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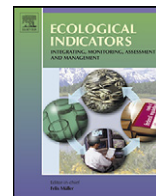
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Linking ecosystem resistance, resilience, and stability in steppes of North Patagonia

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ABSTRACT

The main objective of an ecosystem sustainable management is to preserve its capacity to respond and adapt to current disturbances and/or future changes, and maintain the provision of environmental goods and services. Two very important properties linked to this objective are the ecosystem resilience and resistance to disturbance factors. The *Structural–Functional State and Transition Model* (SFSTM) is a conceptual framework that allows evaluating the ecosystem resilience and resistance based on structural and functional attributes. On the other hand, the *Landscape Functional Analysis* (LFA) presents a method to assess the rangeland “health” based on structural vegetation and soil indicators, creating indexes to evaluate the ecosystem functional integrity. The aim of this study is to integrate LFA and SFSTM as an approach to help validate indicators and indexes associated with the resistance, resilience, and stability of a temperate rangeland ecosystem. States and transitions model for a shrubby-grasses steppe of the Western Patagonian District was used as a reference system. Changes in vegetation structure, soil surface, and loss of soil due to erosion were determined in sites with different grazing histories. Based on the SFSTM, we assessed the relationships between ecosystem structural changes with the recruitment process of the plant community and ecosystem integrity indexes (sensu LFA). Our results indicate that the decrease in the recruitment process, related to different grazing histories, was associated with a loss of ecosystem functional integrity. This was associated to a decrease in the ability to retain, store, and use rain water, and also in nutrient cycling. This suggests that the integration of the LFA methodology to the SFSTM can be used for indexes validation, which in turn allows the identification of critical thresholds associated with ecosystem resilience loss. Finally, throughout the integration of indicators of LFA into SFSTM, we established relationships between ecosystem resistance, resilience, and stability in response to a disturbance factor (e.g. overgrazing). Thus, we used this information to define states in *stable*, *unstable*, *mixed-unstable*, and *indifferent-stable dynamic equilibriums*. Our proposed approach provides a tool for ecosystem assessment regarding the identification of states that can be restored and those that might be more susceptible to degradation. Such information might help in the prevention of crossing a critical threshold and be used for sustainable management programs in rangelands.

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1. Introduction

The main objective of an ecosystem sustainable management is to preserve its ecological integrity while conserving its capacity to respond and adapt to disturbances and/or future changes, and maintaining the provision of environmental goods and services. Two very important ecosystem properties linked to this

objective are resilience and resistance (Walker et al., 1981; Müller et al., 2000; Scheffer et al., 2001; CBD, 2008; DDC, 2009). One of the main problems in arid and semiarid regions is the advanced desertification, associated mainly with overgrazing, that produces significant changes in the structure and functioning of the ecosystems (Reynolds and Stafford Smith, 2002; DDC, 2009). Operative tools are needed to identify the threshold associated with the loss of resilience, which might be easy to evaluate and monitor in the field to carry out sustainable management on rangelands and prevent desertification (Briske et al., 2006, 2008).

The resilience is the capacity of an ecosystem to return to the condition previous to a disturbance once it is suppressed, and it

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is related to the self-regulation ability. Complementary, resistance is the ability of an ecosystem to tolerate a disturbance without suffering significant changes in its structure and functioning (Holling, 1973; Westman, 1978; Stringham et al., 2003). Based on the state and transition model (see more Westoby et al., 1989), López et al. (2011) proposed the *Structural–Functional State and Transition Model* (SFSTM), as a conceptual framework to evaluate the resilience and resistance attributes of an ecosystem, based on structural and functional axes. Resilience is assessed by the attributes of elasticity and amplitude of the ecosystem (Westman, 1978; Williams et al., 1993). The SFSTM allows the identification of a critical threshold (structural and functional) that defines the amplitude of the ecosystem associated with the loss of the original resilience. This threshold is determined when an increase in the disturbance intensity and/or frequency causes important changes in vegetation structure and/or soil (e.g. erosion), and also with a significant increase in the loss rate of ecosystem functions. Moreover, the model can be useful to identify resistance based on the ecosystem changes promoted by a disturbance factor, estimated as the inverse of the speed and magnitude of degradation produced in a negative transition (shift from one state to another more degraded). This assessment helps to identify the types of response for different ecosystems. For example, if the same disturbance factor (overgrazing) on two ecosystems produces different types of degradation, the one with a higher speed and/or magnitude of degradation is less resistant.

An ecosystem that is resistant and resilient to disturbance factors would keep a species composition and productivity relatively stable throughout time. The stability of an ecosystem is a concept that has been defined and discussed as an important characteristic in state and transition models (Holling, 1973; Williams et al., 1993; Bestelmeyer et al., 2003; Stringham, 2003; Hobbs and Suding, 2009). Different approaches have been developed regarding stability, such as in definition of stability scales (local and global), and types (stable and unstable state or equilibrium) (Ludwig et al., 1997; Beisner et al., 2003; Jorgensen et al., 2004; Justus, 2008; Hobbs and Suding, 2009). Although no consensus has been reached (see Grimm and Wissel, 1997), we consider that greater ecosystem stability is related to a greater resistance and resilience to a disturbance factor (Williams et al., 1993; Stringham et al., 2003). While ecosystems are dynamic (Briske et al., 2003; López et al., 2011), the use of the concept of stability can contribute in understanding the dynamics of an ecosystem in relation to disturbance factors, and hence their vulnerability to degradation.

Tongway and Hindley (2004) (*Landscape Functional Analysis*: LFA) and Herrick et al. (2005) presented a methods to evaluate the “rangeland health” based on structural indicators of vegetation and soil states. These indicators are used to indirectly estimate indexes that evaluate the ecosystem functional integrity in relation to water infiltration, soil nutrient recycle, and resistance of the soil to wind and water erosion. Because the functions of an ecosystem are difficult to assess on the field, the operability is one of the main advantages of these rangeland health methodologies (Havstad and Herrick, 2003; Tongway and Hindley, 2004; Briske et al., 2005). For adequate monitoring and evaluation we think that these indexes can be validated and calibrated for each ecosystem mainly integrating two issues: (1) the evaluation of the type of relationship between ecosystem structural degradation (vegetation and soil) and indexes that indirectly estimate functional integrity and (2) the comparison between issue-(1) and the relationship of the ecosystem structural degradation and its key functions (e.g.: rain use efficiency or recruitment of key species).

The different state and transition models and approaches such as LFA had a parallel development and with little integration among them (Briske et al., 2005). Therefore, our aim was to integrate LFA and SFSTM to help the validation of indexes associated with

the decrease or loss of resilience, and to evaluate the ecosystem resistance and stability. For this purpose, we used the shrubby-grass steppe from the Western Patagonian District as reference ecosystem for these analyses of resilience–resistance–stability relationships. Intensive sheep grazing has caused a severe degradation of vegetation and soil. We determined the changes associated with the different grazing histories on the vegetation structure and soil surface (*sensu* LFA), and the loss of soil due to erosion. Based on the SFSTM, we evaluated the relationship between the ecosystem structural changes with the emergence process of plant community's new individuals (key demographic process), and indexes of infiltration, nutrient recycling, and stability (*sensu* LFA). Finally, we established a relationship between resistance, resilience, and stability to disturbance factor by the integration of the LFA indicators to the SFSTM.

