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Generalized and Specific State-and-Transition Models to Guide Management and Restoration of Caldenal Forests

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ABSTRACT

Management impacts and natural events can produce ecosystem state changes that are difficult to reverse. In such cases, a detailed understanding of drivers, thresholds, and feedback mechanisms are needed to design restoration interventions. The Caldenal ecoregion in central Argentina has undergone widespread state change, and restoration is urgently needed, but as yet there has been no knowledge synthesis to support restoration actions. In this paper, we provide evidence-based guidelines for ecological restoration of the Caldenal forest derived from a general to local conceptual understanding of ecosystem dynamics. We develop a Caldenal forest state transition model based on a generalized fire-mediated savanna-woodland transition model. The generalized model depicts global similarities in fire-grass feedback loops as a primary factor controlling savanna to woodland transition (thicketization) in semiarid savannas around the world. An open forest is considered to be the reference state of the Caldenal that developed under a historical regime of frequent low-intensity fire. The introduction of large livestock herds in the region disrupted the positive fire-grass feedback loop and increased dispersal and recruitment of *Prosopis caldenia,* creating conditions for thicketization of the forest. Controlled, low-intensity fire can be used to build the resilience of an open forest state. Restoring open forest states from woodland states requires a large-scale selective thinning and pruning operation. Long-term restoration requires breaking the positive livestock-thicketization — high-intensity fire feedback and reestablishing the positive grass-low intensity fire feedback to ensure the persistence of a restored open forest state.

Introduction

Restoration from a degraded to a desired ecological state requires the identification of processes causing degradation and the development of methods to reverse degrading processes (Hobbs and Norton, 1996). These methods often involve interventions that provide competitive advantage to dominant plants of a desired community and generate conditions for their persistence (Briske et al., 2008; Hobbs and Suding, 2009). In systems exhibiting alternative states, interventions often require an understanding of ecological feedbacks between dominant plants and the environmental processes that support their dominance (Suding et al., 2004), such as the feedback between savanna states and the frequent fires that maintain them (Staver et al., 2011; Batllori et al., 2015). Conceptual models of alternative states and the causes and constraints to transitions, known as *state-and-transition models* (STMs), can be used to synthesize scientific knowledge about the drivers and ecological feedbacks involved in transitions and how to manage them (Briske et al., 2008; Bestelmeyer et al., 2017).

An STM can assist land managers in developing strategies to promote desired transitions and prevent undesirable ones (Bestelmeyer et al., 2010). However, the local emphasis of many STMs precludes theory development with regard to ecosystem dynamics. The consequent exclusion of STMs in the scientific literature has negative impacts on the relationship between theoretical and applied ecology. In this paper, we illustrate the use of generalized STMs that describe the mechanisms of ecosystem dynamics for a broad class of ecosystem (savannas) and refine this model to create a local STM that can be used by managers. The local STM for the Caldenal forest is a particular realization of generalized fire-driven catastrophic transitions that occur in savannas globally. The Caldenal STM is then linked to specific management and restoration actions including 1) designing interventions for reducing the resilience of a degraded state, 2) identifying opportunities for restoration actions, and 3) recognizing variations of states that are most susceptible to transition.

The Caldenal forest occurs in a transition zone between the humid Pampean grasslands and the arid Monte shrubland in central Argentina, intermixed with other vegetation types including shrub savannas,

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shrublands, and grasslands (Cabrera, 1976; Fernández and Busso, 1999; Paruelo et al., 2001). The forest was historically dominated by open forests of the endemic tree *Prosopis caldenia*. This species is typically found on valley floors, slopes, and piedmont landforms with deep soils. Climate conditions are continental, characterized by a northeast to southwest rainfall gradient (from 700 to 400 mm). The forest has experienced significant human impacts, through deforestation and fragmentation (Morris and Ubici, 1996; Menéndez and La Rocca, 2007; González-Roglich et al., 2015). Over the past 2 centuries, the forest has undergone an increase in the density of woody plants, known as thicketization (Archer et al., 1995) triggered by the introduction of cattle grazing following deforestation and changes in the fire regime. The high rate of land degradation has altered historical ecological structure and composition of the Caldenal forest that was predominant in the past (Dellafiore, 2017). Given the extent of degradation and its tendency to facilitate land-use transitions in the Caldenal, restoration of degraded remained forest ecosystems is an urgent priority (Fernández et al., 2009; González-Roglich et al., 2015). Nonetheless, existing information has not been synthesized to support restoration decisions.

