



Changes in agriculture-biodiversity trade-offs in relation to landscape context in the Argentine Chaco

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Abstract

Context Better balancing agricultural production and biodiversity conservation is a central goal for many landscapes. Yet, empirical work on how to best achieve such a balance has focused mainly on the local scale, thereby disregarding that landscape context might mediate biodiversity-agriculture trade-offs.

Objectives Focusing on vertebrates in the Argentine Chaco, we evaluate how trade-offs between agriculture and biodiversity vary with landscape context, from landscapes where agricultural and natural areas are separated to landscapes where both are interspersed.

Methods We modelled the distributions of 226 vertebrates and use the resulting maps to describe the species richness of ecosystem-service providing guilds. We calculated three agricultural intensity metrics, and evaluated how both species richness and agricultural intensity vary along a gradient of landscape configuration, while controlling for landscape composition.

Results Species richness and agricultural yields both varied with landscape configuration. Biodiversity was highest in mixed landscapes where agricultural and natural area are interspersed, whereas agricultural yields showed a more heterogeneous response, with some yield metrics highest in mixed and others in separated landscapes. As a result, agriculture/biodiversity trade-offs depended strongly on landscape

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configuration, irrespective of landscape composition. We also identified large areas with low vertebrate richness *and* agricultural yields, suggesting considerable potential for improving in at least one dimension. **Conclusions** Agriculture/biodiversity trade-offs varied with landscape configuration, suggesting that landscape design can balance these trade-offs. Our simple and broadly applicable approach can provide baseline information for landscape planning aimed at realizing co-benefits between agriculture and biodiversity—in the Gran Chaco and elsewhere.

Keywords Agricultural production · Contagion index · Landscape composition · Land sparing vs. land sharing · Vertebrate richness · Yields

Introduction

Land-use change is a major driver of global environmental change, including the ongoing biodiversity crisis (Brook et al. 2008; Maxwell et al. 2016). Most fertile lands are already used for agriculture, either for cropping or grazing (Foley et al. 2005; Ramankutty et al. 2008). As the global human population continues to increase, and consumption rises even more strongly, the pressure on remaining natural ecosystems surges (Tilman et al. 2011; Meyfroidt et al. 2014). Finding pathways to shift to more sustainable modes of agriculture that allow to produce more, while at the same time lowering pressure on biodiversity, is thus an urgent research issue (Foley et al. 2011; Kehoe et al. 2017).

Much of the debate around how to best minimize trade-offs between agriculture and biodiversity has focused on whether these two competing goals should be integrated in the same place (i.e., wildlife-friendly farming or land sharing) or should better be separated in space (i.e., land sparing; Green et al. 2005; Fischer et al. 2008). The latter approach relies on the assumption that by intensifying agriculture in one place, less agricultural area is needed overall, so that larger areas without agriculture would then be available for biodiversity. A land sharing strategy, on the other hand, combines production and conservation on the same land. Agricultural yields in such a strategy tend to be lower, so larger areas are needed for cultivation (Hodgson et al. 2010; Phalan et al. 2011).

Yet, empirical work on the question of which strategy minimizes the agriculture/biodiversity trade-offs has provided mixed results (Kremen 2015).

Most studies have focused on analyzing agriculture/biodiversity trade-offs based on local-scale data, that is, agricultural yields and biodiversity measured at the plot level (Kremen 2015), including global-scale extrapolations of such local relationships (Newbold et al. 2015; Kehoe et al. 2017). This is particularly problematic for species that have larger home ranges, such as many vertebrates, because the share of habitat at the landscape-scale might be more important for their survival (Fahrig 2013). Many species of conservation concern are simply unable to survive in farmland, even under wildlife-friendly management, and thus the protection of large patches of natural habitat is needed in both sparing and sharing landscapes (Kleijn et al. 2011; Phalan et al. 2011). Most studies have assumed homogenous landscapes, which disregards landscape heterogeneity (Butsic et al. 2020). Empirical work has also typically focused on a specific landscape (Phalan et al. 2011; Mastrangelo and Gavin 2012; Kamp et al. 2015; Dotta et al. 2016; Williams et al. 2017), with a particular mix of agricultural and natural areas, but have not addressed how different landscape configurations impact trade-offs. In addition to landscape configuration (i.e. the spatial arrangement of habitat patches within the landscape; Gustafson 1998), landscape composition (i.e., the shares of habitat types in the landscape) determines spatial patterns of both biodiversity and agriculture, and thus how agriculture/biodiversity trade-offs play out (Martin et al. 2019; Macchi et al. 2020). Yet, no study has sought to disentangle the effects of configuration and composition on these trade-offs. Finally, some global-scale work exists, but has been carried out at resolutions too coarse to adequately consider landscape context (Kehoe et al. 2015; Delzeit et al. 2017; Egli 2018; Zabel et al. 2019). How the trade-off between yields and biodiversity varies with landscape context, that is, with the amount, composition and configuration of natural vs. agricultural areas, remains weakly understood (Butsic and Kuemmerle 2015; Macchi et al. 2020).

This knowledge gap is a major shortcoming, because it prevents identifying those scales and configurations that are potentially most relevant for mitigating the agriculture/biodiversity trade-off through land-use planning (Grau et al. 2013; Ekroos

et al. 2016). Importantly, these scales likely differ depending on a region's social-ecological context (Ramankutty and Rhemtulla 2013; von Wehrden et al. 2014). There is increasing evidence that landscape-scale planning can deliver better outcomes than either of the pure strategies of land sparing or land sharing (Fischer et al. 2008; Butsic and Kuemmerle 2015; Kremen 2015; Macchi et al. 2020). For example, simulation work highlights that land-use strategies allowing for a combination of intensified and low-intensity agricultural land, together with undisturbed natural areas, outperform both pure sharing or sparing landscapes (Butsic and Kuemmerle 2015; Butsic et al. 2020). Similarly, land-use policies that foster land-use mixes at different levels of intensity also provide better outcomes than pure sparing or sharing, as exemplified in Indonesia (Law et al. 2017). Such findings are encouraging, because real landscapes often fall on an intermediate point between pure sparing and sharing (Fischer et al. 2008; Tscharrntke et al. 2012). However, while these studies highlight the benefit of broad-scale planning for assessing the agriculture/biodiversity trade-off, none of them has systematically assessed how trade-offs vary with changing landscape context.