2. Materials and methods

2.1. Study area

The study was carried out in the Pilcaniyeu Campo Anexo of EEA INTA Bariloche, Río Negro, Argentina (70°35'21"8W, 41°01'42"S). The principal activity of the region is extensive animal husbandry. The historical mean annual precipitation is 266 mm (70% during autumn–winter) and average annual temperature is 7.7 °C (Bustos, 2006). Three sites were selected within this area that have shrubby-grassland steppe with *Poa ligularis* and *Mulinum spinosum* representative of the Patagonian Western District (León et al., 1998). In each site, two paired sectors with different grazing history were delimited. Based on each grazing history (stocking rate and time), the states and transitions defined by Bonvissuto et al. (1993), and preliminary vegetation sampling, each sector within each site was labeled as follows: S1-I (site 1, state I) and S1-II (site 1, state II); S2-I (site 2, state I) and S2-III (site 2, state III); S3-I (site 3, state I) and S3-IV (site 3, state IV) (higher Roman numbers indicate most degraded states, Table 1).

2.2. Experimental design

In order to control the effect of a slight slope a Completely Randomized Block Design (DBCA) (four blocks) was used within each site.

2.2.1. Structural attributes

Following the LFA methodology (Tongway and Hindley, 2004), in four 30 m-transects in each state (one per block), the following state variables were evaluated: total and species cover; grass, shrubs and litter cover; patch basal length (PBL) and patch width (PW); density, cover and height of patch; patch symmetry index (PSI-ratio: width of patch/patch basal length) and inter-patch length (IPL-bare soil). To evaluate the loss of soil due to erosion in each state, the soil depth down to a water impervious layer was determined in four profiles (one per block).

2.2.2. Functional attributes

In each state, four plots with dimensions 2 m × 1 m (one per block) were arranged. In April 2007, 2008, and 2009 the seedling emergence for the main perennial species of the community was evaluated. In each year, all the seedlings were marked in order to assess their survival. The survival of the cohort-2007 (seedling emergence April 2007) until April 2009 was determined in September (late winter), December (late spring), and April (late fall) for each year.

Table 1

Study sites with paired sectors: excluded livestock sectors versus grazing history sectors (ranged from 700 to 900 ha). Based on the grazing history (stocking rate and time), sectors were labeled according to the state (I–IV) in the state and transition state model proposed by Bonvissuto et al. (1993).

Site with paired sectors	Excluded livestock sector (exlosures)	Grazing sector ^a
Site 1	S1-I: Grass-shrub steppe of <i>Poa ligularis</i> and <i>Mulinum spinosum</i> (2 ha without grazing for over 15 years)	S1-II: Grass-shrub steppe of <i>Poa ligularis</i> , <i>Stipa speciosa</i> vr. <i>speciosa</i> and <i>M. spinosum</i> , (moderate stocking rate: 0.3 sheep ha ⁻¹ year ⁻¹ for over 15 years)
Site 2	S2-I: Grass-shrub steppe of <i>Poa ligularis</i> and <i>Mulinum spinosum</i> (2 ha without grazing for over 30 years)	S2-III: Shrubby-grasses steppe of <i>M. spinosum</i> , <i>Senecio</i> spp. and <i>Stipa speciosa</i> (high stocking rate: between 0.6 and 0.7 sheep ha ⁻¹ year ⁻¹ for over 80 years)
Site 3	S3-I: Grass-shrub steppe of <i>Poa ligularis</i> and <i>Mulinum spinosum</i> (38 ha without grazing for over 30 years)	S3-IV: Subshrubby-grasses steppe of <i>M. spinosum</i> , <i>Senecio</i> spp. and <i>Stipa</i> sp. (very high stocking rate: about 0.8 sheep ha ⁻¹ year ⁻¹ for over 80 years)

^a Stocking rates associated with states II–IV are within the ranges used for many ecosystems of Patagonia (see more Paruelo et al., 1993) and these are annual average.

2.3. Data analysis

2.3.1. Structural indexes

By combining all the assessed variables according to the LFA and the soil depth data, a Structural Degradation Index (SDI) (proposed by López et al., 2011) was calculated. The Mahalanobis distance (MD) matrix (Legendre and Legendre, 1998) between all the *i*th sampling points of the different states (four blocks per state, $n = 24$) was calculated. The index was composed as follows: $SDI_i = [(MD_i \times 100) \times (MD_{max})^{-1}]$, where MD_i is the MD between the *i*th sampling point and the sampling point that had the greatest total vegetation cover. The MD_{max} corresponds to the maximum value of the registered MD. Based on MD_{max} , all the MD values were standardized, determining that SDI varied between 0 and 100%. The following variables were taken into account to calculate the MD's: cover of soil-total, species, grass, and shrubs; patches 'cover, basal length, width, height, density, and symmetry; inter-patch length; and soil depth.

In order to integrate the variables of patch structure, we propose two new indexes: the vegetation heterogeneity index (VHI) and vegetation connectivity index (VCI). Their formulas are defined as:

$$VHI = \left\{ \left(\frac{S.D. PBL}{PBL} + \frac{S.D. PW}{PW} + \frac{S.D. PSI}{PSI} \right) \times \frac{\text{Total cover}}{100} \right\} + \left(\frac{S.D. IPL}{IPL} \times \frac{\text{Inter-patch cover}}{100} \right);$$

$$VCI = \frac{\text{Total cover}}{100} \times \frac{PBL}{IPL};$$

where S.D. indicates standard deviation.

Li and Reynolds (1995) defined spatial heterogeneity based on the variability of the patches type and configuration. These authors indicated two important characteristics of the spatial heterogeneity that were considered in the proposed VHI: the grain and size of a variable (e.g. patch basal length, inter-patch length) and its variability (standard deviation). A patch mosaic with high standard deviations on patches basal length, width, and patch symmetry index, will have high patch heterogeneity and therefore a high VHI. On the other hand, patches more heterogeneously arranged determine a standard deviation increase of the inter-patch length, determining the grouping and spatial configuration of the patches. The standard deviation of each variable was standardized by its average. Finally, the heterogeneity of the patch structure was standardized based on the proportion of its total cover, while the inter-patch heterogeneity was standardized based on its cover proportion.

The LFA evaluates the structure of patches regarding how it affects the process of gains/losses of the soil, organic matter, and water in the ecosystem. Therefore, the proposed VCI provides more integrated information regarding how different patches are connected, which is associated with the balance of gains/losses of matter and energy. The patches are more "connected" to each other when the inter-patch length decreases (closer patches) and patches basal length increases (higher border effect of the patches on the inter-patch). Connectivity increases with increasing vegetation cover. The number of patches was not taken into account in this formula since it was redundant.

2.3.2. Functionality indexes

To estimate ecosystem functionality, the infiltration, nutrient recycles and stability indexes were estimated using the LFA methodology. These indexes were estimated based on different combinations of the following variables: soil cover, patch basal cover, litter (cover, origin, decomposition degree), cryptogams cover, crust brokenness, erosion (type and severity), deposited materials, micro-topography, surface resistance to disturbance, slake test, and soil texture (see Tongway and Hindley, 2004).

