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The South American dry Chaco is a mosaic of woody vegetation and grasslands with high deforestation rates in recent decades. Considering forests and grasslands as the main natural habitats, we assessed the trade-offs between bird populations and agricultural production to compare the potential consequences of different land use strategies ('sharing', 'sparing', and intermediate) for populations of bird species sensitive to agriculture, while attaining a regional production target. We evaluated how populations responded to scenarios with different proportions of forest and grasslands, considering three reference states (100% forest, 80:20% and 50:50% forest and grasslands, respectively); and scenarios capable of meeting three after-farming scenarios, with land destined to reach a regional production target with three variations of forest:grasslands within spared land. We fitted curves to relate bird abundance to agricultural yield along a gradient of meat production intensity; and we classified bird species as 'losers' (if their populations were lower than the baseline population in the reference state, at any level of production) and 'winners' (if their current populations were higher than the baseline population). At the 'current' (c. 2010) level of regional agricultural production, we found a similar number of loser species maximized by land-sparing and land-sharing strategies; while intermediate strategies were the least favourable to balance production and bird populations. Under the most probable scenarios of increases in regional meat production, most loser bird species populations were maximized by a land-sparing strategy, suggesting that if meat production targets are going to increase in the region, this can be more efficiently achieved by combining well-protected forests and grasslands, and high-yielding mechanized agriculture (e.g. soybean). Our results highlight the importance of assessing all the important natural habitats (e.g. forests and grasslands) of a region to explore conservation strategies at a regional scale.

Keywords: sustainability science; land use change; ecological indicators; South America; semi-arid environment; land sparing; land sharing; conservation strategies

1. Introduction

Balancing food production and biodiversity conservation has become a major objective in applied ecological research. By comparing the potential effects on wildlife populations of land use schemes in which agriculture and biodiversity conservation objectives co-occur spatially (land sharing) to systems where highly productive agriculture is separated in the space from comparatively well-preserved areas (land sparing), it offers one way to assess

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the potential consequences of different land use schemes (Grau, Kuemmerle, & Macchi, 2013; Phalan, Balmford, Green, & Scharlemann, 2011a; Tscharntke et al., 2012). This conceptual framework has been tested in previous studies considering a single yield gradient, from one type of dominant 'natural' habitat (generally forest) to intensive productive systems.

Tropical and subtropical dry-forest and savannahs, including the dry Chaco, are among the biomes most threatened globally by agricultural expansion (Hansen et al., 2013; Lambin et al., 2013), and are typically characterized by a mosaic of natural and semi-natural land cover types, in which both forests and grasslands provide habitat for biodiversity (Adámoli, Senhauser, & Rescia, 1990; Eldridge et al., 2011). The few studies aiming to assess the balance between food production (mostly oriented to meat) and biodiversity in the Chaco (Grau, Gasparri, & Aide, 2008; Mastrangelo & Gavin, 2012) have largely ignored this variation within natural habitats.

Food production is a primary threat to biodiversity (Phalan, Balmford, Green &, Scharlemann, 2011a), primarily through degradation/deforestation process derived from land use changes (Lambin et al., 2013). To evaluate the balance between food production and biodiversity, species population densities are compared in different natural and productive land scenarios (Green, Cornell, Scharlemann, & Balmford, 2005). Using information on the agricultural productivity of these land cover types, these data can be used to build a density-yield function for each species, which can identify the land use design or strategy that maximizes the total population size, considering the combination of natural and productive land at any given target of food production. The original sparing/sharing model proposed by Green et al. (2005) incorporates two compartments: unfarmed land (e.g. forest) and farmland, where yields vary in the farmland compartment. This simple dichotomy, often represented by forests and agriculture, is replicated in most sparing/sharing studies. Here, we considered two 'reference' natural land cover categories (forests and grasslands) in different proportions of the landscape, as well as different systems of agricultural production with varying yields and habitat quality for birds.

Several authors suggest that, while present-day Chaco vegetation is largely dominated by woodlands, this could be the consequence of woody encroachment resulting from domestic livestock expansion in the early twentieth century, as the pre-European landscape was a mosaic of forests and open savannahs (Adámoli et al., 1990; Bucher & Huszar, 1999; Grau et al., in press; Morello & Saravia Toledo, 1959). The region experienced successive fluctuations between dry and humid periods during the Late Pleistocene and Holocene, with dry periods associated with reductions in forest cover and expansion of open areas (Iriondo & Garcia, 1993; May, Argollo, & Veit, 2008). Thus, a considerable proportion of the biota in the Chaco ecoregion could have evolved in landscapes more similar to savannahs rather than woodlands (Short, 1975). Recent analysis showed that far more dry Chaco birds are associated with grasslands than with woodlands (Torres, Gasparri, Blendinger, & Grau, 2014). While current conservation schemes in the area (e.g. National 'Forest Law', REDD+, Protected Areas policies) are largely forest-centred, recent analyses (Macchi, Grau, Zelaya, & Marinaro, 2013; Torres et al., 2014; Grau et al., in press) suggest that grasslands habitats also merit conservation. Our analysis specifically assesses the potential role of grasslands in a conservation scheme that also considers the balance with agriculture production.