Much of the recent work on agriculture/biodiversity trade-offs also typically assumes that the two are independent, conflicting goals. In reality, biodiversity underpins various ecosystem services, contributing to local people's livelihoods via providing food and fiber, as well as to agriculture via pollination, pest control, and maintaining soil fertility (Perfecto and Vandermeer 2010; Bommarco et al. 2013). Conservation typically focuses on maintaining viable populations of focal species, or total richness, but less on species that maintain ecosystem services. Analyzing how agriculture/biodiversity trade-offs vary across service-providing guilds (e.g. seed dispersers, pest controllers) would thus provide new insights into the possible co-benefits between agriculture and biodiversity at the landscape scale.

We here develop an approach to analyze agriculture/biodiversity trade-offs in relation to ecosystem services at the regional scale. We do so for the Dry Chaco region in Cordoba Province, Argentina, which provides a unique setup to explore these issues. There, widespread agricultural expansion and intensification have translated into very high deforestation rates recently (Zak et al. 2008; Aide et al. 2012; Kuemmerle

et al. 2017), with widespread biodiversity loss, translating into an urgent need for conservation planning (Torres et al. 2014; Nori et al. 2016; Semper-Pascual et al. 2018). Existing, local-scale work on the biodiversity/agriculture trade-offs in the Chaco is inconclusive, with some studies suggesting land sparing and others land sharing might minimize trade-offs more (Mastrangelo and Gavin 2012; Macchi et al. 2013; Núñez-Regueiro et al. 2015; Marinaro et al. 2017). An assessment of how agriculture/biodiversity trade-offs play out at broader scales, and are impacted by landscape configuration and composition, is still missing. Recognizing this, we focused on vertebrates in the Argentine Chaco to ask:

1. How do the trade-offs between agriculture and biodiversity vary with changing landscape configuration?
2. How does this variation depend on landscape composition?

Methods

Study area

Our study region corresponds to the north of Córdoba Province, Central Argentina, covering 11 districts (Fig. 1a, b). Climate there is subtropical with average minimum and maximum temperatures of 11 °C and 27 °C, respectively (Capitanelli 1979). The predominantly flat relief is interrupted by the *Sierras de Córdoba* mountain range (700 to 1800 m a.s.l.), running from north to south and resulting in marked rainfall differences (> 700 mm east of the mountains and < 550 mm to the west). Rainfall is concentrated in summer.

We focused on the area below 500 m a.s.l., where most of the conversion of natural vegetation to agriculture has taken place. The area's vegetation has been described in detail by Sayago (1969) and Zak and Cabido (2002) and we here provide only a brief summary. The study area belongs to the Chaco Phytogeographical Province (Cabrera, 1976): the lowlands are part of the Western Chaco District, while the mountain ranges are part of the Sierra Chaco District. The dominant vegetation in the lowlands is *Aspidosperma quebracho-blanco* and *Schinopsis lorentzii* xerophytic forests, alternating with patches of

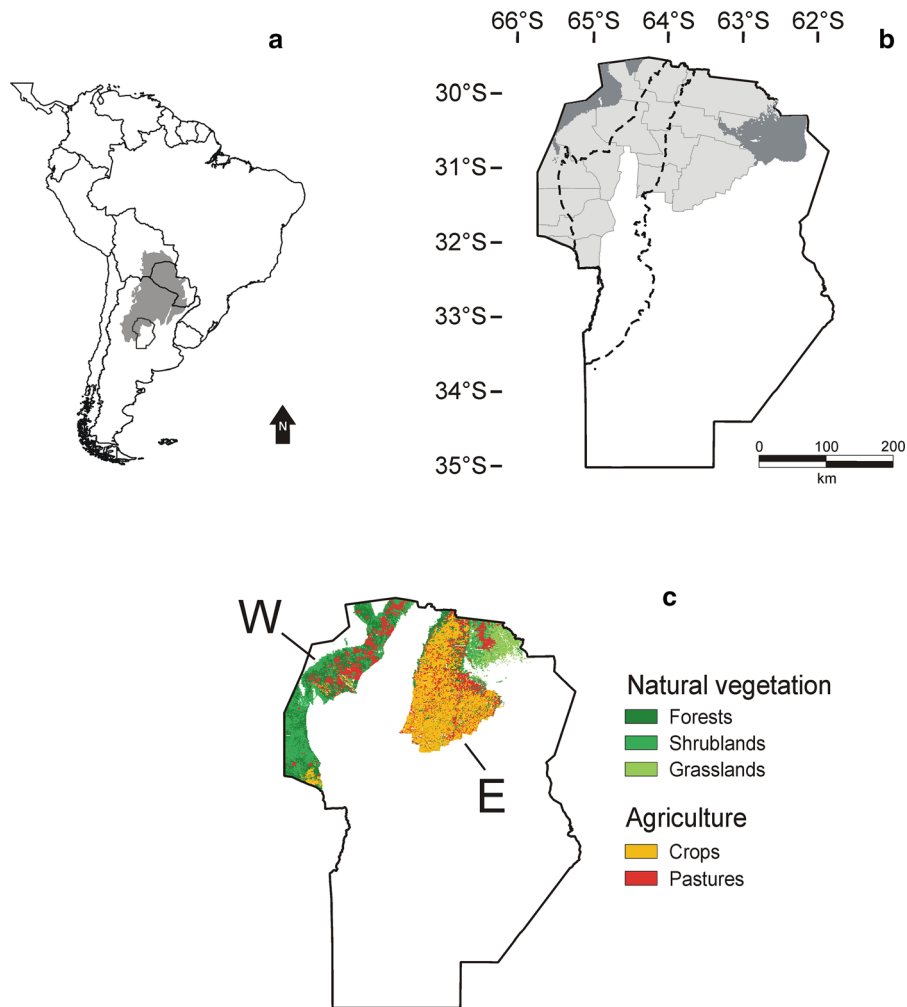


Fig. 1 Overview of the study region. **a** Location of Córdoba province in Argentina, with the shaded area corresponding to the Gran Chaco region *Source* Olson et al. (2001); **b** Córdoba province, with districts making up the study region in light gray. The dashed line indicates areas above 500 m a.s.l. and dark areas indicate inland lakes and salt plains (all not considered in

the study); **c** Vegetation classes in the study area (for 2017/18), including natural habitats suitable for conversion to agriculture (forests, shrublands and grasslands) and agricultural areas (crops and pastures). W = western sub-region; E = eastern sub-region

secondary woodlands and scrubs in a matrix of cultivated lands. Historically, these forests were used for timber extraction, but today most remaining forest patches are used for livestock grazing (mainly cattle and goats), leading to a dominance of grazing-resistant, thorny bushes (Adámoli et al. 1990).