2.3.3. Inferential statistical analysis

First, variance analyses (ANOVAS) were performed considering only the sheep exlosures to assess whether there are differences related to the topography of the three sites. Then, for structural vegetation and soil variables, a model with an Exclosure factor with three levels (S1-I, S2-I, and S3-I) was analyzed.

Then, using information from each sampling point of all states, regression models were fitted between the SDI's (explanatory variable) and each of the following dependent variables: cohort-2007 seedlings density (seedling emergence), infiltration, nutrient recycles, and stability indexes, VHI, and VCI. Additionally, for model simplicity, seedling emergence, infiltration and nutrient recycles indexes were adjusted with piecewise regressions, which helped to determine a threshold response between the analyzed variables (Clements et al., 2010).

Variance analyses were performed for each one of the assessed variables, comparing each grazed state with its paired exlosure. In these ANOVA models, the State factor was analyzed with two levels per site: Site 1 = S1-I and S1-II; Site 2 = S2-I and S2-III; and Site 3 = S3-I and S3-IV.

Finally, in order to make statistical inferences between the different degradation states (S1-II, S2-III, and S3-IV) for each variable, ANOVA were performed comparing the three sites. In these analyses, within each block (B), we considered the differences between

the value of each variable from the state with grazing and the value of its paired enclosure. For example, in Site 1, this *difference* variable is represented as follows: $(S1-II_{B1}-S1-I_{B1})$, $(S1-II_{B2}-S1-I_{B2})$, $(S1-II_{B3}-S1-I_{B3})$, $(S1-II_{B4}-S1-I_{B4})$. The sub-indexes B1–B4 represent the block where they belong. The same applies for the calculation of this *difference* variable for Sites 2 and 3.

The analyses were carried out using the SAS program (version 8.0) with a significance level of $\alpha=0.05$. In the cases in which significant differences for the Site factor were detected, the Bonferroni test was applied. In order to reach normality and variance homogeneity assumptions, some variables were transformed with: $\arcsin(\sqrt{x})$ or $\arcsin(\sqrt{x+1})$ (for some cover variables); $\ln(x)$ (for some patch variables); and x^2 (for some seedling survival variables).

3. Results and discussion

Between the enclosures of the three sites, there were no differences in none of the variables analyzed ($p>0.05$), indicating that the enclosures would represent the same state (S-I) as the one defined by Bonvissuto et al. (1993). Therefore, the enclosures were a proper control for making biological and statistical inferences between different sites; allowing the assessment of a degradation states gradient in regression analyses.

The regression of the seedling emergence, indexes of infiltration, nutrient recycling, and vegetation connectivity in relation to the SDI, were adjusted to a non-linear regression (sigmoid with three parameters) (p -values ≤ 0.05) (Fig. 1a–c and e). The regression model fitted between the stability index and SDI was a polynomial quadratic model (p -value ≤ 0.05) (Fig. 1d). In addition, the vegetation heterogeneity index (VHI) and SDI fitted a logistic regression model (Lorentzian) (p -value ≤ 0.05) (Fig. 1f).

The seedling emergence, infiltration and nutrient recycling indexes, and VCI decreased when SDI increased, (Fig. 1a–c and e), whereas VHI increased from state I to S1-II and decreased toward S3-IV (Fig. 1f). On the other hand, as SDI increased, stability index decreased to a minimum value in S2-III ($SDI \approx 60$), then it increased toward S3-IV (Fig. 1d). The type of response between seedling emergence, infiltration and nutrient recycling indexes in relation to SDI corresponded to a sigmoid curve, similar to the curve of ecosystem function loss, while increasing the disturbance factor, proposed by Tongway and Hindley (2004). Based on the piecewise regressions for the seedling emergence, infiltration and nutrient recycling indexes in relation to SDI, a threshold can be defined for values of SDI between 43 and 48% (p -values ≤ 0.05) (y_1 values in Fig. 1a–c). This would indicate that the system could tolerate approximately 45% of change in vegetation and soil variables in relation to the reference state before the key ecosystem processes significantly decrease. From the threshold (after S1-II), the process of seedling emergence decreases significantly; this would determine a critical threshold associated with a decrease in ecosystem resilience (López et al., 2011). A similar response of seedling emergence, infiltration and nutrient recycling indexes, would indicate that the indexes of LFA are useful for monitoring the functional integrity in this type of ecosystems and also to define critical thresholds. A critical threshold is integrated by the relationship between a structural threshold and a functional threshold (Briske et al., 2005; López et al., 2011). The structural threshold would be associated with: (i) a biotic component with changes in patch structures, grass forage decreases, and shrubs increase in the system (Figs. 2 and 3); and (ii) an abiotic component with loss of soil due to erosion (Bisigato and Bertiller, 1997, 2004b; Briske et al., 2005; Hobbs and Suding, 2009). The functional threshold would be associated with the loss of key ecosystem processes such as recruitment (Figs. 1a and 4) and rain use efficiency (Briske et al., 2005; López et al., 2011).

3.1. Structural attributes of the critical threshold

The biotic factors of the structural threshold were related to changes in the vegetation heterogeneity, a decrease in vegetation cover (less than 45%) and connectivity, density and basal cover of patches, and an increase in the inter-patch length (p -values ≤ 0.05) (S2-III and S3-IV, Figs. 1–3). This biotic threshold would be associated with a modification in the competitive dynamics and a plant–plant and plant–herbivore interactions (Beisner et al., 2003; Briske et al., 2006). In state I the vegetation spatial heterogeneity was mainly related to the irregular form of large patches (low symmetry index) (Figs. 1d,f and 2g). The heterogeneity would increase with moderate grazing pressure (S1-II) due to a greater variability of the symmetry index and size of the patches. This could be due to differential grazing between palatable and less-palatable species, which promoted fragmentation in some patches and/or changes in the floristic composition, increasing the variability (S.D.) within each transect (Fig. 1f). In this study, the fragmentation was evidenced with the decrease in the patch width (Fig. 2e) (p -value ≤ 0.05). Furthermore, heterogeneity might also increase due to differential grazing of sectors within the community. For example, intensive grazing near water sources (Adler et al., 2001; Morici et al., 2003; Oesterheld et al., 2005; Cingolani et al., 2005) would increase the standard deviation of structural variables between transects within each state. The results agree with the theory of “intermediate disturbance”, which poses that in some ecosystems with low or moderate disturbance intensities a species diversity and community’s heterogeneity increase might occur (Paine, 1966; Adler et al., 2001; Cingolani et al., 2005). A similar process has been registered for edaphic variables, where intermediate grazing pressures have increased the heterogeneity of some variables (e.g. soil organic carbon) (Gaitán, 2009).

