



Trade-Offs between Cattle Production and Bird Conservation in an Agricultural Frontier of the Gran Chaco of Argentina

MATIAS E. MASTRANGELO* AND MICHAEL C. GAVIN†

Victoria University of Wellington, School of Geography, Environment, and Earth Sciences, P.O. Box 600, Wellington 6140, New Zealand, email matias.mastrangelo@vuw.ac.nz

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 may be required to maintain cattle yield, bird diversity, and conservation of forest-restricted species in this agricultural frontier.*

Keywords: dry forests, food production, land-use planning, silvopastoral systems

Compromisos entre la Producción de Ganado y la Conservación de Aves en una Frontera Agrícola del Gran Chaco de Argentina

Resumen: *La intensificación de la producción de alimento en paisajes tropicales en ausencia de planificación del uso de suelo puede constituir una amenaza mayor para la diversidad biológica. Las decisiones de integrar tierras espacialmente o segregarlas para la producción y la conservación dependen, en parte, de las relaciones funcionales entre la diversidad biológica y la productividad agrícola. Medimos la diversidad, densidad y composición de especies a lo largo de un gradiente de intensificación de la producción en una frontera agrícola en el Chaco argentino, donde los bosques secos son talados para la producción de ganado. La diversidad de especies de aves en bosques intactos fue mayor que en cualquier tipo de sistema de producción ganadera. La riqueza de especies de aves decreció no linealmente a medida que incrementó la producción ganadera. Los sistemas silvopastoriles de intensidad intermedia, aquellos en los que el sotobosque es talado selectivamente para cultivar pastura de plantas no nativas debajo del dosel de los árboles, produjeron 80% de la*

*Current address: Unidad Integrada INTA Balcarce, Facultad de Ciencias Agrarias, Universidad Nacional de Mar del Plata, P.O. Box 276, Balcarce 7620, Argentina

†Current address: Department of Human Dimensions of Natural Resources, Colorado State University, Fort Collins, CO 80523-1480, U.S.A. Paper submitted March 8, 2011; revised manuscript accepted April 11, 2012.

producción media de ganado obtenida en pasturas en áreas taladas, y fueron ocupadas por 70–90% de las especies de aves presentes en los fragmentos de bosque más cercanos. Las densidades de >50% de las especies de aves fueron significativamente menores en pasturas abiertas que en los sistemas silvopastoriles. Por lo tanto, los sistemas silvopastoriles de intensidad intermedia pueden tener el mayor potencial para sustentar la producción de ganado y conservar un alto porcentaje de especies de aves. Sin embargo, en comparación con los sistemas de producción de baja intensidad, en los que la estructura y extensión del bosque estaba intacta, los sistemas silvopastoriles de intensidad intermedia soportaron significativamente menos especies de aves restringidas a bosques y menos aves frugívoras. Estos datos sugieren que en esta frontera agrícola se requiere la integración de la producción y la conservación mediante sistemas silvopastoriles de intensidad intermedia en combinación con la protección de fragmentos de bosque para mantener la producción de ganado, la diversidad de aves y la conservación de especies restringidas a bosques.

Palabras Clave: bosques secos, planificación de uso del suelo, producción de alimento, sistemas silvopastoriles

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) (Mattison & Norris 2005; Fischer et al. 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. 2011). 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). 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 to account for identity and ecological roles of species (Phalan et al. 2011). 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). They 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.

Methods

Study Area

The Bermejo-Pilcomayo Interfluvium 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. 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, rainfall 1000–800 mm), *umbral* (transition area) (elevation 379–260 m, rainfall 800–600 mm), and *chaco* (elevation <260 m, 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 *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% mestizo).

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 land-holdings) provided by local government agencies and nongovernmental organizations 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. 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. 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 (to which served as baseline land cover) 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. 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). 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