The strong east–west rainfall gradient influences land use. In the west, ranching dominates, typically based on implanted pastures with exotic grasses. As a result, the landscape is composed of a mosaic of natural vegetation patches (mainly forests and shrublands) and implanted pastures, as well as some

cropland. In contrast, the eastern area, where rainfall is higher, is dominated by agri-business agriculture, including intensified, large-scale cropping (mainly soybean and maize), and cattle ranching for meat and milk, with few interspersed patches of natural vegetation (Fig. 1c).

Biodiversity assessment

We focus on terrestrial vertebrates (mammals, birds, amphibians, reptiles) and specifically on those vertebrate guilds that can provide ecosystem services:

fossorials (water infiltration, nutrients capture), frugivores (seed dispersal), insectivores (insect-pest control), nectarivores (pollination), predators (rodent and avian-pest control), scavengers (disease control), and species valued by local communities (i.e., consumed by rural people in the Chaco; hereafter: *local-livelihoods species*). For a detailed description of guilds and species selection see Appendix S1 and Table S1 in the Supplementary Material. We note that our focus here was on the trade-offs between agriculture and the richness of service-provisioning vertebrate guilds, not the ecosystem services themselves.

We used species distribution models to predict the range of a total of 255 terrestrial species. Occurrence data stemmed from extensive field surveys across Córdoba province, conducted in 154 randomly selected locations between January 2010 and June 2014, from museum collections, the literature and other field databases (Giayetto and Zak 2020). We also added records from online databases from 2014 and 2019 (see Appendix S2.1 for details). We generally only retained occurrence records collected after 2010, assuming that they fit best with the land-cover map we used (from 2017 to 2018, see below). However, we included some older records from locations where no land-cover change had occurred. We also dropped species with less than five occurrence points. As predictor variables, we used a total of eight variables capturing topography, climate, and land cover at a resolution of 30 arc-seconds (ca. 1 km × 1 km in our study area; see Appendix S2.2 for details on predictor variables).

We modelled species' distributions using Maxent (Phillips et al. 2017) as implemented in the 'wallace' package (Kass et al. 2018) in R (R Core Team 2019). Model performance was evaluated using the area under the curve (AUC) of the receiver operating characteristic curve (Fielding and Bell 1997; Manel et al. 2001; McPherson et al. 2004). We applied a threshold per species to separate suitable from unsuitable habitat, and stacked the resulting binary maps to generate richness maps per guilds. As a threshold we used the suitability value at the 5th percentile of the suitability value distribution at occurrence points, which provided the most similar distribution maps to known species distributions. Further details on the modeling protocol, model evaluation, thresholding, and validation of the richness maps are provided in Appendices S2.3 and S2.4. Once all richness

indicators were calculated, we compared average species richness between agricultural areas (croplands and pastures) and natural areas (forests, shrublands and grasslands) using the Mann–Whitney U test.

Agricultural production metrics

We calculated three agricultural intensity metrics: beef yields, pork-meat yields, and energy yields, and derive spatial representations of them for our study area. Thus, we assigned beef-yield values to pixels of pastures and natural grasslands, and pork-meat yields to pixels of croplands, as soybean (the crop that dominates the study region) is primarily used for that purpose (Wesz 2016). Averaged values (2015 to 2018) of beef yields and soybean yields at the district (i.e., *department*) level were calculated based on official yield estimations by the National Government of Argentina (<http://www.agroindustria.gov.ar/sitio/areas/bovinos/modelos/>; <https://datos.magyp.gov.ar/dataset/estimaciones-agricolas>). For soybean, we distinguished between soybean meal (79%) and oil (18%) according to the Soya and Oilseed Bluebook (Soyatech 2010). We then converted the soybean-meal fraction to its pork-meat equivalent following Macchi et al. (2013). We calculated pork-meat yields using a conversion rate of 5.5 kg of soybean to 1 kg of pork-meat (Smil 2013). We estimated the energy yield of pastures and natural grasslands using an average energy content of 8.3 MJ/kg of beef (USDA 2019). To convert soybean production to energy yields, we used an average energy content of 18.7 MJ kg⁻¹ for soybean meal (USDA 2019). For assigning energy yield values to agricultural pixels, we summed the energy yield values obtained for beef and pork-meat per pixel.

Forests and shrublands (hereafter: *woodlands*) in our study area also provide both food and energy to local communities and we therefore calculated meat-equivalents and energy yields for woodlands as well. Regarding meat production, we assumed average annual yields of 4.8 kg ha⁻¹ of beef (Bocco et al. 2007). Regarding energy yields, we used the same conversion factors mentioned above for beef.

Comparison between species richness and yields across different landscape configurations and compositions

Using the measures above, we assessed the trade-off between biodiversity (i.e., richness per guild) and agriculture (i.e., beef, pork-meat, and energy yields) across landscapes with varying levels of separation or integration of five land-cover classes, two corresponding to agriculture (pastures and crops) and three to natural areas (all land-cover classes suitable for conversion to agriculture: forests, shrublands and grasslands). To assess landscape configuration, we used the Contagion Index (CI; Li and Reynolds 1993), which measures the degree of clumping of a landscape (see Appendix S2.5 in Supplementary Material for details). Low values of CI (CI = 1–20%) indicate high intermixing of land-cover classes, whereas high values (CI = 80–100%) indicate separation of them. We calculated the CI in circular moving windows of 3 km, 5 km and 10 km using Fragstats v4.2 (McGarigal et al. 2012). We here only show the results for the 5-km radius, as results were very similar for the other two.

We assessed the relative importance of landscape composition and landscape configuration on determining distributional patterns of species richness and agricultural yields. Specifically, we fitted MARS (Multivariate Adaptive Regression Splines) models, which allow to evaluate the effect of multiple, non-linear predictors, including the interactions between them (Hastie et al. 2009). We ran MARS models with species richness and agricultural yields as dependent variables, and the shares of land-cover classes and the CI as predictors. Correlation between our predictors was not high ($r < 0.7$ in all cases) and MARS has been showed to be robust to collinearity among predictors (Dormann et al. 2013). Once models were fit, we evaluated predictor importance for each of our dependent variables (see Appendix S2.6 in Supplementary Material for further details). We also generated scatterplots between the mean percentages of each of the five land-cover classes at 5-km radius from each cell vs. species richness.

