Agriculture / Pasture
Secondary forest / Silvopasture
Forest
0 5 10 20Km
B
0 2.5 5 10Km
C
0 1 2 3Km

Figure 2.2.

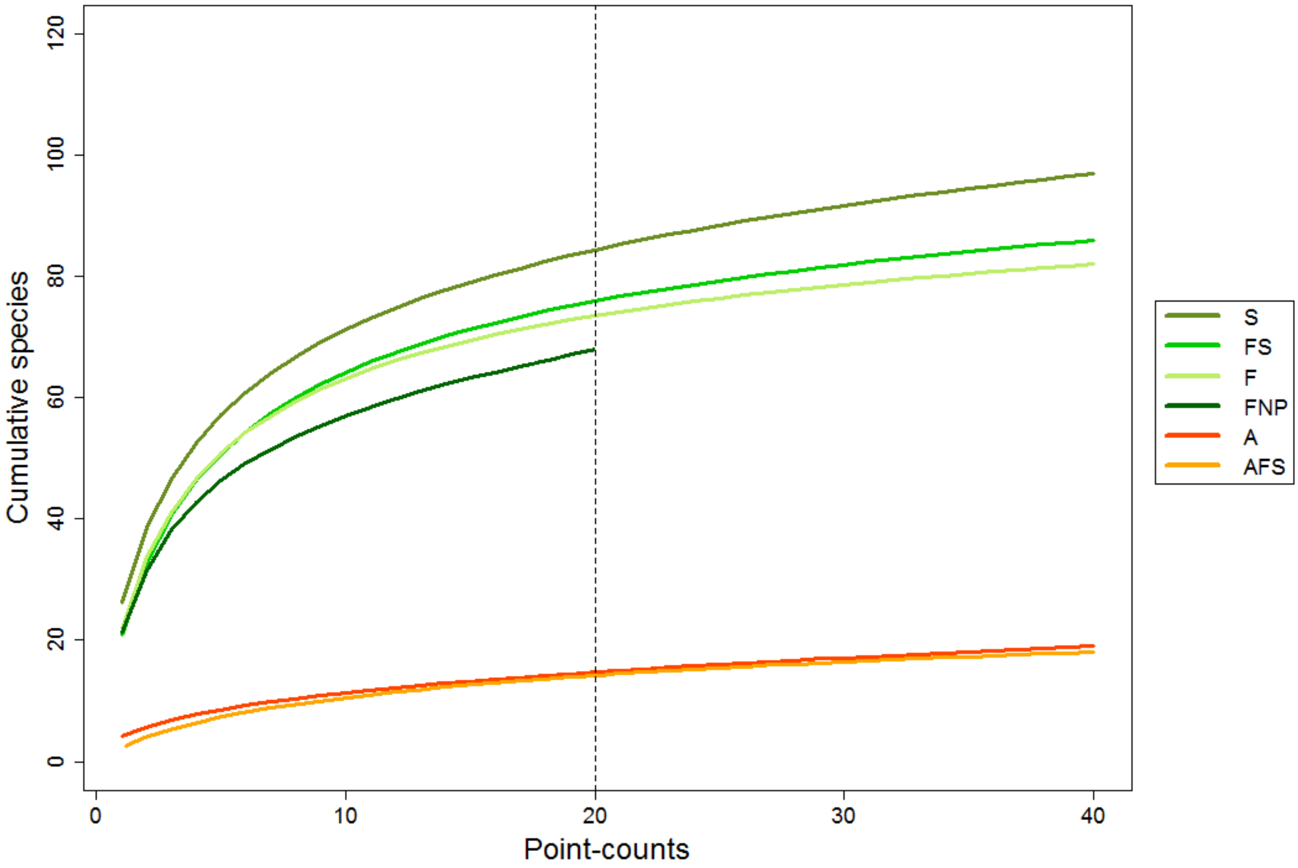

Cumulative species
0
20
40
60
80
100
120
0
10
20
30
40
Point-counts
S
FS
F
FNP
A
AFS

Figure 2.3.

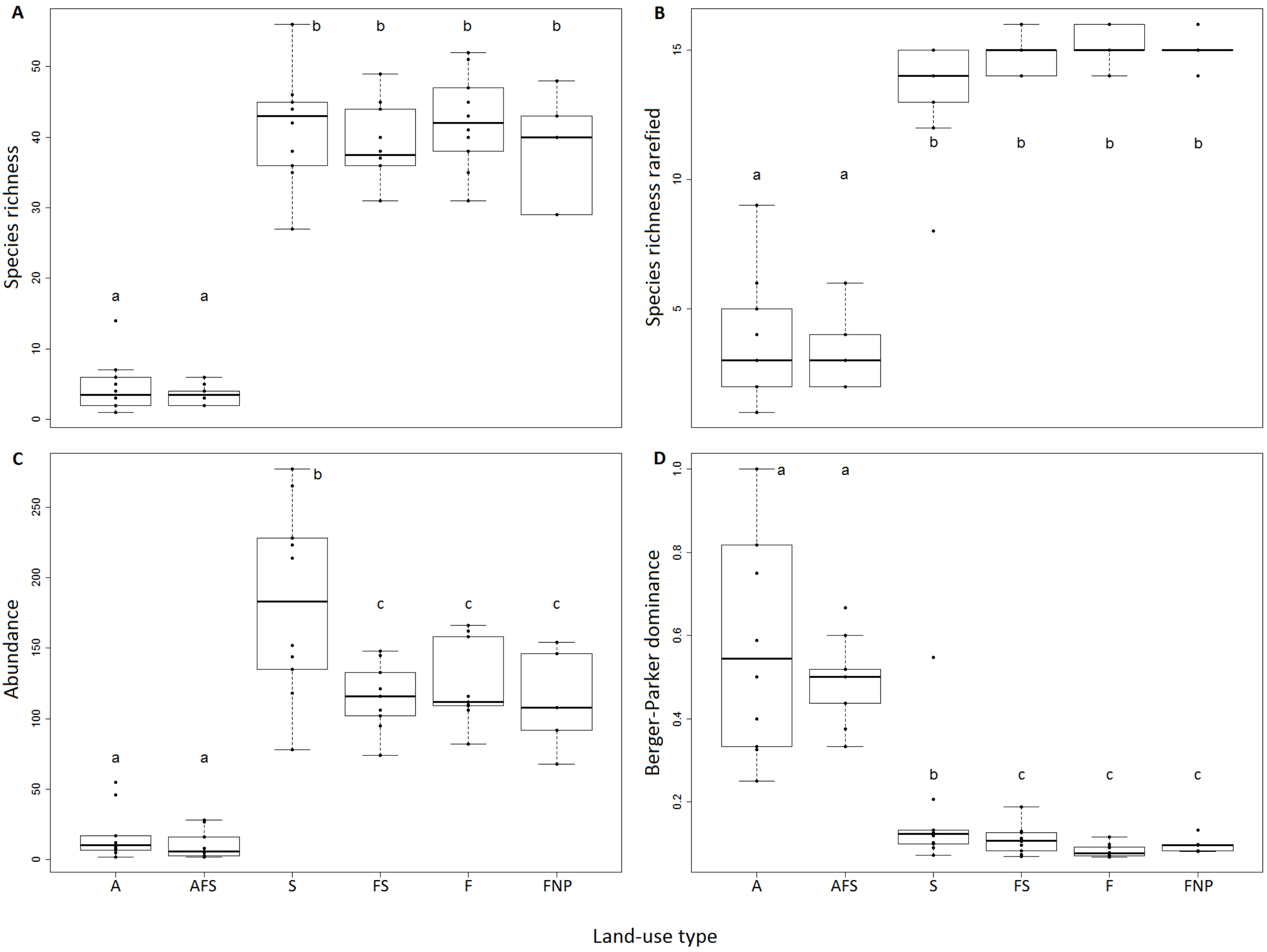

A
Species richness
0
10
20
30
40
50
a
a
b
b
b
b
B
Species richness rarefied
5
10
15
a
a
b
b
b
b
C
Abundance
0
50
100
150
200
250
a
a
b
c
c
c
D
Berger-Parker dominance
0.2
0.4
0.6
0.8
1.0
a
a
b
c
c
c
A
AFS
S
FS
F
FNP
A
AFS
S
FS
F
FNP
Land-use type

Figure 2.4.

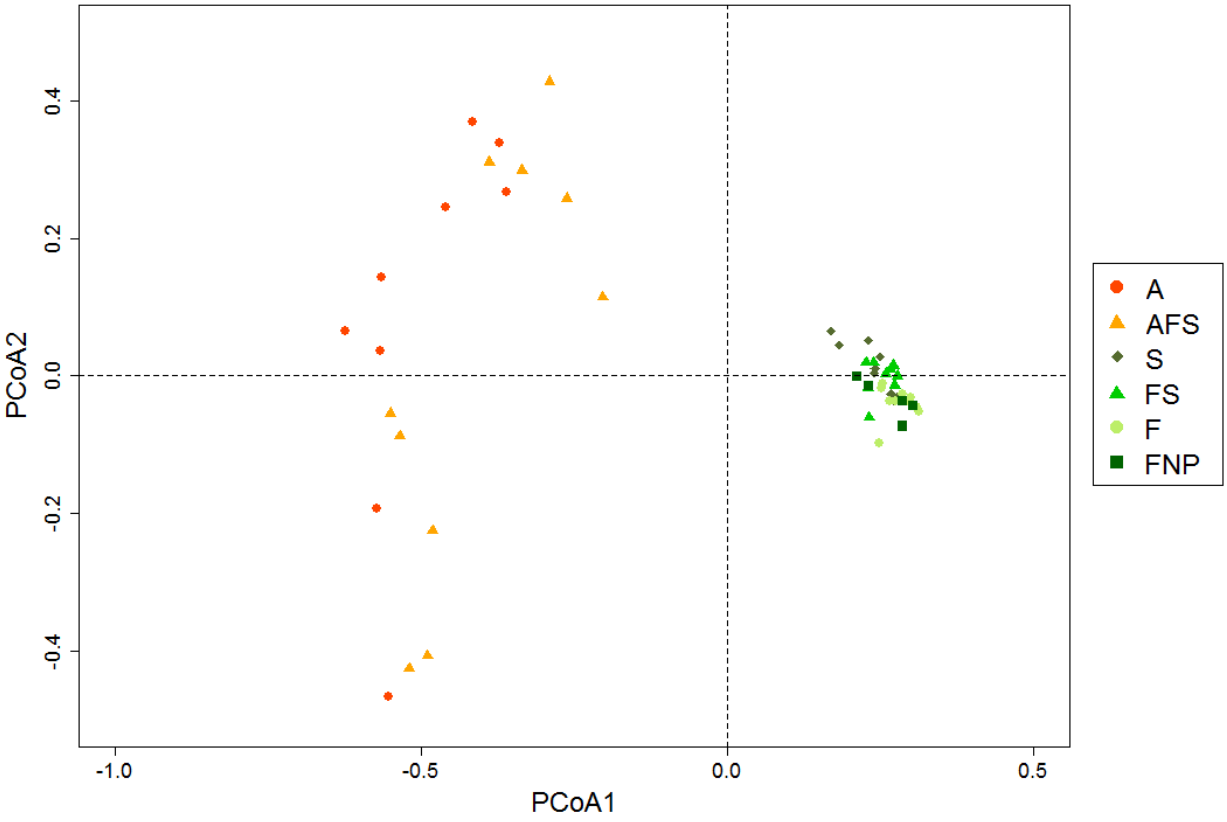


Figure 2.5.

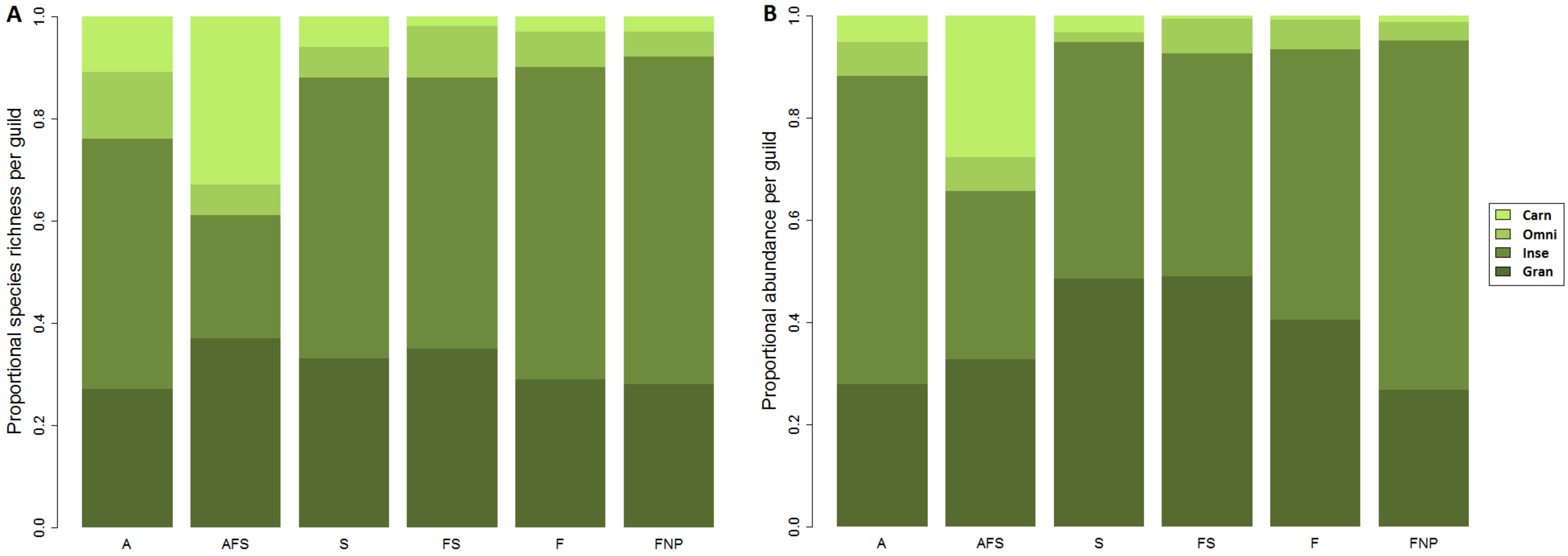
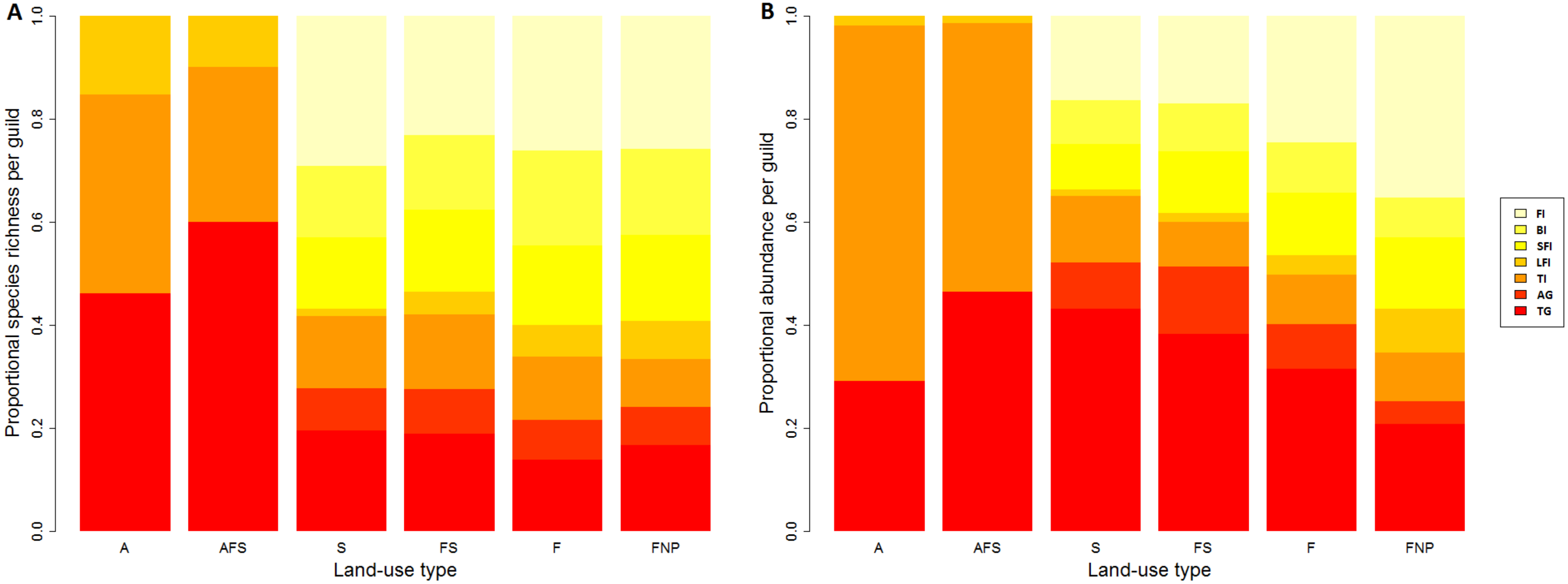

A
Proportional species richness per guild
0.0
0.2
0.4
0.6
0.8
1.0
A
AFS
S
FS
F
FNP
B
Proportional abundance per guild
0.0
0.2
0.4
0.6
0.8
1.0
A
AFS
S
FS
F
FNP
Carn
Omni
Inse
Gran

Figure 2.6.


A
B
Proportional species richness per guild
Proportional abundance per guild
0.0
0.2
0.4
0.6
0.8
1.0
A
AFS
S
FS
F
FNP
Land-use type
FI
BI
SFI
LFI
TI
AG
TG

2.5. Supplementary information

Table 2.S1. Bird species observed during the whole fieldwork period 2011 and 2012 inside the study area in the semiarid Chaco Region. Families are listed in alphabetical order. Species are listed by their scientific and English name. Trophic guild shows the original classification in seven guilds. However, analysis were done by grouping frugivores with granivores; nectarivores with omnivores, and scavengers with carnivores. Category specifies the conservation status under the criteria of IUCN (IUCN 2014). The first 126 species listed were registered during the point-count sampling period; species registered outside the sampling period were not classified by trophic guild, and are listed for the record.

	Family	**Species**	**English Name**	**Trophic guild**	**Category**
1	Accipitridae	*Buteogallus meridionalis*	Savanna Hawk	Carnivore	LC
2	Accipitridae	*Buteogallus urubitinga*	Great Black Hawk	Carnivore	LC
3	Accipitridae	*Elanus leucurus*	White-tailed Kite	Carnivore	LC
4	Accipitridae	*Parabuteo unicinctus*	Harris's Hawk	Carnivore	LC
5	Accipitridae	*Rupornis magnirostris*	Roadside Hawk	Carnivore	LC
6	Apodidae	*Chaetura meridionalis*	Southern Swift	Insectivore	LC
7	Ardeidae	*Syrigma sibilatrix*	Whistling Heron	Carnivore	LC
8	Bucconidae	*Nystalus maculatus*	Chaco Puffbird	Insectivore	LC
9	Caprimulgidae	*Antrostomus rufus*	Rufous Nightjar	Insectivore	LC
10	Caprimulgidae	*Setopagis parvula*	Little Nightjar	Insectivore	LC
11	Cardinalidae	*Cyanocompsa brissoni*	Ultramarine Grosbeak	Granivore	LC
12	Cardinalidae	*Piranga flava*	Hepatic Tanager	Insectivore	LC
13	Cardinalidae	*Saltator coerulescens*	Greyish Saltator	Granivore	LC
14	Cariamidae	*Chunga burmeisteri*	Black-legged Seriema	Omnivore	LC
15	Cathartidae	*Cathartes aura*	Turkey Vulture	Scavenger	LC
16	Cathartidae	*Coragyps atratus*	Black Vulture	Scavenger	LC
17	Cathartidae	*Sarcoramphus papa*	King Vulture	Scavenger	LC

18	Charadriidae	*Vanellus chilensis*	Southern Lapwing	Insectivore	LC
19	Columbidae	*Columbina picui*	Picui Ground-Dove	Granivore	LC
20	Columbidae	*Leptotila verreauxi*	White-tipped Dove	Granivore	LC
21	Columbidae	*Patagioenas maculosa*	Spot-winged Pigeon	Granivore	LC
22	Columbidae	*Patagioenas picazuro*	Picazuro Pigeon	Granivore	LC
23	Columbidae	*Zenaida auriculata*	Eared Dove	Granivore	LC
24	Corvidae	*Cyanocorax chrysops*	Plush-crested Jay	Omnivore	LC
25	Cotingidae	*Pachyramphus viridis*	Green-backed Becard	Insectivore	LC
26	Cracidae	*Ortalis canicollis*	Chaco Chachalaca	Frugivore	LC
27	Cuculidae	*Guira guira*	Guira Cuckoo	Omnivore	LC
28	Emberizidae	*Ammodramus humeralis*	Grassland Sparrow	Granivore	LC
29	Emberizidae	*Arremon flavirostris*	Saffron-billed Sparrow	Insectivore	LC
30	Emberizidae	*Embernagra platensis*	Great Pampa-Finch	Insectivore	LC
31	Emberizidae	*Rhynchospiza strigiceps*	Stripe-capped Sparrow	Granivore	LC
32	Emberizidae	*Zonotrichia capensis*	Rufous-collared Sparrow	Granivore	LC
33	Falconidae	*Caracara plancus*	Southern Crested-Caracara	Carnivore	LC
34	Falconidae	*Falco sparverius*	American Kestrel	Carnivore	LC
35	Falconidae	*Milvago chimachima*	Yelow-headed Caracara	Carnivore	LC
36	Falconidae	*Milvago chimango*	Chimango Caracara	Carnivore	LC
37	Fringillidae	*Euphonia chlorotica*	Purple-throated Euphonia	Frugivore	LC
38	Fringillidae	*Sporagra magellanica*	Hooded Siskin	Granivore	LC
39	Furnariidae	*Asthenes baeri*	Short-billed Canastero	Insectivore	LC
40	Furnariidae	*Campylorhamphus trochilirostris*	Red-billed Scythebill	Insectivore	LC
41	Furnariidae	*Coryphistera alaudina*	Lark-like Brushrunner	Insectivore	LC
42	Furnariidae	*Cranioleuca pyrrhophia*	Stripe-crowned Spintail	Insectivore	LC
43	Furnariidae	*Drymornis bridgesii*	Scimitar-billed Woodcreeper	Insectivore	LC
44	Furnariidae	*Furnarius cristatus*	Crested Hornero	Insectivore	LC
45	Furnariidae	*Furnarius rufus*	Rufous Hornero	Insectivore	LC
46	Furnariidae	*Lepidocolaptes angustirostris*	Narrow-billed Woodcreeper	Insectivore	LC

47	Furnariidae	*Leptasthenura platensis*	Tufted Tit-Spintail	Insectivore	LC
48	Furnariidae	*Phacellodomus ruber*	Greater Thornbird	Insectivore	LC
49	Furnariidae	*Phacellodomus sibilatrix*	Little Thornbird	Insectivore	LC
50	Furnariidae	*Phacellodomus striaticollis*	Freckle-breasted Thornbird	Insectivore	LC
51	Furnariidae	*Pseudoseisura lophotes*	Brown Cacholote	Insectivore	LC
52	Furnariidae	*Schoeniophylax phryganophila*	Chotoy Spintail	Insectivore	LC
53	Furnariidae	*Sittasomus griseicapillus*	Olivaceous Woodcreeper	Insectivore	LC
54	Furnariidae	*Synallaxis albescens*	Pale-breasted Spintail	Insectivore	LC
55	Furnariidae	*Synallaxis frontalis*	Sooty-fronted Spintail	Insectivore	LC
56	Furnariidae	*Tarphonomus certhioides*	Chaco Earthcreeper	Insectivore	LC
57	Furnariidae	*Xiphocolaptes major*	Great Rufous Woodcreeper	Insectivore	LC
58	Hirundinidae	*Progne tapera*	Brown-chested Martin	Insectivore	LC
59	Icteridae	*Agelaioides badius*	Bay-winged Cowbird	Insectivore	LC
60	Icteridae	*Cacicus chrysopterus*	Golden-winged Cacique	Frugivore	LC
61	Icteridae	*Cacicus solitarius*	Solitary Cacique	Frugivore	LC
62	Icteridae	*Icterus cayanensis*	Epaulet Oriole	Insectivore	LC
63	Icteridae	*Molothrus bonariensis*	Shiny Cowbird	Insectivore	LC
64	Icteridae	*Molothrus rufoaxillaris*	Screaming Cowbird	Insectivore	LC
65	Icteridae	*Sturnella supercilliaris*	White-browed Blackbird	Insectivore	LC
66	Incertae sedis	*Saltator aurantiirostris*	Golden-billed Saltator	Granivore	LC
67	Incertae sedis	*Saltatricula multicolor*	Many-coloured Chaco-Finch	Granivore	LC
68	Melanopareiidae	*Melanopareia maximiliani*	Olive-crowned Crescentchest	Insectivore	LC
69	Mimidae	*Mimus triurus*	White-banded Mockingbird	Insectivore	LC
70	Motacillidae	*Anthus chacoencis*	Pampas Pipit	Insectivore	LC
71	Motacillidae	*Anthus lutescens*	Yellowish Pipit	Insectivore	LC
72	Parulidae	*Setophaga pitiayumi*	Tropical Parula	Insectivore	LC
73	Picidae	*Campephilus leucopogon*	Cream-backed Woodpecker	Insectivore	LC
74	Picidae	*Colaptes campestris*	Field Flicker	Insectivore	LC
75	Picidae	*Colaptes melanochloros*	Green-barred Woodpecker	Insectivore	LC

