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Woody Plant-Cover Dynamics in Argentine Savannas from the 1880s to 2000s: The Interplay of Encroachment and Agriculture Conversion at Varying Scales

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Abstract

Woody plant-cover dynamics can alter the provisioning of ecosystem services that humans rely on. However, our understanding of such dynamics today is often limited by the availability of reliable and detailed land-cover information in the past, before the onset of remote sensing technologies. In this study, we carefully extracted information from historical maps of the Caldenal savannas of central Argentina in the 1880s to generate a woody cover map that we compared to a 2000s dataset. Over about the last 120 years, woody cover increased across approximately 12,200 km^2 (14.2% of the area). During the same period, about 5,000 km^2 of the original woody area was converted to croplands and around 7,000 km^2 to pastures, about the same total land area as was affected by encroachment. A smaller area, fine-scale analysis between the 1960s and the 2000s revealed that tree cover increased overall by 27%, shifting from open savannas to a mosaic of dense woodlands along with additional agricultural clearings. Statistical models indicate that woody cover dynamics in this region were affected by a combination of environmental and human factors. Over about the last 120 years, increases in woody plant cover have stored significant amounts of C (95.9 TgC), but not enough to compensate for losses from conversions to croplands and pastures (166.7 TgC), generating a regional net loss of 70.9 TgC. C losses could be even larger in the future if, as predicted, energy crops such as switchgrass, would trigger a new land-cover change phase in this region.

Key words: *Prosopis caldenia*; caldén; caldenal; Pampa; semiarid; historical maps; deforestation; agriculture frontier.

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Introduction

Human population and the demand for goods and services have increased dramatically in the last centuries, and are only expected to increase more in the near future (Haberl and others 2007). To satisfy this demand, some ecosystems have experienced large changes in land use and land cover, contributing to current global environmental change (Foley and others 2005). Changes in land cover affect the persistence of biodiversity, soil properties, and water cycles, and modify climate at varying spatial and temporal scales, ultimately affecting the provision of ecosystem services on which humans rely (Li and others 2007). Rangelands comprise approximately 45% of the global land surface (Bailey 1996), and changes in their cover can have consequences from local to global scales. Hence, it is important to understand past land-cover dynamics in semiarid regions, including both causes and consequences, to better manage natural resources for the future.

Human-induced land-cover changes typically take one of two forms: (1) concrete changes in cover due to a planned intervention, or (2) gradual changes over time. As an example of the first, conversion to agriculture turns millions of hectares of forest, savannas, and grasslands to croplands to increase food and fiber production (Ramankutty and Foley 1999). On the other hand, increases in woody plant cover in grasslands and savannas, a process called woody plant encroachment (WPE), is a much more gradual process that can occur over decades or even centuries. WPE is considered one of the most extensive forms of rangeland land-cover change (Blaum and others 2007), affecting vast portions of arid and semiarid regions worldwide (Asner and others 2004). It has been related to local land use and management (Lunt and others 2010), with the introduction of cattle and changes in fire regimes being two of the most commonly cited drivers (Asner and others 2004). Woody plant clearing and encroachment are two processes usually studied independently, but active agriculture frontiers in semiarid regions, where both occur simultaneously, offer a unique opportunity for understanding complex woody plant-cover dynamics and their consequences.

Shifts between wooded and non-wooded plant communities change the composition, structure, and functioning of ecosystems. A higher density of woody plants typically increases plant water use (Kim and Jackson 2011; Nosetto and others 2012), modifies the energy balance in the ecosystem through changes in albedo (Beltran-Przekurat and others 2008) and can change the size and speed of nutrient cycling (McCulley and Jackson 2012). Net total ecosystem C stock generally increases with woody plant cover (Eldridge and others 2011), whereas ecosystem C is lost when natural woodlands are converted to agriculture (Don and others 2011). Given that wooded ecosystems represent a significant portion of the terrestrial C stocks, spatially explicit studies of woody plant dynamics are essential to understand the long-term variability in C source-sink dynamics at regional scales.

The timespan of land-cover studies is limited in most cases by the availability of reliable information from the past. Most studies of changes in woody plant cover use remotely sensed information such as aerial photos and satellite images as the primary data source (for example, Browning and others 2008), limiting the time of comparison to the onset of the technology used. Historical accounts and maps can extend the time frame of land use and land-cover change studies (Bender and others 2005), and have been widely used in Europe and North America, where systematic records have been collected and preserved for centuries (Yang and others 2014). For example, information registered in the USA General Land Office Records has been used to describe changes in land cover in different regions of the USA, although few studies have used such data to study increases in woody cover (for example, Andersen and Baker 2005). This type of historical dataset is not common in the developing world, and as a consequence reliable long-term land-cover reconstructions are hard to generate in these regions.