The spatial heterogeneity decreased with high or very high grazing pressure due to patches becoming more symmetric, more evenly arranged, and with more space among them (p -values ≤ 0.05) (E2-III and E3-IV, Figs. 1f and 2f,g). Thereby, the standard deviation of the inter-patch length was lower in relation to their high average value by transect, where the relative weight of this variable in VHI increased due to the lower vegetation cover (p -values ≤ 0.05) (Figs. 2a,f and 3a,b). Then, from high to very high grazing pressures a homogenization of the system occurred, possibly due to intensive and frequent grazing in most patches and a decrease of patch density (Figs. 1f and 2c,g). This simplification of the ecosystem was associated with less cover and species richness (data not published), which would affect the ecological integrity of the system (Müller et al., 2000). This change in the spatial structure associated with grazing has been registered in other arid and semi-arid ecosystems (Bisigato and Bertiller, 1997; Bestelmeyer and Wiens, 2001; Bisigato et al., 2005; Cipriotti and Aguiar, 2005; Gaitán, 2009), where grazing produced fragmentation of patches and changes in the floristic composition and/or edaphic variables, affecting the diversity and heterogeneity of the ecosystem.

The decrease of the heterogeneity in highly degraded states was also associated with an increase in the shrub cover (with more cover of *M. spinosum* and *S. filaginoides* in S3-IV than in S3-I) (p -values ≤ 0.05) (Fig. 3c). This could happen because the increase of shrubs in the ecosystem would increase the grain or size of the patches (Cross and Schlesinger, 1999; Bisigato et al., 2005; Gaitán, 2009). Thus was evidenced by a lower patch density with fewer small grassy patches, dominated by large more symmetric shrubby patches, and with a lower variation coefficient in the patch dimension in highly degraded states of our study (see VHI formula; Figs. 2c,d,f,g and 3c).

Studies carried out in shrub steppes of the Monte Austral (Bisigato et al., 2005) suggest that changes in heterogeneity, associated with grazing, are due to an increase in the fragmentation and

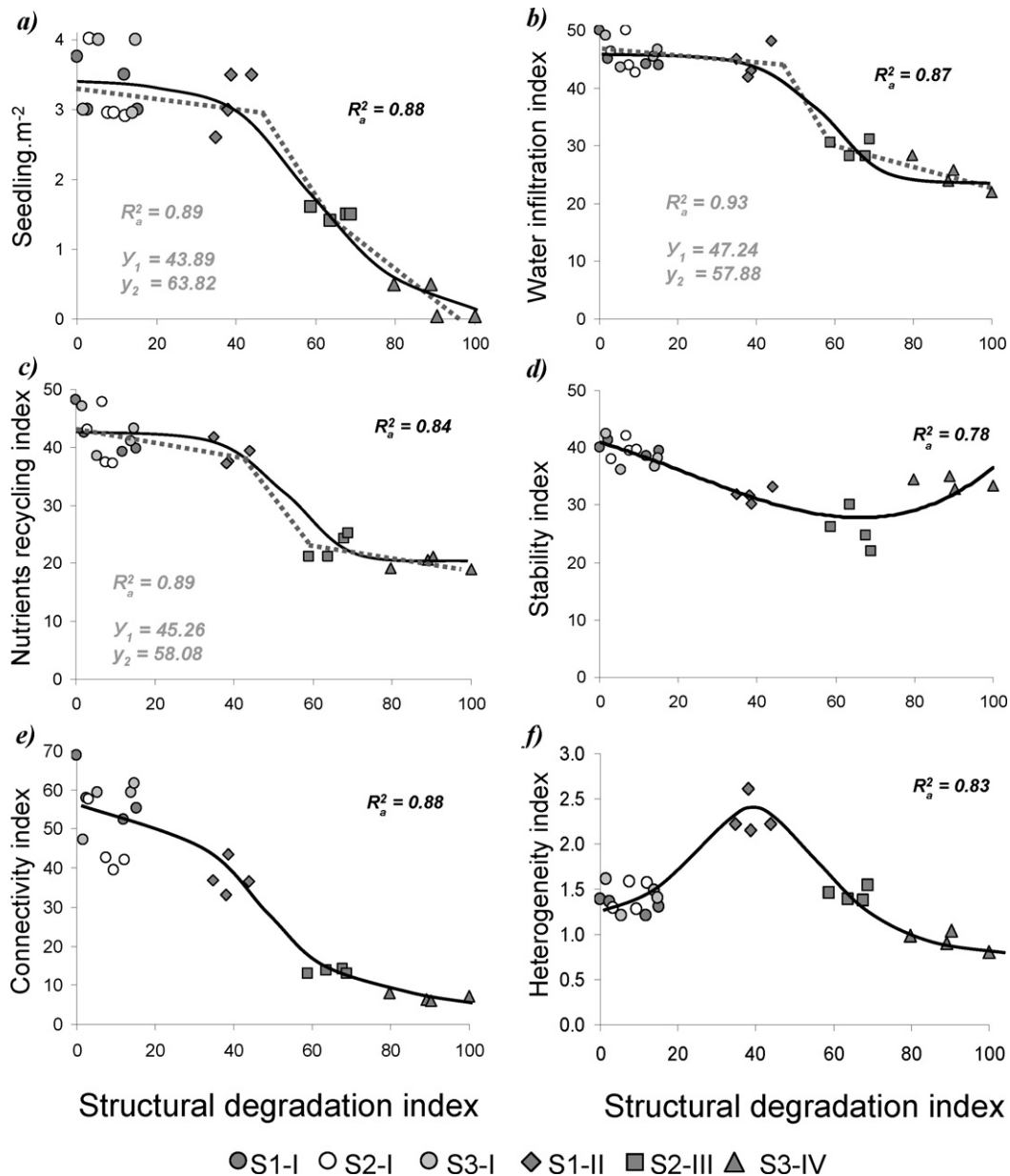


Fig. 1. Sigmoid curve regression (black line) between structural degradation index (SDI) and (a) seedling density of perennial species (no. m⁻²), (b) water infiltration index, (c) nutrients recycling index, and (e) vegetation connectivity index. (d) Quadratic polynomial regression between SDI and stability index. (f) Logistic regression (Lorentzian) between SDI and vegetation heterogeneity index. We report the R^2 -adjusted; in a, b and c is plotted the estimated curve by piecewise regressions (dashed gray line and gray value R^2), y_1 and y_2 are the first and second inflection point, respectively; ($\alpha = 0.05$).

a decrease in density and connectivity of the vegetated patches. In our study, the decrease of the patches connectivity between S1-I and S1-II (Fig. 1e) would have been due to a fragmentation of the patches and a cover decrease. Then, with high or very high grazing pressures (S2-III and S3-IV), the decrease of total cover was fostered, promoting a decrease in patch density and an increase in the inter-patch length; and consequently a marked decrease in connectivity (p -values ≤ 0.05) (Figs. 1e, 2c,f, and 3a,b).

The structural changes (e.g. less connectivity among vegetated patches) decrease the capacity to accumulate sediments in the ecosystem and increase soil loss by erosion (abiotic component of the structural threshold) (Whitford, 2002; Bestelmeyer et al., 2003; Ludwig et al., 2004; Tongway and Hindley, 2004). Our study showed evidences of a decrease in soil depth in the states with high and very high grazing pressures, S2-III and S3-IV had less soil depth than their paired exclosures (S2-I and S3-I, respectively)

(p -values ≤ 0.05). Site differences were found only between sites 1 and 3, where S3-IV had less depth than S1-II (p -value ≤ 0.05). The average values (\pm S.E., standard error) were: S1-I = 40.5 (± 1.0) cm and S1-II = 40.0 (± 0.9) cm; S2-I = 40.0 (± 0.7) cm and S2-III = 35.0 (± 0.8) cm; and S3-I = 41.8 (± 1.0) cm and S3-IV = 30.0 (± 0.6) cm.

