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Environmental Research Letters



LETTER

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OPEN ACCESS

RECEIVED

16 August 2016

REVISED

20 February 2017

ACCEPTED FOR PUBLICATION

23 February 2017

PUBLISHED

28 March 2017

Sofía Marinaro^{1,4}, H Ricardo Grau¹, Néstor Ignacio Gasparri¹, Tobias Kuemmerle^{2,3} and Matthias Baumann²

¹ Instituto de Ecología Regional, Universidad Nacional de Tucumán and CONICET, CC 34, 4107 Tucumán, Argentina

² Geography Department, Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany

³ Integrative Research Institute on Transformations of Human-Environment Systems (IRI THESys), Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany

⁴ Author to whom any correspondence should be addressed.

E-mail: sofiamarinaro@gmail.com

Keywords: conservation of biodiversity, farming, forest biomass, indigenous communities, neotropical dry forests, protected areas zoning

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Abstract

Rising global demand for agricultural products results in agricultural expansion and intensification, with substantial environmental trade-offs. The South American Dry Chaco contains some of the fastest expanding agricultural frontiers worldwide, and includes diverse forms of land management, mainly associated with different land tenure regimes; which in turn are segregated along environmental gradients (mostly rainfall). Yet, how these regimes impact the environment and how trade-offs between production and environmental outcomes varies remains poorly understood. Here, we assessed how biodiversity, biomass stocks, and agricultural production, measured in meat-equivalents, differ among land tenure regimes in the Dry Chaco. We calculated a land-use outcome index (LUO) that combines indices comparing actual vs. potential values of 'preservation of biodiversity' (PI), 'standing biomass' (BI) and 'meat production' (MI). We found land-use outcomes to vary substantially among land-tenure regimes. Protected areas showed a biodiversity index of 0.75, similar to that of large and medium-sized farms (0.72 in both farming systems), and higher than in the other tenure regimes. Biomass index was similar among land tenure regimes, whereas we found the highest median meat production index on indigenous lands (MI = 0.35). Land-use outcomes, however, varied more across different environmental conditions than across land tenure regimes. Our results suggest that in the Argentine Dry Chaco, there is no single land tenure regime that better minimizes the trade-offs between production and environmental outcomes. A useful approach to manage these trade-offs would be to develop geographically explicit guidelines for land-use zoning, identifying the land tenure regimes more appropriate for each zone.

Introduction

Land use has substantially modified ecosystems across the globe, mainly to increase the provision of food, fiber, timber and biofuels (Millennium Ecosystem Assessment 2005, Foley *et al* 2011, Erb *et al* 2016). As global population continues to grow and diets keep shifting towards more animal-based protein (Tilman *et al* 2011), agriculture is expected to continue to expand and intensify (Foley *et al* 2011, Cassidy *et al*

2013, Erb *et al* 2016). This trend results in substantial trade-offs between agricultural production and the conservation of natural ecosystems, their functions and biodiversity (DeFries *et al* 2004, Torres *et al* 2014, Grau *et al* 2015), and there is a growing need to manage and mitigate these trade-offs (DeFries *et al* 2004, Foley *et al* 2011, Wright *et al* 2012).

How these trade-offs vary among land systems (Václavík *et al* 2013, Meyfroidt *et al* 2014, Stürck *et al* 2015), and between alternative land-use strategies

(Phalan *et al* 2011, Tschardt *et al* 2012, Grau *et al* 2013), has received considerable attention. At the heart of this research lies the quest for identifying land-use practices and configurations that minimize the loss of non-provisioning ecosystem services and biodiversity for a given production goal, or conversely, that maximize agricultural production for given conservation targets (Chan *et al* 2006, Polasky *et al* 2008, Koh and Ghazoul 2010, Polasky *et al* 2014).

Due to social, cultural and economic factors, land-use practices can differ strongly among land tenure regimes (Kuemmerle *et al* 2009, Baldi *et al* 2015). For example, deforestation (Dolisca *et al* 2007, Nagendra *et al* 2008, Kittredge *et al* 2003), forest gain (Southworth and Tucker 2001, Nagendra 2007), and logging intensity (Banana and Gombya-Ssembajjwe 2000, Kittredge *et al* 2003) can vary substantially among private, communal or public lands (Tucker *et al* 2007, Nagendra *et al* 2008, Bonilla-Moheno *et al* 2013, Ceddia *et al* 2015). Likewise, different modes of farming, such as agri-business farming vs. medium-sized farming vs. subsistence farming, which are tightly connected to different tenure regimes, result in vastly different farm sizes, land-use patterns, and associated trade-offs (Rodriguez and Wiegand 2009, Dannenberg and Kuemmerle 2010, Graesser *et al* 2015, Fahrig *et al* 2015). But, while the role of land tenure in modulating trade-offs between agriculture and the conservation of natural resources is widely acknowledged, the role of different tenure regimes in lowering trade-offs remains unclear (Ostrom and Nagendra 2006, Altrichter and Basurto 2008, Ceddia *et al* 2015).