To compare our biodiversity metrics and agricultural metrics across the CI gradient, we first generated pairwise scatterplots between all metrics and the CI, and second described these relationships by fitting Generalized Linear Models (GLMs). When fitting the GLMs, we allowed for linear and polynomial

relationships, and picked the best model based on the sample-size corrected Akaike Information Criterion (AIC_c; Konishi and Kitagawa 2008). Given that low CI values indicate a high level of intermixing of agriculture and natural areas, positive slopes in the relationships between CI and guild-wise richness or agricultural yields indicate that separating land-cover classes benefits either biodiversity or agriculture, or both. Conversely, a negative relationship indicates benefits are higher in more integrated landscapes. Unimodal responses indicate biodiversity or agriculture are highest for intermediate landscape configurations.

Given that biodiversity and agricultural metrics are not directly comparable, we rescaled the predicted values for species richness and agricultural yields between 0 and 1 for better visual comparison. We then plotted the rescaled richness of each vertebrate guild vs. the rescaled agricultural intensity metrics for increasing CI values. Based on these plots, we then selected the point where both curves (i.e., biodiversity metrics vs. CI; agricultural metrics vs. CI) intersect. These intersection points can be interpreted as those landscape configurations that maximize agricultural production and species richness at the landscape scale: beyond these points, further increases in one dimension must lead to decreases in the other. The intersection points, thus, represent those landscape configuration with the smallest trade-offs between biodiversity and agriculture, while configurations with high agricultural yields but low species richness, and vice versa, represent areas where large trade-offs exists.

Results

Both the visual inspection (Fig. 1c) and a quantitative summary of the landscape composition (Table 1) showed that the western sub-region was mainly covered by natural vegetation, while the eastern sub-region by agriculture. Our sub-regions also differed to some extent in the shares covered by the different classes within the natural vegetation classes and with agricultural areas. For instance, natural grasslands had a similar proportion than forests and shrublands in the eastern sub-region, but were almost absent from the western sub-region. Likewise, pastures were the main

Table 1 Mean (standard error) percentage of landscape covered by each land-cover type, agricultural metrics, and Contagion Index in randomly selected cells, as well as

comparisons (Mann–Whitney U tests) between the western (W) and the eastern (E) sub-regions (N = 1000 in each sub-region)

	Mean W	Mean E	Z_{adj}	p
% landscape ^a				
Forests	26.7 (18.9)	6.9 (10.6)	25.8	< 0.001
Shrublands	34.0 (23.9)	10.4 (15.4)	26.5	< 0.001
Grasslands	0.2 (1.2)	15.1 (26.8)	– 18.8	< 0.001
Pastures	26.3 (26.2)	18.4 (17.0)	3.6	< 0.001
Crops	5.3 (15.0)	40.7 (34.4)	– 23.1	< 0.001
Yields (kg ha ⁻¹ year ⁻¹)				
Beef	14.5 (12.7)	19.3 (36.1)	– 7.5	< 0.001
Pork meat	24.6 (98.0)	168.2 (219.4)	– 17.3	< 0.001
Energy yield (MJ ha ⁻¹ year ⁻¹)	579.7 (1805.5)	3308.2 (3990.2)	– 17.9	< 0.001
Contagion Index (%) ^a	32.5 (0.6)	42.7 (0.5)	– 12.8	< 0.001

^a% at 5-km radius from each cell

agricultural land cover in the west, whereas crops dominated in the east.

Comparing the agricultural intensity metrics between the two sub-regions revealed marked differences. All agricultural intensity metrics showed higher mean values in the eastern sub-area, but also higher variation (Table 1). In both sub-regions, energy yields follow closely pork-meat yields, with high values in the south of the western sub-region, and in almost all the eastern sub-region except the northeast (Fig. 2). Beef yield had moderate values in the northern half of the western sub-region, and high values in the southeast and moderate values in the northeast of the eastern sub-region (Fig. 2).

Regarding our biodiversity assessment, we found the Maxent models for 226 species (from a total of 255) to be robust and reliable for the purpose of our analyses, given the high goodness-of-fit measures (i.e. an AUC \geq 0.65, or a p -value \leq 0.05 in species with small sample size; see Appendix S2.3). We based all subsequent analyses on these 226 species. Combining the individual species maps revealed that the highest richness values in general occurred where natural cover prevailed. Thus, species richness in general was higher and more evenly distributed in the western sub-region (with a dominance of pastures in a matrix of natural vegetation) than in the eastern one (dominated by croplands and intensified pastures with patches of natural vegetation) of the study area (Table 2; Fig. 2).

This was the pattern for most guilds (notably in fossorials and local-livelihoods species), except for predators and scavengers whose richness was higher in the eastern sub-region (Table 2), with higher values in the eastern margins of the western sub-region and in the periphery of the eastern one (Fig. 2). Also, the variation in richness was higher in the eastern sub-region in all guilds (Table 2). Analyzing the richness of natural and agricultural areas separately showed a similar pattern, with almost all guilds with higher richness values in the western sub-region, except for predators and scavengers (Table 2). No clear relationship between guild-level species richness and agricultural metrics was observed in the western sub-region (Fig. S3). This was different in the eastern sub-region, where the relationship between species richness and beef yields was slightly positive, and negative for pork-meat and energy yields, in all guilds (Fig. S4).

Evaluating the response of richness to each land-cover class separately revealed a general increase in richness with the percentage of forest, and a decrease with the percentage of shrublands, across all guilds, in the western sub-region (Fig. S5). No clear relationships were observed for the other classes. In the eastern sub-region, we also found a positive relationship of richness with the percentage of forests, as well as with shrublands and pastures, and a negative relationship with the percentage of grasslands (Fig. S6). As can be expected, beef yields showed a