76	Picidae	*Dryocopus schulzi*	Black-bodied Woodpecker	Insectivore	**NT**
77	Picidae	*Melanerpes cactorum*	White-fronted Woodpecker	Insectivore	LC
78	Picidae	*Melanerpes candidus*	White Woodpecker	Frugivore	LC
79	Picidae	*Picumnus cirratus*	White-barred Piculet	Insectivore	LC
80	Picidae	*Verniliornis mixtus*	Checkered Woodpecker	Insectivore	LC
81	Polioptilidae	*Polioptila dumicola*	Masked Gnatcatcher	Insectivore	LC
82	Psittacidae	*Amazona aestiva*	Turquoise-fronted Amazon	Granivore	LC
83	Psittacidae	*Myiopsitta monachus*	Monk Parakeet	Granivore	LC
84	Psittacidae	*Pionus maximiliani*	Scaly-headed Parrot	Granivore	LC
85	Psittacidae	*Thectocercus acuticaudatus*	Blue-Crowned Parakeet	Granivore	LC
86	Rhinocryptidae	*Rhinocrypta lanceolata*	Crested Gallito	Insectivore	LC
87	Strigidae	*Athene cunicularia*	Burrowing Owl	Carnivore	LC
88	Strigidae	*Glaucidium brasilianum*	Ferruginous Pygmy-Owl	Carnivore	LC
89	Strigidae	*Pseudoscops clamator*	Striped Owl	Carnivore	LC
90	Thamnophilidae	*Myrmorchilus strigilatus*	Stripe-backed Antbird	Insectivore	LC
91	Thamnophilidae	*Taraba major*	Great Antshrike	Insectivore	LC
92	Thamnophilidae	*Thamnophilus caerulescens*	Variable Antshrike	Insectivore	LC
93	Thraupidae	*Coryphospingus cucullatus*	Red Pileated-Finch	Granivore	LC
94	Thraupidae	*Paroaria coronata*	Red-crested Cardinal	Granivore	LC
95	Thraupidae	*Poospiza melanoleuca*	Black-capped Warbling-Finch	Granivore	LC
96	Thraupidae	*Poospiza torquata*	Ringed Warbling-Finch	Granivore	LC
97	Thraupidae	*Sicalis flaveola*	Saffron Yellow-Finch	Granivore	LC
98	Thraupidae	*Sicalis luteola*	Grassland Yellow-Finch	Granivore	LC
99	Tinamidae	*Crypturellus tataupa*	Tataupa Tinamou	Omnivore	LC
100	Tinamidae	*Nothoprocta cinerascens*	Brushland Tinamou	Omnivore	LC
101	Tinamidae	*Nothura maculosa*	Spotted Nothura	Omnivore	LC
102	Trochilidae	*Chlorostilbon lucidus*	Glittering-billied Emerald	Nectarivore	LC
103	Trochilidae	*Heliomaster furcifer*	Blue-tufted Starthroat	Nectarivore	LC
104	Trochilidae	*Hylocharis chrysura*	Gilded Sapphire	Nectarivore	LC

105	Troglodytidae	*Troglodytes aedon*	House Wren	Insectivore	LC
106	Turdidae	*Turdus amaurochalinus*	Creamy-bellied Thrush	Frugivore	LC
107	Tyrannidae	*Camptostoma obsoletum*	Southern Beardless-Tyrannulet	Insectivore	LC
108	Tyrannidae	*Casiornis rufus*	Rufous Casiornis	Insectivore	LC
109	Tyrannidae	*Elaenia parvirostris*	Small-billed Elaenia	Frugivore	LC
110	Tyrannidae	*Empidonomus aurantioatrocristatus*	Crowned Slaty Flycatcher	Insectivore	LC
111	Tyrannidae	*Euscarthmus meloryphus*	Tawny-crowned Pygmy-Tyrant	Insectivore	LC
112	Tyrannidae	*Hemitriccus margaritaceiventer*	Pearly-vented Tody-Tyrant	Insectivore	LC
113	Tyrannidae	*Inezia inornata*	Plain Tirannulet	Insectivore	LC
114	Tyrannidae	*Knipolegus striaticeps*	Cinereous Tyrant	Insectivore	LC
115	Tyrannidae	*Machetornis rixosus*	Cattle Tyrant	Insectivore	LC
116	Tyrannidae	*Myiarchus tyrannulus*	Short-crested Flycatcher	Insectivore	LC
117	Tyrannidae	*Myophobus fasciatus*	Bran-coloured Flycatcher	Insectivore	LC
118	Tyrannidae	*Pitangus sulphuratus*	Great Kiskadee	Insectivore	LC
119	Tyrannidae	*Pyrocephalus rubinus*	Vermilion Flycatcher	Insectivore	LC
120	Tyrannidae	*Serpophaga griseiceps*	Grey-crowned Tyrannulet	Insectivore	LC
121	Tyrannidae	*Serpophaga subcristata*	White-crested Tyrannulet	Insectivore	LC
122	Tyrannidae	*Stigmatura budytoides*	Greater Wagtail-Tyrant	Insectivore	LC
123	Tyrannidae	*Sublegatus modestus*	Southern Scrub-Flycatcher	Insectivore	LC
124	Tyrannidae	*Suirirí suirirí*	Suiriri Flycatcher	Insectivore	LC
125	Tyrannidae	*Tyrannus savana*	Fork-tailed Flycatcher	Insectivore	LC
126	Vireonidae	*Cyclarhis gujanensis*	Rufous-browed Peppershrike	Insectivore	LC
127	Accipitridae	*Accipiter bicolor*	Bicolored Hawk	*	LC
128	Accipitridae	*Accipiter striatus*	Sharp-shinned Hawk	*	LC
129	Accipitridae	*Buteo brachyurus*	Short-tailed Hawk	*	LC
130	Accipitridae	*Chondrohierax uncinatus*	Hook-billed Kite	*	LC
131	Anatidae	*Sarkidiornis melanotos*	African Comb Duck	*	LC
132	Caprimulgidae	*Hydropsalis torquata*	Scissor-tailed Nightjar	*	LC
133	Cariamidae	*Cariama cristata*	Red-legged Seriema	*	LC

134	Columbidae	*Columba livia*	Rock Dove	*	LC
135	Cuculidae	*Coccyzus melacoryphus*	Dark-billed Cuckoo	*	LC
136	Cuculidae	*Crotophaga ani*	Smooth-billed Ani	*	LC
137	Falconidae	*Falco femoralis*	Aplomado Falcon	*	LC
138	Furnariidae	*Anumbius annumbi*	Firewood-gatherer	*	LC
139	Parulidae	*Geothlypis aequinoctialis*	Masked Yellowthroat	*	LC
140	Passeridae	*Passer domesticus*	House Sparrow	*	LC
141	Picidae	*Celeus lugubris*	Pale-crested Woodpecker	*	LC
142	Picidae	*Piculus chrysochloros*	Golden-green Woodpecker	*	LC
143	Psittacidae	*Pyrrhura frontalis*	Reddish-billed Parakeet	*	LC
144	Recurvirostridae	*Himantopus mexicanus*	Black-necked Stilt	*	LC
145	Rheidae	*Rhea americana*	Greater Rhea	*	**NT**
146	Strigidae	*Asio flammeus*	Short-eared Owl	*	LC
147	Strigidae	*Megascops choliba*	Tropical Screech-owl	*	LC
148	Thraupidae	*Pipraeidea bonariensis*	Blue-and-yellow Tanager	*	LC
149	Thraupidae	*Thraupis sayaca*	Sayaca Tanager	*	LC
150	Tinamidae	*Eudromia elegans*	Elegant Crested Tinamou	*	LC
151	Turdidae	*Turdus rufiventris*	Rufous-bellied Thrush	*	LC
152	Tyrannidae	*Lathrotriccus euleri*	Euler's Flycatcher	*	LC
153	Tyrannidae	*Xolmis cinereus*	Grey Monjita	*	LC
154	Tyrannidae	*Xolmis irupero*	White Monjita	*	LC

Abbreviations: LC, least concern; NT, near threatened

**, species observed in the study area outside the sampling period, not considered for the analysis.*

Table 2.S2. Distribution of species and individuals per feeding group in each land use. Species richness represents the total number of species, and abundance represents the total number of individuals registered for each trophic guild in each land-use type.

Land-use type	**Total species richness**				**Total abundance**			
	Gran	**Inse**	**Omni**	**Carn**	**Gran**	**Inse**	**Omni**	**Carn**
Agriculture	6	7	3	3	44	107	15	7
Agriculture with forest strips	6	4	3	5	32	37	17	17
Silvopasture	25	52	7	13	919	822	35	58
Forest strip	24	50	8	4	573	499	76	8
Forest	20	51	6	5	492	654	77	10
Forest inside National Park	17	41	5	3	151	388	23	6

Abbreviations: Gran: granivores; Inse: insectivores; Omni: omnivores; Carn: carnivores.

Table 2.S3. Distribution of species and individuals per guild in each land use. Species richness represents the total number of species, and abundance represents the total number of individuals registered for each trophic guild in each land-use type.

Land-use type	**Total species richness**							**Total abundance**						
	TG	**AG**	**TI**	**LFI**	**SFI**	**BI**	**FI**	**TG**	**AG**	**TI**	**LFI**	**SFI**	**BI**	**FI**
Agriculture	6	0	5	2	0	0	0	44	0	104	3	0	0	0
Agriculture with forest strips	6	0	3	1	0	0	0	32	0	36	1	0	0	0
Silvopasture	14	6	10	1	10	10	21	740	154	220	23	152	145	282
Forest strip	13	6	10	3	11	10	16	391	134	89	17	123	95	175
Forest	9	5	8	4	10	12	17	344	95	105	41	133	106	269
Forest inside National Park	9	4	5	4	9	9	14	108	23	49	44	72	40	183

Abbreviations: TG: terrestrial granivores; AG: arboreal granivores; TI: terrestrial insectivores; LFI: long-flight insectivores;SFI: short-flight insectivores; BI: bark insectivores; FI: foliage insectivores.

Mammal species captured on camera-traps[4]

3 MAMMAL COMMUNITY RESPONSE TO A GRADIENT OF LAND USE INTENSIFICATION

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[4] Some mammal species captured in the study area. Pictures belong to INTA. From left to right: *Myrmecophaga tridactyla; Eira barbara; Catagonus wagneri; Leopardus geoffroyi; Mazama gouazoubira.*

Summary

The semiarid Chaco landscapes have undergone severe modifications for pastoral and agricultural development through intensification and enlargement of farmed areas. More than 150 mammal species have been recorded for the Chaco Region. However, several studies suggest that distinctive species like the jaguar (*Panthera onca*), the giant armadillo (*Priodontes maximus*) and the endemic Chacoan peccary (*Catagonus wagneri*), have suffered major population declines. A good knowledge of the presence and distribution of species is crucial for planning and developing conservation strategies. Our main objective was to assess the effects of land use on mammal community structure. For that purpose, we associated these effects with the main habitat types and with landscape composition in the area surrounding the sampling sites. We deployed camera trap stations inside seven different land-use types (forest inside National Park; grassland inside National Park; forest; silvopasture; forest strip and two types of agricultural plots) during winter and spring season in 2012 and 2013. A total of 4217 camera trap nights captured 26 different species (approximately 78 % of the mammals reported for the region). Mammal distributions were most strongly correlated with local land-use characteristics. Species richness and relative abundance were highest in habitats with dense forest vegetation. Whereas land uses with moderate (silvopasture) to high human intervention (agriculture) showed a significant drop in number of species and capture frequency (an indicator of relative abundance). The National Park accounted for the highest mean species richness and capture frequency. Arable fields (agriculture with and without forest strips) were similar in their low number of species and capture frequency. Intermediate intensification land uses (i.e. silvopasture) maintained similar species composition to forested habitats, including those in the National Park, demonstrating that this type of agroforestry represent a good option to combine production with high levels of mammal diversity. We hope to use this information to promote land-use practices that will allow mammal species to persist within heavily managed areas in this region.

3.1. Introduction

Landscape transformation is the main factor contributing to biodiversity decline (Fahrig 2003; Tscharntke et al. 2005), acting through the quality reduction of habitats and habitat loss, together with the increasing homogeneity of the farmed landscape and more intensive field management (Andrén 1994; Fahrig 2003). The effects of these changes on the abundance and quality of food resources, shelter, and breeding habitat are likely mechanisms underlying species distribution. Their responses to habitat conditions and human pressures result from complex interactions and can be manifested in different ways and at different spatial scales (Andrén 1994; Woodroffe 2000; Gehring & Swihart 2003; Fracassi 2009). Several studies have demonstrated strong relationships between land cover and the presence of mammal species. A large scale study across Central and North America (Flynn et al. 2009) concluded that both species richness and functional diversity of mammals declined significantly with land use intensification; emphasizing that changes from natural to agricultural production systems can reduce the functional diversity of animal communities beyond mere changes in species richness, potentially affecting the provision of ecosystem services. Coincidentally, mammal assemblages in Mexico have shown a high degree of correlation with specific land-cover types, making their long-term persistence in the region critically dependent to modifications on land use trends (Cuaron 2000). In savannahs of Tanzania (Kiffner et al. 2014) and Australia (Kutt & Gordon 2012; Woinarski & Ash 2002), similar results suggest that native mammal communities are negatively affected by anthropogenic ground cover changes, where the highest species richness and abundance of species were found inside protected areas, whereas settlement and farmed areas had the lowest diversity.

Percentage and conservation status of the forest cover (Pardini et al. 2009; Wearn et al. 2012; R. Cassano et al. 2014), the degree of connectivity between habitats (Gehring & Swihart 2003; Barlow et al. 2010; Minor & Lookingbill 2010), and the level of human pressure (Woodroffe 2000; Altrichter & Boaglio 2004; Altrichter 2005; Paviolo et al. 2009) are among the most important drivers of mammal species persistence.

In South America, dry forest and savannah biomes have experienced extensive deforestation during the last decades (Aide et al. 2013). Most of the loss in woody vegetation cover was concentrated in Bolivia, Paraguay, and northern Argentina where several studies have linked changes in landscape with deforestation for agribusiness (Boletta et al. 2006; Gasparri & Grau 2009). In the semiarid Chaco Region of Argentina, changes in climate conditions, grain prices and technology applied to production favour agribusiness, leading to a rapid conversion from natural ecosystems (grasslands and native forest) to planting areas in one of the most important temperate dry forests in the continent.

Mammalian community in the semiarid Chaco

The impact of agricultural intensification on wildlife in the Chaco Region has been the subject of increasing concern, particularly over the last decade (Zak et al. 2004; Gasparri & Grau 2006; Adamoli 2006; Codesido et al. 2009; Mastrangelo & Gavin 2012; Macchi & Grau 2012; Macchi et al. 2013; Torres et al. 2014). This mosaic of agricultural and natural land provides habitat for at least 30 medium-sized and large mammalian species, represented by 13 families (Myrmecophagidae, Dasypodidae, Canidae, Mustelidae, Mephitidae, Felidae, Procyonidae, Didelphidae, Tapiridae, Cervidae, Tayassuidae, Chinchillidae, and Leporidae).

There are many emblematic species in the region with unique characteristics and requirements. A number of these species are listed on the IUCN Red List of Threatened Species (IUCN 2014) as well as on the Red List of Endangered Mammals of Argentina (Ojeda et al. 2012). For example, all three species of peccaries are present in the Chaco Region (collared peccary, *Tayassu tajacu*; white-lipped peccary, *Tayassu pecari*; and Chacoan peccary, *Catagonus wagneri*) with the latter being the rarest and most vulnerable, categorized as Endangered (Ojeda et al. 2012; Altrichter et al. 2014; IUCN 2014). These species play an important role as prey of top predators and, as ecosystems engineers, disperse the seeds of several fruiting trees and shrubs (Altrichter & Boaglio 2004; Tobler et al. 2009; Altrichter et al. 2014). Armadillos are the most diverse family with 8 species; one globally Vulnerable and regionally Endangered (giant armadillo, *Priodontes maximus*) and two Near Threatened (Chacoan naked-tailed armadillo, *Cabassous chacoensis;* and southern three-banded armadillo, *Tolypeutes matacus*) (Ojeda et al. 2012; Noss et al. 2014). These species feed almost exclusively on ants and termites and are mainly found in undisturbed environments (Wetzel 1985; Bolkovic et al. 1995; Soibelzon et al. 2007; da Silveira Anacleto 2007; Abba & Superina 2010; Abba et al. 2012; Trujillo & Superina 2014). On the other hand, the most common armadillo species (*Dasypus novemcinctus*, *Chaetophractus vellerosus*, *Chaetophractus villosus*, and *Euphractus sexcinctus*.) are opportunistic insectivores, feeding occasionally on other items (i.e. other invertebrates such as worms and larvae, and also carcasses) (da Silveira Anacleto 2007; Soibelzon et al. 2007; Abba & Superina 2010; Abba et al. 2012; Trujillo & Superina 2014). Also from the order of Xenarthrans and the insectivores guild, two species of anteaters inhabit the semiarid Chaco: the giant anteater, currently assessed as Vulnerable (*Myrmecophaga tridactyla,* IUCN 2014), and the collared anteater (*Tamandua tetradactyla*). These charismatic species require large areas for their survival, given their dietary specificity.

Top predators in this region are represented by two species of felids; the jaguar (*Panthera onca*) and the puma (*Puma concolor*) (Taber et al. 1997; Maffei et al. 2004; Romero-Muñoz et al. 2010). The former is present in northern Argentina at its southern limit of distribution, although in extremely low densities (Altrichter et al. 2006; Quiroga et al. 2013; Quiroga 2013), it has been categorized as Critically Endangered at regional scale (Ojeda et al. 2012). Another eight species of mesopredators can be found, three canids (crab-eating fox, *Cerdocyon Thous*; Pampas fox, *Lycalopex gymnocercus*; and the Near Threatened maned wolf, *Chrysocyon brachyurus*) (Rodden et al. 2008), two mustelids (the tayra *Eira barbara*; and the lesser grison, *Galictis cuja*), and three cats (Geoffroy's cat, *Leopardus geoffroyi*; jaguarundi, *Puma jagouaroundi*; and the ocelot, *Leopardus pardalis*). In addition to those mentioned earlier, a handful of other species play the role of prey (e.g. grey brocket deer, *Mazama gouazoubira*; white-eared opossum, *Didelphis albiventris*; forest rabbit, *Sylvilagus brasiliensis*, hog-nosed skunk, *Conepatus chinga*) (Parera 2002; Canevari & Vaccaro 2007; Barquez et al. 2007).

Most of these medium- and large-sized mammals are species with large area requirements, and this determines that a mosaic landscape is generally inhabited by this taxa. Given their high mobility and their extensive home ranges, many mammalian species may be particularly sensitive to land-use changes. Some others might be more resistant to human pressures and habitat modification as a result of a broader trophic niche, or a higher intrinsic population growth rate, which might represent an advantage in human-altered landscapes (Gehring & Swihart 2003). However, the progressive destruction of habitat for agriculture and cattle ranching, as well as timber extraction, and the high hunting pressure upon several of these species are among the factors repeatedly cited as the main causes of population decline (Ojeda et al. 2012; IUCN 2014). A considerable problem confronting the mammal community conservation in this environment is the lack of information. Very few studies exist on mammal communities inhabiting human-modified habitats in the semiarid Chaco. Apart from a small number of targeted studies focused on particular species (Altrichter & Boaglio 2004; Altrichter et al. 2006; Chillo et al. 2010; Torres & Jayat 2010; Serbent et al. 2011), or big predators and their prey in protected areas (Quiroga et al. 2013) or species outside Argentina (Stallings 1984; Taber et al. 1997; Maffei et al. 2004; Maffei et al. 2007; Dillon & Kelly 2008; Kelly et al. 2008; Silveira et al. 2009; Romero-Muñoz et al. 2010).

The aim of this chapter is to understand how mammalian communities change in response to anthropogenic management, and to further investigate the influence of the surrounding landscape. This represents one of the first studies to explore the influence of land use intensification on mammal distributions using camera traps. We assessed the effect of three different types of agricultural management on the components of mammals' diversity, and compared them with non-production ecosystems. Only by examining such relationships and patterns on a local scale we can start to comprehend the effects of land use change on these communities. Nonetheless, species responses to habitat alterations and human pressures result from complex interactions and can be affected by different factors acting at different spatial scales (Gehring & Swihart 2003; Boscolo & Metzger 2009, R. Cassano et al. 2009). Therefore, in this study we compared mammal community structure and composition using variables from local and landscape scales. Given that the physical and spatial characteristics of the sites sampled were strongly related with land-use type, we employed two continuous variables to test for a potential stronger effect or a better correlation with the mammal community metrics than land-use type itself. These two local scale measures were: area of the patch and distance to the nearest edge. Similarly, the importance of variables at landscape scale was evaluated by including percentage of forest cover and habitat diversity into the model selection procedure.

We expect that intensified land uses, surrounded by highly altered environments would support poor communities with reduced species diversity, as fewer food and shelter resources would be available. We also predict that land uses with intermediate level of modification (i.e. silvopasture) would present average values for the community metrics as a result of a higher offer of different types of vegetation cover. Whereas a species-rich and well-structured mammal community would be present in low- and non-productive environments (i.e. forest patches and forest within a National Park).

The mammal community under study is formed by species with a broad range of requirements, some of them with large territories (for instance the felid species) and some others with smaller territories (e.g. forest rabbit, armadillos, etc.), for this reason some of the individualistic species responses to the landscape variables might be masked when we consider the community as a whole. On the other hand, the emergent properties of community composition will be best represented in the complete assemblage; therefore we expect that the amount of forest cover surrounding the study sites will be a good predictor independently of the species included in the assemblages.

3.2. Methods

Study site

This study was carried out in the semiarid Chaco Biogeographic Province (Cabrera 1971), in Chaco and Santiago del Estero Provinces, Argentina. The region is a flatland characterized by semi deciduous xeromorphic forests, and natural grasslands running along ancient river beds. The climate is seasonal semiarid, with 400-800 mm of annual rainfall concentrated in spring and summer (October-March) and a dry season in autumn and winter (April-September). Mean annual temperature is near 22°C, with maximum temperatures over 45°C, and below zero in winter (Cabrera 1971). Sampling was partly conducted in a 6,000 km2 agricultural landscape (26° 24’ S, 61° 09’ W) in the southern portion of Almirante Brown Department, Chaco Province. This area is a mosaic of patches of forest and a matrix of productive land represented by agricultural fields and cattle ranches (silvopastures). The remaining stands of forest are intermixed with cropland and connected with each other by strips of forest surrounding agricultural plots. Forest patches have undergone varying intensity and timing of log extraction and extensive livestock management, generating a range of intermediate to old second-growth forest and different heterogeneity at habitat level (Bucher & Huszar 1999). In addition, we sampled an adjacent portion of protected forest inside Copo National Park (25° 46’ S, 61° 47’ W), Santiago del Estero Province. This control area is located 50 km away from the agricultural landscape (Figure 1.2, see Chapter 1) and constitutes a continuous and well preserved stand of protected forest with moderate to low intensity exploitation.

Mammals’ data collection

We collected mammal community data using camera-traps. This type of survey had never been done before in the area. It is a particularly efficient technique, suitable for a broad set of different studies ranging from inventories of species richness (Silveira et al. 2003; Trolle & Kéry 2003; Silver et al. 2004; Tobler et al. 2008), to studies documenting the presence of rare or presumed-extinct animals (Silveira et al. 2009; Kierulff et al. 2004); for abundance estimations (Karanth & Nichols 1998; Carbone et al. 2001; Rowcliffe et al. 2008; Pereira et al. 2011) or animal traits and ecology studies (Di Bitetti et al. 2010; Rowcliffe et al. 2014). Despite relatively high initial costs, camera trapping is preferred over other techniques like track surveys and direct counts (Silveira et al. 2003) allowing a rapid faunal assessment.

We employed 24 cameras triggered by an infrared heat-motion detector (Reconyx PC800 Hyperfire Professional IR^{TM}). Cameras were deployed at 132 sites during winter and spring season (July to December 2012 and 2013), for an average 32 (± 11) camera-trap nights (CTNs), resulting in a total effort of 4217 CTNs (Table 3.1). Typically studies focused on estimating the densities of a single species using capture-recapture analysis, (Karanth 1995; Karanth & Nichols 1998), place cameras along travel routes or trails used by the target species, in order to maximized the number of records (Maffei et al. 2002; Silveira et al. 2003; Maffei et al. 2004; Di Bitetti et al. 2008; Tobler et al. 2009). However, studies focused on measuring species diversity, ideally should avoid biasing the sampling strategy by limiting it to trails, in order to sample the diversity of habitats in the region (Rowcliffe & Carbone 2008; Wearn et al. 2013). A trail-based sampling approach may limit one’s ability to generalize the results from the study sites to the larger area. Recent studies have explored the advantages and disadvantages of a strictly-random versus an optimal deployment of camera-traps. Blake & Mosquera (2014) found no difference in the overall capture and species composition between trail and off trail cameras suggesting that species are equally likely to use trails as not in their study area; Wearn et al. (2013), however found significant differences in the relative abundances between random locations and on trail locations, with some important threatened species showing a tendency to avoid trails.