Previous studies in the Chaco evaluated bird responses along a gradient from forest to different livestock systems, suggesting that planted pastures with remaining tree canopy (silvopastures) combined with protection of forest fragments was the strategy that would best balance meat production and bird diversity (Mastrangelo & Gavin, 2012;

Mastrangelo & Laterra, 2015). Silvopastures would represent an intermediately productive alternative for the region, between extensive livestock (land sharing) and high yield agriculture (land sparing). However, adding soybean crops to the forest-agriculture gradient indicated that at the community and ecological guild levels the combination of soybean crops and forest areas was the best strategy to conserve forest birds; while along the grasslands-agriculture gradient an intermediate production strategy with silvopastures was optimal (Macchi et al., 2013). Here we go further, integrating two natural habitats and all the most representative land uses of the region, considering each species' response to assess the production–conservation trade-off.

We used relative abundance as a proxy of bird population densities along a yield gradient for the dry Chaco, and developed scenarios with different proportions of forest and grasslands in the reference state and on spared land. Our aim was to explore the consequences of different combinations of agricultural and non-agricultural land use for bird populations, along a range of plausible agricultural production targets. Our specific research objectives were: (1) to estimate the relative abundance of bird species in each natural habitat, and along a gradient of livestock and agricultural production, expressed as meat yield, (2) to fit abundance–yield curves for each bird species along the yield gradients, (3) to identify the strategy that maximizes the populations of birds for each species for different farming scenarios in which the forest–grasslands proportions varied, for current and future estimates of production (2020) and (4) to describe bird species population changes as influenced by the different reference states and scenarios.

2. Methods

2.1. Study area and sampling design

The Gran Chaco ecoregion covers a total of ~120 million hectares in Argentina, Bolivia and Paraguay. This study was conducted on the Northern dry Chaco of Argentina (22° S to 27° S; 59.5° W to 65° W), considered as part of the semi-arid subregion of the Argentine Chaco. The area includes the west of Formosa and Chaco Provinces, the east of Salta Province and the north of Santiago del Estero Province; spanning over 17 million hectares (Figure 1). The area has a subtropical seasonal climate. Mean annual temperature ranges between 20°C and 23°C, with average temperatures of 28°C and 16°C for the hottest (January) and coldest (July) months, respectively. Annual rainfall ranges between 500 and 900 mm, with a strong pattern of monsoonal precipitation seasonality in which ~80% of the rain falls between November and March; and the winter and early spring are characterized by water deficit (Minetti, 1999).

Forest is the most widespread land cover category presently occupying ~75% of the study area according to different studies (Clark, Aide, Grau, & Riner, 2010; Gasparri & Grau, 2009). Grasslands have a much smaller extension (~7% of the study area). There are ~1500 extensive livestock operations named *puestos* spread across the area, mostly in forested areas (Grau et al., 2008), each of them estimated to impact approximately 5000 hectares of forest (~43% of the study area) through human activities like livestock grazing, wood extraction and hunting (Morello & Saravia Toledo, 1959). *Puestos* produce severe vegetation and soil transformation within a 500 m radius from the artificial water ponds next to inhabited areas (Macchi & Grau, 2012). Intensive agricultural systems are difficult to distinguish from each other using satellite information: altogether crops and planted pastures occupy ~10% of the study area (Clark et al., 2010; Gasparri & Grau, 2009).

