A state and transition model for the Caldenal subregion, Espinal ecoregion, Argentina

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Regional characteristics

This state-and-transition model applies to the Caldenal is a subregion of the Espinal ecoregion in the center of Argentina between the humid Pampas grasslands to the east and the arid Monte Desert in the west (Fernández and Busso 1999). Climate is temperate semi-arid with a trend toward more arid conditions to the southwest. Mean annual precipitation ranges from 400-700 mm and mean annual temperature from 14-16 ^{o}C (Casagrande and Conti 1980) (Instituto Nacional de Tecnología Agropecuaria 2004). Landforms are gently undulating plains, dune lands and plains (plateaus) intermixed with narrow depressions called transversal valleys. The region is entirely covered by late Quaternary aeolian deposits(Zárate and Tripaldi 2012). Soils are Mollisols in the east part of the area and Entisols in drier areas or on steep slopes.

Guide to narrative sections

The organization of the STM generally follows that recommended by Bestelmeyer et al. (2010), but 1) transient dynamics within states are described as part of "state" narrative where important, 2) the transition narrative elements are simplified to improve readability, and 3) "context dependence" is added to describe how soil or climate variation can modify transitions because this model was generalized to a relatively broad land area. Following US conventions, "transitions" refer to usually unintentional state transitions whereas "restoration" refers to deliberate recovery of a desired state.

Description. A general description of each state.
Plant community characteristics. Quantitative and descriptive characteristics that can be used to distinguish states.

Resilience management. Management strategies to 1) sustain a state and prevent a transition and 2) sustainably manage resources provided by the state under its dominant land use.

Mechanisms. The specific causes of transitions, including drivers, controlling variables, triggers, and feedbacks.

Constraints to recovery. Variables or processes that preclude recovery of the former state.

Context dependence. Spatially or temporally varying factors that cause variations in transition or restoration likelihood and contribute to uncertainty.

Restoration strategy. Specific strategies used to restore a previous state.

States and transitions (Fig 1)

State 1. Open Forest

Description. Sparse *Prosopis caldenia* trees with a well-developed grass understory depending upon management (see below), and a very low cover of shrubs. Soils are deep with high organic matter content and soil water storage capacity that provide favorable growing conditions for *P. caldenia* trees. Tree density is limited by a low density of seed dispersing animals, especially cattle (Dussart et al. 1998, Dussart et al. 2011). Crown fires are prevented by low tree and shrub density.

Plant community characteristics. Tree density varies from a few individuals up to about 200 individuals ha^{-1} ; shrub density is typical low, but can reach up to 500 individuals ha^{-1}. Grass composition varies according to grazing management (Llorens 2013). In sites with low stocking rates (0.1 animal units [AU] ha^{-1}), the herbaceous stratum is dominated by C3 short grasses that can reach a maximum height of 50 cm, composed of *Poa ligularis, Piptochaetium napostaense,* and *Nasella tenuis* (Cano 1988). Continuous grazing at a moderate stocking rate (0.2 AU ha^{-1}) will favor the increase of midgrass species (Llorens 2013). Plants in this group can reach a maximum height of 100 cm, and include *Jaraba ichu, Nasella tenuisima,* and *Amelichloa brachychaeta* (Cano 1988). Moderate stocking rates with grazing during the fall-winter-spring period (April-October) provide opportunities for the establishment of C4 (summer) grasses (Llorens 2013) and development of mixed grass strata (co-dominance of C4 and C3 grasses).

Summer grasses in the caldenal are about 80 cm tall and include *Setaria leucopila, Digitaria californica, Trichloris crinita,* and *Sporobolus subinclusus* (Cano 1988). Summer grasses are more common in the warmer areas of the caldenal distribution and in sandy soils. High stocking rates (0.8 – 1 AU ha^{-1}) cause a decline in perennial grass cover and an increase in annuals or perennial forbs. Degraded herbaceous strata can have a large cover of palatable annuals including grasses *(Bromus brevis, Hordeum* sp.*)* and forbs *(Plantago* sp.*).* In this condition, livestock grazing can significantly increase the cover of bare soil. Alternatively, degraded herbaceous strata can be dominated by unpalatable forbs *(Chenopodium album, Baccharis ulicina, Solanum eleagnifolium)* or *Cenchrus spinifex* in sandy soil.

Resilience management. Resilience management is focused on 1) avoiding woody plant thicketization and 2) maintaining a high cover of short grass or mixed grass species; these two goals involve distinct management actions. Control of woody plant establishment can be accomplished by limiting cattle grazing during the fruit-shedding period (March- April), especially in paddocks where *P. caldenia* fruiting plants are abundant. Management could also include targeting grazing during the fruit-shedding period with an herbivore, such as sheep, that are less effective calden dispersers. This will reduce the number of pods without significantly increasing seed dissemination. There is limited evidence that sheep are much less effective dispersers than cattle, but experimental studies are lacking (Dussart et al. 1998). Targeted browsing by sheep or goat on seedlings can also be used to control woody recruitment. The maintenance of high grass cover is a complementary strategy to limit woody plant recruitment (Distel et al. 1996, de Villalobos et al. 2005).