In this study, we used a random placement strategy where possible. However, almost all the potential sites inside the agricultural matrix were situated on private land, and we were not always granted the permission to work there. We therefore used the following procedure to select camera trap sites: we mapped and numbered all the potential sites inside the agricultural landscape for five different land uses (agriculture, A; agriculture with forest strips, AFS; silvopasture, S; forest strip, FS; and forest, F). We visited all of the sites to check that they had the required characteristics, and to ask for the owner's approval to conduct the study. Subsequently, 20 sites for each land use (and their correspondent spatial coordinates) were randomly selected (Figure 3.1). Additionally, we sampled two different habitats inside Copo National Park as control sites. These were forest (FNP) and natural grassland (GNP). A major issue for these control sites was the lack of internal roads and poor facility development in the park, restricting the chances of reaching totally random points. Consequently, all the potential sites in these land-use types were restricted to those that could be reached on foot, posing a trade-off between the time needed to set a minimum number of cameras, and the strict randomization of the sites. As a result, 12 out of 20 sites in protected forest were located on abandoned roads inside the park, opened more than 10 years ago for oil prospecting (presenting canopy cover, in advanced successional state, 3-4 metres width, Tálamo et al. 2012), whereas the remaining 8 were located off-road deep in the forest (Table 3.1, Figure 3.2). The park preserves some of the last stands of natural grasslands in the region. Forest vegetation is interrupted by belts (approximately 1 km wide) of natural grasslands arranged in a NW-SE direction. These grasslands are scarce inside the park, they present a well-established grass community dominated by *Elionurus spp*. (Lopez de Casenave et al. 1995) that grows in dense clumps up to 1 metre high, obstructing the deployment of the camera trap. Therefore, we tried to improve detectability by attaching the camera trap to a wooden stick at 70 cm height, tilted downwards, and by removing the vegetation in the first 3 metres right in front of the camera. We were able to access only four of these grasslands; hence, a fewer number of points was set in this land use (Table 3.1). All sites, inside and outside the park were reached on foot, by opening a small track (<1 meter wide) when needed, and using a GPS receiver (Garmin GPS Map 62s, Olathe, Kansas, USA). We deployed one camera-trap per site at an average height of 30 cm, almost always facing south (to avoid the sun reflection when the station was in an open space, such as agriculture). For sampling stations in AFS, camera-traps were deployed pointing towards the forest strip (regardless of the cardinal points). Cameras were attached to trees or wood poles, no bait was used, and vegetation was cleared in front of the camera to facilitate the recognition of species and individuals. The mean distance between nearest sites was 1.7 km (Table 3.1), to capture the range of all the species included in the mammal assemblage. Camera-traps were set to take 10 consecutive pictures at each trigger event, with no delay period between triggers, and a time lapse of 12 h (10 pictures automatically triggered at noon and midnight) to be sure that cameras were functioning even when no capture was made that day. When possible, camera stations were visited to check for any malfunction, to replace batteries or to download pictures. In the event that either the batteries or flash card memory ran out (e.g. resulting from cattle presence or vegetation in silvopasture plots which continuously triggered the camera), we excluded the gap from total camera-trapping effort.

Predictor variables: local and landscape scales

Explanatory variables were measured for each site at two different scales. Local variables included: (i) land-use type (categorical variable with 7 levels: A, AFS, S, FS, F, FNP and GNP); (ii) total area of the habitat patch (Log transformed, LogAREA); and (iii) distance to the nearest edge (Log transformed, LogEDGE). Patch area was calculated by carefully digitizing polygons of homogeneous land cover holding each of the 132 sites. Distance to the edge was calculated as the straight-line distance from the sampling point to the nearest boundary with a dissimilar habitat type. This procedure was done using the software Quantum GIS 2.0.1 (QGIS Development Team 2014), on 2013 Landsat 8 OLI/TIRS and Quickbird satellite imagery (available at GoogleEarthTM, http://earth.google.com). Landscape scale variables included: (i) proportion of forest cover (FC) and habitat diversity (H) within four circular buffers of radii 500 m, 1000 m, 1500 m, and 3000 m around the sampling point. Forest cover measures including only primary and well preserved forest areas (FC) was used as a predictor for mammal species richness, whereas forest cover including primary, secondary forest, and silvopasture areas (SFC) was used as a predictor for relative abundance. To measure these variables, we developed a land cover map for 2013 from Landsat 8 OLI/TIRS images obtained from the U.S Geological Survey (http://glovis.usgs.gov/, see Supplementary Information for a detailed description). Five classes were identified: forest (mature primary forest in good condition), agriculture (winter and summer annual crops), pasture (exotic pastures growing in plots with zero or very low density of trees per hectare), silvopasture (secondary forest, degraded forest and forest under use for timber harvesting or livestock production), and natural grassland (native grasses growing along ancient river beds). Forest cover was calculated using FRAGSTATS (McGarigal et al. 2012) and Shannon-Wiener Index was appraised as a diversity measure of land-use types (Gehring & Swihart 2003; Krauss et al. 2003; Bennett et al. 2006; De Angelo et al. 2011) using package vegan in R (Oksanen et al. 2012).

Data analysis

All the images captured in the 132 sites during the 4281 camera trap nights were reviewed using an image management software (Reconyx MapView Professional, version 3.1.2080). All photographs including large- and medium-sized mammals that we were able to identify, were considered in the analysis. The only small mammal registered and identified during the study (i.e. the common yellow-toothed Cavy, *Galea musteloides*) was also considered part of the assemblage since it plays an important role as prey of carnivore species. For every picture taken, useful data was automatically added by the camera-trap (e.g. date, time, infrared illumination, temperature, moon phase, etc.) and specific data was incorporated (e.g. site, species, sex, number of individuals, etc.). To assess the effectiveness of our survey for inventorying mammal species, we used the graphical method of species accumulation curves. These plots show the cumulative number of species detected against the sampling effort per unit time, which in the case of camera-traps can be CTNs. Species were accumulated by land-use type using 10,000 random iterations without replacement (Soberon & Llorente 1993; Gotelli & Colwell 2001). To compare among land uses we plotted the results against the number of camera-trap nights, and to evaluate the completeness of our survey we compared the total number of species registered with a list of known species from previous studies at the study area (Wetzel 1985; Bolkovic et al. 1995; Parera 2002;

Altrichter & Boaglio 2004; Canevari & Vaccaro 2007; Barquez et al. 2007; Abba et al. 2012; Quiroga 2013; Quiroga et al. 2013).

Based on the pooled pictures of 2012 and 2013, we determined the number of species observed (hereafter, species richness) and the capture frequency (c) for each site. Capture frequency, detection frequency, trap success or trapping rate are different names for the same relative abundance index (Carbone et al. 2001; Silveira et al. 2003; O'Brien 2008; Rowcliffe et al. 2008; Rovero & Marshall 2009). The application of this index is controversial because does not take into account the probability of detection (Jennelle et al. 2002; Carbone et al. 2002). More robust indexes can be obtained when individuals (those previously marked or presenting a natural coat pattern) can be recognized (Karanth & Nichols 1998; Karanth et al. 2004; O'Connell et al. 2011). The use of capture-recapture models provides, in such cases, unbiased density estimates (Jennelle et al. 2002), but excludes from the computation species without individual markings. Based on Carbone et al. (2001), and Rowcliffe et al. (2008) we devised the study design to reduce the differences in detection probability between sites in each land use. First, we set camera stations in at least 20 sites per land-use type (only 10 sites for GNP given methodological restrictions). Second, we set camera stations randomly, avoiding increasing detection probability by optimal deployment. Third, the camera detection zone did not vary greatly across sites because the terrain was always flat and also because vegetation was cleared creating an average area of 15 m^2 in front of the camera, independently of the habitat.

We calculated capture frequency for a given site as the number of independent captures divided by the number of CTNs for that site, and standardizing the value to 100 CTNs. Independent captures were defined if individuals of the same species, appearing in subsequent images, could be unambiguously distinguished, or if the interval between captures was longer than 1 hour.

Statistical analysis

To investigate the effects of land use intensification and landscape variables on the mammal community we used species richness and capture frequency as response variables (Magurran & McGill 2011; Carbone et al. 2001). We controlled for the pseudoreplication in our data by pooling together and averaging the 2012 and 2013 records. As count data, species richness does not usually follow normal distributions; therefore, we used generalized linear models (GLM) with Poisson errors and a log link function. Whereas capture frequency (c +1) was log transformed and modelled using normal distribution of errors (Zar 1996; Crawley 2007; Zuur et al. 2009).

Single variable regressions were used in a multiscale approach to assess for the contribution of each factor to the models (Gehring & Swihart 2003; Banks-Leite et al. 2013; De Angelo et al. 2013). We also compared linear, quadratic, and cubic functions to test possible non-linear adjustments for each continuous predictor variable. To organize model selection, we grouped the hypothesis hierarchically, starting with the single regression models for local scale variables, and followed by regression models for landscape composition-related metrics (refer to Table 3.2 for a complete list of the models tested). To examine for dependencies of predictor variables we used both visual (matrix of scatterplots of every variable against every other) and analytical methods (Pearson's correlation analysis). We found high correlation among all the landscape metrics (FC and H at the four radii, Supplementary information Table 3.S1), thus we performed a Principal Components Analysis (PCA) to reduce the number of variables into uncorrelated axes that incorporated the variation in the landscape metrics. PCA axes were obtained by previously scaling all the variables to have a zero mean and unit variance. We used these axes in the regressions to assess the importance of forest cover and habitat diversity combined.

To describe the relationship of community similarity among land uses in terms of mammal species composition, we used a Principal Coordinates Analysis (PCoA) based on a matrix of Sørensen dissimilarities. Changes in mammal community were measured at site level using incidence data. We used one-way ANOVA to test for differences among land-use types in the scores of the PCoA, and checked which land uses were significantly different from each other with Tukey's Honestly Significant Difference test (Tukey HSD) (Faith et al. 1987; Quinn & Keough 2002).

Hypothesis testing for the model including the categorical variable "land-use type" was performed by sequentially grouping the levels of the variable from the full model and testing for a significant increase in deviance. The factor level grouping followed an *a priori* description of biological sensible hypothesis (Table 3.3). If the result was significant we retained the levels separately in the final model. To select the best fitting function for each variable we used the Akaike Information Criterion corrected for small samples (AICc), comparing the differences of the AICc values between the models with the lower AICc, where AICcmim is the AICc value for the best-fitting model (Burnham & Anderson 2002; Crawley 2007; Zuur et al. 2009). All analysis were performed in R v.3.1.1 (R Core Team 2014). Species accumulation curves, Sørensen dissimilarity matrix, and PCoA were calculated using package "vegan" (Oksanen et al. 2012). GLM were calculated using package "lme4" (Bates et al. 2014).

3.3. Results

Species list and accumulation curves

During the total sampling period, we obtained c.27,281 photos, consisting of 1,367 independent captures of 26 species of mammals. We registered 22 species in 2012 and 25 species in 2013. The latency to first detection in 2012 was 1 day, and 2 days for 2013; whereas the average time to reach 80% of the species was 37.5 days. The most commonly photographed species was the Pampas fox, (*Lycalopex gymnocercus*), followed by the forest rabbit (*Sylvilagus brasiliensis*), and the gray brocket deer (*Mazama gouazoubira*). Whereas the rarest and most elusive species were photographed only once: the giant armadillo (*Priodontes maximus*), the Chacoan peccary (*Catagonus wagneri*) and the South American tapir (*Tapirus terrestris*); or twice: the white-lipped peccary (*Tayassu pecari*), and the collared anteater (*Tamandua tetradactyla*) (Table 3.4).

Two more species were found in the study area without being registered by the camera-traps, these were the Chacoan naked-tailed armadillo (*Cabassous chacoensis*) classified as Near Threatened (Ojeda et al. 2012; IUCN 2014), which was identified through an incidental sighting of a single individual crossing a narrow trail inside a forest patch (26° 28′ 36′′ S, 61° 32′ 38′′ W). There was also an individual maned wolf (*Chrysocyon brachyurus*), found drowned in a water reservoir, inside a cattle ranch (25° 07′ 29′′ S, 61° 40′ 50′′ W). Our total count species includes 28 species. Approximately, between 33 and 34 species of medium to large terrestrial mammals have been reported for the region (Parera 2002; Altrichter & Boaglio 2004; Altrichter et al. 2006; Canevari & Vaccaro 2007; Barquez et al.

2007; Quiroga et al. 2013). This study successfully registered 80 % of the species in that list (without considering the common yellow-toothed cavy, as it is a small mammal species).

The highest absolute number of species was recorded for sites inside the forest (FS= 21, FNP= 19 and F= 17), followed by a second group represented by wider open land uses like silvopasture and grasslands (S= 10, GNP= 8), with the agricultural plots holding the lowest species richness of all (AFS= 8, A=7) (Table 3.5). This result matched the species accumulation curves (Figure 3.3) where A and AFS yielded fewer species per trapping day than the rest of the land uses. Only A, AFS and S seemed to reach an asymptote at low species richness. The relatively high number of species in GNP, according to the camera trapping effort, produced an accumulation curve that did not level off, indicating a potentially higher species richness for this land use, maybe close to or even higher than S. The steepness of the curves showed a very rapid increase in species richness for FS, FNP and F reaching high values in few trapping nights. Whereas the number of species in forest seemed to have plateaued, species richness for FS and FNP could be even higher than the one registered.

Determinants of mammal diversity

Land-use type was the variable that best explained mammal species richness and relative abundance of individuals not only when local scale variables were analysed but also when landscape scale metrics were compared. There was no evidence that any factor had a consistently higher contribution to explaining the response variables. From the single regression models the minimum adequate model for species richness revealed significant differences between three main groups of habitats (AICc=518.3, AIC weight=1.0; Table 3.6). We found that mean species richness increased gradually from agriculture, to forest covered land uses (Figure 3.4 A). Agricultural environments showed the lowest average species richness (A=1.5 ± 0.9, AFS=2.1 ± 1.4) which did not differ from each other nor from species richness in natural grasslands (GNP=1.4 ± 1.2). Intermediate-intensified land uses, like silvopastures, showed a small but significant increase in the number of species (S=3.1 ± 1.6) and all forested habitats together had the most diverse mammal assemblage (F=4.3 ± 2.2, FS=5.4 ± 2.4, FNP=6.2 ± 1.8). At landscape level, percentage of forest cover within 500 metres was the most important variable explaining species richness. A non-linear cubic model best described the relationship (Supplementary information Figure 3.S1, Table 3.6), where species richness rapidly increased with forest cover until a local maximum; after which the number of species decreases (corresponding with grasslands inside National Park sites), to start increasing again for habitats with high forest cover. This pattern reflects a specific response that can only be explained considering the particular landscape composition present inside the National Park, where a long- and narrow-shaped open habitat, like natural grasslands, are closely surrounded by primary forest (Supplementary information Figure 3.S2). Therefore, the percentage of forest cover within 500 metres ranges from 30% to 80% but the number of species registered is low, as in the rest of the open habitats, forcing a local minimum.

Looking at capture frequencies we found that the two types of agricultural plots did not vary greatly (A=15.5 ± 10.8, AFS=14.9 ±11.7); however, the relative abundance of individuals increased significantly for S, and land uses with forest outside the National Park (F and FS); followed by an even greater relative abundance in FNP (Figure 3.4 B, Table 3.7). Considering this result, and in the search of potential stronger relationship, we decided to include silvopasture and secondary forest cover when calculating the forest cover metric for each of the distance radii (SFC- 500, 1000, 1500 and 3000). At landscape level, the percentage of forest cover SFC-1000 metres was the most relevant predictor variable (Table 3.7).

The first two axes of the PCA performed on the landscape variables explained 61 and 35% of the variation respectively. However, visual inspection of the data revealed an uninformative second axis determined by a horse-shoe shaped distribution (Supplementary information Figure 3.S3); therefore we only used the first PCA axis in the analysis. The interpretation of the first principal component was: positive values were associated with low FC (for all radii, the same for SFC) and high habitat diversity at 500 m. Negative values were associated with high FC (constant through all radii, the same for SFC) and low land use diversity. When included in the model selection procedure, neither species richness nor capture frequency presented a strong relationship with this variable (Table 3.6 and 3.7).

Community composition

Community composition was measured as a single axis of a PCoA which explained nearly 40% of the variation among the 132 sites. Because it was performed on an incidence matrix, mainly reflected changes in species richness and in species with low capture rates. A clear division was observed along axis 1, with the scores for forested sites (FS, F and FNP) positioned in the range of negative values, silvopasture sites scattered from positive to negative values, and agricultural plots mostly grouped in positive values (Figure 3.5 A). Mammal community composition was significantly different among all land-use types ($F_{6,117}$= 40.61, p<0.005), with the exception of S, FS, and FNP that presented similar mammal assemblages (Figure 3.5 B).

To get a more detailed understanding of community composition, we produced two more figures. Firstly, we graphically combined the information of capture frequency and occurrence of species using the grouped categories obtained from the best capture frequency model (Figure 3.6). Both types of arable fields (A and AFS) had a very uneven community with the Pampa's fox (*Lycalopex gymnocercus*) as the most abundant species (Table 3.5) and also sharing other species that were less common. The grey brocket deer (*Mazama gouazoubira*) was the most abundant species in silvopasture closely followed by the Pampa's fox, whereas the capture frequencies for the rest of the species detected in this habitat were approximately evenly distributed (Figure 3.6). Inside forest strips, the Pampa's fox and the forest rabbit (*Sylvilagus brasiliensis*) were the most abundant species, with the latter being the most frequently recorded in F as well. Inside the National Park, sites located in forest had five species dominating the community with very high relative abundances for the forest rabbit and the Pampa's fox, whilst the gray brocket deer was the most commonly photographed species in natural grasslands (Figure 3.6).

Secondly, the distribution of endangered mammal species was summarized in a graph of the total number of species and their relative abundance along the gradient of land use intensification (Figure 3.7). Only species categorized under one of the global and/or regional endangered classes (i.e. near threatened, vulnerable, and endangered) were included. Both, the highest number of endangered species as well as the highest abundance was found inside forest in the National Park, with seven different species and a capture frequency of 15.7 individuals per 100 CTN. Forest strips and forest outside the National Park followed, with only one-species difference between them. We registered less endangered species in silvopasture plots than in GNP, although the relative abundance was higher. Only one mammal species, the giant anteater (*Myrmecophaga tridactyla*, Vulnerable), was present in AFS with a very low capture frequency of 0.16 individuals per 100 CTN, and no endangered species was found inside intensified arable plots. The pattern in the number of species correlated with the pattern for relative abundance, except in the case of grassland inside the National Park, where four different species were present in very low numbers (only 1 or 2 independent captures per species); therefore the number of species registered was relatively higher than the capture frequency for those sites.

3.4. Discussion

A great deal of the existing research has been conducted to assess the effects of alterations in the natural environment on wildlife biodiversity (Tscharntke et al. 2005; Fischer & Lindenmayer 2007; Henle et al. 2008; Macchi & Grau 2012; Fischer et al. 2011; Lira et al. 2012; Moura et al. 2013), and more specifically, on medium and large mammal communities (Kinnaird et al. 2003; Michalski & Peres 2007; Kelly et al. 2008; Paviolo et al. 2009; Ahumada et al. 2011; Samejima et al. 2012; De Angelo et al. 2013). However, few studies have focussed directly on the analysis of the complete mammal assemblage in human-modified habitats (Altrichter & Boaglio 2004; R. Cassano et al. 2012; R. Cassano et al. 2014). This study provides the first community estimates for mammals along a gradient of land use intensification resulting from the main human activities in comparison with natural forest in the semiarid Chaco Region.

We assessed the entire mammal assemblage acknowledging that species-specific responses might go undetected; nonetheless using composite measures of community diversity allowed us to retain species that were rarely detected and to include in the modelling potential effects of interspecific interactions that constitute an important property of communities (Tscharntke et al. 2005; Ewers et al. 2009). Accordingly, the randomized sampling design of the study proved to be successful as we obtained registers for most of the species present in the area, and more importantly, it allowed us to calculate un-biased relative abundances for small-scale habitat comparisons (Wearn et al. 2013; Blake & Mosquera 2014).

Our results were broadly concordant with several studies showing negative effects of human managed environments on mammal assemblages (Gehring & Swihart 2003; Daily et al. 2003; Šálek et al. 2009; Kiffner et al. 2014). The most important factor influencing mammal communities was land-use type, and its explanatory power has proved to be stronger than any other variable. Medium-sized mammal assemblages in semiarid Chaco did not respond as expected to the landscape context (percentage cover of forest and habitat diversity) at any of the spatial scales measured (500, 1000, 1500 and 3000m radius around sampling point); while parameters related to local management intensification had the most important negative effects on this group. This result supports the idea that ecology studies are highly context-dependent. Andrén (1994) concluded in his review that, the importance of changes in local forest cover may depend on the surrounding landscape. Moreover, in landscapes with a considerable large area (more than 30%) of suitable habitat, the spatial arrangements of its elements will be of secondary importance. The comparison of our results with previous studies addressing this issue for mammal assemblages (R. Cassano 2014) suggests that our study area is placed in a favourable context. As a result, the impact of the amount of remaining forest on species richness and abundance was less important compared to that shown by different land-use types.

We found a decreasing relationship between species richness and abundance in relation to human disturbance. As expected, the lowest numbers were registered within agricultural fields. All the species present there are usually associated to open habitats and benefit from the physical conditions in farmlands mainly due to their feeding habits (Parera 2002; Canevari & Vaccaro 2007; Superina et al. 2010; Abba et al. 2012). In arable fields we registered three of the most common species of armadillos (*Chaetophractus vellerosus*, *Chaetophractus villosus*, and *Euphractus sexcinctus*), where soil condition probably facilitates foraging for food as some of the individuals were photographed digging borrows. The hog-nosed skunk (*Conepatus chinga*), and the European hare (*Lepus europaeus*) were also recorded, with the latter being an exotic species only present in this habitat. Lastly, both species of canids (crab-eating fox *Cerdocyon thous*, and Pampa's fox *Lycalopex* *gymnocercus,* Figure 3.6) appear capable of moving among all components of the landscape (Gehring & Swihart 2003).

Mammal species richness and relative abundance showed very little variability between A and AFS, that basically shared the same assemblage of species (with the exception of the European hare). Although, the presence of forest dweller species in AFS revealed the influence of the surrounding forest strips as we also registered the giant anteater (*Myrmecophaga tridactyla*) and the grey brocket deer (*Mazama gouazoubira*). Giant anteaters required large areas for their survival mostly inhabiting forest patches, the same as the grey brocket deer (Figure 3.6); however both species can venture into open areas to forage (Parera 2002; Canevari & Vaccaro 2007; Superina et al. 2010; Trujillo & Superina 2014). In this case, the presence of a neighbouring forest strip could have encouraged these individuals to go into the agricultural plot (Barlow et al. 2010; Šálek et al. 2009). In this regard, Redford & da Fonseca (1986) suggested that gallery forest in the Brazilian Cerrado provide refuge, food and water for species not necessarily confined to this environment. Another habitat with similar low records was natural grassland inside National Park. However, significant differences were found in community composition between this land-use type and the arable fields (A and AFS, Figure 3.5 B). Moreover, two species were exclusive of this environment, the lesser grisson (*Galictis cuja*) and the white-lipped peccary (*Tayassu pecari,* Figure 3.6). Low records in GNP might also be related to the vegetation structure that probably affected detectability in these sites.

Silvopastoral systems integrate trees and pastures for production purposes providing a buffer from deforestation (Dagang & Nair 2003; Perfecto & Vandermeer 2008). Many combinations of agroforestry can be found in other regions (e.g. shaded cacao, coffee and rubber plantations) and numerous studies have highlighted their role in providing ecosystems services as well as a matrix that can maintain biodiversity and movement of organisms (Saunders et al. 1991; Perfecto et al. 2005; Perfecto & Vandermeer 2008). Coincidentally R. Cassano et al. (2012), found high mammal species diversity in cabrucas (cacao agroforestry systems in Brazil), as we found that silvopasture plots in the semiarid Chaco harboured a more diverse mammal community than intensified land uses; whilst, also as in R. Cassano et al. (2012), the assemblage structure was similar to that in forested sites (FS and FNP). Moreover, two species of conservation concern were registered in silvopastures (the three-banded armadillo *Tolypeutes matacus*, and the Geoffroy's cat *Leopardus geoffroyi,* Figure 3.6). These results support the importance of silvopastures as productive systems with conservation value simultaneously holding an interesting mammal community and cattle ranching activities.

Forest is the primary habitat for most of the species registered in this study and, consequently, it presented the highest diversity values. Forest strips, and forest in and out the National Park had similar number of species but differed in abundance and community composition. As Barlow et al. 2010, we also detected higher mammal activity in forest strips than in continuous forest patches outside the National Park. In this case, detection probability might have been increased by the linear shape and dimensions of this environment which may have concentrated animal movements leading to an overestimation of the relative abundance of individuals. Therefore we should be cautious in drawing conclusions and comparing the final numbers. However, our results are consistent with Šálek et al. (2009) and Gehring & Swihart (2003) who showed that predators in fragmented agricultural landscapes tend to use hedgerows in higher proportion. As well as having a possible role as corridors, hedgerows can provide habitat for a rich community of smaller mammals. In our study, two of the most photographed species in forest strips were the Pampa's fox and the forest rabbit (*Sylvylagus brasiliensis,* Figure 3.6); the former is an open-habitat species that probably takes refuge and use these strips to move around or to hunt; whereas the latter is a forest-restricted species. Both species find in forest strips a suitable habitat according to their very different traits.