On the one hand, the ability to expand and intensify agriculture should increase as the economic capacity of actors does (e.g. access to machinery, workforce, technology and credits). This would suggest increasing local trade-offs between agriculture and conservation, from subsistence to mechanized farming (Altrichter and Basurto 2008, Meyfroidt *et al* 2014, Ceddia *et al* 2015, Macchi *et al* 2013, Mastrangelo and Gavin 2012). Land tenure regimes that crucially depend on ecosystem services provided by natural ecosystems (e.g. community-based resource management, hunting and gathering conducted by indigenous communities) might therefore result in lower trade-offs (Arenas 2003, Schwartzman and Zimmerman 2005, Nepstad *et al* 2006). However, there are also examples where such land-use practices result in ecosystem degradation (Macchi and Grau 2012, Barsimantov and Antezana 2012, Bonilla-Moheno *et al* 2013) or where mechanized farming can spare land for conservation (Aratrakorn *et al* 2006, Grau and Aide 2008).

The South American Chaco, the largest remaining continuous tropical dry forest (Eva *et al* 2004, Portillo-Quintero and Sánchez-Azofeifa 2010), provides an interesting case to explore this question. Extending into Argentina, Paraguay and Bolivia, the Dry Chaco

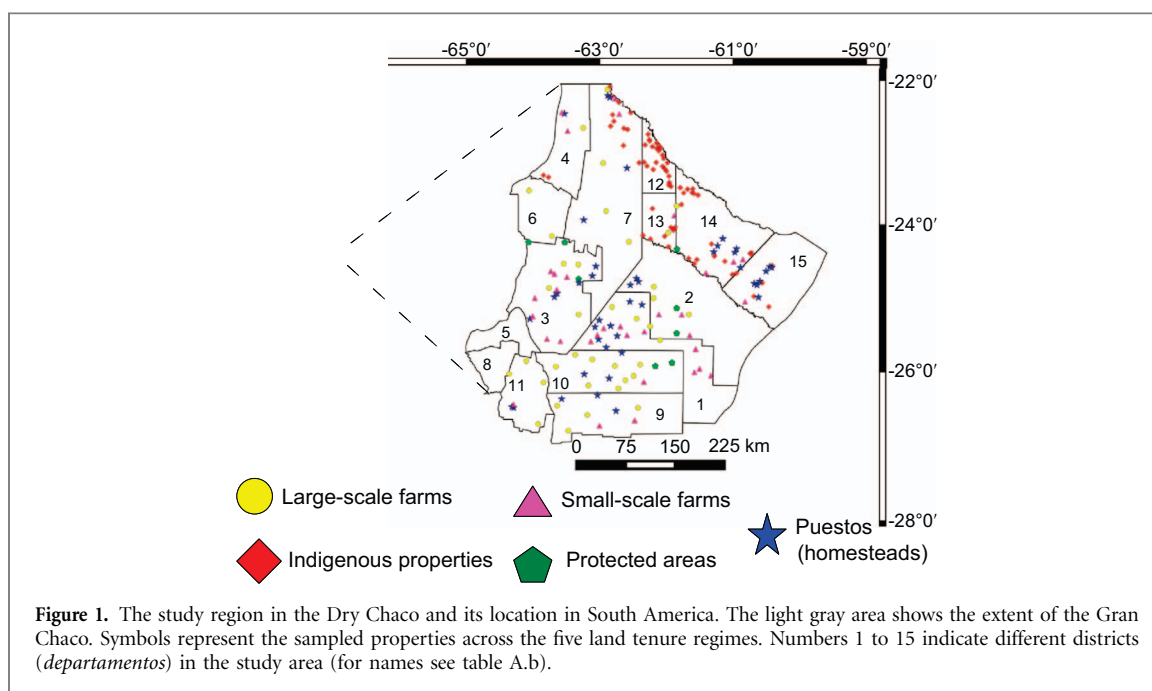
has faced accelerated deforestation since the 1970's as a consequence of the expansion of mechanized agriculture, especially for cattle ranching and soybean cultivation (Grau *et al* 2005, Altrichter and Basurto 2008, Gasparri and Grau 2009). The Chaco is presently characterized by five key tenure regimes, which in turn are closely associated with specific management practices: (1) large-scale farms, (2) medium-sized farms, (3) *puestos* (i.e. subsistence farming and extensive cattle ranching), (4) indigenous communities, and (5) protected areas (Grau *et al* 2008, Gasparri and Baldi 2013, Baldi *et al* 2015). Large-scale farming is characterized by intensified, mechanized agriculture, mainly for soybean crops and pastures, where management is mainly carried out by agri-business companies. In contrast, medium-sized farms are typically family-managed and have a more diversified production. The *puestos* (homesteads) are the traditional way of extensive cattle ranching in the Chaco. Indigenous communities are represented mainly by *Wichí*, but also *Toba qom* and *Pilagá* communities, all practicing traditional hunting, gathering and subsistence agriculture. Finally, protected areas in the Dry Chaco are scarce and relatively young, but in some cases constitute a barrier against the advance of mechanized agriculture.

