

# DEGRADATION INFLUENCES EQUILIBRIUM AND NON-EQUILIBRIUM DYNAMICS IN RANGELANDS: *IMPLICATIONS IN RESILIENCE AND STABILITY*

<sup>1</sup>López D.R.\*, <sup>1,2</sup>Cavallero L., <sup>3</sup>Willems P., <sup>4</sup>Bestelmeyer B.T. and <sup>5</sup>Brizuela M.A.

<sup>1</sup>INTA- Estación Forestal Villa Dolores (EEA Manfredi); <sup>2</sup>CONICET- CCT Córdoba; <sup>3</sup>INTA-EEA Bariloche (retired); <sup>4</sup>USDA-ARS Jornada Experimental Range and Jornada Basin LTER- New Mexico State;

<sup>5</sup>Universidad Nacional de Mar del Plata (retired).

\*[lopez.dardor@inta.gob.ar](mailto:lopez.dardor@inta.gob.ar)

## ABSTRACT

Question: Plant communities are structured by both equilibrium and non-equilibrium dynamics, which interact at different spatio-temporal scales. The influence of external factors on internal regulation processes might depend on ecological state, and thus, on system resilience. We asked if well conserved (reference) states have higher resilience to external factors than degraded states, considering the greater capacity for self-regulation expected of reference states.

Location and Methods: During four years, we assessed the influence of an external factor (rainfall variability) on internal regulation processes (seedling recruitment, growth of main perennial species, and three resilience proxies) in two alternative states (one reference and another degraded) of graminous-subshrubby steppes of northern Patagonia (Argentina). Specifically, we assessed the response of alternative states to simulated high rainfall events (irrigation).

Results: The degraded state was more sensitive to rainfall variability than the reference state.

Specifically, in the degraded state the density of surviving seedlings, the growth of shrubs and

*Papostipa speciosa*'s relative tiller production and cover increased in response to irrigation;

whereas seedling emergence and survival, and grass growth were low or even null without

irrigation. Finally, resistance and elasticity were lower whereas malleability was greater in degraded than in reference states.

Conclusions: The degraded state was less resilient (low resistance and elasticity; high malleability)

to stochastic weather events, in response to either increases or decreases in water availability. In

contrast, the reference state had a great capacity to respond to rainfall variability. However,

demographic processes such as seedling recruitment and vegetative growth were compensated by

competition and mortality, suggesting a lower sensitivity to external drivers, and thus, a greater stability. By influencing the balance between equilibrium and non-equilibrium dynamics, degradation might affect the resilience and stability of the ecosystem. Thus, to prevent rangeland degradation, management plans should plan for climatically favorable and unfavorable periods.

**Keywords:** *Alternative States, Amplitude, Elasticity, Grazing, Malleability, Rainfall Events, Resistance, States and Transitions Model, Thresholds.*

**Species nomenclature:** Flora Argentina (<http://www.floraargentina.edu.ar/>).

## INTRODUCTION

Equilibrium and non-equilibrium paradigms are generally used to explain vegetation dynamics in response to both internal and external drivers. These paradigms underpin two ecological models alternatively used to support management decisions in rangelands. On the one hand, the Range Condition Model (Dyksterhuis 1949) was widely applied in rangeland management until 1990s. This model is based in the equilibrium paradigm (Briske 2003, Briske 2017), and asserts that vegetation dynamics are mainly driven by internal regulation processes through *negative feedback mechanisms* (e.g. intra- and inter-specific interactions as herbivory and competition; see the explanation of feedback mechanisms on Glossary and Figs. S1 and S4 of Supplementary file) (Wu and Loucks 1995; Briske *et al.* 2003, 2005, Briske 2017; Derry and Boone 2010). On the other hand, the State and Transition Model (Westoby *et al.* 1989) was widely applied to arid and semiarid rangelands in the last two decades. This model is mainly associated with the non-equilibrium paradigm. It proposes that ecosystems have a limited internal regulation capacity, and thus, vegetation dynamics largely driven by external drivers. Under this paradigm, stochastic and periodic climatic events would drive great vegetation changes (Westoby *et al.* 1989; Derry and Boone 2010). However, new advances in State and Transition Model claim that vegetation dynamics can be compatible with both paradigms because communities are structured by both, internal- (e.g. herbivory, competition) and external- (e.g. stochastic weather events) regulation

processes which interact at different spatio-temporal scales (Briske *et al.* 2003; López *et al.* 2011; Briske 2017).

