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Review

Grazing ecology and the conservation of the Caldenal rangelands, Argentina

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A B S T R A C T

Grazing by domestic livestock in the Caldenal rangelands has been threatening the ecological balance of this unique biome located in the semiarid zone of central Argentina. The aim of this review was to describe and explain the floristic changes observed in grazed rangelands in the southern Caldenal, discuss management alternatives for the conservation of desirable plant communities, and identify gaps in current knowledge of this distinctive ecosystem. Grazing-induced modification in the species composition entails the replacement of palatable grasses by unpalatable grasses and/or woody plants. Coarse grass and shrub encroachment represents discontinuous stable changes that lead to undesirable regimes in terms of functionality of primary ecological processes, species diversity, carrying capacity, and the economic productivity of livestock operations. Recovery of the desirable regime dominated by palatable grasses requires active restoration technology, which is often constrained by climatic and economic factors. Conservation of the regime dominated by palatable grasses calls for flexible stocking rates and intermittent grazing in replacement of current fixed stocking rates and continuous grazing. However, there is a basic need for more research related to restoration alternatives, grazing management, and for the development of simulation models to encompass the complexity of the system and assess the ecological and economic consequences of different management options of the southern Caldenal rangelands.

Contents

1. Introduction

In arid and semiarid environments land use is intensified during wet cycles, and a relatively high pressure on natural resources is normally maintained in dry cycles (Stafford Smith et al., 2007). Under extensive livestock farming, the maintenance of a high grazing pressure in dry years is associated with accelerated loss of plant cover, soil erosion, and replacement of palatable by unpalatable plant species (Schlesinger et al., 1990; Archer and Smeins, 1991; Fuls, 1992; O'Reagain and Scanlan, 2013). These floristic and edaphic changes can be persistent (i.e. regime shift, *sensu* Scheffer

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and Carpenter, 2003), and potentially reversible only through the application of costly and time consuming restoration efforts (Whisenant, 1999; Suding and Gross, 2006; Tongway and Ludwig, 2011).

The Caldenal rangelands in central-east Argentina experience an irregular pattern of wet and dry cycles at different temporal scales (Viglizzo, 2010; Bohn et al., 2011). The dominant production system is a cow-calf commercial operation based on rangeland utilization (AACREA, 2010). Stocking rate is normally set according to the forage availability in wet years, and it is carried over into dry years, except in food emergency situations that threaten animal life (Morris and Ubici, 1996). Overgrazing has caused soil and vegetation degradation (SAyDS, 2007), with consequent losses in the livestock carrying capacity and economic productivity of cattle operations. My objective was to describe and explain the floristic changes observed in the southern Caldenal rangelands used for livestock grazing, discuss management alternatives for the conservation of desirable plant communities, and identify gaps in current knowledge of this distinctive ecosystem.

2. Study region

The southern Caldenal rangelands are located in the southeast of La Pampa province and the southern part of Buenos Aires province (36–40° S latitude and 63–65° W longitude), Argentina. The main features of the climate, soils, geomorphology and vegetation are described in the Natural Resources Inventory of La Pampa province (INTA et al., 1980). The climate is temperate and semiarid. Mean annual air temperature is 15 °C. Long-term average annual precipitation is 400 mm (30% CV), and mean annual potential evapotranspiration 800 mm. The landscape is composed of extensive plateaus intersected by lowlands. The dominant soils in the plateaus present a sandy loam texture, limited horizon development, weak structure, and a petrocalcic horizon at less than a meter below the soil surface. Lowland soils are silty loam in texture, and deeper and better structured than in the plateaus.

Phytogeographically, the region falls within the Caldén District (commonly named "Caldenal"), which is part of the Espinal province (Cabrera, 1976). Present vegetation physiognomy varies between grassland and shrubland in the plateaus, and tree savanna and woodland in the lowlands. The herbaceous vegetation can be grouped functionally as palatable perennial grasses (e.g., *Poa ligularis*, *Piptochaetium napostaense*, *Stipa clarazii*, *Stipa tenuis*), unpalatable perennial grasses (e.g., *Stipa speciosa*, *Stipa ichu*, *Stipa tenuissima*, *Stipa ambigua*, *Stipa brachychaeta*), and annual grasses and forbs (e.g., *Hordeum* sp., *Bromus* sp., *Schismus barbatus*, *Medicago minima*, *Erodium cicutarium*). On the other hand, woody vegetation can be classified as deciduous (e.g., *Prosopis caldenia*, *Prosopis flexuosa*) and evergreen (e.g., *Larrea divaricata*, *Condalia microphylla*, *Chuquiraga erinacea*). Grass species names follow Rúgolo de Agrasar et al. (2005), whereas the rest of species names are according the Flora Argentina (2015).