Here, we analyzed how agricultural production and environmental outcomes vary among these five different land tenure regimes, and which system is best in reducing or avoiding trade-offs between these outcomes. For the purpose of this work, we use the term land tenure regimes to refer to differences in property rights, but also in farm size, land management practices, and actors associated with these tenure regimes in the Chaco. We defined a land-use outcome index (LUO) that combines three variables: species richness (as a proxy for the preservation of biodiversity), standing stock of biomass (as a proxy for carbon sequestration), and meat production (as a proxy for agricultural production). Specifically, we pursued three objectives: (1) to develop and map the three outcome components; (2) to generate and map an integrated land-use outcome index as a measure of the intensity of these trade-offs; and (3) to compare our indices among the five land tenure regimes.

Methods

Study region and land tenure regimes

Our study region is located in the Northern Argentine Dry Chaco, and covers 172 800 km² across 15 districts (*departamentos*) belonging to four provinces: the eastern part of Salta province, the northern part of Santiago del Estero and the western Chaco and Formosa provinces. Annual rainfall ranges from 400 to 900 mm, 80% of which typically falls between November and March. Mean annual temperature is 20 °C–23 °C with maximum temperatures reaching



48 °C in the summer (Minetti 1999). The landscape is a mosaic dominated by medium-tall, semi-deciduous dry forests. *Aspidosperma quebracho-blanco*, *Schinopsis lorentzii*, and *Bulnesia sarmientoi* dominate the tree layer of 16–18 m of height; while the shrub layer is dominated by species of the genus *Acacia*, *Mimosa*, *Prosopis*, *Celtis*, *Opuntia* and *Cereus* (Bucher 1983). Some natural grassland and flooded savannas with *Copernicia alba* palms also occur (Cabrera 1976). Biodiversity includes 46 tree species (Giménez *et al* 2011), over 400 bird species (Short 1975), over 30 amphibian species (Kacoliris *et al* 2006) and around 145 mammal species (Bucher and Huszar 1999).

The study region has a long history of human use by indigenous and campesinos (*puestos*, homesteads). Traditional human uses are characterized by subsistence fishing and hunting, charcoal and fuel wood production (Bucher and Huszar 1999, Morello *et al* 2007); and since the 20th century, extensive livestock ranching, mainly of cattle (Rearte 2010). The location of the different land systems across the study area is uneven, as a consequence of land use history and land quality. Indigenous properties are mainly located in western Formosa, where potential agriculture productivity represents only the 33% of the same variable of Santiago del Estero province (the most fertile area). In contrast, large and medium-sized agriculture farms are mostly located in the areas most suitable for agriculture. While *puestos* is the land tenure regime more evenly distributed across the region, protected areas are relatively young and were created in comparatively more degraded and less agroecologically suitable places (Marinaro *et al* 2015).

Land production systems in the Chaco are closely related to land tenure, although these systems differ in much more than property rights (Baldi *et al* 2015). Land tenure regimes differ in scale, technology,

integration into national and global markets, and land management practices (Hecht 1993, Beaumont and Walker 1996, Pacheco 2009, Homewood *et al* 2011, Baumman *et al* 2016). Tenure regimes are thus an interesting template for comparing the trade-offs between agriculture and the environment across diverse actor groups.

Modern farming is characterized by mechanized and technologically sophisticated agriculture, mainly for soybean crops and cattle production. Two main types of farms exist: large-scale, agri-business farms, and medium-sized to small, family-type farms. Livestock ranching (mainly cattle) and crop cultivation (soybean, wheat, maize and sorghum) are the main activities of these farms (INTA 2006, Volante *et al* 2006, Grau *et al* 2008). Livestock systems often use sown pastures or silvopastures, typically involving exotic grass species *Panicum maximum* cv. Gatton panic and *Cenchrus ciliaris* (Grau *et al* 2015). To make these activities profitable, medium-sized farmers tend to convert their entire property into crops or pastures, while large-scale farmers usually leave patches and strips of forests within their properties. This difference translates into specific configurations of the landscape associated to a particular farm size. A third farming system is *puestos* (homesteads), the traditional way of subsistence farming in the Chaco, mainly focused on extensive cattle and goat grazing into natural vegetation, which typically results in severe forest degradation but not complete deforestation. Some *puestos* also cultivate crops, albeit on small areas and mainly to feed the livestock during winter. Indigenous communities mainly remain in Formosa province, where the communities of the *Toba qom*, *Pilagá* and *Wichí* manage their land (Bucher and Huszar 1999). These communities typically consist of several families that communally share the land and its resources.

Table 1. Attributes of the five land tenure regimes. Acronyms: n = sample size, PI = preservation of biodiversity index; BI = biomass index; MI = meat production index; with their respective variances (Var).