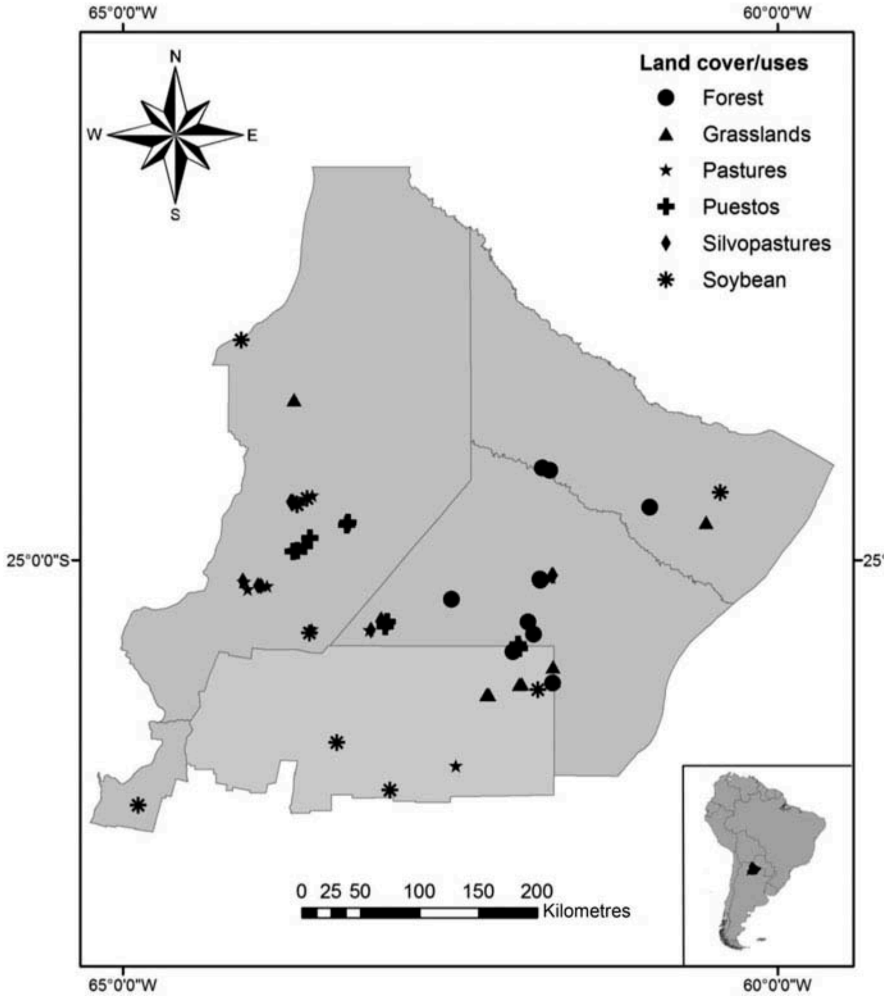

Figure 1. Study area corresponding to the northern sector of the Argentine dry Chaco. Bottom left Inset shows study area location in South America.

We surveyed the relative abundance of bird species in six land use categories of the dry Chaco: (1) protected forests, (2) natural grasslands, (3) woodlands with extensive livestock (*puestos*), (4) silvopastures (planted pastures under an open canopy of remaining trees), (5) planted pastures with few or no trees and (6) soybean crops. Fieldwork was conducted in nine fieldtrips between 2009 and 2011, distributed in different sectors of the study area during the winter season for logistical reasons: intensive rains in summer block the roads. We sampled 10 plots in each land use. Each plot was 1 km^2 square. Within each plot we registered presence/absence data in 9 point counts of birds separated by 300 m each, resulting in a relative abundance from 0 to 9. Plots were distanced by a minimum of 5 km^2; we did not to make surveys in more than two plots for each land use systems within each field trip to minimize spatial autocorrelation. Each point count lasted 10 minutes, during which we recorded the presence of bird species, and from this we calculated the relative abundance of the species in each plot (0 to 9). Observers waited 5 minutes in each point count before starting each survey. All point counts occurred during the first two hours after dawn. We counted all individuals seen or heard within a radius of 20 m around each point, a radius small enough to ensure visual detection of all the species present at each point count. Individual birds flying through were not considered within the sampling. We considered the relative abundance as a proxy of bird density (Stephens, Pettorelli, Barlow, Whittingham, & Cadotte, 2015). We considered relative abundance an intermediate between presence/absence and density data, suitable for regional scale analysis and curve fitting statistical analysis.

2.2. Current and potential agricultural production in the dry Chaco

We estimated regional production based on each land use area and meat yield, assuming all forage goes to feed cattle and all soybeans goes to feed pork. Extensive livestock systems such as the *puestos* could be considered as a template for 'land sharing' in the dry Chaco (although they were created without conservationist purposes), in which free-ranging livestock forage in semi-natural vegetation. Planted pastures (whether silvopastoral systems or pastures without trees) are intermediate yield options, with silvopastures having higher bird diversity. Finally soybean crops (mostly used for pig feed) are the most productive agriculture type in the region, producing twice as much meat per hectare as the most intensive pasture-based systems (Macchi et al., 2013).

