CONSERVATION ON THE FRONTIER: UNDERSTANDING AND INFLUENCING HOW CATTLE PRODUCTION IMPACTS AVIAN DIVERSITY IN THE DRY CHACO FORESTS OF ARGENTINA

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ABSTRACT

This thesis combines the identification of land-use strategies that provide high yields and high biodiversity with the identification of the psycho-social drivers of land-use decisions in an agricultural landscape. I visited 116 landholdings in two agricultural landscapes of the Dry Chaco region in Argentina. In 27 landholdings producing beef cattle in production systems of different land-use intensity, I collected empirical information on: (i) cattle yields, (ii) avian diversity, density and composition, and (iii) structural attributes of habitat in the agricultural matrix. The Chaco avifauna responded non-linearly to increasing cattle production intensification as bird species richness was relatively unchanged from forests to intermediateintensity silvopastoral systems and decreased sharply at high-intensity pasture systems. This pattern indicated the presence of a threshold in habitat quality for birds when native tree cover falls below 30%. The concave trade-off function suggests that land-sharing through the integration of native trees and pastures in silvopastoral systems has more potential than landsparing to simultaneously provide high cattle yields and high bird diversity. Intermediateintensity silvopastoral systems may represent a matrix type of high habitat quality for most bird species due to the lower frequency and intensity of disturbances resulting from agricultural management, compared to high-intensity systems. Bird functional groups responded differently to agricultural intensification and habitat modification. Forest-restricted and fruit-eating bird species occurred at low density in intermediate-intensity silvopastoral systems and disappeared from high-intensity pasture systems. Therefore, low-intensity systems and forest fragments (larger than 1000 ha) should be maintained in the landscape to provide habitat for species of high conservation concern and potentially contributing to forest regeneration.

In 89 landholdings varying in landholding size and land tenure condition, I interviewed landholders and collected information about their beliefs, values and perceptions regarding conservation of remnant forest fragments. Based on this information, I tested the ability of three social psychological models and nine psycho-social constructs to explain landholders' conservation intentions. The Theory of Planned behaviour provided a parsimonious and plausible explanatory model of landholders' intentions to conserve remnant forest fragments in their landholdings. A model integrating self-interest and pro-social motives as proximal predictors and self-identity as the ultimate predictor explained 42% of the variance in landholders' conservation intentions. The perceived pressure from relevant others to conserve

forests (i.e. social norms) and the tendency to value forests favourably or unfavourably (i.e. attitudes) directly and significantly influenced landholders' willingness to set-aside remnant forests in their landholdings. Landholders' self-identity and their level of awareness of the scale and consequences of deforestation underlay the effects of social norms and attitudes on conservation intentions. Policy interventions aimed at influencing the behaviour of landholders towards more conservation-oriented outcomes would be more effective if tailored to the characteristics of landholder identity groups. Influencing conservation intentions of high-intensity, productivist landholders may require policy incentives and regulations that link better environmental performance with agricultural production outcomes and can become peer-enforced in the long-term. Conservation and development outcomes can be jointly enhanced for low-intensity, pre-productivist landholders through policies that secure their land tenure and facilitate the implementation of silvopastoral systems.

Key words: conservation planning, agricultural landscapes, dry forests, silvopastoral systems, avian diversity, cattle production, land-sharing, land-use policy, psycho-social factors.

PREFACE

This thesis is a tale of two personal journeys. The one that started earlier is my personal journey to the nature of the Chaco region. I was raised in the Argentine Pampas, a very different context than that of the Chaco. The rural landscape of the Pampas is flat, open and homogeneous, and was intensively modified by agriculture for more than a hundred years. Historically, it is the region of the country with closer links with the developed world due to immigration, trade and cultural exchange. This is why it is known as the most "Europe-like" region of Latin America. In contrast, my vision of the Chaco region as a child was of an undomesticated, torrid and thorny place, more similar to the character of Latin American landscapes before Europeans arrived. During my childhood, I imagined the Chaco as full of life, with giant anteaters, jaguars and crowned eagles wandering in impenetrable Quebracho woodlands. My appeal for the Chaco originated in this contrast. My visits to Chaco national parks and nature reserves as a teenager substantiated my depictions of the Chaco and even exceeded my expectations. However, as I grew up and my visits and walks took me beyond the boundaries of protected areas, I started to realize the growing threat posed by forest clearing for agriculture on Chaco biodiversity.

I initiated my second journey with the realization that the loss of Chaco biodiversity was seen as an unavoidable side-effect of expanding industrial agriculture to foster national economic development. At this point, I was already an undergraduate student of Biological Sciences in Mar del Plata, my home city located by the Atlantic sea and very far from Chaco woodlands. By the end of my undergraduate studies, I was more focused on the behavioural physiology of mammals and birds than in the ecology of agriculture and conservation. But deep inside me was always the hope that someday I would have the opportunity to use my knowledge and skills in biological sciences to find ways for reconciling conservation and agricultural production objectives in the Chaco region. Nevertheless, I felt that my scientific training in biology would not suffice to answer questions about a multidimensional problem, a problem characterized by complex links between biodiversity conservation, economic development and social equity. The opportunity came with a postgraduate scholarship granted by the New Zealand Agency for International Development to undertake the Master in Environmental Studies. Then I upgraded to the PhD in Conservation Biology and here are the results.

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CHAPTER 1: INTRODUCTION



Cattle and forests in a Chaco agricultural frontier. Photo by the author.

GLOBAL FOOD AND BIODIVERSITY CRISES

Conserving habitats in private, arable lands has become a priority for many governments, organizations and individuals in view of the importance of habitat quality outside protected areas for species persistence (Tschartnke et al. 2005), and the high rates of land conversion for the production of food, fibres and biofuels (Lambin & Meyfroidt 2011). Habitat conservation in agriculture is typically framed as a social dilemma given that two seemingly conflicting objectives are posed on a finite amount of land. On the one hand, it is frequently asserted that the current global extent of protected areas (12%) will not be enough to save biodiversity (Chape et al. 2005, Perrings et al. 2010). Therefore, conserving habitats in the more than two-thirds of global land area already used for agriculture will be critical for meeting global targets of halting the loss of biodiversity and degradation of ecosystem services (Tscharntke et al. 2005). On the other hand, feeding the world population will need 70 to 100% more food by 2050 (Godfray et al. 2010) and may require expanding global agricultural area from the current 5.1 billion ha to 5.4 billion ha in 2030 (Wirsenius et al. 2010). Examining regional differences in these global trends further complicates the scenario. Doubling food production by 2050 will likely be insufficient to alleviate the hunger of the three billion people malnourished or undernourished today, because food security is more closely linked to the lack of access to food (especially for the rural poor in developing countries) and less related to the quantity of food produced globally (Chappell & LaValle 2011). Evidence for this is that the total area of cropland and permanent pasture has increased by over 20% in developing countries while it has shrunk in developed countries in the last 50 years (Green et al. 2005). This means that improving food distribution and reducing food waste would be more effective at securing access to food than increasing food production (Chappel & LaValle 2009). However, most land-use decisions at all institutional levels (from farmers to governments) are still guided by the amount of food produced (Balmford et al. 2005).

Agriculture in developing countries has mainly expanded into tropical and subtropical native ecosystems with high levels of biodiversity, driven by demand from developed and emerging countries with high levels of *per capita* consumption (Lambin & Meyfroidt 2011). In these areas, the relationship between agricultural production and biodiversity conservation is highly complex and conflictive as diverse stakeholders compete for the use of land in a weak institutional context (Barrett et al. 2001). Poor farmers relying heavily on biodiversity and

ecosystem functions to sustain production at the subsistence-level usually coexist with wealthy landholders who intensively modify the ecosystem to maximize agricultural yields and land rent (Diaz et al. 2010). As land and production factors are highly concentrated on wealthy landholders, ecosystem degradation resulting from the expansion of industrial agriculture threatens the livelihoods of the rural poor, creating the paradox of high poverty levels in biodiversity hotspots (Fisher & Cristopher 2007). In turn, as a growing proportion of tropical and subtropical landscapes are managed for agricultural production, habitat quality and the persistence of a large number of species depends increasingly on farmers' land use decisions (Fearnside 2005).

In this thesis, I explore the ecological and social dimensions of biodiversity conservation in the Argentine portion of the South American Gran Chaco, an understudied biome that is experiencing rapid agricultural expansion and intensification (Zak et al. 2004). My aim is to improve our understanding about the complex relationships between agriculture and biodiversity, and to provide scientific evidence relevant to inform the implementation of conservation policies and plans in the Argentine Chaco and similar areas. In this introductory chapter, I will firstly provide an overview of the drivers, pressures, impacts and responses concerning agricultural expansion and intensification into biodiversity-rich regions. After that, I will focus on potential responses to minimize biodiversity impacts of agricultural change by describing and comparing two alternative land-use strategies to reconcile production and conservation: land sharing and land-sparing. As the relative utility of these strategies is highly context-dependent, I will follow with a review of the environmental history of the Chaco region (my study area) to get an accurate depiction of the current socioecological context. Finally, I will present my thesis aims and briefly outline chapters' content.

The relationship between agriculture and biodiversity conservation originates from the temporal and spatial intersection between a human activity aimed at producing ecological output in the short-term and a human activity aimed at conserving medium and long-term ecological processes, respectively (Reboratti 2010). Ecologists traditionally viewed an essentially antagonistic relationship arising from this scale mismatch, with little scope for synergistic interactions (Perfecto & Vandermeer 2008). This created a divided culture of agronomists working at the plot scale towards increasing output in the short term and conservation biologists in pristine or semi-natural areas dealing with the long-term persistence of endangered species (Banks 2004). Disciplinary segregation and a treatment of

the biodiversity crisis as a problem independent from the food crisis have impeded acknowledging the strong interdependence between agriculture and biodiversity, leading to the implementation of production systems that erode biological diversity and put agricultural sustainability at risk (Cunningham et al. 2013).

Moving the relationship from strong antagonisms to positive interactions (weak trade-offs or synergisms) is critical to tackle the twin challenges posed by food insecurity and biodiversity loss (Chappell & LaValle 2010). Integrated conceptual and analytical frameworks are needed to grasp the complexities of the agriculture-biodiversity relationship. Here I will frame production systems as coupled human and natural systems comprising multiple dimensions, including the social, ecological, economic and institutional (Stokols et al. 2013). The socioecological systems framework allows us to consider the multidimensional and multi-scale character of agriculture-biodiversity interactions by relating processes occurring at the plot and landholding (micro-scale), the landscape and province (meso-scale) and the region and globe (macro-scale).

Global food production has doubled in the last 40 years driven by growth in population numbers and *per capita* consumption, which have been enabled by yield increases from the "Green Revolution" (Tilman et al. 2002) and, more prominently, as a result of increases in agricultural land cover (Pretty 2008). Meat consumption increased from 47 million tonnes in 1950 to 260 million tonnes in 2005, raising global *per capita* meat consumption from 17 to 40 kg per year (Brown 2006). Feeding seven billion people with such levels of *per capita* meat consumption is posing threats on remaining arable lands, despite considerable efforts at closing the gap between achievable and realized yields (Cunningham et al. 2013). A cross-scale view of this global problem shows a geographical separation between production and consumption regions, with an increasing proportion of the demand from developed and emerging countries (the "new consumers", Myers & Kent 2003) being supplied by food imports from developing countries. Examples of this global displacement of land use and export of environmental degradation include China's soybean imports from Brazil and Argentina for feeding pork and poultry (Naylor et al. 2005) and New Zealand's imports of palm kernel expeller from South East Asia for feeding dairy cattle (Burger et al. 2012).

In the case of beef cattle, international market demand is also being met via extensive land conversion in subtropical and tropical Latin America, a process that is enabled by trade

liberalization (McAlpine et al. 2009). Global interconnections mediated by trade in beef exert pressure on local socio-ecological systems through two main paths. The direct path of beefdriven land conversion involves the spatial expansion of pastures intensively managed for cattle grazing. The indirect path entails the extensive cultivation of rainfed grain crops, mostly soybeans and maize, for the production of feedstock to raise cattle in feedlots. Furthermore, extensive crop cultivation for feedstock and biofuel production is replacing rangelands and pastures and pushing cattle production systems further into forest ecosystems of the Amazon and Gran Chaco (Morton et al. 2006, Adámoli et al. 2008). Indeed, more than half of the new agricultural land across the tropics came at the expense of intact forests, and another 28% came from the conversion of disturbed forests during the 1980 to 2000 period (Gibbs et al. 2010). Deforestation in Latin America during this period was mainly driven by wealthy cattle ranchers and soybean farmers with abundant access to land, technology and financial resources, in contrast to archetypal scenarios of deforestation driven by poor and landless farmers elsewhere (Rudel 2007). As a consequence, different social motivations, spatial patterns of land-use and environmental impacts characterize smallholder and largeholder-led land conversion (Pacheco 2013).

Extensive agricultural land use is allowing humans to appropriate 23.8% of Earth's net primary productivity annually (Haberl et al. 2007). Such a high level of global land-use intensity makes agriculture one of the most important causes of species extinctions and wild population declines as it represents both a direct cause of habitat loss and an indirect driver of climate change (Green et al. 2005). In fact, habitat loss and degradation driven by agriculture is the main cause for the status of 96% of threatened bird species and the cause of 15% of bird species extinctions globally (Szabo et al. 2012). Agricultural land use often reduces the structural complexity of the ecosystem and the wider landscape to reduce competition and increase productivity (Tilman et al. 2002). In addition to impacts on water and soils, this simplification causes homogenization of biotic communities by favouring a few species with general feeding and habitat preferences and hindering those with specialized life history traits, such as endemics (McKinney and Lockwood 1999). Biodiversity declines can have significant disruptive effects on ecological processes and functions, as the functional capacity of ecosystems becomes impaired when a certain threshold in biodiversity level is crossed (Tschartnke et al. 2012). Furthermore, diversity declines in functional groups can have negative cascade effects on human well-being via the disruption of ecological functions that

provide direct benefits to individuals and society (i.e. ecosystem services) and/or that underlie the capacity of the ecosystem to absorb shocks and maintain its integrity (i.e. ecosystem resilience) (Diaz et al. 2006).

A strengthening of private stakeholders and a weakening of public institutions in Latin American countries during the last 20 years created conditions for global drivers and pressures to threaten socio-ecological sustainability at the meso and micro-scale (Manuel-Navarrete et al. 2009). In view of potential and actual feedback effects from widespread environmental change such as landslides, floods, droughts and social conflict, some responses to reverse the degradation trend have been put forward in the last years at different institutional scales. At the national scale, large producing countries experiencing extensive deforestation such as Brazil and Argentina updated their environmental legislation and established more stringent land-use regulations. Then, federal jurisdictions responsible for law enforcement implemented systems of licensing for logging and clearing, and satellitebased monitoring of deforestation. The implementation of these top-down measures has reduced but not stopped deforestation, due to low compliance, corruption and unexpected effects such as land use displacement (Lambin & Meyfroidt 2011, Seghezzo et al. 2011). In Mato Grosso, pressure from international environmental organizations and demand from environmentally-aware consumers induced agro-industrial corporations to prohibit exports of soybeans, beef and leather from recently deforested areas (Macedo et al. 2012).

At the regional and landscape scale, governments are attempting to implement land-use policies aimed at regulating the allocation of land to agricultural production and biodiversity conservation at different spatial scales. In the Brazilian Amazon, the Forest Code demands landholders to set-aside forests in 20 to 80% of the landholding area ("Reserva Legal"; Nepstad et al. 2010). In the Argentine Chaco, the Forest Law passed in 2008 requires provinces to implement land-use zoning on forest lands and allocate areas for production, conservation and sustainable use ("Ordenamiento Territorial"; Seghezzo et al. 2011). Next, I will describe alternative land use planning strategies, with regard to their theoretical underpinnings and the potential and drawbacks related to their implementation.

RECONCILING CONSERVATION AND PRODUCTION

A review of the scientific literature shows a spectrum of planning strategies that differ on the spatial scale and the degree to which different land uses (i.e. agriculture vs. biodiversity

conservation) are integrated or segregated. A strong debate also exists about the relative utility of contrasting planning strategies to reconcile production and conservation. Some authors argue that the spatial segregation of high-intensity farmland on fertile areas and natural protected areas on land marginal for agriculture (i.e. land-sparing) is the optimal strategy to minimize the trade-off between agriculture and biodiversity (Green et al. 2005, Phalan et al. 2011a,b). In contrast, other authors argue that the integration of agricultural use and conservation management on the same land (i.e. land-sharing) has the greatest potential to jointly achieve food security and biodiversity targets (Perfecto & Vandermeer 2010, Tscharntke et al. 2012). In the following, I will review the rationale, potential and drawbacks related to land-sparing and land-sharing strategies.

LAND SPARING

Supporters of land-sparing rely on the biophysical potential of combining land-use intensification (increasing yields and producing on less land) and agricultural adjustment (producing on the most fertile lands) to release marginal lands from production and spare these for nature conservation and net reforestation. If this biophysical potential is realized, two socio-political processes need to concur for land sparing to deliver conservation and production benefits. First, human pressure on spared lands should decrease as a consequence of land-use intensification on fertile lands. Second, abandoned marginal lands should be protected to secure biodiversity conservation. Previous studies have shown that land intensification and/or agricultural adjustment were associated with a transition from net deforestation to net reforestation in Western Europe, North America and Japan. There, early economic development created technology advances to intensify production and enough offfarm jobs to pull farmers off marginal lands (Mather 1998). More recent forest transitions in developed and developing countries were not associated with land-use intensification and rural-urban migration but with food and timber imports compensating for reductions in area under production and/or with stringent conservation policies on spared lands (Lambin & Meyfroidt 2011). Land sparing is promoted from the production side on the basis of prospects for continued increases in agricultural yields and the development of high-yielding production systems with high environmental performance (Trewavas 2001, Borlaug 2007). From the conservation side, land sparing is promoted based on empirical evidence from tropical agricultural landscapes showing that many bird species are sensitive to low-intensity

agriculture and can only persist in undisturbed areas (Waltert et al. 2004, Phalan et al. 2012, 2013).

From its recent revival by conservation scientists, the land-sparing strategy has been criticized on ecological as well as social grounds. Two lines of critique point to the weak links among land-use intensification, rural depopulation and reforestation, which constrain the actual delivery of benefits hypothesized under the land-sparing strategy. First, it is argued that land-use intensification alone seldom reduces human pressure on marginal lands. To the contrary, it has been shown that intensification and associated infrastructure development attracts rather than deters farmers, causing further agricultural expansion (Angelsen & Kaimowtiz 2001, Castella et al. 2011). Second, it is argued that rural-urban migration and consequent depopulation of marginal lands do not necessarily lead to forest regrowth and a transition to net reforestation. Landholding expansion and concentration is a common practice among the more efficient and wealthy farmers, who switch to extensive land uses on marginal lands, thereby configuring landscapes devoid of people ("hollow frontiers"; Sloan 2007). Overall, this evidence suggests that the occurrence of land sparing is highly dependent on contextual factors such as institutional capacity and social diversity, and that agricultural expansion and deforestation may also occur amid depopulation and land-use intensification. When land sparing actually occurs, it has been pointed out that the biodiversity benefits on spared lands are usually offset by biodiversity costs on farmland. This may happen because of irreversible changes of ecosystems state on spared lands (e.g. shift from forest to savannah) leading to low biodiversity levels and/or to agricultural management in farmland leading to "sacrifice zones" for conservation (Brannstom et al. 2009). Furthermore, as agriculture intensifies its ecological footprint increases exponentially relative to the land it occupies, limiting its conservation potential due to negative effects on non-farmed land such as environmental toxification (Tilman et al. 2002) and greenhouse gas emissions (Matson et al. 2006).

LAND SHARING

Alternative forms of food production combining traditional and modern knowledge and practices emerged in response to negative environmental effects of high-intensity agriculture. Under various labels such as agroecological, integrated management or low-input, these systems share the priority of building resilient and sustainable agriculture through increased

reliance on ecosystem functions rather than external inputs. Supporters of land-sharing strategies argue for the presence of synergies between agriculture and biodiversity, which can be seized by managing agriculture to enhance habitat quality and managing biodiversity to supply services for agriculture (Perfecto & Vandermeer 2008). Land-sharing originated as a strategy to reconcile conservation and production objectives at the agricultural plot and farm scale. Its underlying principles were more recently integrated to advances in landscape ecology, such as metapopulation theory, and scaled up to become an alternative option for landscape planning (Perfeto & Vandermeer 2010). Unlike the binary landscape emerging from land-sparing, land-sharing promotes the formation of a fine-grained mosaic of production systems of varied land-use intensity (i.e. the agricultural matrix) interspersed with fragments of native ecosystems (Fischer et al. 2008). The development of heterogeneous landscape mosaics under land-sharing responds to a societal demand for maintaining the supply of multiple ecosystem services (i.e. multifunctionality) beyond agriculture and habitat conservation (Tschartnke et al. 2012).

Research on the ecology of agriculture-biodiversity interactions has found substantial evidence in favour of land-sharing strategies. Studies comparing species diversity among production systems of different land-use intensities show that many species are able to persist in low and intermediate-intensity production (e.g. Maestas et al. 2003, Harvey et al. 2008). Biodiversity retention in integrated production systems and landscapes has been associated with the spatial continuity of suitable habitat in the agricultural matrix due to low contrast between farmed and non-farmed land. Spatial continuity of habitat facilitates species movements such as dispersal and recolonization, and reduces regional extinction thresholds in habitat amount (Fahrig 2001). Planning for habitat connectivity through, for instance, a network of small but numerous reserves within the agricultural matrix also helps retain ecological memory, that is, the ability of ecosystem states to recover after disturbances (Bengtsson et al. 2003). Biodiversity in matrix habitats is a conservation objective in itself, and is also important due to the insurance effect on ecosystem functions and contribution to human well-being. The supply of various ecosystem services was shown to be enhanced under land-sharing, for instance, protection against natural hazards (Holt-Giménez 2002) and diseases (Mendenhall et al. 2012), biological control (Perfecto et al. 2004) and pollination (Carvalheiro et al. 2010).

The main critique to land-sharing is that it necessarily leads to lower yields compared to high-intensity agriculture and thus to the need to use more land to achieve production targets (Balmford et al. 2008, Phalan et al. 2012). It follows that if more farmland is needed, then the pressure on remaining undisturbed habitats will increase along with the extinction risk of species sensitive to even low-intensity agriculture. This highlights the key role of the relationship between biodiversity and agricultural yield in determining the relative utility of land-sparing and land-sharing. Overall, this review shows that the effectiveness to reconcile conservation and production of land-use planning strategies depends on the spatial scale and socio-ecological context in which these operate.

AGRICULTURAL FRONTIERS

Landscapes in tropical regions of the developing world represent the context and scale at which agriculture drives the most rapid changes in biodiversity as it actively expands into biodiversity-rich ecosystems (Lambin & Meyfroidt 2011). Such areas are usually known as agricultural frontiers, forest frontiers or forest-agriculture frontiers. Historically, agricultural frontiers expanded from fertile to more marginal lands in response to political aims such as increased natural resource use for national economic development and state control over remote or contested territories. Frontier evolution has taken many forms depending on the geographical and historical context, and has been almost invariably associated with ecosystem degradation leading to biodiversity declines, and with conflicts among sociocultural groups around tenure and access to land (Pacheco 2013). Frontier expansion until 1980s was typically driven by state-led colonization projects whereby poor families migrated to "unoccupied" or "idle" lands to practice small-scale farming. During the 1980s, economic liberalization and a weakening of state governments in many developing countries created the conditions for foreign investment and local elites to purchase public lands and develop large-scale agricultural enterprises (Rudel 2007).

Most frontier landscapes in the developing tropics are the result of successive and simultaneous waves of agricultural expansion driven by the interests of stakeholder groups that differ widely in their social, cultural and organizational characteristics (Sloan 2007). Today, these groups are the agents of continuing land-use change and their decisions largely determine production and conservation outcomes in the agricultural frontier. Factors affecting agents' decisions can be classified as: i) macro-scale factors such as land distribution policies

and international food demand, ii) meso-scale factors such as access to land, labour and technology, and iii) micro-scale factors such as landholders knowledge, intentions and attitudes towards land use (Jepson et al. 2010). Given how different frontier development has been in different tropical locations, I will now focus my description on the historical process of frontier evolution and the agents driving current land-use changes in the Argentine Chaco.

FRONTIER EXPANSION IN THE ARGENTINE CHACO

The Gran Chaco is the second largest ecoregion of Latin America after the Amazon, spanning over ca. 1,000,000 km² at the centre of South America (Clark et al. 2010). The Gran Chaco contains the largest continuous tract of Neotropical dry forests and 60% of it is in Argentina (Eva 2004). The Argentine Chaco is a mosaic of seasonal dry forest, scrubland and grassland over a plain that extends from the foothills of the Andes range in the west to the Paraná and Paraguay rivers in the east. The region hosts a great deal of cultural diversity, with 25 indigenous groups of six language families and hundreds of communities of European immigrants. Biological diversity of the Gran Chaco did not change substantially until the early 20th century owing to low population density, remoteness from urban centres and unfavourable conditions for human settlement. However, one hundred years ago a combination of climatic, demographic, technological and geopolitical events initiated an intense process of human occupation and agricultural use in the Argentine Chaco (Morello et al. 2005). In the last 20 years, further socio-economic changes have intensified the process of agricultural expansion and ecosystem conversion, to the extent that 22% of the Argentine Chaco had been converted to agricultural uses by 2008 (Adámoli et al. 2008). Next, I will firstly provide an overview of the physical and biological characteristics of the Dry Chaco of Argentina. After that, I will draw on Morello et al. (2005) to provide an overview of the historical processes leading to current production and conservation outcomes by describing five successive and simultaneous stages of frontier expansion in the Argentine Chaco: (i) indigenous use (500-1000 years BP – today), (ii) smallholder occupation (1860-present), (iii) extraction by large-scale enterprises (1900-present), (iv) incipient agricultural expansion (1970-1995) and (v) agricultural expansion and intensification (1996-present).

CHARACTERISTICS OF THE DRY ARGENTINE CHACO

The Chaco region consists of a large sedimentary plain of about 1,000,000 km². During the upheaval of the Andean range, the region received volcanic ash rain from the neighbouring

Andes. Deposited loess was later mixed with sand and lime carried by rivers (Morello et al. 2012). Fluvial erosion has been an important factor shaping the relief of the Chaco region, due to the relatively flat topography of the region (with a regional slope of 20-40 cm km⁻¹) and the markedly seasonal and torrential nature of river flooding (Morello et al. 2012).

The climate is hot and dry, with a mean annual temperature of 23°C in the northern tip of the Argentine Chaco and of 18°C in its southern tip. The region contains the hottest spot of South America at the core of the Dry Argentine Chaco, where maximum temperature reaches above 47°C in summer. Rainfall in the Dry Argentine Chaco ranges between 400 and 800 mm, 80% of which fall between October and April (monsoonal regime) (Morello et al. 2012).