The semiarid savannas of central Argentina offer a unique opportunity to study long-term woody plant-cover dynamics in an agriculture frontier region where both WPE and clearing for agriculture have occurred. A systematic land survey undertaken in the 1880s recorded detailed vegetation information and was used to generate a baseline dataset of woody plant cover. The objectives of the present study were to: (1) assess the usefulness of historical records to study woody plant-cover dynamics in semiarid savannas ecosystems over +120 years; (2) determine the magnitude of WPE and clearing in this dynamic agriculture frontier; (3) identify factors affecting each of those two processes; and (4) estimate the consequences of woody cover dynamics for regional C stocks.

Methods

Study Area

The Caldenal of central Argentina (Figure 1) is a semiarid savanna ecosystem of 190,000 km^2 dominated by the *caldén* tree (*Prosopis caldenia*). It has an understory of perennial grasses frequently interspersed with dunes, wetlands, and lakes (Cabrera 1994). The climate is temperate with a mean

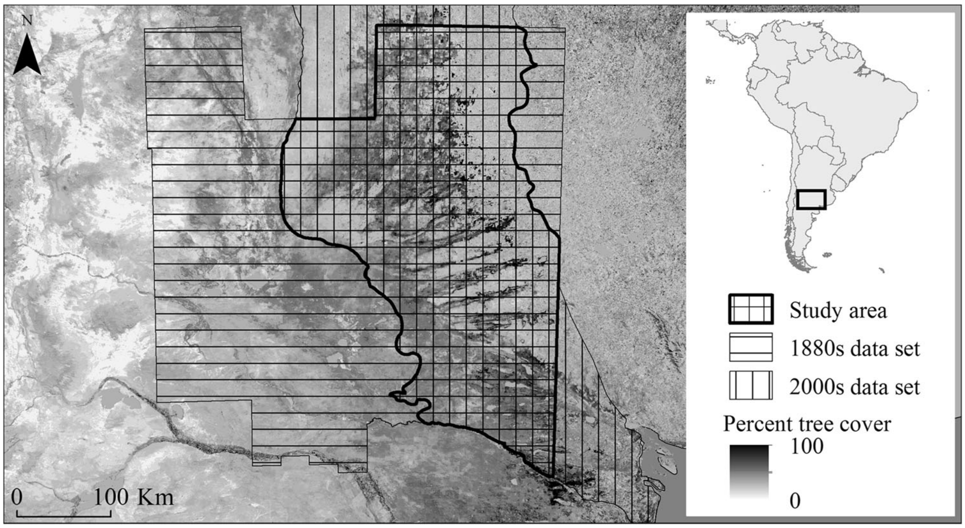

Figure 1. Study area in the Caldenal ecosystem in La Pampa province in central Argentina. Percent tree cover from the MODIS Vegetation Continuous Fields product Collection 5 version 1 from 2009 is presented as the background.

annual temperature of 15°C; mean monthly temperature of the hottest month is 24°C and of the coldest month is 8°C (Cano and others 1980). The region is flat or slightly rolling and is formed mainly of a deep mantle of loessic sediments (Soriano and others 1991). The area is characterized by a SW-NE rainfall gradient ranging from 300 to 700 mm/y, concentrated mostly in summer months, with year-round water deficits (Cano and others 1980).

The area has been occupied for at least 8,500 years by hunters and gatherers (Zink 2008). With the arrival of Europeans to Buenos Aires in the 16th century, cattle appropriation, herding, and trading became primary economic activities (Zink and Salomon Tarquini 2008). The Caldenal is central to what was an important colonial trade route that connected Buenos Aires to Chile (Ramos and others 2009). Major land-cover and land-use changes occurred with the arrival of new settlers at the end of the 19th century, when the Argentine government seized control of the region, and have intensified since then (Alonso 2009). Some of these changes include replacement of natural systems with agriculture, extractive logging, introduction of non-native species, overgrazing by livestock, alteration of fire regimes (Medina 2007; Mendez 2007b), and encroachment of native woody plants into grasslands and savannas (Baldi and Paruelo 2008; González-Roglich and others 2012).

Regional Land Cover in the 1880s

Once the federal government seized control of what is currently La Pampa province, surveyors systematically characterized the terrain between 1882 and 1884 (Lluch 2008). They delineated the vertices of 1,784 10- by 10 km townships (called

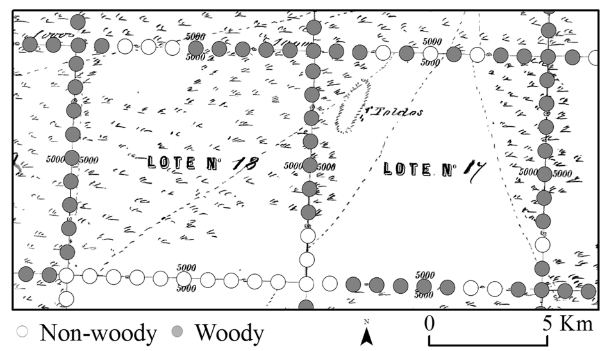

Figure 2. Example of the Points method used for land-cover information extraction from the 1880s historical maps.

lotes in Spanish). For each township, they drew a map and wrote a description of the vegetation they found along the edges of each township, totaling 2,710 pages of information. We digitized these pages, and georeferenced each individual map in a geographic information system.