Internal and external drivers may both influence vegetation dynamics, with one or the other prevailing in different situations. In this sense, internal regulation processes may mediate the response of vegetation to external drivers. For example, herbivory (grazing) is an internal regulation factor, but if stocking rate is unbalanced with the ecosystem's carrying capacity, it can negatively affect the structure and functioning of an ecosystem, decreasing plant cover while promoting soil erosion, reducing in turn, forage productivity (Paruelo and Sala 1992; Noy-Meir 1995; Fernández-Gimenez and Allen-Diaz 1999). High grazing pressure can also decrease rain use efficiency (Hein 2006; Retzer 2006). Consequently, degradation caused by overgrazing, by altering the structure and function of an ecosystem (i.e., internal regulation ability), will modify the ecosystem's ability to respond to external factors such as droughts or high rain events.

Alternatively, climatic variability can drive ecosystem functioning (Kemp 1989; Pake and Venable 1996; Ludwig *et al.* 1999). Stochastic rain events can modulate the dynamics of plant communities (Noy-Meir 1973; Westoby 1979, 1989; Chesson *et al.* 2004) at distinct scales (Schwinning and Sala 2004). The occurrence and intensity of rainfall events can affect internal regulation processes via biogeochemical cycles at ecosystem scale and biological interactions and recruitment processes (Guterman 1993) at the community scale (Noy-Meir 1973; Gebauer and Ehleringer 2000; Novoplansky and Goldberg 2001; Chesson *et al.* 2004), and may even trigger recovery processes, plant succession (Schwinning and Sala 2004) or degradation. External factors usually drive vegetation dynamics in arid and semiarid ecosystems (Fuhlendorf *et al.* 2001; Briske *et al.* 2003; Bestelmeyer *et al.* 2004). These types of ecosystems are characterized by high spatio-temporal variability, mainly in climate (Romero *et al.* 1998; Ramos and-Martínez-Casasnovas 2006). However, the consequences of climate uncertainty in the functioning of plant communities has been rarely tested. Consequently, in a scenario of climate change, in which a greater variability of rain events is predicted, it is important to assess the influence of external factors (e.g. droughts or

abundant rain events) on internal regulation processes (Chesson *et al.* 2004, Gillespie and Loik 2004).

From a management perspective, the influence of external factors on internal regulation mechanisms might depend on rangeland ecological state, and thus, on resilience. External factors can increase or decrease resource availability (e.g. very wet years or droughts, respectively), and may even trigger recovery or degradation transitions. Consequently, studying the response of alternative states of an ecosystem to external factors is essential to assist decision making in productive rangelands as well as to generate new knowledge to be able to understand their resilience to environmental drivers. Under this framework, for the same reference ecosystem (i.e. same *ecological site*, see Glossary on Supplementary file), we hypothesize that degraded states will have less ability to respond to external factors than reference (better conserved/less altered from historical conditions) states. This would be mainly associated with a lower soil cover in degraded than in reference states, with less soil and organic matter as a consequence of erosion processes. However, since reference states are postulated to have higher self-regulation capacity (e.g. associated with the inter and intra-specific competition of adult and young individuals) with respect to both ecosystem structure and functions (López *et al.* 2013), the response magnitude to external factors will be lower in reference than in degraded states. This is due to the fact that better conserved states are associated with high resilience, given by a high capacity for self-regulation and self-organization after disturbances or stochastic weather events, that allows them being more stable and thus, to persist or remain in its current state of dynamic equilibrium (López *et al.* 2013).

The experimental manipulation of rainfall events (i.e., quantity and/or frequency) can be a useful approach to understand how degradation affects the response capacity of ecosystems to environmental drivers (Chesson *et al.* 2004; Gillespie and Loik 2004). In this study, we simulated high rainfall events in two alternative states of graminous-subshrubby steppes of northwestern Patagonia (Argentina). The aim of the study was to assess the response of alternative states (reference vs. degraded *sensu* López *et al.* 2013) of graminous-subshrubby steppes to an external driver (rainfall), with the hypothesis that these states differ in resilience and stability. Specifically,

we recorded the effect of irrigations (simulating high rainfall events) on internal regulation processes as: (i) seedling emergence and survival of perennial species, (ii) growth of main perennial species; and (iii) three resilience proxies (resistance, elasticity and malleability indices). Thus, the experimental assessment of the response of alternative states to an external driver allows us to infer the mechanisms that drive the underlying differences in their resilience to disturbance and/or management factors.

