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Original Research

Effect of Climoedaphic Heterogeneity on Woody Plant Dominance in the Argentine Caldenal Region☆,☆☆

Lauren N. Svejcar [a,b,*,1], H. Raul Peinetti [c], Brandon T. Bestelmeyer [b]

[a] Department of Plant and Environmental Sciences, New Mexico State University, New Mexico, USA
[b] US Department of Agriculture —Agricultural Research Service, Jornada Experimental Range, Las Cruces, New Mexico, USA
[c] Facultad de Agronomía, Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina

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ABSTRACT

Woody plant encroachment is widespread throughout drylands of the world, but rates and patterns of encroachment at the regional scale can be mediated by soil and climate. Climoedaphic properties may therefore help to explain patterns of woody plant dominance. In the Caldenal region of central Argentina, which is experiencing widespread woody plant encroachment, we used stratified and targeted inventory of vegetation and soils alongside climate data to classify vegetation states and then identify factors indicating resistance to woody plant encroachment. We found that three climoedaphic contexts differed in the degree of woody plant dominance. Sandsheet landforms had the lowest likelihood of a shrub thicket state. Within loamy soils, sites with deep soil carbonates in warmer and wetter climates were less likely to feature a shrub thicket state than sites with shallow carbonates in cooler and drier climates. These contexts serve as a basis for recognizing different ecological sites to assist mapping and prioritization of management interventions in the Caldenal region. Simple inventory-based approaches can be helpful for designing land management recommendations in other ecosystems.

Introduction

Spatial variation in soil and climate (climoedaphic) properties can cause spatial heterogeneity in woody plant dominance and the likelihood of state transitions from grassland or savanna to woody-plant dominated states (Walker et al., 1981). The potential for tree-dominated states in mesic savannas increases with mean annual precipitation (Hirota et al., 2011; Sankaran et al., 2005), whereas shrub-dominated states may be favored where dry conditions limit fuel continuity and fire spread (Bond, 2008; Buck and Monger, 1999). Because woody plants have extensive root systems, soil properties that promote deep water infiltration and storage, such as on coarse-textured soils, tend to favor woody plants over shallow-rooted herbaceous species (McAuliffe, 1994; Ward et al., 2013). Conversely, woody plant growth can be constrained (and herbaceous plants favored) on soils with relatively high subsoil clay content and limited deep infiltration (Archer et al., 1995; Bestelmeyer et al., 2006, 2011). Petrocalcic (cemented carbonate) soil horizons occurring at shallow depths also limit deep water infiltration and rooting by woody plants (Browning et al., 2012). Abundant run-on water in lower landscape positions, however, may override soil texture effects and promote woody plant dominance on soils otherwise resistant to encroachment (Wu and Archer, 2005). Thus, climoedaphic variations may help to explain and predict patterns of woody plant encroachment (Bestelmeyer et al., 2011).

Information about how plants respond to climoedaphic variations can be used in management decision making. Land classification systems such as ecological sites in the United States (Bestelmeyer et al., 2009) use data on plant-soil-climate relationships to categorize land areas that differ in the likelihoods of state transitions and how they can be managed. Ecological sites are differentiated on the basis of soil-landscape and climate properties that can be mapped. The classification and mapping of ecological sites can assist in prioritizing management or policy interventions.

Here, we use an inventory dataset from the Caldenal region of central Argentina to test if the occurrence of vegetation states is predictably related to soils and climate. Changes in vegetation composition, specifically an increase in woody plants, have been clearly documented for the past 2 centuries in the Caldenal (Dussart et al., 2011). Human impacts from the European settlement period (120 years ago) to the present, such as logging, agricultural development, grazing, and alterations in the fire regime, have created a mosaic of vegetation states featuring

☆ Nomenclature is based on the US Department of Agriculture Plants Database (http://plants.usda.gov/java/; accessed 12 March 2014).

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* Correspondence: Lauren N. Svejcar, School of Veterinary and Life Sciences, Murdoch University, 90 South St, Murdoch, Western Australia, Australia.
E-mail address: lauren.svejcar@bgpa.wa.gov.au (L.N. Svejcar).
[1] Current address: Lauren N. Svejcar, School of Veterinary and Life Sciences, Murdoch University, 90 South St, Murdoch, Western Australia, Australia, and Biodiversity Conservation Center, Kattidj Close, Kings Park, Western Australia, Australia.

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variations in woody plant dominance and herbaceous composition (González-Roglich et al., 2015). Changes in historic fire regimes and seed dispersal of woody plants across the region have led to a gradual infilling of woody plants (closed forest states) including *Prosopis caldenia* and *Condalia microphylla* and shifts to shade-tolerant, unpalatable grasses. High-intensity fire within closed forest states can lead to a shrub thicket (locally known as *fachinal*) due to resprouting by woody plants, very slow self-thinning, and feedbacks causing more frequent fire (Bóo et al., 1996; Dussart et al., 1998).

The objectives of this paper were to 1) quantitatively characterize alternative vegetation states and 2) determine if the occurrence of different vegetation states was related to climoedaphic variations within the Caldenal region. Disturbance and management history are the most widely accepted explanations for differences in vegetation (Bogino et al., 2015; Busso, 1997; Distel and Boo, 1996; Dussart et al., 1998, 2011; Llorens, 1995). However, variation in climoedaphic conditions may result in distinct vegetation states under similar management and disturbance regimes, due to variations in resistance to shrub encroachment (Bestelmeyer et al., 2006). We used an inventory dataset and a variety of statistical approaches to classify vegetation states of the Caldenal region and then tested the hypothesis that landform, soil, and climate variables can explain the distribution of different states. Given the well-documented history of woody plant proliferation in the region, we used this analysis to infer the factors conferring resistance to woody plant proliferation as a basis for ecological site classification.