Spatially continuous land-cover representations, such as polygons, are easier to interpret than points or lines. In this case, however, we only had certainty that the surveyors had walked the perimeters of each township, and therefore we considered that the information along those perimeters would be more accurate than the information further away from the edges. To address that limitation, we developed a Points method to extract land-cover information. A grid of points spaced 1 km apart and located along the edges of the townships was overlaid on the map (Figure 2); if the point was in the proximity (<500 m) of a woody plant symbol (that is, trees and shrubs), then the point was classified as covered by woody plants (Table 1). For

Table 1. Datasets Used for the Different Spatio-temporal Analysis

Period	Data set	Year	Spatial resolution	Cover data extracted
1880s	Historical maps	1882–1884	Coarse	Woody
1960s	Aerial photographs	1961–1967	Fine	Tree
2000s	Forest inventory map	2005–2006	Coarse	Woody
2000s	CBERS images	2009	Fine	Tree

display, we estimated proportional woody cover at the township level as the proportion of points classified as covered by woody plants. Given the lack of independent data sets, we were not able to assess the accuracy of the 1880s map. However, visual inspection of the overall spatial pattern did not highlight any systematic artifacts such as surveyor or area bias.

Regional Land Cover in the 2000s

As part of the first National Forest Inventory in Argentina, the Caldenal region was resurveyed in the early 2000s (Mendez 2007a). Using remotely sensed data and extensive field surveys, a land-cover map of the region was developed (Mendez 2007c). Using a vector version of the map, we recoded land-cover classes as woody (shrubland, savanna, and forest) or non-woody (other land-cover types). We selected the same point locations used to describe the 1880s vegetation to characterize woody plant cover in the 2000s. The accuracy of this simplified dataset aggregated to woody–non-woody was estimated based on the error matrix provided by the authors (Mendez 2007c).

Fine-Resolution Spatial Patterns in the 1960s and 2000s

To examine woody plant-cover dynamics at a finer spatial resolution than in the regional land-cover maps, we used 100 16-km^2 quadrats distributed throughout the study area. The size of the quadrats was determined by the footprint of the 1960s aerial photos. We assessed changes in tree cover and tree aggregation by comparing panchromatic aerial photographs from the 1960s (scale 1:30,000) to the panchromatic CBERS-2B images from the 2000s. The 1960's aerial photographs were scanned and georeferenced, and then resampled up to 2.5 m to match the spatial resolution of the CBERS images. The spatial resolution of this dataset limited our ability to identify shrubs (that is, woody plants of smaller size), and for that reason we were limited to identification of trees with canopy diameters larger than 5 m. Each image from both datasets was then manually thresholded to generate binary maps of tree/non-tree cover.

Thresholding can introduce errors due to subjectivity at the moment of defining the threshold and the effect of shadows. In an effort to control for such error, all the thresholding was performed by the same person for the 1960s and 2000s datasets. Given that our objective was to assess changes between the 1960s and the 2000s, consistency in processing was fundamental. We used field data estimating percent tree cover at 35 50- by 50-m square field plots within the study area (for details see González-Roglich and others 2014) to compare CBERS tree cover estimated aggregating to 50 m pixels. We estimated the root mean square error (RMSE) and the mean absolute error (MAE) as relative measures of the precision of the thresholding method for the 2000s dataset. Given that the analysis performed to the 1960s images was the same as the one applied to the 2000s images, we assume that the error estimates should be relatively similar for both datasets.

For each quadrat and time period, we determined indices which provide quantitative descriptions of the landscape pattern (O'Neill and others 1988; Swenson and Franklin 2000): percent tree cover, mean patch size, and clumpiness. The clumpiness index ranges from −1 when the focal patch type (woody vegetation) is maximally disaggregated, to 1 when the patch type is maximally aggregated, and produces a value of zero for a random distribution of trees across the landscape, regardless of the proportion of the area occupied by that particular class (McGarigal and others 2012). Patch statistics were computed in FRAGSTATS V4 (McGarigal and others 2012). Paired t-tests were used to assess the change between the 1960s and the 2000s (Sokal and Rohlf 1994).