Different management practices can be used to favor the dominance of palatable grass species and reduce the cover of grasses featuring low forage quality (Llorens 1995, Busso 1997, Tizon et al. 2010). Management practices depend on the current composition of herbaceous stratum. When the stratum is dominated by short grass species, management should avoid overgrazing via high stocking rates or uneven use of the paddock. Overgrazing significantly reduces the size and density of plants (Sala et al. 1986). Stocking rates should be low or grazing deferred during early fall to provide conditions for the increase in the crown size of palatable plants during their vegetative growth period. Early spring deferment will improve seed production because stem elongation and fruit ripening occur during this period.

Summer grazing is used to benefit short grass species within mixed grass strata. Strata dominated by mid grasses will provide very low forage quality for livestock. In this case, late summer fire (February- March) followed by a short-duration of grazing at a moderate stocking rate (0.2 AU ha^{-1}) is used to consume growing tillers of burned mid grass plants which will promote the growth of short grass plants already present in the community by reducing interspecific competition. Higher stocking rates or longer duration of grazing will have negative consequences, however, because animals will graze on short grass plants. When the density of short grass plants is very low, overgrazing on the resprouting mid grass plants through high instantaneous stocking rate (0.5 to 1 UA ha^{-1}) is used to weaken mid grass plants and open spaces for the establishment of the short grass species (Llorens 2013).

State 2. Closed forest/herbaceous understory

Description. High density of trees with closed canopy cover. Relative to the open forest, grass cover is reduced due to the increase in competition with woody plants for light and soil nutrients. Shade tolerant midgrass or annual species are favored in low light conditions (Estelrich et al. 2005). Low light levels in the understory limits *P. caldenia* establishment (de Villalobos et al. 2007). Competition for light produces tall and thin trees. Low tree mortality rate results in a high density of uneven-aged individuals with similar height but with varying crown diameter.

Plant community characteristics. Tree density is between 200 to 2000 individuals ha^{-1} and shrub density is low--no more than 500 individuals ha^{-1}. Herbaceous cover is dominated by *Jarava ichu* or the annuals forbs *Chenopodium album* and *Conizia bonaeriensis* when overgrazed or in very dense woody sites (Svejcar et al., in review).

Resilience management. In order to prevent a transition to the fachinal (shrub thicket) state following a catastrophic fire, managers attempt to reduce the likelihood of fire occurrence by limiting ignitions though firebreaks or reducing fuels (grass biomass). Woody plant establishment can be limited via the timing of grazing in open patches. For example, reducing stocking rates in years of high *P. caldenia* fruit production or introducing livestock 4-6 months after the fruit shedding period (March – April) can be used to limit woody plant establishment. The number of viable seed in unconsumed pods declines rapidly due to bruchid beetle or fungus attacks (Lerner and Peinetti 1996).

State 3. Closed forest/shrubby understory

Description. High density of trees with partially closed canopy cover and high shrub cover. Grass cover is variable and usually dominated by shade-tolerant mid grasses of low palatability intermixed with patches of palatable short grasses, depending on grazing management (Morici et al. 2009). Burned trees typically resprout through the development of numerous basal buds which change the growth form from tree to shrub morphology (Bóo et al. 1996, Dussart et al. 1998). Shrub forms do not revert to tree morphology. Long-term persistence of tree strata will depend on individuals that survive fires and resprout.

Plant community characteristics. Tree density varied from a few individuals in areas that had been affected by repeated fires to densities of 1000 individuals ha^{-1} dominated by *P caldenia* and featuring *Prosopis flexuosa*, *Schinus* sp., and *Jodina rombifolia* as associated species. Shrub density is high, ranging from 1000-2000 individuals ha^{-1} that includes multistemmed *P. caldenia*, *Condalia microphylla*, and *Schinus fasciculatus*. Herbaceous cover is patchy overall and dominated by midgrasses, but includes short or mixed grass species as minor components. (Distel and Boó 1995, Llorens 1995).

Resilience management. Control of woody plant establishment and herbaceous composition is achieved as described for the Open Forest and Closed Forest/herbaceous states. The cover of shortgrass patches can be increased through flexible livestock management combined with fire (Llorens 1995). Controlled fire can be used to favor palatable grass species or reduce fire risks, however, fire should be applied in small areas and under strict supervision to avoid catastrophic fire outbreak.