	Large-scale farming properties	Medium-sized farming properties	<i>Puestos</i>	Indigenous properties	Protected areas
$N = 192$	$n = 38$	$n = 34$	$n = 43$	$n = 69$	$n = 8$
Median property size (ha)	10 819	2536	1029	2713	16 569
Range of property size (ha)	>4500	1201 to 4500	<1200	59 to 16 460	7782 to 122 903
Median PI	0.720	0.720	0.670	0.680	0.750
Var PI	0.006	0.005	0.010	0.006	0.002
Median BI	0.850	0.750	0.785	0.810	0.900
Var BI	0.034	0.102	0.033	0.070	0.045
Median MI	0.100	0.150	0.100	0.350	0.090
Var MI	0.004	0.015	0.060	0.088	0.011
Median LUO	1.650	1.580	1.580	1.870	1.750
Var LUO	0.020	0.080	0.060	0.040	0.090

Indigenous communities practice hunting, fishing and fruit gathering, charcoal and firewood production, and handicrafts manufacturing mostly based on ‘chaguar’ fibers (from two species of Bromeliaceae, *Bromelia hieronymi* and *B. urbaniana*) and ‘palo-santo’ wood (*Bulnesia sarmientoi*) (Arenas 2003). Indigenous communities also cultivate crops on small fields and breed small numbers of cattle and goats (Bucher and Huszar 1999) mostly for own consumption.

Finally, our study region includes several protected areas, without agricultural land use (with the exception of a few isolated *puestos* in Copo National Park). In many cases, protected areas in the study region contain degraded ecosystems, due to their recent establishment and their previous use based on extensive livestock ranching and wood extraction (Marinaro *et al* 2015).

Sampling design

To calculate our index of land-use outcomes, we first selected properties spread across the five land tenure regimes we considered: large-scale farming properties, medium-sized farming properties, *puestos*, indigenous properties and protected areas (figure 1, table 1). Based on spatial distribution of land tenure regimes, on the availability of cadastral and other spatial information, on our field knowledge and on visual interpretation of high-resolution images (available in Google Earth and the Landsat archive), we selected 192 properties to be included in this study (see appendix A.1 available at stacks.iop.org/ERL/12/045003/mmedia). We included all protected areas within the study region.

Land tenure regimes are not evenly distributed across our study region, and our sample is therefore imbalanced along environmental gradients. *Puestos* are the most evenly distributed tenure regime across our study region, and medium and large-scale farms are scarce in northern Salta and western Formosa, where indigenous properties dominate (figure 1). As biophysical conditions also vary across the study area, the uneven distribution of land tenure regimes translates into a biased association between land tenure regimes and

potential agriculture production ($F=76.99$, $p < 0.0001$). Consequently, indigenous communities were the land tenure type with the lowest potential production (median potential production = 168.00; figure A.1.1).

Land-use/cover map

A land-use/cover map for our study area was available from our own previous research (Baumann *et al* 2016). The map contains the following classes: ‘forest’, ‘pastures’, ‘croplands’ and ‘other’, as well as changes among these classes between 1985 and 2013. This map was generated by first deriving Landsat image composites using about 20 000 individual Landsat images, and then classifying these composites into the selected land cover classes with random forests algorithm. The overall classification accuracy of the land-cover map was about 90%, and class-wise user’s and producer’s accuracies ranged between 75% and 94% (Baumann *et al* 2016). For the purposes of this study, we only used the information for the year 2013, and extracted land-cover/use for the area of our 192 properties.

Data on preservation of biodiversity, standing stock of biomass and meat production

To estimate the level of preservation of biodiversity, standing stock of biomass and meat production within our 192 properties, we calculated the potentially reachable value and the actual value for each property for all three aspects. To derive the preservation of biodiversity index (PI), we extracted potential and actual species richness of trees, birds, mammals and amphibians based on an existing species distribution database (Torres *et al* 2014, see appendix A.2 for details). For potential species richness, we assumed no anthropogenic uses in the property: the potential number of species in a property was derived using species distribution models that assessed species’ environmental niche using only climatic, topographic and soil variables. For actual richness we used species distribution models that incorporate land use and land cover as predictive variables (Torres *et al* 2014, see

appendix A.2 for details). The difference between actual and potential richness for each taxa then defines the index of preservation of biodiversity in a particular property.

To calculate the potential standing stock of biomass in each property, we assumed that it was completely covered by undisturbed forest (see appendix A, table A.2.a). Thus, we fitted a regression model using the standing stock of biomass in the higher quartile (average +1 standard deviation) as dependent variable, and the minimum temperature of the coldest month as the independent variable (Gasparri and Baldi 2013), because it was the variable with the highest correlation coefficient. To estimate the actual standing stock of biomass in each property we applied tabulated values to the land covers 'pastures', 'agriculture' and 'other natural vegetated areas' (appendix A.2; table A.2.b). Data of forest biomass came from the standing stock of biomass map for the region, based on remote sensing and field survey plots (Gasparri and Baldi 2013).