Fire represents a phenomenon that has moulded the structure and function of the ecosystem historically (Bóo, 1990). The presettlement fire return interval was about 5 years, and it has increased in post-settlement times (Medina, 2007). Reduction in herbaceous biomass due to grazing by domestic livestock in combination with fire prevention by ranchers may have prolonged the fire return period in the Caldenal rangelands.

The South American camelid *Lama guanicoe* represented the main large herbivore in recent history, but currently it is virtually extinct. Sheep were introduced into the region at the beginning of last century and became replaced by cattle in the second half of the XXth century. Land is privately owned. Ranches are 2500 ha or more in extent, whereas paddock size varies between 650 and 2500 ha. Most landowners lack a long-term management plan. The average stocking rate in the cow-calf operations varies between 5 and 15 ha per cattle equivalent, depending on the condition of rangelands. The weaning rate (around 60% calves weaned per cow exposed) and meat production (10 or less kg/ha/yr) are below the potential values (Morris and Ubici, 1996; Distel and Bóo, 2002).

3. Species replacement

The species replacement process analyzed below is limited to the plateau, which is the dominant landform in the southern Caldenal rangelands.

The historical reconstruction of the vegetation through phytolith analysis in the soil profile showed that *P. ligularis* and *Stipa clarazii* were the dominant herbaceous species in the pristine condition of the southern Caldenal rangelands (Gallego et al., 2004). Both species are mid-tall (40–50 cm) productive perennial grasses of high nutritive value and palatability (Pisani et al., 2000; Cerqueira et al., 2004; Distel et al., 2005, 2008). On the other hand, studies on the long term dynamics of woody species populations suggest a low density of shrubs and trees in the plateau of the Caldenal before the introduction of livestock (Dussart et al., 1999). Moreover, high competitive pressure from mid-tall grasses represents unfavourable conditions for the establishment of woody plants in the Caldenal (de Villalobos et al., 2005). Altogether, the evidence indicates that most probably the physiognomy of the vegetation before European colonization in the plateau of southern Caldenal was a grassland with scattered woody plants. This would have been the rangeland that was first used for livestock production, through heavy and continuous grazing (older ranchers, pers. com.), at the start of the XXth century.

Mid-tall palatable perennial grasses of the Caldenal are sensitive to continuous and frequent grazing, which may explain their low representation in the present communities (Bóo and Peláez, 1991). Plants of *P. ligularis,* defoliated over the growing cycle, showed an exponential reduction in shoot productivity in response to an increasing frequency of defoliation (Didoné and Distel, 2006). Similarly, *P. ligularis* ecotypes from sites with different grazing histories in the Patagonian steppe only partially compensate for an equal proportion of biomass removed (Rotundo and Aguiar, 2008). Other studies (Klich et al., 1996; Busso et al., 2011) have also demonstrated the sensitivity of *P. ligularis* to defoliation. Less is known about the response to defoliation of *S. clarazii*, although this mid-tall perennial grass presents low tiller density and a relatively low production of seeds per plant (Distel and Klich, 1996), which may limit its regrowth capacity and seedling recruitment under heavy grazing. However, tillers located on the periphery of the crown present a low insertion angle, which may confer *S. clarazii* with some resistance to herbivory through grazing avoidance (Briske, 1991).

With increasing grazing intensity, mid-tall palatable perennial grasses are replaced by short palatable perennial grasses (Bóo and Peláez, 1991; Distel and Bóo, 1996). The most representative species of the latter group are *S. tenuis* and *P. napostaense*, which have relatively high productivity (Distel and Fernández, 1986) and nutritive value (Estelrich and Cano, 1996; Pisani et al., 2000; Cerqueira et al., 2004). Both species show grazing avoidance mechanisms (small stature, low tiller insertion angle), grazing tolerance mechanisms (high tiller density), and an elevated reproductive effort, which enhance grazing resistance (Distel and Klich, 1996; Becker et al., 1997). However, continuous heavy grazing atomizes the populations of both species (a few large plants are replaced by a large number of small plants), making them very susceptible to defoliation and drought. Under these conditions, an increase in annual species and bare ground is observed (Bóo and

Peláez, 1991).