State 4. Fachinal (shrub thicket)

Description. Fachinales have a very high cover of shrubs and low cover of grasses. Shrub cover can be dominated by *P caldenia*, be a mix of shrub species, or be dominated *Condalia microphylla*. The grass stratum is poorly represented and mostly limited to the open patches or inside the crown of the shrubs. This state is highly resilient due to the ability of woody plants to resprout following fires which are promoted by the dense shrub cover. After resprouting, all plants grow to a similar size. Limited asymmetric competition prevents the development of tree growth forms and sustains the shrub-dominated state.

Plant community characteristics. Trees are scattered or absent. Shrub density is > 4000 individuals ha^{-1}. Grass cover is low and bare ground cover is higher than in other states (Svejcar et al., in review).

Resilience management. Although repeated fires reinforce the fachinal state, change in woody plant structure would be very slow even without fire. Little can be done to facilitate a transition to another state.

Transition T1

Mechanisms. P. caldenia seed dispersal by cattle (Peinetti et al. 1993, Lerner and Peinetti 1996) in conjunction with low fire frequency or fire absence leads to a gradual infilling of trees.

Constraints to recovery. Longevity of woody plants with very slow self-thinning.

Context dependence. Transition has been more likely on loamy soils with shallow calcium carbonate (calcic) horizons and in cooler, drier parts of the Caldenal than on deep sandy soils with no calcic horizon in warmer, wetter parts of the Caldenal (Svejcar et al., in review).

Transition T2

Mechanisms. P. caldenia seed dispersal by cattle in conjunction with relatively high frequency fires leads to increases in shrub density. Some calden trees can withstand high fire frequency, evident from fire scars typically present in a stem cross section (Medina et al. 2000, Medina 2007, 2008, Dussart et al. 2011, Bogino et al. 2015). Although high intensity fire does not cause mortality of most woody species, it stimulates resprouting and the development of shrub thickets (Bóo et al. 1996, Dussart et al. 1998).

Constraints to recovery. Shrub and tree resprouting after fire, in conjunction with longevity of woody plants, maintain the closed forest/shrubby state. Natural fire events may create favorable conditions for woody plant establishment (Dussart et al. 1998, Bogino et al. 2015).Grazing by cattle favors woody plant establishment through seed dispersal and/or reduction of competition with grasses.

Context dependence. Transition has been more likely on loamy soils with shallow calcium carbonate (calcic) horizons and in cooler, drier parts of the Caldenal than on deep sandy soils with no calcic horizon in warmer, wetter parts of the Caldenal (Svejcar et al., in review).

<u>Transition. T3</u>

Mechanisms. In the context of high fuel loads that accumulate in state 2, fire acts as a trigger that eliminates most aboveground biomass and promotes widespread resprouting of woody plants and repeated fire.

Constraints to recovery. Shrub and tree resprouting after fire (Bóo et al. 1996) in conjunction with longevity of woody plants.

Context dependence. Low intensity fires are less likely to cause widespread mortality and resprouting.

<u>Transition. T4</u>

Mechanisms. A high fire frequency occurring in a community with a dense shrub layer causes tree mortality and precludes their replacement by favoring resprouting, shrubby growth forms.

Constraints to recovery. Shrub and tree resprouting after fire in conjunction with longevity of woody plants.

Context dependence. Without restoration, the transition is inevitable and its rate depends on the frequency of high intensity fires.

Transition. T5

Mechanisms. Conversion to rainfed cropland or planted pasture from forest.

Constraints to recovery. Soil erosion after clearing may limit tree and grass recovery following abandonment by reducing soil water holding capacity and soil organic matter (Buschiazzo et al. 2004).

Context dependence. Historically, conversion to cropland occurred predominantly in the eastern part of the Caldenal in wetter areas, on richer soils (Mollisols) and closer cities whereas conversion to pasture is most common in western areas with lower rainfall and farther from cities (González-Roglich et al. 2015).

Restoration. R1

Strategy. Selective removal of trees followed by targeting browsing to control any resprouting woody plants and strategic grazing or fire management to reduce fuel biomass.

Context dependence. Unknown.

Restoration. R2

Strategy. Mechanical removal of shrubs. Goat grazing can be used to control shrub resprouting after the removal treatment (Pisani et al. 2001). Strategic grazing or fire management can be used to reduce fuel biomass. Once the shrub cover is reduced, trees can be reestablished by planting or using cattle as a seed dispersal vector.

Context dependence. Unknown.

Restoration. R3

Strategy. Mechanical removal of shrubs combined with tree planting after clearing or the use of cattle to introduce calden seeds. Long-term grazing rest following plant establishment can allow an increase in tree recruitment and the increase in grass cover.

Context dependence. On hillslopes with poorly developed soils, shrubland may be the reference state such that increases in grass cover are ephemeral.

Restoration. R4.

Strategy. Same as for R3 without mechanical removal, but little understood.

Context dependence. Soil that has eroded to an infertile or restrictive subsoil horizon may experience limited restoration success.

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Figure 1. State-and-transition model diagram. Transitions (T) and Restoration strategies (R) correspond to entries in the narrative.