To calculate potential meat production we assumed that the property was fully converted into soybean crops (which would give the highest meat yield among all land cover types). For doing this, we acquired potential soybean yield maps from the Global Agro-Ecological Zones Database (v3, IIASA/FAO 2012). For actual meat production we compiled soybean production data (2010-2015; SIIA 2015), and converted soybean production (based on the cropland area of each property) into meat -production-equivalents according to Smil (2000). This assumed 5.5 kg of soybean are equivalent to 1 kg of living pork (see appendix A.2 for details; tables A.2.a and A.2. b). We used this conversion rate since the main destination for Argentine soybean is China and Europe, where it is mainly used to feed pigs (Lapitz *et al* 2004). Moreover, comparing to meat equivalents allows for comparing cropping and grazing systems more easily, as in previous studies in the region (Grau *et al* 2008, Macchi *et al* 2015). For non-cultivated areas, we applied values of livestock yield from Macchi *et al* (2013).

Data analyses and integration to estimate land-use outputs

In order to map a preservation of biodiversity index (PI), a standing stock of biomass index (BI), and a meat production index (MI) (objective 1), we calculated these indices as the ratio between the actual and potential values. We estimated actual and potential values for each property as a whole as the average at the grid level (100 m grid). To do so for the PI required us to first calculate the pi of the individual biological groups (i.e. pi_{trees} , pi_{birds} , $pi_{amphibians}$ and $pi_{mammals}$), based on the actual and potential richness for each taxa at each property (appendix B, figure B.1); and then calculate the mean across the four taxa.

Values of the individual indices PI, BI and MI can reach values from zero to one, with values close to zero

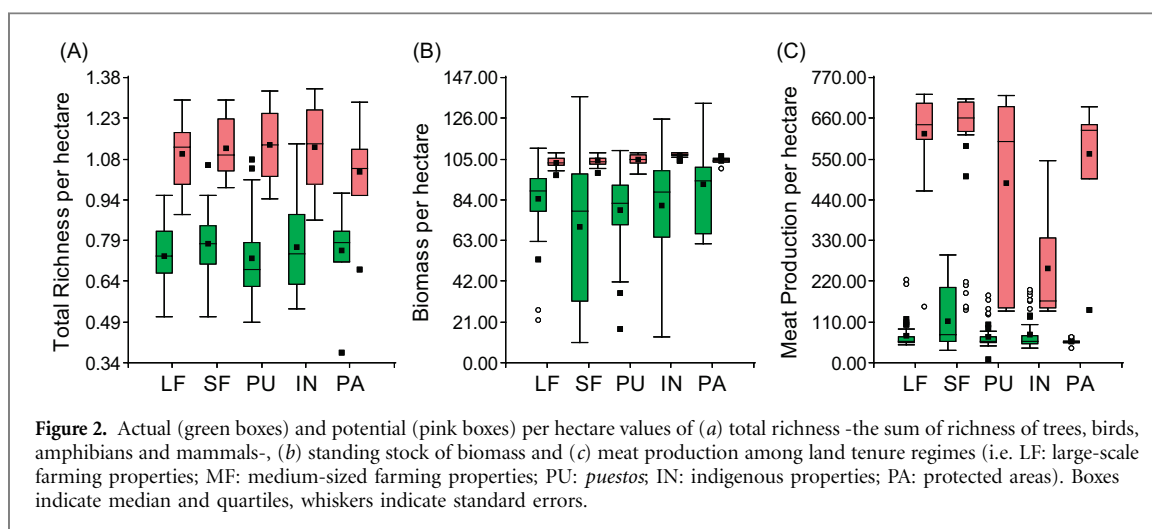
indicating low preservation, low biomass or low meat production, respectively. An index equal to one indicates a property reaches the potential value. In a few cases, indices can exceed one by a small margin, indicating that a particular property performs better than expected under optimal conditions.

Regarding our objective 2, to generate an integrated index of land-use outcomes (LUO), we calculated the sum of the three individual indices as $LUO = PI + BI + MI$. Our LUO thus ranges between zero and three and assumes an equal weight for each subcomponent. The higher the LUO, the higher the outcomes (thus, the lower the trade-offs among our three dimensions). We calculated the LUO for each property and compared median values among land tenure regimes using the Kruskal-Wallis test and pair-wise comparisons (objective 3). We also performed an analysis of variance (ANOVA) and Tukey's test (Tukey 1949) to see if PI for different taxa were significantly different across land tenure regimes. For PI, BI, and MI, as well as for LUO, we performed non-parametric (Kruskal-Wallis) analyses and pair-wise comparisons, because variables were neither normal (based on Q-Q plots) nor homoscedastic (based on a Levene's test; Di Rienzo *et al* 2011).