We estimated the forage production of each land use type based on literature records of the dry Chaco (Macchi et al., 2013). Most estimates were based on systematic forage harvest expressed as dry matter for one year. Protected forests and natural grasslands were assumed to have zero production although in some cases there is very low density of livestock within the national parks and reserves. Although there are other livestock (e.g. goats), cattle is by far the principal regional meat product (Rearte, 2010), and thus we assumed all the forage production was directed to cattle meat production. Meat production of the different livestock land uses was computed as follows:

Secondary production (SP) = $0.08 \times 0.6 \times \text{FB}$

where

SP = meat production (kg ha^{-1} yr^{-1})

0.08 = conversion rate from vegetable to cattle meat (Deregibus, 1988; Martin, 2005)

0.6 = proportion of the plant consumed by cattle (Deregibus, 1988; Martin, 2005)

Forage biomass (FB) = kg ha^{-1} yr^{-1}

In the case of soybean we used a conversion rate of 5.5 from kilograms of soybean to kilograms of pork meat (Smil, 2000, 2013). To estimate the soybean yield we used data from the national government (http://www.siia.gov.ar), considering the average annual harvest of 11 years (period 2000–2010) for the provinces of Chaco (mean = 1900 ± 0.5 kg ha^{-1} yr^{-1}), Santiago del Estero (mean = 2100 ± 0.6 kg ha^{-1} yr^{-1}), Formosa (mean = 1900 ± 0.5 kg ha^{-1} yr^{-1}) and Salta (mean = 2500 ± 0.4 kg ha^{-1} yr^{-1}). Argentina is the third largest global exporter of soy grain. Most of it is destined as pig and chicken feed; soybean is also used for flours and oils, destined to the European Union, China and India (Lapitz, Evia, & Gudynas, 2004). To estimate meat production based on soybean yields, we assumed that all this production goes to feed pigs, because: (1) pig feed is the number one use of soybean; (2) in contrast with chicken (the second most important use of soybean) from both culinary and nutritional (calories, proteins, fat) point of view pork is fairly similar to beef; (3) it is intermediate in terms of food-meat transformation efficiency, being about twice as efficient as cattle, and approximately half as efficient as chicken (Smil, 2013). We computed the area required to reach the current regional production level under each land use, and how much land could potentially be preserved as unused natural forest or grasslands in each case.

Based on the agricultural production trends from the period 1994 to 2010, we used linear extrapolation to estimate a plausible production target for the year 2020 which resulted in an estimated increase of 71%. We estimated the area required to reach this production level under minimum, intermediate and maximum yield systems within the allowable yield. We considered the remaining area destined to conservation purposes for three forest–grasslands ratios: 100% forest, 80:20 and 50:50 forest and grasslands. It is important to differentiate that with *yield* we refer to production per unit area of a specific land use, while with *regional production* or *production target* we refer to the total production (current or projected) from the entire study area.

2.3. Abundance-yield models

2.3.1. Model parameterization

With the maximum likelihood method (MLE) we fitted linear regression models relating the relative abundance of each species (counts 0–9) in each sampling site as the dependent variable to meat production (kg ha^{-1} yr^{-1}) as the independent variable. We used two alternative formulas:

$$(\mathrm{A})\ y = \exp\left(b_0 + b_1(x^{\alpha})\right)$$

and

$$(\mathrm{B})\ y = \exp\left(b_0 + b_1(x^{\alpha}) + b_2(x^{2\alpha})\right)$$

where y is the relative abundance of counting points of each species (0–9). The variable x represents the yield in kg of meat ha^{-1} yr^{-1}, and b_0, b_1, b_2 and α are constant parameters estimated from the data. We assumed that the yield values (x) are constant within each land use category, therefore not accounting for environmental heterogeneity (for details of fittings see Phalan, Onial, Balmford, & Green, 2011b, Supplementary Information).

2.4. Estimating relative bird populations under alternative scenarios

We compared the estimated total population of each species within a region after farming, calculated by the sum of its population in the different land use/cover categories (forest-grasslands and farmland systems), to baseline populations in different reference states. We estimated a baseline population of each species for three combinations of natural habitats. First, we considered a reference state in which the entire region (100%) was covered by forests; we used the expected relative abundance from each species yield–abundance curve and multiplied it by the whole forest area to produce a baseline population estimate. Then we considered 80:20% and 50:50% forests to grasslands ratios, from which we estimated species baseline populations. In the case of forest, we used the expected population value based on the curve fitting; and for grasslands we took the mean population value from field surveys in that habitat.

In order to compare the conservation strategies, we quantified bird species' relative abundances in hypothetical landscapes where all production comes from farming at different intensities (*land sharing, intermediate, land sparing*). Any level of regional production can be achieved within a range defined by the minimum and maximum allowable yields. For each production level, the minimum allowable yield (land sharing) is obtained by dividing the production target by the total region area. We also assumed that there is a maximum allowable yield (land sparing), set by the maximum possible production of crops (i.e. soybean mean yield). Within the allowable range of yields, productive land area is obtained by dividing the production target by the assumed yield.

Next, we calculated a total relative population size estimate after farming at minimum (sharing), intermediate and maximum (sparing) yields for each production target (regional production). Populations were estimated from the combination of natural habitats and farmland based on abundance–yield curves, summing population estimates from forest, grasslands (average value) and agricultural land in each case. We assumed that the land not used to meet the production target could be allocated to non-productive forest or grasslands in three scenarios: (1) 100% forest, (2) 80:20 and (3) 50:50 forest and grasslands. We expressed each estimate as a proportion of the corresponding baseline population which allowed us to estimate the 'optimal yield' for any level of regional production (production target). Therefore, we compared bird populations for each of the three reference states with respect to three possible forest–grasslands combinations in spared land at minimum, intermediate or maximum yields.