The original vegetation consisted of a mosaic formed by xerophytic forests, gallery forests, and soil-determined or fire-generated savannas (Adamoli et al., 1972). Before recent agricultural expansion, changes in vegetation resulted mainly from two processes: i) changes in herbaceous/woody species caused by overgrazing, fire and droughts, and ii) gallery forest dynamics resulting from intensive river-bed migration processes. More recently, forest degradation and fragmentation have introduced abrupt changes in the composition and configuration of native vegetation cover (Torrela et al. 2013).

The Chaco region hosts a large diversity of plant and animal species. It is home to 3,400 plant species, approximately 500 bird species, 150 species of mammals, 120 species of reptiles, and approximately 100 species of amphibians (TNC et al. 2005). Chaco forest types are classified based on the species of quebracho tree that dominate the high arboreal stratum. The drier Western Chaco forests are dominated by *Schinopsis lorentzii* and the more humid Eastern Chaco forests by *Schinopsis balansae*. In the central Chaco, "three-quebrachos" forest are co-dominated by these two species and another quebracho tree (*Aspidosperma quebracho-blanco*) (Torrela et al. 2011). The middle and lower arboreal strata are dominated by species of algarrobo trees (*Prosopis* spp.).

These forests are inhabited by a relatively large number of mammal species. Redford et al. (1990) report the occurrence of 30 species of medium ($\geq 1~\rm kg$) and large ($\geq 10~\rm kg$) mammal species at a 2,000 ha study site close to the Argentina-Paraguay border covered by Dry Chaco forests, and of another 23 mammal species elsewhere in the Chaco. For comparison, these authors report that the Manu National Park in Peru, generally regarded as the richest site in the Neotropical region, is inhabited by 34 species of large and medium sized mammals. This

comparison highlights the high conservation value of Dry Chaco forests, as this non-rainforest ecosystem is as rich as tropical rainforests in terms of numbers of larger mammalian species. Moreover, the conservation value of these forests increased in 1974 with the discovery of *Catagonus wagneri*, a peccary species endemic to the Western Argentine Chaco previously known only from fossils, which is now at risk of extinction (Redford et al. 1990).

Dry Chaco forests also host a comparatively high avian diversity. Short et al. (1974) reported that about 409 bird species are resident or breed in the Chaco region, including 22 that barely reach its borders. Taxonomically, there are 218 non-passerine birds, 100 sub-oscine passerines, including 52 tyrant flycatchers, 20 oscine passerines of Old World groups, and 71 New World nine-primaried oscines (Short et al. 1974). Notwithstanding its high diversity, the Chaco region hosts few endemic bird species. Almost 60% of its bird species are endemic in South America, 28% reach Mesoamerica, 12% are also found in North America and 3% are also in the Old World. Only one species (*Eudromia formosa*) and five subspecies are endemic to the region, while 11 other mainly occur in the Chaco (Short et al. 1974). This low avian endemicity is explained by the central location and accessibility of the Chaco region within South America. The Chaco region neighbours other xeric regions along the "dry diagonal" comprising Chaco, Cerrado and Caatinga regions (Bucher 1982), and also highly diverse mesic regions such as the Yungas, Atlantic and Amazon rainforests, with which it shares many bird species.

In this thesis, birds are used as the response variable of the study system for two main reasons. First, bird species and communities are good indicators of ecosystem status as they show a high sensitivity to disturbances, such as those produced by land-use intensification (Sekercioglu et al. 2002, Tscharntke et al. 2008). Previous studies reported significant changes in the richness and composition of Chaco avifauna in response to the presence of vegetation edges, such as those produced by total forest clearing (Lopez de Casenave et al. 1998), and to the removal of shrub vegetation (Codesido et al. 2009). Secondly, birds are an important conservation target owing to their high intrinsic, functional and utilitarian value (Sekercioglu 2006, Whelan et al. 2008). Chaco avifauna have been exposed to multiple conservation threats, with the exception of species invasions (i.e. the few exotic species found in the Chaco do not represent a conservation threat for native birds, Lopez de Casenave et al. 1998). Habitat degradation due to agricultural intensification, hunting and pet trade, among

other factors, jeopardize the regional status of many bird species. The Bermejo-Pilcomayo Interfluve in the Western Chaco hosts populations of regionally threatened bird species highly valued as food (e.g. *Ortalis canicollis*), pets (e.g. *Amazona aestiva*), or that play important functional roles as top predators (e.g. *Harpyhaliaetus coronatus*) (Di Giacomo & Abril 2005).

INDIGENOUS USE

Human occupation of the Chaco occurred between 500 and 1000 years before present (Morello & Adámoli 1970). The region was described as dominated by woody vegetation in some locations and by herbaceous vegetation in others (Estrada 1906 in Morello & Saravia Toledo 1959). The balance between woody and herbaceous vegetation was controlled by periodic fires, geomorphologic processes, and climatic stochasticity (Adámoli et al. 1990). Fire use among indigenous people shaped the landscape for purposes as diverse as herding, preparation of sites for temporary settlement, communication and warfare (Barquez 1997). By various burning events both in space and time indigenous inhabitants created a mosaic of grassland patches at different successional stages in order to maintain a regular supply of ecosystem goods and services throughout the year (Morello et al. 2005). Indigenous livelihoods were radically altered after several waves of planned and unplanned occupation of the Chaco in mid-19th century, following the independence of Argentina (Leake 2008). Immigrants and their cattle herds imposed physical and social barriers to the mobility of indigenous groups and initiated the degradation of their resource base (Van Dam 2002). Increased competition for the land along with incipient ecosystem degradation forced indigenous people to become less mobile and eventually sedentary (Leake 2008). This set of factors had a profound disrupting effect on the indigenous mode of living, leading to the high vulnerability to agricultural expansion found today among remaining indigenous people in the Chaco (Leake 2008).

SMALLHOLDER OCCUPATION

In early 19th century, the first Argentinean governments distributed public lands in the Chaco region among influential people from the burgeoning Pampas, and the formation of large landholdings (i.e. *latifundios*) ensued. For many decades, landowners were usually absentees from *latifundios* as these were mostly used for speculative purposes, such as gaining access to credit. Native families with Spanish descent (i.e. *criollos*) employed in *latifundios* gradually

took control over the land and used it as a common pool resource for low-intensity cattle grazing (Morello et al. 2005). State-led colonization of the Chaco region was initiated in the 1860s with the establishment of pastoral colonies along the large rivers Bermejo and Pilcomayo. Large increases in cattle numbers led to overgrazing of riverine grasslands, land abandonment and dispersion of criollo families along the interfluves (i.e. lands between rivers) of the Bermejo and Pilcomayo (Barbarán & Arias 2001). In the interfluves, criollo families developed a cattle production system, known as puesto, that consisted of houses, a well and corrals, and a portion of land ranging from 500 to 5000 ha without perimeter or internal fences (Camardelli 2003). In a *puesto* system, this portion of land is the daily foraging range of cattle of up to 5 km from the *puesto* centre. By 1940, expansion of *puestos* reached areas too dry or too hot for cattle ranching and the production capacity of the ecosystem became saturated (0.2 head of cattle/ha, Adámoli et al. 1990). Overstocking led to two conspicuous landscape changes. In combination with fire suppression, extensive grazing stimulated the expansion of fire-sensitive, woody vegetation on savannahs (Adamoli et al. 1990). The concentration of livestock around water sources in the *puesto* centre created areas of heavily degraded vegetation and soil around *puestos*, locally known as *peladares* (Morello et al. 2005).

LARGE-SCALE ENTERPRISES

By the turn of the 20th century, rapid growth in population, consumption and production levels in the Pampas brought about high demand for different types of forest products: charcoal and firewood for domestic use, posts for fencing rural properties, timber for furniture production and sleepers for railway construction. These forest products were mostly supplied by small and medium enterprises, which were labour-intensive and promoted the development of railrways along the Chaco region (Morello et al. 2005). A radically different mode of forest exploitation ensued with the arrival of large foreign companies dedicated to the extraction of high-tannin-yielding tree species such as *quebrachos* (*Schinopsis* spp.). The unprecedented extent and intensity of logging activities of large foreign companies is illustrated by the British "Forest Land, Timber and Railways Company" which arrived in 1904 and exploited 2 million ha of *quebracho* woodlands in the Central Chaco (Morello et al. 2005). By 1963, this company exhausted the resource and moved to exploit the mimosa tree in South-West Africa leaving behind ghost towns and degraded scrubland (Morello et al. 2005). By the 1970s, another large-scale extractive activity arrived to the Chaco region. State

and foreign companies extended a profuse network of oil exploration roads and extraction stations, where oil spills and open oil wells were common (Morello et al. 2012). However, the largest influence of oil extraction activities on Chaco landscapes has been indirect, by facilitating access to loggers, hunters and pet traders, who found in oil exploration roads a way to penetrate into forest areas that would otherwise be inaccessible (Barbarán & Arias 2001).

INCIPIENT AGRICULTURAL EXPANSION

Crop cultivation in the Chaco region during the first half of the 20th century had been smallscale and localized in colonies of European immigrants in the Eastern Chaco dedicated to cotton production. By the 1960s, the so-called Green Revolution brought about the possibility of significantly increasing crop yields through the use of short-cycle cultivars, machinery and potent agrochemicals. In the Argentine Chaco, the adoption of these technologies combined with the presence of large tracts of fertile lands, despite a century of extensive cattle ranching. It also coincided with increases in rainfall by 20-30% above levels during the first half of the 20th century. Adoption of "Green Revolution" technologies was stimulated by a political context of economic liberalization and land privatization (Grau et al. 2008). These conditions fueled the large-scale cultivation of beans and soybeans in the Western Sub-humid Chaco and of cotton in the Central Sub-humid Chaco (Van Dam 2002). The expansion of conventional agriculture involved for the first time the employment of a production system that required a complete replacement of the native ecosystem. Land conversion for extensive cropping led to deforestation rates of 110, 000 ha/year for the Western Chaco during the period 1977-1997 (Paruelo et al. 2011). In addition, environmental toxification was incipient in already converted lands as production systems became highly mechanized and subsidized with external inputs (such as fertilizers and pesticides) to substitute for ecosystem functions (such as soil regeneration and biological control) that were impaired by land conversion (Pengue 2005).

AGRICULTURAL EXPANSION AND INTENSIFICATION

In the 1990s, technological, economic and institutional changes in a context of globalization and urbanization gave rise to a fundamentally different stage of frontier expansion. The most prominent technological change was the introduction of transgenic soybean cultivars with resistance to a powerful herbicide (glyphosate) in 1996 and the diffusion of no-till farming,

which offered wealthy farmers a more simple and profitable cropping system (Manuel-Navarrete et al. 2009). Soybean cultivation could now be managed with fewer human resources and be implemented on areas that were previously marginal for rainfed agriculture. Furthermore, the technological suite formed by GM soybeans, glyphosate and zero tillage did not require intercropping or fallow periods and allowed more intensive use of the land by cropping it all year round (Aizen et al. 2009). Economic changes related to the formation of an agro-industrial chain oriented to the export of soybeans and soybean-based products (oil, feedstock and biodiesel) to developed and emerging countries, especially China (Manuel-Navarrete et al. 2009). Institutional changes consisted of the reduction in government investment in agricultural research, technological development and rural extension services, which along with weak environmental governance of rural areas set the stage for an increasing influence of private actors (e.g. agricultural firms, seed and agrochemical companies) in determining land-use choices available to farmers (Manuel-Navarrete et al. 2009).

The organization and logic of decision making of the agricultural enterprise also changed radically. The large amount of financial and physical capital required to cultivate soybeans along with rising land prices increased the minimum planted area that a production enterprise needed to be profitable (Reboratti 2008). Concentration of land and production ensued with transnational as well as large national firms buying latifundios and public lands and investment funds known as "sowing pools" leasing land to medium- and small-holders. These changes were so widespread that more than 50% of croplands in Argentina are dedicated to GM soybean cultivation (Aizen et al. 2009). Traditional rangelands of the Pampas were replaced with soybean fields and cattle stocks were displaced to the Chaco region. Lands already cleared in the Chaco region for the cultivation of beans and cotton in the Western and Central portions were replaced with soybean fields. Soybean cultivation pushed cattle pastures further into the agricultural frontier to the extent that 79% of the regional agricultural expansion (6 million ha) occurred through the conversion of native ecosystems by 2008 (Ginzburg 2009). Agricultural area increased from 5.12 M ha in 1992 (10% of the region) to 11.11 M ha in 2008 (22%) and regional deforestation rates tripled between the 1992-2002 period (182,000 ha/year) and 2002-2008 period (518,000 ha/year). Annual deforestation rates for the Western Chaco reached 2% in 2008, surpassing Latin American and world averages

(0.5 and 0.2, respectively) and coincident with the imminent passing of the Forest Law (Seghezzo et al. 2011).

THE FUTURE OF AGRICULTURE AND BIODIVERSITY IN THE CHACO

The review of the environmental history of the Argentine Chaco highlights critical aspects of the socio-ecological context that influence the potential effectiveness of land-use planning strategies aimed at reconciling biodiversity conservation and agricultural production. First, it shows that substantial social and cultural heterogeneity is present in the Chaco region, which means that researchers should meaningfully consider the diversity of values, beliefs and perceptions towards land-use when evaluating land-use strategies. It also requires planners and policy-makers to balance the interests of multiple stakeholders in the implementation of such strategies. Second, it demonstrates the consistently low capacity of Argentine government institutions to improve conservation outcomes in arable, private lands. To be effective, land-use planning interventions should therefore not rely exclusively on top-down approaches for biodiversity conservation. Third, it helps visualize the complex dynamics of Chaco ecosystems both due to intrinsic variability in biophysical processes (e.g. current trend of rainfall increase) and in response to exogenous anthropogenic disturbances (e.g. past woody expansion due to overgrazing). In this light, the design of conservation planning strategies should be based on sound ecological research and on the application of transdisciplinary research approaches combining insights from ecological, agronomic and social sciences (Kaimowitz 2010).

Unfortunately, few attempts have been made to apply transdisciplinary research approaches to the study of agriculture and biodiversity relationships in agricultural frontier regions in general, and in the South American Gran Chaco in particular (Zak et al. 2004, Kaimowitz 2010). Ecological research on the relationship between biodiversity and agriculture has significant gaps and biases that constrain the development of sound evidence relevant for conservation planning. First, it is geographically biased either towards temperate regions where agriculture has already cleared most of the landscape such as Europe (Martin et al. 2012) or to tropical regions where agriculture expands into pristine or charismatic ecosystems such as the Amazon (Hecht 2010). This has left tropical dry forest ecosystems such as the Chaco largely understudied, despite being one of the most endangered ecosystems globally (Sanchez Azofeifa et al. 2005). Second, it is biased towards the evaluation of cropping

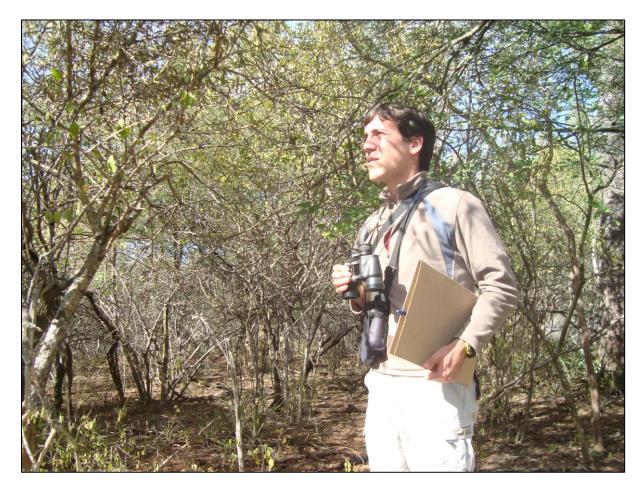
systems (Balmford et al. 2012), leaving the study of land-based livestock systems under a "long shadow" (Naylor et al. 2005, Steinfeld 2006). Third, the quantitative relationship between food productivity and biodiversity levels across land-use intensity gradients remains unknown for most taxa and agricultural systems (Perfecto & Vandermeer 2008). Knowing this relationship has been identified as a research priority both in the conservation (Sutherland et al. 2009) and agriculture literature (Pretty et al. 2010). Fourth, biodiversityproductivity relationships have been mostly assessed on the basis of aggregate measures of biodiversity (e.g. species richness) and indirect measures of productivity (e.g. land-use intensity) (Phalan et al. 2011a). This has constrained the possibility of exploring the contribution of biodiversity and agricultural productivity to ecosystem services and human well-being (Tschartnke et al. 2012). Fifth, of the few studies assessing biodiversityproductivity relationships, none of them have explicitly evaluated the spatial scale of the ecological processes influencing conservation outcomes such as the habitat quality of agricultural matrix types (Cunningham et al. 2013). Finally, to my knowledge no attempts have been made to assess the conservation potential of land-use options and then to evaluate the social factors influencing the choice of pro-conservation land-use options.

Here I will contribute to filling these research gaps by evaluating the ecological and social dimensions of the trade-offs between food production and habitat conservation at two agricultural frontiers expanding into tropical Chaco dry forests. More specifically, Chapter 2 presents the first assessment across the globe of the functional relationship between biodiversity and agricultural productivity in a dry forest ecosystem and across gradient of cattle production intensity. This assessment provides empirical evidence on the relative utility of land-sparing and land-sharing as strategies to reconcile production and conservation in the agricultural frontier of the Bermejo-Pilcomayo Interfluve, Western Argentine Chaco.

Chapter 3 presents an analysis of the spatial scale of the ecological processes influencing conservation outcomes through an assessment of the relative influence of agricultural management (local) and landscape level factors on habitat quality for birds of different agricultural matrix types. This analysis helps identify the type and spatial scale of changes in habitat quality with higher effect on the persistence of bird species in the agricultural matrix. Chapter 4 presents an evaluation of the psycho-social factors influencing landholders' intentions to conserve forest fragments in the agricultural frontier of the Chaco Impenetrable, Central Argentine Chaco. This evaluation is the first use of social psychological models to

understand pro-conservation intentions in the context of agriculture, globally. Chapter 5 presents a discussion on the main findings of the thesis and its contribution to improve our understanding of agriculture-biodiversity relationships. It also proposes a series of planning and policy recommendations to reconcile production and conservation objectives at Chaco agricultural frontiers. Two of these chapters are published (Chapters 2 and 4) and submission for publication of Chapter 3 is imminent. These chapters are therefore placed in the thesis in the style and formats that was published or will be submitted for publication. The manuscript formats mean some repetition in Methods and Study site description.

CHAPTER 2: TRADE-OFFS BETWEEN CATTLE PRODUCTION AND BIRD CONSERVATION IN AN AGRICULTURAL FRONTIER OF THE GRAN CHACO OF ARGENTINA



Watching birds in dry Chaco forests. Photo by the author.

This chapter is formatted in the style of Conservation Biology where it was first published online on 2 August 2012 as Mastrangelo, M. E., & Gavin, M. C. 2012. Trade-Offs between Cattle Production and Bird Conservation in an Agricultural Frontier of the Gran Chaco of Argentina. Conservation Biology, 26(6), 1040-1051. For this chapter, I collected all data, conducted analyses and did all the writing, while Gavin, M. C. provided advise.

ABSTRACT

Intensification of food production in tropical landscapes in the absence of land-use planning can pose a major threat to biological diversity. Decisions on whether to spatially integrate or segregate lands for production and conservation depend in part on the functional relations between biological diversity and agricultural productivity. We measured diversity, density, and species composition of birds along a gradient of production intensification on an agricultural frontier of the Argentine Chaco, where dry tropical forests are cleared for cattle production. Bird species diversity in intact forests was higher than in any type of cattle production system. Bird species richness decreased nonlinearly as cattle yield increased. Intermediate-intensity silvopastoral systems, those in which forest understory is selectively cleared to grow pastures of non-native plants beneath the tree canopy, produced 80% of the mean cattle yield obtained in pastures on cleared areas and were occupied by 70-90% of the number of bird species present in the nearest forest fragments. Densities of >50% of bird species were significantly lower in open pastures than in silvopastoral systems. Therefore, intermediate-intensity silvopastoral systems may have the greatest potential to sustain cattle yield and conserve a large percentage of bird species. However, compared with low-intensity production systems, in which forest structure and extent were intact, intermediate-intensity silvopastoral systems supported significantly fewer forest-restricted bird species and fewer frugivorous birds. These data suggest that the integration of production and conservation through intermediate-intensity silvopastoral systems combined with the protection of forest fragments at the landscape scale may be required to maintain cattle yield, bird diversity, and conservation of forest-restricted species in this agricultural frontier.

Introduction

Producing food sustainably while conserving biological diversity is becoming more challenging as demand for livestock and feedstock increases globally (McAlpine et al. 2009). In South America, this challenge is particularly acute given that a significant portion of the global supply of beef and soybeans comes from large Neotropical ecoregions with diverse species: Amazonia, Gran Chaco, and Cerrado (Brannstrom 2009). Policy and management decisions to minimize effects of land-use on biological diversity require increased understanding of the interactions between human pressure (e.g., production intensity) and response factors (e.g., species diversity, ecosystem services) (Fischer et al. 2008; Mattison & Norris 2008). This gap in understanding is recognized as a top research priority in the conservation (Sutherland et al. 2009) and agriculture (Pretty et al. 2010) literature.

The search for spatial arrangements of land uses that can achieve both conservation and production objectives has been the subject of much theoretical debate, but limited empirical research. Some authors support spatial segregation of lands allocated to production and conservation, arguing that strong conflicts between these objectives are inevitable (Green et al. 2005; Phalan et al. 2011a). They suggest developing high-yield agriculture on fertile areas and protecting abandoned or undeveloped lands on marginal areas to increase production efficiency and conservation effectiveness, respectively (Grau et al. 2008). Others support spatial integration of conservation and production management, arguing that high-priority species may persist in agricultural areas (Daily et al. 2001; Perfecto & Vandermeer 2010). They suggest developing a fine-grained mosaic of low- and intermediate-intensity production and fragments of native land cover to increase the permeability of the landscape to species dispersal. The few existing efforts to model the functional relation between species diversity and yield (e.g., Vandermeer et al. 1998; Green et al. 2005) have produced 2 testable predictions: if values of biological-diversity response variables decrease sharply at low levels of agricultural intensification, then land-use segregation is most likely to achieve conservation and production objectives and if values of biological-diversity response variables only decrease at high levels of agricultural intensification, then land-use integration is most likely to achieve conservation and production objectives.

The relation between biological diversity and agricultural productivity along intensification gradients provide a valuable framework for land-use planning; however, these relations have

not been evaluated for the vast majority of taxonomic groups and agricultural systems (Perfecto & Vandermeer 2008). Empirical studies in which this framework has been applied across intensification gradients of multiple production systems are few (Clough et al. 2011). By December 2012, Grau et al. (2013) reported only nine published studies providing empirical evidence on trade-offs between biodiversity and agricultural yields. In turn, there is a need to expand the range of measures of biological diversity used to explore the response of biological diversity to agricultural productivity in order to account for identity and ecological roles of species (Phalan et al. 2011a). We applied and expanded existing methods to quantify the effect of different production systems on cattle yield and on species diversity and composition of birds in the Gran Chaco, Argentina. This region contains one of the largest tracts of tropical dry forests, a highly threatened and poorly studied ecosystem (Sanchez-Azofeifa et al. 2005). We used our results to suggest options for land-use planning in the area.

In the Argentine Chaco (approximately 700,000 km² and 60% of the Gran Chaco region), the combination of strong international-market demand for beef and soybeans, increasing rainfall, national policies encouraging land privatization and agricultural exports, and weak environmental governance of rural lands stimulated the expansion of industrial crop and cattle production. Forest clearing for growth of pastures planted with non-native species and for planting genetically modified soybeans is driving the advance of the deforestation frontier from subhumid areas to the semiarid core of the Argentine Chaco. From 2005 to 2010, annual deforestation rates in the Chaco (1.5-2.5%) surpassed Latin American and world averages (0.51 and 0.20, respectively) (Seghezzo et al. 2011). On the deforestation frontier, industrial systems of high-intensity cattle grazing of African grasses (e.g., Panicum maximum) planted on cleared areas displace traditional ranching systems in which cattle browse forests and shrublands at low intensity. Some ranchers use an integrated silvicultural and pastoral (i.e. silvopastoral) system that combines cattle production with management of forest structure and functions (e.g., native shade trees). Ranchers selectively remove woody understory to allow grass to regenerate or sow grass beneath the tree canopy. We empirically assessed trade-offs between bird conservation and cattle production along a gradient of agricultural and pastoral intensification from low-intensity traditional systems to 2 variants of silvopastoral systems, to industrial high-intensity systems (see Chapter 1 - Characteristics of the Dry Argentine Chaco for reasons for the selection of birds as the response variable).

METHODS

STUDY AREA

The Bermejo-Pilcomayo Interfluve covers approximately 2 million ha in the central-west South American Gran Chaco, extending from *yungas* (lower-elevation Andean humid forest) eastward toward *chaco* (dry plains forest) (Fig. 2.1). It contains the most rapidly expanding agricultural frontier in northwestern Argentina. Differences in elevation and mean annual rainfall create a distinct longitudinal gradient in forest structure and potential agricultural productivity that delineate the division of the study area into 3 zones: premontane forest (elevation 500-380 m, per annum rainfall 1000-800 mm), *umbral* (transition area) (elevation 379-260 m, per annum rainfall 800-600 mm), and chaco (elevation <260 m, per annum rainfall <600 mm). The forest overstory is dominated by hardwoods (red quebracho [*Schinopsis quebracho-colorado*] and white quebracho [*Aspidosperma quebracho-blanco*]) and to a lesser degree by *palo blanco* (*Calycophyllum multiflorum*) and *palo amarillo* (*Phyllostylon rhamnoides*) in humid areas and by *palo santo* (*Bulnesia sarmientoi*), floss silk tree (*Chorisia speciosa*), and algarrobos (*Prosopis* spp.) in drier areas. The ecotone between yungas and chaco forests has relatively high species richness and supports a culturally diverse human population (30% indigenous and 20% of mixed European and indigenous ancestry).

CLASSIFICATION OF CATTLE RANCHES

We defined cattle-production intensification as the process of increasing cattle live weight over time (annual) per unit area (hectare) through changes in management. Actual live-weight yield in frontier areas is difficult to measure because production data are limited and production is highly variable over time and space. In Chaco frontiers, methods for clearing forests (selective clearing and complete clearing) and for increasing forage availability (native grass regeneration and planting of non-native grass) have the greatest influence on cattle yield (Berti 2009). We classified cattle ranches by production strategy on the basis of these practices as a surrogate measure of cattle yield. We validated this classification later by comparing methods for clearing forests and for increasing forage availability with cattle yield declared by ranchers.