Results

Estimated levels of actual biodiversity, biomass and meat production varied markedly across the five land-tenure regimes we studied. However, these differences were often not statistically significant (i.e. p -values of >0.05 from the Kruskal-Wallis test for preservation of biodiversity and standing stocks of biomass values; figure 2). In terms of biodiversity, protected areas and medium-sized farms had the highest median actual richness (i.e. the sum of the richness of trees, birds, amphibians and mammals per hectare; 0.78 species ha^{-1}), although we found the maximum richness value in indigenous properties (1.14 species ha^{-1}). The lowest median actual total richness was found in *puestos* (0.68 species ha^{-1} , figure 2(a)). With regards to the actual standing stock of biomass, we found the highest median in protected areas (93.99 t ha^{-1}), and the lowest in medium-sized farms (78.41 t ha^{-1} , figure 2(b)). Finally, regarding actual meat production, we found the highest median values in medium-sized farms (77.01 kg $ha^{-1} yr^{-1}$), whereas the four remaining land tenure regimes had similar, but lower median meat production values (between 55.01 and 58.26 kg $ha^{-1} yr^{-1}$; $H = 14.77$, $p < 0.001$; figure 2(c)).

Potential values of biodiversity, biomass and meat production also varied across land tenure regimes. Protected areas had the lowest median potential total richness (1.05 species ha^{-1}), while *puestos*, indigenous properties and large-scale farms had the highest median values (between 1.13 and 1.15 species ha^{-1} ; figure 2(a)). These differences, however, were not



statistically significant ($p > 0.05$). We found the highest median potential standing stock of biomass in indigenous properties (107.31 t ha^{-1}), whereas large and medium-sized farms, as well as protected areas, reached the lowest median potential standing stock of biomass (between 103.25 t ha^{-1} and 104.03 t ha^{-1} ; $H = 84.64$, $p < 0.0001$; figure 2(b)). Potential meat production was highest in large and medium-sized farms and protected areas, and lowest in indigenous properties ($H = 75.95$, $p < 0.0001$; figure 2(c)).

Across the region, and independent from land-tenure regimes, the PI varied between 0.50 and 0.90, with a non-normal distribution and a median value of 0.70 ($\text{Sd} = 0.08$). When comparing PI among land tenure regimes, we found three distinct groups ($H = 9.80$, $p = 0.044$; table 1, figure 3(a)). *Puestos*, indigenous properties and large-scale farms formed the first group with the lowest median PI values, ranging between 0.67 and 0.71. Large-scale farms, medium-sized farms and protected areas, showed the highest median values (between 0.71 and 0.75). With intermediate values, a last group shared members with the other two (large and medium-sized farms and indigenous properties) (table 1, figure 3(a)). When comparing the land tenure regimes across the pi of the individual biological groups, regimes had particular behavior of grouping under the pi_{birds} , $pi_{\text{amphibians}}$ and pi_{mammals} , while pi_{trees} was similar among land tenure regimes (see appendix B, figure B.1 for details).