2.5. Bird classifications based on their response to yield

For each of the three forest–grasslands ratios, we classified the species of birds that responded as 'winners' or 'losers' for all possible production targets. 'Winners' are those species for which the total size of the population of the region was always equal to, or greater than the baseline population. 'Losers' are those species whose total populations when there was some farming were sometimes or always lower than the baseline population. We adopted this classification because winners are expected to have higher populations than in the baseline with the expansion and intensification of agriculture, regardless of the production target and yield. Losers are species whose populations could fall below the baseline population as a result of agricultural expansion or intensification, so their condition is more sensitive to decisions about changing land use in different yields.

For species where the optimal yield (calculated as described above) was the lowest allowable yield, land sharing is the best strategy (i.e. the strategy in which these species have the largest total population). For species where the optimal yield was the highest allowable yield, land sparing is the best strategy. For species whose optimum yield was neither the lowest nor the highest allowable yield, an intermediate strategy would be best. We identified the optimal conservation strategy for each species for the current and for projected future (2020) regional production.

3. Results

The current agricultural production estimated for the dry Chaco during the period 2008–2011, averaged across the entire study area (including farm and nonfarm land) was 32 kg ha^{-1} yr^{-1} (vertical solid line in Figure 2). Based on average yields of each land use, we estimated the area needed to meet this production target and the remaining area of natural habitat. Livestock *puestos* would require ~60% of the region to satisfy the estimated production. Silvopastoral and pastures systems respectively would require 20% and 29% of the area; and soybean would require 8%.

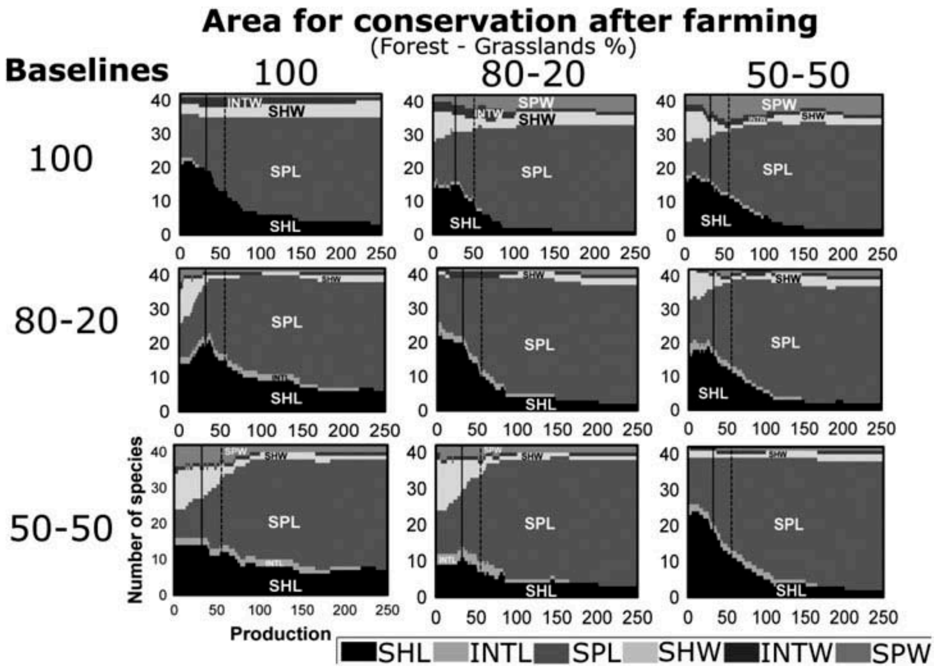

Figure 2. Numbers of winners and losers and of species for which land-sharing or land-sparing or an intermediate strategy gives the highest total population, in relation to production target for different baselines and forest–grasslands proportions after farming. Production targets for 2007 (solid) and 2020 (dashed) are indicated by vertical lines. Fills varies in forest–grasslands proportions from 100% forest to 80:20% and 50:50% forest grasslands. Columns vary in the forest–grasslands proportions after farming 100% forest to 80:20% and 50:50% forest grasslands. Reference from up to down: land-sparing winner (SPW), intermediate winner (INTW), land-sharing winner (LSW), land-sparing loser (SPL), intermediate loser (INTL) and land-sharing loser (SHL).