We analyzed a land-cover map (Landsat TM from September 2009) and cadastral information (map of landholdings) provided by local government agencies and NGOs to

determine for each ranch in the study area the degree to which forests were cleared (i.e., not cleared, cleared understory, or completely cleared) and whether the main source of forage was forest and shrubland, native grasses, or planted non-native grasses. We validated the classification of the degree of clearing and the main source of forage through visual inspection of ranches located along secondary roads during field trips in April through May 2010.

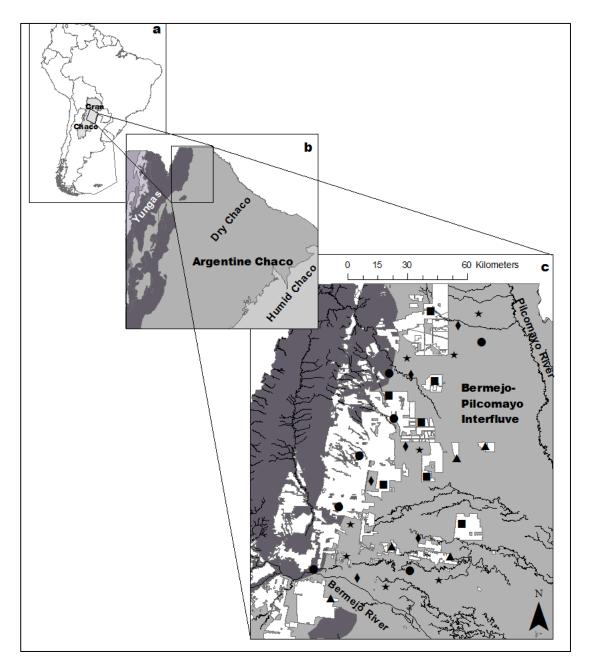


FIGURE 2.1. LOCATION OF (A) THE ARGENTINE CHACO (BLACK PARALLELOGRAM) IN THE SOUTH AMERICAN GRAN CHACO, (B) THE MIDDLE BERMEJO-PILCOMAYO INTERFLUVE (BLACK SQUARE) IN THE TRANSITION BETWEEN THE ARGENTINE CHACO AND THE YUNGAS ECOREGION, AND (C) SITES OF BIRD SAMPLING: DIAMONDS, FOREST FRAGMENTS; STARS, VERY LOW-INTENSITY SYSTEMS; CIRCLES, LOW-INTENSITY SILVOPASTORAL SYSTEMS; TRIANGLES, INTERMEDIATE-INTENSITY SILVOPASTORAL SYSTEMS; SQUARES, HIGH-INTENSITY PASTORAL SYSTEMS.

In this way, we classified each ranch into 1 of 4 types of cattle production systems: very-low-intensity systems, closed forests with free-ranging cattle feeding on understory shrubs and ephemeral grasses; low-intensity silvopastoral systems, open forests with the understory selectively cleared to stimulate regeneration of native grasses; intermediate-intensity silvopastoral systems, stands of native trees of varying densities in which planted non-native grasses have replaced the woody understory; and high-intensity pastoral systems, open pastures of non-native grasses growing on areas completely cleared of native vegetation.

SELECTION OF SAMPLING SITES

We collected data on cattle yield and birds on ranches with different production intensities. Measured from the perimeter, ranches with the same type of production system were at least 50 km apart from each other. At least one ranch in every type of production system was located in each zone (premontane, umbral and chaco) to account for variations in elevation and rainfall. To collect baseline data on birds, we surveyed forest fragments that had not been used for agriculture or intensive logging in the past 5 years, were >1000 ha, and had a canopy cover >70%. Each forest fragment was in the same zone (premontane, umbral or chaco) of a group of 4-5 selected ranches, for which it served as a baseline habitat, and at a distance of 5-50 km from those ranches (measured from the perimeter). This selection process yielded a sample of 7 high-intensity pasture systems, 5 intermediate-intensity silvopastoral systems, 7 low-intensity silvopastoral systems, 8 very low-intensity systems, and 6 forest fragments (Fig. 2.1).

BIRD SURVEYS

We established 6 25-m radius sites in which we conducted point counts in each of the 33 sampling sites (27 cattle ranches and 6 forest fragments) (see Appendix B for explanation on selection of bird survey method). To locate survey sites, we subdivided the total area of each sampling site into a grid of 100-ha square cells (i.e., usual paddock size and shape) and established a point-count site in the center of 6 randomly selected cells. We conducted point counts at sites once during the non-reproductive season (May-August 2010) (see Appendix B for explanation on selection of bird survey season). We detected birds by sight or sound and recorded all individuals staying in, entering, or leaving the site over 20 min. We counted birds when bird activity is greatest, either 3 hours after dawn (51.5% of counts) or 3 hours before dusk (48.5%). We minimized imperfect detection of birds (Martin & McIntyre 2007)

in 2 ways. First, we used fixed-radius point counts instead of, for example, open-radius point counts or transect counts to control for differences in detection range among sampling sites with different vegetation structure. Second, a single observer (M.E.M.) undertook all bird counts, which reduced detection bias associated with differences in observer performance.

INTERVIEWS WITH RANCHERS

We conducted semi-structured interviews with ranch managers of each of the 27 ranches to gather data on management strategies and cattle-production practices. We visited each ranch twice. During an initial visit in April 2010, we validated the classification of ranches into types of production systems and identified the person with the greatest knowledge of the cattle-ranching operations to interview in the future. During the second visit between May and August 2010, we conducted the interviews. In very-low-intensity systems, we interviewed household heads of long-established (40-90 years), family-run operations, locally known as *puestos* (i.e., ranches with undefined boundaries ranging from 800 to 2300 ha). In low-intensity and intermediate-intensity silvopastoral systems, we interviewed owners of recently established (5-10 years) medium-sized *fincas* (i.e., ranches with defined boundaries ranging from 2000 to 5200 ha) responsible for production activities in the field. In highintensity pastoral systems, landowners were often absent from the ranch. Therefore, in these cases, we interviewed the employee in charge of ranching operations. We asked 25 openended questions, delivered in one-on-one conversations in Spanish under a semi-structured design to reduce potential bias associated with cultural differences among respondents and between respondents and the interviewer (Bernard 1994) (survey instrument in Table A2, Appendix A). Questions focused on social (e.g., time of residence and land tenure), technological (e.g., use of agrochemicals, machinery, fire), and agronomic (i.e., number of cattle, live weight at sale) characteristics of ranches.

DATA ANALYSES

We constructed species-accumulation curves and calculated richness estimators at the level of production systems with EstimateS (Colwell 2009). We compared means of 3 diversity measures at the level of ranches and production systems with two-way nested analysis of variance (ANOVA) and the Satterthwaite approximation for unbalanced sample sizes. Then, we performed unplanned comparisons (Tukey-honestly significant difference) at the level of production systems in SPSS 18.0 (IBM, Chicago, USA). The 3 diversity measures were

species richness (number of species recorded in a point count), species richness relative to forest ([number of species in a point count of ranch_i / mean number of species in the forest fragment nearest to ranch_i] * 100), and values of the Shannon diversity index (H):

$$H = -\sum_{i=1}^{S} pi \ln pi, \tag{1}$$

where S is species richness and p_i is the proportion of individuals of the ith species.

We constructed 2 species richness-yield functions to determine whether the relation between species richness and cattle yield was best represented by a concave or a convex function (Fig. 2.2a) (see Appendix C for explanation of curve-fitting method). We calculated the first function with bird species richness and cattle yield expressed in total values and the second with the values of these variables expressed as a percentage of their respective potential values. For the first species richness-yield function, we pooled the number of bird species recorded in the 6 point counts of a ranch to calculate the total species richness of that ranch. We obtained a measure of actual cattle yield from responses of ranchers to interview questions, which was expressed as the live cattle weight produced per hectare per year for the ranch. For the second species richness-yield function, we calculated species richness relative to intact forest at the level of ranches: (total species richness of ranch_i / total species richness of forest fragment nearest to ranch_i) * 100. To calculate actual cattle yield relative to its potential, we used estimations of the potential effect of the interaction between management practices (i.e., type of clearing, type of forage) and biophysical variables (i.e., elevation, rainfall, soil type) on cattle yield (Berti 2009). We divided actual yield of ranch; by the yield that can be obtained through the use of management practices that define the production system of ranch_i in the zone where ranch_i is located and multiplied the quotient by 100. We obtained best-fitting curves and regression coefficients for both richness-yield functions with SPSS 18.0 (see Appendix C for explanation of curve-fitting method).

We examined species composition of bird assemblages across the gradient of agricultural intensification. We evaluated species composition by comparing the Chao-Jaccard abundance-based similarity index (2) between pairs of production systems:

$$J_{abundance\ based} = \frac{UV}{U + V - UV} \tag{2}$$

where U and V are the relative abundances of individuals of the shared species in the 2 assemblages.

We also constructed a curve that depicts the variation in the Jaccard occurrence-based similarity index (3) between bird assemblages of forest fragments and production systems and compared this curve with the species richness-yield curve:

$$J_{occurrence\ based} = \frac{A}{A+B+C} \tag{3}$$

where A is the number of species shared by 2 assemblages, and B and C are the number of species unique to each of them. To evaluate functional composition, we first classified all species recorded with respect to 2 functional attributes, feeding strategies and habitat affiliation (Lopez-Casenave et al. [1998] for chaco species and Blendinger [2007] for yungas species). This classification resulted in 5 feeding guilds (i.e., insectivores, frugivores, granivores, carnivores and omnivores) and 3 habitat-affiliation groups (i.e., forest specialists, generalists, and open-land species). We did not examine species richness in nectarivores because we recorded only one species in this group. We compared means of species richness and abundance within functional groups among ranches and production systems with two-way nested analysis of variance corrected for unbalanced sample sizes and post hoc tests in SPSS 18.0.

We calculated density of species_i as the abundance of species_i at a given point divided by the area sampled (0.02 km²). Then, we compared means of density of all species recorded at the level of ranches and production systems with two-way nested analysis of variance corrected for unbalanced sample sizes and post hoc tests in SPSS 18.0. These analyses revealed associations between density of birds and cattle production intensity, which were stronger between production systems with marked differences in forest structure (e.g., silvopastoral systems of cleared understory and high-intensity pastoral systems completely cleared). Thus, we classified each species into 1 of 3 qualitative types of response (decrease, stable, increase) to each of the 2 forest-clearing classes (cleared understory and completely cleared) on the basis of the quantitative pattern of differences in density resulting from multiple comparisons among types of production systems (Table 2.1).

RESULTS

PRODUCTION INTENSITY, CATTLE YIELD, AND TREE COVER

Ranges for cattle yield were 4-12 kg ·ha⁻¹·year⁻¹ in very-low-intensity systems, 14-30 kg ·ha⁻¹·year⁻¹ in low-intensity silvopastoral systems, 100-140 kg ·ha⁻¹·year⁻¹ in intermediate-intensity silvopastoral systems and 115-180 kg ·ha⁻¹·year⁻¹ in high-intensity pastoral systems. Types of production systems differed significantly in cattle yield (df=3, *F*=96.8, *p*<0.001) and canopy cover (df=158, *F*=263.03, *p*<0.05). Cattle yield was significantly lower in very-low-intensity systems (7 kg ·ha⁻¹·year⁻¹ [SD 2.7]) than in low-intensity silvopastoral systems (20 kg ·ha⁻¹·year⁻¹ [SD 6.6]), both of which had significantly lower yields than intermediate-intensity silvopastoral systems (105 kg ·ha⁻¹·year⁻¹ [SD 16.7])) and high-intensity pastoral systems ((130 kg ·ha⁻¹·year⁻¹ [SD 32.6])). Canopy cover was significantly greater in very-low-intensity systems (81% [SD 14.2]) than in low-intensity silvopastoral systems (56% [SD 22.5]) or in intermediate-intensity silvopastoral systems (37% [SD 9.4]), where canopy cover was significantly greater than in high-intensity pastoral systems (6% [SD 5.4]).

TABLE 2.1. CRITERIA USED TO CONVERT THE QUANTITATIVE DENSITY OF INDIVIDUAL SPECIES OF BIRDS IN DIFFERENT TYPES OF CATTLE PRODUCTION SYSTEMS INTO A QUALITATIVE RESPONSE TYPE FOR EACH SPECIES.

| Production system 1 (PS1) | Production system 2 (PS2) | Density in PS1 versus density in PS2* | Qualitative response type |
|--|---------------------------------------|--|---|
| Forest fragments and very-low intensity | low-intensity and intermediate- | significantly higher | decreased in areas with cleared understory |
| systems | intensity silvopastoral systems | significantly lower | increased in areas with cleared understory |
| | | not statistically different | stable in areas with cleared understory |
| Low-intensity and intermediate-intensity | high-intensity pastoral systems | significantly higher | decreased in areas with cleared understory and trees |
| silvopastoral systems | | significantly lower | increased in areas with cleared understory and trees |
| | | not statistically different | stable in areas with cleared understory and trees |

^{*} Output of post hoc tests for multiple comparisons among types of production system.

We recorded 119 bird species, 97 in forest fragments, 79 in very-low-intensity systems, 78 in low-intensity silvopastoral systems, 63 in intermediate-intensity silvopastoral systems, and 42 in high-intensity pastoral systems (species accumulation curves in Fig A1 and species list in Table A1, Appendix A). Observed species richness was 80% of the estimated true species richness (on the basis of Chao1) in every type of production system. Production intensity was significantly associated with species richness (df=4, F=18.78, p<0.001), species richness relative to forest (df=4, F=17.07, p<0.001), and the Shannon diversity of birds (df=4, F=15.02, p<0.001) (Table 2.2). This association resulted in common patterns of differences among production systems for the 3 measures of diversity. Thus, bird diversity was significantly greater in forest fragments than in all other types of production systems; not statistically different among very-low-intensity systems, low-intensity, and intermediate-intensity silvopastoral systems; and significantly lower in high-intensity pastoral systems than in all other types of production systems.

RICHNESS-YIELD FUNCTIONS

The relation between bird species richness and cattle yields was best described by a concave function, which indicated that the number of bird species was relatively high in low- and intermediate-intensity systems and low in high-intensity systems (see Appendix C for discussion of alternative non-linear models). This was the pattern for species richness and yield expressed as total values (Fig. 2.2b) and as percentage of potential values (Fig. 2.2c). Both when expressed in total and relative values, cattle yield explained over half the variation (57%) in bird species richness. This result suggests that factors associated with cattle yield (e.g., type of forest clearing) are also associated with species richness of birds. Intermediate-intensity silvopastoral systems had the highest combination of yield and species richness. These systems were occupied by 70-90% of the number of bird species present in the nearest forest fragments and produced 60-70% of the cattle yield that could potentially have been obtained with this production system in premontane, umbral, or chaco.

TABLE 2.2. SUMMARY OF RESULTS OF 2-WAY NESTED ANALYSIS OF VARIANCE USED TO EVALUATE ASSOCIATIONS BETWEEN AGRICULTURAL PRODUCTION INTENSITY AND VARIABLES USED TO MEASURE BIRD DIVERSITY AND FUNCTION.

| | Type of pro | duction system, | mean (SD) ^a | | | Variance ra | tio ^b | Variance (%) ^c | |
|---|---------------------------|---------------------------|----------------------------|----------------------------|---------------------------|----------------------|------------------|---------------------------|-------|
| Bird measure | FF ^b | VLIS | LISS | IISS | HIPS | production system | ranch | production system | ranch |
| Diversity | | | | | | | | | |
| total species richness | $10.8 (3)^{\alpha}$ | $8.7 (2.8)^{\beta}$ | $9.2 (2)^{\beta}$ | $9.6 (2.6) \alpha^{\beta}$ | $5.5 (2.1)^{\gamma}$ | 18.78*** | 2.62*** | 48.26 | 11.01 |
| species richness relative to nearest forest | - | $84.8 (30.7)^{\alpha}$ | 84.4 $(21.5)^{\alpha}$ | 88.4 $(23.1)^{\alpha}$ | $46.8 (15.8)^{\beta}$ | 17.17*** | 1.83* | 39.69 | 7.32 |
| Shannon diversity index | $2.2 (0.3)^{\alpha}$ | $2 (0.3)^{\alpha\beta}$ | $2 (0.3)^{\alpha\beta}$ | $2 (0.3)^{\alpha\beta}$ | $1.3~(0.5)^{\gamma}$ | 15.02*** | 2** | 37.92 | 8.89 |
| Species richness within functional gro | oups | | | | | | | | |
| feeding guild | | | | | | | | | |
| granivores | 2.2 (1.2) | 2.3 (1.8) | 2.8 (2) | 3.8 (1.6) | 3 (1.7) | 2.3 | 2.73* | 6.53 | 20.89 |
| insectivores | $5.6 (2.3)^{\alpha}$ | $5.1 (2.3)^{\alpha}$ | $5.1 (2.1)^{\alpha}$ | $4.6 (2.4)^{\alpha}$ | $1.3 (1.3)^{\beta}$ | 14.2*** | 2.27* | 38.64 | 10.77 |
| omnivores | $0.6 (0.6)^{\alpha}$ | $0.3 (0.5)^{\alpha\beta}$ | $0.3 (0.6)^{\alpha\beta}$ | $0.3 (0.5)^{\alpha\beta}$ | $0.3 (0.5)^{\alpha\beta}$ | 3.5* | 0.67 | 4.1 | 0 |
| carnivores | $0.6 (0.6)^{\alpha\beta}$ | $0.3 (0.5)^{\alpha}$ | $0.6 (0.8)^{\alpha}$ | $0.9 (0.9)^{\beta}$ | $0.9 (0.7)^{\beta}$ | 3.5* | 1.43 | 7.82 | 6.19 |
| frugivores | $1.7 (1)^{\alpha}$ | $(1)^{\beta}$ | $0.4 (0.5)^{\gamma}$ | $0.2 (0.4)^{\gamma}$ | O_{λ} | 20.49*** | 1.86** | 44.63 | 6.94 |
| habitat group | | | | | | | | | |
| forest specialist | $6.7 (2.2)^{\alpha}$ | $5(2.3)^{\beta}$ | $3.9 (1.2)^{\beta}$ | $2.3 (1.4)^{\gamma}$ | 0^{δ} | 30.45*** | 3.67*** | 65.51 | 10.62 |
| habitat generalist | $3.4 (1.6)^{\alpha}$ | $3.6 (1.9)^{\alpha\beta}$ | $4.2 (2.1)^{\beta \gamma}$ | $5.2 (2.1)^{\beta \gamma}$ | $2.7 (1.8)^{\alpha}$ | 4.23** | 2.37*** | 13.66 | 16.05 |

| open-land species | $0.6~(0.9)^{\alpha\beta}$ | $0.5 (0.8)^{\alpha}$ | $1.3 (1.3)^{\beta}$ | $2.4 (1.4)^{\gamma}$ | $2.8 (1.3)^{\gamma}$ | 17.32*** | 2.20*** | 43.19 | 9.48 |
|------------------------------------|---------------------------|------------------------|-----------------------|----------------------|-----------------------|----------|----------|-------|-------|
| Abundance within functional groups | | | | | | | | | |
| feeding guild | | | | | | | | | |
| granivores | 5.2 (5.2) | 9.4 (15.7) | 10.1 (9) | 19.3 (16.4) | 41.1 (66.7) | 1.71 | 12.54*** | 7.2 | 61.05 |
| insectivores | $9.3 (4.7)^{\alpha}$ | $8.9 (5)^{\alpha}$ | $10 (6.2)^{\alpha}$ | $8.7 (6.6)^{\alpha}$ | $4.6 (3.4)^{\beta}$ | 3.25* | 1.99*** | 8.89 | 12.91 |
| omnivores | 1.7 (1.9) | 0.8 (1.3) | 0.9 (2) | 0.7 (1.5) | 1.4 (3.4) | 1.52 | 0.26 | 1.49 | 2.78 |
| carnivores | $0.8 (1.2)^{\alpha}$ | $0.3 (0.5)^{\alpha}$ | $0.9 (1.4)^{\alpha}$ | $1.1 (1.2)^{\beta}$ | $1.2 (1.4)^{\beta}$ | 3.6* | 1.11 | 6.72 | 1.69 |
| frugivores | $2.7 (1.8)^{\alpha}$ | $2.3 (2.5)^{\alpha}$ | $0.8 (1.1)^{\beta}$ | $0.5 (0.9)^{\beta}$ | O^{β} | 12.37*** | 2.05** | 33.54 | 9.91 |
| Habitat group | | | | | | | | | |
| forest specialist | $12.3 (5.1)^{\alpha}$ | $12.3 (11.4)^{\alpha}$ | $7.8 (5.1)^{\beta}$ | $5.2 (4.7)^{\beta}$ | 0^{γ} | 6.38*** | 7.32*** | 32.77 | 34.48 |
| habitat generalist | $6.2 (4.8)^{\alpha}$ | $8.5 (8.1)^{\alpha}$ | $11.3 (9.3)^{\alpha}$ | $16.8 (13)^{\beta}$ | $8.7 (7.6)^{\alpha}$ | 2.71* | 3.55*** | 9.81 | 26.93 |
| open land specialist | $1.5(2)^{\alpha}$ | $1.1 (1.8)^{\alpha}$ | $3.6 (4.3)^{\alpha}$ | $8.2 (9.2)^{\alpha}$ | 39.6 $(67.2)^{\beta}$ | 2.41* | 13.17*** | 13.51 | 57.93 |

^a Data are at the level of point counts. Superscript Greek letters show the outcome of multiple comparisons (different letters indicate results that are statistically different at alpha = 0.05). Abbreviations: FF, forest fragments; VLIS, very low-intensity systems; LISS, low-intensity silvopastoral systems; IISS, intermediate-intensity silvopastoral systems; HIPS, high-intensity pasture systems.

^b Comparisons among production systems and among ranches within production systems (* p<0.05, ** p<0.01, *** p<0.001).

^d Percentage of variance explained by differences among production systems and among ranches within production systems

COMPOSITION OF BIRD ASSEMBLAGES

Values of the Chao-Jaccard abundance-based similarity index were higher for pairs of production systems that had similar production intensities (index range 0.78-0.95) than for pairs of production systems that differed by at least at one level of intensification (e.g., a very-low-intensity system and a low-intensity system) (index range 0.6-0.79). Bird assemblages in low-intensity and intermediate-intensity silvopastoral systems were almost identical (similarity index 0.95), despite significant differences in cattle yield. Compositional similarity of bird assemblages in intermediate-intensity silvopastoral systems and highintensity pastoral systems was relatively low (index 0.78). As was the case with patterns of species richness, compositional similarity among bird assemblages in production systems and forest fragments decreased nonlinearly as production intensity increased. Differences in species composition were much greater at higher levels of production intensity. However, the similarity-yield curve decreased more sharply than the species richness-yield curve between low-intensity and intermediate- to high-intensity production systems (Fig. 2.2d). The observation that bird species detected in forest fragments became absent from ranches at a disproportionately higher rate than the overall number of species suggested that other types of bird species incorporated to the assemblages as production intensity increased.

RICHNESS AND ABUNDANCE WITHIN FUNCTIONAL GROUPS

Production intensity was negatively associated with species richness of insectivores, frugivores, carnivores, and omnivores (Table 2.2). Species richness of frugivores and insectivores showed significant declines across the gradient (df=4, p<0.001, F=20.49 and F=14.2, respectively). These declines were explained to a large extent by differences in production intensity (45% and 39%, respectively). The number of frugivore species declined the most in intermediate-intensity systems, whereas insectivores declined at higher levels of production intensity. Species richness of carnivores and omnivores (df=4, F=3.5, p>0.05 for both tests) did not vary significantly along the intensification gradient.

Production intensity had a strong negative association with abundance of frugivores (df=4, F=12.37, p<0.001) and a weaker negative association with abundance of insectivores (df=4, F=3.25, p<0.05). No frugivores were detected in high-intensity pastoral systems. Conversely, the abundance of carnivores and granivores increased as production intensity increased.

Carnivores and granivores occurred at highest abundance in intermediate-intensity systems (df=4, F=3.6, p<0.05), and granivores in high-intensity systems (df=28, F=12.54, p<0.001).

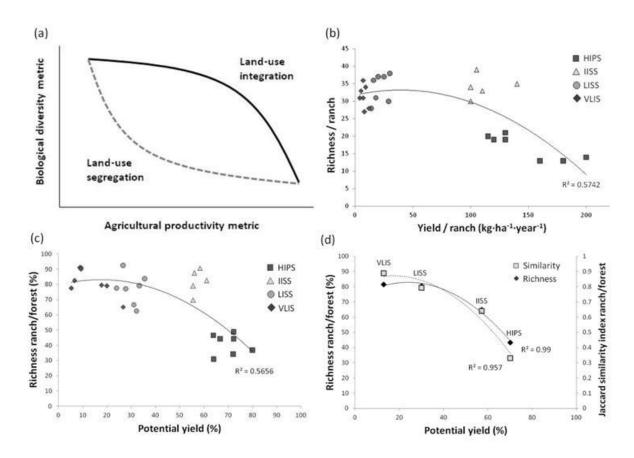


FIGURE 2.2. (A) HYPOTHETICAL TRADE-OFF BETWEEN SPECIES RICHNESS AND AGRICULTURAL PRODUCTIVITY (CONCAVE FUNCTION, –INTEGRATED [I.E. LOW AND INTERMEDIATE-INTENSITY] PRODUCTION SYSTEMS ACHIEVE PRODUCTION AND CONSERVATION OBJECTIVES; CONVEX FUNCTION, –SPATIAL SEGREGATION OF LIGHT-USE AND HIGH-INTENSITY PRODUCTION AREAS ACHIEVES PRODUCTION AND CONSERVATION OBJECTIVES [GREEN ET AL. 2005]). EMPIRICAL BEST-FITTING CURVES AND REGRESSION COEFFICIENTS AT THE RANCH LEVEL FOR THE RELATION (B) BETWEEN BIRD SPECIES RICHNESS AND CATTLE YIELD AND (C) BETWEEN BIRD SPECIES RICHNESS IN THE RANCH RELATIVE TO THE NEAREST FOREST FRAGMENT AND CATTLE YIELD RELATIVE TO ITS POTENTIAL YIELD GIVEN A TYPE OF PRODUCTION SYSTEM AND AREA. (D) COMPARISON OF SPECIES RICHNESS AND CATTLE YIELD (SOLID LINE) AND SIMILARITY OF BIRD COMPOSITION BETWEEN RANCHES AND FOREST FRAGMENTS AND CATTLE YIELD (DOTTED LINE) ACROSS THE DIFFERENT TYPES OF PRODUCTION SYSTEMS. NOTE: BIRD SPECIES RICHNESS IN PANEL C IS THE MEAN RICHNESS OF THE RANCH RELATIVE TO THE MEAN RICHNESS OF THE NEAREST FOREST FRAGMENT, WHILE IN PANEL D IT IS THE ACCUMULATED RICHNESS ACROSS RANCHES OF THE SAME PRODUCTION SYSTEM RELATIVE TO THE ACCUMULATED RICHNESS ACROSS FOREST FRAGMENTS. ABBREVIATIONS: FF, FOREST FRAGMENTS; VLIS, VERY LOW-INTENSITY SYSTEMS; LISS, LOW-INTENSITY SILVOPASTORAL SYSTEMS; IISS, INTERMEDIATE-INTENSITY SILVOPASTORAL SYSTEMS; HIPS, HIGH-INTENSITY PASTORAL SYSTEMS.