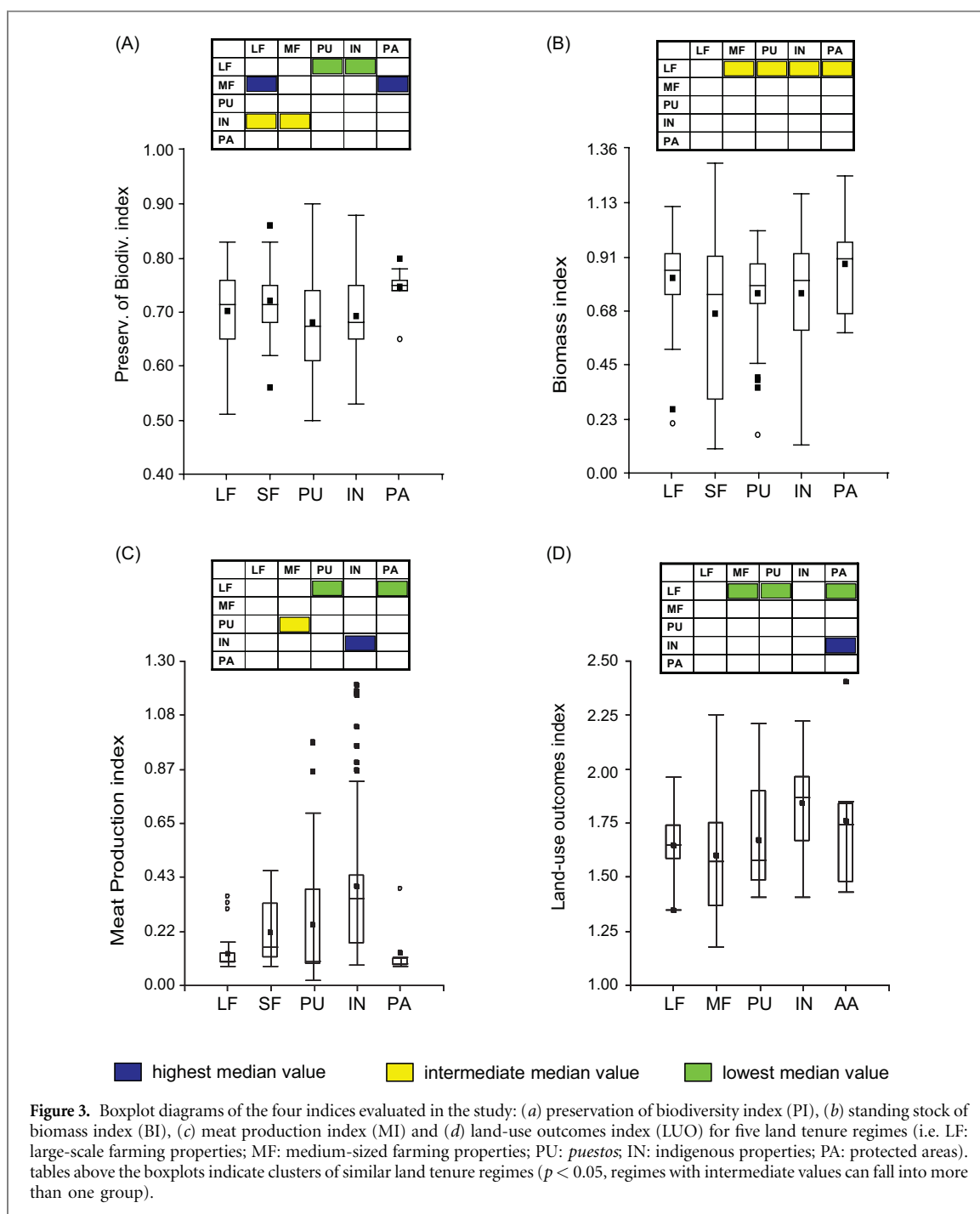
The BI and MI were also not normally distributed. The BI varied between 0.10 and 1.30 ($\text{Mn} = 0.81$, $\text{Sd} = 0.25$), but was not significantly different among land tenure regimes ($p > 0.05$; table 1, figure 3(b)). The MI reached values between 0.02 and 1.20 ($\text{Mn} = 0.14$, $\text{Sd} = 0.25$), and clearly separated three groups of land tenure regimes: (1) large-scale farms, *puestos* and protected areas with the lowest median values; (2) indigenous properties with the highest median value; and finally, (3) medium-sized farms and *puestos* ($H = 56.03$, $p < 0.0001$; table 1, figure 3(c)).

The integrated LUO index reached values between 1.18 and 2.40, with a non-normal distribution and a

median value of 1.68 ($\text{Sd} = 0.24$). The Kruskal-Wallis test showed significant differences between land tenure regimes, resulting in two clearly separated groups (table 1, figure 3(d)). Indigenous properties and protected areas had the highest LUO values (1.87 and 1.75 respectively), but protected areas also joined the remaining land tenure regimes in a second group of lower LUO values (with values between 1.58 and 1.75; $H = 33.70$, $p < 0.0001$; table 1, figure 3(d)).

Discussion

We used the example of the Dry Chaco in Northern Argentina, a global hotspot of land-use change, to explore differences in the trade-offs among agriculture production, biomass stocks and preservation of biodiversity, across five land tenure regimes. Three important insights emerge from our analyses. First, there were substantial differences among land tenure regimes in our indices, and these differences were not consistent across the combined land-use outcomes index and its three components. This implies that there is no land tenure regime that better balances agriculture production and its environmental outcomes in the Chaco. Instead, our results suggest that specific tenure regimes minimize specific trade-offs, and that each tenure regime includes possibilities for mitigating trade-offs further. Second, the highest combined land-use outcomes index (i.e. the lowest trade-offs among our three dimensions) occurred for indigenous communities and protected areas; probably this pattern was largely driven by environmental conditions rather than management. In other words, these two land tenure regimes had low trade-offs as they tend to be found in areas that are marginal for agriculture production (mostly due to lower rainfall), and to some extent naturally poorer in terms of potential biomass and biodiversity. Third, our land-use outcome index varied more across different environmental conditions than across land tenure regimes, and land tenure geography thus



seems to be strongly superimposed with environmental gradients.

The three individual indices that we combined into our land-use outcomes index (LUO), i.e. the preservation of biodiversity index, the standing stock of biomass index and the meat production index, varied independently among land tenure regimes. The preservation of biodiversity index segregated tenure regimes in three different groups, with protected areas and large and medium-sized farms reaching the highest values. This was a surprising finding, since we had expected that large and medium-sized farms to perform worst in this regard. Possible explanations for this may lie in different land-cover/use configurations (Marinero and Grau 2015, Baldi *et al* 2015), with

larger farms likely to have diverse types of land covers inside them. This could reflect the heterogeneity of resources available to biodiversity in different land tenure regimes (Beaumont and Walker 1996, Altrichter and Basurto 2008, Marinero *et al* 2015) (appendix B, figure B.1). The conservation value of larger farms has so far not been recognized widely. Given that private properties occupy a much larger area than protected areas in the region, our results suggest that conservation efforts should also be directed to take advantage of conservation opportunities by improving land-use practices in large farms. Because of their lower number and potentially higher administrative transparency, large farms owners represent a group of decision makers that could be

influenced towards more sustainable management practices at potentially lower costs.