Methods

Study Area

The Caldenal encompasses approximately 10 million ha (Fernández and Busso, 1999) and features level to undulating plains. The landscape is covered by quaternary aeolian deposits (Zárate and Tripaldi, 2012) with soils composed of entisols distributed throughout the region and mollisols, which are limited to the east (Peña Zubiate et al., 1980). The region has a semiarid climate with higher precipitation in the NE trending to more arid conditions in the SW, with mean annual precipitation ranging from 700 to 400 mm along this gradient (Casagrande et al., 1980).

Two woody plant species are dominant throughout the Caldenal: the tree *P. caldenia* and shrub *C. microphylla*. *Prosopis caldenia* can grow to 12 m and forms an open, monospecific tree stratum, with an understory dominated by C3 shortgrasses, or mixed C4 midgrasses, under low livestock grazing (Cano et al., 1980; Estelrich et al., 2005). *Prosopis flexuosa var. flexuosa* can be found as a companion tree. Other shrubs are present at variable densities, including *C. microphylla, Schinus* spp., *Lycium* spp., *Ephedra triandra, Chuquiraga erinacea,* and *Geoffroea decorticans*.

Herbaceous species are locally categorized by ecologists and land managers according to four plant groups (Cano, 1988; Llorens, 1995, 2013). C3 shortgrasses comprise species that attain a maximum height of 50 cm, are highly palatable for livestock, dominate under well-managed conditions (i.e., not overgrazed), and include *Poa ligularis, Piptochaetium napostaense,* and *Nasella tenuis*. C3 midgrasses are more shade tolerant than shortgrasses, are not palatable, reach a maximum height of 100 cm, and include *Jaraba ichu, Nasella tenuisima,* and *Amelichloa brachychaeta.* C4 midgrasses, with a maximum height of 80 cm, are associated with warmer climates and include *Setaria leucopila, Digitaria californica, Trichloris crinita,* and *Sporobolus subinclusus.* Finally, annuals/forbs include annual grasses (*Bromus brevis, Cenchrus spinifex, Hordeum* sp.) and forbs (*Plantago* sp., *Chenopodium album, Baccharis ulicina, Solanum eleagnifolium*).

Inventory Dataset

Sampling was conducted across the entire Caldenal region in order to capture the breadth of vegetation composition and physical conditions (climate, landforms, and soils). Cleared areas or cultivated areas were avoided. Two kinds of sampling were employed to ensure that the variety of vegetation conditions present in the Caldenal was represented in our dataset: stratified-random sampling and targeted sampling. Stratified sampling was based on a coarse soil map consisting of five soil units (Calciustolls, Haplustolls, Torripsamments, Ustipsamments, Ustorthents) at 1:500 000 scale. A spatially random set of 20 points with a randomized visitation order was generated for each soil unit. Rejection rules were defined for each point including lack of accessibility (e.g., owner could not be contacted), cleared or similar disturbances, and affected by recent (< 4 yr) fires. However, all sampled sites had evidence of historic fires (> 4 yr). Targeted sampling was conducted opportunistically alongside stratified sampling on the basis of the presence of contrasting vegetation near to random sampling sites and areas that are regarded as well managed (Llorens, 2013) and areas that have not been used for livestock grazing in decades. A total of 47 georeferenced sampling points were visited (stratified random sites = 19 and targeted sites = 28). Sample sites in this study are used for livestock production except for four sites placed in a state park (Parque Luro) where livestock grazing was discontinued in the 1950s (Amieva, 1992), but substantial grazing by a large population of introduced deer *(Cervus elaphus)* has persisted. Extensive management history was unavailable for most of the sample points, however, precluding statistical analysis of management effects. At all points, data were collected on landform, soil characteristics, and plant community composition and structure. In addition, average precipitation and temperature data (1950 − 2000) for each point were obtained from the WorldClim database, which features estimates at 1-km spatial resolution (Hijmans et al., 2005).

Each point was categorized to one of the following landform categories. *Lowland:* valley floor; *Slope:* gentle slopes (2 − 8%) on piedmont landforms; *Meseta*: level high plain or mesa; *Sandsheet*: dune lands, sandy undulating plains; and *Plain*: level plain on a basin floor. All landforms were recorded in the field and verified on the basis of digital elevation models (Jarvis et al., 2008) and Google Earth elevation profiles.

A soil pit was excavated at each point to a depth of 40 cm by shovel, and then a soil auger was used for an additional 60 cm for a total soil depth of 1 m (unless a hardpan or physical obstruction deterred reaching 1 m). Soil classification was conducted following Schoeneberger (2002). Samples were collected from each horizon (≈40 g). Laboratory analyses on horizon samples for percent silt and clay followed the Bouyoucos (1962) hydrometer method. Carbonate stage for each horizon, depth to carbonate reaction (i.e., effervescence using 1-N HCl), depth to petrocalcic horizon (a cemented $CaCO_3$-rich layer), and maximum clay content of the soil profile were recorded. Soil temperature regime was mesic for the entire area and derived from La Pampa soil survey information (Peña Zubiate et al., 1980).