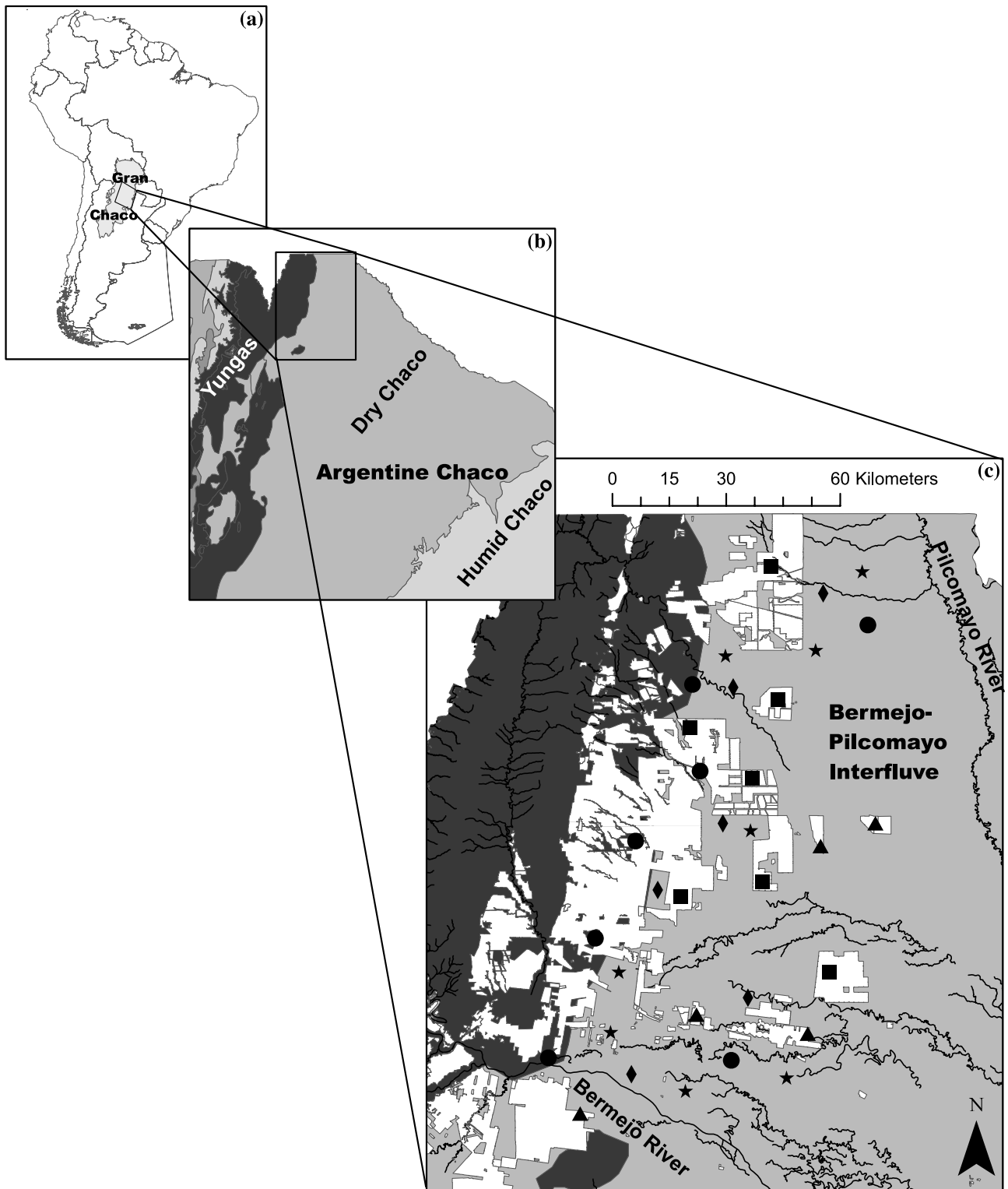


Figure 1. Location of (a) the Argentine Chaco (square) in the South American Gran Chaco, (b) the Middle Bermejo-Pilcomayo Interfluve (square) in the transition between the Argentine Chaco and the Yungas ecoregion, and (c) sites of bird sampling (diamonds, forest fragments; stars, very low-intensity systems; circles, low-intensity silvopastoral systems; triangles, intermediate-intensity silvopastoral systems; squares, high-intensity pastoral systems).

center of 6 randomly selected cells. We conducted point counts at sites once during the nonreproductive 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 is greatest, either 3 h after dawn (51.5% of counts) or 3 h 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 semistructured 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 the initial visit, 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, 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 high-intensity 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 open-ended questions, delivered in one-on-one conversations in Spanish under a semistructured design to reduce potential bias associated with cultural differences among respondents and between respondents and the interviewer (Bernard 1994) (survey instrument in Supporting Information). 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 2-way nested analysis of variance (ANOVA) and the Satterthwaite approximation for unbal-

anced sample sizes. Then, we performed unplanned comparisons (Tukey-honestly significant difference) at the level of production systems in SPSS 18.0 (IBM, Chicago, Illinois). 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)

$$H = - \sum_{i=1}^S p_i \ln p_i, \quad (1)$$

where S is species richness and p_i is the proportion of individuals of the i th 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. 2a). We calculated the first function with bird species richness and cattle yield expressed in total values and the second function 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_{*i*} 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.