The similarity in the standing stock of biomass index across all land tenure regimes was also a surprising result. We expected that the actual biomass in all properties were the result of particular land management practices, typical for a specific tenure regime, and thus to find the highest relative biomass stocks in indigenous communities and protected areas, where no deforestation takes place. Yet, even though indigenous communities had the highest potential biomass values, this tenure regime also showed to have only intermediate values of actual biomass. This could be the result of the long history of forests' use by indigenous people, with trees being an important source of charcoal and firewood (Bucher and Huszar 1999). Medium-sized farms reached the lowest actual biomass, but also had the lowest potential; thus, we could not state that their land-use practices impact on actual biomass values. Finally, protected areas reached the highest actual biomass albeit their potential biomass was the lowest. Thus, it seems that in relative terms protected areas were the most efficient tenure regime in conserving biomass.

Our results for agricultural production also yielded some unexpected findings. Although, a priori, we expected indigenous communities to have lower production because of their subsistence practices and limited access to technology, we found the highest index values (proportion of relative to potential) for this tenure regime. This result can be explained by the uneven distribution of our land tenure regimes along the Chaco's strong environmental gradients. Indigenous communities are typically located in those regions of the Dry Argentine Chaco that have the lowest potential agricultural production, suggesting that even modest agricultural production leads to high efficiency as measured by our index. Our findings, however, also imply that under such marginal conditions, traditional agricultural production systems may not necessarily underperform and may be able to take better advantage of the given environmental conditions than more intensified systems.

According to our analyses, the LUO as measured by our combined index reached highest values in protected areas and indigenous properties. Overall, these tenure regimes (mainly located in marginal agriculture areas) are the ones that showed the lowest trade-offs between agriculture and conservation. Indeed, a key finding was that the LUO varied more according to environmental factors than across the five tenure regimes we studied. A *posteriori* analyses (Spearman correlation between potential production and LUO) also showed that no land tenure regimes by itself, but instead the ecological potential production, better defined the LUO in a property. The higher the potential production, the lower the LUO ($r = -0.71$, $p < 0.0001$). The uneven distribution of land tenure regimes across our study region, due to historical,

political and economic reasons, contributes to explaining this somewhat unexpected finding. Potential production seems to be the key factor explaining the outliers that indigenous properties often constitute, since these properties are located where potential production is the lowest in the region. In addition, the historical evolution of land tenure regimes in the Dry Chaco strongly determines the economic and cultural choices and possibilities (Redo 2013, Baldi *et al* 2015), meaning that there is limited flexibility of social actors to shift roles and modes of production across a wide range of biophysical conditions (Alix-Garcia *et al* 2012).

Overall, our findings suggest that the current geographic distribution of land tenure regimes in the Argentine Dry Chaco to some extent reflects social and technological adaptations to the prevailing environmental gradients, in particular potential agriculture productivity. This finding should be considered in terms of land-use planning seeking to encourage and/or limit the development and spread of different land-use systems in the Chaco. In the context of the current zoning for the Chaco (Argentine 'Forest' Law 26 331) and possible REDD + projects (Reducing Emissions from Deforestation and forest Degradation), an approach for land management and zoning could involve the promotion of land tenure regimes that minimize trade-offs, for each particular ecological zone in the Chaco. In practical terms, our results suggest that intensifying agriculture on already deforested areas appears to be useful for increasing agricultural outputs, since those areas have already 'paid' high ecological costs in terms of biomass and biodiversity loss. This should be especially the case in areas that are highly suited for agriculture such as northern Santiago del Estero and western Chaco province. Conversely, in more marginal areas, such as western Formosa, less intensified modes, including subsistence farming and indigenous communities of production appear to lower trade-offs between agricultural production and environmental impacts. On a more general level, this highlights that trade-offs can vary substantially in space, and no single land-use strategy is likely to minimize these trade-offs across large and environmentally heterogeneous regions.

Acknowledgments

We acknowledge funding by the Argentine Research Council (CONICET), the Argentina National Agency of Science and Technology Research (PICT 2006 #1693 and PICTO 2011 OTNA #98), the Environmental Conservation Fund of the Argentine Galicia Bank (FOCA program 2011), Rufford Small Grants for Nature Conservation (RSG 57.11.08 and RSG 10.12.05), Einstein Foundation Berlin, the German Federal Ministry of Education and Science (BMBF; project PASANOVA, 031B0034A), and the German

Research Foundation (DFG, project KU 2458/5-1). Sofia Nanni helped with language revision. We also thank two anonymous reviewers for thorough, constructive, and encouraging comments on prior manuscript versions.

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