Belt transects (30 m long) were used to record mature woody plant density and composition. At each sample point, the belt transect was strung north to south on level sites (< 1% slope) or perpendicular to > 1% slopes. Sample points were visually determined to be in one of the following base/trunk cover classes: high (> 50% woody plant base/trunk cover), low (< 50% woody plant base/trunk cover), and savanna (< 5% woody plant base/trunk cover). High, low, and savanna classes were measured with 5-m, 10-m, and 20-m-wide belt transects, respectively, in order to sample an adequate number of plants. Woody plants with > 50% of the canopy falling inside the belt were tallied by species (and summed to plant group where needed), and the height of each individual was measured.

Line-point intercept transects (20-cm record intervals, 30-m length) were used to estimate cover of herbaceous species. Transects were placed inside and parallel to belt transects. Canopy cover was calculated for each of the four herbaceous groups described earlier.

The belt transect and line point intercept data were used to quantify the relative importance of seven plant groups in the characterization of vegetation states, including three woody plant groups: 1) *Prosopis* trees

(*P. caldenia* and *P. flexuosa* var. *flexuosa*), 2) *C. microphylla,* and 3) all other shrub species; and four groups of herbaceous plants: 1) C3 shortgrasses, 2) C3 midgrasses, 3) C4 midgrasses, and 4) annuals/forbs. Plant density and height were used for woody vegetation and foliar canopy cover for herbaceous species.

Data Analysis

We conducted our analysis in two steps. First, we asked if broad (and easily mapped) landforms were related to major differences in vegetation states, climate, and soils. Second, we conducted a more detailed classification of vegetation states and tested for relationships between vegetation and climoedaphic variables when landform classes were uninformative (i.e., where there were no clear differences in soils, climate, and vegetation among landforms). In the first step, relationships between landforms, plant groups, and soil/climate variables were visualized using redundancy analysis (RDA), a canonical ordination method. We determined the significance of canonical axes using a Monte Carlo permutation test (1 000 permutations) with CANOCO 5.X. Differences in soil/climate and vegetation variables among landforms was tested using Kruskal-Wallis tests followed by post-hoc Wilcoxon tests when overall differences were significant ($P \leq 0.05$).

For landforms whose sampling points did not differ in vegetation, soil, or climate variables, we conducted more detailed analyses in a second step. We first classified vegetation states using hierarchical cluster analysis (Ward's minimum variance method) to group points on the basis of the cover/density of the seven plant groups described earlier. Since we used different metrics for quantifying woody (density) and herbaceous (cover) plant groups, data were standardized by subtracting the plant group mean and dividing by the standard deviation.

In addition, we used fuzzy set functions to classify forest structure (woody plant density and heights) at all plots to aid in describing vegetation states. Fuzzy sets can be used to estimate the degree to which an element belongs to a set. Values represent the degree of membership and range from no membership (value = 0) to complete membership (value = 1) (Cox, 1994). Each point was classified to one of three

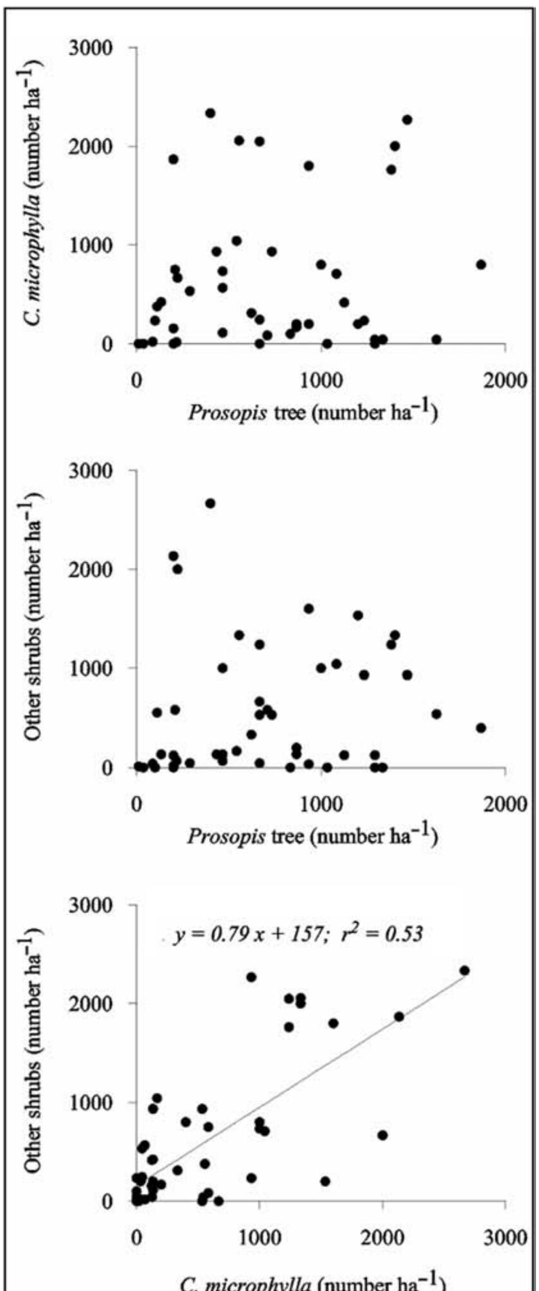

Figure 1. Relationships between density of woody plant groups (*Prosopis* trees, *C. microphylla*, and other shrub species) in sites sampled throughout the Caldenal.