The mammal species list recorded in forest inside National Park included all the species previously found in a recent study (Quiroga 2013) with the addition of the nine-banded armadillo (*Dasypus novemcinctus*), the crab-eating fox (*Cerdocyon thous*), and the Chacoan peccary (*Catagonus wagneri,* Figure 3.6). Sites inside the park presented the highest mean species richness and capture frequency of all environments. However, both measures could be probably an underestimation of true values due to methodological constraints: first, the lack of roads inside the park prevented us from reaching sites in the core area; and second, the sampling effort was the result of a compromise between time availability and number of camera traps deployed. Regardless of the values, the importance of the protected area for the conservation of endangered species is supported by the exclusive records of the giant armadillo (*Priodontes maximus*), the White-lipped Peccary, and the Chacoan peccary inside the protected area, as well as the fact that the highest number of endangered mammal species was recorded inside the limits of Copo National Park (Figure 3.7). The decline in the range and numbers of these species is probably due to a combination of factors including hunting by humans, habitat destruction, and diseases. Of these, hunting pressure undoubtedly has the most negative impact (Altrichter & Boaglio 2004; Altrichter 2005; IUCN 2014); therefore, the preservation and implementation of exclusion areas like reserves and national parks are key to the conservation of these species in the semiarid Chaco. Nonetheless, other important species considered scarce in the study area were also registered outside the National Park (e.g. the South American tapir *Tapirus terrestris,* the Tayra *Eira barbara*, and the collared anteater *Tamandua tetradactyla*). In this regard, several studies have suggested that the amount of forest cover in the surrounding landscape influences species responses to local management intensification (Andrén 1994; Bennett et al. 2006; Fischer et al. 2011; R. Cassano et al. 2014) by maintaining viable populations of species that move along corridors and “wildlife-friendly” productive environments, using mainly well preserved forest patches. The mammal distribution patterns registered in our study support this hypothesis and numerous records of several species photographed with their offspring (e.g. puma *Puma concolor*, collared peccary *Tayassu tajacu;* giant anteater; grey brocket deer, and the South American tapir) are proof that species find in this landscape suitable habitats to breed.

To summarize, this study encompassed an important area of high agricultural activity were habitat transformation is extending over natural land at an alarming rate. Our results demonstrates that the pattern in distribution of mammal assemblages follows the intensification gradient and that land-use type associated with level of intensification is the most important factor driving mammal diversity and community composition. Conservation strategies should consider the use of intermediate modified habitats such as silvopasture and the maintenance of forest patches and strips in order to minimise the impacts of agricultural practices on important and charismatic mammal species of the Chaco Region.

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Table 3.1. Sampling effort for each land-use type studied: total number of sites surveyed; camera trap night per year, total for both years, and averaged (± standard error) per land-use type; mean distance between sites was calculated for camera-traps in the same land-use type (km ± se); and number of camera traps deployed on and off existing trails

Land-use type	**Number of sites**	**CTNs per year**		**Total CTNs**	**Average CTNs**	**Average distance between sites**	**Camera placement**	
		2012	**2013**				**On trail**	**Off trail**
Agriculture	20	128	422	550	27.5 ± 10	1.8 ± 0.5	-	-
Agriculture with forest strip	20	261	370	631	31.5 ± 9.3	2 ± 0.6	-	-
Silvopasture	22	278	365	643	29.2 ± 8.6	1.6 ± 0.4	-	-
Forest strip	20	283	404	687	34.3 ± 7	1.9 ± 0.4	3	17
Forest	20	282	405	687	34.3 ± 7	2.2 ± 1	0	20
Forest in National Park	20	271	492	763	38.1 ± 14.4	1.5 ± 0.4	12	8
Grassland in National Park	10	117	139	256	29.1 ± 16	1.1 ± 0.3	-	-
Total	**132**	**1649**	**2632**	**4217**	**32 ± 10.7**	**1.7 ± 0.4**	**15**	**45**

CTNs: camera trap nights was defined as the total number of complete 24-hour periods during which the camera was functioning.

Table 3.2. List and description of all the models considered in relation to local and landscape predictor variables. Each particular model was described by GLM or LM (depending on the response variable). We used model selection based on the Akaike Information Criterion to compare the set of candidate models, with deletion tests (Wald's chi-square test for species richness and F-test for capture frequency) to assess the significance of the increase in deviance that resulted when a given term was removed from the current model.

Model	**Local scale predictor variable 1 = AREA**
m1	Log (AREA)
m2	Polynomial (Log (AREA),2)
m3	Polynomial (Log (AREA),3)
	Local scale predictor variable 2 = EDGE
m1	Log (EDGE)
m2	Polynomial (Log (EDGE),2)
m3	Polynomial (Log (EDGE),3)
	Landscape scale predictor variable 1 = FC
m1	FC 500
m2	Polynomial (FC 500,2)
m3	Polynomial (FC 500,3)
m4	FC 1000
m5	Polynomial (FC 1000,2)
m6	Polynomial (FC 1000,3)
m7	FC 1500
m8	Polynomial (FC 1500,2)
m9	Polynomial (FC 1500,3)
m10	FC 3000
m11	Polynomial (FC 3000,2)
m12	Polynomial (FC 3000,3)
	Landscape scale predictor variable 2 = H
m1	H 500
m2	Polynomial (H 500,2)
m3	Polynomial (H 500,3)
m4	H 1000
m5	Polynomial (H 1000,2)
m6	Polynomial (H 1000,3)
m7	H 1500
m8	Polynomial (H 1500,2)
m9	Polynomial (H 1500,3)
m10	H 3000
m11	Polynomial (H 3000,2)
m12	Polynomial (H 3000,3)
	Landscape scale predictors 1 and 2 combined
m1	PCA1

Polynomial (x, num): fits a polynomial model with predictor x to the power of the number.
Log AREA: area (ha.) of the land-use patch log-transformed.
Log EDGE: distance to the nearest edge (metres) log-transformed.
FC- 500, 1000, 1500 and 3000: percentage of forest cover within each radii (SFC included secondary forest and was analysed in the same way).
H- 500, 1000, 1500 and 3000: land-use diversity within each radii.
PCA1: Principal Component Analysis axis one.

Table 3.3. List and description of models for the categorical variable “land use”. Factor level arrangements were based on a set of *a priori* hypothesis that ensured biological interpretation of the results. Each particular model (hypothesis) was described by GLM or LM (depending on the response variable). We used model selection based on Akaike’s Information Criterion to compare candidate models, with deletion tests (Wald’s chi-square test for species richness and F-test for capture frequency) to assess the significance of the increase in deviance that resulted when a given term was removed from the current model. (Adapted from Table 2.1, Chapter 2).

Model	**Factor level arrangement**	**Particular hypothesis justification**
m1	A, AFS, S, FS, F, FNP, GNP	Each land-use type has a particular effect at local scale, mainly given to their specific vegetation cover and management regime.
m2	A + AFS, S, FS, F, FNP, GNP	Intensive arable systems (A and AFS) are not different from each other in their mammal community, mainly because habitat availability in these land uses is very low despite local differences in forest strips surrounding AFS plots. The rest of the land uses present a distinctive mammal community.
m3	A + AFS, S, FS, F + FNP, GNP	Intensive arable systems (A and AFS) are not different from each other. Land-use types presenting a well-preserved forest cover (F and FNP) are not different from each other. Natural grasslands inside National Park present a distinctive mammal assemblage.
m4	A + AFS, S + FS, F + FNP, GNP	Intensive arable systems (A and AFS) do not differ. Intermediate intensity land uses (S and FS) are grouped accordingly to their habitat alteration level and disturbance regime. Land uses with a well-preserved forest cover (F and FNP) are not different from each other. Natural grasslands inside National Park present a distinctive mammal assemblage.
m5	A + AFS, S, FS + F + FNP, GNP	High-intensity land uses (A and AFS) do not differ. Intermediate intensity land uses, where forest cover has been significantly reduced (S) hold a distinctive mammal community. Land uses presenting a well-preserved and structured forest cover, regardless of size (FS, F and FNP) are not different from each other. Natural grasslands inside National Park present a distinctive mammal assemblage.
m6	A + AFS, S + FS + F, FNP, GNP	High-intensity land uses (A and AFS) do not differ. Sites inside protected areas (FNP and GNP) hold a different mammal community than the rest of forested land-use types (with reduced or well-preserved vegetation cover) outside the National Park.
m7	A + AFS, S + FS + F + FNP, GNP	Intensive arable systems (A and AFS) are not different from each other. The category of protection does not affect mammal community assemblages: land-use types presenting a range of intermediate forest cover (S), good forest cover outside protected areas (FS and F) and well-preserved forest cover inside National Park (FNP) do not differ. Natural grasslands inside National Park present a distinctive mammal assemblage.

Abbreviations: A: agriculture; AFS: agriculture with forest strips; S: silvopasture; FS: forest strip; F: forest; FNP: forest inside Copo National Park; GNP: Grassland in National Park.

Table 3.4. Mammal species registered during 2012 and 2013 in the semiarid Chaco. Family, scientific and common name for the total 28 species registered during the survey, global and regional category of threat, and number of direct sightings. Number of photos is the total number of pictures taken for each species, number of independent captures considers only images of different individuals or images obtained more than one hour apart. Capture frequency (relative abundance) is calculated as total number of independent captures per 100 camera trap nights. Naive occupancy is the proportion of sampled sites at which the species was detected. Scientific names follow Barquez et al. 2007. Regional status assessment taken from Ojeda et al. 2012.

Family	**Scientific Name**	**Common Name**	**IUCN Red List Category**	**Regional Assessment Category**	**Direct sightings**	**Camera trapping**			
						Number of photos	**Independent captures**	**Capture frequency (c)**	**Naive occupancy**
CANIDAE	*Cerdocyon thous*	Crab-eating Fox	LC	LC	1	772	57	1.33	0.220
CANIDAE	*Chrysocyon brachyurus*	* Maned Wolf	NT	EN	1	0	0	0.00	0.000
CANIDAE	*Lycalopex gymnocercus*	Pampas Fox	LC	LC	0	4532	297	6.94	0.598
CAVIIDAE	*Galea musteloides*	Common Yellow-toothed Cavy	LC	LC	0	67	4	0.09	0.030
CERVIDAE	*Mazama gouazoubira*	Grey Brocket Deer	LC	LC	4	6750	164	3.83	0.485
DASYPODIDAE	*Cabassous chacoensis*	* Chacoan Naked-tailed Armadillo	NT	NT	1	0	0	0.00	0.000
DASYPODIDAE	*Chaetophractus vellerosus*	Screaming Hairy Armadillo	LC	LC	0	286	28	0.65	0.076
DASYPODIDAE	*Chaetophractus villosus*	Large Hairy Armadillo	LC	LC	5	99	13	0.30	0.091
DASYPODIDAE	*Dasypus novemcinctus*	Nine-banded Armadillo	LC	LC	0	108	9	0.21	0.053
DASYPODIDAE	*Euphractus sexcinctus*	Yellow Armadillo	LC	LC	2	732	57	1.33	0.205
DASYPODIDAE	*Priodontes maximus*	Giant Armadillo	VU	EN	0	6	1	0.02	0.008
DASYPODIDAE	*Tolypeutes matacus*	Southern Three-banded Armadillo	NT	NT	2	1709	112	2.62	0.326
DIDELPHIDAE	*Didelphis albiventris*	White-eared Opossum	LC	LC	0	118	6	0.14	0.030

(*) Indicates species observed in the study area outside the sampling period, not considered for the analysis.
IUCN: International Union for the Conservation of Nature. NE: not evaluated; LC: least concern; NT: near threatened; VU: vulnerable; EN: endangered.

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Family	Scientific Name	Common Name	IUCN Red List Category	Regional Assessment Category	Direct sightings	Camera trapping			
						Number of photos	Independent captures	Capture frequency (c)	Naive occupancy
FELIDAE	*Leopardus geoffroyi*	Geoffroy's Cat	NT	NT	2	1074	70	1.64	0.280
FELIDAE	*Puma concolor*	Puma	LC	LC	0	205	18	0.42	0.083
FELIDAE	*Puma yagouaroundi*	Jaguarundi	LC	LC	0	61	7	0.16	0.053
LEPORIDAE	*Lepus europaeus*	European Hare	LC	-	0	63	6	0.14	0.030
LEPORIDAE	*Sylvilagus brasiliensis*	Forest Rabbit	LC	LC	0	5213	277	6.47	0.326
MEPHITIDAE	*Conepatus chinga*	Hog-nosed Skunk	LC	LC	0	776	77	1.80	0.295
MUSTELIDAE	*Eira barbara*	Tayra	LC	NE	2	78	5	0.12	0.023
MUSTELIDAE	*Galictis cuja*	Lesser Grison	LC	VU	2	22	4	0.09	0.015
MYRMECOPHAGIDAE	*Myrmecophaga tridactyla*	Giant Anteater	VU	VU	7	2171	121	2.83	0.341
MYRMECOPHAGIDAE	*Tamandua tetradactyla*	Collared Anteater	LC	NT	0	40	2	0.05	0.015
PROCYONIDAE	*Nasua nasua*	South American Coati	LC	LC	0	41	3	0.07	0.015
TAPIRIDAE	*Tapirus terrestris*	South American Tapir	VU	EN	0	50	2	0.05	0.008
TAYASSUIDAE	*Catagonus wagneri*	Chacoan Peccary	EN	EN	0	3	1	0.02	0.008
TAYASSUIDAE	*Tayassu tajacu*	Collared Peccary	LC	VU	2	2266	24	0.56	0.053
TAYASSUIDAE	*Tayassu pecari*	White-lipped Peccary	VU	EN	0	39	2	0.05	0.015

IUCN: International Union for the Conservation of Nature. NE: not evaluated; LC: least concern; NT: near threatened; VU: vulnerable; EN: endangered.

Table 3.5. Summary statistics for the data collected during 2012 and 2013 in the semiarid Chaco. The table lists: mammal species richness for each land use calculated as total and mean number of species, mean capture frequency (c), and the most abundant species (scientific name) captured in each land use.

Land-use type	**Total number of species**	**Mean species richness (± se)**	**Mean capture frequency (± se)**	**Most abundant species**
Agriculture	7	1.55 ± 0.94	15.53 ± 10.83	*Lycalopex gymnocercus*
Agriculture with forest strip	8	2.1 ± 1.41	14.95 ± 11.7	*Lycalopex gymnocercus*
Silvopasture	10	3.14 ± 1.61	26.31 ± 21.23	*Mazama gouazoubira*
Forest strip	21	5,45 ± 2.4	44.63 ± 31.25	*Lycalopex gymnocercus*
Forest	17	4.35 ± 2.23	30.03 ± 24.53	*Sylvilagus brasiliensis*
Forest in National Park	19	6.2 ± 1.85	63.33 ± 30.44	*Sylvilagus brasiliensis*
Grassland in National Park	8	1.4 ± 1.17	10.58 ± 13.6	*Mazama gouazoubira*

Table 3.6. Summary of model selection for mammal species richness. For each spatial scale (local and landscape), and predictor belonging to that scale, the table lists only the best minimum final model; a complete list of the models compared is shown in Table 3.2. An offset term was included in the models (camera trap nights) to standardize for sampling effort per site. Models were fitted using GLM with Poisson error and log-link. We report AICc: Akaike Information Criterion value corrected for small samples; ∆ AIC: difference in AICc values between each model and the best model, and *w*: the percentage of model weight attributed to each model. The best model selected is shown in bold.

Response variable: Species richness	**AICc**	**∆ AIC**	***w***
Null model	577.7		
Local scale			
Polynomial (Log AREA,2)	540.2	21.8	0.00
Log EDGE	568.6	50.3	0.00
Land use factor m5 (GNP, A+AFS, S, FS+F+FNP)	**518.3**	**0.0**	**1.00**
Landscape scale			
Polynomial (FC 500,3)	560.0	0.0	0.68
FC 1000	563.4	3.4	0.12
FC 1500	568.6	8.6	0.01
Polynomial (FC 3000,3)	565.6	5.6	0.04
Polynomial (H 500,3)	564.9	4.9	0.06
Polynomial (H 1000,2)	564.5	4.5	0.07
H 1500	579.8	19.8	0.00
Polynomial (H 3000,2)	572.6	12.6	0.00
PCA1	567.7	7.7	0.01

Polynomial (x, number): fits a polynomial model with predictor x to the power of the number (e.g. Polynomial (x, 2) is a quadratic polynomial for x).
Log AREA: area (ha.) of the land-use patch log-transformed.
Log EDGE: distance to the nearest edge (metres) log-transformed.
GNP: Grassland in National Park; A: agriculture; AFS: agriculture with forest strip; S: silvopasture; FS: forest strip; F: forest; FNP: forest inside National Park.
FC-500, 1000, 1500 and 3000: percentage of forest cover within each radii.
H-500, 1000, 1500 and 3000: land use diversity measured with Shannon-Weiner index, basically a measure of proportion of different habitats within each radii.
PCA1: Principal Component Analysis axis one.

Table 3.7. Summary of model selection for mammal capture frequency. For each spatial scale (local and landscape), and predictor belonging to that scale, the table lists only the best minimum final model; a complete list of the models compared is shown in Table 3.2. Because capture frequency already takes into account the sampling effort, no offset term was necessary. Models were fitted using LM with Normal error distribution. We report AICc: Akaike Information Criterion value corrected for small samples; Δ AIC: difference in AICc values between each model and the best model, and *w*: the percentage of model weight attributed to each model. The best model selected is shown in bold.

Response variable: Log Capture frequency (+1)	**AICc**	**Δ AIC**	***w***
Null model	402.3		
Local scale			
Polynomial (Log AREA,2)	375.3	22.4	0.00
Log EDGE	400.1	47.1	0.00
Land use factor m6 (GNP, A+AFS, S+FS+F, FNP)	**353.0**	**0.0**	**1.00**
Landscape scale			
Polynomial (SFC 500,3)	389.9	0.0	0.44
Polynomial (SFC 1000,3)	390.4	0.5	0.35
Polynomial (SFC 1500,3)	395.9	6.0	0.02
Polynomial (SFC 3000,3)	394.3	4.4	0.05
H 500	393.6	3.7	0.07
Polynomial (H 1000,2)	399.7	9.8	0.00
H 1500	403.8	13.9	0.00
H 3000	403.0	13.1	0.00
PCA1	393.5	3.6	0.07

Polynomial (x, number): fits a polynomial model with predictor x to the power of the number (e.g. Polynomial (x, 2) is a quadratic polynomial for x).
Log AREA: area (ha.) of the land-use patch log-transformed.
Log EDGE: distance to the nearest edge (metres) log-transformed.
GNP: Grassland in National Park; A: agriculture; AFS: agriculture with forest strip; S: silvopasture; FS: forest strip; F: forest; FNP: forest inside National Park.
SFC-500, 1000, 1500 and 3000: percentage of forest cover (considering primary and secondary forest together) within each radii.
H-500, 1000, 1500 and 3000: land use diversity measured with Shannon-Weiner index, basically a measure of proportion of different habitats within each radii.
PCA1: Principal Component Analysis axis one.

Figure legends

Figure 3.1. Land cover map of the study area. (A) a 100 x 60 km agricultural landscape inside which 100 camera trapping sites were deployed (red dots), (B) detail showing several sampling sites scattered within different land-use types, (C) detail of the sites located in two different land-use types: forest strip and agriculture. Different vegetation cover is represented by different colours.

Figure 3.2. Land cover map showing (A) Copo National Park and its borders depicted in grey, and (B) close-up detail of several sites inside the park. Red dots mark sites where camera traps were deployed. Different vegetation cover is represented by different colours.

Figure 3.3. Mammal species accumulation curves for each land use showing the total number of species recorded with increasing sampling effort (camera trap nights, CTNs). Species were accumulated by number of camera trap nights. The dashed vertical line indicates a species richness comparison standardized to the minimum camera trap effort, and corresponds to 256 CTNs, the total CTNs for GNP. A, agriculture; AFS, agriculture with forest strip; S, silvopasture; FS, forest strip; F, forest; FNP, forest inside National Park, and GNP, grassland inside National Park.

Figure 3.4. Variation in diversity measures for each land use. (A) Mammal species richness; (B) Capture frequency. Thick lines represent the median, boxes represent the interquartile range and whiskers represent minimum and maximum values, points represent sites (replicates). A, agriculture; AFS, agriculture with forest strip; S, silvopasture; FS, forest strip; F, forest; FNP, forest inside National Park; GNP, grassland inside National Park. Statistical differences in the mean of the variable are true when letters differ between factor levels (Tukey HSD at alpha= 0.5).

Figure 3.5. Result of a Principal Coordinates Analysis (PcoA) based on a Sørensen dissimilarity matrix for all 132 sites and 26 mammal species. (A) Plot of the first two axes of the PCoA. Highly modified environments (A and AFS) had community composition with

positive scores in the first axis. Forest-like land uses mostly presented negative values. Sites are shown in coloured symbols; each character corresponds to a different land-use type. (B) Results from an ANOVA of community composition (PCoA axis 1) and land-use type. Open habitats (GNP, A and AFS) presented significant changes in composition among them and also with the rest of the land uses, whereas mammal assemblages in forests did not vary significantly (S=FS=FNP). Thick lines represent the median, boxes represent the interquartile range and whiskers represent minimum and maximum values, points represent sites (replicates). Land uses marked with the same letter did not showed significant differences in community composition (Tukey HSD at alpha=0.05). A, agriculture; AFS, agriculture with forest strip; S, silvopasture; FS, forest strip; F, forest; FNP, forest inside National Park; GNP, grassland inside National Park.

Figure 3.6. Capture frequencies distribution per land use for each species registered during the study. Records are drawn following the subdivision in groups according to the best model selected for capture frequency (i.e. A and AFS grouped together; S, FS and F grouped together, and FNP separately). All 26 species registered are listed in the horizontal axis. Vertical axes are scaled differently for each group, with the broader range corresponding to FNP. Different colours represent different land uses. A, agriculture; AFS, agriculture with forest strip; S, silvopasture; FS, forest strip; F, forest; FNP, forest inside National Park; GNP, grassland inside National Park.

Figure 3.7. Mammal species of conservation concern distributed along the gradient of land use change. Bars represent number of species and relative abundance of mammal species within a category of threat following the IUCN criteria and the regional status assessment (near threatened, vulnerable; or endangered, IUCN 2014; Ojeda et al. 2012). Slate gray bars (scaled axis to the left) represent total number of species, and light gray bars (scaled axis to the right) represent capture frequency, both obtained for each land-use type. The dotted line was added to facilitate the identification of the land covers located inside the National Park. A, agriculture; AFS, agriculture with forest strip; S, silvopasture; FS, forest strip; F, forest; FNP, forest inside National Park; GNP, grassland inside National Park.

Figure 3.1.


A
B
C
N
Natural grassland
Agriculture / Pasture
Secondary forest / Silvopasture
Forest
0
10
20
40 Km
0
2.5
5
10 Km
0
0.5
1
2 Km

Figure 3.2.

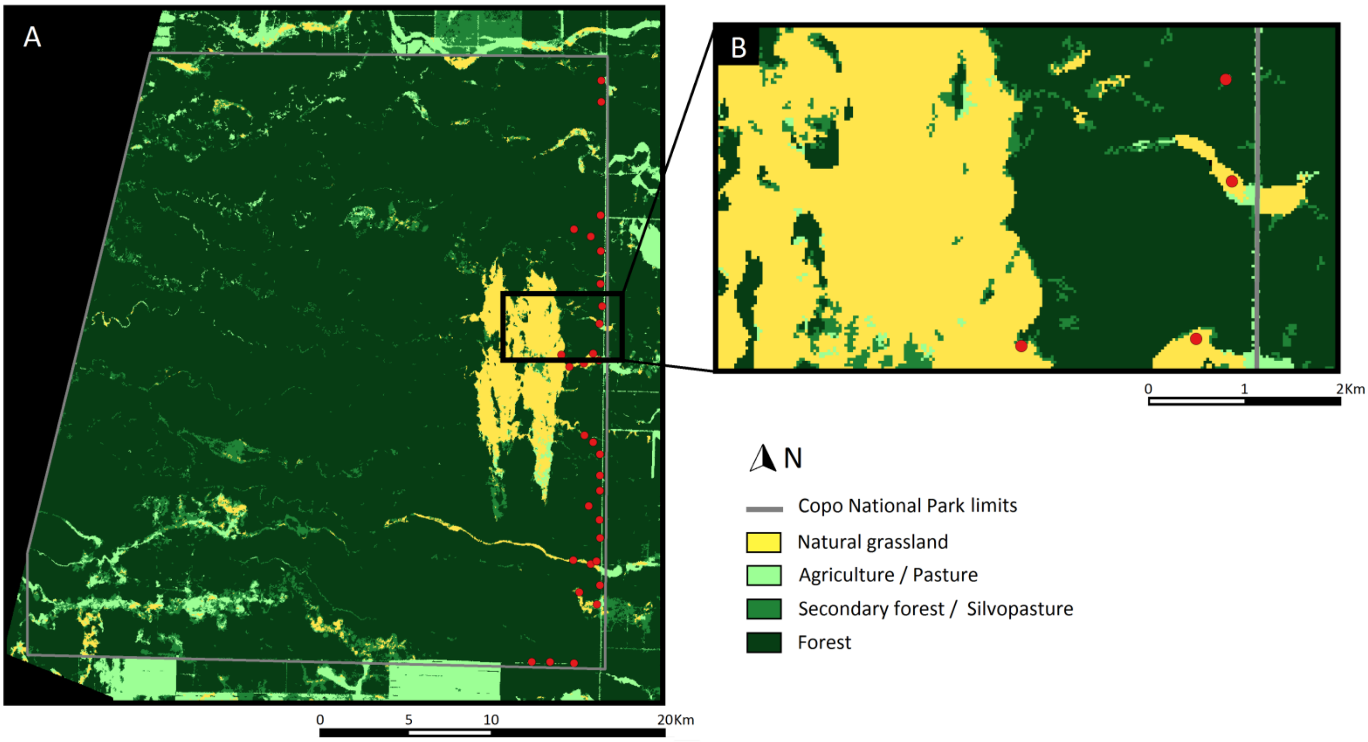

A
B
0
1
2Km
0
5
10
20Km
N
Copo National Park limits
Natural grassland
Agriculture / Pasture
Secondary forest / Silvopasture
Forest

Figure 3.3.