3.2. Functional attributes of the critical threshold

The decrease in the infiltration index after the threshold, as SDI increase (Fig. 1b), was associated with a decreasing of soil cover (vegetation and litter) (Fig. 3a and d; p -values ≤ 0.05) and vegetation heterogeneity (less patch density and greater inter-patch length; Fig. 2c and f), which would increase the surface water runoff (Heady and Child, 1994; Tongway and Hindley, 2000; Briske et al., 2006). These changes along with low soil depth in the more degraded states (S2-III and S3-IV), lead to less water storage and less

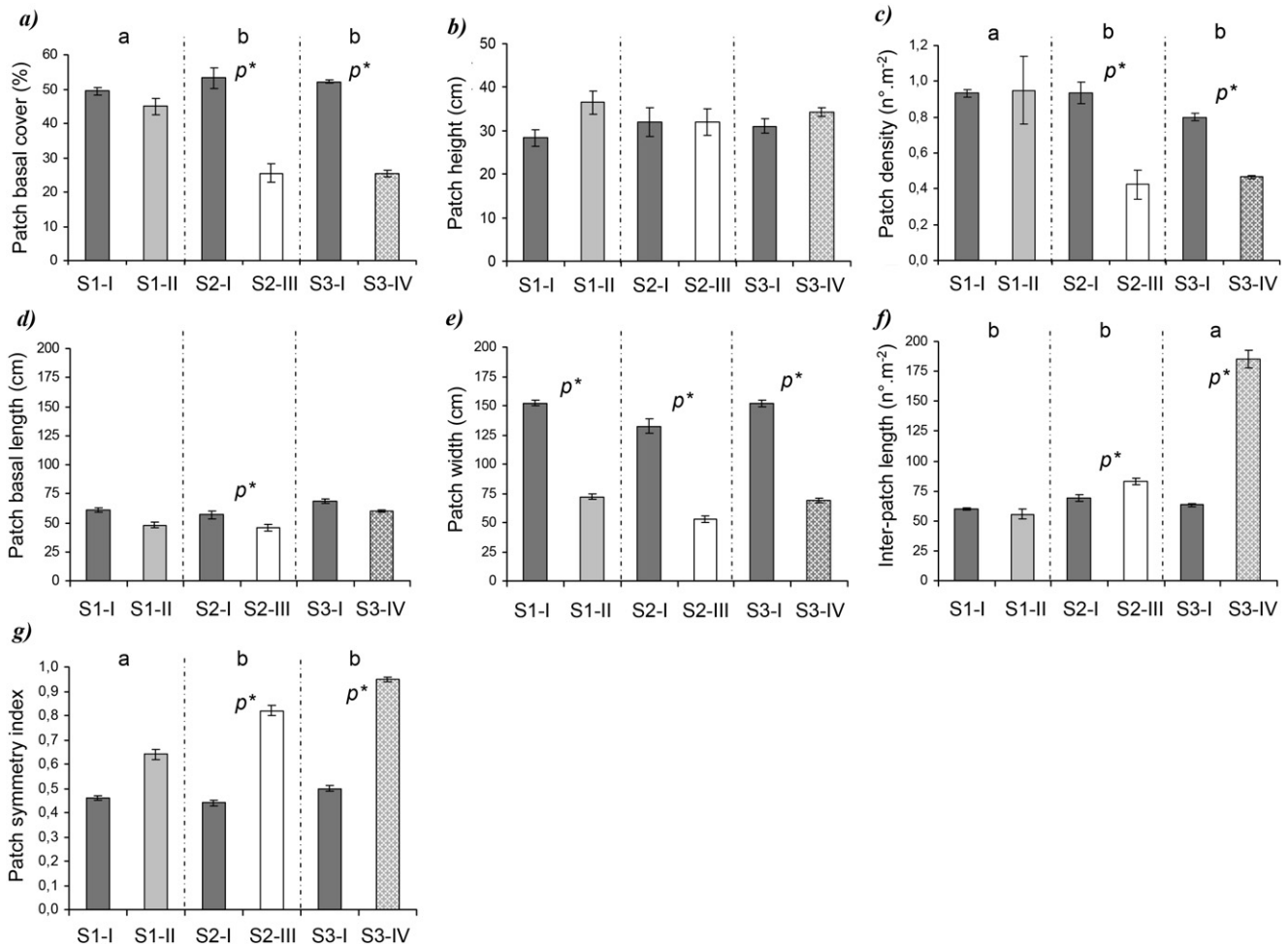


Fig. 2. Mean values (\pm S.E.) of (a) Patch basal cover, (b) patch height, (c) patch density, (d) patch basal length, (e) patch width, (f) inter-patch length and (g) patch symmetry index (patch basal length/width patch) in states (I, II, III and IV) of Site 1 (S1-I and S1-II), Site 2 (S2-I and S2-III) and Site 3 (S3-I and S3-IV). Significant differences within each site are indicated by p*. Significant differences between the Sites (difference variable) are indicated with different lowercase letters; ($\alpha = 0.05$).

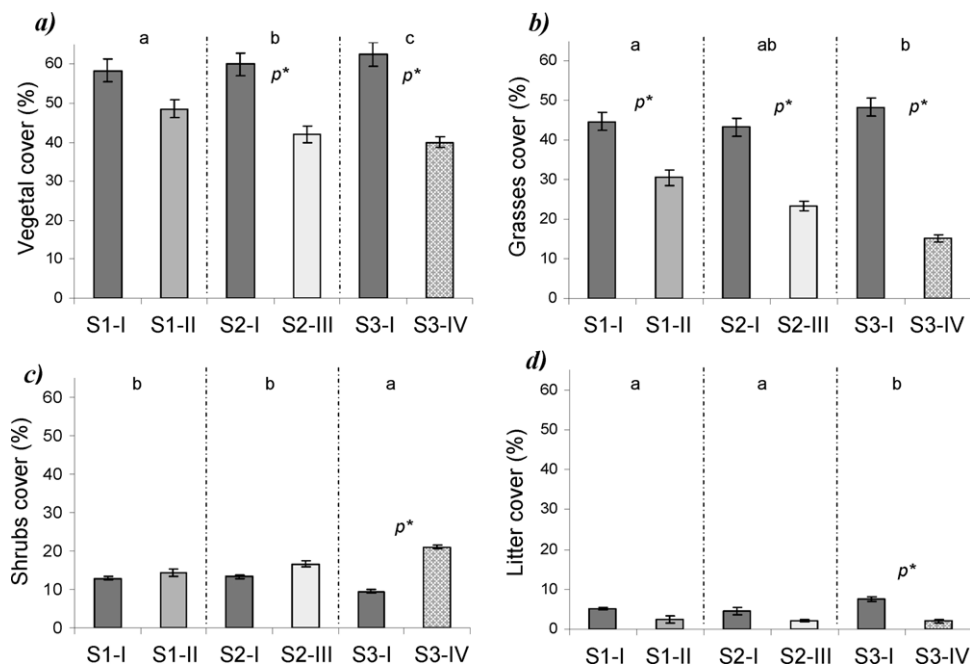


Fig. 3. Characterization of vegetation (for states I–IV), within Site 1 (S1-I and S1-II), Site 2 (S2-I and S2-III) and Site 3 (S3-I and S3-IV), based on ($\bar{X} \pm$ S.E.): (a) Vegetation total cover; (b) grass cover; (c) shrub cover and (d) litter cover. Significant differences within each site are indicated by p*. Significant differences between the Sites (difference variables) are indicated with different lowercase letters; ($\alpha = 0.05$).

