A conceptual model for changes in floristic diversity under grazing in semi-arid Patagonia using the State and Transition framework

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ABSTRACT

Effect of grazing on plant diversity was studied based in 92 sites of the semiarid Magellan Steppe, South Patagonia, Argentina. 85 species were registered, 96% of them perennials and mostly native and endemic, with only 7.6% exotics. Cover of tussock grass Festuca gracillima was used as a Proxy variable for grazing intensity. Maximum likelihood analysis of diversity vs. tussock cover selected a quadratic function with a maximum at intermediate grazing intensities, closer to predictions of equilibrium models (MSL) for sub humid environments with a long history of grazing than those for semi arid-short evolutionary grazing history. State and Transition (ST) models indicate that the most diverse areas have probably lost tussock cover by intense use in their grazing history but are at present under lower grazing pressure, as this induces gain of diversity of short grasses without reestablishing tussock cover. A new model is proposed combining previous MSL and ST models. It shows a smaller increase in diversity with intermediate/high grazing, loops in the trajectory and multiple alternate states under low grazing depending on the management history. It may be an example of non-linear models that are supposed to be common in semiarid areas but have few published examples.

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1. Introduction

Grazing domestic herbivores are a major ecological factor that shape structure and function of the remaining natural rangelands in the world (McNaughton, 1979; Mack and Thompson, 1982). Biodiversity of rangelands has received particular attention because it relates to productivity and stability (Folland et al., 1986; Tilman, 1996). While heavy grazing in semi-arid rangelands generally leads to a reduction in diversity, the effects of intermediate grazing pressures differ. Some ecosystems such as shrublands in Israel (Naveh and Whittaker, 1980; Noy-Meir et al., 1989) or sagebrush steppes in Montana (Meuggler, 1984) reach maximum diversity at intermediate stocking rates; while others show maximum values in exclosures and grazing even at moderate stocking rates generates diversity reduction, as in most arid Australia (Lunt et al., 2007).

Milchunas et al. (1988) in their well-known graphical model suggest that diversity is determined by grazing intensity following a response function that depends on two factors: evolutionary history of the site and moisture. Grazing semiarid areas that have evolved under high pressure from native herbivores causes a small effect on community composition, while grazing those with a shorter evolutionary history induces loss of diversity at much lower grazing intensities and at a higher rate. They offered as examples of the former the US shortgrass prairie and of the latter, Patagonian steppes. On the other hand, grazing in sub humid grasslands gives way to an increase in diversity, and the level of grazing that supports higher diversity increases with site productivity (Proulx and Mazumder, 1998; Kondoh, 2001; Stewart and Pullin, 2008).

The Milchunas, Sala and Lauenroth (1988) model (MSL model hereafter) postulates a single equilibrium value for each grazing pressure in a continuous reversible process, but as Westoby (1979) suggests, in arid and semi-arid lands the response time to grazing may vary widely and changes may be irreversible (Illius and O'Connor, 1999). Grazing for a short time may cause a temporary reduction that disappears when stocking rates are relaxed (i.e.: the community is resilient), but higher stocking rates or longer periods may induce transitions between discrete

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"States" in the community. The State and Transition Model (STM hereafter) (Westoby et al., 1989) includes irreversible transitions and alternate states and may be more suitable to represent their dynamics.

Cingolani et al. (2005a) point out that there is a contradiction arising between these models, as MSL predicts a single equilibrium of diversity for each grazing level, while the STM allows for alternate equilibrium points. They suggest that systems with long evolutionary grazing history are more likely to show resilience to grazing and reversible transitions, conforming to the single equilibrium state of the MSL model. On the other hand, those with short evolutionary history probably show irreversible transitions that generate additional branches to the MSL trajectories, generating two or more States with different levels of diversity for a given grazing intensity depending on the history of the site.

In order to test the pattern of the relation of diversity in response to grazing, field data and a strategy to statistically compare different response functions are required. While diversity is readily assessed, grazing intensity is difficult to evaluate as consistent historical records of stocking rates in particular sites are rarely available, and because herbivores in commercial paddocks generate grazing gradients that complicate the estimation of grazing pressure at any singular point (Bailey et al., 1996). Stocking experiments are limited to one or a few sites, explore a reduced number of grazing intensities and are limited in time frame (Ash and Smith, 1996). Fence contrasts have been also been used with this purpose (Naveh and Whittaker, 1980; Todd and Hoffman, 1999; Cesa and Paruelo, 2011) but they are limited in distribution and may represent border effects. The third strategy is to use surrogate (Proxy) variables for grazing intensity such as distance to watering points (Ludwig et al., 1999) used in "piosphere" studies (Lange, 1969), or total vegetation cover (Perelman et al., 1997). In this study, cover of the main tussock grass was used as a Proxy, as *Festuca gracillima* cover is known to decrease under heavy grazing (Anchorena, 1985; Faggi, 1985; Roig and Faggi, 1985; Cingolani et al., 1998; Anchorena et al., 2001; Covacevic, 2001; Cingolani et al., 2002). Demographic model projections for the Magellanic Steppe show that under high stocking rates (0.65 sheep·ha^{-1}) half of the tussock cover would be lost in 37 years (Oliva et al., 2005). The gradual reduction in tussock cover that is initially thought to have been in the order of 30% or more in the *Festuca gracillima* grasslands of the Magellanic Steppe (Faggi, 1983) may then indicate the historical intensity of grazing.