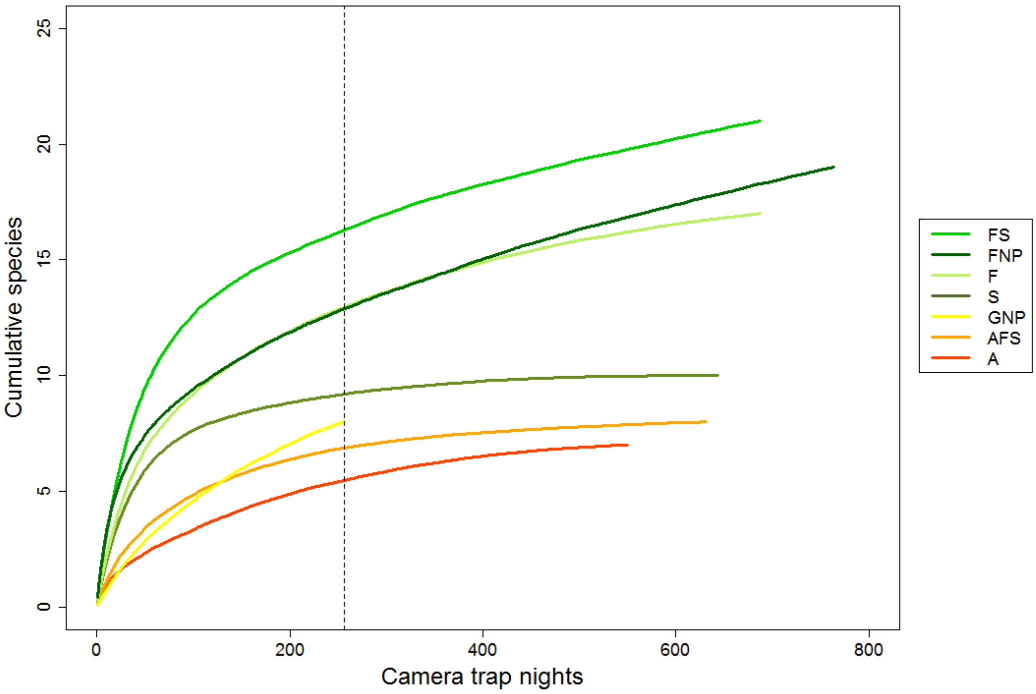

Cumulative species
0
5
10
15
20
25
0
200
400
600
800
Camera trap nights
FS
FNP
F
S
GNP
AFS
A

Figure 3.4.

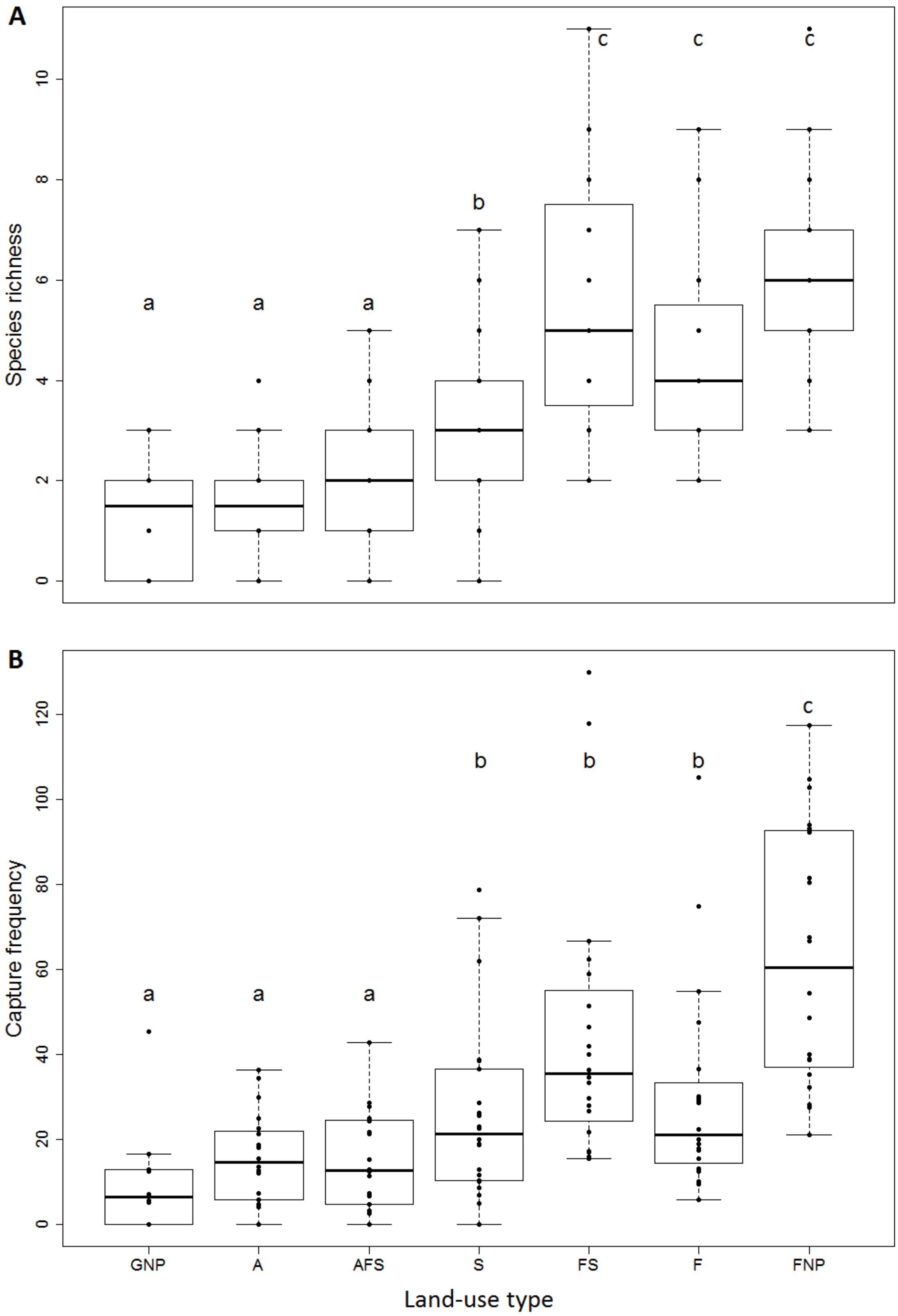

A
Species richness
0
2
4
6
8
10
a
a
a
b
c
c
c
B
Capture frequency
0
20
40
60
80
100
120
a
a
a
b
b
b
c
GNP
A
AFS
S
FS
F
FNP
Land-use type

Figure 3.5.

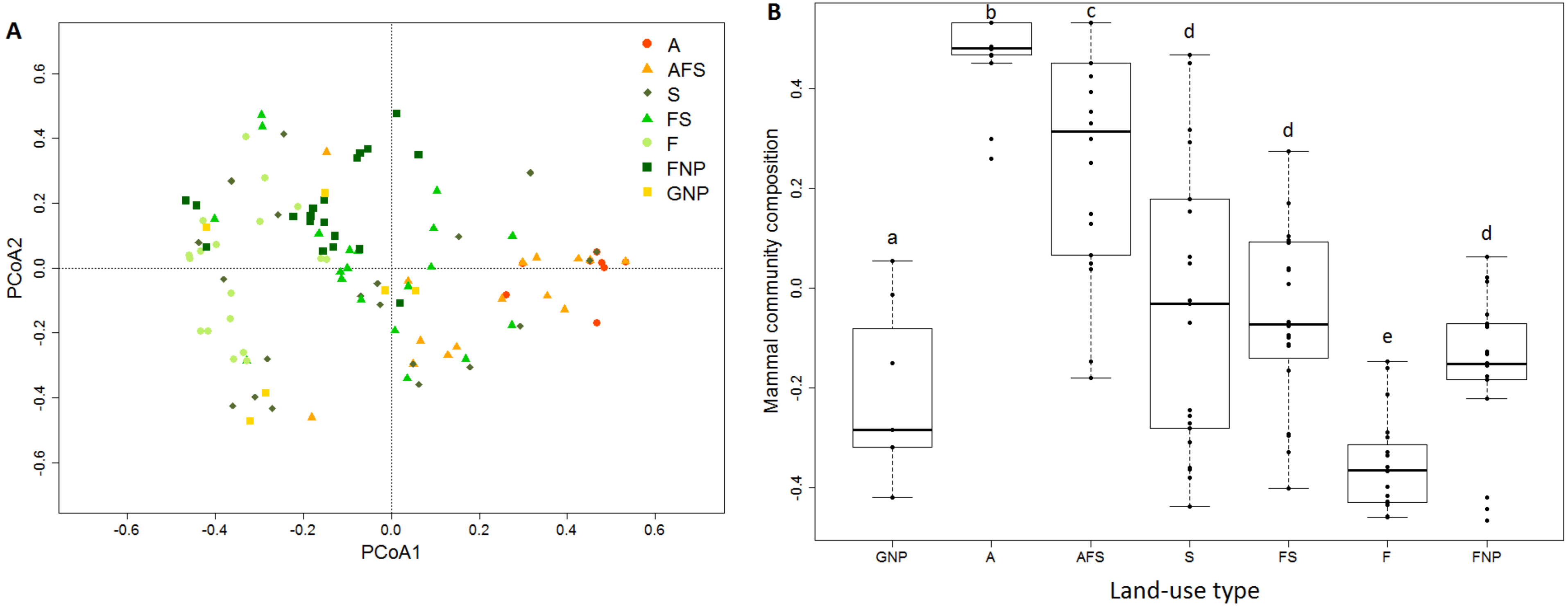

A
PCoA2
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
PCoA1
A
AFS
S
FS
F
FNP
GNP
B
Mammal community composition
0.4
0.2
0.0
-0.2
-0.4
a
b
c
d
d
e
d
GNP
A
AFS
S
FS
F
FNP
Land-use type

Figure 3.6.

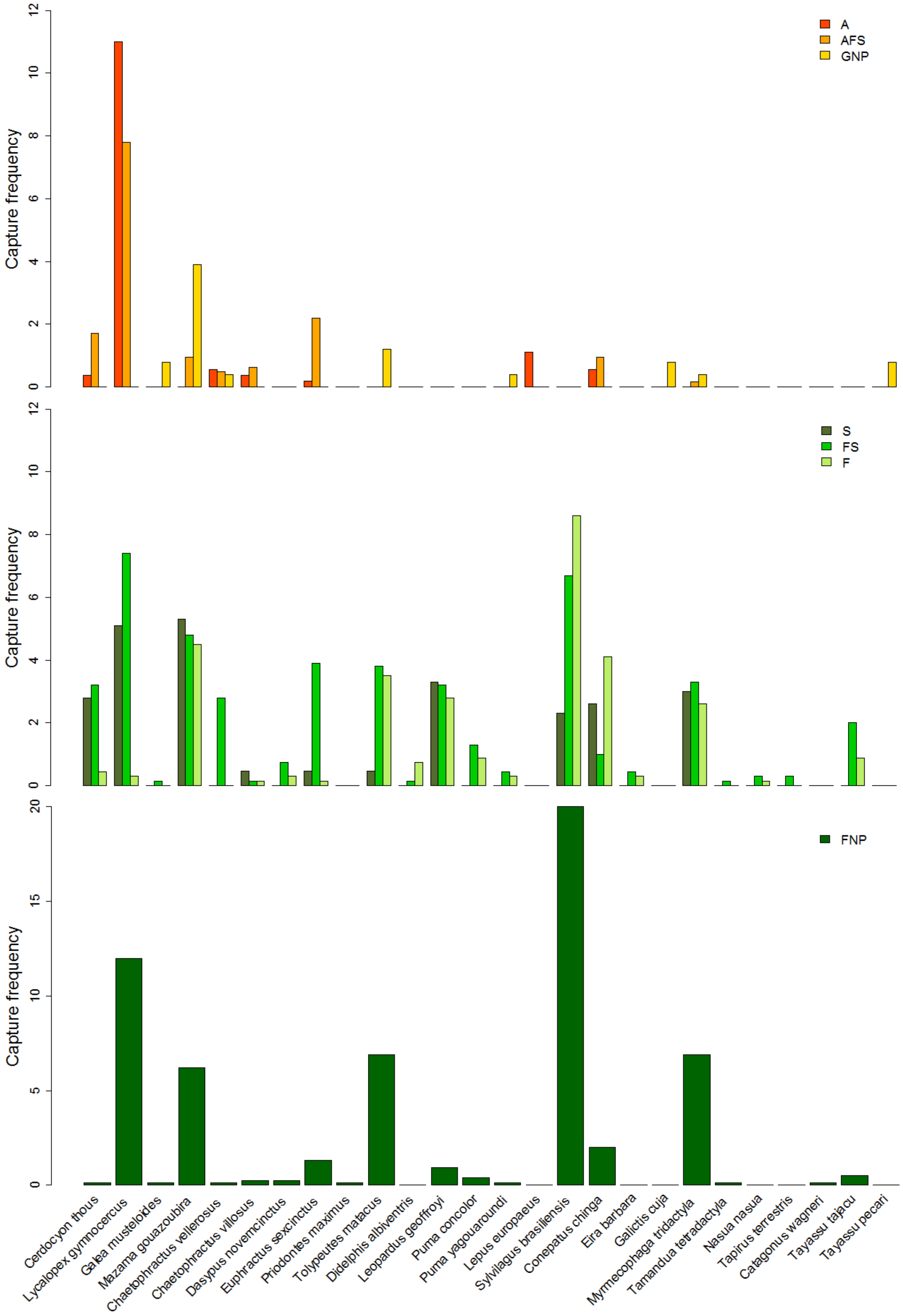
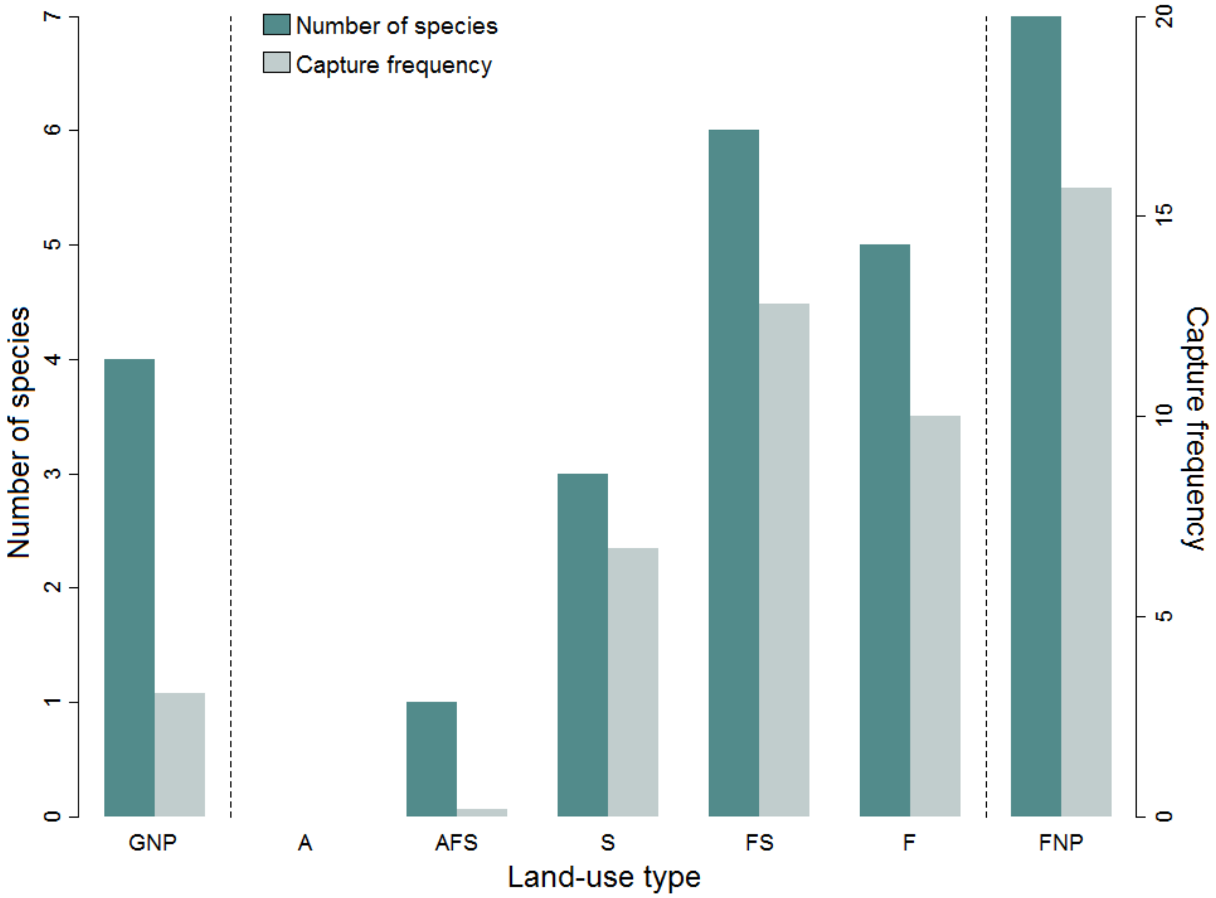

Capture frequency
0
2
4
6
8
10
12
A
AFS
GNP
Capture frequency
0
2
4
6
8
10
12
S
FS
F
Capture frequency
0
5
10
15
20
FNP
Cerdocyon thous
Lycalopex gymnocercus
Galea musteloides
Mazama gouazoubira
Chaetophractus vellerosus
Chaetophractus villosus
Dasypus novemcinctus
Euphractus sexcinctus
Priodontes maximus
Tolypeutes matacus
Didelphis albiventris
Leopardus geoffroyi
Puma concolor
Puma yagouaroundi
Lepus europaeus
Sylvilagus brasiliensis
Conepatus chinga
Eira barbara
Galictis cuja
Myrmecophaga tridactyla
Tamandua tetradactyla
Nasua nasua
Tapirus terrestris
Catagonus wagneri
Tayassu tajacu
Tayassu pecari

Figure 3.7.


Number of species
Capture frequency
Number of species
0
1
2
3
4
5
6
7
Capture frequency
0
5
10
15
20
GNP
A
AFS
S
FS
F
FNP
Land-use type

3.5. Supplementary information

Land cover map for 2013

A land cover map was derived from three Landsat 8 OLI/TIRS scenes (path: 228, Row: 78; 30-m pixel size) for 2013 (30th July, 17th October, 3rd November), and one scene for 2014 (7th February) in order to account for changes in the phenology of the vegetation and facilitate the classification. Cloud free images were obtained from the United States Geological Survey website (http://glovis.usgs.gov/), and re-projected to UTM 20 South using software ArcGIS 9.1 (ESRI 2005). Six multispectral bands (3 visible bands, the near-infrared band and 2 medium infrared bands) from all images were combined into a single stack of 24 layers. Land cover maps were produced through a supervised classification scheme based on ground truth data taken during the camera trap sampling period and complemented with Quickbird images available in Google Earth (earth.google.com). Training areas for five different classes were digitized on the raw images using Quantum GIS 2.0.1 (QGIS Development Team 2014). From the total training sites per class, a random sample of 70% of the pixels was selected to run the classification. The remaining 30% was used to validate the map. Five classes were mapped: natural grasslands (native grassland vegetation occurring in the sandy soils of ancient river beds or in forest gaps generated by fire, and dominated by *Elyonorus* cf. *adustus*, *Trichloris crinita, Gouinia latifolia,* and *Setaria macrostachya,* Tálamo et al. 2012); primary forest (well preserved primary xerophytic forest and old-growth secondary forest formed by *Schinopsis lorentzii, Aspidosperma quebracho-blanco, Bulnesia sarmientoi, Ziziphus mistol, Prosopis alba and Prosopis nigra*, Cardozo et al. 2011; Tálamo et al. 2012); silvopasture (included silvopasture management, highly modified forests stands and secondary forest); agriculture (included several crops in different phenological stages: wheat, soybean, sorghum, maize, sunflower, oats, cotton, and also bare soil); and pastures (exotic perennial pastures dominated by the dwarf variety of *Panicum maximum* (Gatoon Panic)). Images were classified using a Maximum Likelihood algorithm in the software ERDAS 9.1 (ESRI 2005). To eliminate small misclassifications, patches of less than four pixels were assigned to the dominating surrounding class. Maps were validated with error matrices, overall accuracies, user's and producer's accuracies and the area adjusted kappa statistics (Congalton 1991; Foody 2002; Olofsson et al. 2013).

Commission and omission errors ranged between 0.6 - 42.2, and 0.1 – 45.3 respectively for all the classes. The overall classification accuracy of the map was 90.14 % with an overall area adjusted Kappa statistic of 0.86.

Table 3.S1. Pearson's correlation matrix for local and landscape scale variables. Measured metrics were calculated using the software QGIS (AREA and EDGE), and software Fragstats. Non significant correlations are indicated in bold red.

	AREA	**EDGE**	**FC 500**	**FC 1000**	**FC 1500**	**FC 3000**	**H 500**	**H 1000**	**H 1500**	**H 3000**
AREA	1.000									
EDGE	**-0.050**	1.000								
FC 500	0.640	**-0.090**	1.000							
FC 1000	0.650	**-0.100**	1.000	1.000						
FC 1500	0.750	-0.170	0.880	0.900	1.000					
FC 3000	0.810	**-0.170**	0.750	0.780	0.940	1.000				
H 500	-0.620	**-0.170**	-0.800	-0.800	-0.720	-0.620	1.000			
H 1000	-0.270	-0.600	**-0.130**	**-0.120**	**-0.090**	**-0.100**	0.570	1.000		
H 1500	-0.470	-0.470	**-0.160**	**-0.160**	-0.210	-0.290	0.450	0.790	1.000	
H 3000	-0.690	-0.230	-0.350	-0.360	-0.450	-0.540	0.480	0.510	0.840	1.000

AREA: area of the land-use patch (ha.).
EDGE: distance to the nearest edge (metres).
FC- 500, 1000, 1500 and 3000: percentage of forest cover within each radii.
H- 500, 1000, 1500 and 3000: land-use diversity measured with Shannon-Weiner index, basically a measure of proportion of different habitats within each radii.

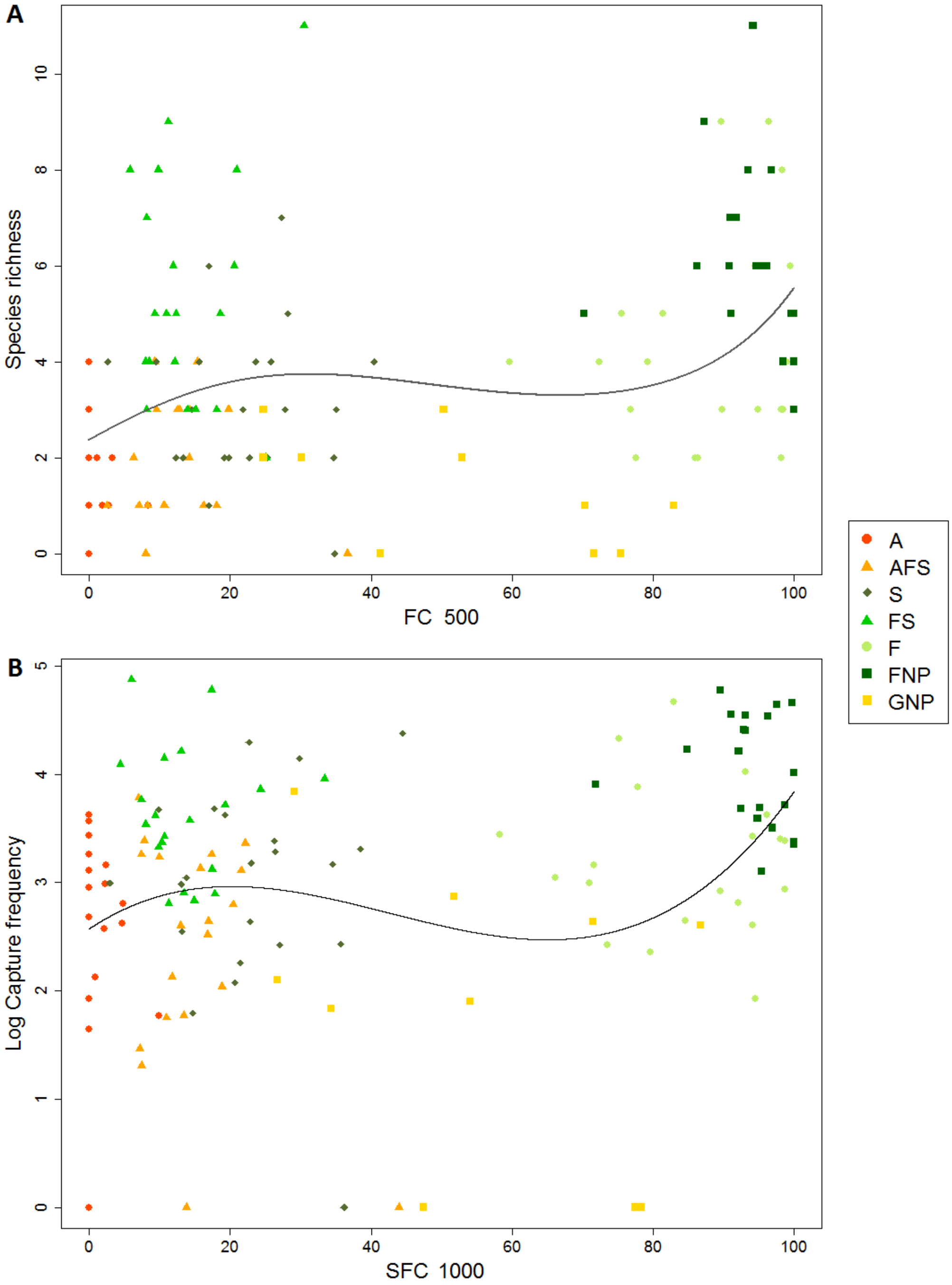


Figure 3.S1. Mammal diversity metrics and landscape variables. A) Species richness response to forest cover within 500 metres (FC 500) from the camera trap site. B) Capture frequency (log transformed) response to forest cover within 1000 metres (SFC 1000). Each point represents a site with the shape and colour of the character indicating land-use type. The line represents the predicted response according to the best model selected for each variable.