## **MATERIALS AND METHODS**

### ***Study area***

The study was carried out in Patagonian steppes, located in Río Negro province, Argentina, southern South America. The vegetation of this area is characterized by mixed grass-shrub steppes (Western Patagonian District of the Patagonian Steppe *sensu* León *et al.* 1998), with a soil cover of around 50 % dominated by tussock grasses. Climate is characterized by cold wet winters (coldest month mean temperature is 2.1°C) with temperate dry summers (hottest month mean temperature is 15°C). Mean annual precipitation is  $265 \pm 82.5$  mm, and more than 70% of the precipitation falls during autumn and winter (Bustos and Rocchi 1993; Bustos 2006). In this area, stochastic high rainfall events are common (Golluscio *et al.* 1998; Oesterheld *et al.* 2001; Schwinning and Ehleringer 2001; Schwinning and Sala 2004; Tables A and B on Supplementary file). Specifically, in the last 30 years, four wet periods were recorded (i.e. rainfall was more than one standard deviation greater than the historical average, Table A, Supplementary file). Fieldwork was done in Pilcaniyeu, at a 7800 ha area belonging to Estación Experimental Agropecuaria Bariloche of INTA, located in Río Negro, Argentina (41° 01' 42" S, 70° 35' 21" W). In this study, we focused on graminous-shrubby steppes of *Poa ligularis* and *Mulinum spinosum* (León *et al.* 1998), which is a key forage steppe of Western Patagonian District.

### ***Experimental design***

Throughout the study landscape, we selected four areas, and within each area we delimited two paired sectors representing two alternative vegetation states: one reference state (i.e., well conserved) and one degraded state. These alternative states were also described as State I and II in state and transition models developed for the area (López *et al.* 2013, López and Cavallero 2017). The vegetation of the sectors in reference state is graminous-shrubby steppe of *P. ligularis* and *M. spinosum*. These sectors are excluded to sheep grazing since 1975 (i.e., > 30 years without livestock grazing). Plant cover is greater than 60 %, dominated by *P. ligularis* (the main forage species with ~ 30 % cover) and *Pappostipa speciosa* (covering ~ 7%). In degraded sectors, the plant community is a subshrubby-grass steppe of *M. spinosum*, *Senecio spp.* and *P. speciosa*, generated by an interaction between high grazing pressure (i.e., 0.6-0.7 sheep. ha<sup>-1</sup>.yr<sup>-1</sup>) for more than 25 years and recurrent droughts. Specifically, plant cover is near 40 %, with 20 % *P. speciosa*, and 1.5 % *P. ligularis*. In this state, soil erosion and the decrease in plant cover affected the functional integrity of the ecosystem, thus it was classified as an alternative state that crossed a degradation threshold (i.e., post-threshold state *sensu* López *et al.* 2013).

In order to control the effects of a slight slope (< 3%) in the landscape, we used a Completely Randomized Block Design (Steel and Torrie, 1980). We established four blocks including both states in each: Reference and Degraded (n = 4 replications for rangeland state factor). The experimental design and replicate number were the same as used by López *et al.* (2013) and López and Cavallero (2017). During the experiment, all blocks remained without sheep grazing (thus rangeland state reflects historical rangeland degradation). The reference state was excluded from grazing for > 30 years. In the degraded state, we installed four 25 x 25 m enclosures in October 2005 (adjacent to reference state), one enclosure in each block (n = 4 enclosures in degraded state). Within each block and state, we delimited two 2 x 2 m sub-plots and irrigation treatments (with irrigation, hereafter 'I'; and without irrigation, hereafter 'NI') that were randomly assigned to each sub-plot (n = 4 replications for Irrigation factor). Thus, the experimental design includes two factors: rangeland state with two levels (Reference State and Degraded State) and irrigation with two levels (i.e. with and without simulation of high rain events). The rangeland state

was assigned as the main plot (plots arranged in a blocks) and Irrigation as the sub-plot. The dimensions of main plots were  $25 \times 25$  m, and of sub-plots were  $2 \times 2$  m. In each sub-plot we assessed (i) density of emerged seedlings of perennial species their survival, (ii) grass and shrub growth, and (iii) plant cover (at the beginning and at the end of the experiment).