Drivers of Woody Cover Change

We used logistic regression models to identify factors affecting woody plant-cover change between the 1880s and the 2000s. A set of 15 candidate explanatory variables addressing dispersion, topography, water availability, soil type, and human influence was identified (Table 2). To simplify the interpretation of both the direction and the magnitudes (effect sizes) of the estimates, variables were standardized to z-scores (Grueber and others 2011). Three sets of models were constructed, one for WPE, one for conversion from woody cover to cropland, and one from woody cover to pasture. For each set of models, we first performed univariate logistic regression analysis (GLM with logit-link and binomial error) on each potential predictor. Predictors with $p < 0.10$ for univariate logistic regression or those with higher p-values but of known ecological importance were selected for multivariate analysis (Hosmer and others 2013). To avoid potential multicollinearity, no single pair of variables with correlations higher than 0.75 were included in the models. When such situations emerged, the variable with the most direct effect on woody plant dynamics, based on the literature, was selected for the model. We used the Akaike Information Criterion (AIC) for model selection (Burnham and Anderson 2002) and model averaging to incorporate model selection uncertainty by weighting the influence of each model by the strength of its supporting evidence (Gutierrez and others 2013). To evaluate the model's spatial dependence, we analyzed the spatial autocorrelation of the residuals in the averaged model using Moran's I spatial correlograms with the spatial weight matrix based on the inverse Euclidean distance.

Goodness of fit of the final model was assessed using The Hosmer–Lemeshow Test (Hosmer and others 2013). To evaluate the predictive performance of the final averaged model, we used the receiver operating characteristics (ROC) analysis (Fielding and Bell 1997). The area under the ROC curve (AUC) is typically used as a general measure of predictiveness (Fawcett 2006). AUC values close to 0.5 indicate no discrimination, and values close to 1 indicate exceptional discrimination (del Hoyo and others 2011). Statistical analysis was performed in R version 3.0.2 using the AICcmodavg for model averaging (R Core Team 2013).

Carbon Stocks

To assess the effect of changes in woody plant cover on total C stocks across the Caldenal region, we first identified the percent area affected by each land-cover transition. C stocks for natural vegetation covers were obtained from recent local field surveys (González-Roglich and others 2014). For cropland, we considered only soil organic C (SOC), which was estimated to be 50% of the SOC of the original land cover (Zach and others 2006). Changes were estimated as the difference between the total C stock of the land cover in 1880s and the 2000s, and then converted to regional stocks in TgC.

Results

Regional-Scale Changes

We fully mapped, for the first time, woody plant cover in the Caldenal Savannas of central Argentina as it was in the 1880s (Figure 3). Before the

Table 2. Variables Considered for the Logistic Regression Models

Type	Variable	Description
Dispersion	DWO	Distance to the closest pixel covered by woody plants in the 1880s. Derived from the 1880s' data set
Topography	ELE	Elevation derived from the 90 m SRTM DEM (Jarvis and others 2008)
	SLO	Slope in percent. Derived from ELE
	TPI	Topographic position index: continuous variable that ranges between −1 (valleys) and 1 (ridges). Derived from ELE following Jenness (2006)
	ASP	Aspect: 1 (north facing slopes), 0 (no slope), and −1 (south facing slopes). Derived from ELE
Water	MAP	Mean annual precipitation from Hijmans and others (2005)
	ARI	Aridity index: ratio between mean annual precipitation and mean annual evapotranspiration. From Zomer and others (2008)
	WTD	Water table depth from Fan and others (2013)
	PET	Potential evapotranspiration from Zomer and others (2008)
Soil	SOD	Soil order: 0 = molisols, and 1 = entisols. From Cano and others (1980)
Human	DSE	Distance to the closest 1880s' native American settlement. Derived from 1880s' map
	DTR	Distance to the closest 1880s' trail. Derived from 1880's map
	DCI	Distance to the closest city with a population of at least 1,000 in the year 2000. Population center data from CIESIN (2011)
	DRO	Distance to the closest paved road in the year 2000 from DPV (2012)
	DRR	Distance to the closest rail road track. Rail road data from IGN (2013)

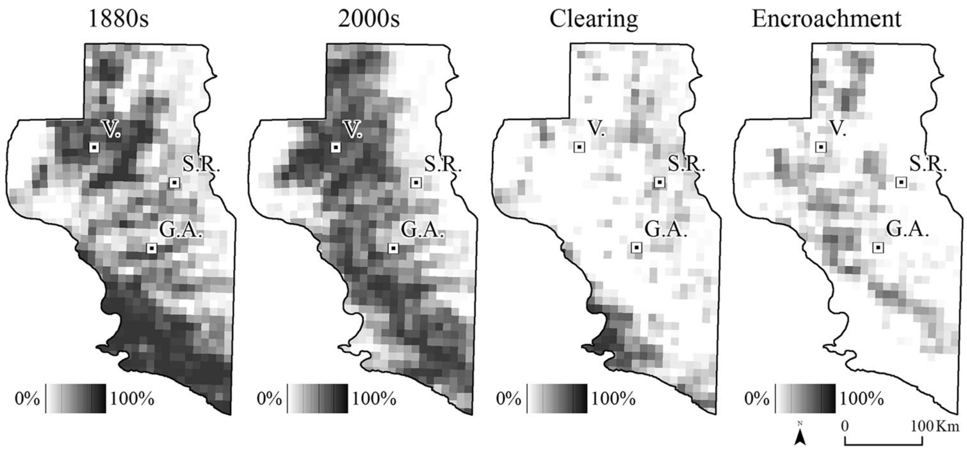

Figure 3. Woody cover averaged at the township level for the 1880s and 2000s, and changes over that period attributable to clearing for agriculture and woody encroachment. The three major cities in the area are presented as a reference: Santa Rosa (S.R.), General Acha (G.A.), and Victorica (V.).