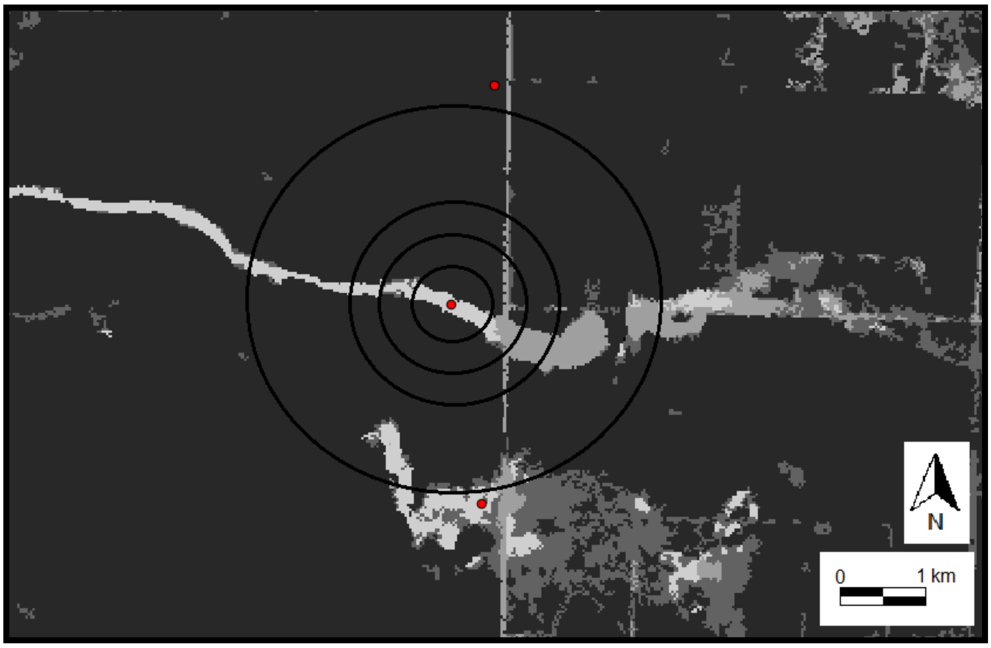


Figure 3.S2. Detail of one camera trap site located within grassland in National Park (GNP). Red dots mark a camera trap station. Concentric circles indicate buffers at 500, 1000, 1500 and 3000 metres from the point for which proportion of forest cover was measured. Pale grey: natural grassland; grey: agriculture; the two darkest grey shades belong to forest (primary and secondary).

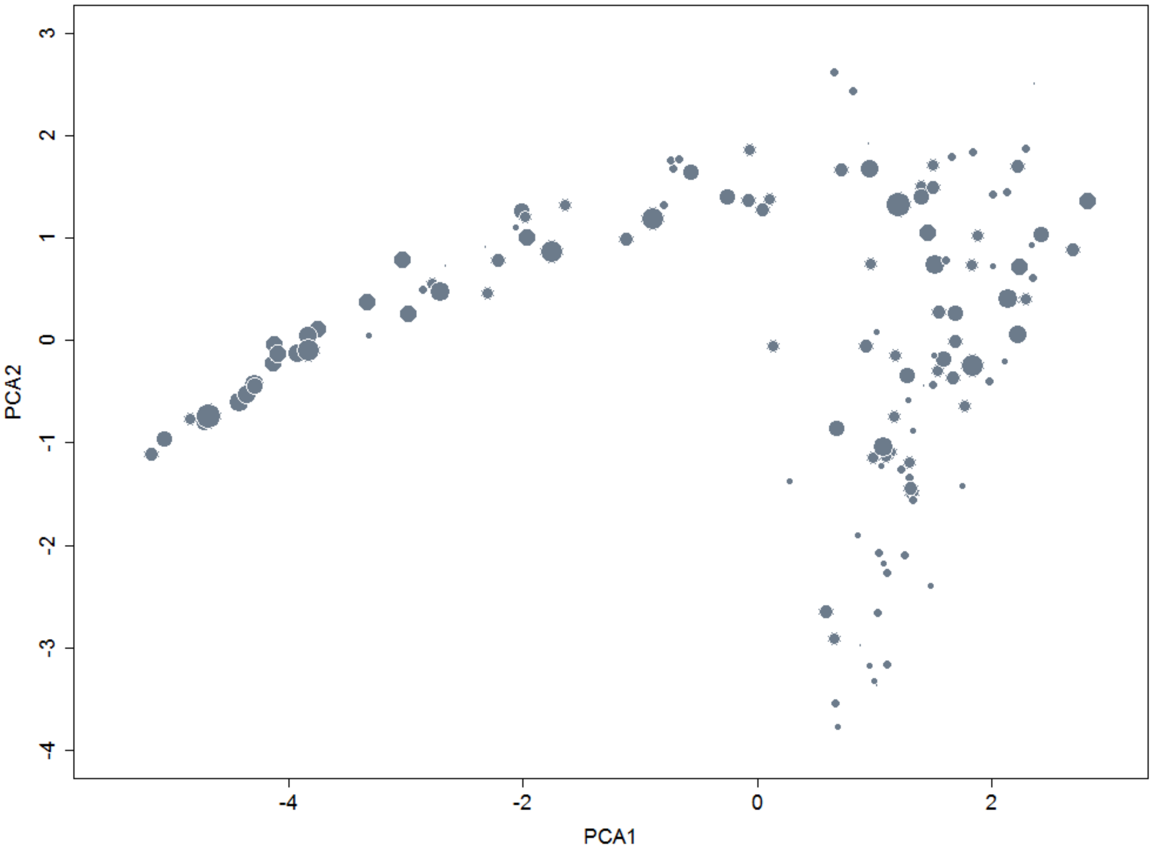


Figure 3.S3. Principal Component Analysis plot obtained for forest cover and land-use diversity variables. A distinctive horse-shoe effect is noticeable along the second axis. Bubbles represent each of the sites sampled, with their size matching the value of species richness for that site.

Agricultural environments in the semiarid Chaco[5]

4 BALANCING BIODIVERSITY AND AGRICULTURAL PRODUCTION: CONSERVATION OF BIRD AND MAMMAL COMMUNITIES IN AN AGRICULTURAL FRONTIER

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[5] Pictures by the author, otherwise stated in brackets. From left to right: Soybean field-forest edge; Silvopasture; Soybean field in the front and forest being burned further behind; White quebracho *Aspidosperma quebracho-blanco* standing alone in a soybean field; Agriculture field edge, a grey brocket deer, in the front, and some Chaco chachalacas, in the back, ventured out from the forest strip (Blas Fandiño).

Summary

Large areas once occupied by natural ecosystems are being transformed to cropland and pastures worldwide. Moreover, the United Nations' Food and Agriculture Organization (FAO) recognise that by the year 2050, the demand of food and goods will increase by 70%. The expansion of agribusiness for crop production and cattle ranching in the South American Chaco in particular has resulted in one of the highest rates of global forest loss. In this scenario, land use planning and the strategic assessment of agricultural landscape design is crucial to accommodate food production and manage resources in a sustainable fashion while minimizing negative impacts on species diversity. We studied the relationships between gradients of agricultural intensification (with associated profitability) and species richness, abundance, and community integrity in birds and mammals in the Chaco Region. Biodiversity data for both taxa and agricultural productivity data were recorded in six different land-use types during a three year period (2011-2013). We analysed crop and meat production to evaluate the relationship between land use management and economic revenue, and we related those results with diversity measures for birds and mammals to understand the trade-offs between agricultural productions and biodiversity. The economic revenue obtained from each land-use type differed markedly from extensive practices, with intermediate-to-high intensification, to industrialized silvopastures and agriculture plots. All diversity measures for both bird and mammal assemblages were negatively associated with profit increases but trends differed among taxa. Overall, bird diversity was highest in primary forest and kept similar values for low- to intermediate-profit management practices. It was only at much higher levels of intensification that dramatic declines in bird diversity were observed, with an average 90% reduction in species richness, abundance and community integrity for highly intensified land uses. Diversity values for the mammal community changed gradually: a significant increase in profit (from extensive cattle ranching to low-intensity silvopasture systems) caused a 40% decline in species richness and abundance, and a 20% change in community integrity. Whereas a further 36% increase in profit (from silvopasture to mechanized agriculture) produced a 45% decline in the number of species and individuals and 70% change in community composition. Although broadly, our results highlight that there are important differences in the species' responses and

validate the need of considering more than one unique group to evaluate the effects of habitat alterations on biodiversity. We conclude that a combination of land sparing and wildlife-friendly farming provides the best compromise between biodiversity and profit.

4.1. Introduction

Across the globe, land conversion of natural ecosystems for human activities has been proposed as one of the major causes of biodiversity loss and threaten of ecosystem functions (Tilman 1999; Sala 2000; Foley et al. 2005). Worldwide agricultural production is projected to double over the next 50 years in response to human population demands, increasing direct and indirect negative impacts on biodiversity (Balmford et al. 2005).

Recently, the study of the potential integration of conservation and food production has been divided between two main strategies: a land sparing approach, and a combined wildlife-friendly farming approach (Figure 1.1, see Chapter 1) (Green et al. 2005). In land sparing, wildlife conservation and agricultural production are maintained in separate locations with high yield and heavily mechanized agriculture in areas not expected to sustain high biodiversity levels. In turn, unmodified habitats, are set aside ("spared") for biodiversity conservation. Alternatively, wildlife-friendly farming combines conservation and agriculture, promoting low impact practices (e.g. reduced use of agrochemicals) and increasing fine-grain heterogeneity (e.g. including patches of native vegetation scattered throughout the landscape). Land sparing is typically managed for commodity production maximizing yield per unit area, whereas wildlife-friendly farming reduces yields, therefore, larger areas are required to meet a given production target.

The challenge for ecological research is to identify the most appropriate land management strategy for an area that attains effective biodiversity conservation in the face of land-use change driven by agriculture. Green et al. (2005) proposed a model to quantify the trade-offs between species diversity and yield, based on the assumption that the ecological and biological characteristics of the species determine the shape of the response along the intensification gradient. The model highlights two basic patterns: if diversity metrics for a given community fall dramatically with little habitat disturbance (Function type I in Figure 1.1, Chapter 1), then land-sparing is the best option. However, if species are resilient to low levels of disturbance and a sharp decline in species diversity is only observed at much higher levels of intensification (Function type II in Figure 1.1, Chapter 1), then wildlife-friendly farming would be the most appropriate approach to concurrently achieve conservation and production objectives. Framed in this dichotomy, different studies have supported land sparing (Balmford et al. 2005; Green et al. 2005; Ewers, Scharlemann, et al. 2009) or wildlife-friendly farming (Dorrough et al. 2007; Makowski et al. 2007; Clough et al. 2011; Tscharntke et al. 2012). However, these attempts have not always covered the whole range of possibilities. Based on their study in oil palm plantations, Koh et al. (2009) proposed to expand the approach to incorporate discontinuous responses in which dramatic changes in ecosystem composition results from a small increment in the intensification level (Function type III in Figure 1.1, Chapter 1). Perfecto and Vandermeer (2012) also pointed out that factors other than biodiversity (e.g. socio-economic needs of the smallholders living in the agricultural landscape) should be considered when using this framework to decide the best strategy for conservation and production.

In this context, the South American Chaco provides a good setting to study the relationship between biodiversity and revenue coming from agricultural production. The semiarid Chaco Region has suffered intense transformation from agricultural development and cattle ranching (Bucher & Huszar 1999; Gasparri & Grau 2009; Portillo-Quintero & Sánchez-Azofeifa 2010) and is one of the least studied and protected ecosystems in the continent. Furthermore, since 1970, this region has suffered the combined consequences of an increase in rainfall, which has eliminated environmental limitations for crop growth; a rise in agricultural commodity prices that generates high profits; and the adoption of new technologies, like genetically modified crops, chemical fertilizers and pesticides, that provide high-yielding cultivars and lower production labour costs (Grau et al. 2005; Torrella & Adamoli 2006; Zak et al. 2008).

The expansion and intensification of agriculture in former forested areas generated a growing concern for the potential biodiversity loss in natural habitats and, as a consequence, a “Forest Law” was enacted in 2007. From this point, environmentally-sensitive farming was encouraged by favouring less intensive silvopasture practices over intensive agricultural management. In addition, regulations were put in place to maintain forest strips between agriculture plots, and to protect existing forest patches. The resulting landscape design presented a combination of spared land for biodiversity conservation (forest patches and forest strips) and shared land with a less intensive management approach (silvopasture) as well as intensively produced croplands.

The availability of empirical information is important to understand the benefits and limitations of land-sparing and wildlife-friendly farming to provide appropriate guidelines in accordance with the local conditions. To our knowledge only two previous studies have assessed the relationship between biodiversity and yield in agricultural systems of the Chaco Region (Mastrangelo & Gavin 2012; Macchi et al. 2013). Both studies found that bird richness remained relatively high for low and intermediate levels of intensification, favouring the integration of environmental-friendly practices into the production system. However, their results differed when analysing community similarity; whereas Mastrangelo and Gavin (2012) results supported the same strategy as for species richness, Macchi et al. (2013) found that even low intensification levels resulted in highly altered bird assemblages. Bird community has been the focus of extensive research given its well know biology and the accessible sampling techniques employed for studying it. Here, we investigate the relationship between production revenue (i.e. economic profit) and bird community data gathered in the semiarid Chaco Region, and we also provide the first assessment for medium- and large-sized mammals in the context of the land sparing/land sharing approach. Examining community diversity metrics from these two taxonomic groups would shed light on the question of whether any of the proposed strategies is suitable to achieve conservation and agricultural targets.

We met four critical points that would allow us to meaningfully assess the biodiversity-yield relationship (Phalan, Balmford, et al. 2011): (1) both taxa were extensively sampled across the land-use gradient, from highly disturbed to pristine habitats; (2) community-wide metrics were calculated to consider optimal farming solutions at the community level; and (3) quantitative measures of crop yield were combined with meat production to obtain direct information of the economic output per site, facilitating the integration of different production systems in the land-use intensification gradient; (4) measurements of biodiversity in a baseline habitat (i.e. forest inside National Park) was included. In this chapter we specifically aim to assess the responses of community measures (species richness, abundance and community integrity) for birds and mammals along the gradient of production profit, to analyse economic profit differences between farming systems, and ultimately, to evaluate a potential unified strategy that takes into account the ecological requirements of two distinctive taxonomic groups. Agricultural production–biodiversity relationships of these two taxa across the range of existing land uses in the semiarid Chaco Region would increase understanding of the response of biodiversity to human managed habitats, and in turn, would be useful to inform decisions on the adoption of land sparing and wildlife-friendly farming to preserve biodiversity and improve sustainability.

4.2. Methods

Study area

The study area comprises about 600,000.00 ha of an agricultural landscape in the western limit of Chaco Province (26° 24’ S, 61° 09’ W), and an additional portion of c. 118,120.00 ha of protected forest and grasslands in Copo National Park (25° 46’ S, 61° 47’ W), Santiago del Estero Province, Argentina. The area is part of the “Gran Chaco”, one of the most extended seasonally-dry forests in South America. The Semiarid part of Chaco Region in Argentina was once a mosaic of dense forest and grassland (Morello & Saravia-Toledo 1959; Bucher & Huszar 1999; Morello et al. 2006), however after more than three decades of unplanned use of the resources and forest clearing, much of the region is now reduced to degraded forest patches inserted in a matrix of arable fields, implanted pastures and agro forestry managements (Zak et al. 2004; Aizen et al. 2009; Aide et al. 2013). Currently the area represents one of the most active and expanding agricultural frontiers in Argentina (Zak et al. 2008; Aide et al. 2013; Piquer-Rodriguez et al. 2015), and in consequence it has been the focus of active political debate centred in the conflict between modern agriculture production and nature conservation.

The topography of the area is predominantly flat; the climate is seasonal semiarid, with rainfalls concentrated in summer. Mean annual temperature is around 22°C, with maximum temperatures above 45°C (Cabrera 1971). For more details about the study area refer to Methods in Chapters 2 and 3.

Bird and mammal surveys

Birds and mammals were surveyed in sites spread across the agricultural landscape as well as in control sites inside Copo National Park. We sampled in five land-use types that appropriately represented the range of environments and production systems in the area (agriculture (A); agriculture with forest strips (AFS); silvopasture (S); forest strip (FS), and forest (F)). Additionally to quantifying biodiversity across the range of farming systems, we took samples inside the National Park that were considered as a baseline (Phalan, Balmford, et al. 2011), given the relatively good status of conservation of the forest stand (Tálamo et al. 2012).

Birds were sampled during spring in 2011 and 2012 in a total of 55 sites, 10 in each of the land uses for the agricultural landscape (A, AFS, S, FS, and F) and 5 sites in FNP. Each randomly selected site encompassed a homogeneous habitat. All birds seen or heard during a 10 minutes period were registered using a point count methodology (100 m fixed-radius) (Hill 1973; Hutto et al. 1986; Bibby et al. 1992; Sutherland 2006). Mammals were sampled using camera traps deployed from July to December in 2012 and 2013. The same arrangement of land-use categories surveyed for birds were used for mammals, with 20 replicates per land use (A, AFS, S, FS, F and FNP). Sites sampled for this taxon were also randomly selected. Camera-traps were attached to trees or wood poles, no bait was used, and vegetation was cleared in front of the camera to facilitate the recognition of species and individuals. An averaged 32 (± 11) camera-trap nights (CTNs) per site resulted in a total effort of 4281 CTNs. For a detailed explanation of the bird and mammal sampling methods refer to Methods in Chapters 2 and 3 respectively.

Profit assessment

We analysed crop and meat production for all sites (55 for birds and 120 for mammals, from which 41 overlapped in both studies). We obtained data on production (mean harvested mass in tonnes per year) of four of the most frequent crops found in the sites visited (soybean; corn; sunflower, and sorghum, Table 4.1.A). Cotton and oats fields were present in very low numbers and were considered as soybean to facilitate calculations. Given that both taxa were surveyed in a different sequence of years (birds: 2011-2012; mammals: 2012-2013) and that crop rotation is a frequently adopted practice in the area, even those sites with shared bird-mammal sampling resulted in a different combination of crops (for instance, if the sequence of planted crops for a given site surveyed for both taxa was: soybean to corn to sorghum in 2011, 2012 and 2013 respectively, then yield will be the averaged combination of soybean-corn for birds and corn-sorghum for mammals generating a slight variation in the revenue). Similarly, we calculated livestock production (mean meat in kilograms per year) for the whole range of cattle ranching alternatives, from extensive systems inside forest patches to more industrialized silvopasture plots (Table 4.1.B and C). Sites in protected forest (FNP) and inside forests strips were assumed to have zero production, although in some cases there was small number of cattle foraging in these environments.

Crop and meat production were converted from mass to economic output (United State dollars per hectare per year, US$ ha^{-1}.year^{-1}). We used it as a proxy of yield to facilitate comparisons and combinations among land uses, and we refer to it throughout the chapters as profit (Balmford et al. 2005; Phalan, Balmford, et al. 2011). In the case of agriculture, profit was calculated for each site as the economic input derived from the production averaged for both years (Supplementary information Table 4.S1). For livestock production, the difference in the capacity to produce meat was given by the technological level and development of the ranch. In this case, profit reflected the average yearly revenue obtained in each site (Supplementary information Table 4.S1).

Biodiversity measures

We computed three community diversity measures: species richness, abundance and community integrity. Bird and mammal species richness for each site was calculated as the observed number of species. The total number of bird individuals registered in a given site was considered as the total abundance for that site. Whereas for mammals we incorporated differences in sampling effort among sites by calculating a relative abundance index: capture frequency was the number of independent captures divided by the number of CTNs for that site, standardizing the value to 100 CTNs. Images sequences were considered independent if they contained different individuals or if they were separated by an interval longer than 1 hour.

Following Ewers et al. 2009, and Banks-Leite et al. 2014 we calculated the averaged similarity of community composition relative to the control sites (FNP) using the Sørensen index, that measures incidence-based similarity between ecological communities (Magurran & McGill 2011), we called this measure “community integrity” (Banks-Leite et al. 2014) . The

Sørensen index takes values between zero and one, with zero indicating that a community has no species in common with the control sites, and one representing an assemblage similar to those found inside protected forest. Some level of natural turnover is expected even among control sites due to the heterogeneity in the environment and natural differences among sites; therefore, we re-scaled the values of similarity among sites in FNP to equal the mean value of Sørensen index for those sites. Sørensen similarity values were calculated using the package “vegan” in R v.3.1.1 (Oksanen et al. 2012; R Core Team 2014).

All three diversity measures were calculated using the pooled data for both years in which each group was sampled.

Statistical analysis

We analysed per area annual productivity variations among land-use types by comparing means of profit at site level. We used general linear models (LM) and *a posteriori* multiple comparisons using Tukey’s HSD tests to determine the significant differences among land uses. Normality and homogeneity of variance were checked using standard graphical methods (Quinn & Keough 2002; Crawley 2007).

We fitted separate biodiversity-profit functions for each taxa with species richness, abundance (or capture frequency for mammals), and community integrity as the response variables, and profit as the predictor variable. We assessed whether these measures were best described by a convex, concave or sigmoid function (Type I, II or III curves in Figure 1.1, see Chapter 1). We used alternative formulations of linear and non-linear functions (Supplementary information Table 4.S2) to test a wide range of shapes for the curves relating diversity to profit. Bird and mammal diversity measures were modelled using Generalized Linear Models (GLM) for linear, quadratic and cubic polynomials of the response variable. Error distribution for species richness was modelled with Poisson and log-link, whereas abundance and community integrity were modelled with normal distribution. Other exponential and logistic functions were fitted using non-linear regression (nls). Only capture frequency was log transformed to achieve normality of the residuals. GLMs were run in R v.3.1.1 (R Core Team 2014) using package “lme4” (Bates et al. 2014). To find the value of profit that separated the diversity data in distinctive levels we run a *post hoc* tree model analysis in R using package “tree” (Ripley 2014; Crawley 2007).

To select the best fitting function for each variable we employed the Akaike Information Criterion value corrected for small samples (AICc), and delta AIC (Δ AIC) and Akaike weights (w), which we used in model comparisons (Burnham & Anderson 2002; Crawley 2007). We also report the explained deviance (pseudo-R^2) as a measure of the explanatory power of the models.

4.3. Results

Production intensity gradient and profit

In sites where we measured diversity of birds and mammals, mean annual profit ranged from zero to c. 435 US$ ha^{-1} with a similar pattern of differences between land uses for both groups (comparing profit among land uses: $F_{5,49}$=236.8 birds, and $F_{5,115}$=641.5 mammals, p<0.001). Sites inside forest categories (FS, F, and FNP) produced the lowest profit with protected forest and forests strips generating zero direct revenue, and a non-significantly higher profit made in forests used for extensive livestock production (mean profit of 4.2 and 2.9 US$ ha^{-1}.year^{-1} for birds and mammals respectively, Table 4.2, Figure 4.1). Silvopastures followed the gradient of intensification with a profit c. 82 times higher than that in forests for both birds and mammals (Table 4.2, Figure 4.1). The following transition from silvopastures to agriculture was much more moderate yet significant, increasing c. 150 US$ ha.$^{-1}$ year^{-1} for bird sites and c. 68 U$S ha.$^{-1}$year^{-1} for mammal sites, whereas, as expected, different types of agriculture had the highest profit in the whole range, and revenue was similar for the two types of arable systems (A and AFS) (Table 4.2, Figure 4.1).

Birds, mammals and profit relationships

We registered a total of 126 bird species (5067 individuals) and 26 medium- and large-sized mammal species (1367 independent captures) in the agricultural landscape and the protected forest (Table 4.3).

All bird diversity measures showed significant correlations with profit. Species richness ($F_{1,53}$=78.6, p<0.001), abundance ($F_{1,53}$=19.0, p<0.001), and community integrity ($F_{1,53}$=159.5, p<0.001) decreased abruptly in high-profit land uses showing values about 85-90% lower than in forested habitats. Species richness and abundance initially increased with low levels of intensification (4% increase in species richness, and 35% increase in abundance), showing a local maximum, whilst community integrity responded always negatively (20% decrease). However, these changes were not important enough to be significant. As a result, the best selected model describing the data was a logistic (sigmoid) function (Table 4.4), indicating that low and medium levels of land-use production did not alter significantly the bird assemblages up until a point were higher intensification resulted in a sharp decline in the number of species and individuals, and a significant change in community integrity (Figure 4.2.A to C). The value explaining the maximum deviance in the tree model was 360.35 U$S ha.$^{-1}$year^{-1}, indicating that any production system with profits above that threshold were expected to have a significant negative impact in the bird assemblage in this landscape.

Overall for the mammal community, diversity measures declined with agricultural intensification. However, this decline followed a different pattern for each measurement (Figure 4.3), and an inflexion point was not as clear as the one observed for birds. The number of species and capture frequency for mammals decreased around 70% from FNP to agriculture land uses ($F_{1,119}$=533.4, p<0.001; $F_{1,119}$= 52.9, p<0.001), and community composition changed around 50% ($F_{1,119}$= 109, p<0.001). Mammal species richness showed a similar response to bird species richness, as it was best fitted by a logistic model (Table 4.4) with an S-shaped curve (Figure 4.3.A) that presented a threshold at 239.55 U$S ha.$^{-1}$year^{-1}. Capture frequency maintained a relatively high number of species in low- and intermediate-intensity systems, and decreased the most in high-intensity systems (Table 4.4, Figure 4.3.B).