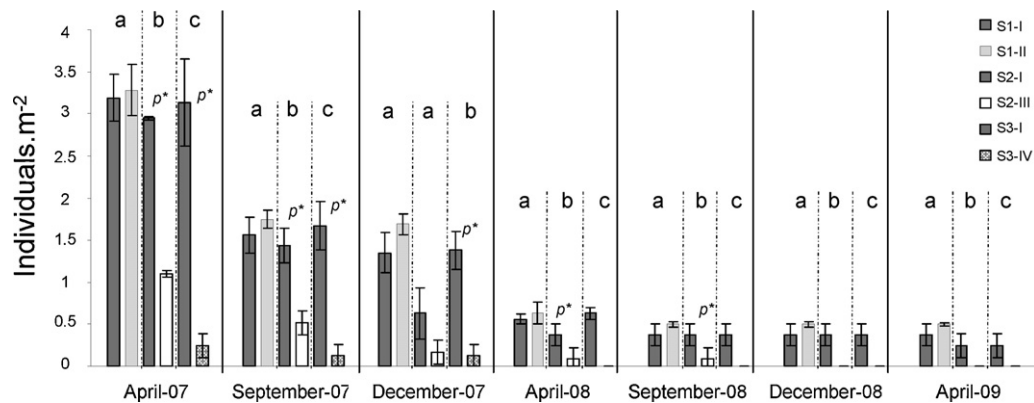


Fig. 4. Density of individuals of perennials species (number m^{-2}) in states (I, II, III and IV) within Site 1 (S1-I and S1-II), Site 2 (S2-I and S2-III) and Site 3 (S3-I and S3-IV). Emergence of cohort-2007 (April 2007) and survival of cohort-2007 until April 2009 ($\bar{X} \pm S.E.$). ANOVAs were performed separately for each month. Significant differences within each site (between the grazing state and their paired state I) are indicated by p^* . Significant differences between the Sites (difference variable) are indicated with different lowercase letters; ($\alpha = 0.05$).

use by the ecosystem (Thurow, 1991; Heady and Child, 1994). Similarly, the decrease of the nutrient recycle process (Fig. 1c) would be associated with soil and organic matter loss due to erosion, and a lower contribution of vegetation due to less cover and biological activity (Figs. 2 and 3; p -values ≤ 0.05) (Tongway and Hindley, 2000, 2004; Whitford, 2002; Bestelmeyer et al., 2003; Ludwig et al., 2004).

On the other hand, the functional threshold was related to a lower recruitment rate of new individuals, with an approximately value of 2.5 seedling m^{-2} (in years with rainfall near the historical average) (Fig. 1a). The seedling density in April 2007 (cohort-2007) and its survival density decreased in the states with high and very high grazing pressure (lower in S2-III and S3-IV, p -value ≤ 0.05), where after two years no survivors were registered. No differences were found between exclosure (S1-I) and the state with moderate grazing pressure (S1-II) during the whole period ($p > 0.05$), reporting surviving individuals in April 2009 (Fig. 4). The seedling density of cohort-2008 (April 2008) was very low in all the states and no statistical inferences could be made (average value no. of seedlings $m^{-2} \pm S.E.$): S1-I = 0.13 ± 0.13 ; S1-II = 0.25 ± 0.14 ; S2-I = 0.13 ± 0.13 ; and S3-I = 0.25 ± 0.14 ; no plants were recorded in S2-III and S3-IV. In September 2008, no survivor individuals were detected from the cohort-2008 in either state. In cohort-2009 (April 2009), the only seedlings registered were in the exclosures and S1-II (between 1.7 and 3.3 seedlings m^{-2}), with no differences between S1-I and S1-II ($p > 0.05$). The values of seedling emergence and registered survival were suited within the ranges registered in other rangelands of Patagonia (Defossé et al., 1997; Bisigato and Bertiller, 2004a,b) and the Mediterranean (García-Fayos and Gasque, 2006), indicating that as in such ecosystems the recruitment of new individuals is a process involved in the maintenance of this type of rangeland (López et al., 2011). Specifically for the cohort-2007, in the pre-threshold states (E-I and E1-II), at the paddock level, survived between 3.000 and 5.000 individuals per ha at end of period (Fig. 4).

Overgrazing would have a direct effect on the recruitment of new individuals due to trampling and/or grazing and a decrease in the seed production (O'Connor, 1991; O'Connor and Pickett, 1992; Bertiller, 1994; Bisigato and Bertiller, 2004a,b). In steppes, the recruitment process occurs mainly in the center and periphery of the patches (Bisigato and Bertiller, 2004a; López, 2011). Therefore, the loss of soil and vegetation cover, lower patch cover and density, and less heterogeneity and symmetry of patches (fewer patch borders) would reduce the quantity of safe-sites for the establishment of new individuals, indirectly affecting the recruitment process (cohorts 2007 and 2009 in S2-III and S3-IV) (Schlesinger

et al., 1996; Fernández and Busso, 1997; Kinloch and Friedel, 2005; Bisigato and Bertiller, 2004a).

Considering the cohort-2007, after the 2nd year the individual density remained constant in the exclosures and states with moderate grazing pressure (S-I and S1-II), and even after the registered drought during summer–autumn 2008 (Villagra et al., 2009). This suggests that these individuals are already established and with a good opportunity for reaching maturity. The absence of surviving individuals after 2008 in the more degraded states (S2-III and S3-IV, Fig. 4), and the lack of emergence in April 2009, would indicate that these states would be very vulnerable because the recruitment process was affected, compromising the sustainability of the plant community (Scheffer et al., 2001; Bisigato and Bertiller, 2004a; Kinloch and Friedel, 2005). The low emergence and null survival of cohort-2008 might be a result of the drought registered during this period which affected a large area of the region (Villagra et al., 2009). Weather conditions during the remainder of the study were close to average values.

In the less degraded states (state I), a high stability index (Fig. 1d) could be due to the protective effect of the soil cover to erosive agents, and low symmetry and high connectivity of patches (large and irregular) (Figs. 1e, 2c,g and 3a). Beyond the critical threshold, the stability index reached lower values toward S2-III (Fig. 1d), which was related to the vegetation degradation, measured as a decrease in vegetation cover, basal cover, width, length and density of patches (Figs. 2 and 3a), leading to loss of soil and organic matter by erosion (Whitford, 2002; Bestelmeyer et al., 2003; Ludwig et al., 2004; Tongway and Hindley, 2004). The stability index includes the gains and losses of the system sediments and ground cover of vegetation and rocks (Tongway and Hindley, 2004). Thus, the stability index increases when there has been great soil loss, little sediment to be transported by wind and/or water, and more exposed rock surface (S3-IV, Fig. 1d). Possibly at this point another critical structural threshold (*sensu* López et al., 2011) may have been crossed, which is defined mainly by an abiotic component such as high soil loss (Beisner et al., 2003; Briske et al., 2005; Hobbs and Suding, 2009).