Table 3. Top Ranking Models Predicting Grassland to Woodland Transition Between the 1880s and 2000s as Assessed by Akaike's Information Criterion (AIC)

Model Grassland to Woodland	K	AIC	ΔAIC	AIC_w
DWO + ELE + SLO + WTD + MAP + SOD + DTR + DSE + DCI	10	386.27	0.00	0.507
DWO + ELE + SLO + SOD + DTR + DSE + DCI	8	387.35	1.07	0.297
DWO + ELE + SLO + WTD + MAP + DTR + DSE + DCI	9	389.71	3.43	0.091
DWO + ELE + SLO + DTR + DSE + DCI	7	389.85	3.57	0.085
DWO + ELE + SLO + WTD + MAP + SOR	7	393.12	6.84	0.017

Distance to woody (DWO), elevation (ELEV), slope (SLO), mean annual precipitation (MAP), water table depth (WDP), soil order (SOD), distance to settlements (DSE), distance to trails (DTR), and distance to cities (DCI). Number of estimated parameters including intercept (K), AIC, the difference in AIC (ΔAIC), and the AIC weights (AIC_w) are provided.

influx of European settlers at the end of the 19th century, 44.1% of the area was covered by woody plant communities. The overall area occupied by woody communities remained relatively consistent over the last 120 years, representing 43.8% in the 2000s (overall accuracy for the 2000s dataset = 96.5%, Kappa = 0.92). However, this consistent woody cover proportion is the result of two opposite processes: increases in woody plant cover in some areas and losses in others. Between the 1880s and the 2000s, woody plants occupied 12,181 km^2 (14.2% of the study area). The increase in woody plant cover occurred primarily in the central portion of the study area (NW–SE diagonal, Figure 3), both in areas where woody plants were present in the 1880s, but are now found at increased density, and in areas where they were absent previously. Woody plant-cover loss, on the other hand, occurred primarily at the eastern and western edges of the Caldenal, affecting 11,970 km^2 (13.9% of the study area). Of these areas, 40.4% were converted to croplands (5,045 km^2), and 59.6% to pasture (6,925 km^2), according to the land-cover information provided by the 2000s land-cover map.

The increase in woody plant cover in the Caldenal region has been influenced by several factors. Of the set of models considered (Table 3), the averaged model presented acceptable fit ($\chi^2 = 8.87$, df = 8, p value = 0.35, Table 4) and high discrimination (AUC = 0.86). The Moran's I autocorrelation coefficient decreased from 0.126 for the response variable to 0.025 for the residuals. The spatial correlogram showed no discernible problematic patterns. According to this model, the probability of encroachment was higher in grasslands closer to sites with woody plants in the 1880s, and at locations with higher elevations, steeper slopes, poorer soils (that is, entisols), or closer to Native American trails (Table 4). Mean annual rainfall, water table depth, distance to settlements, and distance to cities also had effects, but given that the 95% CI in each case included zero, we consider these effect to be less conclusive.

Woody cover loss occurred in two distinct regions within the study area. Although conversion to cropland occurred toward the east, conversion to pastures occurred mostly in the west (Figure 3). Consequently both processes were modeled independently. Of the set of models evaluated for the woodland to cropland transition (Table 5), the

Table 4. Variable Estimates of the Averaged Grassland to Woodland Transition Model

Variable	Averaged coefficient	Standard error	95% CI	Variable importance
Intercept	**−1.02**	**0.24**	**(−1.49, −0.54)**	**1.00**
DWO	**−0.89**	**0.24**	**(−1.35, −0.42)**	**1.00**
ELE	**1.01**	**0.18**	**(0.66, 1.35)**	**1.00**
SLO	**1.48**	**0.26**	**(0.97, 1.98)**	**1.00**
MAP	−0.06	0.29	(−0.62, 0.50)	0.62
WTD	0.35	0.23	(−0.10, 0.80)	0.62
SOD	**0.86**	**0.41**	**(0.05, 1.67)**	**0.82**
DSE	−0.17	0.17	(−0.49, 0.16)	0.98
DTR	**−0.43**	**0.17**	**(−0.77, −0.10)**	**0.98**
DCI	−0.03	0.20	(−0.42, 0.36)	0.98