The loss of palatable perennial grasses depresses interspecific competition and favours encroachment and dominance of unpalatable perennial grasses and woody plants (Distel and Bóo, 1996). Studies conducted under natural and controlled conditions have demonstrated the superior competitive ability of perennial palatable grasses as compared with perennial unpalatable grasses (Moretto and Distel, 1997) or woody species (Distel et al., 1996; de Villalobos et al., 2005). However, heavy selective grazing of palatable grasses reduces their competitive ability (Moretto and Distel, 1999), facilitating the growth of established plants and seedling recruitment of both unpalatable grasses (Moretto and Distel, 1998) and woody plants (de Villalobos et al., 2005). Similar grazing-induced modifications in the species composition have been documented in many rangelands throughout the world (Archer, 1989; Noy-Meir et al., 1989; Westoby et al., 1989; Noble, 1997; Roques et al., 2001).

We have only anecdotal evidence on the composition and dynamic of the unpalatable grass and woody communities. These floristic groups can be strongly dominant or can co-dominate in the communities. The composition of unpalatable grass communities shows a strong association with soil type. Species with narrow leaf blade (e.g., *S. ichu*, *S. tenuissima*) dominate in sites with sandy loam soils, whereas species with more wide leaf blades (e.g., *S. ambigua*, *S. brachychaeta*) dominate in sites with silty loam soils. On the other hand, woody communities are rich in species, and frequently dominated by *Prosopis* spp. Cattle ingest pods of *Prosopis* species favouring dispersal and seed germination. Most of the seedling emergence occurs in cow dung. These observations on unpalatable grass and woody communities raise implicit questions that deserve to be addresses in future studies.

The replacement of mid-tall palatable perennial grasses by short palatable perennial grasses, and the increase in the abundance of annual species with increasing grazing intensity can be explained by the classical plant succession model (Clements, 1916), which assumes continuous and reversible biophysical changes. Transitions between communities dominated by these floristic groups in the southern Caldenal rangelands can be assumed to be reversible by controlling the causal disturbance (i.e., grazing). Although there is no confirmatory experimental evidence, floristic changes observed in grazing exclosures are consistent with the assumed reversibility of vegetation changes induced by grazing. It has been a common observation that sites dominated by short grasses and annual species that are protected from grazing end up being dominated by mid-tall palatable perennial grasses. The communities dominated by mid-tall grasses, short grasses or annuals would represent the vegetation dynamic within the "Palatable Grass Regime" (regime or attractor *sensu* Scheffer and Carpenter, 2003) (Fig. 1).

On the other hand, the encroachment of unpalatable grasses and woody plants represents vegetation changes that exceed the explanatory power of the succession model, because of their discontinuity and irreversibility (Fig. 1). These types of changes adjust better to a different conception of ecosystem dynamics, such as the one that proposes the existence of alternative regimes in the same ecological site (Holling, 1973; Noy-Meir, 1975; Westoby, 1980; Walker and Salt, 2012; Bestelmeyer et al., 2015). The encroachment of unpalatable grasses and shrubs represent regime shifts due to their persistence. Once communities in the Caldenal rangelands become dominated by unpalatable grasses and/or woody vegetation, a disturbance other than grazing (e.g., fire or mechanical) is necessary to start turning the transition back to the "Palatable Grass Regime" (Bóo et al., 1996, 1997). The unpalatable grass and shrub regimes most probably derive from the annual communities within the palatable grass regime since, as already mentioned, the loss of palatable perennial grasses depresses interspecific competition and favours encroachment of unpalatable perennial grasses and woody plants.

4. Restoration of degraded rangelands

Most of the Caldenal rangelands are currently in the process of crossing, or have already crossed, thresholds to alternative regimes dominated by unpalatable grasses and/or woody plants, with the consequent losses in the livestock carrying capacity and economic productivity of cattle operations (SAyDS, 2007). However, restoration of the "Palatable Grass Regime" is potentially possible since a regime shift to either unpalatable grasses or woody vegetation attractors does not involve irreversible soil degradation in the Caldenal rangelands (Villamil et al., 2001). Transition from these undesirable regimes to the "Palatable Grass Regime" needs a disturbance other than grazing due to strong hysteresis in forward and backward switches over the grazing intensity gradient (Distel and Bóo, 1996). Controlled burning has been successfully utilized to reduce the aerial cover and density of both woody vegetation (Bóo et al., 1997) and unpalatable grasses (Bóo et al., 1996). Mechanical control (roller chopping) of shrubs has also contributed to increasing the dominance of desired species and the productivity of the ecosystem (Adema et al., 2004). Even so, disturbance methods (fire or mechanical) need to be repeated through time since regrowth or sprouting of undesirable plants, and expectedly accompanied with proper control of grazing in order to achieve dominance of the desired plant species. However, although potentially possible, restoration of the "Palatable Grass Regime" should be visualized as a lengthier process constrained by climatic and economic factors. For instance, woody plant encroachment control increases pasture productivity and thus expected income, but could also increase the farmer's income risk under variable climates (Lukomska et al., 2014). Further research is needed to address how the interaction between disturbance (fire or mechanical) and grazing influences recovery of palatable grasses.