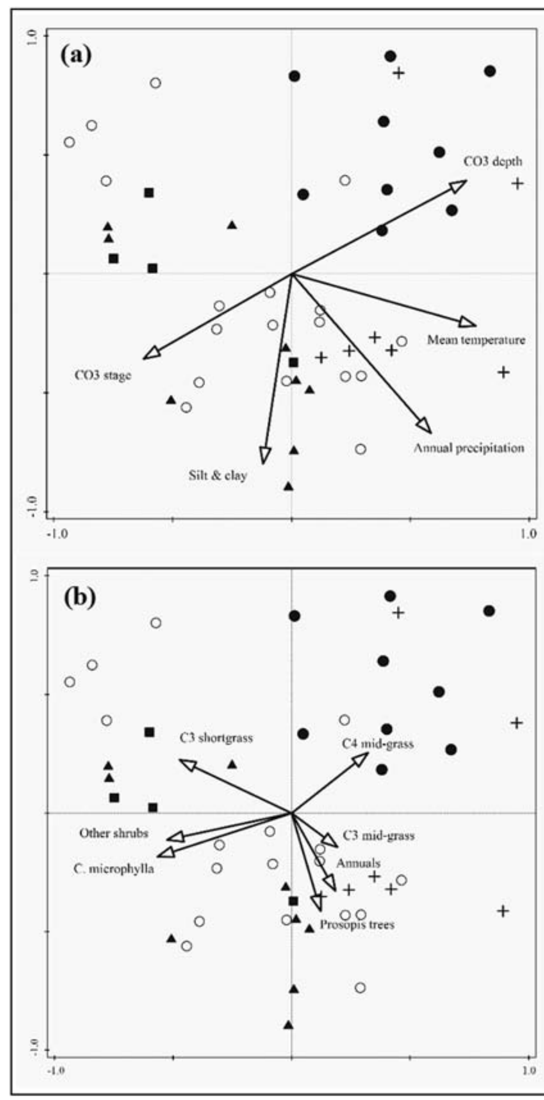

Figure 2. Representation of sampled sites with environmental variables (CO3 equals carbonate) (**a**) or plant groups (**b**) in the first two axes of the ordination diagram (RDA). Sampled sites correspond to lowland (triangle), meseta (square), plain (cross), sandsheet (filled circle), and slope (open circle).

Table 1
Median of soil and climate properties across sampled landforms in the Caldenal.

Environmental properties	Lowland	Slope	Meseta	Sandsheet	Plain
Silt + clay of A horizon (%)	$43^{A,1}$ (35, 61)[2]	34^{B} (27, 39)	27^{B} (24, 31)	6^{C} (5, 7)	42^{B} (19, 67)
Carbonate stage	2^{A} (1.5, 2)	$2^{A,B}$ (1.5, 2)	3^{B} (2, 4)	0^{C} (0, 0)	$2^{A,B}$ (0, 2)
Depth to carbonate reaction (cm)	58^{A} (2, 68)	52.5^{A} (8.6,75)	15^{A} (3, 51.5)	> 100^{B}	52^{A} (4, > 100)
Maximum clay content (%)	24^{A} (11, 29)	$20^{A,B}$ (7, 28)	19^{A} (12, 24)	5^{B} (4, 13)	$10^{A,B}$ (5, 27)
Mean annual temperature (°C)	15.5^{A} (15, 15.7)	$15.3^{A,B}$ (15.1, 15.5)	14.9^{B} (14.8, 15.2)	15.4^{A} (15.1, 15.6)	16.1^{C} (16, 16.3)
Mean annual precipitation (mm)	547^{A} (496, 572)	$554^{B,C}$ (499, 572)	$507^{A,C}$ (507, 575)	$543^{B,C}$ (504, 556)	$579^{B,C}$ (558, 617)

[1] Different letters indicate significant differences at $P \le 0.05$ using pairwise Wilcoxon tests given that the overall Kruskal-Wallis test was significant at the $P \le 0.05$ level.
[2] Lower and upper quartiles values.

woody plant density categories—open forest (OF), closed forest (CF), and thicket (TH; Table A.1) —and three height categories based on the height of the tallest woody plants in the plot: short (Sh), medium (Md), or tall (Tl; Table A.2). Mean fuzzy membership values for the density and height categories were calculated for each cluster with μ^{OF}, μ^{CF}, and μ^{TF} referring to mean membership value of open, closed, and thicket forest, respectively, and μ^{Sh}, μ^{Md}, and μ^{Tl} referring to mean membership value of short, medium, and tall tree height, respectively.

The relationship between soil and climate variables and vegetation states was then evaluated using Kruskal-Wallis and post-hoc Wilcoxon tests. Cluster analysis and nonparametric tests were conducted in SAS JMP 11.0, SAS Institute, Inc.

Results

Environmental and Woody Plant Characteristics

Mean annual temperature at sample sites across the region ranged from 14.6°C to 16.3°C, and annual precipitation ranged from 440 mm to 630 mm. Higher values of both variables were found in the NE sector of the sample region, as expected. Soils sampled ranged from very sandy (96% sand content) to silt loam (30% sand content; Table B.1). Depth to a petrocalcic horizon was < 1 m in only 4 out of 47 sites; however, most soils had a calcic (carbonate-enriched) horizon.