The objective of this paper was to a) verify the properties of states in the previously developed State and Transition models for the Magellanic Steppe b) examine how species diversity metrics vary among states, evaluated with respect to predictions of the MSL model and c) propose a new combined conceptual model that relates diversity and grazing and better adjusts to the observed patterns. Patagonia classifies as semiarid (Noy Meir, 1973) with low-productivity, and has been used as an example of short evolutionary grazing history (Milchunas et al., 1988). The initial hypothesis, according to the MSL model for short history of grazing and low productivity sites were that (1) grazing reduces diversity (2) the relation between grazing and diversity is linear with negative slope and a maximum in ungrazed or slightly grazed sites. Additionally and based on Cingolani et al. (2005a) model we hypothesised that (3) the system shows low resilience, with irreversible transitions and alternate states in equilibrium with a single grazing intensity. Field observations and state and transition hypothesis were combined in order to construct a graphical model that explains some of the particularities of complex vegetation dynamics that may be common in other semiarid ecosystems.

2. Materials and methods

2.1. Study area

Dry Magellanic Steppe (Leon et al., 1998; Oliva et al., 2001) is included in the Patagonia Phytogeographic province (Cabrera, 1976), and occupies 1.17 M ha of tertiary sedimentary plateaus, quaternary glacial terraces, and basaltic flows in southern Patagonia, north of the Magellan Strait (Fig. 1).

Soils are mostly Borolic haplargids (Salazar Lea Plaza and Godagnone, 1990), sandy and rich in organic matter in the top 10 cm, and argilic in depth. Climate is maritime, with a range of 170 and 240 mm of rain and is classified as a semi-arid site (Noy-Meir, 1973). Analysis of long term records for Rio Gallegos (Servicio Meteorológico Nacional, 1930—2010) indicate 239 (63 SD) mm annual rainfall with an even monthly distribution and 26% inter-annual coefficient of variation. Temperatures are low, 12.7 °C in summer 1.4 °C in winter (De Fina et al., 1968), and winds are constant (27 km/h yearly mean). *Festuca gracillima* Hook. f. tussock grass steppes with up to 70—80% total vegetation cover are the dominant vegetation type (Roig and Faggi, 1985). With an annual net productivity (ANNP) of 148 g m^{-2} (Cibils et al., 2005; Ferrante, 2011), they classify well below the 200 g m^{-2} threshold of systems of low productivity sites on global scale analysis of ecosystems (Milchunas and Lauenroth, 1993; Cingolani et al., 2005a). Sheep were introduced in the region around 1880 (Barbería, 1995), with high initial stocking rates of over 0.70 sheep ha^{-1}. Grazing pressure was gradually reduced in the second part of the XX century in an effort to maintain production in degrading rangelands, and mean stocking rates reached 0.30 sheep ha^{-1} from 1978 on (Oliva et al., 2012).

2.2. State and transition model

Changes in the dominant *Festuca gracillima* communities have been summarized in a STM by Borrelli and Oliva (2001) that has seven States (Fig. 2 and Table 1). In this scheme, the principal, vertical axis is related to cover of tussocks and the secondary one is associated with cover of short grasses and graminoids.

Floristic evaluations were performed in 91 sites that represent a sample of the real situations in the Dry Magellanic Steppe ecological site (Table 2). Observations date from 1987 to 2013, and used the line intercept method (Levy and Madden, 1933) with 500 points and 50 m transects. Species were identified following Nicora (1978).

Species were classified into Growth Habits: forb/herb, graminoid (including grasses), shrub and subshrub following NRCS (2004), but tussock grasses were further distinguished from graminoids. Origin was classified as endemic, native or exotic in the South American flora; perennity as perennial or annual and nomenclature was updated following Zuloaga et al. (2008). Life form (Raunkiær, 1934) was obtained from Roig and Faggi (1985).

In order to apply the ST model, transects were classified into States, initially using the State and transition catalog for Dry Magellanic Steppe in (Fig. 2 and Table 1) Borrelli and Oliva (2001), that provides a cover range for different functional groups: Tussocks, short graminoids and forbs/herbs and subshrubs. This classification was tested using ordination of the matrix of 66 species × 91 transects. Rare (<1% cover) species were removed from this analysis and Principal Components Analysis of PRINCOMP procedure (SAS/STAT Institute, 1998) was used.

2.3. Grazing vs. diversity models

In order to test the MSL model, the proposed shape of the