3.3. Linking ecosystem resistance, resilience, and stability

Taking into account what Laycock (1991), Reynolds and Wu (1999), Scheffer and Carpenter (2003) suggested and making an analogy with thermodynamic systems (i.e. Tschoegl, 2000), we differentiated two levels of stability: stability of the ecosystem, and stability of each state of the ecosystem. To a disturbance factor, an ecosystem with high resistance (low degradation velocity and

magnitude) and resilience (great elasticity and amplitude) would be a meta-stable ecosystem, or from an LFA's approach it would be a robust ecosystem. At another level, each alternative state of an ecosystem could be in different situations of 'dynamic equilibrium (*sensu* López et al., 2011)', such as stable, unstable, mixed-unstable, or stable-indifferent. We can interpret these stability degrees of different states in dynamic equilibrium for an ecosystem by integrating the LFA and SFSTM approaches. To do this the following stability properties should be evaluated:

- The magnitude of the structural–functional change produced by a disturbance factor. When a particular grazing pressure on an ecosystem state affects its structure, the state would be less stable if this structural change causes a major functional change, rather than a small functional change. In this sense, the assessment of the recruitment process in key species of a given plant community, helps to infer if the community in each state will remain over time (keeping its replacement rate), or if it will tend to decline due to the small or null recruitment of individuals (O'Connor, 1991) (e.g. S2-III, Fig. 4).
- The susceptibility of a state to be degraded. In our study this can be estimated through the resistance of the soil to erosion (stability index). Given that the speed of the erosion process increases with the decrease in vegetation, litter and rock cover, and the increase of quantity of fine sediments, the stability index would allow us to infer the velocity at which an ecosystem can be degraded.
- Type of response of the ecosystem in dynamic equilibrium when the disturbance factor is removed. For example, if the grazing is excluded in state III of the studied ecosystem (Bonvissuto et al., 1993), there would be less stability if a positive transition is triggered toward a different state than if nothing occurs.

In this context, the stability concept at the ecosystem state level would also be related to the resilience and resistance (Williams et al., 1993; Stringham et al., 2003), since they are associated with the resistance (point a and b) and the resilience (point-c) concepts. Based on these three points of stability properties, we adopted the states and transitions proposed by Bonvissuto et al. (1993) as a model of reference to define and exemplify the different types of stability for each state of the studied ecosystem. Then, according to the mentioned points, a state such as state I would be in stable dynamic equilibrium, because: (a) a structural change produces little functional change (between states I and II, Fig. 1a–c), (b) the stability index is high (high erosion resistance, Fig. 1d), and (c) any state suited before the critical threshold, once the disturbance factor is removed, tends to return to the state I (e.g. state II, Bonvissuto et al., 1993). The stability of state I would be associated with the original stability. While there is no significant losses in functions and/or processes (point-a) toward the critical threshold, the stability would decrease because the resistance to erosion decreases (e.g. stability index of state II, Fig. 1d) (point-b) and because if grazing is interrupted a transition toward S-I is triggered (point-c) (Fig. 5). The interrelation between original stability, ecosystem amplitude and elasticity, and resistance (before crossing the critical threshold) allow assessing the meta-stability.

In general, the states beyond critical threshold would be unstable because: (a) the slope between structural degradation and functions of the ecosystem become more accentuated. Small structural changes produce great functional changes (Fig. 1; gray square Fig. 5a); (b) the resistance of the soil to erosion is low (Fig. 1d); and (c) the interruption of grazing would trigger a positive transition to another state, which for our ecosystem would be more grassy but dominated by *S. speciosa* instead of *P. ligularis* (López, 2011) (Fig. 5a and c). Thus, for the studied ecosystem, the state III would be in an unstable dynamic equilibrium. If the elimination of the

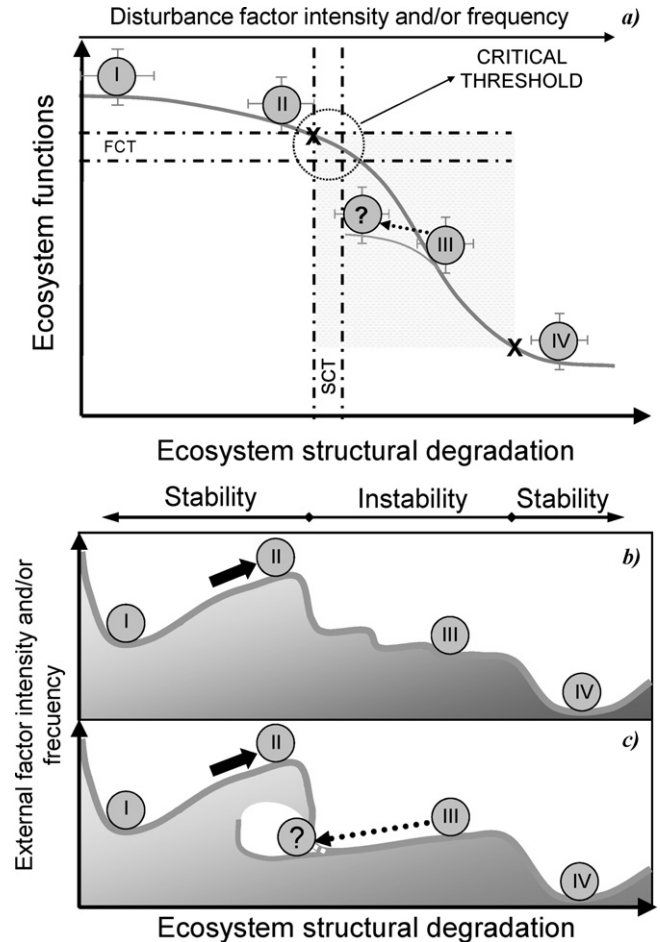


Fig. 5. Schematic representation of the stability of different states in dynamic equilibrium of grass-shrub steppe of *P. ligularis* and *M. spinosum*, based on: (a) Structural-Functional State and Transition Model (López et al., 2011); (b and c) cup-ball model. A state in dynamic equilibrium is represented: stable = state I (a, b and c); unstable = state III (a and c); mixed-unstable = state III (b); indifferent-stable = state IV (a–c). Gray balls represent the states, most degraded are shown with higher Roman numbers. The black arrow represents disturbance factor (e.g. grazing pressure). The gray ball with the (?) symbol represents the state to where it triggers a positive transition (dashed arrow) from an unstable dynamic equilibrium state, when grazing is removed. In (a), the bars of gray balls represent the “state amplitude (López et al., 2011)”. SCT: Structural Critical Threshold; FCT: Functional Critical Threshold. The intensity and/or frequency of the external factor (b and c) indicate the amount of pressure needed to degrade the system (e.g. grazing pressure) or the amount of external factor needed to trigger a positive transition either by climatic events (e.g. mm rain) or active restoration (e.g. re-vegetation costs).

grazing pressure on a state such as state III does not trigger a positive transition, we consider that this state is in a mixed-unstable dynamic equilibrium; this is because it would have an unidirectional stability (i.e. it does not recover), but it is unstable regarding degradation (Fig. 5b). Finally, states such as S-IV would be in an indifferent-stable dynamic equilibrium (Fig. 5) because they are severely degraded and have little forage available for the animals and little vegetation to be degraded (Fig. 3) (Bonvissuto et al., 1993). Possibly beyond this degradation state the system would collapse and the use of grazing would be unlikely (Archer, 1989). The erosion resistance is high, because there is no material to be eroded, and the exposed rocks on the surface would increase the protection against erosive agents (point-b). In such states, if grazing is suppressed, the probability for a positive transition is very low (point-c) (e.g. Archer, 1989; Westoby et al., 1989; Bonvissuto et al., 1993).