Sites with low total woody density were dominated by *Prosopis* trees, but as woody density increased, *C. microphylla* and other shrub species were an increasingly dominant proportion of woody plants. This pattern is reflected in the lack of linear relationship between densities of *Prosopis* trees and *C. microphylla* or other shrubs ($P = 0.31$ and 0.46, respectively), and a significant linear relationship between *C. microphylla* and other shrubs ($P < 0.001$ $r^2 = 0.53$) (Fig. 1).

Variation in Climate, Soil, and Vegetation Among Landforms

The canonical axes of the RDA ordination explained a large fraction of the variation in the plant composition ($P = 0.002$; explained fitted variation = 85%) for all sites. The ordination also illustrated that the sandsheet landform was distinctive in both climoedaphic conditions and vegetation, but such differences among other landforms were not obvious (Fig. 2). Compared with other landforms, sandsheet soils had lower silt and clay content in A horizons, and there was no calcic horizon development in the top meter of soil (Table 1, Fig 2a). Climate tended to be warmer and drier in the sandsheet compared with the other landforms. The sandsheet had a far lower woody plant density than any other landform. *C. microphylla* was nearly absent, and while herbaceous groups did not exhibit significant differences among landforms, C4 midgrasses were abundant on the sandsheet (Fig. 2b, Table 2). Forest structure was characterized as open ($\mu^{OF} = 0.8$; $\mu^{CF} = 0.2$; $\mu^{TF} = 0.1$) dominated by *Prosopis* trees of medium to tall height ($\mu^{Sh} = 0.0$; $\mu^{Md} = 0.6$; $\mu^{Tl} = 0.4$). On the basis of the correspondence of distinct soil properties, low woody plant cover, and the absence of an important encroaching shrub species, we considered the sandsheet to be a distinct ecological site featuring an Open forest state. The remaining landforms, however, did not consistently differ from one another in soil and vegetation, so were subject to cluster analysis and additional comparisons of climate and soil properties as a second step.

Vegetation States on Nonsandsheet Landforms

While the cubic clustering criterion indicated that seven clusters were optimal, examination of raw data, ordination, and fuzzy set classification indicated that five clusters resulted in more interpretable vegetation groupings. Five nonsandsheet vegetation states were identified with the following characteristics (Table 3):

1. Moderately closed/C4 midgrass: Moderately closed forest ($\mu^{OF} = 0.4$; $\mu^{CF} = 0.6$; $\mu^{TF} = 0.10$) dominated by *Prosopis* trees of medium height ($\mu^{Sh} = 0.2$; $\mu^{Md} = 0.6$; $\mu^{Tl} = 0.3$), with few *C. microphylla* or other woody species in the shrub strata. Herbaceous strata were dominated by C4 midgrasses.
2. Moderately closed/C3 shortgrass: Moderately closed forest ($\mu^{OF} = 0.4$; $\mu^{CF} = 0.6$; $\mu^{TF} = 0.0$) dominated by *Prosopis trees.* Most sites had well-developed tree strata of medium height ($\mu^{Sh} = 0.3$; $\mu^{Md} = 0.6$; $\mu^{Tl} = 0.2$), except sites that were in long-term recovery from fire, which had a relatively sparse cover of trees. Other shrub species were usually well represented but typically had lower densities than *Prosopis* trees. Herbaceous strata were dominated by C3 shortgrasses.
3. Closed/C3 midgrass: Dense forest ($\mu^{OF} = 0.0$; $\mu^{CF} = 0.5$; $\mu^{TF} = 0.4$) with a higher woody plant density than moderately closed forest

Table 2
Median woody density (plant ha^{-1}) and herbaceous foliar canopy cover (%) across sampled landforms in the Caldenal.

Plant groups	Lowland	Slope	Meseta	Sandsheet	Plain
Prosopis trees	$1033^{A,B,1}$ (200, 1 208)[2]	644^{A} (450, 1 208)	$900^{A,B}$ (300, 1 633)	217^{B} (119, 667)	833^{A} (433, 1 292)
Condalia microphylla	422^{A} (99, 1 288)	700^{A} (225,1 833)	588^{A} (244, 1 550)	0^{B} (0, 64)	100^{A} (42, 750)
Other shrub species	$125^{A,B}$ (94, 1 187)	933^{A} (191, 1 261)	$478^{A,B}$ (200, 1 339)	44^{B} (6, 333)	33^{B} (0, 583)
Total woody plants	$1458^{A,C}$ (789, 3 517)	2304^{A} (1 258, 3 946)	$2133^{A,C}$ (1 083, 4 017)	300^{B} (119, 1 078)	1375^{C} (1 167, 1 500)
C4 midgrass	$5^{A,B}$ (2, 12)	$2^{A,B}$ (0, 18)	11^{A} (4, 27)	25^{B} (8, 41)	$13^{A,B}$ (11, 24)
C3 shortgrass	$21^{A,B}$ (7, 34)	11^{B} (0, 40)	$42^{A,B}$ (21, 74)	9^{A} (0, 50)	2^{A} (0, 7)
C3 midgrass	6^{A} (3, 14)	3^{B} (0, 19)	14^{A} (2, 45)	1^{A} (0, 17)	$21^{A,B}$ (8, 29)
Annuals	7^{A} (0, 15)	4^{A} (0, 37)	0^{A} (0, 10)	3^{A} (0, 11)	3^{A} (0, 6)

[1] Different letters indicate significant differences at $P \le 0.05$ using pairwise Wilcoxon tests given that the overall Kruskal-Wallis test was significant at the $P \le 0.05$ level.
[2] Lower and upper quartile values.