Production intensity was negatively associated with species richness of forest specialists and positively associated with species richness of open-land species (Table 2.2). In intermediate-intensity systems, the number of forest specialist species decreased sharply (df=4, F=30.45, p<0.001) and the number of open-land species increased (df=4, F=17.32, p<0.001). Sixty-five percent and 43% of the variation in species richness of forest specialists and open-land species, respectively, was explained by level of production intensity. Abundance of forest

specialists decreased as production intensity increased (df=4, F=6.38, p<0.001), whereas the abundance of open-land species increased as production intensity increased (df=4, F=2.41, p<0.05). Species richness and abundance of habitat generalists was highest in intermediate-intensity systems and lower at both ends of the intensification gradient (df=4, F=2.71, p<0.05).

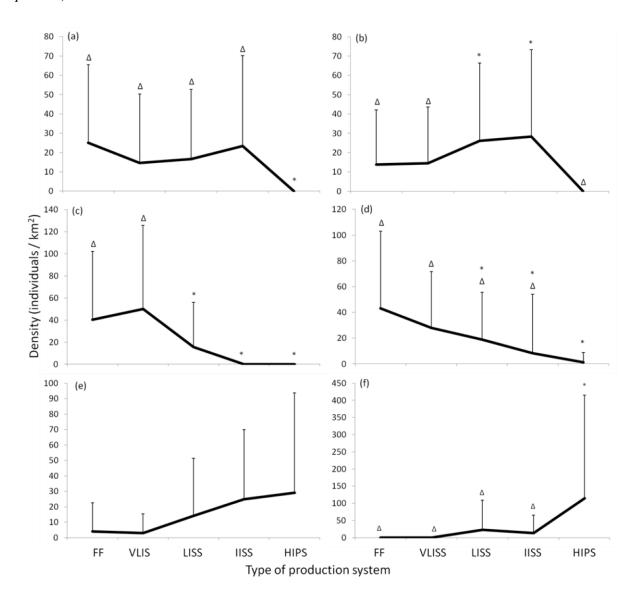


FIGURE 2.3. CHANGE IN DENSITY (INDIVIDUALS/KM²) OF BIRD SPECIES ALONG A GRADIENT OF INCREASING AGRICULTURAL PRODUCTION INTENSITY (FF, FOREST FRAGMENTS; VLIS, VERY LOW-INTENSITY SYSTEMS; LISS, LOW-INTENSITY SILVOPASTORAL SYSTEMS; IISS, INTERMEDIATE-INTENSITY SILVOPASTORAL SYSTEMS; HIPS, HIGH-INTENSITY PASTORAL SYSTEMS): (A) HEPATIC TANAGER (PIRANGAFLAVA) (B) WHITE-FRONTED WOODPECKER (PIRANGAFLAVA) (B) GREATER WAGTAIL-TYRANT (PIRANGAFLAVA) (C) CHACO CHACHALACA (PIRANGAFLAVA) (D) GREATER WAGTAIL-TYRANT (PIRANGAFLAVA) (S) MANY-COLOURED CHACO FINCH (PIRANGAFLAVA) (D) GREATER WAGTAIL-TYRANT (PIRANGAFLAVA) (S) HINY COWBIRD (PIRANGAFLAVA) (S) ARE SHOWN ONE-SIDED FOR CLARITY, BUT THEY ARE SYMMETRICAL. DIFFERENT SYMBOLS ABOVE BARS INDICATE STATISTICALLY SIGNIFICANT DIFFERENCES AMONG GROUPS AT ALPHA = 0.05.

SPECIES RESPONSES

Densities of 92 of the 119 species recorded (77%) varied significantly among types of production systems. Densities of the majority of species (70%) did not change in the absence of understory. This result was common among species that feed in the forest canopy (e.g., Hepatic Tanager [*Piranga flava*]) (Fig. 2.3a). Densities of 16 species (17% of the species that varied significantly in density across the gradient) increased in silvopastoral systems (e.g., White-fronted Woodpecker [*Melanerpes cactorum*], which preys on insects that occur on tree bark) (Fig. 2.3b). Densities of 12 species (13%) decreased in areas with cleared understory, especially species restricted to forests that feed on fruits of understory plants (e.g., such as the Chaco Chachalaca [*Ortalis canicollis*]) (Fig. 2.3c).

Conversely, densities of the majority of species decreased in completely cleared areas (55%). This was the case for most forest-restricted insectivores (e.g., Greater Wagtail-tyrant [Stigmatura buditoydes]) (Fig. 2.3d). Densities of 22 species (24%) remained stable in high-intensity systems. In particular, densities of generalists that feed on seeds in pastures or neighbouring cropland (e.g., Many-coloured Chaco Finch [Saltatricula multicolour]) remained stable (Fig. 2.3e). Densities of 19 species (21%) increased in open pastures, and most of these species had wide geographical ranges (e.g., Shiny Cowbird [Molothrus bonariensis]) (Fig. 2.3f).

DISCUSSION

Bird diversity, the composition of bird assemblages, and cattle yield all responded nonlinearly to intensification of cattle production. The limited overlap in cattle yield among types of production systems indicates that management practices and yield were closely associated and supports our choice of the type of forest clearing and source of forage as determinants of production intensity. Richness-yield functions indicated 3 significant changes in the strength of the associations between these variables along the intensification gradient. First, small decreases in bird diversity were consistent with small increases in cattle yield between forest fragments and low-intensity production systems. Second, little change in bird diversity accompanied large yield increases between low-intensity and intermediate-intensity silvopastoral systems. This relative stability in bird diversity was associated with the maintenance of a relatively high density of overstory trees, which may be providing spatial continuity of habitat for birds and facilitating movement among fragments, thus creating a

high-quality agricultural matrix (Perfecto & Vandermeer 2010). In turn, synergistic interactions between native trees and high-yielding grasses growing beneath the canopy (e.g., microclimate regulation, nutrient cycling) are thought to underlie yield increases in intermediate-intensity silvopastoral systems (Berti 2009). Third, a sharp decline in bird diversity occurred along with minor or no productivity gains between intermediate-intensity systems and high-intensity systems. Low bird diversity at these high levels of intensification was associated with a decrease in canopy cover to below 30%. This suggests a threshold in habitat quality for birds, which is consistent with results of studies on Australian grassy woodlands that show major declines in bird diversity when native cover decreases to 10-30% of the patch or landscape (Radford 2005).

Evaluating species' responses to production intensification on the basis of aggregate measures, such as species richness, may mask differences in the responses of individual species. Hence, we expanded our analyses to changes in species composition and functional composition of bird assemblages. Of the species present on ranches with cleared understory, more than 60% were not detected on ranches where native vegetation was completely cleared, whereas only an average of 42% less species were detected in high-intensity pastoral systems than intermediate-intensity silvopastoral systems. Similarly, the difference between intermediate-intensity silvopastoral systems and high-intensity pastoral systems in the number of species shared with nearest forest fragments (31%) was larger than the difference in the richness relative to nearest forest (21%). These results suggest that not only species richness but also species composition changed significantly at the highest level of production intensity. In addition, disproportionate changes in species richness within functional groups indicated compositional changes that may affect ecosystem functions. The relatively large change in species richness of insectivores associated with the simplification of vegetation structure (30% decrease between intermediate-intensity silvopastoral systems and highintensity pastoral systems) that we found also occurs in other tropical agroecosystems (Tschartntke et al. 2002). This change may have a negative impact on biological pest control (Philpott et al. 2009). The large difference in species richness of frugivores associated with selective forest clearing (60% decrease between very-low-intensity systems and low-intensity silvopastoral systems) probably occurred because most frugivores feed on the forest understory. This decrease in species richness of frugivores may negatively affect tree regeneration in silvopastoral systems. Therefore, intensification may not only drive species

distributions, but it may also be linked to species turnover because ecological conditions in more intensive production systems may hinder the persistence of habitat specialist and trophic specialist species and increase the probability of colonization by generalist species.

The fate of biological diversity in agricultural landscapes ultimately depends on individual choices of multiple landholders among several land-use options. In the Argentine Chaco, conflicting visions for development exist and the capacity of existing land-use plans to balance competing objectives is uncertain (Seghezzo et al. 2011). Most studies examining the potential of land-use integration and segregation to achieve conservation and production objectives have assessed biological diversity and productivity measures in 2 contrasting landuse situations (i.e., low-intensity use, high-intensity use [Edwards et al. 2010; Hodgson et al. 2010; Fisher et al. 2011]). We compiled data that can be used to relate measures of conservation value and yield across an intensification gradient of multiple management options at a spatial extent (i.e., individual landholdings) that is relevant for land-use decision making by individuals. However, our bird data originated from unrepeated counts conducted in one season (nonreproductive) in different months (May to August) and in contrasting vegetation classes (from forest to pasture), all of which may have influenced bird detectability. In addition, our yield data originated from subjective, although informed, responses to interview questions. Despite these weaknesses, we believe our assessment points to management options that can conserve birds and have small opportunity costs for cattle ranchers. Intermediate-intensity silvopastoral systems that integrate management of native trees and high-yielding grasses can simultaneously provide high cattle yields and habitat for a a similar number of bird species as are present in forest fragments. In contrast, high-intensity pastoral systems provided yields similar to intermediate-intensity silvopastoral systems and we detected less than half the number of bird species present in forest fragments. The conservation and development potential of integrative land-use plans that focus on intermediate production intensities has also been suggested for other tropical forest regions of Latin America, such as Mesoamerica (Harvey et al. 2008) and Colombia (Murgueitio et al. 2011).

In intermediate-intensity silvopastoral systems, we detected about half the number of forest-restricted species present in low-intensity silvopastoral systems. This result suggests that conservation of forest-restricted species, usually of higher conservation concern, may require areas under low-intensity production or protected areas. Thus, we believe land-use plans at

the regional scale should limit the amount of land allocated to high-intensity pastoral systems and also to intermediate-intensity silvopastoral systems. In general, our results indicated that neither the integration of pastures and native trees in silvopastoral systems nor the segregation of lands for the growth of pastures on cleared areas is sufficient to achieve production and conservation objectives. Instead, a combination of intermediate-intensity silvopastoral systems interspersed with conserved forest fragments will be required to achieve desired cattle yield, bird diversity, and conservation of forest-restricted species. Similar planning approaches have been recommended for Australian woodlands (McIntyre et al. 2002), the Brazilian Cerrado (Mattison & Norris 2005), Indonesian rainforests (Koh & Ghazoul 2010), and the tropics in general (Fischer et al. 2008).

Identifying the relative spatial extent and configuration of lands that can be used for different intensities of cattle production without compromising the persistence of forest-restricted species will require studies of processes operating at larger spatial extents (e.g., source-sink dynamics). In addition, evaluating temporal changes in the relations between biological diversity and cattle yield will be necessary to assess the long-term effects of land-use options on biological diversity. We believe it should be determined whether current levels of tree density and associated bird diversity in intermediate-intensity silvopastoral systems will remain stable over time or whether they correspond to an early stage in these systems that may eventually lead to further reductions in bird diversity. To answer this question, evaluations of the social (e.g., ranchers´ intentions to intensify) and ecological processes (e.g., regeneration capacity of trees) that influence future habitat quality for birds are needed. Finally, assessing intensification effects on additional taxonomic groups and ecosystem services will better inform policy and planning interventions in agricultural landscapes.

CHAPTER 3: IMPACTS OF AGRICULTURAL INTENSIFICATION ON AVIAN RICHNESS AT MULTIPLE SCALES IN DRY CHACO FORESTS



Cattle at the edge between a high-intensity agricultural matrix and a forest fragment. Photo by the author

This chapter is formatted in the style of Journal of Applied Ecology where it will be submitted for publication. For this chapter, I collected all data, conducted analyses and did all the writing, while Gavin, M. C. provided advise.

ABSTRACT

- 1. Agricultural land covers more than two-thirds of the planet's terrestrial surface and is rapidly expanding in subtropical and tropical landscapes. Previous studies have focused more on the agricultural matrix as conduit for inter-fragment migration and less as suitable habitat for native species. Knowledge on the habitat quality of the matrix in agricultural landscapes undergoing land-use intensification is limited. Here I test several hypotheses about the factors influencing bird species occurrence in different types of grazing matrices in an agricultural frontier of the South American Chaco, a threatened and largely understudied region.
- 2. I selected landholdings differing in intensity of forest clearing, cattle yields achieved, location relative to the frontier and size of grazing plots to form a matrix intensification gradient. For each landholding, I measured: (i) overall avian richness and richness of forest specialist birds and (ii) six structural attributes operating either at the plot scale (i.e. tree cover and vegetation complexity), matrix-forest interface (i.e. edge vegetation complexity and distance to edge) or landscape scale (i.e. distance to forest and forest extent), which varied independently along the matrix gradient. I assessed the relative influence of these structural attributes on avian richness using a multi-model selection approach based on AIC.
- 3. I found that local effects are comparatively more important than landscape effects in driving avian richness across the matrix intensification gradient, especially for forest specialist species.
- 4. Tree cover and vegetation complexity at the grazing plot scale were the factors with the highest influence on the occurrence of overall and forest-restricted bird species.
- 5. The intensity of disturbances resulting from local agricultural management practices may have the greatest impact on matrix quality for Chaco avifauna.
- 6. Where a significant proportion of native avifauna has already adapted to novel disturbance regimes, low-intensity systems may provide high quality habitat for birds. Where further cattle production intensification cannot be avoided, development of intermediate-intensity silvopastoral systems through selective methods of forest clearing would limit biodiversity impacts without incurring substantial reductions in cattle yields. Finally, where cattle production intensification has already occurred, ecological restoration via native tree plantings on cleared areas will be needed to recover native bird diversity.

Introduction

The need for conservation planning in agricultural landscapes has never been greater. Today, more than two-thirds of the ice-free global terrestrial surface is used for agriculture (Ellis & Ramankutty 2008). Most of the recent expansion and intensification of agriculture has occurred in subtropical and tropical regions of developing countries (Rudel et al. 2009, Gibbs et al. 2010). Notably, the expansion of soybean cropping and intensification of cattle ranching in the South American Gran Chaco has driven the highest rates of deforestation of the 21st century globally (Hansen et al. 2013). Effective conservation planning in this threatened and understudied biome requires a better understanding of the prominent influence of agriculture-driven landscape modification on biodiversity patterns.

Agricultural intensification modifies biodiversity through processes occurring at multiple spatial scales, from the degradation of patch and matrix vegetation, to the formation of abrupt edges and the loss of native cover at the landscape scale (Tschartnke et al. 2012). Individual species respond differently to these threatening processes according to functional characteristics, such as habitat and diet specialization, and dispersal ability (Henle et al. 2004). Agriculture-driven changes in community composition have cascading effects on ecosystem functions and services, which feedback on human well-being at local to global scales (Diaz et al. 2011). Here we aim to identify the processes influencing bird diversity patterns in an agricultural frontier landscape where cattle ranching intensification is the major driver of modification of Dry Chaco forests.

Modified landscapes have been typically represented as mosaics of patches and corridors of native vegetation within a matrix dominated by human land-use, such as agriculture. This binary view of landscapes explains the focus on patch size and isolation as the main factors threatening species, and the emphasis on increasing landscape connectivity as the major management strategy to mitigate species declines (Fischer & Lindermayer 2007). However, recent studies demonstrate that some types of matrix provide habitat for native species, and that management of matrix habitats can greatly improve conservation outcomes in agricultural landscapes (Perfecto & Vandermeer 2010).

Modified landscapes are increasingly represented as habitat suitability gradients based on substantial evidence showing the retention of native biodiversity in agricultural matrices. This evidence comes from experimental studies testing the dispersal behavior of individual species across different matrix types (i.e. species-oriented approach, e.g. Castellón & Sieving 2005), as well as from those evaluating the relationships between species diversity and landscape metrics (i.e. pattern-oriented approach, e.g. Luck & Daily 2003). Here we employ a pattern-oriented approach to test a set of theory-driven hypotheses to explain species occurrence across a matrix intensification (i.e. habitat suitability) gradient. Hypotheses related to species-specific behaviors are not tested as these can only be evaluated using species-oriented approaches. We aim to answer: i) what is the relative influence of structural attributes operating at the plot, edge and landscape scale on bird occurrence in the matrix, and ii) is the occurrence of habitat specialist (patch-dependent) species and habitat generalist species in the matrix affected differently by structural attributes?

Several hypotheses have been proposed to explain species occurrence in matrix habitats. These focus either on structural attributes exerting their effects at the scale of the landscape (i.e. patches and the surrounding matrix), edges (i.e. patch-matrix interface) or plots (i.e. within the matrix). Most studies have based their explanations on landscape-level processes, especially on the role of the matrix as a conduit for inter-fragment migration (Bender & Fahrig 2005). According to the "dispersal" hypothesis, species occurrence in the matrix is a function of the distance to fragments and the extent of suitable habitat in the landscape (i.e. proximity to and size of source populations, respectively, Tscharntke et al. 2012). More recently, Fahrig (2013) proposed an explanation independent of fragment size and isolation, in which species occurrence in the matrix depends on the extent of suitable habitat at the local and landscape scale ("habitat amount" hypothesis).

In another set of studies, the suitability of the matrix as bird habitat depends on the structural similarity (or contrast) between matrix and patch vegetation. Put simply, this "edge contrast" hypothesis asserts that the more similar the vegetation is at both sides of the edge, the more likely it will be to find patch-dependent species in the matrix (Zurita et al. 2012). This effect occurs because species encounter suitable conditions to disperse, available resources and/or a favorable abiotic environment in the matrix (Driscoll et al. 2013). However, this effect is predicted to change with distance from the edge to the interior of the matrix as conditions, resources and the abiotic environment may become less suitable as species permeate into the matrix ("edge proximity" hypotheses).

Finally, the intensity of disturbances caused by agricultural management at the plot scale is receiving increasing attention as a factor influencing species retention in the matrix (Kennedy et al. 2010). Managing the land for agriculture often involves the simplification of the structure of native vegetation to favor the growth of crops and pastures. Hence, agricultural management practices increase the intensity of disturbances (e.g. vegetation clearing, plant regrowth suppression) and affect the suitability of the matrix for native species. Here we found relatively high support for the "disturbance" hypothesis, indicating that processes operating within the matrix (plot scale) have a strong influence on bird species occurrence in matrix types of Chaco agricultural frontier landscapes. This effect was more pronounced for patch-dependent species, suggesting that planning for the long-term conservation of Dry Chaco forests avifauna should pay attention to the effects of local agricultural management.

METHODS

STUDY SITE

The study area corresponds to the upper portion of the Bermejo-Pilcomayo Interfluve (Salta province, Argentina), a tract of dryland of ca. 2 Mha between the Pilcomayo River to the north and the Bermejo River to the south. The Bermejo-Pilcomayo Interfluve is delimited to the west by the eastern foot of the Andes range (elevation 500–380 m, annual rainfall 1000–800 mm) and extends to the east over the Chaco plains (elevation 380–240 m, annual rainfall 800–500 mm). It is covered by xerophytic semi-deciduous forests dominated by red quebracho (*Schinopsis quebracho-colorado*) and white quebracho (*Aspidosperma quebracho-blanco*) and to a lesser degree by palo blanco (*Calycophyllum multiflorum*) and palo amarillo (*Phyllostylon rhamnoides*) in humid areas, and by palo santo (*Bulnesia sarmientoi*) and *Prosopis* spp. in drier areas. Deforestation from 1977 to 2008 has produced more than 1.5 million ha of cleared areas in Salta province (26% of its area) and 116,200 ha in the Bermejo-Pilcomayo Interfluve (Paruelo et al. 2011). In the Argentine Chaco, annual deforestation rates for the period 2002-2008 ranged between 1.5 and 2.5%, surpassing Latin America (0.51%) and global deforestation rates (0.2%) (Seghezzo et al. 2011).

MATRIX GRADIENT AND STRUCTURAL ATTRIBUTES

A matrix intensification gradient was identified in the study area comprising four types of cattle ranching systems of increasing land-use intensity (very-low, low, intermediate and high). Twenty-seven cattle ranches were selected and six sampling sites were located within the grazing matrix in each cattle ranch (see *Sampling strategy*). Six structural attributes were assessed at each sampling point (n=162). Each attribute varied independently across the matrix intensification gradient due to differences among cattle production systems in: (i) type of clearing used to increase forage productivity; (ii) location within the agricultural frontier, and (iii) size of grazing plots. Two of the structural attributes influenced habitat quality for birds at the plot scale (i.e. plot tree cover and plot vegetation complexity), two of them operated at the edge scale (i.e. distance to edge and edge vegetation complexity) and the remaining two captured landscape-scale effects (i.e. distance to forest and landscape forest cover). The definition and assessment of the six structural attributes was as follows:

- Plot tree cover (PTC): land area covered by the arboreal strata in the grazing matrix, expressed as percentage of the sampling point area (0.2 ha). Tree cover at each sampling point was assessed via ocular estimation using a vertical tube based on Johansson (1985). PTC was expressed as the quotient between zenith observations intercepted by the arboreal strata and total observations (25 per sampling point) multiplied by 100.
- Plot vegetation complexity (PVC): number of vertical strata of vegetation at the grazing matrix. Six strata were identified (bare soil, herbaceous, shrub [1-3 m], lower arboreal [3-5 m], middle arboreal [5-10 m] and higher arboreal [>10 m]), and seven levels of plot complexity were defined based on combinations of vegetation strata (Table 3.2).
- Edge vegetation complexity (EVC): number of vertical strata of vegetation at the edge of the nearest forest patch (definition of strata and complexity level as for PVC).
- Distance to edge (DE): linear distance bewteen the center of the grazing matrix (sampling point) and the nearest area where the vertical complexity of vegetation changes by 2 or more levels (Table 3.2). Distance to edge was measured in the field using a range meter.
- Distance to forest (DF): linear distance between the centre of the grazing matrix (sampling point) and the perimeter of the nearest forest patch. Forest patches were

defined based on FAO (2000) as fragments with trees taller than 3 m, tree cover higher than 50%, and an area larger than 100 ha. Forest patches were identified based on field observations and analysis of satellite images (Landsat TM form September 2009). Distance to forest was measured in ArcGIS (ESRI).

Landscape forest cover (LFC): land area covered by forests that fitted the FAO
definition over a circular buffer area 3 km radius centered in the sampling point. LFC
was calculated as the quotient between forest area and buffer area (≈30 km²),
multiplied it by 100 and expressed this variable as quintiles.

In very-low intensity systems, PLC and PVC were high because native vegetation in the grazing matrix was not cleared (Table 3.1). These systems were located on pre-frontier areas with relatively small agricultural area and large forest area at the landscape scale. Cattle grazing at very low intensity over large areas created an extensive matrix of homogeneous vegetation and thus DE was very large.

In the grazing matrix of low-intensity systems, the forest understory was selectively cleared to stimulate the regeneration of native grasses, leaving a relatively high PLC and intermediate PVC. DF and LFE were intermediate within the gradient as these systems were located in expansion areas where agriculture actively expands into native forests. Cattle grazed over relatively large grazing plots and therefore DE was large.

In intermediate-intensity systems, PLC and PVC were intermediate due to the selective remotion of shrubs and trees to allow for the cultivation of high-yielding grasses beneath the tree canopy. Ranches developing this type of silvopastoral system were located mostly in expansion areas, where LFC and DF were intermediate. Relatively small grazing plots defined short distances between the matrix and nearest edges in intermediate-intensity systems.

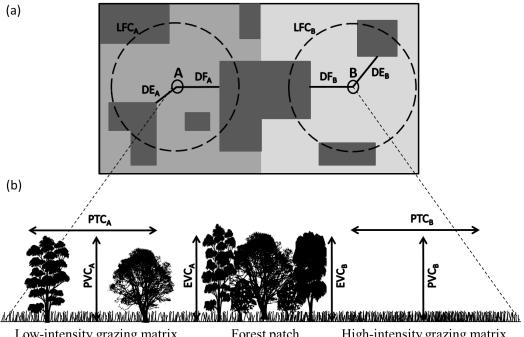
High-intensity systems consisted of intensively grazed pastures completely cleared of native woody vegetation. These systems were located in areas undergoing the formation of large and continuous tracts of agricultural land (i.e. agricultural consolidation), and thus DF was large and LFC was low. DE was intermediate in high-intensity systems as pastures were cultivated over plots of intermediate size within the gradient.

TABLE 3.1. PROPERTIES AND ATTRIBUTES OF MATRIX TYPES ALONG THE CATTLE PRODUCTION INTENSITY GRADIENT

| Properties and attributes of the matrix | Lar | nd-use intensity | in the grazing n | natrix | |
|---|---------------|------------------|--------------------------|---------------|--|
| Properties and attributes of the matrix | Very-low | Low | Intermediate | High | |
| Type of clearing | None | Selective | Selective | Total | |
| Cattle yields (kg.ha ⁻¹ .year ⁻¹ ; range) | 4 - 12 | 14 - 30 | 100 - 140 | 115 - 180 | |
| Frontier location | Pre-frontier | Expansion | Expansion | Consolidating | |
| Management plot size (ha; range) | 600 - 2200 | 200 - 700 | 80 - 260 | 90 - 330 | |
| Plot vegetation complexity (median) | 6 | 5 | 4 | 1 | |
| Plot tree cover (%; mean \pm SD) | 81 ± 14.2 | 56 ± 22.5 | 37 ± 9.4 6 ± 5.4 | | |
| Distance from centre of grazing | | | | | |
| matrix to nearest edge (km; mean \pm | 2.3 ± 0.7 | 0.7 ± 0.5 | 0.2 ± 0.2 | 0.5 ± 0.3 | |
| SD) | | | | | |
| Edge vegetation complexity (median) | 6 | 6 | 5 | 4 | |
| Distance from centre of grazing | | | | | |
| matrix to perimeter of nearest forest | 1.9 ± 1.1 | 2.3 ± 1.7 | 3 ± 2.1 | 4.4 ± 1.7 | |
| patch (km; mean \pm SD) | | | | | |
| Landscape forest cover (quintile; | 00 100 | 40.60 | 20.40 | 0-20 | |
| median) | 80-100 | 40-60 | 20-40 | | |

SAMPLING STRATEGY

We classified cattle ranches of the study area according to their type of cattle ranching system using cadastral data, field observations and satellite images. Then, one ranch of each type was randomly selected and each subsequent random choice was included in the sample only if the closest ranch of the same type was at least 50 km apart (measured from the perimeter) to obtain a substantial coverage of the study area. The resulting sample consisted of seven high-intensity systems, five intermediate-intensity systems, seven low-intensity systems and eight very-low-intensity systems. We also sampled six forest patches to assess the richness of forest specialist species in baseline habitats. We divided the matrix area of each cattle ranch into a grid of 1 km² square cells and a sampling point was established in the centre of six randomly selected cells. We surveyed 162 sampling points once between May and August 2010 for structural attributes and bird species richness, and an additional 36 sampling points in forest patches for bird species richness only.