We recorded a total of 145 species of birds within the six categories of land use. We found 42 species that were present in more than five sites and have significant models according to *F* test ($p < 0.05$, Sup. Table 1). For any regional production target, we described each species response for three nonfarm forest–grasslands ratios in the reference state, and three in spared land (nine possible scenarios for any production target). In all scenarios we found more losers than winner species. For the mean production of the period 2008–2011 (32 kg ha^{-1} yr^{-1}), most loser species populations were maximized by a land-sharing or a land-sparing strategy in each of the nine forest–grasslands ratios. As production increased, most loser species populations were maximized by a land-sparing strategy, including the estimated production for 2020 (55 kg ha^{-1} yr^{-1}) and all future productive scenarios (Table 1, Figure 2).

For the current (2010) production level, most loser species were maximized either by land-sharing or by land-sparing strategies, and clearly not by an intermediate strategy (Table 1). Land sharing maximized loser species populations in 6/9 scenarios varying in the proportions of natural habitat in the reference and future states (Table 1). In all scenarios, most loser species were maximized by land-sharing and land-sparing schemes instead of the intermediate strategy (Table 1). With a reference state of 100% forest, and 100% forest in spared land after farming (100:100–100:100% scenario in Table 1) we found 19 loser species maximized by land sharing and 16 by land sparing. Similarly in the

Table 1. Number of the 42 selected species responding to each strategy for scenarios of 100%, 80% and 50% forests for the PT of 32 and 55 kg ha^{-1} yr^{-1}.

PT	Baseline/Conservation	LSH	LINT	LSP	WSH	WINT	WSP
32	100–100	19	0	16	3	3	1
32	100–80	15	1	15	5	3	3
32	100–50	16	1	12	5	2	6
32	80–100	19	2	16	3	1	1
32	80–80	20	2	17	0	2	1
32	80–50	17	2	17	4	1	1
32	50–100	14	2	11	8	1	6
32	50–80	11	3	15	9	1	3
32	50–50	19	2	18	2	1	0
55	100–100	13	0	22	3	3	1
55	100–80	7	1	24	3	3	4
55	100–50	12	1	18	1	2	8
55	80–100	15	2	22	1	1	1
55	80–80	10	2	27	0	2	1
55	80–50	12	2	25	1	1	1
55	50–100	12	2	19	4	1	4
55	50–80	7	3	24	3	1	4
55	50–50	12	2	25	1	1	1

Notes: Species account corresponds to baseline and farmed landscapes. In the column 'Baseline/Conservation': the first number denotes the forest–grasslands proportion for baselines (100 forest, 80:20 and 50:50 forest grasslands), where the second number denotes the forest–grasslands proportion after farming (100 forest, 80:20 and 50:50 forest grasslands).

PT, production target; LSH, loser land sharing; LINT, loser intermediate; LSP, loser land sparing; WSH, winner land sharing; WINT, winner intermediate; WSP, winner land sparing.

100–50% (100% forest reference state and 50:50–50:50% forest grasslands in spared land in Table 1 and Figure 2), 80:20–100%, 80:20–80:20%, 50:50–100% and 50:50–80:20% scenarios most losers species were maximized by land sharing (16, 19, 20, 14 and 11, respectively) and land sparing (12, 16, 17, 11 and 15, respectively). In the 100–80:20% and 80:20–80:20% scenarios, we found the same number of loser species maximized by land sharing and sparing, and in the 50–80% scenario land sparing maximized most loser species (15/29), followed by a land-sharing strategy (11/29, Table 1). In all cases there were a minor number of species maximized by intermediate strategies (from 0 to 3 species, Table 1).

For the estimated 2020 production for the region (55 kg ha^{-1} yr^{-1}) we estimated the area needed to meet this target and the remaining area of natural habitat based on the 2000–2010 average yields of each land use. Livestock *puestos* would require ~103% of the region to satisfy the estimated production, silvopastoral systems 35% and soybean 13%, respectively. For the production of 55 kg ha^{-1} yr^{-1} land sparing maximized the populations of most loser species for all combinations of reference state and proportions of land cover in spared land (dotted line in Figure 2, Table 1). This pattern becomes stronger with increasing regional production (Figure 2). For the production in 2020 the loser species maximized by land sparing was higher than by a land-sharing strategy in all scenarios (from 1.5 to 3.4 times higher, Table 1), and again the intermediate strategy maximized only a minor number birds loser populations (from 0% to 9% of losers species, Table 1).