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

$$J \text{ abundance based} = \frac{UV}{U + V - UV}, \quad (2)$$

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

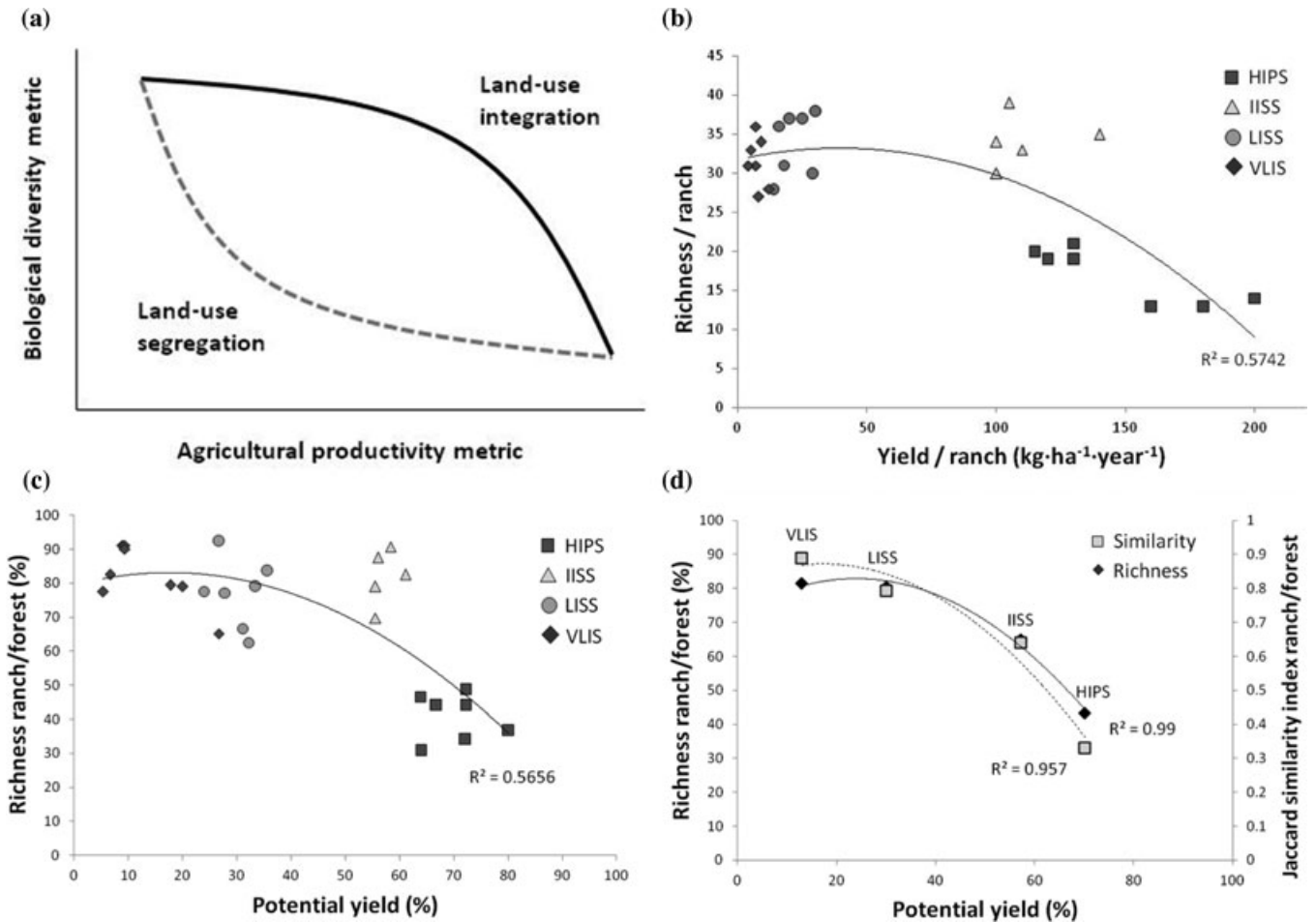


Figure 2. (a) Hypothetical trade-off between species richness and agricultural productivity (concave function, integrated [i.e., low and intermediate-intensity] production systems achieve production and conservation objectives; convex function, spatial segregation of nonuse and high-intensity production areas achieves production and conservation objectives [Green et al. 2005]). Empirical best-fitting curves and regression coefficients at the ranch level for the relation between (b) bird species richness and cattle yield and (c) 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 zone. (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. Abbreviations: FF, forest fragments; VLIS, very-low-intensity systems; LISS, low-intensity silvopastoral systems; IISS, intermediate-intensity silvopastoral systems; HIPS, high-intensity pastoral systems.