Low-intensity grazing matrix Forest patch High-intensity grazing matrix

FIGURE 3.1. SCHEMATIC REPRESENTATION OF STRUCTURAL ATTRIBUTES MEASURED AT SAMPLING POINTS. (A) AERIAL VIEW OF A TYPICAL LANDSCAPE CONFIGURATION AT THE STUDY AREA, WITH FOREST PATCHES (DARK GREY) SCATTERED ALONG THE GRAZING MATRIX. A AND B ARE TWO SAMPLING POINTS (0.2 HA), ONE IN A LOW-INTENSITY GRAZING MATRIX (A) AND OTHER IN A HIGH-INTENSITY GRAZING MATRIX (B). LANDSCAPE FOREST COVER (LFC) WAS MEASURED ON A 3-KM RADIUS CIRCULAR AREA CENTERED IN THE SAMPLING POINT, WHICH NEVER OVERLAPPED WITH THAT OF OTHER SAMPLING POINTS. DISTANCE TO FOREST (DF) WAS MEASURED AS THE DISTANCE FROM THE CENTRE OF THE SAMPLING POINT TO THE PERIMETER OF THE NEAREST FOREST PATCH BASED ON THE DEFINITION OF FOREST BY FAO (2000). DISTANCE TO EDGE (DE) WAS MEASURED AS THE DISTANCE FROM THE CENTRE OF THE SAMPLING POINT TO THE NEAREST AREA OF MARKED CHANGE IN VEGETATION COMPLEXITY (I.E. EDGE) (B) CROSS SECTIONAL VIEW OF THE VEGETATION BETWEEN SAMPLING POINTS A AND B. PLOT VEGETATION COMPLEXITY (PVC) WAS MEASURED AS THE NUMBER OF VERTICAL STRATA OF VEGETATION AT THE CENTRE OF THE SAMPLING POINT. PLOT TREE COVER (PTC) WAS MEASURED AS THE PERCENTAGE OF ZENITH OBSERVATIONS INTERCEPTED BY THE ARBOREAL STRATA. EDGE VEGETATION COMPLEXITY (EVC) WAS MEASURED AS THE NUMBER OF VERTICAL STRATA OF VEGETATION AT THE NEAREST EDGE.

BIRD SAMPLING

We established a 25 m radius count point in each of the 162 sampling sites, where we counted birds once during the non-reproductive season (May–August 2010). We detected birds by sight or sound and recorded all individuals staying in, entering, or leaving the site over 20 min. We counted birds when bird activity was greatest, either 3 h after dawn or 3 h before dusk. Counts were balanced within each type of production system for dawn and dusk sampling. We minimized imperfect detection of birds in two ways. First, we used fixed-radius point counts instead of, for example, open-radius point counts or transect counts to control for differences in detection range among sampling sites with different vegetation structure (Martin & McIntyre 2007). Second, a single observer (M.E.M.) undertook all bird counts, which reduced detection bias associated with differences in observer performance.

We classified the bird species recorded according to their habitat preferences based on Lopez-Casenave et al. (1998) and Codesido & Bilenca (2004). We calculated species accumulation curves for every type of production system.

TABLE 3.2. ORDINAL CATEGORIES USED TO DESCRIBE VERTICAL COMPLEXITY OF THE VEGETATION.

| Level of vegetation complexity | Combinations of | Combinations of vertical strata of vegetation | | | | | | | | | | |
|--------------------------------|-----------------|---|-------|----------|--|--|--|--|--|--|--|--|
| 1 | Н | BS-SH | | | | | | | | | | |
| 2 | H-SH | BS-LA | | | | | | | | | | |
| 3 | H-LA | BS-MA | | | | | | | | | | |
| 4 | H-MA | SH-LA | BS-LA | | | | | | | | | |
| 5 | H-HA | SH-MA | LA-MA | | | | | | | | | |
| 6 | H-MA-HA | SH-LA-MA | MA-HA | SH-LA-HA | | | | | | | | |
| 7 | LA-MA-HA | SH-LA-MA-HA | | | | | | | | | | |

References = H: pasture/herbaceous strata; SH: shrub strata; LA: lower arboreal strata; MA: middle arboreal strata; SA: superior arboreal strata; BS: bare soil

MULTI-MODEL DATA ANALYSIS

We employed an information-theoretic approach to consider uncertainty in the choice of explanatory models. We first created a model set consisting of 13 alternative hypothesis (Table 3.3). Among these, there was the full model containing all predictor variables and six models representing the following hypothesis: (i) disturbance hypothesis containing factors operating at the plot scale (PTC and PVC), (ii) edge effects hypothesis containing factors exerting their influence at the edge, (iii) dispersal hypothesis containing factors operating at the landscape scale (DF and LFE), (iv) edge contrast hypothesis combining plot and edge vegetation complexity, (v) habitat amount hypothesis combining forest cover at the local and landscape scale, and (vi) local effects hypothesis combining factors operating a the plot and edge scale. Finally, we also examined six models contained only one predictor variable each.

We used the overall richness and richness of forest specialist (patch-dependent) species as reponse variables. We plotted all pairs of predictor and response variables (12 pairs) to explore the type of function (linear, binomial quadratic, binomial cubic) that best described their relationship. We calculated goodness of fit indices and the Akaike Information Criterion corrected for small sample sizes (AICc) for the 13 candidate models on each of the two response variables via regression analyses (26 runs) using the appropriate model basis for

each case (linear or non-linear). After that, we ranked the models according to their respective AICc values from smallest to largest and compared model probabilities by calculating the difference in AICc between the first-ranked model and following ones (Δ AICc). All models within two AICc units were considered part of the best model subset and those differing more than 3-4 units from the second one as the best single model. Models with Δ AICc larger than 12 were interpreted as implausible models (Brunham & Anderson 2002). I calculated the weight of evidence carried by each model as:

$$w_i = \frac{\exp(-\Delta AICc_i/2)}{\sum_{r=1}^{R} \exp(-\Delta AICc_r/2)}$$

TABLE 3.3. HYPOTHESES (CANDIDATE MODELS) TESTED USING THE MULTI-MODEL INFERENCE APPROACH

| | Pr | edic | tor | vari | able | es | |
|-------------------------|----|------|-----|------|------|----|--|
| Hypothesis | P | P | Е | D | D | L | Meaning |
| | T | V | V | E | F | F | |
| | C | C | C | | | C | |
| Full model | 1 | 1 | 1 | 1 | 1 | 1 | Factors operating at the plot, edge and landscape determine bird species richness |
| Local effects | 1 | 1 | 1 | 1 | 0 | 0 | Only factors operating at the plot and edge determine bird species richness |
| Tree cover | 1 | 0 | 0 | 0 | 0 | 0 | Tree cover at the plot scale determines bird species richness |
| Habitat amount | 1 | 0 | 0 | 0 | 0 | 1 | Forest cover at the sampling point and landscape scale determines bird species richness |
| Disturbance | 1 | 1 | 0 | 0 | 0 | 0 | Land-use management factors operating at the plot determine bird species richness |
| Local complexity | 0 | 1 | 0 | 0 | 0 | 0 | Vegetation complexity at the plot determine bird species richness |
| Edge contrast | 0 | 1 | 1 | 0 | 0 | 0 | Difference in vegetation structure between plot and edge determine bird species richness |
| Landscape forest extent | 0 | 0 | 0 | 0 | 0 | 1 | Forest extent at the landscape scale determines bird species richness |
| Dispersal | 0 | 0 | 0 | 0 | 1 | 1 | Only factors operating at the landscape scale determine bird species richness |
| Proximity to edge | 0 | 0 | 0 | 1 | 0 | 0 | Distance to edge determines bird species richness |
| Edge effects | 0 | 0 | 1 | 1 | 0 | 0 | Edge complexity and distance to edge determine bird species richness |
| Proximity to forest | 0 | 0 | 0 | 0 | 1 | 0 | Distance to forest determines bird species richness |
| Edge complexity | 0 | 0 | 1 | 0 | 0 | 0 | Vegetation complexity at the edge determines bird species richness |

References: PTC: plot tree cover; PVC: plot vegetation complexity; EVC: edge vegetation complexity; DE: distance to edge; DF: distance to forest; LFC: landscape forest cover

Finally, we estimated the effects of individual predictors following the procedure described by Burnham & Anderson (1998), which consists of: (i) weighting coefficients by multiplying model coefficients and model weight, and (ii) averaging weighted model coefficients across models included in the best subset. We considered coefficients not included in a model as having a value of 0, hence, multi-model- averaged coefficients shrank towards 0 and the extent of the shrinkage depended on the cumulated weight of the models without the variable (Lavoue & Droz 2009). In the case of one single best model, effects were estimated from coefficients of the first-ranked model.

RESULTS

We recorded 119 bird species: 97 in forest fragments,79 in very-low-intensity systems, 78 in low-intensity systems, 63 in intermediate-intensity systems, and 42 in high-intensity systems. In all types of production systems, observed richness represents more than 80% of estimated true species richness using a common estimator (i.e. Chao1). Although species richness per ranch may have been underestimated, the total species inventory of each type of production system is relatively complete (Fig. 3.2).

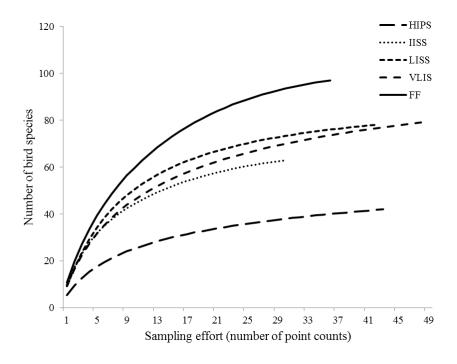


FIGURE 3.2.BIRD SPECIES ACCUMULATION CURVES FOR FOREST FRAGMENTS (FF) AND TYPES OF CATTLE PRODUCTION SYSTEMS: VERY-LOW INTENSITY SYSTEMS (VLIS), LOW-INTENSITY SILVOPASTORAL SYSTEMS (LISS), INTERMEDIATE-INTENSITY SILVOPASTORAL SYSTEMS (IISS), AND HIGH-INTENSITY PASTURE SYSTEMS (HIPS).

We observed a high number and proportion of forest specialist species in production systems where land-use intensity was minimal (in forest fragments: 54 species, 56% of species observed were forest specialists), very low intensity systems (VLISS: 38 species, 49%) and low intensity systems (LISS: 33 species, 43%) (Fig. 3.3). In turn, 20 forest specialist species (31%) were detected in silvopastoral systems of intermediate intensity (IISS). Alternatively, habitat generalist species (23 species, 45%) and species affiliated with open habitats (18 species, 43%) dominated avian communities on pastures in cleared areas.

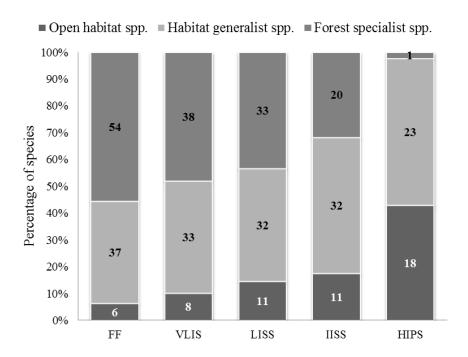


FIGURE 3.3. PROPORTION OF SPECIES WITHIN HABITAT AFFILIATION GROUPS AMONG FOREST FRAGMENTS (FF) AND TYPES OF CATTLE PRODUCTION SYSTEMS: VERY-LOW INTENSITY SYSTEMS (VLIS), LOW-INTENSITY SILVOPASTORAL SYSTEMS (LISS), INTERMEDIATE-INTENSITY SILVOPASTORAL SYSTEMS (IISS), AND HIGH-INTENSITY PASTURE SYSTEMS (HIPS).

FACTORS AFFECTING RICHNESS OF ALL SPECIES

Correlation between all pairs of the six habitat attributes was relatively low (r < 0.5), corroborating that structural attributes varied independently across the matrix intensity gradient. The full model containing all predictor variables explained 44% of the variance in richness of overall bird species. It could be regarded as the best single model because it had the lowest AICc, and Δ AICc between this and other candidate models was relatively high (4.61) (Table 3.4). This model was \approx 10 times more likely to be the best fitting model than the model with the second lowest value (Local effects; evidence ratio = 10.03), indicating moderate support for the full model (Lukacs et al. 2007). The first (Full model) and second

(Local effects) models represent the majority of evidence (99%) arising from this multi-model inference approach. The remaining models can be considered implausible as $\Delta AICc$ between these and the first model is larger than 12.

TABLE 3.4. SUMMARY STATISTICS OF THE MULTI-MODEL INFERENCE APPROACH WITH OVERALL RICHNESS AS THE RESPONSE VARIABLE

| | | P | redio | ctor | var | iable | es | | | | | | | |
|-------------|-------------------------|-------------|-------------|-------------|--------|--------|-------------|---|---|----------------|---------|--------|--------|-------------------|
| Hypothesis | | P T C | P V C | E V C | D E | D F | L F C | p | K | \mathbb{R}^2 | RSS | AICc | ΔΑΙС | Akaike weights |
| | Full model | 1 | 1 | 1 | 1 | 1 | 1 | 6 | 8 | 0.439 | 752.08 | 266.17 | 0 | 0.9071 |
| | Local effects | 1 | 1 | 1 | 1 | 0 | 0 | 4 | 6 | 0.407 | 794.82 | 270.79 | 4.61 | 0.0904 |
| | Local cover* | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0.349 | 872.44 | 279.59 | 13.41 | 0.0011 |
| | Habitat amount* | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 4 | 0.354 | 865.95 | 280.47 | 14.29 | 0.0007 |
| | Disturbance | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 4 | 0.352 | 868.44 | 280.94 | 14.76 | 0.0005 |
| S | Vertical complexity | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 0.321 | 910.80 | 286.60 | 20.42 | < 0.0001 |
| All species | Edge contrast | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 4 | 0.311 | 924.44 | 291.13 | 24.95 | < 0.0001 |
| All | Landscape forest extent | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 0.293 | 948.16 | 293.15 | 26.98 | < 0.0001 |
| | Dispersal | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 4 | 0.172 | 1109.92 | 320.93 | 54.75 | < 0.0001 |
| | Proximity to edge | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3 | 0.082 | 1230.51 | 335.64 | 69.467 | < 0.0001 |
| | Edge effects | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 4 | 0.083 | 1230.14 | 337.69 | 71.52 | < 0.0001 |
| | Proximity to forest | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 3 | 0.054 | 1269.19 | 340.68 | 74.51 | < 0.0001 |
| | Edge complexity | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 3 | 0.015 | 1320.79 | 347.18 | 81.01 | < 0.0001 |

References: PTC: plot tree cover; PVC: plot vegetation complexity; EVC: edge vegetation complexity; DE: distance to edge; DF: distance to forest; LFE: landscape forest extent; p: number of predictors; K: number of parameters; RSS: residual sum of squares. * Models with non-linear basis.

Regression coefficients for all predictor variables were statistically significant (p<0.05; Table 3.5). The largest effects were those of plot vegetation complexity (standardized β =0.861, p<0.001) and plot tree cover (standardized β =0.749, p<0.001). As expected, overall bird richness increased with increasing vertical complexity of the vegetation at the grazing plot, and to a lesser extent at the edge. An increase of four units in plot vegetation complexity led to a gain of five species in the avian assemblage if all other variables are held constant. Also, overall richness increased with increasing tree cover at the plot. An increase of 16% in tree

cover led to a gain of one bird species if all other variables are held constant. Finally, overall richness responded positively to distance to edge and negatively to distance to forest, with an increase of 512 m in distance to edge and a decrease of 2.14 km in distance to forest associated with a gain of one bird species, all other variables being constant.

FACTORS AFFECTING RICHNESS OF FOREST SPECIALISTS

When predicting richness of forest specialist species, several options appeared as likely candidates to be the best model (ie. $\Delta AICc < 3$; Table 3.6). The subset of the four best-ranking models (i.e. local effects, full model, disturbance and habitat amount) provided $\approx 99\%$ of the evidence obtained within the whole set of models tested. Any of the models in the best subset were ≈ 260 times more likely than the others tested to be the best-fitting model, indicating a strong support for them (Lukacs et al. 2007). Explanatory power in the subset of best models was good, with 58% to 61% of the variance explained for the richness of species affiliated with forest habitats.

The model containing all structural attributes and the local effects model were the first and second best models and captured 36% and 35% of the evidence within the model subset, respectively. The third and fourth-ranked models represented the disturbance and habitat amount hypotheses and captured 17% and 10% of the evidence, respectively. The number of times individual factor is present within the best model subset is an indication of the explanatory power of the factor (Stephens et al. 2007). Structural attributes operating at the plot scale were present in the three best-ranked models, of which plot tree cover was also present in the fourth-best model, i.e. habitat amount hypothesis. Habitat attributes operating at the edge were present in the first and second-best models, while landscape forest extent was present in the second and fourth-best models within the best subset. Estimated effects were consistent with these results, as plot-level factors have a significantly higher influence than edge and landscape-level factors on the richness of forest-specialist birds in matrix habitats.

Regression coefficients of plot tree cover, plot vegetation complexity and distance to edge were statistically significant (p<0.05), while landscape forest cover was only marginally significant (p<0.1) (Table 3.5). Richness of forest specialist species responded positively to increases in tree cover and vegetation complexity at the plot scale, with one forest species expected to be added to the assemblage for every 32% increase in tree cover and for every

 ${\tt TABLE~3.5.~SINGLE-MODEL~(ALL~SPECIES)~AND~MULTI-MODEL~AVERAGED~(FOREST~SPECIALIST~SPECIES)}\\ {\tt COEFFICIENTS}$

| Predictor variable | Estimated effects (Standa | rdized β coefficients) | | | |
|----------------------------|---------------------------|--------------------------------|--|--|--|
| riedictor variable | All bird species | Forest-specialist bird species | | | |
| Plot tree cover | 0.749**** | 0.370** | | | |
| Plot vegetation complexity | 0.861**** | 0.314** | | | |
| Edge vegetation complexity | 0.260** | 0.056 | | | |
| Distance to edge | 0.304**** | 0.089** | | | |
| Distance to forest | -0.239*** | 0.034 | | | |
| Landscape forest extent | 0.215* | 0.123* | | | |

References: * p<0.1, ** p<0.05, *** p < 0.01, **** p<0.001

TABLE 3.6. SUMMARY STATISTICS OF THE MULTI-MODEL INFERENCE APPROACH WITH RICHNESS OF FOREST-AFFILIATED SPECIES AS THE RESPONSE VARIABLE

| | | P | redi | ctor | var | iabl | es | | | | | | | |
|---------------------------|---------------------|---|-------------|-------------|--------|--------|-------------|---|---|-------|--------|---------|--------|-------------------|
| · | Hypothesis | | P V C | E V C | D E | D F | L F E | p | K | R2 | RSS | AICc | ΔAICc | Akaike weights |
| | Local effects | 1 | 1 | 1 | 1 | 0 | 0 | 4 | 6 | 0.597 | 438.37 | 173.79 | 0 | 0.3639 |
| | Full model | 1 | 1 | 1 | 1 | 1 | 1 | 6 | 8 | 0.607 | 426.95 | 173.89 | 0.09 | 0.3471 |
| | Disturbance | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 4 | 0.583 | 453.96 | 175.20 | 1.41 | 0.1797 |
| | Habitat amount | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 4 | 0.580 | 456.91 | 176.26 | 2.46 | 0.1059 |
| cies | Landscape cover | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 0.551 | 488.06 | 184.91 | 11.11 | 0.0014 |
| spe | Local cover | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0.546 | 493.17 | 186.60 | 12.81 | 0.0006 |
| ated | Dispersal | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 4 | 0.552 | 486.94 | 186.64 | 12.84 | 0.0005 |
| Forest-affiliated species | Edge contrast | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 4 | 0.55 | 489.73 | 187.57 | 13.77 | 0.0003 |
| Fores | Vertical complexity | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 0.542 | 498.36 | 188.31 | 14.51 | 0.0002 |
| | Edge effects | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 4 | 0.318 | 741.11 | 255.10 | 81.30 | < 0.0001 |
| | Edge complexity | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 3 | 0.279 | 783.61 | 262.08 | 88.29 | < 0.0001 |
| | Proximity to edge | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 3 | 0.145 | 929.42 | 289.90 | 116.10 | < 0.0001 |
| | Proximity to forest | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 3 | 0.136 | 939.14 | 291.600 | 117.80 | < 0.0001 |

References: PTC: point tree cover; PVC: point vegetation complexity; EVC: edge vegetation complexity; DE: distance to edge; DF: distance to forest; LFE: landscape forest extent; p: number of predictors; K: number of parameters; RSS: residual sum of squares

two units of vegetation complexity, if all other variables are held constant. In turn, the number of forest specialist species increased with increasing distance to edge, with an increase of 2 km in distance to edge leading to a gain of one forest specialist species.

DISCUSSION

Ecological research is providing increasing evidence of the important role of some types of matrix in favoring biodiversity retention in agricultural landscapes, moving away from the general conception of agricultural matrices as inhospitable environments and population sinks (Prugh et al. 2008). However, most studies still focus on the effects of the matrix in mediating the persistence of species within habitat fragments, implicitly considering that the only role for an agricultural matrix is to serve as a conduit for inter-fragment migration and not as habitat. Here we present one of the few empirical studies evaluating the factors influencing the habitat quality of several types of agricultural matrices. The evaluation is based on several structural attributes operating at different spatial scales and varying independently across a matrix intensification gradient comprising multiple land-use systems.

Birds are key players in the functioning of forest ecosystems, contributing to the supply of multiple services such as seed dispersal, biological control, pollination and the regeneration of native plant species (Whelan et al. 2008). In the Argentine Chaco, forest clearing for pasture expansion and cattle grazing intensification modifies structural attributes of matrix vegetation at multiple scales (Torrella et al. 2013, Gasparri et al. 2013). Our results indicated that the occurrence of bird species in the grazing matrix was affected by structural changes occurring at the local scale (i.e. plot and edge), and to a lesser extent at the landscape scale. This suggests that Chaco bird species are particularly sensitive to local management factors driving the intensification of the grazing matrix, such as the choice of methods to clear forests (e.g. total vs. selective) and increase forage productivity (grass implantation vs. regeneration).

Structural changes occurring at the local scale had a higher influence on forest specialist species compared to the whole avian assemblage. The variation in species richness of forest specialists was best explained by four models containing two key structural attributes operating at the plot scale: tree cover and vegetation complexity. Clough et al. (2009) also found a prominent influence of local factors in driving bird richness in Indonesian cacao agroforests, with 35% of the variation explained by a model containing tree species richness

and number of tall trees as predictor variables. Our best model subset explained a comparatively high proportion (between 58 and 61%) of the variation in richness of forest specialist birds. This suggests that the disturbances introduced by local management on plot vegetation structure strongly influences the habitat quality of the matrix for patch-dependent species.

The higher plausibility of hypotheses ascribing a larger influence to structural attributes operating within the grazing matrix is in agreement with several studies in tropical and subtropical agricultural landscapes. High tree cover and vegetation complexity in the matrix has been consistently associated with higher avian richness in the Costa Rican countryside (Hughes et al. 2002, Sekercioglu et al. 2008), Australian grazing lands (Manning et al. 2006) and Southeast Asian agroforests (Waltert 2004, Clough et al. 2009). For example, the reduction of shade trees in cacao agroforests from 80% to 40% is associated with the loss of most forest specialist bird species in the matrix (Steffan-Dewenter et al. 2007). Here, an increase in plot vegetation complexity from intermediate to high-intensity systems via native tree plantings can produce a gain of five forest specialist species in the matrix. Native tree plantings can also maintain or even increase cattle yields through the ecosystem services provided by trees in the grazing matrix (e.g. fertilization of pastures, shadow for cattle) (Murgueitio et al. 2011, Kunst et al. 2012).

The potential role of native tree plantings in restoring bird diversity in the grazing matrix highlights the notion that management disturbances are not necessarily detrimental to native avifauna. Planners and managers can benefit from the strong influence of agricultural management by promoting and/or implementing the type of disturbance regimes that are known to increase bird diversity. For example, many decades of cattle grazing has reduced the structural complexity of native vegetation around domestic areas of low-intensity systems. However, Macchi & Grau (2012) found that the abundance of most birds' guilds is high in such areas, potentially in response to the availability of additional resources (water and food sources) and the maintenance of tall trees. Similarly, Mastrangelo & Gavin (2012) found that silvopastoral systems maintaining tree cover above 30% provide habitat for 60-70% of the number of bird species found in nearby forest patches. This means that management disturbances in low and intermediate-intensity systems can be used to favor biodiversity retention in the grazing matrix, without needing to take land out of production.

I found hypotheses ascribing importance to processes operating at the landscape scale (e.g. "dispersal" hypothesis) and to a lesser extent to edge effects to be implausible explanations of bird occurrence in the matrix. This result supports the conclusions of a meta-analysis of 89 studies of terrestrial fauna on six continents, which found that structural attributes indicating the degree of isolation relative to source populations at the landscape scale were poor predictors of occupancy for many species in fragmented landscapes (Prugh et al. 2008). In contrast, the meta-analysis of Prugh et al. (2008) showed that local characteristics of the matrix had a strong influence on occupancy patterns across many taxa, as found here for birds. In turn, the implausibility of explanations related to edge effects can be expected when considering the regional context. The presence of abrupt edges has been a common feature in Chaco landscapes as these consisted of a mosaic of forests, savannah and scrubland before landscape modification by cattle ranching and cropping (Morello et al. 2005). As a result, some Chaco bird species may have evolved preference for, or tolerance to forest edges (Lopez de Casenave et al.1998).