It is important to highlight that the grazing pressure which triggers a negative transition (e.g. from state I to II, Fig. 5; or in the model by Archer (1989) from state A to B), would be different from

the grazing pressure than the ecosystem in *dynamic equilibrium* has in a given state (e.g. state II, black arrow in block, Fig. 5b and c; state B in Archer, 1989). For example, in our studied ecosystem the carrying capacity on state I is 0.6 sheep ha⁻¹ years⁻¹, but if a greater stocking rate is used (e.g. 0.8–1 sheep ha⁻¹ years⁻¹) a negative transition toward state II would occur (Bonvissuto et al., 1993). If this stocking rate is sustained, the degradation of the ecosystem would continue. In order to keep the ecosystem in a dynamic equilibrium in state II, the stocking rate would have to decrease to 0.4 sheep ha⁻¹ years⁻¹ (Bonvissuto, 2008), as the ecosystem has less carrying capacity. This indicates that resistance would be a characteristic associated more to each state and not to the ecosystem in general, as state II resists less grazing pressure than state I. On the other hand, the resilience concept should be applied to a more general level of the system, mainly because the ecosystem amplitude defines a gradient of states in which the ecosystem maintains its original resilience (López et al., 2011).

The decrease in the ecosystem's carrying capacity associated with overgrazing is related to species replacement when grazing pressure increases. First there is a replacement of species from more palatable to less palatable for sheep. In our study *P. ligularis* (more palatable) had the highest values *difference* variable at site 1, and was always less in the grazed state than its paired enclosure (S1-I = 28.1 ± 1.5% and S1-II = 10.1 ± 1.8%; S2-I = 30.0 ± 1.4% and S2-III = 1.7 ± 0.1; S3-I = 29.5 ± 1.3% and S3-IV = 0.2 ± 0.05%), and *S. speciosa* (less palatable) had greater cover in S2-III than S2-I (18.6 ± 0.4 and 8.7 ± 0.3%, respectively) (*p*-values ≤ 0.05). Furthermore, in states with very high grazing pressure there is an increase of "non-desirable" species for sheep (in our study: greater non-forage grasses and shrubs cover in S3-IV than S3-I, 18.6 ± 8.7 and 0.3 ± 0.4%, $\bar{X} \pm EE$, respectively) (*p*-values ≤ 0.05) (S3-IV, Fig. 3) (Bolen, 1998; Bonvissuto, 2008). These changes of species along with less total cover and higher soil loss due to erosion reduce significantly the ecosystem forage production (NRC, 1992; Reynolds and Stafford Smith, 2002; Suttie et al., 2005).

The greatest resistance to grazing in the less degraded states (e.g. more carrying capacity in state I) may be due to these states having species that are more tolerant to grazing (e.g. protected buds, higher growth rate). On the other hand, the increase of relative cover of non-desirable or less palatable species in more degraded states would reinforce the idea of an increasing stability. This is because in these states in stable-indifferent dynamic equilibrium (Fig. 5) there would be an increase in grazing resistance, since many species generally have attributes that make them more resistant to grazing (e.g. spines, silica bodies, pubescence, and cuticle waxes) (Briske, 1991; Cingolani et al., 2005). Besides, according to Grime (2002), better conserved states with low disturbance intensity are generally dominated by species with more competitive/ruderal strategies, which are related to greater ecosystem resilience. In contrast, in the more degraded states due to overgrazing, the dominating species would be less-palatable and stress-tolerant related to a greater resistance of the ecosystem to more xeric conditions.

4. Conclusions

Our study would be indicating that the overgrazing decreased the recruitment process, and it could be associated with a loss of the ecosystem functional integrity, where a response pattern was registered as similar in seedling emergence, infiltration and recycling indexes in relation to SDI. This would be related to a decrease in the capacity to retain, store and use rain water, and to a decrease on the nutrients recycling (Tongway and Hindley, 2004). The results indicate that the integration of the LFA methodology with the SFSTM allow to validate indicators and indexes for the identification of critical thresholds.

This work aimed to contribute in the evaluation of some important ecological concepts (i.e. stability or stability properties) based on a reference ecosystem. While we must perform more studies to make general inferences, the results allow us to raise some interesting perspectives for the analysis and discussion of resilience–resistance–stability relationships: (i) In the less degraded states of an ecosystem, stability would be associated with high resilience and resistance to grazing, and resistance to soil erosive agents. (ii) Beyond the critical threshold, the instability of an ecosystem would be associated with a reduction in resistance and resilience. (iii) In high degraded states, the ecosystem would reach an indifferent-stable dynamic equilibrium. In this state, the increase of the stability would be associated with the increment of the resistance to a disturbance factor (both grazing and drought) and to erosive agents, but with resilience loss.

A valuable contribution to the states and transitions models, particularly in arid ecosystems, is the simplicity to evaluate and include information of the structure and heterogeneity of patches, and vegetation connectivity (Bestelmeyer et al., 2011). Therefore, the heterogeneity and connectivity indexes suggested in this study provide a useful tool to better describe and understand the degradation processes implied in negative transitions, and specifically with thresholds. On the other hand, the analysis of these indexes would help overcome the "dilemma of whether shrub-encroachment is a problem or not in the rangeland degradation (see Maestre et al., 2009)", since the indexes allow us to evaluate degradation as a process of ecosystem homogenization. This is because ecosystem degradation produces a structural homogenization with less diversity of species and/or functional groups. Such degradation affects the functional integrity of the ecosystem, reducing its resilience and ability to maintain the provision of goods and services (Folke et al., 2004; Müller et al., 2000; Reza and Abdullaha, 2011).

The proposed approach is a tool for inferring which states can be restored and which are more susceptible to degradation. For example, in states that are in an unstable dynamic equilibrium, due to their high susceptibility to degradation, the following factors must be assessed: feasibility to manage lower stocking rate than the carrying capacity, and possibility that a positive transition can be triggered in favorable years (e.g. exclusion of grazing during wet years, Westoby et al., 1989). On the other hand, in states with an indifferent-stable dynamic equilibrium, the possible use of grazing must be evaluated adjusting the stocking rate to its low carrying capacity, since recovery might be unlikely.

More studies ought to be made regarding integrating approaches between LFA and SFSTM, in order to move forward in the evaluation of resistance, resilience, and stability, at the level of the ecosystem and the different states of degradation. This type of approach provides the tools for sustainable management of rangelands, allowing us to evaluate and prevent crossing a critical threshold in ecosystems under grazing.

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