Generalized Fire-Mediated Savanna-Woodland Transition Model

Thicketization occurs in many semiarid savannas around the world, and a global body of studies have identified robust generalizations on its causes and management. In thicketization-prone savanna ecosystems, woody plant dominance is constrained in the reference savanna state by positive feedback loops between fire and grass biomass (Archer et al., 2017). State transitions are facilitated by the reduction of grass biomass accumulation and fuel loads associated with continuous heavy grazing (Briggs et al., 2002; Van Langevelde et al., 2003; Wiseman et al., 2004; Joubert et al., 2012; Stevens et al., 2016; Archer et al., 2017). Thicketization may also require other processes that accelerate woody plant recruitment, including a reduction in competition for soil water (Riginos, 2009; Goheen et al., 2010); increased dispersal of woody plant seeds (Brown and Carter, 1998; Dussart et al., 1998; Brown and Archer, 1999); and reduced browsing, seed, and seedling predation (Goheen et al., 2007, 2010). The reference state can be restored relatively easily with fire during the early stages of woody plant encroachment (Noel and Fowler, 2007) or through a combination of factors such as fire and browsing (Trollope, 1974; Midgley et al., 2010) or fire and drought (Roques et al., 2001). Once dense, mature woodland states have developed; however, catastrophic fire (Twidwell et al., 2013) or costly mechanical/chemical treatments (Archer et al., 2017) can initiate restoration. Combinations of other practices over multiyear timeframes, such as seeding, prescribed fire, and grazing management, may be required to reestablish positive grass-fire feedbacks sustaining the reference savanna state.

State-and-Transition Model of the Caldenal Forest

As in other rangeland ecosystems, conventional interpretations of Caldenal forest dynamics in the past were based on a Clementsian successional model of vegetation (Clements, 1916, 1936). The degradation of the Caldenal produced by logging or grazing was considered to be fully reversible by a natural tendency of the vegetation to return to late-successional stages over time (Koutche and Carmelich, 1936; Lasalle, 1966; Orquín et al., 1983). For example, changes in the plant community driven by grazing, such as the decline in short grass species and the increase in unpalatable midgrass species, could be reversed if grazing was discontinued. Similarly, natural self-thinning was thought to reverse thicketization if the forest was left undisturbed. Although this model was not formalized and published, its assumptions have guided traditional range management decisions in the Caldenal forest for decades.

State-and-transition concepts were introduced for herbaceous elements of Caldenal vegetation beginning in the 1990s (Distel and Boó, 1995; Llorens, 1996; Distel, 2016). These STMs represent the effect of livestock grazing on the herbaceous stratum and are used to generate recommendations for livestock management. However, the dynamics of woody vegetation are not explicitly represented in these STMs, even though thicketization is the most prevalent process of degradation of the Caldenal forest and has strong negative effects on livestock production. Thus, a more comprehensive synthesis of the dynamics of the Caldenal forest is needed to improve resilience management and guide restoration actions. Here, we review literature to develop an STM for the Caldenal forest that combines elements of previous models with newly synthesized information on woody plant dynamics to provide a whole-system perspective. The existing evidence for Caldenal STM structure and behavior reflects the generalized fire-mediated savanna-woodland transition described earlier. A general description of the Caldenal STM is presented in Box 1 and described in detail in supplementary material following conventions in Briske et al. (2008) and Bestelmeyer et al. (2010). (See Fig. 1.)