Overall, my findings indicate that the processes that modify the structural attributes of the vegetation within the grazing matrix have a prominent role in driving the distribution of bird species in agricultural frontier landscapes of the Dry Chaco. These results have important implications for planning interventions aimed at conserving Chaco avifauna and the ecosystem services it supports. Where a significant proportion of native avifauna has already adapted to novel disturbance regimes, low-intensity systems should be maintained as these provide high quality habitat for birds. Moreover, functional roles played by birds in this type of matrix can contribute to the stable supply of ecosystem services relevant to local ranchers. Where further cattle production intensification cannot be avoided, selective methods of forest clearing can be promoted to produce a silvopastoral matrix that provides habitat continuity for most bird species and reduces edge contrast. In addition, to minimize impacts on native avifauna, silvopastoral systems can maintain or even increase cattle yields. Finally, where cattle production intensification has already occurred, planting of native trees on cleared areas can encourage the restoration of significant bird diversity. Native tree planting can also increase economic returns by increasing pasture productivity in the long-term. Overall, attention to local-level land-use management and ecological restoration strategies are likely to have lasting effects on avifauna diversity.

CHAPTER 4: PSYCHO-SOCIAL FACTORS INFLUENCING FOREST CONSERVATION INTENTIONS ON THE AGRICULTURAL FRONTIER



A landholder of the Chaco managing goats as part of their low-intensity, diversified production systems. Photo by the author.

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ABSTRACT

Remnant forest fragments are critical to conserve biological diversity yet these are lost rapidly in areas under agricultural expansion. Conservation planning and policy require a deeper understanding of the psycho-social factors influencing landholders' intentions towards conserving forest fragments. We surveyed 89 landholders in an agricultural frontier of the South American Gran Chaco and employed survey data to test three social psychological models: the Theory of Planned Behaviour (TPB) and two modified versions of it, one integrated to the Norm Activation Theory (TPB-NAT) and one including the effect of identity (TPB-NAT-Identity). The TPB was the most parsimonious model and explained a large variance of conservation intentions (41%). Social norms and attitudes had the largest direct influence on intentions across the three models, and identity had a significant role in shaping social norms and attitudes. Interventions aimed at building social capital within landholder networks provide the best hope for influencing pro-conservation norms.

Introduction

One of the major global drivers of biodiversity loss is the expansion and intensification of agriculture into tropical and subtropical ecosystems in developing countries to supply the increasing demand for food, fibres and biofuels from developed and emerging countries (Lambin & Meyfroidt 2011). In areas under agricultural expansion (i.e. agricultural frontiers), landholders decide on the fate of remnant native forests influenced by external or "structural" factors (e.g. land tenure regimes, market forces) and internal or "human agency" factors (e.g. education level, social norms) (Roy Chowdhury & Turner 2006). Considerable evidence exists on the effects of structural factors on agriculture-driven deforestation (e.g. Angelsen & Kaimowitz 2001), but little is known about the role of human agency in determining the configuration of landscapes (St John et al. 2010; Meyfroidt 2012), despite its importance being widely acknowledged (Lambin 2005). Resources for conservation in developing countries are very limited and therefore a better understanding of the human and social processes underlying forest loss is needed to prioritise conservation actions.

The social psychological theory most often used to explain conservation behaviour is the Theory of Planned Behaviour (TPB, Ajzen 1991). According to the TPB, behaviour is mainly motivated by self-interest and its most proximal predictor is behavioural intentions. In turn, behavioural intentions are influenced by attitudes (i.e. tendency to value the behaviour favourably or unfavourably), social norms (i.e. perceived pressure from relevant others to perform the behaviour), and perceived behavioural control (i.e. the extent to which the behaviour is perceived to be under volitional control). The few TPB applications in rural environments have focused on farmers' adoption of practices to conserve soils (Lynne at al. 1995; Wauters et al. 2010) and vegetation on field margins (Beedel & Rehman 1999; Fielding et al. 2005). Applications of TPB should be expanded to explain behaviours that have the greatest effect on biodiversity and that have the potential to change conservation-oriented outcomes (Gardner & Stern 2002). Hence, we apply the TPB to explain the intention of rural landholders to conserve remnants of dry Chaco forests in Northern Argentina threatened by agricultural expansion.

The TPB has been adapted to increase its explanatory power in particular contexts (Ajzen 2011). For example, Bamberg and Moser (2007) have integrated the TPB with the Norm Activation Theory (NAT, Schwartz 1977), which posits that behaviour is pro-socially

motivated with its main predictor being personal norm, characterised by feelings of personal obligation to perform the behaviour. In the context of conservation behaviour, knowledge about environmental problems and awareness of their consequences are probably important cognitive preconditions for triggering personal norms (Bamberg and Moser 2007), and social norms are thought to underlie the activation of personal norms (Bamberg et al. 2007). Therefore, we add personal norms as a proximate predictor of intention, as well as problem awareness (i.e. the knowledge on the scale and severity of a problem) and awareness of consequences (i.e. the perception that an action has negative consequences for others) as underlying factors of the constructs in the TPB, to test a model integrating both self-interest and pro-social motives (i.e. TPB-NAT model).

For conservation behaviour in agricultural systems, Burton and Wilson (2006) propose that identity (i.e. the behaviours that are perceived as part of the self) is a significant factor underlying land-use decision-making. These authors support that identities are multiple and hierarchical (Stryker 1994) and that occupational identities of farmers (e.g. agribusiness person) are the most salient in the hierarchy; this stimulates the adoption of roles and behaviours for which the individual and the group share expectations, such as clearing native vegetation to farm intensively. Past behaviour has been suggested to better measure perceived behavioural control in the context of agriculture (Wauters et al. 2010). Therefore, we also add identity and past behaviour to the integrated TPB-NAT model in order to test a model tailored to the characteristics of agricultural agency (i.e. TPB-NAT-Identity model).

In predicting our target intention, we will make a methodological and theoretical contribution through the use of an information-theoretic approach to directly compare three models: the standard TPB model and two modified versions of it, one adapted to behaviours related to the environment (TPB-NAT model) and one tailored for decisions in the context of agriculture (TPB-NAT-Identity model). Considering that interventions will vary greatly depending on the factors driving landholders' decisions, the identification of the main social psychological drivers will allow for interventions in the Gran Chaco to be more efficiently designed and targeted.

METHODS

The study area covers ca. 10,000 km² in the Chaco province, in the Northwest of Argentina, and corresponds to the eastern portion of The Chaco Impenetrable, one of the largest remnant

tracts of Neotropical dry forests, a globally threatened biome. Government-led colonization programs in the mid 20th century promoted extensive cattle ranching and increased human pressure on this fragile environment, but the magnitude and pace of forest degradation and loss increased exponentially with the arrival of soybean farmers and intensive cattle ranchers from the 1990s (Altrichter & Basurto 2008). In the Chaco province, the deforestation frontier advances today from the sub-humid margins (900-1100 mm of annual rainfall) to the semiarid core (<900 mm), forming an arc from the towns of Miraflores and Juan José Castelli in the northeast, and Concepción del Bermejo and Pampa del Infierno in the southwest of the study area (Fig. 4.1). In a neighbouring province (Salta), agricultural expansion drove the loss of native forests at annual rates of 1.5 - 2% from 2005 to 2010 (Seghezzo et al. 2011), also leading to the violent displacement of peasant and indigenous people. In response, the Argentine government passed a Forest Law in 2008 to regulate the use of forest lands by establishing zones for agricultural production, sustainable use and nature conservation. A previous study suggests that reconciling production and conservation in the ecologically fragile Gran Chaco requires landholders to integrate forest fragments and strips into their food production systems (Mastrangelo & Gavin 2012).

Survey and questionnaire design

We reviewed the literature on land use history of the study area and divide it into four subareas (named after the largest town) from those with older and more extensive deforestation to those with more recent and localized deforestation: Juan José Castelli, Miraflores, Concepción del Bermejo, Pampa del Infierno. Then, we classified landholdings on the basis of analysis of satellite images and cadastral maps in ArcGIS (ESRI). Classification was based on three characteristics of landholdings: (i) sub-area where is located (Miraflores, Juan José Castelli, Concepción del Bermejo or Pampa del Infierno), (ii) size (small: 1-200, medium: 201-2000 and large: >2000 ha), and (iii) land tenure condition (landholdings with complete, incomplete or no cadastral information). Above 80% landholdings in each sub-area corresponded to medium-sized landholdings with complete cadastral information. We randomly selected 25 landholdings within the most frequent size and tenure classes in each sub-area, of which 11 refused to participate, leading to a final sample of 89 landholdings.

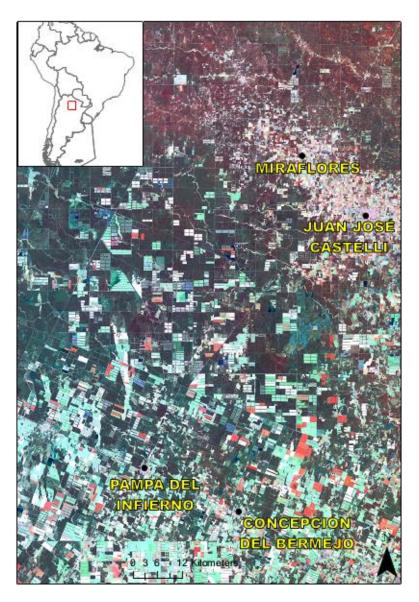


FIGURE 4.1. SATELLITE IMAGE (LANDSAT TM) OF THE STUDY AREA IN THE ARGENTINE CHACO, SHOWING THE DISTRIBUTION OF CLEARED AREAS (LIGHTER RECTANGULAR AREAS) AND OF REMNANT NATIVE DRY FORESTS (DARKER IRREGULAR AREAS). FOREST CLEARING FOR SOYBEAN AND PASTURE EXPANSION ADVANCES FROM EAST (SUB-HUMID, MORE FRAGMENTED) TO WEST (SEMIARID, LESS FRAGMENTED) AND INTO THE CORE OF THE CHACO IMPENETRABLE, ONE OF THE LARGEST REMNANT TRACTS OF NEOTROPICAL DRY FORESTS. INSET: LOCATION OF THE STUDY AREA (RED SQUARE) IN SOUTH AMERICA.

We surveyed landholders in July 2012 using a questionnaire approved by the Human Ethics Committee of Victoria University of Wellington (#19477). Prior to the survey, we collected 33 semi-structured interviews from landholders selected using a snowball sampling method. Interviews elicited salient beliefs, perceptions and/or values that may influence intentions to conserve forest fragments in their landholdings. From the qualitative analysis of interview content, we selected three salient beliefs, perceptions and/or values related to each of the nine theoretical constructs (Table D1 in Appendix D). We then designed a list of 27 questionnaire items following the principle of compatibility (Ajzen 2011), where the target of the action

was forest fragments, the action was their conservation (i.e. no clearing, no intensive timber extraction), the context was the landholding of the respondent, and the time was July 2012-July 2013 (Table D2 in Appendix D). One interviewer (MEM) visited each landholder, to whom he asked questionnaire items in the same order and with the same wording.

In the iterative process of item generation and selection, we sought a balance between developing items that were redundant enough to achieve sufficient internal consistency of constructs and items that were dissimilar enough to capture the salient dimensions of each construct (Graham et al. 2010). We piloted the questionnaire with eight landholders to ensure that statements and scales were clear and relevant. We also employed the questionnaire to collect social (e.g. participation in forums and networks), economic (e.g. access to external fund) and demographic (e.g. age of the landholder) information of landholdings (Tables D3 and D4 in Appendix D).

Structural equation modelling allows testing the validity of the measurement (i.e. relating measured items and theoretical constructs) and structural models (i.e. relating theoretical constructs) in a single step, but requires large sample sizes to test complex models (Byrne 2001). We employed a two-step approach as it reduces the demand for large sample sizes and allows testing complex models in contexts where data collection is very time-consuming, like in our study area. First, we tested construct validity by calculating the contribution of measured items to the corresponding construct using confirmatory factor analysis in AMOS 19 (IBM, Chicago, Illinois) (Schumaker & Lomax 2004). Second, we tested the relationships among constructs using the maximum-likelihood procedure on validated construct scores comprising weighted averages of confirmed measured items in AMOS 19. We employed an information-theoretic approach with the Akaike Information Criterion (AIC) to compare the degree of fit and parsimony of the three social psychological models (Burnham & Anderson 2002)

RESULTS

The majority of landholdings were family enterprises (96.6%), and interviewed landholders were all male, most born in the Chaco region (92%) and residing in the landholding (53%) or in the town nearest to the landholding (44%, Table D3 in Appendix D). Landholders' age (range: 25-75 years), farming experience, time of tenure of the landholding (range: 2-64 years), level of formal education, and participation in forums and networks ranged widely

(Table D4 in Appendix D). Landholdings were located in zones under two conservation categories according to the provincial land-use plan, with 64% on category I (total forest clearing permitted) and 34% on category II (only selective clearing permitted). Most landholders reported no intention to either lease (64%) or sell (81%) all or part of their landholdings in the near future. Landholding size ranged from 180 to 1764 ha. An average landholding was 300 ha, of which 60% was covered by forests (usually used by cattle), 15% by cropland (cereals in winter, soybeans in summer) and 25% by pastures (15% as silvopastoral systems). None of these attributes had a statistically significant correlation with landholders' intentions to conserve forest fragments in their landholdings (p>0.05).

Most landholders (77.5%) reported a positive intention towards conserving forest fragments in their landholdings, which was statistically correlated with the perception of the self as a steward of the land (r=0.415, p<0.001). Landholders' perception of forest clearing as an environmental problem were higher than the scale mid-point (mean score=3.59, t=5.95, p<0.01, Table S4.4 in Appendix B), with stronger perceptions reported by those with less secure conditions of land tenure (r = -0.239, p<0.05), lower access to external funding (r=-0.230, p<0.05) and lower labour to consumer ratio (r=-0.245, p<0.05). Landholders' level of awareness of the negative consequences of forest clearing on native fauna, soils and local climate were high on average (mean scores>3.6, all p<0.01). A higher awareness of the effects on soils was reported by landholders located in sub-areas with more extensive and longer history of deforestation (r=0.322, p<0.001) and of the effects on local climate by younger landholders (r=-0.244, p<0.05).

Landholders' feeling of obligation to conserve forests because of their intrinsic value was higher than neutral (mean scores>3.66, t=4.23, p<0.01), with stronger feelings reported in landholdings with smaller crop, pasture, and total area (r=-0.237, p<0.05) and higher family labour (r=0.305, p<0.01). Landholders' valuation of the aesthetic value of forests was higher than neutral (mean scores>3.96, t=9.23, p<0.01), with higher values reported by landholders with more years in farming (r=0.219, p<0.05), smaller crop area (r=-0.341, p=0.001) and larger silvopastoral area (r=-0.277, p<0.01). Finally, a lighter degree of forest transformation in the landholding from 2009 to 2011 was reported by landholders that participated in a larger number of forums and networks (r=-0.215, p<0.05) and with less secure tenure of land (r=-0.244, p<0.05).

MEASUREMENT AND STRUCTURAL MODELS

The 25 regression coefficients between measured items and their corresponding constructs (i.e. factor loadings) were mostly moderate to high (Table S4.1). Three measured items with factor loadings below 0.25 were not included in the analyses. Cronbach's alpha coefficients were higher than 0.65 for all constructs, which is acceptable in human dimensions research (Vaske 2008). Mean correlation between constructs was low (0.186 [SD=0.29]), indicating that they were measuring different aspects of landholders' cognitions. The TPB model showed moderate fit to survey data ($\gamma^2/df < 5$, SRMR ≈ 0.1 , RMSEA>0.2) but explained 41% of the variance of landholders' intention to conserve forest fragments in their landholding (Table 4.1). Social norms had the largest effect on intentions (β =0.59), followed by attitude $(\beta=0.23)$, and a small negative effect of perceived behavioural control ($\beta=-0.11$) (Fig. 4.2). In contrast, the TPB-NAT model (Fig. 4.3) had a better fit to survey data ($\chi^2/df\approx3$, SRMR ≈1 , RMSEA<0.2), but explained less of the variance (31%) compared to the TPB. The TPB-NAT-Identity model (Fig. 4.4) had a good fit to survey data ($\chi^2/df < 2$, SRMR ≈ 0.1 , RMSEA≈0.1) and explained as much variance of intention as the TPB (42%). Despite its fit, the TPB can be regarded as the best model because: (i) the difference in the AIC with the second best model (TPB-NAT-Identity) was much larger than 2 (AIC=35.7, Table 4.1), the threshold usually used to identify a substantially better model on the basis of its fit and parsimony (Burnham & Anderson 2002), and (ii) it explained a large amount of the variance in behavioural intention.

TABLE 4.1. MODEL FIT INDICES OF THE THREE PSYCHO-SOCIAL MODELS EMPLOYED TO EXPLAIN LANDHOLDERS' INTENTIONS TOWARDS FOREST CONSERVATION,

| Model | Model fit indices | | | | | | | | | |
|--------------------------|-------------------|----------------|-------------|------|------|------|-------|-------|------|----------------|
| • | χ^2 | df | χ^2/df | SRMR | GFI | CFI | RMSEA | AIC | ΔΑΙC | \mathbb{R}^2 |
| TPB | 18.77 | 4 (p=0.001) | 4.69 | 0.17 | 0.89 | 0.65 | 0.23 | 30.71 | | 0.41 |
| TPB- NAT | 28.41 | 9 (p=0.001) | 3.15 | 0.99 | 0.9 | 0.69 | 0.17 | 66.41 | 35.7 | 0.31 |
| TPB- NAT- Identity | 26.54 | 16 (p=0.47) | 1.65 | 0.11 | 0.91 | 0.87 | 0.09 | 66.54 | 35.8 | 0.42 |

SRMR=standardized root mean residual; GFI=goodness of fit index; CFI=comparative fit index; RMSEA=root mean square error of approximation; AIC=Akaike information criterion.

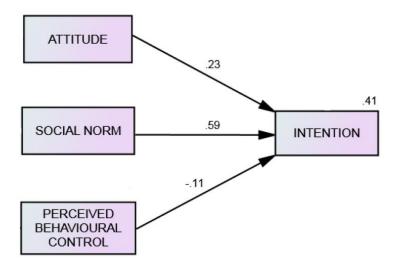


FIGURE 4.2. GRAPHICAL OUTPUT OF THE TPB MODEL SHOWING A LARGE EFFECT OF SOCIAL NORMS (B = 0.59), A RELATIVELY MODERATE EFFECT OF ATTITUDES ON INTENTIONS (B = 0.23) AND A SMALL EFFECT OF PERCEIVED BEHAVIOURAL CONTROL (B = -0.11) ON INTENTIONS. NUMBERS IN THE UPPER RIGHT CORNER OF BOXES FOR CONSTRUCTS ARE COEFFICIENTS OF DETERMINATION (\mathbb{R}^2) AND NUMBERS ON ARROWS ARE STANDARDIZED REGRESSION COEFFICIENTS (B).

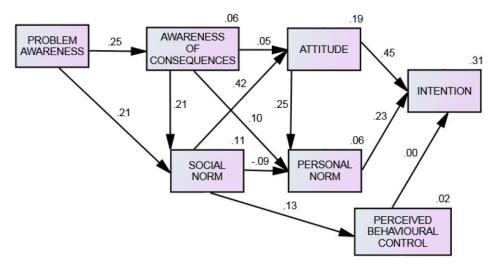


FIGURE 4.3. GRAPHICAL OUTPUT OF THE TPB-NAT MODEL SHOWING THAT THE ADDITION OF PERSONAL NORM AS A PROXIMATE PREDICTOR AND PROBLEM AWARENESS AND AWARENESS OF CONSEQUENCES AS UNDERLYING PREDICTORS DID NOT INCREASE THE AMOUNT OF EXPLAINED VARIANCE IN INTENTION AS COMPARED TO THE TPB MODEL. TO THE CONTRARY, EXPLAINED VARIANCE OF THIS MODEL WAS 10% LOWER THAN THE TPB DUE TO A MORE INDIRECT INFLUENCE OF SOCIAL NORMS ON INTENTIONS. NUMBERS IN THE UPPER RIGHT CORNER OF BOXES FOR CONSTRUCTS ARE COEFFICIENTS OF DETERMINATION (R²) AND NUMBERS ON ARROWS ARE STANDARDIZED REGRESSION COEFFICIENTS (B).

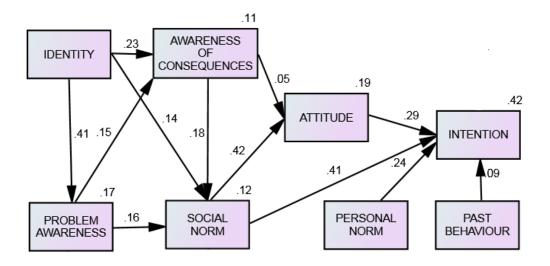


FIGURE 4.4. GRAPHICAL OUTPUT OF THE TPB-NAT-IDENTITY MODEL SHOWING THAT SOCIAL NORMS HAD THE LARGEST OVERALL EFFECT ON INTENTION BOTH DUE TO A DIRECT EFFECT (B=0.41) AND AN INDIRECT EFFECT MEDIATED BY ATTITUDES (B=0.54). IDENTITY HAD A LARGE EFFECT ON INTENTION, VIA ITS EFFECTS ON SOCIAL NORMS (B=0.14), PROBLEM AWARENESS (B=0.41) AND AWARENESS OF CONSEQUENCES (B=0.23). NUMBERS IN THE UPPER RIGHT CORNER OF BOXES FOR CONSTRUCTS ARE COEFFICIENTS OF DETERMINATION (R^2) AND NUMBERS ON ARROWS ARE STANDARDIZED REGRESSION COEFFICIENTS (B).

DISCUSSION

We integrated components of basic social psychological theories oriented to explain behaviour driven by self-interest and pro-social motives to build candidate models *a priori* more or less tailored to explain conservation behaviour in the context of agriculture. Other social psychological theories such as the Value-Belief-Norm Theory (Stern et al. 1999) derive from these basic theories and seek to explain general conservation behaviours, and thus were not employed here. Previous research has mostly relied on socio-economic attributes to explain land use behaviour (e.g. Roy Chowdhury & Turner 2006), but our findings showed that none of the landholder attributes surveyed was associated with their conservation intentions. Instead, landholders' intention towards remnant habitats was influenced by psycho-social factors.

The information-theoretic approach is particularly useful in environmental psychology where it allows for a direct comparison of the many different constructs and models that have been proposed to influence a variety of behaviours. To our knowledge, this is the first use of this approach to examine the drivers of land use intentions. Our findings indicate that TPB had the highest degree of fit and parsimony. The variance of intention explained here by the TPB (41%) was higher than the explained variance found (27%) in a meta-analysis of 185 independent TPB studies (Armitage & Conner, 2001). The model more tailored to explain

conservation behaviour in agriculture (TPB-NAT-Identity) explained a similar amount of variance than the TPB (42%). This means that in this context TPB is able to explain a similar proportion of the variance usually explained by social psychological models in other behavioural domains, providing a simple and comprehensive framework for identifying key variables relevant for the design of conservation interventions (St John et al. 2010).

Social norms had the most prominent influence on intention in both the TPB (β =0.59) and TPB-NAT-Identity (β =0.41) models, reinforcing the notion that farmers constitute a judgemental peer group (de Snoo et al. 2012). Attitude had an important role as driver of intention across the three models (β =0.23-0.45), similar to studies using TPB to explain the choice of agricultural (Fielding et al. 2005, Wauters et al. 2010) and silvicultural practices (Karppinen 2005). Perceived behavioural control did not influence conservation intentions, suggesting the absence of factors inhibiting the behaviour (Wauters et al. 2010). The positive effect of past behaviour supports the notion that perceived difficulty rather than perceived control influences conservation intentions in agriculture (Primmer & Karppinen 2011). Contrary to Wall et al. (2007), the integration of the TPB and NAT models did not increase the explanatory power, due in part to weak effect of social norms on personal norms. Identity had a significant underlying influence on conservation intentions through a positive effect on awareness of the problem and of the consequences of landholders' behaviour. These results suggest that social norms and identity are important determinants of intentions to conserve habitats in productive lands, in line with Primmer and Karpinnen (2010) and Lokhorst et al. (2011).

Most landholders in our sample hold positive intentions towards conserving forest fragments in the near future. However, a significant proportion of them (22.5%) reported a weak conservation intention, which means that they probably plan to clear forest fragments in their landholding. Encouraging this significant proportion of landholders to alter their behaviour towards more conservation-oriented outcomes requires informed behaviour change interventions. Our findings suggest that (re)establishing social norms that reward conservation behaviours within groups of landholders to which they identify with may be critical to achieve long-term conservation of dry Chaco forests.

Social norms are shared understandings and expectations among group members on how to behave when faced with individual choices relevant to the group (Ostrom 2000). In general,

behaviour of land users can be influenced by: (i) providing economic incentives, (ii) enforcing government legislations, or (iii) building social capital (de Snoo et al. 2012). Economic incentives based on market mechanisms or government contracts in the Argentine Chaco will seldom drive lasting changes in conservation behaviour because of their temporary and volatile nature. Moreover, economic incentives can erode social norms by turning behaviours motivated by social norms into behaviours financially motivated (de Snoo et al. 2012). Government legislations can lead to the internalization of pro-conservation norms and rules if accepted by the majority of landholders and implemented for a long term (Stobbelaar et al. 2009). However, land use plans in the Argentine Chaco are ignored or perceived as illegitimate by most landholders because of their passive participation (if any) in the planning process (Seghezzo et al. 2011), reducing the chance for existing regulations to exert long-lasting normative influences.

To be effective, interventions aimed at influencing social capital should be implemented based on an in-depth knowledge the context and dynamic of existing social groups and networks (Minato et al. 2010). In the Argentine Chaco, two broad types of social networks or participatory processes exist (Garcia-Lopez & Arispe 2010). On the one hand, commercial producers operating over large landholdings participate in networks initiated by multinational corporations and international NGOs (top-down process), where they learn about new technological inputs and compare outcomes against peers. In this case, individuals and organizations in Argentina and importing countries concerned about deforestation in the Chaco should demand better environmental performance of large commercial landholders to foster higher environmental benchmarks within their peer networks (de Snoo et al. 2010). On the other hand, peasant smallholders participate in self-organized networks (bottom-up process) that work towards securing land tenure and food sovereignty. Local NGOs and government extension agencies working with peasant smallholders should promote existing knowledge and norms, which are intrinsically compatible with forest conservation, and grant land property rights so they can exert safe stewardship on their lands.

CHAPTER 5: DISCUSSION



Cattle at the front, birds and forests on the back: a depiction of Chaco agricultural landscapes. Photo by the author.

Previous chapters presented empirical analyses of the ecological and social drivers of avifaunal change in agricultural frontiers of the Argentine Dry Chaco. Taken together, this new evidence has important implications for conservation planning in the South American Gran Chaco and other tropical regions undergoing rapid agricultural intensification. In the following, I present a set of ten conclusion statements that capture the main contributions of this thesis for conservation science. Each statement in this concluding decalogue is followed by a brief discussion.