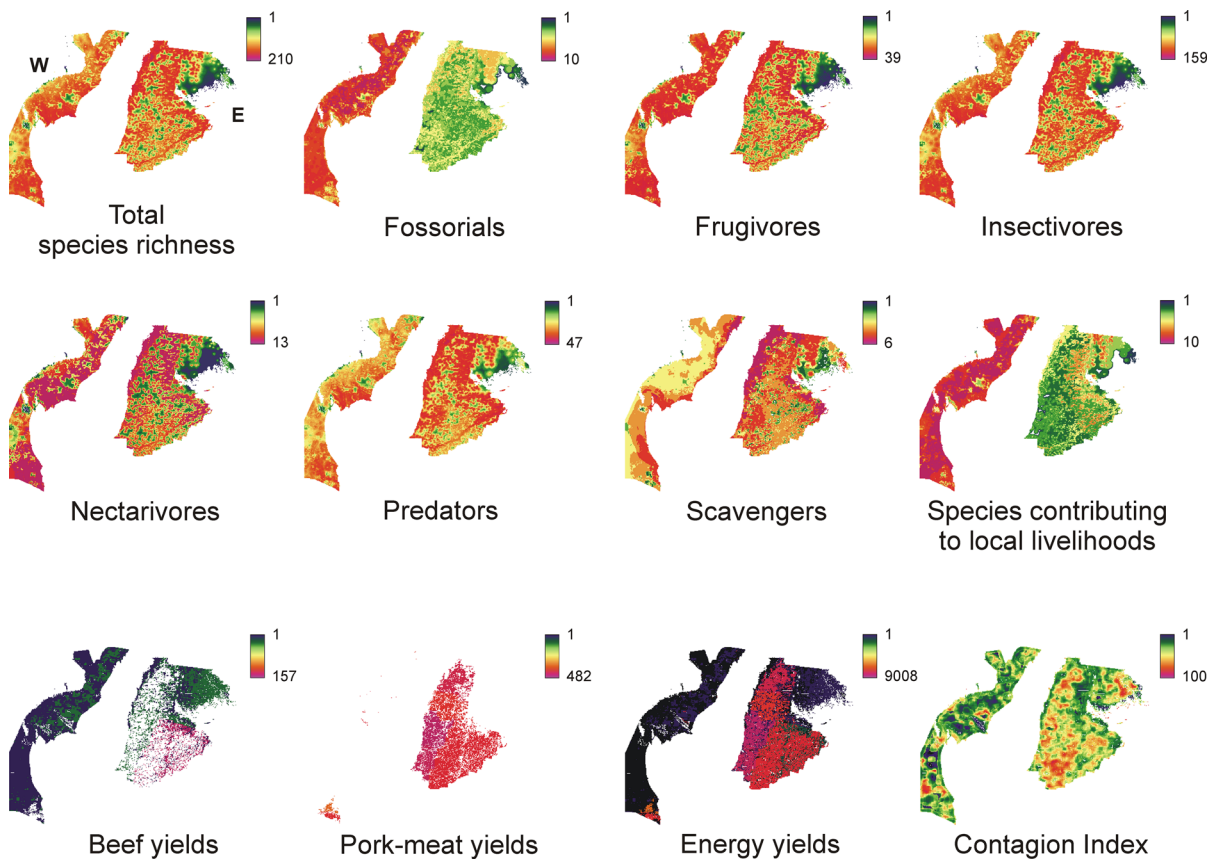


Fig. 2 Species richness for all species and guilds, agricultural intensity metrics (beef and pork-meat yields in $\text{kg ha}^{-1} \text{ year}^{-1}$), energy yield (in $\text{MJ ha}^{-1} \text{ year}^{-1}$) and contagion index for the western (W) and eastern (E) sub-regions (as in Fig. 1c)

strong positive relationship with the percentage of pastures, and pork-meat and energy yields with the percentage of crops, in both sub-regions (Fig. S5 and Fig. S6). However, while no clear relationships between agricultural yields and the other vegetation classes were observed in the western sub-region, in its eastern counterpart beef yields showed a unimodal relationship with the percentages of forests, shrublands, and crops, while pork-meat and energy yields decreased to reach minimal values at low percentages of the first two land cover classes (Fig. S6).

The importance of landscape composition (i.e., the share of each land-cover class surrounding a cell) vs. landscape configuration (i.e., the arrangement of these land covers, as measured by the CI) in determining spatial patterns of species richness and agricultural yields varied between sub-regions. Landscape configuration was selected by final MARS models in all cases; however, compositional variables were

important for most vertebrate guilds in the western sub-region, while CI was more important in the eastern sub-region for most guilds (Fig. 3). Agricultural yields depended strongly on the amount of agricultural land (i.e., pastures in the case of beef yields and crops in the case of pork-meat and energy yields). The importance of the landscape configuration for beef yields was relatively low, but configuration strongly determined pork-meat and energy yields (Fig. 3).

Regarding spatial patterns of CI, low values dominated the western sub-region, excepting small areas in the center and the south part. In the eastern sub-region, in turn, we found most of the area covered by high CI values, except for some areas in the north-center of this sub-region (Fig. 2). The eastern sub-region had a larger mean CI than the western sub-region, confirming a greater degree of separation between agriculture and natural areas (Table 1). Species richness in almost all groups showed

Table 2 Mean richness of vertebrate guilds in randomly-selected cells, and comparison (Mann–Whitney U tests) between the western (W) and the eastern (E) sub-region of the study region

Guilds	Mean W (SD)	Mean E (SD)	Z _{adj}	P
Total^a				
Fossorials	8.2 (1.2)	4.0 (1.4)	– 36.7	< 0.001
Frugivores	30.1 (6.5)	23.1 (10.7)	– 13.7	< 0.001
Insectivores	110.3 (23.1)	96.3 (39.7)	– 5.3	< 0.001
Nectarivores	10.0 (3.3)	7.7 (4.2)	– 11.9	< 0.001
Predators	29.7 (3.3)	30.9 (10.1)	5.6	< 0.001
Scavengers	3.7 (0.9)	4.1 (1.4)	9.6	< 0.001
Local-livelihoods species	8.9 (1.4)	3.7 (1.9)	– 36.5	< 0.001
Natural areas^b				
Fossorials	8.4 (1.1)	3.9 (1.9)	– 26.2	< 0.001
Frugivores	30.8 (6.4)	21.5 (13.1)	– 8.5	< 0.001
Insectivores	112.7 (22.3)	86.4 (49.2)	– 5.0	< 0.001
Nectarivores	10.4 (3.1)	7.1 (5.0)	– 9.3	< 0.001
Predators	30.4 (6.0)	29.1 (12.4)	0.7	0.499
Scavengers	3.9 (0.9)	4.0 (1.6)	3.9	< 0.001
Local-livelihoods species	9.2 (1.1)	4.0 (2.3)	– 26.0	< 0.001
Agricultural areas^b				
Fossorials	7.9 (1.6)	4.0 (1.0)	– 26.0	< 0.001
Frugivores	29.3 (6.6)	24.3 (7.8)	– 9.9	< 0.001
Insectivores	107.8 (23.7)	104.6 (26.7)	– 1.6	0.121
Nectarivores	9.5 (3.3)	8.2 (3.4)	– 6.1	< 0.001
Predators	28.9 (6.6)	32.5 (7.3)	7.5	< 0.001
Scavengers	3.5 (0.9)	4.2 (1.2)	10.2	< 0.001
Local-livelihoods species	8.5 (1.6)	3.5 (1.4)	– 26.2	< 0.001