5. Stocking rate and grazing regime

Southern Caldenal rangelands have historically suffered high, fixed stocking rates (Morris and Ubici, 1996; older ranchers, pers. com.), as in many arid and semiarid rangelands around the world (Illius et al., 1998). However, under conditions of highly variable precipitation the least risky decision in stocking rate management is to set the number of animals according to a level of forage production with a high probability of occurrence (i.e., conservative stocking rate). In an analysis for the southern Caldenal rangelands that comprised a period of 30 years, Cecchi (1995) concluded that setting the stocking rate of reproductive cows 20% below the average value of forage production markedly reduces the periods with forage deficit. The same author argued that this conservative stocking rate would allow the continuance of high reproductive efficiency even in dry years due to stockpiling forage from wet years, except under conditions of extreme multi-year droughts. Studies conducted around the world consistently showed that conservative stocking rates reduce the probability of overgrazing and improve the economic productivity in the mean- and long-term, compared to stocking rates adjusted to the average or over average forage production (Janssen et al., 2004; Higgins et al., 2007; Quaas et al., 2007; Teague et al., 2008; Quiroga et al., 2009; Richardson et al., 2010; Ash et al., 2011; Orr and O'Reagain, 2011). A conservative stocking rate provides flexibility which is just as important. In average or above average rainfall years any excess forage can be used to feed and grow young animals (stockers) (Díaz-Solís et al., 2009; Torell et al., 2010), to recover the vigour of

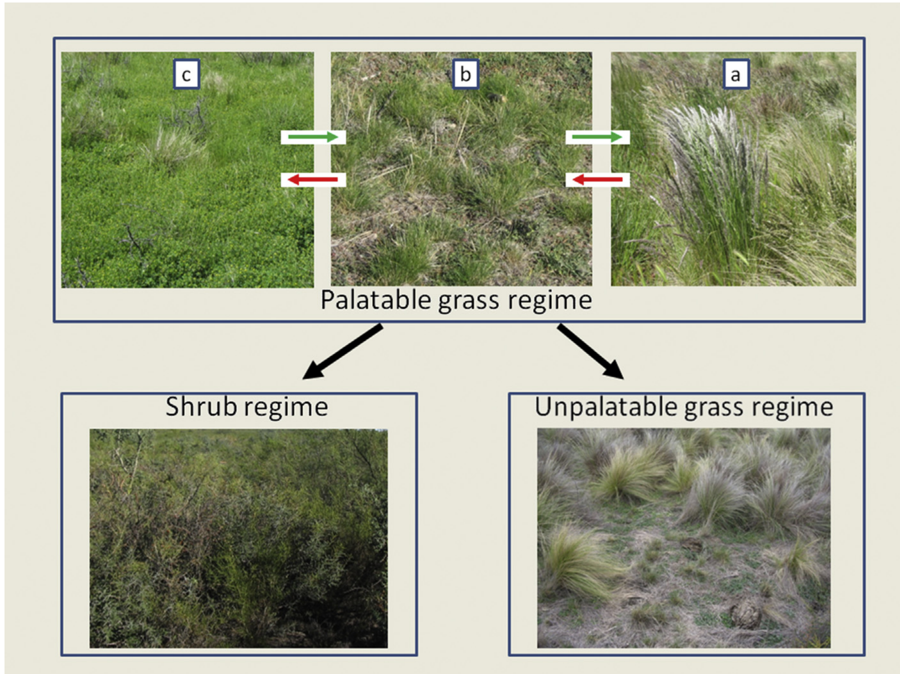

Fig. 1. Regime shifts observed in the southern Caldenal rangelands. Green and red arrows stand for reversible community pathways within the "Palatable Grass Regime": (a) mid-tall palatable grasses, (b) short palatable grasses, (c) annual species. Black arrows stand for irreversible transitions to either a "Shrub Regime" or "Unpalatable Grass Regime". (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the more preferred grasses (Müller et al., 2007; Scanlan et al., 2011; Ash et al., 2011) or for burning to control encroachment of undesirable species (Ansley et al., 2010; Limb et al., 2011; Lohmann et al., 2014).