1. Cattle yields increase non-linearly with increasing land-use intensity. In intermediate-intensity systems allow for the coexistence of native trees and pastures and produce as much cattle yields as pastures on cleared areas. In turn, cattle production intensification should proceed via the adoption of silvopastoral systems to increase cattle yields while retaining native tree species in the grazing matrix.

I described and characterized the diversity of modes in which landholders use and combine their capital assets to produce beef cattle in the Dry Chaco region. Traditional systems produced comparatively low levels of cattle yields, and depended heavily on the natural productivity of forage in native ecosystems. Land privatization and the clearing of native ecosystems in the last two decades drastically reduced the spatial extent of grazing lands to which traditional landholders could access, rendering them highly vulnerable to ecosystem collapse (Camardelli 2003). Investment of financial, physical and human capital for the development of silvopastoral systems (e.g. technology and knowledge to implement selective forest clearings) raised cattle productivity by a factor of 3 to 9 compared to traditional systems. The cultivation of high-yielding grasses in the understory of stands of native trees allows for positive interactions among trees, cattle and pastures (e.g. increased soil fertility due to tree litter decomposition, reduced heat stress in cattle under the tree shade, Radrizzani & Renolfi 2004). Further financial investments in the form of total vegetation clearing did not necessarily increase economic returns in the form of higher cattle yields within high-intensity systems compared to silvopastoral systems. For these reasons, reducing the vulnerability of traditional systems and increasing their development options in the Chaco agricultural frontiers may involve: i) promoting the adoption of silvopastoral systems among traditional landholders to raise cattle productivity while

conserving native trees, and ii) limiting the expansion of high-intensity systems to prevent further displacement of traditional systems and loss of native forests.

2. Bird species richness at the grazing matrix relative to the nearest forest decreases non-linearly with increasing land-use intensity. High bird species richness and high cattle yields co-occur in intermediate-intensity systems. Land-sharing via the development of silvopastoral systems can provide "win-win" outcomes for bird conservation and cattle production.

The empirical assessment of the trade-off model proposed by Green et al. (2005) provides fundamental information to explore the relative utility of land-sharing and land-sparing as strategies for planning biodiversity conservation in agricultural landscapes. I assessed the trade-off model to describe the pattern of bird diversity change as a function of cattle production intensification. Following a path of increasing land-use intensity, bird species richness relative to the nearest forest were high in very-low, low and intermediate-intensity systems, likely in response to the maintenance of native tree cover in the grazing matrix. The retention of significant levels of native biodiversity in agroforestry systems has been also reported for silvopastoral systems in Colombia (Murgueitio et al. 2011) and Mexico (Harvey et al. 2006), cocoa agroforests in Indonesia (Clough et al. 2009), and coffee agroforests in Mexico (Perfecto et al. 2004). Intermediate-intensity silvopastoral systems in the Argentine Dry Chaco provided habitat for 70-90% of the bird species found in nearby forests and produced 60-70% of the cattle yields that can be achieved under particular soil, rainfall and management conditions. In contrast, bird species richness was very low in high-intensity systems (i.e. 30-50% compared to nearby forests). This 20-60% decline in bird diversity in response to the total clearing of native vegetation was accompanied by minor or no increases in cattle productivity between intermediate and high-intensity systems. Increasing land-use intensity in lands already cleared for pasture cultivation and intensive cattle grazing did not affect bird species richness negatively. The pattern of bird diversity change described above was also reported recently in an independent study applying a similar sampling design in the same study area (Macchi et al. 2013). This evidence indicates that intermediate-intensity silvopastoral systems offer a "win-win" option for bird conservation and cattle production in Chaco agricultural frontiers.

3. Bird functional groups differ in the responses to increasing cattle production intensity. Forest specialist and frugivorous birds are sensitive to intermediate-intensities of land-use. Land-sharing should be combined with the protection of remnant forest fragments to conserve these habitat and trophic specialist species.

Bird species differ in their responses to cattle production intensification. Higher sensitivity has been consistently associated with the presence of certain functional traits, such as habitat and diet specialization (Henle 2004). Some of the functional traits that confer enhanced sensitivity also underlie the performance of ecological functions that contribute to ecosystem services (Tschartnke et al. 2012). For this reason, I expanded the simple tradeoff model of Green et al. (2005) to evaluate the responses of individual species and functional groups of birds to increasing cattle production intensity. The density of individuals in the grazing matrix declined at higher proportions for those species with specific habitat and feeding preferences. Similarly, the number of species within functional groups experienced a larger decrease for groups characterized by specialized life-history strategies. For example, the number of insectivorous bird species declined by 30% between intermediate and high-intensity systems. Frugivorous and forest specialist birds were absent in high-intensity systems and rare in silvopastoral systems, owing to a decline by 63% and 60% between very-low and low-intensity systems, respectively. The combination of some functional traits appeared to be associated with enhanced sensitivity. Large-bodied frugivores such as Ortallis canicolis and Penelope obscura, highly valued for their meat, were abundant in low-intensity systems and very scarce in intermediate-intensity systems. The richness and density of individuals playing similar ecological roles indicates the functional redundancy within groups, which contributes to stability in the supply of ecosystem services provided by birds (Yachi & Loreau 1999). Frugivorous bird species, for instance, play an important role as seed dispersers and may contribute to tree regeneration in silvopastoral systems and open pastures. As the relative importance of ecosystem services provided by birds differs among cattle production systems, the decline of functional redundancy within groups may have different impacts on landholders' livelihoods (Diaz et al. 2011). The conservation of forest remnants is important to maintain

source populations of species sensitive to land-use intensification that provide valuable ecosystem services.

4. Bird species richness decreases sharply when tree cover falls below 30%.

Maintaining tree cover above 30% and developing a silvopastoral matrix on the remaining land produces the highest combination of bird diversity and cattle yields at the landscape scale. Land-sharing can spare land for biodiversity conservation.

The analysis of changes in cattle yields and the richness of avian assemblages and functional groups across the intensification gradient allowed me to project alternative policy scenarios and explore the relative merits of land-use planning strategies to balance bird conservation and cattle production objectives. The richness-yield curve showed a threshold in the habitat quality of the grazing matrix that led to a 40% decline in bird species richness relative to the nearest forest when native tree cover fall below 30%. Assuming that a tree cover above 30% of the landscape area provides habitat for all forest specialist species, I compared the conservation and production outcomes of five policy scenarios (Table 5.1). Under the industrial agriculture scenario, the maximization of production outcomes via high-intensity systems created a landscape devoid of native vegetation and only inhabited by less than one third of the bird species found in forests, all except one being habitat generalist species, which are usually of lower conservation concern. The land-sharing scenario provided only 13.1% less yields than the industrial agriculture scenario, while it created a matrix that was used by one-quarter of the bird species restricted to forest habitats and two-thirds of the habitat generalist species native to the Chaco region. Cattle yields under the land-sparing scenario were 16.9% lower than under the land-sharing scenario. This result contradicts the widely held notion that integrating production and conservation on the same land (land-sharing) produces lower yields than combining land set-asides and land-use intensification (land-sparing). Under the land-sparing scenario, setting aside a forest area not lower than 30% of the landscape provided core habitat for all bird species detected, although high land-use intensities in the 70% of the landscape created a matrix with very low avian conservation value. The traditional ranching scenario allowed for the conservation of a large proportion of the forest specialist (62.6%) and habitat generalist species (84.8%) found in undisturbed forests.

Larger populations of these bird species may be supported under the traditional ranching compared to the land-sparing scenario as forest area in the former was 3.3 times larger than in the latter. However, a landscape dominated by traditional ranching systems provided 8.7 and 7 times lower cattle yields than the land-sharing and land-sparing scenario, respectively. Finally, the scenario combining land-sharing and conservation on the same landscape simultaneously provided; (i) core habitat for all Chaco avifauna in the 30% of undisturbed forest area, and (ii) a high-quality matrix in the 70% of area covered by silvopastoral systems, which allowed for the conservation of 23.8% and 36.5% more forest specialist and habitat generalist species in the matrix compared to the land-sparing scenario. These larger conservation outcomes came at the cost of achieving only 9% less yields than under the land-sparing scenario

TABLE 5.1. COMPARISON OF PRODUCTION AND CONSERVATION OUTCOMES OF FIVE POLICY OPTIONS FOR SIMULTANEOUSLY INCREASING BIRD DIVERSITY AND CATTLE YIELDS IN CHACO AGRICULTURAL FRONTIERS.

| Policy | Land-use composition of | | | | Production | Conservation outcomes (%) | | | | |
|--------------|-------------------------|-----|-----|-----|-------------------|---------------------------|--|---------|--|--|
| option | scenarios (%) | | | | outcome (%) | Conservation outcomes (%) | | | | |
| | | | | | Forest specialist | | Habitat generalist | | | |
| | FF | LIS | IIS | HIS | Beef cattle | Core | Matrix | Core | Matrix | |
| | 1.1. | LIS | 113 | шэ | productivity | habitat | habitat | habitat | Habitat | |
| Industrial | 0 | 0 | 0 | 100 | 100 | 0 | 0.6 | 0 | 29.5 | |
| agriculture | | | | | | | | | | |
| Land sharing | 0 | 0 | 100 | 0 | 86.9 | 0 | 24.4 | 0 | 66 | |
| Land sparing | 30 | 0 | 0 | 70 | 70 | 100 | 0.6 | 100 | 29.5 | |
| Land sharing | 30 | 0 | 70 | 0 | 61 | 100 | 24.4 | 100 | 66 | |
| conservation | 30 | Ü | 70 | Ü | 01 | 100 | 2 | 100 | 00 | |
| Traditional | 0 | 100 | 0 | 0 | 10.4 | 62.6 | 0 | 84.8 | 0 | |
| ranching | | ,,, | | | | | , and the second | | , and the second | |

References: FF, forest fragments; LISS, low-intensity systems; IIS, intermediate-intensity systems; HIS, high-intensity systems.

5. Management disturbances within the grazing matrix have a strong influence on bird species richness in matrix habitats. Minimizing disturbances that reduce the structural complexity of vegetation in the grazing matrix, and promoting those that increase it, should be a priority in the design of conservation plans.

Agricultural intensification in the agricultural matrix influences avian diversity via multiple processes operating at local to landscape scales, known as matrix effects. Previous studies have mostly focused on the effect of the matrix as a barrier for species dispersal between habitat patches (Vandermeer & Carvajal 2001). I evaluated the relative influence of several matrix effects on bird occurrence in the grazing matrix by testing and comparing a set of theory-driven hypotheses. The dispersal hypothesis did not provide a plausible explanation, suggesting that processes other than those operating at the landscape scale may be driving bird species distributions. The variation of structural attributes of vegetation within the grazing matrix had the largest effect on bird diversity. Therefore, disturbances introduced by local agricultural management may have the greatest influence on the habitat quality of the matrix. Total clearing, frequent fires, intensive grazing and the cultivation of exotic grasses are likely to act synergistically to the detriment of habitat quality for birds in highintensity systems, as it was described for Australian grazing lands (Hobbs et al. 2001). However, conservation plans should also focus on at least two other types of management disturbances in the grazing matrix. First, selective clearing of native vegetation for the opening of silvopastoral plots should be carefully regulated as small variations in the cover and structural complexity of the vegetation can have significant effects on habitat quality. Highly selective methods such as those employing roller-choppers (Kunst et al. 2012) should be promoted in order to maintain dense and diverse stands of native trees and seedlings (>120 adult trees per ha). In contrast, bulldozers should not be employed to clear the forest understory as this method only leaves highly scattered trees of few species and with low chances of regeneration. Second, plantings of native tree species that are abundant in the forest and are valued by landholders for their timber (Schinopsis spp.) and forage (*Prosopis* spp.) should be promoted in already cleared lands in order to restore significant bird habitat while yielding benefits for landholders.

6. Socio-economic attributes of landholders are associated with their perceptions and beliefs regarding forest conservation. Psycho-social factors have a strong direct influence on landholders' intentions to conserve remnant forest fragment. Policy interventions should be tailored not so much to the socio-economic profile of landholders, but to their psycho-social characteristics.

Social research in the context of agriculture and land-use shows that landholders' decisions about land allocation to alternative uses are influenced by three types of factors. Macrolevel or "structural" factors operate at global to regional scales, and are therefore exogenous to the landholder (Roy Chowdhury & Turner 2006). Landholders vary widely in the level of exposure to the influence of structural factors (e.g. commodity price fluctuations in international markets) depending on their production systems. Meso-level or "access" factors operate at regional to local scales, and result from the interactions of the landholder with institutions and organizations (Jepson et al. 2010). Property rights, land-use contracts and farmers associations are some of the meso-level factors that constrain or enable access of landholders to the capital assets needed for agricultural production (e.g. land, technology, knowledge). Finally, micro-level or "agency" factors operate within the individual landholder and his/her social group. Psycho-social theory posits that individuals' intentions are proximally determined by a set of discrete factors such as attitudes, norms, etc. (i.e. psycho-social constructs, Ajzen 2011). My survey questionnaire collected data on socio-economic attributes of landholders representing macro and meso-level factors, and on psycho-social constructs representing micro-level, agency factors. Correlation analyses revealed few strong associations between socio-economic attributes and psycho-social constructs. Among these, a small landholding size was strongly associated with positive attitudes towards forest conservation. In contrast, structural equation analyses showed that some psycho-social constructs were consistently associated with forest conservation intentions across alternative models. In light of this evidence, tailoring policy interventions based on classical agent characterizations of socio-economic profiles may be misleading. Psycho-social data may provide a more realistic description of landholders' conservation behaviour to inform the design of policy incentives and regulations.

7. The Theory of Planned Behaviour is useful to explain the conservation behaviour of landholders. Social norms and attitudes are the most important proximate predictors of landholders' conservation intentions. Behaviour change interventions should target both the pro-social and self-interest motivations behind land-use decisions.

According to psycho-social theory, the intention to perform a particular behaviour related to the environment is influenced by either self-interest (e.g., to pursue a land-use strategy that maximizes one's economic rent) and/or pro-social motives (e.g. to prevent pollution that may cause risks for other's health) (Bamberg & Moser 2007). Psycho-social models vary in the importance given to these motives as determinants of intentions. Previous research shows that the relative influence of self-interest and pro-social motives on proenvironmental intentions depends on the behaviour under study (Bamberg & Moser 2007). The Theory of Planned Behaviour (TPB) integrates self-interest (i.e. attitude) and prosocial motives (i.e. social norms) and has been commonly used to explain proenvironmental behaviour. Other pro-social motives such as moral norms and problem awareness proposed by Schwartz (1977) in the Norm Activation Theory were also found to be significant drivers of pro-environmental behaviour (Bamberg et al. 2007). Finally, the self-identification according to the role played in social groups (i.e. identity) was found to bear importance in shaping decisions in the context of agriculture (Burton & Wilson 2006). Among the psycho-social models tested in Chapter 4, the TPB explained the largest amount of variance in landholders' intentions to conserve remnant forests in their landholdings. Among individual factors, social norms had the strongest effect on conservation intentions, closely followed by attitudes. Therefore, both pro-social and self-interest motives appear to be underlying the formation of forest conservation intentions among Chaco landholders.

8. Landholder's self-identification is a key factor underlying their conservation behaviour. Identity influences intentions via multiple paths. Existing social networks and forums within identity groups provide a fertile ground to influence behaviour towards more conservation-oriented outcomes.

Research approaches from rural sociology to understand landholders' conservation behaviour have focused on the role of farmers' self-identification as a driver of land-use decisions (Burton & Wilson 2006). Wilson (2007) proposed that a salient identity across a group of farmers consists of shared expectations on the set of management practices that they should implement and the resulting outcomes in terms of productivity and biodiversity. For this reason, I tested a psycho-social model including the identity construct as the ultimate factor influencing landholders' conservation intentions. It was measured as the degree to which landholders self-identified as stewards of the land, efficient land-user and commercial (profit-maximizing) food producers. A self-identification as steward of the land was strongly associated with positive intentions to conserve forest fragments. This effect was mediated by three main relationships. First, landholders' self-identity positively influenced their awareness of the scale of deforestation in the Chaco region and of the consequences of forest clearing on soils, fauna and climate. Second, landholders' selfidentity and their awareness of the scale and consequences of deforestation significantly influenced social norms, that is, their perceived pressure to conserve forests from relevant others such as family, neighbours and media referents. Third, social norms positively influenced landholders' tendency to value forest fragments favourably or unfavourably (i.e. attitude) regarding their aesthetic, regulatory or provisioning value. These results suggest that social interactions within identity groups may have a prominent role in determining landholders' conservation intentions. Existing social networks and forums may provide a fertile ground to influence behaviour towards more conservation-oriented outcomes.

9. The integration of concepts and methods from social and ecological disciplines yielded key insights into the dynamics of socio-ecological systems in the agricultural frontier, with important implications for conservation planning. A mix of top-down, regulatory approaches and bottom-up interventions aimed at changing landholders behaviour may be needed to foster land-use transitions towards more balanced conservation and production outcomes.

The empirical evidence presented in this thesis indicates that three types of land-use transitions contributes towards reconciling cattle production and bird conservation in Chaco

agricultural frontiers. Moreover, my findings allow identifying planning and policy actions that may foster these transitions.

The transition from low to intermediate-intensity systems has the potential to significantly increase cattle production outcomes without reducing bird diversity (Fig. 5.2, right-pointing arrow). A necessary pre-condition for traditional landholders to implement silvopastoral systems entails securing their access and tenure of land, so they can safely invest human and financial capital in the selective clearing of the forest understory and the cultivation of high-yielding pastures. Non-governmental organizations (NGOs) and peasant associations have been increasingly asking the provincial government to grant land titles to traditional landholders in the last years (REDAF 2012). In parallel, rural extension agencies have been working in facilitating access to seeds of high-yielding grasses (e.g. Panicum maximum) and training landholders in the utilization of light machinery such as rollerchoppers (Kunst et al. 2012) to selectively clear the forest understory. Increasing the adoption of silvopastoral practices among traditional landholders will require an intensification of current efforts by NGOs and rural extension agencies. In addition, it will require complementing the focus on facilitating access to natural and physical capital with a focus on conserving the cultural capital of traditional landholders (i.e. pro-conservation identities, norms and knowledge).

The transition from high to intermediate-intensity systems has the potential to significantly increase conservation outcomes without reducing cattle yields (Fig. 5.2, upward-pointing arrow). One of the main barriers to promote this land-use transition relates to how are decisions to develop total forest clearings usually made. The strategy of landholders in high-intensity systems usually involves maximizing economic returns from agricultural production in the short-term, selling the cleared lands and buying new lands to clear (Seghezzo et al. 2011). This pervasive behaviour can only be counteracted by creating more stringent land-use regulations, for example, prohibiting forest clearing in lands marginal for agriculture as part of the National Forest Law (Paruelo et al. 2011). For those landholders without this pervasive behaviour, native tree planting may represent a cost-effective option to restore cattle productivity on already cleared lands. Economic incentives in the form of payments for ecosystems services may further motivate profit-maximizing landholders to

plant native trees (Pagiola et al. 2007). Designing payment schemes will require increased research efforts for the ecological and economic valuation of ecosystem services provided by silvopastoral systems. Finally, raising awareness of the negative consequences of high-intensity systems on native avifauna through media campaigns may trigger positive attitudes among landholders towards native tree planting on cleared lands.

The set-aside of remnant forest fragments in landholdings with intermediate and highintensity systems is critical for the long-term conservation of forest specialist bird species, and for the regeneration of native trees in the grazing matrix (Fig. 5.2, left-pointing arrow). Provincial legislations already mandate the protection of native forest reserves over a variable (20-50%) proportion of the landholding area; however, these regulations are weakly enforced in practice and therefore, compliance is very low (Seghezzo et al. 2011). National universities are working towards the improvement of satellite-based monitoring of forest area within landholdings in order to provide the technical means for a more effective enforcement of native forest reserves (Volante et al. 2011). On the other hand, bottom-up incentives for forest conservation such as ecotourism and birdwatching may represent an increasingly important land-use option for landholders as public demand for observation of Chaco fauna is increasing (Seghezzo et al. 2011). Beyond economic incentives, the internalization and peer enforcement of pro-conservation norms among landholders provides the best hope for the long-term conservation of native ecosystems (Stobbelaar et al. 2009). Chaco landholders ascribed importance to the opinion of peers and the public in the formation of their forest conservation intentions. Therefore, raising public awareness about the need to conserve remnant forests within landholdings may create the social pressure required for the internalization of pro-conservation norms among landholders.

High conservation outcomes Low production outcomes

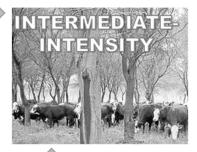
• Grant property rights to secure land tenure

• Facilitate access to machinery and seeds

• Promote the diffusion and strengthening of existing pro-conservation norms and identities

High conservation outcomes
High production outcomes





- Prohibit total forest clearing on marginal lands
- Provide incentives for native tree planting
- Raise awareness about the negative consequences of high-intensity systems on native avifauna.



Low conservation outcomes High production outcomes

Mandate forest reserves within landholdings

• Promote alternative land-uses (e.g. bird watching)

• Exert social pressure in favour of forest conservation so that it is internalized and becomes peer enforced

FIGURE 5.1. LAND-USE TRANSITIONS THAT MAY CONTRIBUTE TO RECONCILING CATTLE PRODUCTION AND CONSERVATION OBJECTIVES IN CHACO AGRICULTURAL FRONTIERS AND THE POLICY AND PLANNING ACTIONS THAT MAY FACILITATE THESE LAND-USE TRANSITIONS.

10. Improving conservation outcomes in agricultural frontier landscapes in the Argentine Chaco requires increased research efforts. Future research should adopt and refine inter and trans-disciplinary approaches if it is to inform the design of effective interventions to halt biodiversity loss in the Chaco region.

Reconciling conservation and production objectives on agricultural frontier landscapes is an increasingly challenging task for conservation research and planning. Therefore, it will require the investment of more resources and better approaches to improve our understating of biodiversity-agriculture relationships and to inform land-use planning and policy. This thesis sets the stage for multiple research directions that should be prioritized in Chaco agricultural frontiers and similar socio-ecological contexts in order to increase the effectiveness of conservation efforts in agricultural landscapes. These are:

- Trade-off models could be further applied to assess the impacts of agricultural production on multiple conservation objectives. Taxa other than birds such as plants, arthropods and mammals should be assessed for their responses to agricultural intensification. Where possible, such assessments should be based on primary data collected over multiple seasons and years.
- Trade-offs between agricultural production and regulatory ecosystem services such as
 pollination and biological control should be assessed to evaluate the sustainability and
 multifunctionality of land-use systems.
- Social studies are needed to evaluate the preferences of stakeholders for the different combinations of production and conservation outcomes along the trade-off curve.
 This knowledge will be critical for the design of socially fair and legitimate land-use planning and policies.
- Long-term research projects integrating social and ecological disciplines will be
 needed to assess temporal changes in the biodiversity value of land-use systems, for
 example, in response to the intensification of silvopastoral systems. Longitudinal
 studies could be designed to assess changes in the identities, norms and attitudes of
 landholders regarding biodiversity and land-use, for example, in response to
 behaviour change interventions.
- Social surveys should be designed to collect potential responses of landholders to different policies aimed at producing more conservation-oriented outcomes. These responses could be used to predict future land-use change under alternative policy

scenarios. Finally, trade-off functions could be integrated into spatially-explicit landuse scenarios to explore potential impacts of policy interventions on biodiversity and agricultural productivity.

In addition to fostering research in the above directions, I plan to work in the design and implementation of the interventions recommended in this thesis. Therefore, I will be involved in the following actions:

- Running of workshops with environmental non-governmental organizations and rural extension agencies with the purpose of establishing networks and forums for the diffusion of pro-conservation norms among landholders.
- Writing and publication of reports in Spanish summarizing the main findings of his
 thesis and making this available to landholders and other decision-makers (i.e. policymakers, planners). These reports will be oriented towards raising awareness about the
 need to foster the land-use transitions described in Conclusion statement #9 if we are
 to reconcile bird conservation and cattle production outcomes in the agricultural
 frontier.
- Formation of inter- and trans-disciplinary research teams and networks to increase our capacity to increase our knowledge of the socio-ecological dynamics of the Dry Chaco region and produce policy-relevant information to mitigate biodiversity loss.

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APPENDIX A

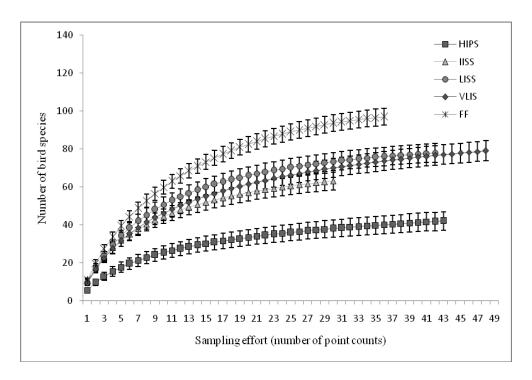


FIGURE A1. ACCUMULATION CURVES OF BIRD SPECIES WITH INCREASING SAMPLING EFFORT. NOTE THAT ALL CURVES ASYMPTOTE, INDICATING THAT SPECIES ASSEMBLAGES WERE EXHAUSTIVELY SAMPLED IN ALL TYPES OF PRODUCTION SYSTEMS. ABBREVIATIONS: VLIS: VERY LOW-INTENSITY SYSTEMS; LISS: LOW-INTENSITY SILVOPASTORAL SYSTEMS; IISS: INTERMEDIATE-INTENSITY SILVOPASTORAL SYSTEMS; HIPS: HIGH-INTENSITY PASTORAL SYSTEMS.