The reference state of the Caldenal STM is an open forest dominated by *P. caldenia* and an herbaceous layer of a cool-season perennial grasses (shortgrass). Evidence to establish this community as a reference state comes from historical observations and descriptions of well-managed Caldenal sites, alongside its desirability for regional managers (Koutche and Carmelich, 1936; Estelrich et al., 2005; Fernández et al., 2009; González-Roglich et al., 2015). Open forest was the dominant state in the late 19th century based on historical records and tree ring reconstructions; however, closed forest states may have been common before that period (Dussart et al., 2011). In open forest, trees can reach 10- to 12-m in height and 1.5-m trunk diameter. Shrubs including *Condalia microphylla, Lycium* spp., and *Schinus* spp. are usually present but at very low density. Short-statured perennial C_3 cool-season grasses (shortgrass) include *Piptochaetium napostaense, Poa ligularis,* and *Nassella tenuis*. These grasses have low shade tolerance, are preferred by livestock, and have a high survival rate after fire. Longer-term overgrazing of short grasses can create an "open forest — midgrass" community characterized by the dominance of unpalatable midgrass species (*Jarava ichu, Nassella tenuissima, Achnatherum brachychaetum*) (Llorens, 1995; Busso, 1997; Distel, 2016). These species have a similar phenology to shortgrasses, but they are favored by grazing due to their low palatability (Cerqueira et al., 2004). Very heavy grazing within the midgrass community could cause transitions in the herbaceous stratum toward annual grass dominance and forbs.

The open forest state is associated with a historical regime of frequent low-intensity fire. Ground fires will not produce severe damage to trees but can limit shrub and tree recruitment, thereby promoting the resilience of the open forest state. This region has no records of presence of large herbivores since the end of the Pleistocene period (Bucher, 1987). The lack of grazing in the past and the high productivity of grasses in the Caldenal forest create the conditions for a strong grass-fire positive feedback loop. Anthropogenic ignitions may have also favored high fire frequency in the pre-European period. The introduction of large livestock herds in the region since the 17th century weakened the positive grass-fire feedback loop, creating conditions promoting thicketization (Dussart et al., 2011). Livestock disrupted the fire regime and also released seed dispersal constraints by feeding on seed pods and accelerating establishment rates of *P. caldenia* (Lerner and Peinetti, 1996; Dussart et al., 1998).

Thicketization in the absence of fire is represented as the transition to a "closed forest/herbaceous understory" state characterized by a high density of trees (up to 2 000 plants ha^{-1}) and low shrub density (T1, see Box 1). Thicketization combined with limited fires (T2, see Box 1) favors *P. caldenia* shrubs, creating a "closed forest/shrubby understory" state (Bóo et al., 1997; Dussart et al., 1998; Bogino et al., 2015). Fire damage on young *P. caldenia* trees stimulates resprouting from basal buds and the development of several vigorous stems, none of which becomes the leader. This growth pattern represents a permanent morphologic shift from a tree to shrub life form (Dussart et al.,

Box 1
State-and-transition model for the Caldenal forest (See Fig. 1).