Table 3
Median woody density (plant ha^{-1}) and herbaceous foliar canopy cover (%) in the five clusters distinguished by Wards cluster analysis for nonsandsheet sites.

Plant groups	1. Moderately closed/C4 midgrass	2. Moderately closed/C3 shortgrass	3. Closed/C3 midgrass	4. Closed/ annuals	5. Thicket/ mixed grass
Prosopis trees	$833^{A,1}$ (378, 1 313)[2]	583^{A} (133, 867)	1008^{A} (821, 1 142)	589^{A} (222; 1 233)	1381^{A} (533, 1 433)
Condalia microphylla	233^{A} (71, 683)	298^{A} (156, 422)	454^{A} (142, 1 254)	700^{A} (233, 800)	2048^{B} (2 014, 2191)
Other shrub species	33^{A} (0, 117)	133^{A} (122, 200)	1288^{B} (813, 1 567)	967^{B} (542, 1 333)	1238^{B} (1 085, 1 952)
Total woody plants	1167^{A} (911, 1 563)	1122^{A} (689, 1 500)	2884^{B} (2 104, 3 634)	2400^{B} (1 500, 3 417)	4666^{C} (4 166, 5 067)
C4 midgrass	28^{A} (18, 45)	4^{BC} (2, 5)	11^{B} (7, 13)	0^{C} (8, 0)	5^{A} (0, 27)
C3 shortgrass	7^{A} (3, 21)	39^{B} (30, 54)	6^{A} (0, 17)	0^{C} (0, 1)	40^{A} (20, 58)
C3 midgrass	17^{A} (13, 24)	3^{B} (0, 7)	54^{C} (47, 57)	6^{AB} (3, 19)	0^{B} (0, 4)
Annuals	6^{A} (0, 18)	0^{A} (0, 3)	0^{A} (0, 1)	36^{B} (16, 50)	0^{AB} (0, 6)

[1] Different letters indicate significant differences at $P \le 0.05$ using pairwise Wilcoxon tests given that the overall Kruskal-Wallis test was significant at the $P \le 0.05$ level.
[2] Lower and upper quartiles values.

clusters. *Prosopis* trees were of medium height ($\mu^{Sh} = 0$; $\mu^{Md} = 0.9$; $\mu^{Tl} = 0.1$). C3 midgrasses were the dominant herbaceous species.

4. Closed/annuals and forbs: Closed forest ($\mu^{OF} = 0.0$; $\mu^{CF} = 0.7$; $\mu^{TF} = 0.3$) of medium to tall height ($\mu^{Sh} = 0.1$; $\mu^{Md} = 0.5$; $\mu^{Tl} = 0.5$). Structure was similar to cluster 3 (closed/C3 midgrass), but with larger variation in the relative proportions of different woody species and with generally taller trees. Herbaceous strata were dominated by annuals/forbs or codominated by C3 midgrasses.
5. Thicket/mixed grass: Very high density of woody plants ($\mu^{OF} = 0.0$; $\mu^{CF} = 0.0$; $\mu^{TF} = 1.0$) of short to medium height (i.e., shrubby growth forms; $\mu^{Sh} = 0.7$; $\mu^{Md} = 0.3$; $\mu^{Tl} = 0$). *C. microphylla* (2 000 to 2 500 plants ha^{-1}) and other shrubs species were dominant. *Prosopis* spp. density varied from ca. 500 to 1 400 plants ha^{-1}. The herbaceous layer was characterized by C3 shortgrasses with some C4 midgrasses.

Vegetation State-Environment Relationships

Sites representing the moderately closed/C4 midgrass state had higher temperature and rainfall and deeper depth to carbonates compared with the thicket/mixed grass state (Fig. 3). The moderately closed/C3 shortgrass, closed/C3 midgrass, and closed/annuals and forbs states did not differ from one another in any environmental variable examined and were generally intermediate between the moderately closed/C4 midgrass and thicket/mixed grass states with respect to rainfall, temperature, and depth to carbonates (see Fig. 3), reflecting broad distributions across the study area (Fig. 4). There were no overall differences among states in silt and clay content of the A horizon, maximum clay content, or maximum carbonate development stage.

The moderately closed/C4 midgrass state occurred in all landforms of the northern Caldenal, whereas the thicket/mixed grass cluster was found only in lowland and slope landforms in the south (see Fig. 4, Table B.2). Open forests of the sandsheet were found in the west part of the Caldenal, while closed forest states occupied more humid eastern areas.

Discussion

Vegetation States of the Caldenal Region

Woody plant encroachment in the Caldenal is commonly thought to involve an increase in *P. caldenia* density in forests and bordering semiarid grasslands (Cano, 1988; Dussart et al., 1998). Our data indicate that *Prosopis* trees are not necessarily the dominant woody plants at high overall woody plant densities and that other woody species significantly contribute to states locally deemed as encroached, particularly *C. microphylla* (see Fig. 1). Seeds of both *P. caldenia* and *C. microphylla* require acid scarification, such as through ingestion by cattle, to germinate (Peinetti et al., 1993; Peláez et al., 1996). However, *C. microphylla* has reduced seedling establishment in warmer temperatures (Peláez et al., 1996), suggesting that reduced ambient temperatures occurring below tree canopies might provide ideal growing conditions for this species. Our observations suggest conventional views regarding the processes driving woody plant proliferation in the Caldenal region may be incomplete and indicate a need for population models of woody plant species other than *Prosopis* trees. In addition, our classification confirms the notion that dominance by unpalatable C3 midgrasses and annuals is associated with relatively closed canopy forest (Estelrich et al., 2005; Morici et al., 2009). Palatable C4 midgrasses and C3 shortgrasses, on the other hand, were associated with the relatively well-insolated conditions of open and moderately closed forests and open patches occurring within thickets. Utility of closed forests for