(3) between bird assemblages of forest fragments and production systems and compared this curve with the species richness-yield curve

$$J \text{ occurrence based} = \frac{A}{A + B + C}, \quad (3)$$

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 & Alvarez 2009 for yungas species). This classification resulted in 6 feeding guilds (i.e., insecti-

vores, frugivores, granivores, carnivores, omnivores, and nectarivores) and 3 habitat-affiliation groups (i.e., forest specialists, generalists, and open-land species). We compared means of species richness and abundance within functional groups among ranches and production systems with 2-way nested ANOVA 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 2-way nested ANOVA corrected for unbalanced sample sizes and post hoc tests in SPSS 18.0. These analyses revealed associations between

Table 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.

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

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

density of birds and cattle production intensity, which were stronger between production systems with marked differences in forest structure (e.g., silvopastoral systems with cleared understory and completely cleared high-intensity pastoral systems). 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 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 higher 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 higher than in high-intensity pastoral systems (6% [SD 5.4]).

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

(Supporting Information). 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). This association resulted in common patterns of differences among production systems for the 3 measures of diversity. Thus, bird diversity was significantly higher 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. This was the pattern for species richness and yield expressed as total values (Fig. 2b) and as percentage of potential values (Fig. 2c). 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.

Composition of Bird Assemblages

Values of the Chao-Jaccard abundance-based similarity index were higher for pairs of production systems that had

Table 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.

Bird measure	Type of production system, mean (SD) ^a					Variance ratio ^b		Variance (%) ^c	
	FF	VLIS	LISS	IISS	HIPS	production system	ranch	production system	ranch
Diversity									
total species richness	10.8 (3) ^α	8.7 (2.8) ^β	9.2 (2) ^β	9.6 (2.6) ^{αβ}	5.5 (2.1) ^γ	18.78 ^{***}	2.62 ^{***}	48.26	11.01
species richness relative to nearest forest	-	84.8 (30.7) ^α	84.4 (21.5) ^α	88.4 (23.1) ^α	46.8 (15.8) ^β	17.17 ^{***}	1.83 [*]	39.69	7.32
Shannon diversity index	2.2 (0.3) ^α	2 (0.3) ^{αβ}	2 (0.3) ^{αβ}	2 (0.3) ^{αβ}	1.3 (0.5) ^γ	15.02 ^{***}	2 ^{**}	37.92	8.89
Species richness within functional groups									
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) ^α	5.1 (2.3) ^α	5.1 (2.1) ^α	4.6 (2.4) ^α	1.3 (1.3) ^β	14.2 ^{***}	2.27 [*]	38.64	10.77
omnivores	0.6 (0.6) ^α	0.3 (0.5) ^{αβ}	0.3 (0.6) ^{αβ}	0.3 (0.5) ^{αβ}	0.3 (0.5) ^{αβ}	3.5 [*]	0.67	4.1	0
carnivores	0.6 (0.6) ^{αβ}	0.3 (0.5) ^α	0.6 (0.8) ^α	0.9 (0.9) ^β	0.9 (0.7) ^β	3.5 [*]	1.43	7.82	6.19
frugivores	1.7 (1) ^α	1 (1) ^β	0.4 (0.5) ^γ	0.2 (0.4) ^γ	0 ^γ	20.49 ^{***}	1.86 ^{**}	44.63	6.94
habitat group									
forest specialist	6.7 (2.2) ^α	5 (2.3) ^β	3.9 (1.2) ^β	2.3 (1.4) ^γ	0 ^δ	30.45 ^{***}	3.67 ^{***}	65.51	10.62
habitat generalist	3.4 (1.6) ^α	3.6 (1.9) ^{αβ}	4.2 (2.1) ^{βγ}	5.2 (2.1) ^{βγ}	2.7 (1.8) ^α	4.23 ^{**}	2.37 ^{***}	13.66	16.05
open-land species	0.6 (0.9) ^{αβ}	0.5 (0.8) ^α	1.3 (1.3) ^β	2.4 (1.4) ^γ	2.8 (1.3) ^γ	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) ^α	8.9 (5) ^α	10 (6.2) ^α	8.7 (6.6) ^α	4.6 (3.4) ^β	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) ^α	0.3 (0.5) ^α	0.9 (1.4) ^α	1.1 (1.2) ^β	1.2 (1.4) ^β	3.6 [*]	1.11	6.72	1.69
frugivores	2.7 (1.8) ^α	2.3 (2.5) ^α	0.8 (1.1) ^β	0.5 (0.9) ^β	0 ^β	12.37 ^{***}	2.05 ^{**}	33.54	9.91
Habitat group									
forest specialist	12.3 (5.1) ^α	12.3 (11.4) ^α	7.8 (5.1) ^β	5.2 (4.7) ^β	0 ^γ	6.38 ^{***}	7.32 ^{***}	32.77	34.48
habitat generalist	6.2 (4.8) ^α	8.5 (8.1) ^α	11.3 (9.3) ^α	16.8 (13) ^β	8.7 (7.6) ^α	2.71 [*]	3.55 ^{***}	9.81	26.93
open land species	1.5(2) ^α	1.1 (1.8) ^α	3.6 (4.3) ^α	8.2 (9.2) ^α	39.6 (67.2) ^β	2.41 [*]	13.17 ^{***}	13.51	57.93