Ecological states

State 1. Open forest. Low tree density with nonoverlapping canopies. Scattered shrubs and high grass cover dominated by palatable or unpalatable species depending on management.
Feedback and ecological processes. Tree recruitment is constrained by absence or reduced number of seed-dispersing animals. Crown fire is prevented by limited vertical fuel continuity.
Resilience management. Control seed dispersal of woody plants and maintain the dominance of palatable grasses though managed grazing.
State 2. Closed forest/herbaceous understory. Dense tree population with complete canopy cover. Shrub stratum is poorly developed. Grasses are dominated by shade-tolerant perennial midgrasses or annual forbs.
Feedback and ecological processes. Competition for light produces tall and thin trees. Low tree mortality rates result in a high density of uneven-aged individuals with similar height. High tree canopy cover gives a competitive advantage to shade-tolerant herbaceous species.
Resilience management. Reduce fire risk through firebreaks, reduce woody biomass, and prevent fine fuel accumulation through managed grazing.
State 3. Closed forest/shrubby understory. Moderate tree population with partially closed canopy and high shrub cover. Grass stratum is well developed and dominated by perennial midgrasses of low palatability intermixed with patches of palatable grasses.
Feedback and ecological processes. Fire promotes shrub growth forms through basal resprouting. Long-term persistence of the forest stratum relies on individuals that survive fire without resprouting.
Resilience management. Reduce fire risk through firebreaks, removal of woody biomass, and prevention of fine fuel accumulation through managed grazing.
State 4. Shrub thicket. Shrub-dominated community. Trees are scattered or absent and grass cover is low to very low. *Prosopis* spp. and *Condalia microphylla* are the dominant woody species.
Feedback and ecological processes. Shrubs can survive recurrent fire through resprouting. Woody plants have similar sizes and no individuals monopolize enough resources to outcompete others. Repeated fires prevent any asymmetric competition and maintain a thicket state. Dense woody plants prevent grass establishment.
Resilience management. Reduce erosion risk by preventing bare soil expansion due to fire or grazing.

State transitions

Transition 1 (T1). *Mechanisms. P. caldenia* seed dispersal by cattle with low fire frequency or no fires.
Constraints to recovery. Long-lived woody plants. Very slow self-thinning.
Transition 2 (T2). *Mechanisms. P. caldenia* seed dispersal by cattle with moderate fire frequency.
Constraints to recovery. Plant resprouting and very slow self-thinning.
Transition 3 (T3) and Transition 4 (T4). *Mechanisms*. Severe fires that trigger significant tree resprouting.
Constraints to recovery. Very low fire-induced tree mortality and an absence of asymmetric competition that maintains a shrub thicket state in the face of fire and other disturbances.

Ecological restoration

Restoration 1 (R1). Selective mechanical or manual thinning of trees. Strategic grazing and fire can be used after thinning to increase short grass species.
Restoration 2 (R2). Mechanical or manual selective removal of shrubs. Targeted pruning of vigorous multistemmed individuals stimulates the development of a leader stem.
Restoration 3 (R3). Removal of a large fraction of shrubs combined with pruning of selected vigorous individuals. Planting *Prosopis* spp. trees and sowing exotic grass species to promote soil stabilization and facilitate the establishment of native grass species. Roller chopping or fire can be used to reduce the initial woody biomass.

1998; Peláez et al., 2012). The shade provided under the canopy of closed forest states creates conditions for the dominance of midgrasses or annuals even without heavy grazing pressure.

The structural changes produced by these transitions (T1 and T2, see Box 1) are associated with a shift from frequent low-intensity fires to pyrophytic high-severity crown fires (see also Kitzberger et al., 2016). The pyrophytic closed forest state is due to the high fuel load created by a dense woody biomass and ungrazed midgrass. A large biomass accumulation alongside vertical continuity increases the risk of high-severity crown fire, which is not suitable for tree persistence. High fire intensity in a closed forest state will lead to woody plant resprouting and a transition to a "shrub thicket" state. Total woody density can be similar to the closed forest state, but trees are sparse or absent. Due to high shrub density, the herbaceous layer is sparse or limited to open patches. A new shrub-fire positive feedback loop is generated, which causes recurrent *P. caldenia* tree resprouting and an increase in the density of fire-tolerant native shrubs including *C. microphylla*, *Schinus* spp., and *Lycium* spp.

The open forest and shrub thicket states are both resilient to fire disturbance, but fire has distinct effects in each state. High-intensity crown fire is unlikely in an open forest due to the lack of vertical fuel continuity. Ground fires will not produce severe damage to trees but can limit shrub and tree recruitment, thereby promoting the resilience of the open forest state. Similarly, the shrub thicket states are resilient to fire due to resprouting stems from basal buds (Bóo et al., 1997; Dussart et al., 1998). Dormant basal buds constitute an important trait that builds resilience to frequent disturbances in several woody plants species (Clarke et al., 2013; Enright et al., 2014; Pausas and Keeley, 2014). In contrast, high fuel load and continuity imparts low resilience to the closed forest state, and a rapid transition to a shrub thicket state can be triggered by fire events.