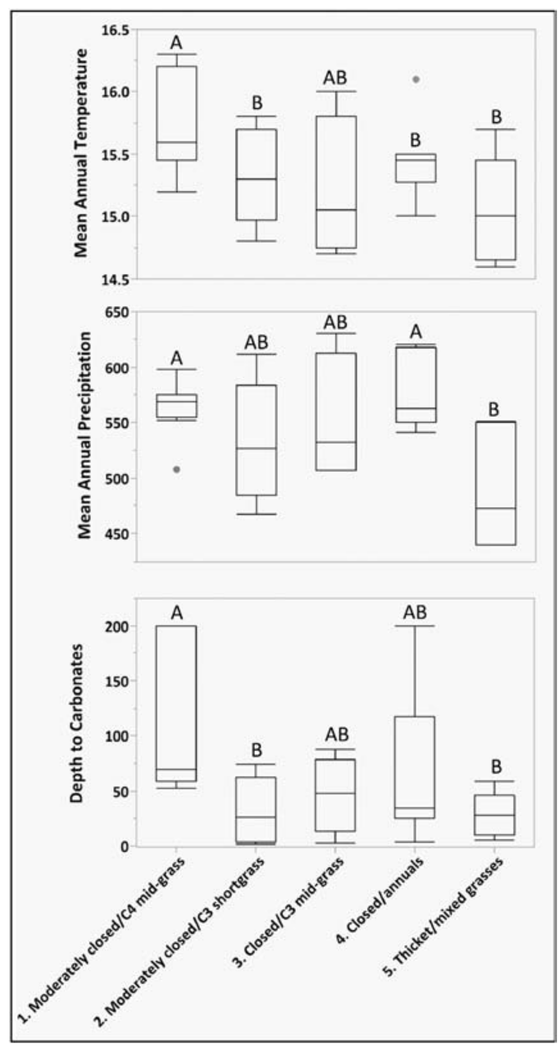

Figure 3. Variation in climate (temperature and precipitation) and depth to a calcium carbonate—rich horizon among vegetation clusters. Different letters indicate significant differences at $P \le 0.05$ using pairwise Wilcoxon tests given that the overall Kruskal-Wallis test was significant at the $P \le 0.05$ level.