The best model for community integrity of mammal species (ΔAIC=0, and w=0.31) was represented by an exponential function (Table 4.4), although a linear model also had a good fit to the data (ΔAIC=0.6, and w=0.23). We maintain the exponential model as the selected one since it showed a higher probability (w) of being the best model, and also because the number of parameters estimates in both models was the same. However, we acknowledge that the decreasing trend may not be as steep as the function type would be indicating (Figure 4.3.C).

4.4. Discussion

Profitability gradient of the agricultural landscape

The economic revenue obtained in each type of production management in the study area showed a marked division between very-low intensification practices and intermediate-to-high intensification practices. In turn, this resulted in a gradient of profit lacking intermediate values, despite having used several measures to capture as much variability as possible in the calculation (e.g. crop rotations and silvopasture categorization, see Table 4.1.A to C, and Table 4.2). Using averaged estimates to calculate net profit doubled this effect. On the one hand, mean values are appropriate as yield commonly fluctuates between years depending on climate, with dry years resulting in poor harvests, therefore profit calculated for a period of time more accurately represents the economic revenue of agricultural activities. On the other hand, averaged values could have masked significant differences in crop types and silvopasture categories because values of costs were available only for some crops and some categories of ranches. However, all land-use types under production generated different yearly economic revenue, with the exception of the two agricultural systems.

Several different options could be considered to smooth the relationship between land-use type and profit. First, in this study A and AFS did not vary significantly in their economic gain because profit was considered by area and time unit (i.e. U.S dollars per hectare per year) and only gains coming from farmed areas were used in the calculations. If a measure of profit incorporating the total area of the plot would have been used instead, then AFS would have had lower profit. This approach is similar to consider the profitability of a landscape rather than specific land-use types. The question in this case would be if locally sparing land would reduce profit significantly and increase biodiversity in the system at the same time (Balmford et al. 2012), in which case the shape of the biodiversity-profit function should not change. However, if the reduction in profit is non-significant but a considerable increment in biodiversity is achieved, then the relationship would be significantly altered. A similar idea with a different approach was studied in cacao agroforestry systems in Indonesia (Clough et al. 2011) where the biodiversity-yield relationship was not affected by the landscape context.

Second, low-to-intermediate intensity practices should be added to the profit gradient. In this study, low intensification practices were represented by a few sites with extensive livestock production. Any other low or intermediate intensification practice was too scarce to be considered in the sampling design. Macchi et al. 2013 collected relevant production data from low intensification silvopastoral systems (locally called “puestos”) and from grasslands in a nearby area in the semiarid Chaco. However, those land-use types were not common in our area. Probably, the advanced conversion of land and reduction of forest patches made extensive cattle ranching impracticable in our study area.

Third, economic revenue coming from systems different than agricultural ones could also be included. For instance, profit coming from nature-based tourism activities developed in Copo National Park. Currently, admission to National Parks in Argentina are free of cost, yet indirect regional economic returns could be taken into account by considering the money spent in hotel bookings, restaurants, and other local businesses that could benefit from tourism and the outdoor recreation industry (Heberling & Templeton 2009).

Several studies working with economic revenues from agricultural activities presented similar values of profit, confirming that our calculations were representative. Banks-Leite et al. 2014 reported a median gross profit of 467 US$ ha^{-1}year^{-1} for agricultural land in the Brazilian Atlantic Forest, whereas Koh et al. 2009 found that farmers in Indonesia collected from corn an average 580 US$ ha.$^{-1}$ during 2006. More local and closely related studies reported similar meat production values for silvopasture systems (Mastrangelo & Gavin 2012), and agricultural land-use gradients (Macchi et al. 2013) in the Chaco Region.

Bird community relationships

In this study the development of human-managed production systems in the semiarid landscape of Chaco Region was associated with loss of bird diversity. These observations coincide with numerous studies worldwide (Aratrakorn et al. 2006; Gordon et al. 2007; Phalan, Onial, et al. 2011) and supports the theory of a trade-off between conservation and agricultural production (Green et al. 2005; Balmford et al. 2005; Ewers, Scharlemann, et al. 2009). As expected, bird community responded negatively to intensification, showing consistent similar patterns for the complete set of diversity measures under consideration.

Bird species richness, abundance and community integrity changed nonlinearly with increasing land-use intensification. The shape of the best-fitting functions obtained for each measure can be analysed as follows: the highest values of all measures are reached in low intensity land uses, not surprisingly protected forests and forest with relatively low disturbance levels (FS) had the most diverse and complete assemblages. When moving from low- to intermediate-intensity managements, bird community characteristics remain stable, indicating that wildlife-friendly farming would be a good strategy to maximize conservation and production. However, if intensification increases, the shape of the relationship changes and further interventions in the production system cause a rapid decline in bird diversity leading to a new state of equilibrium for the community.

Recent studies suggested either a land sharing (Mastrangelo & Gavin 2012) or a land sparing (Macchi et al. 2013) strategy for the Chaco region. Our results coincide with Mastrangelo & Gavin 2012 in that silvopastures (wildlife-friendly cattle production) support relatively well preserved bird assemblages, and therefore, this system would represent the best strategic option to maintain production and biodiversity integrated in the same landscape. Agroforestry schemes have been confirmed as valuable wildlife-friendly farming option mainly in developing countries (Mattison & Norris 2005) where profitable species of plants (i.e. cacao, rubber, coffee) and animals (i.e. livestock) can share resources and benefit from ecosystem services (Koh et al. 2009) provided by native plants (Dorrough et al. 2007; Makowski et al. 2007), insects, bats, and birds, among other vertebrates (Perfecto et al. 2003; Harvey et al. 2006; Fischer et al. 2008; Clough et al. 2011).

At the same time, our analyses uphold the findings of Macchi et al. 2013 in that higher modification and intensification accompany a detriment in bird assemblages composition in which case some land should be spared from production in order to guarantee the preservation of healthy bird communities including habitat specialist that rely upon resources only provided by unaltered forests or native patches of grassland (Aratrakorn et al. 2006; Kleijn et al. 2009; Phalan, Onial, et al. 2011).

Interestingly, all three measures of bird diversity responded with the same pattern to land-use intensification. Whilst variance in species richness and community integrity was small for all land-use types, the range in abundance values for silvopasture was wider and also held the highest mean abundance. The difference in the number of individuals registered in this environment is likely due to a methodological constraint. The lack of understorey vegetation could have facilitated the detection of individuals, whereas in forested land uses detection and identification relies mainly on sound as most of the individuals are hidden in the vegetation.

Overall, the results found for birds facilitate the analysis about which strategy is best to maximize production and conservation at the same time. In the case of bird assemblages in the semiarid Chaco landscapes, species richness, abundance and community integrity only show substantial declines at high intensification levels.

Mammal diversity-profit relationship

Our results provide the first direct, quantitative estimation of a profitability-biodiversity relationship for medium- and large-sized mammals in the semiarid Chaco Region. As was found in birds, variation in mammal community diversity showed a strong decline with increasing production intensity.

Mean mammal species richness was highest in unmodified forest patches and did not change in habitats converted to low-intensity production. However, with further modification of the habitat, the number of mammal species decreased sharply. It is important to notice that mammal species richness declined at a lower intensification level than that for birds, moreover, only two silvopasture sites presented species richness similar to unaltered forest, whereas the rest of sivopastures were mingled among high intensification agricultural plots presenting low number of species. This difference may arise for a few reasons: (1) birds and mammals did not share all the locations during sampling. In some sites only sampled for mammals, the profit generated in highly developed cattle ranches equalled the profit generated in intensively farmed areas. These cattle ranches presented similar structural characteristics to the ones that yielded lower profits, but employed diet supplementation and paddock rotation to improve productivity. With basically the same level of intervention in the environment, these highly developed cattle ranches obtained better revenues. (2) Costs associated to farming activities increased between 17-36% from 2011-2012 to 2012-2013 (Table 4.1.A) reducing the net profit of agriculture sites and closing differences in revenue between livestock production and farming. (3) Lastly, and more importantly, wildlife sensitivity to environmental changes are determined by their requirements and their tolerance to habitat alterations, and in turn, requirements and tolerance change for different groups depending on their ability to move throughout the landscape (Andrén 1994; Fahrig 2003). The response threshold for mammal species richness was found to be lower than the threshold for birds, indicating that intermediate intensification practices cause a significant decline in the number of mammal species.

The capture frequency-profit function indicated that small decreases in mammal relative abundance corresponded to small increases in profit between forest patches and low-intensity production systems. Further small changes in mammal abundance accompanied large profit increments between low- and intermediate-intensity silvopastures. This kind of win-win situation has been reported in agroforestry systems elsewhere, in studies focusing on large mammals (R. Cassano et al. 2012; R. Cassano et al. 2014) and other vertebrates (Perfecto et al. 2003; Harvey et al. 2006; Clough et al. 2011) where the heterogeneity of the habitat and the structure of the canopy cover provide key resources potentially benefiting the persistence and dispersion of this group in agricultural landscapes.

Community integrity among sites inside forest in National Park (i.e. the land-type taken as baseline) was lower for mammals (54%) than for birds (72%); however mammal community integrity decrease steadily with increasing profit. Highly intensified managements, producing the highest profits, had the lowest community integrity. In the Atlantic Forest of Brazil, R. Cassano et al. 2012 found highly valuable communities of large mammals inhabiting cacao agroforestry systems, where a high number of species and similar composition to primary forest was also accompanied by the presence of some endemic and threatened mammal species. However, they also recognised that potentially altered communities in control sites (i.e. “original” habitats impoverished by previous use and/or hunting pressure) may have an important role in the interpretation of the results and should be considered. In this study, an important number of threatened species were only registered in FNP and, albeit they presented very low numbers, their presence inside the National Park validate the use of this habitat as a reference to compare community integrity. Based in these results, the most suitable approach to balance production and conservation would be land sparing (Barlow et al. 2007; Harvey & González Villalobos 2007).

Diversity measures for the mammal community showed different responses along the gradient of production intensification. This results support the idea that more than a single strategy should be considered to achieve production targets and, at the same time, preserve mammal communities. The easiest way would be to adopt land sparing, excluding some areas from economic revenues and intensifying at the same time production in other lands. Nonetheless, this option neglects other important factors arising from environmental-friendly practices, such as, ecosystem services, smallholders' livelihood provision, and coarse-grain landscape connectivity.

Balancing strategies

This study represents a first step to understand the effects of land use intensification on the diversity patterns of birds and mammals, and to evaluate those effects in light of the land sparing versus wildlife friendly farming approach.

In the agricultural landscapes of semiarid Chaco Region wildlife-friendly practices generate lower revenues than high-yielding agriculture. Additionally, both communities of birds and mammals presented a negative association with land-use intensification, resulting in highly altered values of diversity for the most productive systems, and posing a consequent trade-off between wildlife conservation and productivity. Our results showed that bird and mammal communities in the semiarid Chaco can benefit from wildlife-friendly farming to maintain highly diverse assemblages favoured by the provision of habitat and resources at a local scale, and a heterogeneous matrix that facilitates movements and dispersion of individuals at landscape scale. At the same time, the exclusion of some areas from modification and production activities must be ensured in order to preserve a wider range of forest-dependent and threatened species. Overall this research supports the idea that wildlife-friendly farming and land sparing are not mutually exclusive options, but should be recognized to offer potentially complementary advantages for land management.

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Table 4.1.**A.** Agricultural input data used for calculations of profit per site in the study area. Mean yield values were calculated using information of average yields of each crop type harvested in Almirante Brown Department (Chaco Province, Argentina) during the period 2011 to 2013. Mean crop price represents FAS values (free alongside ship values) paid for grain in Argentina averaged for the period 2011 to 2013. Mean yield and mean price values were taken from the official website of the Ministry of Agriculture, Livestock and Fisheries of Argentina. Production costs represent labour costs associated to crop management (i.e. seeds, agrochemicals, machinery leasing). Values were available only for soybean and corn; therefore, we consider that sunflower and sorghum had the same costs as soybean given that corn is always the crop with the highest costs.

A	**Agricultural production**				
Crop type	**Mean yield (ton/ha.year)**	**Mean crop price (AR$/ton)**	**Production costs (AR$/ha)**		
	2011-2013	**2011-2013**	**2011**	**2012**	**2013**
Soybean (SB)	1.62	1571.28	636.10	810.35	998.42
Corn (C)	3.79	931.75	656.75	892.29	1075.22
Sunflower (SF)	1.68	1559.32	-	-	-
Sorghum (SG)	3.25	745.31	-	-	-
Source	1	2	3		

B. Cattle ranching input data used for calculations of profit per site in the study area. Cattle ranch type indicates the kind of management: subsistence livestock production in forest patches or more industrialized management in silvopasture plots. Each site inside either forest or silvopasture was classified accordingly to their level of intensification. The classification was made based on interviews with the owners, on professional assessment made by a local agronomist, and on personal knowledge of the sites. Sites were assigned to one of five categories based on the number of paddocks present (i.e. high number of paddocks means higher production associated to a bigger space and higher availability of pastures), and on diet supplementation. Mean cattle production was assessed based on interviews with the owners, and on information provided by a local agronomist of the National Institute of Agricultural Technology (INTA).

B	**Livestock production**			
Cattle ranch type	**Category**	**Number of paddocks**	**Supplementary fodder**	**Mean cattle production (kg/ha.year)**
Extensive, inside forest	0	0	No	10
Silvopasture	1	0	No	20
Silvopasture	2	1-2	No	90
Silvopasture	3	>2	No	250
Silvopasture	4	>2	Yes	400-500

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C. Cattle ranching input data used for calculations of profit per site in the study area. Mean cattle price is presented for each year and averaged. Values correspond to the General Index of Livestock Production (from the Spanish words: Indice General de Cria e Invernada, IGCeI). This index represents the averaged price paid per kilogram of live cattle. Production costs represent labour costs associated to cattle ranching (i.e. veterinary services, fodder, workers wages). Values were taken from the official website of the Ministry of Agriculture, Livestock and Fisheries of Argentina.

C	**Livestock production**				
		Year		**Mean value**	**Source**
	2011	**2012**	**2013**		
Mean cattle price (AR$/kg)	11.17	11.43	11.38	11.33	4
Production costs (AR$/kg)	-	6.66	8.53	7.60	4

The following table lists the websites where the input data, before mentioned in tables **A** and **C**, was taken from.

Source	**Website**
1	http://www.siia.gov.ar/_apps/siia/estimaciones/estima2.php
2	http://www.minagri.gob.ar/new/0-0/programas/dma/precios_referencia/precio_ref_acum/01_valores_acum_2012.php
3	http://www.margenes.com
4	http://www.minagri.gob.ar/site/ganaderia/bovinos/05=Mercados/01=Hacienda%20en%20Pie/index.php

Table 4.2. Productivity of land-use types sampled in the semiarid Chaco. Land management systems vary in size and annual production. Values show the averaged profit (± standard error) in sites surveyed for birds and mammals.

Land-use type	**Mean patch size (ha)**	**Birds**	**Mammals**
		Mean profit (US$ / ha. year)	**Mean profit (US$ / ha. year)**
Agriculture	297.1 ± 75.9	419.2 ± 5.0	360.8 ± 4.6
Agriculture with forest strip	67.0 ± 30.3	434.3 ± 5.1	366.2 ±4.6
Silvopasture	42.5 ± 6.8	285.6 ± 6.6	298.3 ± 4.8
Forest strip	12.2 ± 6.4	0.0 ± 0.0	0.0 ± 0.0
Forest	470 ± 237.5	4.2 ± 0.4	2.9 ± 0.4
Forest in National Park	118,118	0.0 ± 0.0	0.0 ± 0.0

Table 4.3. Summary statistics for bird and mammal diversity and economic output data registered for six representative land uses present in the semiarid Chaco Region. For each taxonomic group we present averaged values (± standard error) per land-use type of species richness, abundance, and community integrity. In the bottom row we show: total number of species for the whole survey for birds and mammals, total number of bird individuals, and total number of independent captures for mammals.

Land-use type	**Birds**			**Mammals**		
	Species richness	**Number of individuals**	**Community integrity**	**Species richness**	**Capture frequency**	**Community integrity**
Agriculture	4.6 ± 3.8	17.3 ± 20.3	0.03 ± 0.04	1.5 ± 0.9	15.5 ± 10.8	0.24 ± 0.03
Agriculture with forest strip	3.5 ± 1.3	10.3 ± 9.9	0.05 ± 0.04	2.1 ± 1.4	15.0 ± 11.7	0.26 ± 0.10
Silvopasture	41.4 ± 7.8	183.4 ± 66.8	0.51 ± 0.05	3.3 ± 1.5	27.5 ± 21.0	0.37 ± 0.13
Forest strip	39.3 ± 6.7	115.6 ± 22.8	0.55 ± 0.02	5.4 ± 2.4	44.6 ± 31.2	0.47 ± 0.12
Forest	42.3 ± 5.3	123.3 ± 28.3	0.61 ± 0.04	4.3 ± 2.2	30.0 ± 24.5	0.45 ± 0.11
Forest in National Park	37.8 ± 8.5	113.6 ± 36.2	0.72	6.2 ± 1.8	63.3 ± 30.4	0.54
Total	**126**	**5067**	**-**	**26**	**1367**	**-**

Community integrity was based on Sørensen index and shows the similarity of the community in each land-use type in relation to the assemblages found in forest sites inside the National Park (control sites).

Table 4.4. Summary of regression model selection applying the land sparing / wildlife-friendly farming approach for birds and mammals. Only the best minimum model for each predictor variable is shown. Each model shows the estimated parameters ± standard error. We report df: degrees of freedom for each model, AICc: Akaike Information Criterion value corrected for small samples; Δ AIC: difference in AICc values between each model and the best model, w: the percentage of model weight attributed to each model, and explained deviance (pseudo-R^2): as a measure of statistical significance.

Taxon	**Response variable**	**Best Model**	**Df**	**AICc**	**Δ AIC**	**W**	**Explained deviance**
Birds	Species richness =	40.8 (± 1.1) - 38.8 (+ 2.7) / (1 + exp (36.2 (± 0.4) - *profit*))	52	363.5	0.00	1.00	0.89
	Abundance =	136.9 (± 7.5) - 131.2 (+ 19.4) / (1 + exp (36.5 (± 0.8) - *profit*))	52	576.8	0.00	1.00	0.65
	Community integrity =	0.57 (± 0.01) - 0.54 (+ 0.02) / (1 + exp (36.9 (± 0.3) - *profit*) / 0.07 (+ 0.18))	51	-152.6	0.00	0.95	0.95
Mammals	Species richness =	1.8 (± 0.2) + 0.5 (+ 0.5) / (1 + exp (28.3 (± 0.9) - *profit)*)	117	489.3	0.00	0.39	0.46
	Log(Capture frequency) =	3.14 (± 0.07) - 5.9 (± 0.8) * *profit* - 2.0 (± 0.8) * *profit* ^2	117	294.9	0.00	0.64	0.89
	Community integrity =	0.52 (± 0.01) * exp(-0.017 (± 0.002) * *profit*)	117	-158.7	0.00	0.31	0.46

Figure legends

Figure 4.1. Mean economic output along the land use intensification gradient in the semiarid Chaco. Mean profit was calculated for each land-use, and separately for each taxonomic group given that (A) birds, and (B) mammals were sampled in different sites (represented by points, replicates). Thick lines represent the median, boxes represent the interquartile range and whiskers represent minimum and maximum values. Land-use types are sorted from the least to the most productive systems: FNP, forest inside National Park; FS: forest strip; F: forest; AFS: agriculture with forest strips; A: agriculture. Statistical differences in the mean of the variable are true when letters differ between factor levels (Tukey HSD at alpha= 0.5).

Figure 4.2. Diversity-profit functions for the bird community showing the changes in: (A) species richness, calculated as total number of species in each site, (B) abundance, calculated as total number of individuals registered in each site, and (C) community integrity, calculated as species composition per site (using Sørensen index) in relation to species composition in control sites (i.e. sites in forest inside National Park). Each point with a distinctive shape and colour represents a replicate for a given land-use type. The line represents the predicted values obtained from the best model selected for each diversity measure (Table 4.4). Points for some of the land uses overlapped (mainly those corresponding to profit=0 US$), therefore the shape and colour that predominates is the one belonging to the last land-use type added to the graph hiding underneath the rest of the points for other land uses.

Figure 4.3. Diversity-profit functions for the mammal community showing the changes in: (A) species richness, calculated as total number of species in each site, (B) capture frequency, calculated as the number of independent captures of all species present at a site per 100 camera trap nights, and (C) community integrity, calculated as species composition per site (using Sørensen index) in relation to species composition in control sites (i.e. sites in forest inside National Park). Each point with a distinctive shape and colour represents a replicate for a given land-use type. The line represents the predicted values obtained from

the best model selected for each diversity measure (Table 4.4). Points for some of the land uses overlapped (mainly those corresponding to profit=0 US$), therefore the shape and colour that predominates is the one belonging to the last land-use type added to the graph hiding underneath the rest of the points for other land uses.

Figure 4.1.

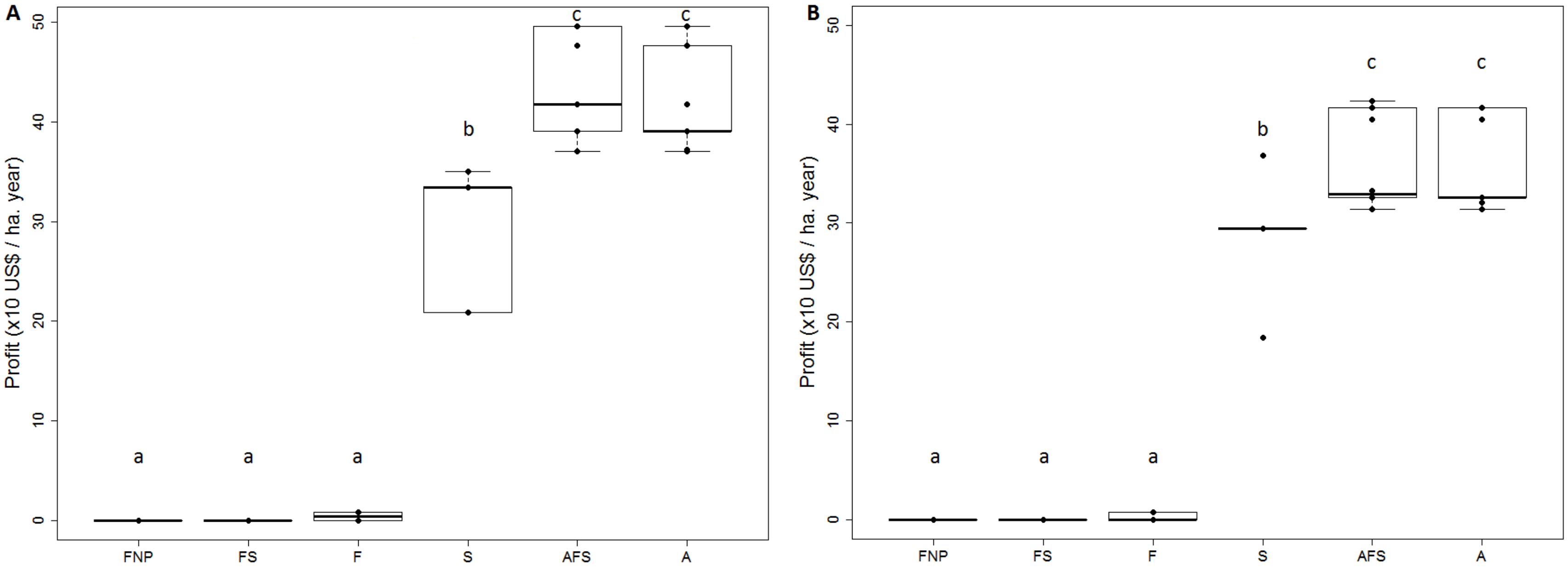


Figure 4.2.