^aData are at the level of point counts. Superscripted 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.

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

^cPercentage of variance explained by differences among production systems and among ranches within production systems.

similar production intensities (index range 0.78–0.95) than for pairs of production systems that differed by at least 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 high-intensity 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. 2d). That bird species detected in forest fragments were absent from ranches at a disproportionately higher number than the

overall number of species suggested that other types of bird species were added 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). We did not examine species richness in nectarivores because we recorded only one species in this group. Species richness of frugivores and insectivores declined the most ($df = 4$, $p < 0.001$, $F = 20.49$ 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 experienced a slight increase in abundance in intermediate-intensity systems ($df = 4$, $F = 3.6$, $p < 0.05$), and abundance of granivores was high in high-intensity systems ($df = 28$, $F = 12.54$, $p < 0.001$).

Production intensity was negatively associated with species richness of forest specialists and positively associated with species richness of open-land species (Table 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 ($df = 4$, $F = 2.71$, $p < 0.05$).

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. 3a). Densities of 16 species (17%) increased in silvopastoral systems (e.g., White-fronted Woodpecker [*Melanerpes cactorum*], which preys on insects that occur on tree bark) (Fig. 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. 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 buditoyses*]) (Fig. 3d). Densities of 22 species (24%) remained stable in high-intensity systems. In particular, densities of generalists that feed on seeds in pastures or neighboring cropland (e.g., Many-colored Chaco Finch [*Saltatricula multicolor*]) remained stable (Fig. 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. 3f).

Discussion

Bird diversity, the composition of bird assemblages, and cattle yield all responded nonlinearly to intensification of cattle production. The little 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