^aN = 1000 cells in each sub-region

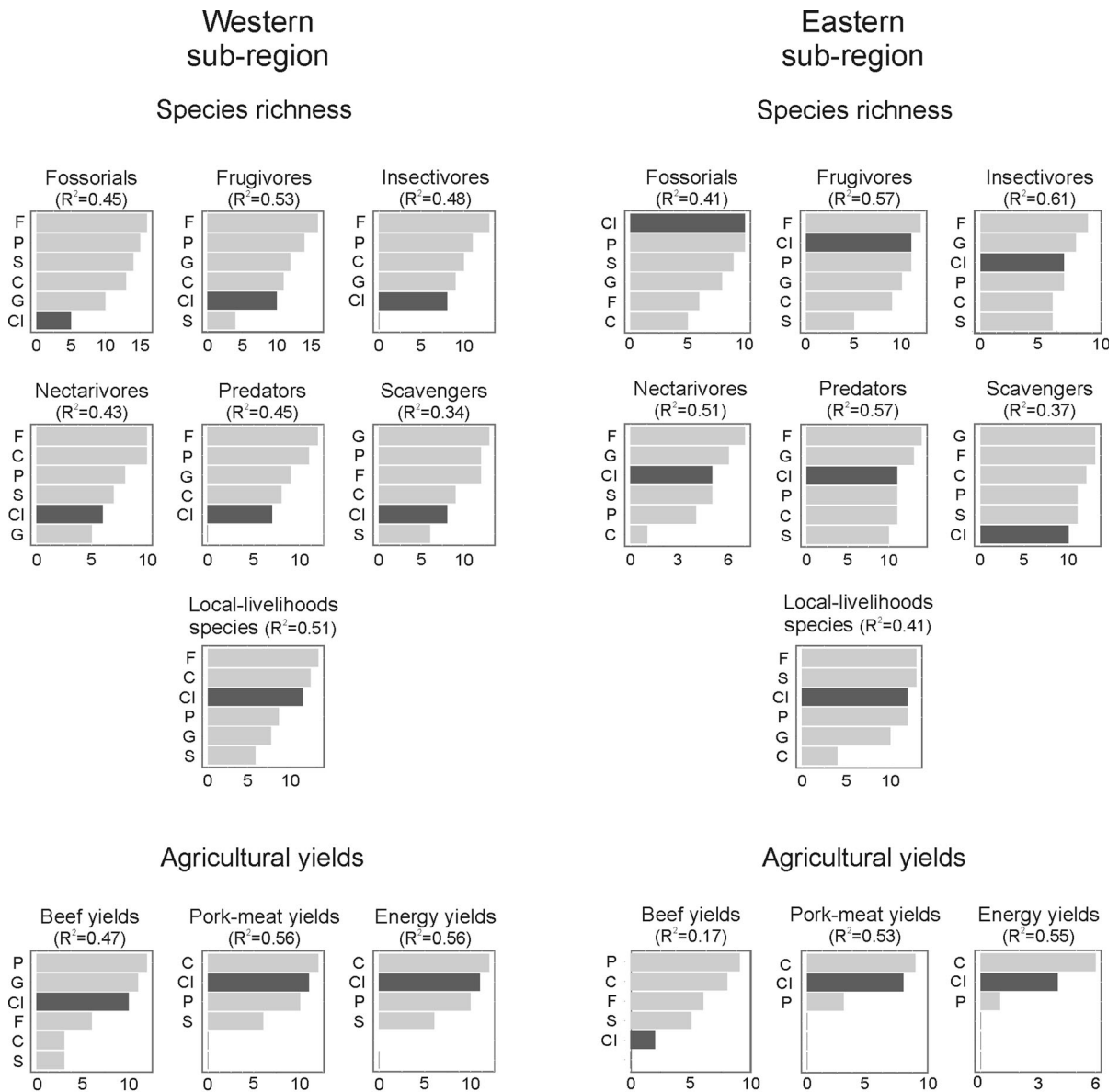
^bNatural areas = forests + shrublands + grasslands; Agricultural areas = crops + pastures; N = 1000 cells in each sub-region

unimodal curves along the CI gradient, peaking at low values of CI in both sub-regions and decreasing markedly towards highest CI values (Fig. 4, and Table S2). Yet, some guilds (fossorials, predators and scavengers) maintained high richness values (> 80%) along the CI gradient.

The relationship between agriculture intensity and CI differed between agricultural intensity metrics. Beef yields showed bimodal curves, and although these curves were different between sub-regions, they consistently had highest values in landscapes with high intermixing of land cover classes (that is, at low CI values), irrespective of the sub-region (Fig. 4c, d). Likewise, pork-meat and energy yields showed unimodal curves and peaked at intermediate CI values in both sub-regions (Fig. 4e–h), suggesting moderate

separation of agriculture and natural areas co-occur with higher yields. The distance between mean and maximum observed values of species richness and agricultural yields across the different CI gradient showed consistent patterns across guilds and intensity metrics (Fig. S7), with larger gaps between actual and potential richness in all guilds (particularly in more shared landscapes) and yield values (especially in more separated landscapes) in the eastern sub-region.