Distance to woody (DWO), elevation (ELEV), slope (SLO), mean annual precipitation (MAP), water table depth (WDP), soil order (SOD), distance to settlements (DSE), distance to trails (DTR), and distance to cities (DCI). The 95% confidence interval (CI) for coefficients in bold did not include 0. Hosmer and Lemeshow goodness of fit test: $\chi^2 = 8.87$, *df = 8, p value = 0.35. AUC = 0.89.*

Table 5. Top Ranking Models for Woodland to Cropland Transition between the 1880s and 2000s as Assessed by Akaike's Information Criterion (AIC)

Model Woodland to Cropland	*K*	AIC	ΔAIC	AIC_w
SLO + MAP + SOD + DCI	5	129.82	0.00	0.532
MAP + SOD + DCI	4	130.59	0.76	0.364
SLO + MAP + DCI	4	135.17	5.35	0.037
MAP + DCI	3	135.67	5.84	0.029
SLO + SOD + DCI	4	135.89	6.06	0.026

Slope (SLO), mean annual precipitation (MAP), soil order (SOD), and distance to cities (DCI). Number of estimated parameters including intercept (K), AIC, the difference in AIC (ΔAIC), and the AIC weights (AIC_w) are provided.

Table 6. Variable Estimates of the Averaged Woodland to Cropland Transition Model

Variable	Averaged coefficient	Standard error	95% CI	Variable importance
Intercept	**−3.79**	**0.64**	**(−5.03, −2.54)**	**1.00**
SLO	−0.65	0.42	(−1.48, 0.17)	0.60
MAP	**0.83**	**0.33**	**(0.18, 1.48)**	**0.96**
SOD	**−1.79**	**0.78**	**(−3.33, −0.26)**	**0.93**
DCI	**−1.83**	**0.48**	**(−2.76, −0.90)**	**1.00**

Slope (SLO), mean annual precipitation (MAP), soil order (SOD), and distance to cities (DCI). The 95% confidence interval (CI) for coefficients in bold did not include 0. Hosmer and Lemeshow goodness of fit test: $\chi^2 = 3.88$, *df = 8, p value = 0.86. AUC = 0.90.*

averaged model presented acceptable fit (Chi squared = 3.88, df = 8, *p* value = 0.86) and discrimination (AUC = 0.90, Table 6), as did the model for the woodland to pasture transition ($\chi^2 = 9.99$, df = 8, *p* value = 0.26, and AUC = 0.81, Tables 7 and 8). The Moran's I autocorrelation coefficient decreased from 0.057 for the response variable to 0.008 for the residuals in the first model, and from 0.060 to 0.010 in the second. The spatial correlogram showed no discernible problematic patterns. Wooded areas experienced a higher probability of being converted to agriculture if they were in areas with higher mean annual rainfall or richer soils (that is, molisols) and if they were closer to cities. On the other hand, if wooded areas had lower rainfall and were further away from cities, they were more likely to be converted to pasture.

Fine-Scale Changes

Between the 1960s and the 2000s, we found at the finer spatial resolution that mean tree cover area

Table 7. Top Ranking Models Predicting Woodland to Pasture Transition Between the 1880s and 2000s as Assessed by Akaike's Information Criterion (AIC)

Model Woodland to Pasture	*K*	AIC	ΔAIC	AIC_w
SLO + MAP + DCI	4	215.47	0.00	0.416
SLO + MAP + SOD + DCI	5	215.64	0.17	0.382
SLO + MAP + SOD	4	218.66	3.18	0.085
MAP + DCI	3	219.31	3.83	0.061
MAP + SOD + DCI	4	220.59	5.11	0.032

Slope (SLO), mean annual precipitation (MAP), soil order (SOD), and distance to cities (DCI). Number of estimated parameters including intercept (K), AIC, the difference in AIC (ΔAIC), and the AIC weights (AIC_w) are provided.

Table 8. Variable Estimates of the Averaged Woodland to Pasture Transition Model

Variable	Averaged coefficient	SE	95% CI	Variable importance
Intercept	**−2.82**	**0.44**	**(−3.68, −1.95)**	**1.00**
SLO	**−0.57**	**0.26**	**(−1.07, −0.07)**	**0.90**
MAP	**−0.85**	**0.28**	**(−1.40, −0.29)**	**0.98**
SOD	0.70	0.51	(−0.31, 1.70)	0.51
DCI	**0.57**	**0.23**	**(0.13, 1.02)**	**0.91**

Slope (SLO), mean annual precipitation (MAP), soil order (SOD), and distance to cities (DCI). The 95% confidence interval (CI) for coefficients in bold did not include 0. Hosmer and Lemeshow goodness of fit test: χ^2 = 9.99, df = 8, p value = 0.26. AUC = 0.81.