The best strategy for all loser species for which sharing was best changed to sparing as regional production increased. As expected, open habitat species populations fared best in scenarios with higher grasslands proportions in spared land, as the case of *Agelaidoides badius, Aratinga acuticaudata, Columbina picui, Coragyps atratus, Embernagra platensis, Melanopareia maximiliani, Mimus saturninus, Myiopsitta monachus* (Sup. Table 2). In contrast, forest species such as *Campylorhampus trochilirostris, Chunga burmeisteri, Cyanocorax chrysops, Cyclarhis gujanensis, Dryocopus shulzi, Heliomaster furcifer, Hemitriccus margaritaceiventer, Knipolegus aterrimus, Knipolegus striaticeps, Myiophobus fasciatus, Myrmorchilus strigilatus, Nystalus maculatus* and *Piranga flava* had higher populations when spared land was dominated by forest (Sup. Table 2). The relative changes in populations were affected by the forest–grasslands proportion in the reference case, and the difference in each species' abundance in the two natural habitats. For example, *Melanopareia maximiliani*, a species with high abundance in grasslands and no record in forest, "experienced" population "explosions" after incorporating grasslands into landscapes (Sup. Table 2); and similar scenarios of population boom are expected for forest-dependent species such as *Aratinga leucophthalma, Hemitriccus margaritaceiventer, Knipolegus aterrimus* and *Knipolegus striaticeps* with higher populations in scenarios with 100% forest (Sup. Table 2).

4. Discussion

This study provides a novel analysis of the trade-offs between agricultural production and biodiversity response in complex landscapes characteristic of South American semi-arid regions. We were able to extend previous analytical models that relate agricultural production with species abundance, by considering scenarios that describe different proportions of forest and grasslands in reference states and in spared land after-farming, under different productive systems of the Argentinean dry Chaco. Such heterogeneity including forests and grasslands as distinctive natural habitats, as well as the specific analysis of meat production, makes the model more realistic for ecoregions within the dry forest biome, one of the most threatened by the expansion of agriculture (Aide et al., 2013; Hansen et al., 2013; Lambin et al., 2013).

Three major results emerge from this study: (1) conservation strategies oriented towards satisfying a certain regional production target while maintaining species populations depend on the level of these production targets, species abundance in natural and agricultural habitats, the yields of each productive system, and proportion of natural habitats in baselines and spared land; (2) for the current (c. 2010) regional production levels, we found that most loser species (those negatively affected by agriculture expansion) would benefit from land-sharing or land-sparing strategies, but not by an intermediate strategy (i.e. the expansion of silvopasture systems, as has been proposed by previous research, Mastrangelo & Gavin, 2012); (3) as the region is subjected to higher targets of meat production (as is expected to happen, Lambin et al., 2013), loser species populations would be increasingly benefited by a land-sparing strategy, combining high-yielding production (e.g. soybean croplands) and protection of large extensions of natural habitats, rather than land-sharing systems based on *puestos* or intermediate livestock systems. Of course, this does not imply that allowing the free expansion of modern agriculture will result in the automatic 'sparing' of land for nature conservation, but instead high-yield farming needs to be accompanied by active conservation-oriented land use planning (Grau et al., 2013).

For the current levels of production a similar number of species was maximized by sparing as by sharing strategies. This result implies that if food production were maintained at the present level, the *puestos* (land sharing) can contribute to the conservation of bird populations similarly than under a land-sparing scheme. Previous studies found that the *puestos* promote degradation of vegetation diversity and biomass, and habitat quality for vertebrates (Altritcher, Boaglio, & Perovic, 2006; Blanco, Biurrun, & Ferrando, 2005; Grau et al., 2008). For birds, the *puestos* have shown an ambiguous pattern: while the abundance of most bird guilds was higher around the *puestos*, possibly due to the presence of water, food and open spaces, rare or low abundance species were positively related to the distance to the *puestos* (Macchi & Grau, 2012). *Puestos* have very low meat productivity in comparison to other livestock systems which have appeared more recently in the Chaco. It is precisely because of the low meat productivity that the *puestos* system was unable to maximize bird populations for future regional production targets. In this study we considered the *puestos* as the local example of a land-sharing scheme; however, this system has not been implemented with conservation purposes in mind, as a real land-sharing strategy would be. Our results suggest that if the region does not increase its production targets, *puestos* can be compatible with conservation policies oriented to reconcile wildlife protection with rural societal goals; that could be implemented for example through ecosystem services payments (e.g. carbon sequestration) coupled with improvements in livestock management. But, this would not be an effective way to reconcile production and biodiversity conservation under scenarios of higher regional meat production.