Comparing biodiversity and agricultural intensity metrics across the CI gradient revealed both similarities and differences between sub-regions. As species richness and agricultural yields showed non-linear relationships with CI, guild-level richness intersected twice with the agricultural yield curve in many cases. At any rate, the highest richness and beef yields



Importance of landscape composition vs landscape configuration

Fig. 3 Importance of compositional (light gray) and configurational (dark gray) components of the landscape in determining spatial patterns of species richness and agricultural yields. Importance was assessed via the reduction in the generalized cross-validation error estimate in MARS models (see Appendix

coincided in both sub-regions (Fig. 4c, d), suggesting low trade-offs between them. Instead, highest pork-meat and energy yields occurred far away from richness peaks in both sub-region (Fig. 4e–h), thus with high trade-offs between them. In the western sub-

S2.6). F = %forests, S = %shrublands, G = %grasslands, C = %crops, P = %pastures and CI = Contagion Index (all calculated within a 5 km-radius from each cell), in 1000 cells randomly extracted from each sub-region

region beef yields and richness curves intersect in clustered landscape configurations (CI values of 0–20% and 20–40%), which prevail over much of this sub-region (23% and 50%, respectively; Fig. 4c, e, g). In the eastern sub-region, beef yields and richness

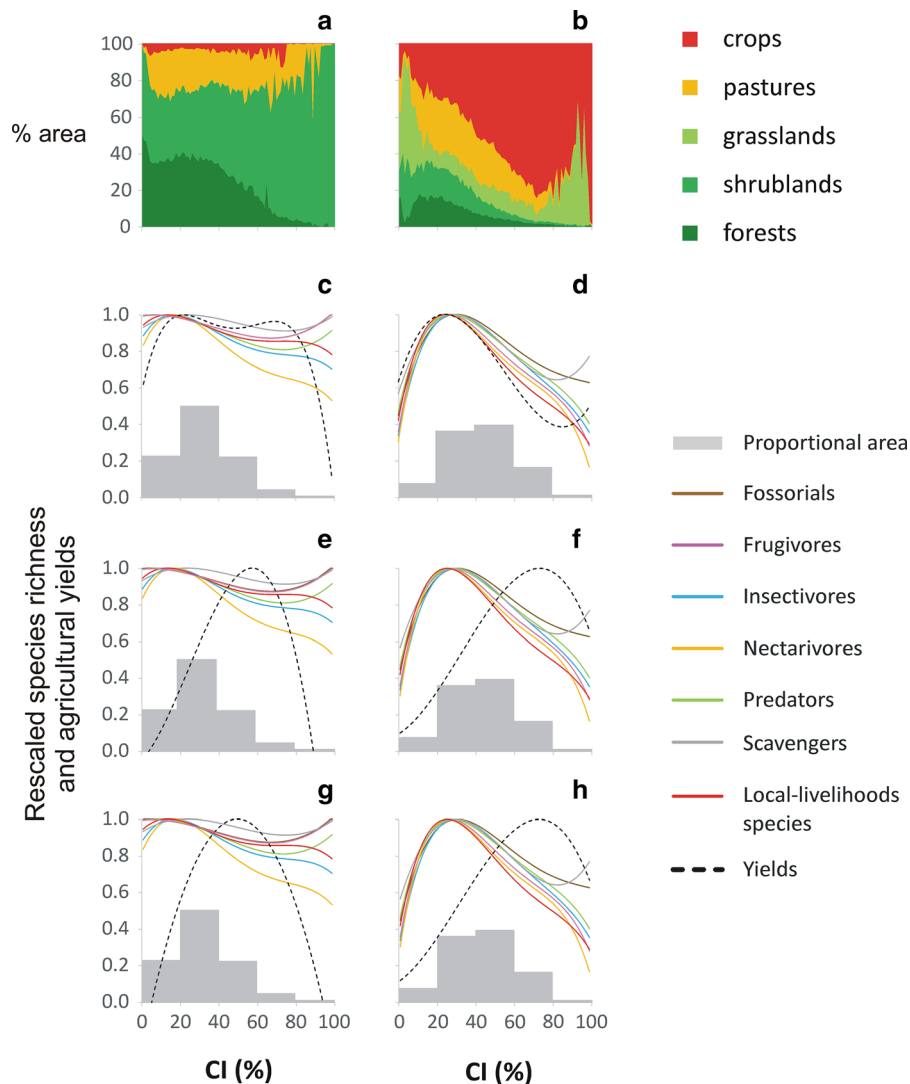


Fig. 4 Percentage of area covered by natural habitats (forests, shrublands and grasslands) and agricultural areas (crops and pastures) for the western (**a**) and eastern (**b**) sub-regions; Species richness for vertebrate guilds (continuous lines) and agricultural intensity metrics (dashed lines; **c** and **d** = beef yields; **e** and **f** = pork-meat yields; **g** and **h** = energy yields) across the gradient of landscape configuration (as measured by the Contagion Index; CI), for the western (**c**, **e** and **g**) and eastern

(**d**, **f** and **h**) sub-regions. Richness and agricultural metrics were rescaled between 0 and 1 for comparison. Grey areas in each graph represent the proportional area covered by each of five CI intervals in the specific sub-region (eastern or western). These proportional areas and the species richness curves do not differ along columns and are provided in each graph for reasons of comparison to the agricultural intensity metrics

curves also intersected at clustered landscape configurations (CI 20–40%, found across 36% of this sub-region; Fig. 4d, f, h). Pork-meat and energy yields intersect with richness curves at intermediate CI levels in both sub-regions (Fig. 4e–h).

Discussion

Like many other tropical or sub-tropical dry forests across the globe, the Chaco is currently facing rapid deforestation as a result of agricultural expansion (Banda-R et al. 2016; Kuemmerle et al. 2017; Powers et al. 2018). Agricultural frontiers advance predominantly outwards from already converted areas,

although leapfrogging also occurs (Volante et al. 2016; le Polain de Waroux et al. 2018). Together, this generates a wide range of landscape configurations, from regions dominated by agriculture, to regions still dominated by natural areas (Macchi et al. 2020). As elsewhere, assessments of agriculture/biodiversity trade-offs in the Chaco have so far exclusively relied on local data (Mastrangelo and Gavin 2012; Macchi et al. 2013, 2016), thereby neglecting that these trade-offs may vary with landscape composition and configuration. Here, we analyzed how vertebrate richness and agriculture intensity vary from landscapes where natural areas and agriculture are interspersed to landscapes where they are separated, and how these relationships vary depending on the regional landscape context.

Unsurprisingly, natural habitats harbored higher biodiversity (vertebrate richness in our case) than agricultural areas (Table 2) and regions with more natural habitat (i.e., the western sub-region) thus hosted higher numbers of vertebrates. There, spatial patterns of richness of most guilds were more sensitive to landscape composition than landscape configuration (Fig. 3). Composition was also important in the eastern sub-region, where agriculture dominates, but we found lower richness and a stronger effect of landscape configuration there. Overall, this highlights the central importance of habitat amount (Fahrig 2013; De Camargo et al. 2018) and the strong biodiversity trade-offs that agricultural expansion can bring about (Carrasco et al. 2017; Morán-Ordóñez et al. 2017).