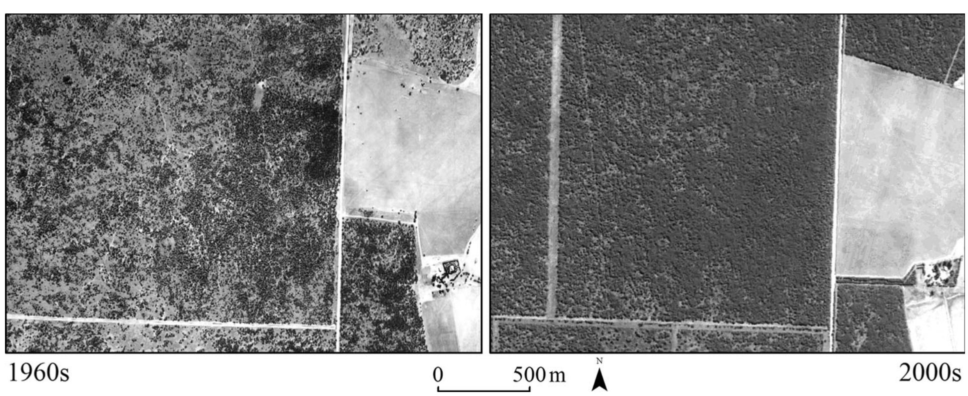

Figure 4. Example of changes in the spatial pattern of woody plant cover from the 1960s (aerial photograph at left) to the 2000s (CBERS image at right). Some areas experienced clearing for agriculture, whereas others experienced increased density in woody plant cover.

increased in the sampled area from 11.6 to 14.7% ($t = -1.79$, p value = 0.07). The agreement between the 2000s tree-cover estimate and the field data was relatively high, RMSE = 0.151 and MAE = 0.111. Although tree cover increased by 27%, mean tree patch size increased almost 300%, from 249 m^2 in the 1960s to 954 m^2 in the 2000s ($t = -8.63$, p value <0.01). During the same period, mean number of tree patches decreased, from 5.2 to 2.2 patches per ha ($t = 6.58$, p value <0.01), and mean tree clumpiness increased 17% from 0.68 to 0.80 ($t = -11.4$, p value <0.01). Over the last 40 years, tree cover increased and changed from a disaggregated spatial pattern to a more aggregated one, becoming dominated by either cleared areas or closed woodlands (Figure 4).

Changes in C Stocks

Land-cover dynamics have affected C stocks in this region (Table 9). The increase in woody plant cover in former grasslands captured almost 96 TgC, although that sink was not enough to compensate for the losses due to conversion to cropland and

Table 9. Land-cover Transitions in the Caldenal Savannas Between the 1880s and the 2000s: Total Area, Changes in C Stocks per Unit Area and Total Regional Stock Change

	Area (km^2)	C stock change	
		(kg C m^{-2})	(TgC)
Woodland–Woodland	25,467	–	–
Woodland–Pasture	6,925	−7.87	−54.5
Woodland–Crops	5,045	−8.10	−40.9
Grassland–Grassland	10,734	–	–
Grassland–Crops	23,866	−2.99	−71.4
Grassland–Woodland	12,181	7,87	95.9
Other land covers	1,801	–	–
Regional total	86,019		−70.9

pasture. Per unit area, conversion from woodlands to croplands had the single largest effect (8.1 kgC m^{-2} loss), but overall conversion of grasslands to croplands generated a larger loss (71.4 TgC) due to the extended area experiencing this change. Regionally, Caldenal savannas have lost about 71 TgC over the last 120 years due to changes in land cover in rural areas.

Discussion

Detailed historical maps generated by systematic surveys offer a unique opportunity for understanding long-term vegetation dynamics. By extracting information from 1880s land surveys, we were able to document the extent of woody plant cover across about 86,000 km^2 of the Caldenal savannas of central Argentina. Although we found that the total area occupied by woody plants has remained similar across the last 120 years there are two processes at play: woody plant encroachment in areas previously covered by grasslands and open savannas (14.2% of the study area) and the loss of woody plant cover due to conversion to cropland and pastures (13.9% of the area). Of the areas that lost woody plant cover, approximately 40% were conversions to croplands in the eastern part of the study area next to the Pampa grasslands and 60% were conversions to pasture in the southwestern portion of the study area (Figure 3).