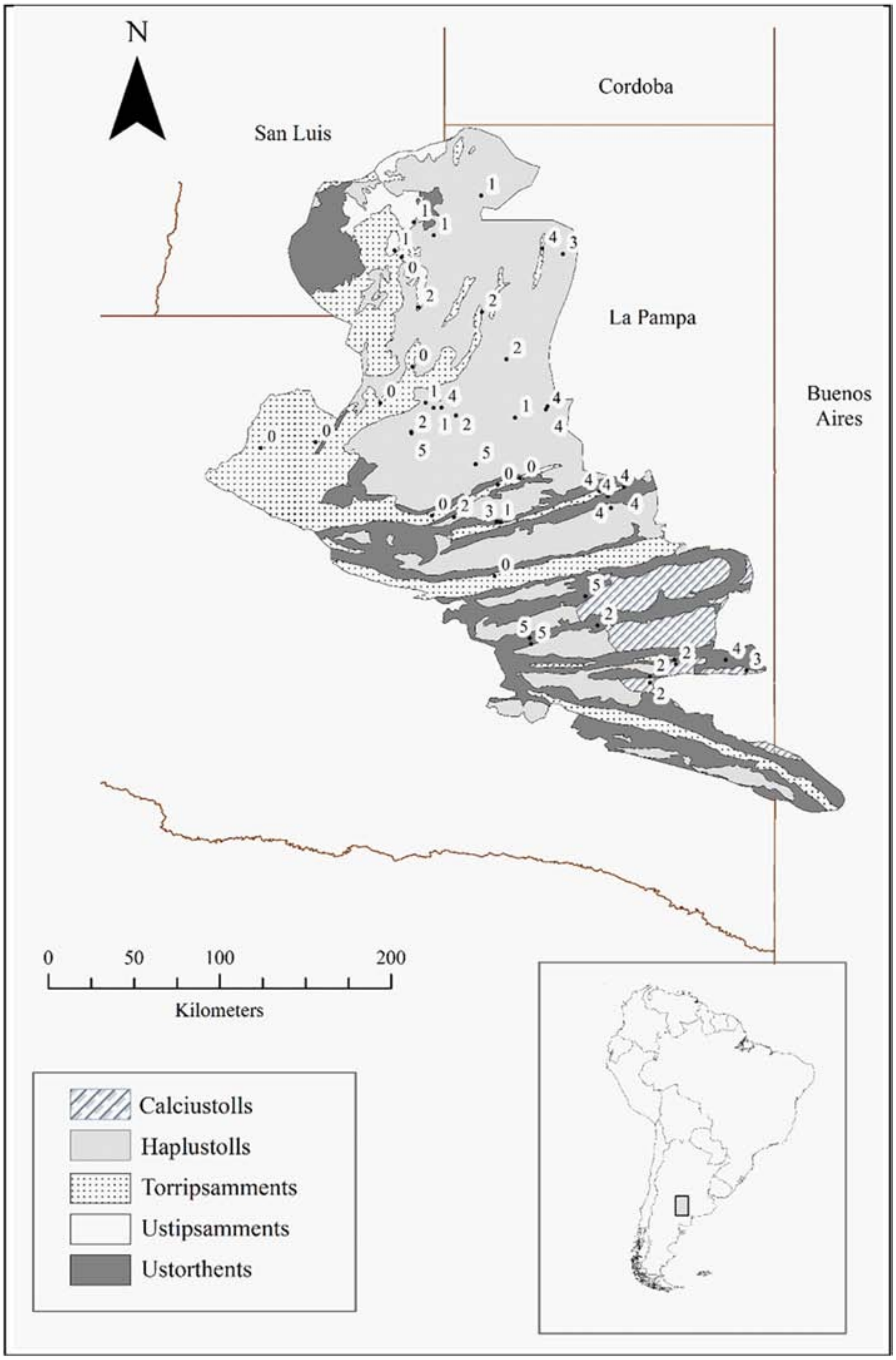

Figure 4. Distribution of sample points (numbers) in the Caldenal region within the geographic boundaries of Argentinian provinces. Numbers indicate vegetation types: 0. Open forest, 1. Moderately closed/C4 midgrass, 2. Moderately closed/C3 shortgrass, 3. Closed/C3 midgrass, 4. Closed/annuals and forbs, and 5. Thicket/mixed grass.

grazing is therefore limited, while open patches within thickets are difficult for livestock to access (Adema and Babinec, 2002; Rucci and Iglesias, 1990).

Climoedaphic Effects on Distribution of Vegetation States

Our inventory dataset supports the hypothesis that woody encroachment in the Caldenal region is influenced by variations in climoedaphic conditions. The deep coarse soils of the sandsheet had few trees and shrubs. *Prosopis* was the dominant woody plant group in open forests of the sandsheet, with a low density of shrubs and dominance of C4 species in the herbaceous stratum. Valley floors, gentle slopes, and plains landscapes exhibited greater densities of trees/shrubs than the sandsheet, and these landforms are generally considered favorable for Calden forest development (Cano et al., 1980). Woody plant density and cover are often negatively related to soil clay content (Browning et al., 2012; Sankaran et al., 2005). However, like Wu and Archer (2005), we found that coarse-textured upland soils are likely more resistant to increases in woody plant density than fine-textured lowland soils. Wu and Archer (2005) attribute this pattern to the augmentation of soil water availability on fine-textured soils due to runoff from adjacent uplands. A similar mechanism, involving runoff or subsurface hydrology that we did not measure, may explain the patterns observed.

Stages of woody plant encroachment in the Caldenal are thought to progress from an open forest state to moderately closed, to closed, to a persistent thicket state (González-Roglich et al., 2015). Open forest is generally poorly represented in the region due to past encroachment (González-Roglich et al., 2015) and, in our study, limited to sandsheet landforms. Moderately closed and closed forests did not differ consistently from other states in climoedaphic factors, suggesting that they are true alternative states (i.e., different vegetation that can occupy the same environment) (Peterson, 1984; Petraitis, 2013). Our data, however, suggest that only certain moderately closed states regularly transition to a thicket state in the same environment. The moderately closed/C4 midgrass state, which features greater rainfall, higher temperatures, and greater depth to soil carbonates, appears to exist in a climoedaphic environment that is distinct from that of the thicket/mixed grass state. The role of soil carbonate depth is unclear, but it may influence (or be influenced by) soil water dynamics (McAuliffe, 1994; McDonald et al., 1996; Royer, 1999) and soil phosphorous availability (Schachtman et al., 1998; Shariatmadari et al., 2006; Tunesi et al., 1999) in ways that favor certain shrubs, as has been observed for *Larrea* shrubs in southwestern deserts of North America (Bestelmeyer et al., 2009). On the other hand, moderately closed/C3 shortgrass state and closed/C3 midgrass state did not differ from the thicket/mixed grass state in any variable considered. However, the closed/annuals and forbs state tended to occur in wetter environments than the thicket/mixed grass state. These results indicate that moderately closed and closed states featuring C3 grasses, and sometimes annuals, occur within the same climoedaphic conditions as thicket states and are at risk of transition to these states. Thus, moderately closed and closed states occurring in the context of low rainfall, cool temperatures, and shallow soil carbonates should be considered priorities for taking actions to avoid the development of thicket states (Adams, 2013). Predicting where further woody plant encroachment is more or less likely to occur would help guide future management investments.

Implications

Vegetation state change is jointly controlled by the magnitude of drivers and the climoedaphic context within which drivers act (Bestelmeyer et al., 2006; McAuliffe, 1994). Our study of the distribution of vegetation states in the Caldenal region suggests that three climoedaphic variations are especially important: sandsheet landforms that do not demonstrate the existence of woody plant dominance; loamy soils with deep carbonates in warmer, wetter climates that support C4 grasses and are not likely to develop into thicket states; and loamy soils in cooler, drier climates featuring C3 grasses and shallow carbonates where transitions to thicket states occur. These distinct contexts can be considered as three ecological site classes (Bestelmeyer et al., 2009) that can serve as a basis for mapping and management recommendations in the Caldenal. Analyses based on stratified and targeted inventory approaches can prove useful for developing resilience-based management recommendations in many kinds of ecosystems (Bestelmeyer et al., 2017; Kachergis et al., 2011; Miller et al., 2011).

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Supplementary data

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