Resilience Management and Restoration Guidelines

Preventing undesirable state transitions (i.e., managing for resilience) and restoring desirable ecological states are primary strategies for sustaining the provision of multiple ecosystem services in a landscape (Bullock et al., 2011; Alexander et al., 2016). In this section, we provide evidence-based guidelines for management and restoration of the Caldenal forest ecosystem stemming from general

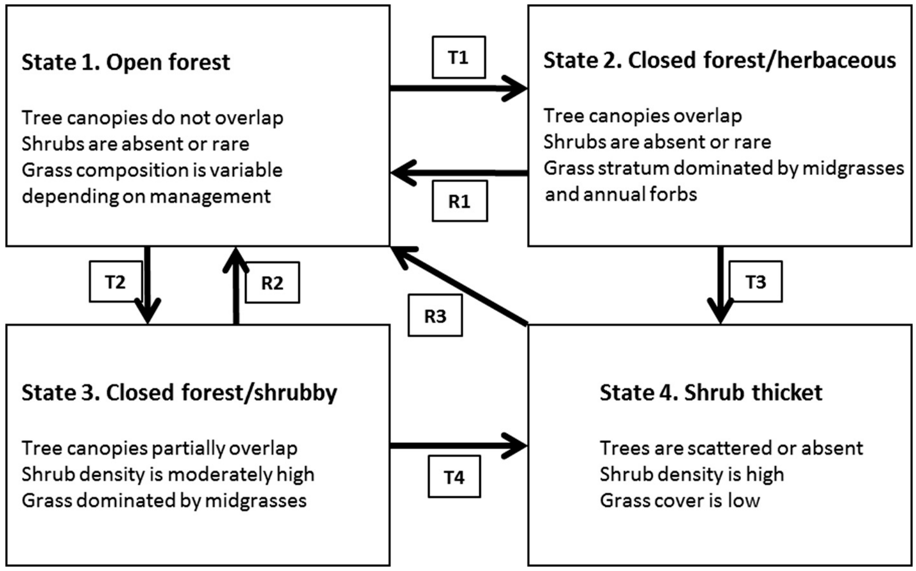

Figure 1. State-and-transition model for the Caldenal forest. T indicates state transition; R, ecological restoration.

and local STMs. A decision support tree derived from the guidelines is presented in Box 2.

Building Resilience of the Open Forest State

One of the primary goals of management and restoration is to increase resilience to thicketization of remaining open forest states. Resilience management can be achieved by providing conditions for the development of a healthy tree population, controlling the recruitment rate of woody plants, and maintaining a high cover of short grass species. Primary management recommendations include:

1. *Restore fire regime.* The reintroduction of low-intensity fire at early stages of tree recruitment can prevent thicketization. The use of prescribed fire in open forest has a low likelihood of affecting adult trees, but its frequency must be timed to reduce a negative effect on a natural rate of tree recruitment (Chidumayo, 2013; Collins et al., 2014). Controlled fire can also be used to depress the competitive dominance of midgrass species and promote short grasses (Llorens, 1996). Wildfires occurring in an open forest with a shortgrass understory should be of lower intensity compared with the open forest—midgrass community phase.
2. *Use strategic livestock grazing to control postfire recovery of midgrasses.* Vigorous tillering of midgrasses is typically observed after fire when there is sufficient soil water, such as when a fire event is followed by high rainfall. New growth of midgrass plants is palatable to livestock, so there is an opportunity to weaken the plants by depleting stored carbohydrates that support the recovery of photosynthetic tissues. Very high stocking rate (≥ 3× above that recommended for the area) can be used to consume tillers generated after the fire (Llorens, 1995). Increasing the recovery time of midgrasses will lengthen the recruitment window for shortgrass species.
3. *Defer livestock grazing during the* Prosopis *fruit-shedding period to limit excessive woody plant recruitment rate. P. caldenia* dispersal is promoted when pods are consumed by cattle, which separates seeds from the indehiscent pod, accelerates scarification (Peinetti et al., 1993), and reduces the risk of predation by bruchid beetles (Lerner and Peinetti, 1996). Bruchids constitute one of the most important seed predators documented for the genus *Prosopis* (Kingsolver et al., 1977). Adults lay their eggs on the developing pods, and the young larvae burrow and feed in the developing seeds. After pupation in the seeds, the adult beetles emerge through a small hole infecting other seeds. Bruchid predation may constitute a critical constraint for *P. caldenia* dispersal. Cattle consumption of pods diminishes this natural constraint (Coe and Coe, 1981; Lerner and Peinetti, 1996).
4. *Time grazing events to maximize benefits to desired herbaceous plants.* Alternating grazing with resting periods is generally recommended in the Caldenal forest (Llorens, 2013). However, rotational grazing can be adjusted to accomplish specific management goals. For example, grazing during the fall (February—March) should be avoided if the goal is to favor production of existing cool season shortgrasses. If the goal is to increase plant density, grazing should be avoided during the spring-summer flowering-fruiting period (September—January).
5. *Adapt ecological restoration to landscape heterogeneity.* The Caldenal forest occurs in a wide range of climoedaphic conditions. This variation seems to be associated with varying resistance to woody plant increase in different soils. For example, coarse-textured upland soils are likely more resistant to thicketization than fine-textured lowland soils (Svejcar et al., 2018). Therefore, efforts to manage woody plants can be prioritized on fine-textured soils.

Restoring Open Forest from Alternative States

Within closed forest states, restoration to open forest requires reduction of woody plant density through selective thinning and the establishment of favorable conditions for the recruitment of large trees. Selective thinning involves the choice of a target plant to promote and the removal of all other woody plants within a predefined distance, by cutting below the crown level to control resprouting. Pruning of target plants is required if they are multistemmed, leaving only one large stem as the leader. Additional pruning is required after thinning to remove resprouted stems. Pruning to reduce branching and stimulate apical dominance can promote faster height increase in young individuals. Thinning of the forest also stimulates radial growth in young and mature *P. caldenia* trees (Dussart et al., 2011). Pilot studies indicate that this thinning strategy can recover an open forest structure, but restoration of the herbaceous stratum may require seeding (Ernst et al., 2015).

Restoration of shrub thicket states requires substantial intervention that includes the removal of most woody plants, soil stabilization through sowing grass species, and planting trees. Programs for cultivation of native grasses alongside nursery practices and planting techniques to guide establishment of native *Prosopis* trees are under way. Alternatively, livestock feeding on Caldenal sites with high production of *Prosopis* spp. pods can be used as a seed dispersal agent to a restoration site (Bistolfi, 2016). Due to the labor and cost required, large-scale

Box 2
Decision tree to forest restoration derived from the STM of the Caldenal forest (see Box 1).