Modeling ecological processes is intrinsically complex. Given the coarse grain of our analysis, our primary research goal was to identify variables that could help us understand the underlying drivers of the dynamics identified. Our model of grassland-to-woodland transition revealed that environmental factors had the most important influence on where WPE occurred. Proximity to areas already covered by woody plants in the 1880s was the single most important factor in areas that experienced woody encroachment. The fact that *caldén* seeds are mostly dispersed by cattle (Lerner 2004) supports the notion that distance to seed sources is an important factor controlling expansion. Topographic factors were also important, although their individual effects were smaller than that of proximity to existing woody plants. A higher probability of encroachment was found at higher elevations. Because elevation in the study area decreases to the east, where precipitation is higher and soils more fertile, conversions to agriculture may have prevented WPE in lower elevation areas. Encroachment was less likely to occur in Molisols than in Entiols. Soil intrinsic physical (for example, texture) and secondary properties (for example, fertility) have been found to affect the development and abundance of woody plants in North American grasslands (Liu and others 2013). Our coarse-scale modeling results seems to reflect the preference of *Prosopis caldenia* for coarse textured and well-drained soils (Cano and others 1980), confirming the effect of soil properties in WPE dynamics. Slope also showed a strong effect, with WPE having a higher probability of occurrence in areas with steeper slopes, consistent with previous studies that found denser woodlands on slopes than in flat areas (Cano and others 1980).

Rainfall is the single most important factor affecting water availability in this semiarid region. Given that agriculture here is almost exclusively rainfed, mean annual rainfall was an important factor explaining the conversion from woodlands to crops and pastures. Croplands were located in areas with higher water availability, whereas pastures were primarily in the drier areas to the west. Mean annual precipitation was not identified as an important factor affecting the increase in woody plant density. However, increased precipitation in the last century seems a likely factor to have affected WPE in this region. Regionally, precipitation has shown a 20% increase between the first and the second half of the 20th century (Tripaldi and others 2013), which could have favored the establishment and development of woody plants (Munson and others 2013).

Most current landscapes have been shaped directly or indirectly by human activities (Antrop 2005). In the present day, proximity to urban centers and roads highly influence the intensity of land use. Nonetheless, activities that took place decades and centuries ago can generate legacy effects that shape the development of plant communities over time (Marcucci 2000). Historically, Native Americans intensively used the Caldenal. We identified 54 settlements in the historical maps and a trail system over 6,500 km long, which they used to transport cattle from the Pampa grasslands to Chile (Ramos and others 2009). The probability of encroachment was higher closer to these trails, which suggests the existence of a legacy effect. Calden seeds are dispersed by cattle, increasing the establishment of new seedlings and the development of denser woodlands. As for the current human influences we tested, we found none affecting the probability of encroachment, but we did find that conversion to agriculture was more likely closer to cities. The opposite was found for conversion to pasture.

In this study, we were able to assess woody plant cover dynamics in the Caldenal savannas over 120 years and to identify several environmental and human factors that contributed to those dynamics. However, two important factors could not be modeled in our analysis but likely played a role in land-cover dynamics across this region: management and fires. Livestock type and density influence the establishment and development of woody plants (Dussart and others 1998), but we were unable to incorporate management practices implemented by individual land owners due to lack of detailed historical data for such a large area. Fire is another factor which influences the structure of savanna ecosystems (Gordijn and others 2013), and we know that both fire intensity and frequency have changed since the arrival of settlers in the region (Medina 2007). The lack of a spatially explicit dataset of fire occurrence for the last 120 years prevented us from incorporating this factor into the models.

Vegetation dynamics play a key role on the global C cycle (Beer and others 2010). Although large amounts of C have been released to the atmosphere from deforestation and conversion to agriculture (Houghton 2013), plant growth in woody ecosystems has been responsible for a significant C uptake (Ballantyne and others 2012). We found that in the Caldenal savannas, conversion of grasslands and woodlands to agriculture has converted the region into a net C source, losing around 10% of the total C stocks available in the 1880s. That loss would have been even larger if woody plant communities had not developed in grasslands and open woodlands. In the last century, the agriculture frontier has been limited by the relatively arid conditions of the western portion of the study area, but recent studies have indicated the suitability of the region for the development of energy crops such as switchgrass (Diogo and others 2014). Such a transformation could trigger massive land-cover changes and, consequently, a release of C to the atmosphere much larger than that seen in the last century.

Conclusion

Over the last 120 years, the Caldenal savannas have experienced significant changes in land use and cover. Using maps from the 1880s and the 2000s, we identified important changes in land cover, with large areas being converted to agriculture and others experiencing increases in woody plant cover. Between the 1960s and the 2000s, our fine spatial resolution analysis showed that tree-cover area increased by 27%, changing from sparsely covered savannas to a mosaic of dense woodlands interspersed with intensive agriculture. This change in land cover has altered the regional carbon balance. Over the last 120 years the Caldenal savannas have lost approximately 10% of the C stock available in the 1880s, and that loss could potentially be much larger in the future if energy crops are introduced in the region (Diogo and others 2014). Moreover, the consequences of the new spatial configuration of communities in this region expand far beyond C storage. The development of high-density woodlands combined with natural habitat loss due to agriculture conversion would also reduce the provision of suitable habitat for native wildlife and potentially affect the water and energy balances in the region.

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