Such higher regional production targets are very likely to reflect the near future. Based on our production projections, the continued increases in local and global demand for agricultural products, the relatively high suitability for mechanized agriculture (Lambin et al., 2013) and the interest of the national government to increase agricultural production in the coming decades (Plan Estratégico Territorial, 2008), agricultural production will most probably continue rising in the dry Chaco. Our study showed that bird populations would fare better in a land-sparing strategy for all scenarios if regional production increases; thus implying that high-yield mechanized agriculture can play a role in regional land use planning aimed to balance production and conservation. But, this role is unlikely to emerge spontaneously. The expansion of soybean crops and pastures in Latin America have been considered the main drivers of deforestation in Argentina, Brazil, Paraguay and Bolivia (Aide et al., 2013; Grau, Gasparri, & Aide, 2005; Greasser, Aide, Grau, & Ramankutty, 2015). At the local level, intensification that raises profitability and returns can provide incentives to further expand cultivated area – Jevon's paradox (Byerlee, Stevenson, & Villoria, 2014; Grau, Kuemmerle, Macchi, 2013; Lambin & Meyfroidt, 2011). In the case of the dry Chaco, the effects of soybean on deforestation are not limited to the fine-scale proximate effect on each particular plot; but also to the overall economic effect on agricultural activity, including indirect and time-delayed effects such as displacement of livestock and other crops (Gasparri, Grau & Gutierrez Angonese, 2013; Grau, Gasparri, Aide, 2008). Therefore, to take full advantage of the potential benefits of high-yielding agriculture in a regional planning scheme, production targets must be constrained, agricultural expansion must be controlled and degraded ecosystems restored, in particular in areas identified as high biodiversity or habitat quality, including both forests and grasslands (Grau et al., in press).

The silvopastoral systems were proposed as an intermediate-intensity system based on their yield values and to their bird composition similarity with respect to forest (Macchi et al., 2013). Considering a productivity gradient of extensive cattle ranching (*puestos*, silvopastures and pastures), silvopastures were considered as the 'optimal' strategy to balance trade-offs between meat production and bird diversity (Mastrangelo & Gavin, 2012). In this case silvopastures were proposed as the land-sharing option for the dry

Chaco instead of the *puestos* systems as in this study. In contrast, our results, when production gradient is extended by the inclusion of soybean croplands, showed that intermediate productive strategy maximizes populations fewer bird species populations, in comparison to both *puestos* (full sharing system) and land-sparing schemes based on high-yield agriculture. In the dry Chaco, silvopastures are a novel productive system that include different management practices, from those with a high density of native trees (more consistent with land-sharing conception); to those with low tree density and high tree mortality, more similar to pastures without canopy (Kuntz et al., 2014). Such heterogeneity was not considered in our study, and we believe there is potential of some specific silvopastoral systems to balance meat production with biodiversity conservation and other ecological functions (e.g. soil and water conservation, wood extraction). Our results provide little support for the idea that silvopastures are a promising option to maintain bird populations and meat production.

While croplands are very likely to expand in the coming decades in the study region, such expansion will be partially constrained by the national zonation law (*Ley de Bosques*). The current zonation considers three land use categories: non-use (forest), 'sustainable' use (*puestos* and silvopastures) and intensive use (pastures and crops). The implementation of a sparing scheme (the most efficient in a scenario of higher production targets) would require a redistribution of the land assigned to each category. In particular, the 'non-use' (red) zones would need to be expanded, since they currently only represent 9% of the study area, and must specifically include the protection of natural grasslands. The current area zoned for conservation is below Argentina's national commitment to habitat conservation (17% according to Aichi target 11; Rode, Wittmer, & Watfe, 2012); and being a forest-centred law, essentially ignore grasslands as conservation targets (Grau et al., in press).

This study does not consider geographic heterogeneity in habitat quality and agricultural productivity, and we assumed there were no systematic relationships between the potential of land for biodiversity and its potential for agricultural production. Soils and climate do vary across this extensive area and likely affect both the yielding patterns of each land use and bird abundance patterns. A more sophisticated analysis should include such spatial heterogeneity of the region, and, coupled with the specific consideration of the legal constraints for land use given by the forest law, should allow for spatially explicit land use recommendations to optimize biodiversity conservation and meat production.

Our model was able to expand the original density-yield model proposed by Green et al. (2005), in particular, by exploring how the inclusion of more than one natural habitat affected estimates of relative change in populations. In regions like the Chaco, where current natural habitats are dominated by forest but grasslands provide habitat for a non-negligible proportion of the biodiversity (Grau et al., in press), not accounting for open habitats could easily lead to wrong estimates of wildlife population values, and in consequence to misleading management guidelines. Further improvements in optimization studies should include a larger set of trade-offs (e.g. carbon storage, watershed protection, human geography and socio-economic conditions) in a spatially explicit and geographically heterogeneous setting.

By assessing the consequences of different production targets and different combinations of natural habitats for bird species populations, we found that for the current regional production both land sharing and sparing have the potential to maximize the agricultural production–bird populations trade-offs; and under ongoing trends of land use change in the dry Chaco, land-sparing strategies could be more efficient for combining agricultural production and bird conservation. Together with the inclusion of grasslands (in addition to forests) as a specific conservation target, our analysis suggests that conservationists and policy-makers should investigate the potential to improve protection for the dry Chaco without compromising food production, through modifications of the government land use zonation and other land use policies.

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Supplemental data

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