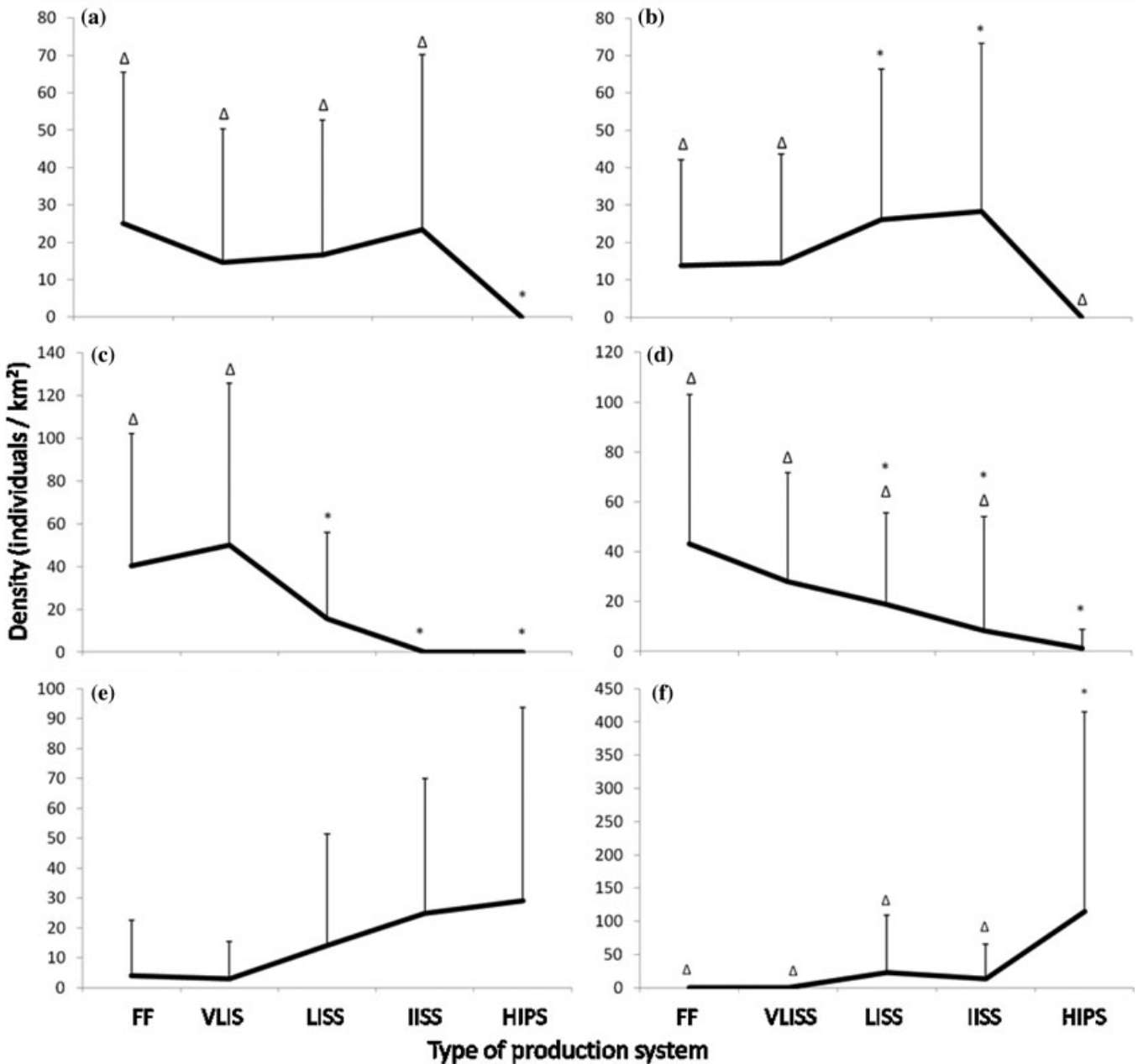


Figure 3. Mean (SD) density of bird species along a gradient of increasing agricultural production intensity (FF, forest fragments; VLIS, very-low-intensity systems; LISS, low-intensity silvopastoral systems; IISS, intermediate-intensity silvopastoral systems; HIPS, high-intensity pastoral systems): (a) Hepatic Tanager (*Piranga flava*) (b) White-fronted Woodpecker (*Melanerpes cactorum*), (c) Chaco Chachalaca (*Ortalis canicollis*), (d) Greater Wagtail-tyrant (*Stigmatura buditoydes*), (e) Many-colored Chaco Finch (*Saltatricula multicolor*), and (f) Shiny Cowbird (*Molothrus bonariensis*). The SD bars are shown one-sided for clarity, but they are symmetrical. Different symbols above bars indicate statistically significant differences among groups at alpha = 0.05.

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 et al. 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 on average 42% fewer

species were detected in high-intensity pastoral systems than in intermediate-intensity silvopastoral systems. Similarly, the difference between intermediate-intensity silvopastoral systems and high-intensity pastoral systems in the number of species shared with the nearest forest fragments (31%) was larger than the difference in species richness relative to nearest forest (21%). These results suggest species richness and species composition changed substantially 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 high-intensity pastoral systems) that we found also occurs in other tropical agroecosystems (Tschartntke et al. 2008). This change may have a negative effect 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 (Seghezze 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 land-use 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), and these factors may have influenced bird detectability. In addition, our yield data originated from subjective, although informed, responses to interview ques-

tions. 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 similar number of bird species 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 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.

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Supporting Information

Species accumulation curves, a species list, and the survey instrument (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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