State 1. Open forest. Total woody density < 1 000 plants/ha dominant tree density < 200 plants/ha.
1.1 Low woody density. Total woody density < 500 plants/ha. Dominant tree density < 200 plants/ha, shrub cover ≤ 20%.
1.1.1 Total herbaceous cover is high > 50%.
1.1.1.1 Shortgrasses dominant.
Maintain current management, site functioning at its potential.
1.1.1.2 Midgrasses dominant.
Controlled fire and episodic grazing to increase shortgrass cover.
1.1.2 Total herbaceous cover is low < 50%.
Opportunistic grazing with long deferment or rest periods.
1.2 Moderate woody density. Total woody density 500 – 1 000 plants/ha. Dominant tree density ≤ 200 plants/ha, shrubs cover > 20%.
Similar to case 1.1 with regard to the herbaceous layer and include the following management actions: deferring livestock grazing during the *Prosopis* fruit-shedding period and thinning, through selective removal of shrubs and young trees, to reach similar woody structure as case 1.1.
State 2. Closed forest/herbaceous understory. Total woody density 1 000 – 2 000 plants/ha. Low shrub cover shrub cover ≤ 20%.
2.1 Total herbaceous cover is dominated by midgrasses.
Thinning. Selective mechanical or manual removal of young trees leaving a woody structure as in case 1.1. Mowing and episodic grazing after thinning.
2.2 Total herbaceous cover dominated by forbs.
Thinning as in case 2.1 followed by a resting during the subsequent growing season of winter grasses. Punctuated by episodic grazing could be used to reduce herbaceous biomass.
State 3. Closed forest/shrubby understory. Total woody density 1 000 – 3 000 plants/ha. High shrub cover > 50%.
3.1 Total herbaceous cover > 20%.
Thinning. Selective mechanical or manual removal of shrubs and some young trees to reach similar woody structure as case 1.1. Controlled fire and episodic grazing after thinning.
3.2 Total herbaceous cover ≤ 20%.
Thinning as in case 4.1 followed by long rest with episodic grazing in productive years.
State 4. Shrub thicket. Total shrub density 1 000 – 3 000 plants/ha. Trees are few or absent.
4.1 Total woody cover is high (> 40%).
Roller chopping and, when the herbaceous cover is low (≤ 20%), sowing grass. Thinning of shrubs may additionally be required. Trees can then be planted to reach a target density of about 200 plants/ha. Conduct recurrent pruning practices until trees are well developed. Use long rest periods with episodic grazing to reduce fire risk.
4.2 Total woody cover is low (≤ 40%).
Similar management as in 5.1 but excluding the use of roller chopping.
Keys to generalized management practices

1. *Controlled fire*. Prescribed burn conducted in late fall, winter, or early spring to reduce midgrass dominance or total grass biomass. It is recommended only in open forest ecological states.
2. *Grazing deferment during* Prosopis *fruit-shedding period.* Prevent grazing during Feb – June period to avoid cattle consumption and dispersal of *Prosopis* spp. seed pods.
3. *Episodic grazing.* Timing grazing events to favor shortgrass dominance. Also used to reduce herbaceous biomass to prevent fire.
4. *Planting*. Establishment of seedlings of native *Prosopis* trees by transplanting.
5. *Pruning*. Removal of resprouting stems to stimulate the apical dominance of a leader stem.
6. *Roller chopping.* Crushing woody plants with a large barrel of 10 – 20 tons weight powered by a tractor. Also used to sow grasses.
7. *Thinning.* Selective removal of small trees and shrubs.
8. *Mowing.* Cutting tall grasses to ground level with a large mower powered by a tractor.

implementation of these approaches is difficult to implement in the current socioeconomic conditions of Argentina.

Selective roller chopping is recommended as a restoration practice within thorn scrub of the adjacent Chaco and Espinal ecoregions (Adema et al., 2004; Kunst et al., 2008, 2012) and is regarded as a valuable tool to restore large areas in those systems (Willcox and Giuliano, 2012). Roller chopping involves the use of a large barrel of 10 – 20 tons pulled by a tractor to crush woody plants and promote the increase of herbaceous plants (Adema et al., 2004). Some of the benefits of using rolling chopping are 1) the debris of fragmented plant biomass can protect the soil from erosion, 2) dead woody biomass can be incorporated into the soil which increases soil organic matter (Martín et al., 2008), and 3) seeds of native grass species can be sowed during the roller chopping treatment (Adema et al., 2004; Anriquez et al., 2005) and woody litter creates favorable conditions for establishment. In the Caldenal, however, woody plant dominance will return after a few years such that recurrent management interventions would be needed. For example, crushing young *Prosopis* trees will promote the development of a shrub lifeform (R. Peinetti, personal observations). Thus, while roller chopping might be combined with other thinning methods, it is not recommended as a stand-alone intervention because it would enhance shrub-fire feedbacks and the transition or return to a shrub thicket state. Roller chopping should be applied only in an early stage of restoration intervention of a "shrub thicket" state.