TABLE A1. LIST OF SPECIES RECORDED, CLASSIFIED ACCORDING TO FUNCTIONAL ATTRIBUTES AND RESPONSE TYPES.

| | Functional § | Functional groups | | onse type ^c |
|-----------------------|----------------------------|-------------------------------------|---------------------|------------------------|
| Scientific name | Feeding guild ^a | Habitat affiliation ^b | Understory clearing | Total clearing |
| Suiriri suiriri | Ins | OF | I | D |
| Molothrus bonariensis | Ins | O | I | I |
| Zenaida auriculata | Gra | O | I | I |
| Falco femoralis | Car | O | I | I |
| Polyborus plancus | Car | OF | S | I |
| Pitangus sulphuratus | Omn | OF | S | S |

| Buteo polysoma | Car | О | S | S |
|----------------------------|-----|----|---|---|
| Columbina picui | Gra | О | I | I |
| Molothrus badius | Gra | OF | I | I |
| Coragyps atratus | Car | OF | S | I |
| Rhea americana | Omn | О | S | I |
| Columba maculosa | Gra | О | I | I |
| Buteo magnirostris | Car | O | S | I |
| Theristicus melanopis | Omn | O | S | I |
| Guira guira | Omn | O | I | I |
| Mimus saturninus | Ins | O | I | I |
| Heterospizias meridionalis | Car | O | I | I |
| Myiopsitta monacus | Gra | OF | I | I |
| Saltraticula multicolor | Gra | OF | I | I |
| Coryphospingus cucullatus | Gra | OF | I | I |
| Zonotrichia capensis | Gra | OF | I | I |
| Sicalis luteola | Gra | OF | I | I |
| Troglodytes aedon | Ins | OF | S | I |
| Polioptila lactea | Ins | OF | D | D |
| Phacellodomus silbilatrix | Ins | OF | S | D |
| Coryphistera alaudina | Ins | OF | I | D |
| Asthenes baeri | Ins | OF | S | D |
| Pseudoseisura lophotes | Ins | OF | S | S |
| Nothoprocta cinerascens | Omn | OF | S | S |
| Falco peregrinus | Car | O | S | I |
| Tyrannus melancholicus | Ins | OF | S | I |
| Embernagra platensis | Gra | O | S | I |
| Spartanoica maluroides | Ins | O | S | I |
| Bubulcus ibis | Ins | O | S | I |
| Xolmis irupero | Ins | O | I | S |
| Stigmatura budytoides | Ins | F | D | D |

| Paroaria coronata | Gra | OF | I | D |
|-------------------------------|-----|----|---|---|
| Furnarius rufus | Ins | OF | S | D |
| Pyrocephalus rubirus | Ins | OF | S | S |
| Pachyramphus polychopterus | Ins | F | S | S |
| Hylocharis chrisura | Nec | OF | S | D |
| Icterus cayennensis | Ins | OF | I | S |
| Saltataor aurantirostris | Gra | OF | S | D |
| Geranoaetis melanoleucus | Car | O | S | S |
| Melanerpes cactorum | Ins | F | I | D |
| Piranga flava | Fru | F | S | D |
| Lepidocolaptes angustirostris | Ins | F | S | D |
| Cyclaris gujanensis | Ins | F | S | D |
| Furnarius cristatus | Ins | OF | S | D |
| Knipolegus hudsoni | Ins | OF | S | S |
| Cathartes aura | Car | OF | S | S |
| Parula pitiayumi | Ins | F | D | D |
| Polioptila dumicola | Ins | F | D | D |
| Sitlasomus griseicapillus | Ins | F | S | D |
| Piculus chrysoclorus | Ins | OF | S | D |
| Serpophaga subcristata | Ins | F | S | D |
| Amazona aestiva | Gra | F | S | D |
| Phylloscartes ventralis | Ins | F | S | D |
| Columbina talpacoti | Gra | F | S | D |
| Melanerpes candidus | Ins | OF | S | S |
| Aratinga acuticaudata | Gra | F | D | D |
| Herpetotheres cachinnans | Car | OF | S | S |
| Drymornis bridgesii | Ins | F | S | D |
| Campephilus leucopogon | Ins | OF | S | D |
| Nystalus maculatus | Ins | F | S | S |
| Camptostoma obsoletum | Ins | F | S | S |

| Chunga burmeisterii | Omn | OF | S | S |
|------------------------------------|-----|----|---|---|
| Phacellodomus rufifrons | Ins | F | S | D |
| Milvago chimango | Car | OF | S | S |
| Elanus leucurus | Car | OF | S | S |
| Serpophaga nigricans | Ins | F | S | D |
| Cyanocorax chrysops | Omn | F | D | D |
| Thraupis sacaya | Fru | F | D | D |
| Turdus amaurochalinus | Fru | F | S | D |
| Passerina brissoni | Gra | F | S | D |
| Turdus rufiventris | Fru | F | S | S |
| Taraba major | Ins | F | D | D |
| Ramphastos toco | Omn | F | S | D |
| Psarocolius decumanus | Omn | F | S | D |
| Knipolegus aterrimus | Ins | F | D | D |
| Pyrrhura frontalis | Gra | F | S | D |
| Thraupis bonariensis | Fru | F | D | D |
| Thlypopsis sordida | Fru | F | S | D |
| Sarcorampuus papa | Car | OF | S | S |
| Arremon flavirostris | Gra | F | S | D |
| Circus cinereus | Car | OF | S | S |
| Ortallis canicollis | Fru | F | D | D |
| Xiphocolaptes major | Ins | F | S | D |
| Campylorhamphus trochilirostris | Ins | F | S | D |
| Crotophaga ani | Omn | OF | D | D |
| Euphonia chlorotica | Fru | F | S | D |
| Buteogallus urubitinga | Car | OF | S | S |
| Vireo olivaceus | Ins | F | S | D |
| Mirmorchilus strigilatus | Ins | F | D | D |
| Busarellus nigricollis | Car | OF | S | S |

| Agelaius thilius | Ins | OF | D | D |
|--------------------------------|-----|----|---|---|
| Certhiaxis cinnamomea | Ins | F | S | D |
| Todirostrum plumbeiceps | Ins | F | S | D |
| Aramides ipecaha | Omn | OF | S | S |
| Saltator coerulescens | Gra | F | S | D |
| Sublegatus modestus | Ins | F | S | D |
| Knipolegus striaticeps | Ins | OF | S | S |
| Phyllomyas uropigialis | Ins | F | S | D |
| Hemitrichus margaritaceiventer | Ins | F | S | D |
| Crypturellus tataupa | Gra | F | S | D |
| Myophobus fasciatus | Ins | F | S | D |
| Picumnus cirratus | Ins | F | S | S |
| Phaeomyias murina | Ins | F | S | D |
| Paroaria capitata | Gra | OF | S | S |
| Elaenia parvirostris | Ins | F | S | S |
| Tiaris obscura | Gra | OF | S | D |
| Pheucticus aureoventris | Gra | F | S | D |
| Lathroticcus euleri | Ins | F | S | D |
| Hirrundinea ferruginea | Ins | F | S | S |
| Penelope obscura | Fru | F | D | D |
| Crotophaga major | Omn | OF | D | D |
| Trogon curucui | Fru | F | S | D |
| Chlorospingus ophtalmicus | Fru | F | S | D |
| Pyrrhomyias cinnamomea | Ins | F | S | D |

^a Guild abbreviations: Gra: Granivore, Ins: Insectivore, Car: Carnivore, Omn: Omnivore, Fru: Frugivore. ^b Habitat affiliation abbreviations: F: occurs in forest habitats, O: occurs in open habitats, OF: occurs in both forested and open habitats. ^c Response abbreviations: D: decreased, S: stable, I: increased.

TABLE A2. CONTENT AND DESIGN OF THE SURVEY INSTRUMENT: SEMI-STRUCTURED INTERVIEWS DELIVERED IN ONE-ON-ONE MEETINGS WITH RANCH LANDOWNERS. QUESTIONS ARE PRESENTED IN ENGLISH (RIGHT), SPANISH (LEFT) AND IN ORDER OF ADMINISTRATION.

Ranch characteristics

- 1. How many hectares does this ranch cover? What types of production system do you develop in this ranch? What is the relative area of each?
- 2. How many cattle heads are in this ranch as an annual average? And now?
- 3. What is the average live weight at sale of the cattle you raise here? How many kilograms of meat yield each cattle head?
- 4. What is the main source of food for the cattle? Is it implanted pastures or natural fodder (native grasses, shrubs, etc.)?
- 5. How do you manage the pastures? How many species do you use?
- 6. Do you make pasture rotations? Describe the rotations scheme. How long are fallow periods?
- 7. Do you use fertilizers or pesticides?

 Describe the input applications scheme.

 How many litres of agrochemicals do you buy per month?
- 8. Do you use machinery? What type of machinery? How often do you use it?
- 9. Did you habilitate plots for cattle production? How did you do it (e.g. understory clearing, forest clearing, prescribed burning)? What type of machinery did you use?
- 10. Do you use timber products from the ranch? And non-timber forest products? Describe.

Ranch trajectory

1. What types of production systems were developed in this ranch in the past? For how long?

Características de la finca

- 1. ¿Cuántas hectáreas cubre esta finca? ¿Qué tipos de sistema de producción desarrolla usted en esta finca? ¿Cuál es el área relativa que ocupa cada sistema?
- 2. ¿Qué promedio anual de cabezas de ganado hay en esta finca? ¿Y en este momento?
- 3. ¿Cuál es el peso vivo a la venta promedio del ganado que usted cría aquí? ¿Cuántos kilos de carne produce cada cabeza de ganado?
- 4. ¿Cuál es la principal fuente de alimento para el ganado? ¿Es pastura implantada o forraje natural (pastos, arbustos nativos, etc.)?
- 5. ¿Qué tipo de manejo hace usted de las pasturas? ¿Cuántas especies utiliza?
- 6. ¿Hace usted rotar las pasturas? Describa el esquema de rotaciones. ¿Qué duración tienen los periodos de barbecho?
- 7. ¿Usa usted fertilizantes o pesticidas?
 Describa el esquema de aplicación.
 ¿Cuántos litros de agroquímicos compra usted por mes?
- 8. ¿Usa usted maquinaria agrícola? ¿Qué tipo de maquinaria? ¿Con qué frecuencia la utiliza?
- 9. ¿Habilitó usted las parcelas para la producción de ganado? ¿Cómo lo hizo (ej. desbajerado, desmonte completo, quemas prescriptas)? ¿Qué tipo de maquinaria utilizó para tal fin?
- 10. ¿Usa usted los recursos maderables? ¿Y otros productos del monte?

Trayectoria de la finca

1. ¿Qué tipos de sistemas de producción fueron desarrollados en esta finca en el pasado? ¿Por cuánto tiempo?

- 2. When agricultural plots were first put under production? How many years elapsed since deforestation?
- 3. How do you plan to use this land in the next 3/5 years? Why?
- 4. How do you plan to use this land in the next 10 years? Why?
- 5. How do you think the land-use planning proposal will affect your land-use plans?

Rancher profile

- 1. What is your role in this agricultural enterprise?
- 2. How old are you?
- 3. Where were you born?
- 4. Where have you resided during the last 20 years? Where do you reside now?
- 5. If you came to the area in recent years, what were the motives for your inversion and establishment in this area?
- 6. How would you describe this type of enterprise? Is the ranch run by your family alone or is it run by a company, corporation, etc.?
- 7. Under what legal conditions are you using this land? Do you own or lease the land you are using? For how long?
- 8. In what type of production system did you work before? Where? For how long?
- 9. Are you assisted by professionals about ranching management decisions? If yes, what type of assistance do you receive?
- 10. Are you enrolled or affiliated to any rancher organization? If yes, which one? What is the mission of that association?

- 2. ¿Cuándo fueron habilitadas las parcelas? ¿Hace cuánto se hizo el desmonte?
- 3. ¿Cómo planea usted usar estas tierras en los próximos 3 a 5 años? ¿Por qué?
- 4. ¿Cómo planea usted usar estas tierras en los próximos 10 años? ¿Por qué?
- 5. ¿Cómo cree usted que la propuesta de ordenamiento territorial va a afectar a sus planes de uso de la tierra?

Perfil del productor

- 1. ¿Cuál es su función en este emprendimiento agrícola?
- 2. ¿Qué edad tiene usted?
- ¿Dónde nació usted?
- 4. ¿Dónde ha residido en los últimos 20 años? ¿Dónde reside usted ahora?
- 5. Si usted vino al área en años recientes, ¿cuáles fueron los motivos de su inversión y establecimiento en esta área?
- 6. ¿Cómo describiría usted este tipo de emprendimiento? ¿Esta finca es manejada por una familia, por una compañía o algún otro tipo de corporación?
- 7. ¿En qué condiciones legales usa usted esta tierra? ¿Es usted dueño de esta tierra o la arrienda? ¿Hace cuánto tiempo?
- 8. ¿En qué tipo de sistemas productivos ha trabajado usted en el pasado? ¿Dónde? ¿Por cuánto tiempo?
- 9. ¿Está usted asesorado por profesionales con respecto a las decisiones en el manejo agrícola? Si lo está, ¿qué tipo de asesoramiento recibe?
- 10. ¿Está usted enrolado o afiliado a alguna organización de productores? Si lo está, ¿en cuál? ¿Cuál es el objetivo de esa organización?

APPENDIX B

Bird survey methods were designed on the basis of results from pilot bird surveys in the study area. I piloted three widely used bird survey methods to compare its ability to yield precise estimates of bird richness across the intensification gradient. These were: i) transect counts, ii) open-radius point counts, and iii) 25 m fixed-radius point counts. The difference between these methods is that transect counts allow for larger area coverage than point counts, while point counts are better suited for relating bird diversity indicators and structural attributes of the environment (Rosenstock et al. 2002). The difference between open and fixed-radius counts reside in the trade-off between detectability and detection range, which varies among habitat types. Open-radius counts allow for larger detection range in open habitats and fixedradius counts reduce problems associated with detectability in closed habitats (Rosenstock et al. 2002). Using the three methods, I surveyed three sites in each of two contrasting habitat types: closed-canopy forests and pastures on cleared land. The number of counts in the pilot phase amounted to 3 (survey methods) \times 2 (habitat types) \times 3 (sites) = 18. I compared the precision (i.e. variance in bird richness among sites of the same habitat type, Gregory et al. 2004) of estimates among the three bird survey methods. Richness estimates obtained through 25 m fixed-radius point counts showed the smallest variance among sites in the two habitat types. As 25 m fixed-radius point counts yielded the most precise estimates among the methods tested, it was selected for subsequent data collection. In an independent study undertaken in the Dry Chaco region of Argentina, Macchi & Grau (2013) chose a similar method (i.e. 20 m fixed-radius point counts) to assess bird species richness and abundance across a gradient of land-use intensity. Therefore, employing a commonly used and precise method of bird sampling increased the comparability and confidence of my richness estimates.

Dry Chaco forests show seasonal variation of climatic and environmental variables, with four months of marked water deficit (June to October) and four months of heavy rains (November to March) (Minetti 1999). Bird counts spanned across four months of the year (from May to August), which means that a significant proportion of intra-annual variation in environmental variables was captured by the survey. The year of sampling (2010) did not show any anomalies in terms of rainfall and temperature, and therefore can be regarded a representative year (González et al. 2012). Bird counts were not undertaken during the reproductive season (from December to March) for two main reasons. First, the reproductive season coincides

with a period of weather instability and heavy rains in the study area (monsoon regime), which frequently causes flooded roads and impedes accessing to landholdings. Second, logistical and budgetary limitations impeded sampling for a longer period and/or undertaking an additional field trip. The absence of repeated counts in different months and years precluded the detection of seasonal and inter-annual variations in the richness and composition of bird assemblages in the study area. For this reason, the results presented in this chapter are accurate only to describe changes in the distribution and density of bird species during the non-reproductive season of Chaco avifauna.

APPENDIX C

I portrayed two contrasting hypotheses for the relationship between bird species richness and cattle yields in Fig. 2.2a based on the literature review of the land-sparing/land-sharing debate presented in Chapter 1 and the Introduction section of Chapter 2. These hypotheses derive from the analysis of Green et al. (2005) of the trade-off between conservation and production targets in agricultural lands. In their conceptual and analytical framework, the relative utility of land-sharing and land-sparing for a particular context depend on the shape of the trade-off function (reviewed by Mattison & Norris 2005 and Fischer et al. 2008). This framework proposes that the conservation target has either a declining phase at low land-use intensity and a stable phase at high land-use intensity (convex function, land-sparing best) or a stable phase at low land-use intensity and a declining phase at high land-use intensity (concave function, land-sharing best). In this study, I adopted the framework proposed by Green et al. (2005) and tested the two contrasting hypotheses. For this reason, I fitted different types of non-linear models (polynomial, exponential, logarithmic) to my empirical data to test whether the relationship between bird richness and cattle yields was best described by a concave or convex function. The best fit (as indicated by r²) was obtained using a second-order polynomial function both for richness and yields expressed in absolute and relative numbers.

For the reasons described above, I did not test the fit of non-linear models with more than two phases (e.g. sigmoidal function) or with abrupt changes in the response variable (e.g. step or threshold functions). However, other non-linear models were shown to provide better fit to the data. For example, a Boltzmann sigmoidal model had a better fit to the data for richness and yields expressed in absolute numbers (r^2 =0.638 [Fig. C1a] compared to r^2 =0.574 for a second-order polynomial model [Fig. 2.2b]) and for these variables expressed as relative to their potential (r^2 =0.820 [Fig. C1b] compared to r^2 =0.565 for a second-order polynomial model [Fig. 2.2c]). The shape of these better-fitting functions reflect a pattern of avian responses to increasing land-use intensity similar to that described in the Results section of Chapter 2, which can be characterized as follows: i) bird species richness maintains stable at low and intermediate land-use intensities, and ii) bird species richness sharply declines beyond intermediate land-use intensities. The new information provided by a sigmoidal

model compared to a polynomial one relate to the stability of bird species richness at high levels of land-use intensity, which suggests that the system reaches an alternative stable state when forests are totally converted to pastures.

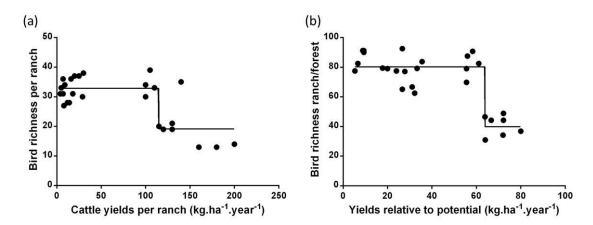


Figure C1. Empirical data fitted to a Boltzmann sigmoidal model to describe the relationship between bird species richness and cattle yields across the intensification gradient for these variables expressed as absolute numbers (a) or relative to their potential (b).

APPENDIX D

TABLE D1. FACTOR LOADINGS (I.E. CORRELATIONS BETWEEN ITEM AND CONSTRUCT SCORES) AND SUMMARY STATISTICS FOR ITEM SCORES AND T-VALUE FOR THE COMPARISON OF MEAN SCORE VS. SCALE MID-POINT (3)

| Social psychological construct | Questionnaire item statement and code | Factor loadings | Ques | Questionnaire item score | | |
|--------------------------------|--|-----------------|------|--------------------------|-----------|--|
| Social psychological construct | Social populotogical construct Questionnaire item statement and code | | Mean | SD | t value | |
| Intention | I) Intention to conserve forest fragments to 2013 | | 3.32 | 1.099 | 2.428** | |
| Problem awareness | PA1) Deforestation as an environmental problem | 0.73 | 3.59 | 0.815 | 5.954*** | |
| | PA2) Deforestation as a national-wide problem | 0.55 | 3.07 | 0.951 | 0.637 | |
| | PA3) Deforestation as a social problem | 0.08 | 3.06 | 1.196 | 0.406 | |
| Awareness of consequences | AC1) Effect of forest clearing on native fauna | 0.29 | 3.87 | 1.078 | 6.639*** | |
| | AC2) Effect of forest clearing on local climate | 0.54 | 3.63 | 1.006 | 5.183*** | |
| | AC3) Effect of forest clearing on soil fertility | 0.90 | 3.62 | 1.023 | 4.981*** | |
| Perceived behavioural control | PBC1) Landholding area as a barrier for materializing own intentions | 0.06 | 2.93 | 1.124 | -0.539 | |
| | PBC2) Government regulations as a barrier for materializing own intentions | 0.87 | 4.25 | 0.799 | 12.904*** | |
| | PBC3) Forest clearing costs as a barrier for materializing own intentions | 0.61 | 4.35 | 0.842 | 13.246*** | |
| Social norm | SN1) Influence of other farmers on forest management decisions | 0.69 | 3.18 | 0.772 | 1.886* | |
| | SN2) Influence of family and friends on forest management decisions | 0.86 | 3.31 | 1.136 | 2.241** | |
| | SN3) Influence of the media on forest management decisions | 0.25 | 3.22 | 0.709 | 2.565** | |

| Self-identity | SI1) Identity of farmer as efficient land-user | 0.63 | 2.04 | 0.721 | -10.927*** |
|----------------|---|------|------|-------|------------|
| | SI2) Identity of farmer as steward of the land | 0.51 | 3.76 | 0.794 | 7.942*** |
| | SI3) Identity of farmer as commercial food producer | 0.44 | 2.69 | 1.213 | -2.100** |
| Past behaviour | PB1) Degree of transformation of forest strips from 2009 to 2011 | 0.81 | 5.50 | 1.072 | 15.384*** |
| | PB2) Degree of transformation of forest fragments from 2009 to 2011 | 0.58 | 4.54 | 1.450 | 5.938*** |
| Personal norm | PN1) Obligation to clear forest fragments due to egocentric arguments | 0.26 | 3.35 | 1.033 | 2.817*** |
| | PN2) Obligation to conserve forest due to biocentric arguments | 0.45 | 3.66 | 1.288 | 4.235*** |
| | PN3) Obligation to conserve forests due to property rights | 0.50 | 3.13 | 1.196 | 0.913 |
| Attitude | AT1) Aesthetic value of forest fragments | 0.43 | 3.96 | 0.854 | 9.230*** |
| | AT2) Regulatory value of forest fragments | 0.71 | 4.09 | 0.640 | 14.015*** |
| | AT3) Provisioning value of forest fragments | 0.17 | 3.87 | 0.689 | 10.384*** |
| | | | | | |

^{*} p<0.1, **p<0.05, ***p<0.01

TABLE D2. STATEMENTS AND SCALES OF ITEMS OF THE QUESTIONNAIRE

| Code | Statement | 5-point Likert scale |
|------|---|---|
| I | My intention to maintain forest remnants undisturbed in my landholding for the next year is | Very strong to very weak |
| PA1 | Forest clearing for agriculture harms the environment | |
| PA2 | Forest clearing for agriculture is the main environmental issue of Argentina | Strongly agree to strongly disagree |
| PA3 | Forest clearing for agriculture displaces local people from rural areas | |
| AC1 | If I clear forest remnants, it is that many native species disappear | |
| AC2 | If I clear forest remnants, it is that weather becomes hotter and drier | Very likely to very unlikely |
| AC3 | If I clear forest remnants, it is soils become less fertile | |
| PBC1 | Considering the size of my landholding, it is to conserve forest remnants in my landholding for the next year | |
| PBC2 | Considering government regulations, it is to conserve forest remnants in my landholding for the next year | Very easy to very difficult |
| PBC3 | Considering the costs of forest clearing, it is to conserve forest remnants in my landholding for the next year | |
| SN1 | Other farmers are of my intentions towards forest remnants in my landholding for the next year | Very |
| SN2 | My family and friends are of my intentions towards forest remnants in my landholding for the next year | supportive to very |
| SN3 | People on the media is of my intentions towards forest remnants in my landholding for the next year | unsupportive |
| SI1 | My role as a landholder is to be an efficient land-user | |
| SI2 | My role as a landholder is to be a steward of the land | Strongly agree to strongly disagree |
| SI3 | My role as a landholder is to be a commercial food producer | |
| PB1 | Between 2010 and 2012, forest strips in my landholding experienced transformations | Very intense |
| PB2 | Between 2010 and 2012, forest fragments in my landholding experienced transformations | to very light |
| PN1 | I feel obligated to clear remnant forests for increasing my welfare | Extremely to |

| PN2 | I feel obligated to conserve remnant forests to care for nature | not at all |
|-----|---|-----------------------|
| PN3 | I feel obligated to conserve remnant forests as I own this land | |
| AT1 | Considering their effect on agricultural yields, it is to conserve forest remnants in my landholding for the next year | Very |
| AT2 | Considering their effect on landscape beauty, it is to conserve forest remnants in my landholding for the next year | beneficial to very |
| АТ3 | Considering their effect on production stability, it is to conserve forest remnants in my landholding for the next year | detrimental |

TABLE D3. FREQUENCIES FOR QUALITATIVE ATTRIBUTES OF SURVEYED LANDHOLDINGS

| Variable | Levels | Frequency |
|--|--|-----------|
| Nearest locality to the farm | 1: Pampa del infierno | 25 |
| | 2: Juan José Castelli | 23 |
| | 3: Concepción del Bermejo | 21 |
| | 4: Miraflores | 20 |
| Type of organization of the | 1: Anonymous company | 3 |
| farm | 2: Family-run company | 19 |
| | 3: Family production unit | 67 |
| Level of access to external | 1: No external funding | 36 |
| funding | 2: Bank credit | 8 |
| | 3: Government subsidy or compensation | 33 |
| | 4: Credit and subsidy/compensation | 12 |
| Conservation category | 1: Type I: total clearing is allowed | 57 |
| | 2: Type II: only selective clearing is allowed | 32 |
| Land tenure condition | 1: De facto occupant | 0 |
| | 2: With occupation act | 4 |
| | 3: Allotee (with property rights but not land title) | 37 |
| | 4: De jure owner (with property rights and land title) | 48 |
| Intention to sell out the farm to 2013 | 1: Intention to sell all the farm | 1 |

| | 2: Intention to sell part of the farm | 17 |
|-----------------------------|--|----|
| | 3: No intention to sell | 72 |
| Intention to lease the farm | 1: Intention to lease all the farm | 1 |
| to 2013 | 2: Intention to lease part of the farm | 31 |
| | 3: No intention to lease | 57 |
| Farmer's place of birth | 1: Extra-regional (outside the Chaco region) | 7 |
| | 2: Regional (in the Chaco region) | 8 |
| | 3: Local (in a locality of the Chaco Impenetrable) | 74 |
| Farmer's place of residence | 1: Extra-regional (outside the Chaco region) | 0 |
| | 2: Regional (in the Chaco region) | 2 |
| | 3: Local (in a locality of the Chaco Impenetrable) | 39 |
| | 4: In the landholding | 48 |
| | | |

TABLE D4. SUMMARY STATISTICS FOR QUANTITATIVE ATTRIBUTES OF SURVEYED LANDHOLDINGS

| Variable | Mean | SD | Min | Max |
|---------------------------------------|-------|-------|-----|------|
| Number of persons working on the farm | 2.6 | 1.1 | 1 | 6 |
| Labour to consumer ratio | 0.6 | 0.3 | 0.2 | 1 |
| Number of participating forums | 1. | 1 | 0 | 4 |
| Total landholding area (ha) | 308.8 | 358.8 | 180 | 1764 |
| Landholding area covered by | | | | |
| Forests (ha) | 219.1 | 264.6 | 30 | 1313 |
| Cropland (ha) | 59.7 | 157.2 | 0 | 970 |
| Pastures (ha) | 34.5 | 56.7 | 0 | 300 |
| Farmer age | 47.5 | 12.8 | 25 | 75 |
| Number of formal education stages | 2.4 | 1.4 | 1 | 6 |
| Number of years in farming | 28.8 | 16.3 | 2 | 64 |
| Number of years in the landholding | 25.8 | 15.9 | 2 | 64 |