Yet, despite different responses to landscape composition among our sub-regions, our results suggest a generally strong response of vertebrate richness to landscape configuration. In fact, highest richness values in all vertebrate groups occurred at low CI values in both sub-regions (Fig. 4), suggesting that vertebrate richness is maximized at mixed landscape configurations. Prior, local-scale studies of agriculture/biodiversity trade-offs found support for both land sparing and sharing. Our work highlights that considering landscape context potentially reconciles these apparently diverging findings, as our work can explain why the results of studies focusing on landscapes with more natural habitat (e.g., Mastrangelo and Gavin 2012) should differ from studies conducted in more transformed landscapes (e.g., Macchi et al. 2013, 2016). Our results are also in accordance with growing evidence highlighting

heterogeneity at the landscape level as a key determinant of regional biodiversity (Moreira et al. 2015; Larkin et al. 2016). In the case of the Chaco, there is increasing evidence that pre-European landscapes included more open habitat types and were patchier than current landscapes (Bucher 1982; Morello et al. 2005). Therefore, Chacoan fauna might be adapted to, and benefit from, more complex landscapes (Grau et al. 2015), in line with our results. This finding has important consequences for landscape planning, given that current zoning does not promote mixed landscapes, but favors a spatial segregation of production and natural areas over wide areas of the Chaco.

Our results also showed that agricultural yields themselves might depend differently on landscape configuration. As with biodiversity, beef-yields showed highest values at low CI values (Fig. 4c, d), suggesting that ranching is favored by mixed landscapes. This is probably because mixtures of pastures and woodlands (i.e., forests plus shrublands) are beneficial for livestock, as woodlands provide shadow and supplementary fodder (Bucher and Huszar 1999; Navas Panadero 2010; Trillo et al. 2014). This finding is thus in line with growing evidence for natural areas providing important ecosystem services to agriculture (González et al. 2016; Rusch et al. 2016; Nicholson et al. 2017). Instead, cropping yields were highest at high CI values (Fig. 4e–h), and thus in more segregated landscapes. This is likely because economies of scale (e.g., benefits of large, high-tech machinery) can be realized better in such landscape configurations, and because transportation costs and costs for sowing, pesticide management and harvesting are lower in such clustered (as opposed to mixed) landscapes.

As both biodiversity and agricultural yields depended on landscape configuration, configuration also strongly mediated the agriculture/biodiversity trade-offs. Generally, we observed that the highest values of species richness and beef-yields coincide along the CI gradient, while highest values of species richness and pork-meat and energy yields did not (Fig. 4). Thus, trade-offs were lower for ranching and stronger for cropping. Finally, we also observed that large areas had low values of biodiversity *and* low agricultural yields, suggesting that landscape planning can increase at least one of these dimensions. These findings have important consequences for land-use planning. In Argentina, the current land zoning (law 26,331 from 2007, also known as the Forest Law)

regulates which land uses are allowed where, with three main categories: zone 1 (green) allows all agricultural land uses, including the conversion of forests to other uses; zone 2 (yellow) allows only for sustainable uses with the forest, but prohibit deforestation; finally, zone 3 (red) prohibits all land uses. However, the zoning is currently implemented at the scale of individual plots and does not take into account landscape configuration. Our study provides evidence of the substantial opportunities that landscape design could have for striking a better balance between agriculture and biodiversity, as recently demonstrated elsewhere in the Chaco (Torrella et al. 2018). Specifically, our study suggests that (1) maintaining major shares of natural habitat is beneficial for mitigating agriculture/biodiversity trade-offs, particularly where cropping dominates and (2) that mixed landscapes are preferable where ranching dominates. These recommendations should be considered in upcoming revisions of the zoning law.

Our study used comprehensive datasets of biodiversity and agricultural intensity to provide new insights into how agriculture/biodiversity trade-offs vary with landscape configuration and composition. Still, a number of limitations need to be mentioned. First, we only relied on species richness, but other metrics such (e.g., abundance metrics) might be interesting to explore in follow-up work (von Wehrden et al. 2014; Socolar et al. 2016). Second, our approach was based on richness maps constructed from binary habitat/non-habitat maps per species. This requires thresholding that can lead to under- or overestimation of true distributions (Pineda and Lobo 2009). Although our validation suggests the species-specific maps and richness maps are reliable, uncertainty in species distributions cannot be fully excluded. Finally, in many places, landowners are the primary actors making decisions about land use and solutions via landscape design might not easily be implemented. However, the current zoning law constitutes a strong, top-down planning mechanism, monitored by provincial governments and penalizing offenders in case of violations. While the implementation of the zoning has been far from perfect (Volante and Seghezze 2017), the zoning law is a major opportunity to influence land users' decisions.

Conclusions

Balancing agricultural production and biodiversity remains a central goal for land-use and conservation planning. Yet, the potential role of landscape design in contributing to this goal is often unclear. Using the case of the Chaco, a global deforestation hotspot, we analyzed how vertebrate richness and agriculture intensity vary from landscapes where natural areas and agriculture are interspersed to landscapes where they are separated. This highlighted that, at the landscape scale, trade-offs between agriculture and biodiversity are context-dependent, that landscape composition and configuration both mediate trade-offs, and that trade-offs were in general lowest in mixed landscapes that still contain sizeable shares of natural vegetation. We furthermore showed that most ecosystem-services providing guilds respond similarly to changing landscape configurations. Finally, we found large areas that had low values of both, biodiversity *and* agricultural yields, suggesting that adequate landscape planning can increase at least one of these dimensions.

Taken together, our analyses showcase how landscape ecology tools can be useful for aligning agriculture and biodiversity at the landscape scale. The central importance of both habitat amount and fragmentation has recently been highlighted for biodiversity (Fahrig 2013; Hanski 2015; De Camargo et al. 2018), ecological functioning, and ecosystem services (Xiao et al. 2016; Auffret et al. 2017; Thompson et al. 2017). Yet, empirical work on agriculture/biodiversity trade-offs has largely ignored this evidence. Our results showed that agriculture/biodiversity trade-offs depend on landscape composition and configuration, and therefore that landscape design should provide opportunities for mitigate these trade-offs (Turner et al. 2013; Law et al. 2015; Torrella et al. 2018). Moving beyond the local scale towards assessing trade-offs in real-world landscapes, and how they vary as these landscapes are transformed, is urgently needed in times of rapid biodiversity loss and land cover change.

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