The Caldenal rangelands have also most frequently been continuously grazed. Under continuous grazing animals regraze the high-quality immature regrowth, which is detrimental to root growth and survival, water and nutrient absorption, growth and survival of tillers, and the accumulation of carbohydrate reserves (Briske and Richards, 1995). In the southern Caldenal, overgrazed communities of palatable grasses are normally composed of a high density of small tussocks, which are particularly susceptible to drought conditions (personal observation). Continuous grazing also depleted residual biomass below the minimum required for adequate plant and soil protection (Fig. 2). Grazed plants require a recovery period that can last for several weeks or months (depending on the inherent characteristic of the species and the biotic and abiotic conditions of the habitat) for re-adjusting their morpho-physiology to attain a normal function (Caldwell, 1984; Richards, 1993; Ferraro and Oesterheld, 2002).

Fig. 2. Continuously grazed southern Caldenal rangeland showing insufficient residual biomass for adequate plant and soil protection.

There is a basic need for research related to stocking rate control and grazing regime in the southern Caldenal rangelands. Information on forage production throughout the year in relation to rangeland condition and precipitation regimen is needed to set safe stocking rates and for timing decisions on retaining or selling stockers. There is information neither on "minimum residual biomass" (BLM, 1999) for plant and soil protection in different ecological sites, nor on simple indicators to determine readiness for grazing after resting. There is also a need for development of simulation models to encompass the complexity of the system and assess the ecological and economic consequences of different management options.

6. Indicators of imminent undesirable ecosystem changes

In the southern Caldenal rangelands, the communities dominated by annual species within the "Palatable Grass Regime" may represent "at risk communities" (*sensu* Walker et al., 2004; Briske et al., 2008), which are the closest to crossing thresholds to alternative regimes (Speed et al., 2010). Reduced competitive pressure from annuals, particularly under drought conditions (Fig. 3), has been observed to favour recruitment of unpalatable grasses (Moretto and Distel, 1999) and woody plants (de Villalobos et al., 2005). In the annual species communities there would be therefore a relatively high probability of transition to alternative undesirable regimes dominated by unpalatable grasses and/or woody species.

Prevention of transition to undesirable regimes requires the

Fig. 3. The loss of perennial grasses caused by overgrazing and drought represents a tipping point for woody plant encroachment in the southern Caldenal rangelands. White arrows show seedling establishment of *Larrea divaricata* at the end of a multi-year drought.

monitoring of ecological indicators that can be used to assess the ecological status and trends in the health of the ecosystem and its component parts. Examples of such indicators are vigour and size of perennial grasses, abundance of annual species, seedling establishment of undesirable species, size and connectivity of denuded soil patches, and soil aggregate stability (Pellant et al., 2005; Chartier and Rostagno, 2006; Stokes et al., 2009; Kaghergis et al., 2011; López et al., 2011; Sasaki et al., 2011). Ecological indicators serve to identify "at risk communities", which should emphasize the necessity to initiate preventive management actions that block undesirable changes in the structure and functioning of the ecosystem. Such actions would entail specific decisions in grazing management in combination with other management decisions (e.g., burning). For instance, for fire-driven rangelands like the Caldenal, resilience-based management prescribes periodic destocking and burning to balance the perennial grass and shrub densities (Anderies et al., 2002; Ratajczak et al., 2014).

There is a big gap in knowledge related to indicators of undesirable ecosystem changes, and preventive management actions, for the Caldenal rangelands. There is an urgent need of research in order to support planning towards the prevention of undesirable ecosystem changes, to avoid costly post hoc restoration actions.

7. Synthesis

There is enough evidence to justify the argument that grazing by domestic livestock has been a primary driver in the degradation of the southern Caldenal rangelands. Rangeland degradation led to crossing thresholds from a desirable regime dominated by palatable perennial grasses to alternative regimes dominated by unpalatable grasses and/or woody plants. These latter regimes are undesirable in terms of safeguarding the functionality of the primary ecological processes, species richness, species diversity, carrying capacity, and economic productivity of livestock operations. Restoration of the "Palatable Grass Regime" in degraded rangelands requires management decisions, such as burning or mechanical control of shrubs and unpalatable grasses, and should be envisaged as a costly mid to long term task. In the transition towards or in the "Palatable Grass Regime", stocking rate and grazing regime represent the primary controlling factors for conserving the Caldenal rangelands. The sustainable utilization of palatable grasses calls for flexible stocking rates and intermittent grazing in replacement of current fixed stocking rates and continuous grazing. Most importantly, decisions need to be made within a framework of adaptive management, in which flexibility plays a crucial role.

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