Intense wildfires can present restoration opportunities of ecological states dominated by woody plants (Twidwell et al., 2016). A wildfire can eliminate almost all aboveground biomass that requires several years to recover. This period can be a window of opportunity for intervention as the openness created by a wildfire can facilitate recruitment of favored plants, as well as access to and removal of undesired plants. The implementation of an effective restoration of severely burned sites will require a combination of the strategies described earlier.

Socioeconomic Constraints to Restoration

Ecological knowledge alone, however, cannot put restoration actions on the ground. Restoration in the Caldenal region is primarily motivated by a desire to improve conditions for livestock production, which is the dominant economic activity. The value of this service by itself, however, has been insufficient to fund much restoration. For example, selective thinning and pruning is an effective approach for restoration to open forests, but at present, it is not economically feasible to restore large areas. Innovative management approaches that account for other ecosystem services may provide incentives to accelerate restoration activities. The use of woody plants as a source of bioenergy might be used to support restoration costs (Park et al., 2012). In addition, a new opportunity for conservation of native forests emerged in 2007 with a new federal law establishing "Minimum Standards for the Environmental Protection of Native Forests," known as Forest Law (Quispe Merovich, 2009). The law was established to control the rapid expansion of agriculture into natural forest areas, especially in the Chaco region (Gasparri and Grau, 2009), and to promote sustainable management of native forest (Juliá, 2010). This law could also serve as a platform to promote restoration actions, potentially via mitigation to offset land conversions in portions of the Caldenal region. Thus, while management strategies to overcome ecological barriers to restoration are clear, the development of policy strategies to promote sustainable forest management and restoration is in its infancy.

Concluding Remarks

Several STMs were created in recent years and have gained acceptance as management tools in Argentina. STM structure has evolved into an increasingly quantitative representation of state and thresholds and richer description of feedback mechanisms that are linked to management interventions. However, STMs tend to be restricted to specific management problems of local interest. Generalized STMs can represent global-level theories and link several STMs representing similar ecosystem behaviors.

The Ecosystem Dynamics Interpretive Tool (EDIT) is a web environment to develop, catalog, and explore STMs (Bestelmeyer et al., 2016). Generalized STMs are being introduced to EDIT to provide guidance on the development of local models at a global extent. A systematic structure for classifying ecological sites and representing state-transition elements will facilitate the sharing of knowledge among local models that are addressing similar problems under comparable ecological contexts. Our hope is that EDIT will accelerate STM development and application and their basis in ecological theory.

Management Implications

The Caldenal forest STM provides a theory-based and logical framework to design management interventions to sustain or restore desirable open forest states. Management should focus first on enhancing ecological resilience to thicketization of remaining open forest states and reduce the risk of state transitions triggered by catastrophic wildfire events. A combination of different management actions would be more suitable than a particular type of intervention. Management needs should be adapted according to climoedaphic context. For example, land managers should prioritize restoration efforts in Caldenal forests in soils of fine texture that are at higher risk of state transition. Management should also be adapted to the ecological state of the forest; for example, prescribed fire can be effective in open forest but in closed forest will only be effective in open patches because the dense canopy favors shade-tolerant midgrass species. However, controlled fire in closed forest presents a high risk of crownfire. Recommended actions to reduce hazardous fuels accumulation in closed forest include thinning and grazing but not prescribed fire. Preventive management actions such as the construction of firebreak barriers can be used to reduce the spread of fire in forest states. In contrast, shrub thicket states can be restored to open forest only with intensive efforts such as shrub removal, tree planting, and soil stabilization through grass seeding. Because of the relatively rich body of research in the Caldenal, the specific management recommendations may prove useful in other savanna ecosystems.

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