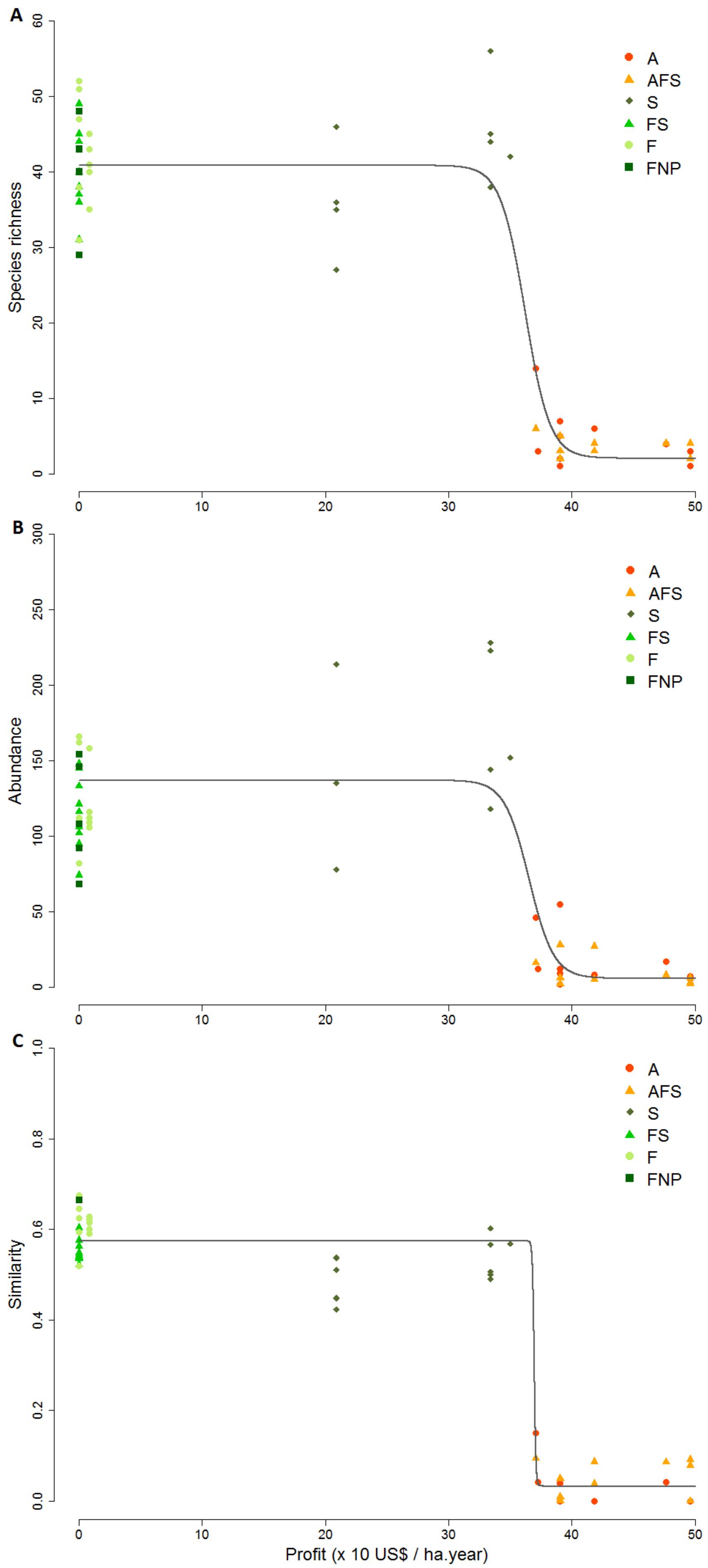
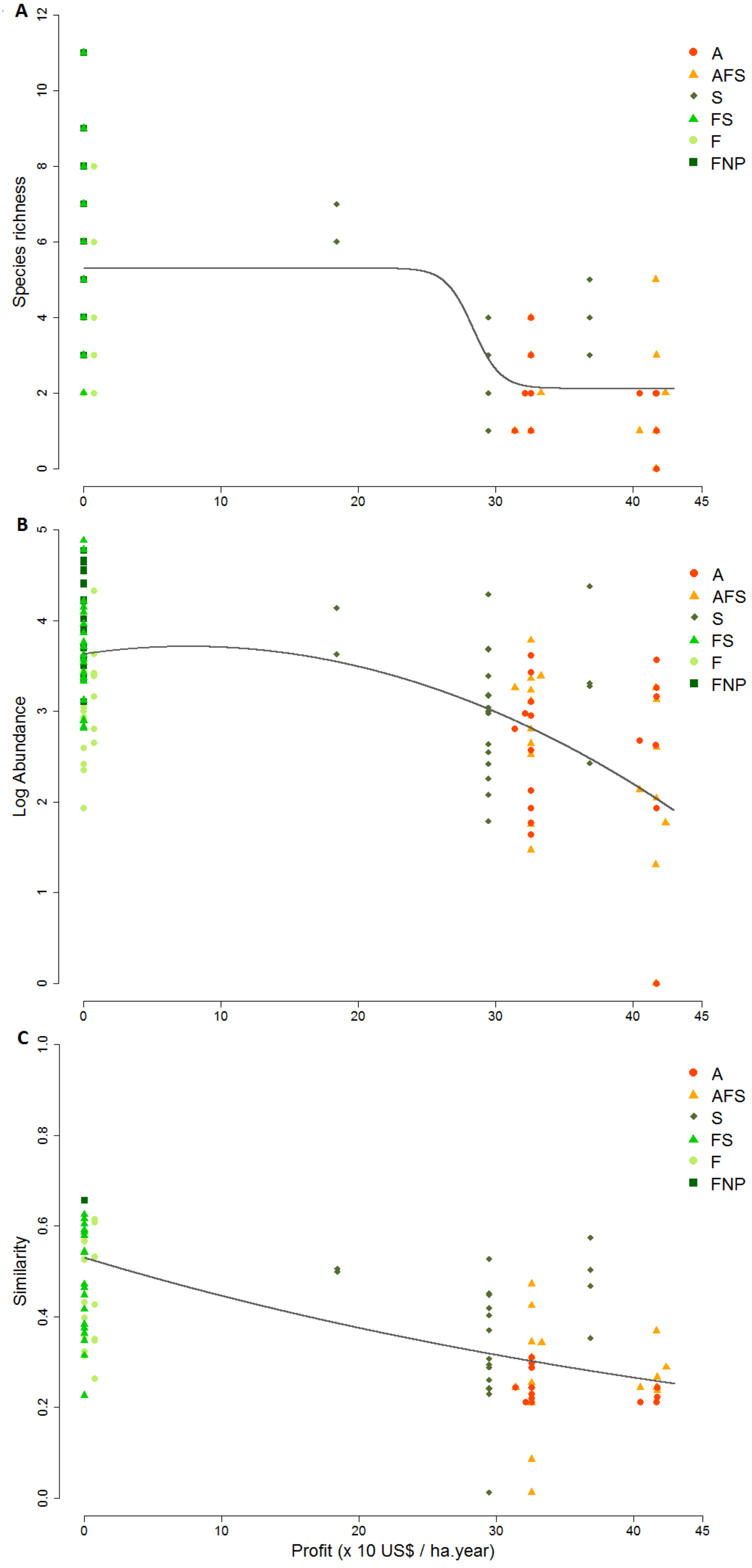

A
Species richness
0
10
20
30
40
50
60
A
AFS
S
FS
F
FNP
0
10
20
30
40
50
B
Abundance
0
50
100
150
200
250
300
A
AFS
S
FS
F
FNP
0
10
20
30
40
50
C
Similarity
0.0
0.2
0.4
0.6
0.8
1.0
A
AFS
S
FS
F
FNP
0
10
20
30
40
50
Profit (x 10 US$ / ha.year)

Figure 4.3.


A
B
C
Species richness
Log Abundance
Similarity
Profit (x 10 US$ / ha.year)
0
2
4
6
8
10
12
0
1
2
3
4
5
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
45
A
AFS
S
FS
F
FNP

4.5. Supplementary information

Table 4.S1. Summary data for the calculations of profit of the sites surveyed in the semiarid Chaco Region. Only data for some of the sites visited during the mammal community survey is shown as an example (profit for sites surveyed for the bird community were attained using the same methodology and input data). Only sites with unique profit values > 0 US$ are listed (i.e. sites inside FNP, FS and some sites in F outside National Park were excluded from the table given their profit was zero). The first row called “Col” was added to facilitate the explanation of calculations, with each letter corresponding to a different column on the table.

- Site correspond to the number allocated to each site sampled and is shown only as a reference, sites are sorted in two groups from smallest to largest values of profit; first, sites with an agricultural land use, followed by sites with livestock production.

- Mean yield for each crop type represents the average weight of grain harvested per year (during 2011 to 2013) according to the crop sown in the corresponding year of sampling. Based in values from Table 4.1.**A**.

- Mean grain price represents the economic value of each crop type averaged for the years 2011 to 2013, according to the crop sown in the corresponding year of sampling. Based in values from Table 4.1.**A**.

- Gross profit A represents the economic output of agriculture obtained in a given year. It was calculated as G= C*E, and H=D*F.

- Mean gross profit is the averaged economic revenue obtained between 2012 and 2013. It was calculated as I= (G+H)/2.

- Production costs per year represent the costs associated to farming depending on the crop type sown each year. Based in values from Table 4.1.**A**.

- Mean production costs are the values of costs averaged per year. It was calculated as L= (J+K)/2.

- Cattle ranch category was assigned to each site located either in forest or silvopasture dedicated to livestock production. The classification was based on interviews with the owners, on professional assessment made by a local agronomist, and on personal knowledge of the sites. Based in values from Table 4.1.**B**.

- Mean cattle production represents the average production per year depending on the ranch category (infrastructure and development). Based in values from Table 4.1.**B**.

- Mean cattle price is the economic value of livestock averaged for the years 2011 to 2013. Based in values from Table 4.1.**C**.

- Gross profit B represents the economic output of cattle ranching obtained in a given year. It was calculated as P= N*O.

- Production costs A represents the costs associated to cattle ranching expressed in Argentine pesos per kilogram. Based in values from Table 4.1.**C**.

- Production costs B represents the costs associated to cattle ranching expressed in Argentine pesos per hectare per year. It was calculated as R= N*Q.

Lastly, profit is the net economic output per site according to each production averaged for 2012 and 2013. It takes into account gross profit and costs of production according to the land use and its history of management. Initially calculated using Argentine currency, it was later transformed to United State dollars (US$) using a value of 5.02 as conversion rate (based on averaged rates from 2011 to 2013 acquired from official site http://www.bcra.gov.ar/index.asp). We subtracted averaged annual costs from annual value of produce to get net estimates of profit as follows, **S (for agriculture) =** (I-L)/5.02; **S (for cattle ranching) =** (P-R)/5.02.

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Col	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
Site	**Crop type**		**Mean yield (ton/ha.year)**		**Mean grain price (AR$/ton)**		**Gross profit A (AR$/ha.year)**		**Mean gross profit 2012-2013 (AR$/ha.year)**	**Production costs (AR$/ha.year)**		**Mean production costs 2012-13 (AR$/ha.year)**	**Cattle ranch category**	**Mean cattle production (kg /ha.year)**	**Mean cattle price 2011-2013 (AR$/kg)**	**Gross profit B (AR$/ha.year)**	**Production costs A (AR$/kg)**	**Production costs B (AR$/ha.year)**	**Profit (US$/ha.year)**
	2012	**2013**	**2012**	**2013**	**2012**	**2013**	**2012**	**2013**		**2012**	**2013**								
81	SG	SB	3.25	1.62	745.31	1571.28	2422.26	2539.19	2480.72	810.35	998.42	904.39	-	-	-	-	-	-	314.01
110	SG	SF	3.25	1.68	745.31	1559.32	2422.26	2611.86	2517.06	810.35	998.42	904.39	-	-	-	-	-	-	321.25
121	SB	SB	1.62	1.62	1571.28	1571.28	2539.19	2539.19	2539.19	810.35	998.42	904.39	-	-	-	-	-	-	325.66
38	SF	SB	1.68	1.62	1559.32	1571.28	2611.86	2539.19	2575.52	810.35	998.42	904.39	-	-	-	-	-	-	332.90
28	C	SG	3.79	3.25	931.75	745.31	3533.20	2422.26	2977.73	892.29	998.42	945.36	-	-	-	-	-	-	404.85
120	C	SB	3.79	1.62	931.75	1571.28	3533.20	2539.19	3036.19	892.29	998.42	945.36	-	-	-	-	-	-	416.50
129	SB	C	1.62	3.79	1571.28	931.75	2539.19	3533.20	3036.19	810.35	1075.22	942.79	-	-	-	-	-	-	417.01
83	C	SF	3.79	1.68	931.75	1559.32	3533.20	2611.86	3072.53	892.29	998.42	945.36	-	-	-	-	-	-	423.74
3	-	-	-	-	-	-	-	-	-	-	-	-	0	10	11.3	113	7.6	76	7.37
126	-	-	-	-	-	-	-	-	-	-	-	-	3	250	11.3	2825	7.6	1900	184.26
109	-	-	-	-	-	-	-	-	-	-	-	-	4	400	11.3	4520	7.6	3040	294.82
12	-	-	-	-	-	-	-	-	-	-	-	-	4	500	11.3	5650	7.6	3800	368.53

Abbreviations: SG: sorghum; SB: soybean; SF: sunflower; C: corn. AR$: Argentine currency (peso).

Table 4.S2. List of mathematical functions tested during the model selection procedure. Response variable corresponded to species richness, abundance (Log [capture frequency], for mammals) and community integrity for each taxa. The equation shows the mechanistic relationship of the independent variable “profit” with the corresponding response variable; k is the number of parameters estimated from the model, and Name describes the type and shape of the function.

Variable	**Equation**	**k**	**Name**
Response	a + b * *profit*	2	Linear
Response	Polynomial (*profit*, 2)	3	Quadratic
Response	Polynomial (*profit*, 3)	4	Cubic
Response	a * exp (-b * *profit*)	2	Exponential
Response	a + b * exp (-c * *profit*)	3	Exponential
Response	exp (a + b * *profit*) / (1 + exp (a + b * *profit*))	2	Logistic
Response	a + (b - a) / (1 + exp (c - profit))	3	Logistic
Response	a + (b - a) / (1 + exp ((c - profit) / d))	4	Logistic

Polynomial (x, number): fits a polynomial model with predictor x to the power of the number (e.g. Polynomial (x, 2) is a quadratic polynomial for x).

5 GENERAL DISCUSSION

Biodiversity and ecosystems around the world are being threatened by increasing human pressure to generate food and goods (Sala 2000). Therefore, assessing the conservation potential of human-dominated landscapes is crucial, and requires investigating the activities, movements, and persistence of species not only in remnants of native habitat, but also in the full array of productive agricultural systems (Saunders et al. 1991; Henle, Lindenmayer, et al. 2004). The main aim of this thesis was to identify the patterns and processes underlying species persistence and distribution in human-altered environments. In previous chapters we empirically analysed the status and occurrence of bird and mammal species in one of the last remaining dry forest extensions in South America, that is being currently threatened by habitat loss and modification through rapid expansion of agricultural lands in the region (Grau, Gasparri, et al. 2005; Portillo-Quintero & Sánchez-Azofeifa 2010; Aide et al. 2013). Overall, this body of work constitutes an important step in the study of wildlife communities that survive in the heterogeneous mosaics of the semiarid Chaco Region.

Bird species diversity across a gradient of agricultural intensification

In Chapter 2 we found that relatively large forest tracts, inside and outside a National Park, forest strips, and silvopastures immerse in the agricultural matrix, hold the highest species richness among land uses, with a steep fall of diversity from these forested environments to heavily managed crop fields. Whereas, species richness responded similarly in several studies elsewhere (Harvey et al. 2006; Maas et al. 2009; Tscharntke et al. 2008; Macchi & Grau 2012; Banks-Leite et al. 2012; Moura et al. 2013), a great proportion of these studies have also pointed out the importance of analysing species composition, as significant differences in the structure of assemblages have been detected for secondary forests (Harvey et al. 2006; Banks-Leite et al. 2012). In this study, variation in bird community was strongly correlated with land-use type and the employment of several diversity measures reinforces this conclusion. These results indicated that communities in forest outside the National Park retained a composition of species similar than communities in protected areas. This could be related with the amount of remaining forest at the landscape scale (Andrén 1994; Martensen et al. 2012) which has been proved to be an important predictor affecting the response of several groups to local habitat variables (Pardini et al. 2009; Tscharntke, Tylianakis, et al. 2012). We did not measure forest cover at landscape scale, however, the relatively large remnant patches (>200 ha) in the study area could be determining the presence of forest specialist species, not only in forested land uses, but also in other land-use types within the agricultural matrix. In that regard, a sound knowledge of the community composition in natural or more pristine habitats is key to accurately compare integrity between land-use types (Gardner et al. 2009).

Possible factors influencing the estimates of bird species richness in modified land-use types

Estimates of bird species diversity in this study may have been partially biased by habitat structure in different agricultural environments. A more open vegetation structure in silvopasture plots, for example, could have led to the detection of a higher number of individuals, simply because it is easier to see birds in this setting than in the more closed forest. The sampling method employed in this study (i.e. 100 metres fixed radius point-count station) is designed to minimise this bias by limiting the survey to a relatively small area (Bibby et al. 1992). However, the probability of spotting a bird that is not singing or moving in an open habitat like silvopasture is likely to be higher than for more dense vegetation.

Total and averaged bird abundance was higher in silvopastures, consistent with the intermediate disturbance hypothesis (Connell 1978) where medium levels of intensification can create high local habitat diversity playing a significant role in the maintenance of larger numbers of individuals and species. Macchi & Grau 2012 found that human-modified habitats provided important additional resources (e.g. water and food) for bird species, resulting in highly diverse communities associated to low-intensity livestock production. Similarly, the high diversity measures registered in forest strips could be related to the enhanced variety and availability of food resources found in these edge habitats (Lopez de Casenave et al. 1995). Forest strips may also provide a greater opportunity for dispersal and foraging movements among habitats (i.e. spill over) leading to a higher species richness and abundance in these areas (Tscharntke, Tylianakis, et al. 2012). This effect is highly probable if we consider that forest strips frequently surround silvopasture plots as well as arable fields, possibly providing food and shelter, and in addition, some of these strips connect to larger forest patches.

Neighbouring tracts of forest can often enhance local diversity in lower quality habitat patches by spill over from source environments. Additionally, periodically high productivity and resource availability inside the field, when crops emerge, can attract certain functional groups (i.e. pollinators, seed eaters, predators) from the edges and into the fields (Tscharntke et al. 2008; Tscharntke, Tylianakis, et al. 2012). In this study, such effects were not strong enough to significantly increase bird species diversity inside the agricultural plots; however, the intrinsic value of forest strips was demonstrated by the high diversity measures registered for this land use. Notwithstanding, to accurately assess the potential spill over of individuals from the forest edge to the arable plot, measures should be taken in a different season or based on a different sampling design, one which focuses on fine scale movements of birds from crop edges. To our knowledge, this study is the first one contributing to the evaluation of forest strips as an important element influencing bird species diversity in an agricultural mosaic.

Factors influencing mammal species richness and abundance across agricultural landscapes

Although understanding the influences of land use intensification on medium- and large-sized mammals is increasing (Daily et al. 2003; De Angelo et al. 2011; R. Cassano et al. 2012; Msuha et al. 2012; De Angelo et al. 2013), few large-scale studies have evaluated the conservation potential of human-modified landscapes for mammal communities. Undertaking such studies is particularly important in the Chaco Region, where a major fraction of its biodiversity is threatened by habitat loss and fragmentation (Zak et al. 2004; Portillo-Quintero & Sánchez-Azofeifa 2010). From the analysis made in Chapter 3 we conclude that the mammal assemblage responded with a gradual change across land-use types, showing significant differences between three main groups. High intensity land uses (agriculture, and agriculture with forest strips) did not differ in the number of mammal species. Intermediate intensity land uses, were forest cover has been reduced (silvopasture), harboured significantly higher mammal species than arable fields. Land-use types presenting a well preserved and structured forest cover, independently of size (forest strip, forest, and forest inside National Park) followed with the highest species richness; and lastly, natural grasslands inside National Park presented a distinctive mammal assemblage, characteristic of open habitats, with fewer species. Relative abundance (capture frequency) of mammals varied in a slightly different way to that of birds, with the smallest assemblages being found in high intensity land-use types (agriculture and agriculture with forest strips), and forest inside National Park holding the most abundant community. The rest of forested land-use types with reduced or well preserved vegetation cover (silvopasture, forest strips and forest) contained intermediate values of mammal abundance.

Influence of local and landscape scale factors on mammal species distributions

The inclusion of landscape variables in the analysis showed that their importance was not strong enough to override the effect of land-use type. This finding corroborates the results discussed for birds, in which the study area, still presenting a relatively well preserved network of forest patches, can maintain mammal community diversity at landscape scale (Daily et al. 2003; Pardini et al. 2009). The complementary analysis of capture frequency distributions (Figure 3.6, Chapter 3) showed that forest patches are contributing to the persistence of the mammal community as well as forest strips and silvopasture plots. First, although not significant, the presence of forest-dependent species in agricultural fields (i.e. *Myrmecophaga tridactyla* and *Mazama gouazoubira*) indicated that mammals may eventually venture from favourable habitats (forest strips) to less favourable habitats (agriculture with forest strips) most probably searching for food (Gehring & Swihart 2003; Fahrig 2007). Second, species richness and abundance of mammals inside forest strips were amongst the highest of all land uses. This suggests that mammal species are moving across land uses, using forest strips to traverse the agricultural landscape. Coincidentally Barlow et al. 2010 found high mammal activity with associated dung beetle abundance in forest strips linking nearby forest remnants, suggesting in turn, its great value for conservation.

Modified environments as well as native forest are important for mammal community conservation

Forest inside National Park and forest strip together accounted for 24 out of the 26 total species registered during the study; emphasizing the importance of these environments associated to the persistence of the mammal community. Recent studies have highlighted the important role of secondary forest and agroforestry systems as alternative habitats holding highly diverse mammal assemblages (R. Cassano et al. 2012; R. Cassano et al. 2014; Banks-Leite et al. 2014). In this study, the mammal community inhabiting silvopasture systems presented significantly less species than forested land uses; however, records of predator species and species classified under threat (IUCN 2014) indicate its important role in maintaining a friendly agricultural matrix to facilitate the movements of species with broad home-ranges, and to provide alternative environments for the conservation of compromised species.

Evidence of direct human pressure e.g. hunting, persecution and disturbance.

Direct human disturbance has been pointed out as an important factor of altered large mammal assemblages. High capture frequency of domestic dogs negatively affected mammals in cacao agroforestry systems in the Atlantic Forest (R. Cassano et al. 2014); several wild mammal species were killed as they were perceived to endanger domestic animals in Costa Rica (Daily et al. 2003), whereas the abundance of all three species of peccaries decreased significantly with the number of human settlements in a previous research in our study area (Altrichter & Boaglio 2004). In this study, we registered a few events of human disturbance inside the different environments. In highly intensified systems (agriculture and agriculture with forest strips), human presence was evident by records showing the use of heavy machinery. Despite silvopasture represented a less altered land-use type than arable fields, it inevitably had some level of disturbance: firstly, by the cattle using the plots and the people in charge of their management (i.e. horse-back riders with dogs); and secondly, by machinery used for shrubs removal. Lastly, neither inside forest strips, forest patches nor forest sites in the National Park we registered significant human presence on the camera traps. We detected only low levels of intervention in these habitats during our walks to reach the sampling station (i.e. footprints, cut twigs and branches, abandoned objects, etc.). In this study we did not specifically collect evidence to assess the direct effects of human disturbance (i.e. hunting pressure, domestic dogs, and fires). However, a comparison could be made among silvopasture plots with and without cattle presence using the data gathered by the camera traps since a negative association between cattle presence and Chaco wildlife has been suggested (Altrichter & Boaglio 2004) but remains unknown.

Economic revenues, levels of agricultural production and changes in biodiversity

Strong differences in the economic revenue arising from alternative production systems in the semiarid Chaco posed a compromise between biodiversity and profit (Green et al. 2005; Phalan, Malvika, et al. 2011). We linked biodiversity estimates of bird and mammal communities to a management indicator (i.e. profit) on a large number of agricultural fields, agroforestry systems and natural forests, thereby covering the full range from very extensive to highly intensive land uses. In extensive cattle ranching, producers keep their livestock using the resources from the forest, in this case, the economic revenue is extremely low in comparison with the lowest level of income for silvopasture plots, and is mainly developed as livelihood. Disturbance is kept at a minimum, and therefore, the associated diversity of birds and mammals and the community integrity for both taxa was not affected. Development of silvopasture systems requires some level of financial investment (i.e. selective forest clearance, sowing of grasses) and this translates into a significant increment in productivity. Low-intensity silvopasture production reaches intermediate profits approximately 82 times higher (i.e. from an averaged 3.5 US$ ha.$^{-1}$ year^{-1} to c.292 US$ ha.$^{-1}$year^{-1}) than traditional livestock husbandry. Changes made to the environment include delimiting the paddocks, selectively clearing the forest inside the paddock, mechanically removing the understorey and implantating exotic grasses. Further intensification involve increasing the number of paddocks and supplementing the diet of the cattle. Low-intensity silvopasture maintain high diversity of both taxa, indicating that profit can be significantly increased whilst keeping bird and mammal diversity and community integrity practically unchanged, with the exception of mammal community integrity that decreased almost linearly even at low levels of intensification. The last step between low-to-intermediate intensity levels and high intensification practices leads to higher profitability and the consequences on the bird and mammal community varied in different ways for both taxa, although always resulting in low diversity values.

Combining conservation efforts for bird and mammal communities inhabiting agricultural landscapes in the semiarid Chaco

We found that logistic (sigmoid) functions more accurately described bird diversity than linear or exponential functions (Koh et al. 2009). This implies that effects of land-use change are small for low- and intermediate-intensity systems and most pronounced after a threshold of habitat modification and human intervention is reached. A quadratic declining function gave the best fit for mammal abundance along the intensification gradient. This suggests that intermediate intensification can maintain a high number of mammals in agricultural landscapes. Whereas community integrity declined almost linearly with increasing economic output indicating that mammal assemblages outside protected and well preserved forest patches could be equally favoured by land sparing or wildlife-friendly farming (Green et al. 2005; Phalan, Balmford, et al. 2011; Phalan, Malvika, et al. 2011). Therefore, what are the most important implications of the observed relationships between biodiversity and profit? First, we suggest that high biodiversity of both taxa are largely restricted to protected forest patches or to areas where wildlife-friendly practices are developed. Second, very low levels of bird and mammal diversity are associated with high-intensive and profitable managements, whereas community integrity in those land uses is seriously compromised. Third, strategies incorporating conservation into the agricultural landscape are cost-effective when production outcomes are below the maximum profit for both taxa. Intermediate levels of intensification can support bird communities with up to 90% of the total species, abundance and community integrity; whereas approximately 70% of species richness and abundance, and only 50% of the community integrity, are maintained for mammals.

In summary, bird and mammal communities in the semiarid Chaco can benefit from wildlife-friendly farming to maintain highly diverse assemblages favoured by the provision of habitat and resources at a local scale, and a heterogeneous matrix that facilitates movements and dispersion of individuals at landscape scale. At the same time, the exclusion of some areas from modification and production activities must be maintained in order to ensure the preservation of a wider range of forest-dependent and threatened species.

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