### ***Sampling procedure***

#### *Perennial species recruitment*

During four years (2006 to 2009) we assessed seedling emergence in autumn (April), and survival at the end of winter (September) and in spring (December) and autumn (April) of the subsequent year. Seedling emergence was recorded by counting the number of new individuals of the main perennial species in each sub-plot. Recording seedling density in distinct seasons allows its association with different demographic processes as emergence and survival. April seedling counts reflect seedling emergence because seed germination occurs as a pulse during the beginning of the wet period, since soil humidity increases and temperatures are high enough to trigger germination processes (López 2011; López *et al.* 2013). Later in the year, temperatures are below  $0^{\circ}\text{C}$  (Bustos 2006) and metabolic processes in plants decrease significantly. Thus, seedling counts made in September (i.e., end of winter) and December (i.e., end of spring) reflect seedling survival because cold winters and windy dry springs represent the main abiotic filters that seedlings must overcome to become established (López 2011). Therefore, seedling emergence was assessed by counting the number of individuals younger than one year (i.e., seedlings with less than three leaves, López 2011), in April 2006 and 2007, which were the years in which we simulated high summer rainfall events. Each recently emerged seedling was marked to assess its survival at the end of winter and spring seasons. Seedling survival was assessed by counting the number of marked individuals that were alive during the subsequent three years in September, December and April. Thus, survival of the seedling cohort that emerged in April 2006 was assessed in September and December 2006, 2007, 2008; and in April 2007, 2008 and 2009. Survival of the seedling cohort that emerged in April 2007 was assessed in September and December 2007 and 2008, and in April 2008 and 2009.

## *Plant growth*

Grasses: In September 2005, 2006 and 2007, we selected two individuals of *P. ligularis* and two of *P. speciosa* in each sub-plot. All selected individuals belonging to the same species were of similar size. On each plant we marked four tillers (with three expanded leaves), two located at the center and two at the edge (one in the eastern edge and another in the western). During three years (2006, 2007, and 2008), at the end of April, we recorded the following variables in each marked tiller: (a) tiller production, (b) leaf production, and (c) length of the longest leaf of each tiller (O' Reagain 1993; Gittins 2011). To estimate tiller production, we counted the number of secondary tillers arising from each marked tiller. Leaf production was estimated by counting the number of leaves including marked and secondary tillers. Leaf length was measured with a digital caliper in marked and secondary tillers and the length of the longest leaf of each tiller was summed to obtain a single value for each marked tiller. To calculate these variables, the initial tiller- and leaf-number, and initial leaf length recorded in September were subtracted to final values recorded in April of the subsequent year. To be able to compare between sub-plots having distinct cover of each grass species, we estimated relative tiller production per sub-plot. Thus, tiller production was relativized by species cover in each state:

$$\text{Relative tiller production per sub-plot} = [\text{Total number of tillers produced} \times (\text{Total number of marked tillers})^{-1}] \times \text{Species cover in each plot} \times 100^{-1}.$$

In estimating the cover of each species in each plot, we only considered the plant parts that were green (i.e., live) (see below: *sampling of Plant cover*).

Shrubs: In each sub-plot we selected one individual of *M. spinosum* and other of *S. filaginoides*. In shrub selection we attempted to reduce between-plot shrub size variation within each species. In each plant, in September of 2005, 2006, and 2007, we randomly selected 12 branches, and marked the last internode in each one of them. With a digital caliper we measured the initial length of the distal portion of each branch, which included from the last internode to the end



of the branch. Then, at the end of April of the following year (i.e., at the end of the growing season; in 2006, 2007, 2008), we measured the final length of the distal portion of each branch, also adding the length of all secondary branches arising from each marked branch. Therefore, we estimated seasonal growth by subtracting the initial length to the final length of the distal portion of each branch. To estimate bud production, we counted the number of secondary branches arising from the marked branch. Finally, in *M. spinosum* we recorded leaf production in 12 branches randomly distributed in each plant, because the green new leaves produced each year are easily distinguished from dry leaves of previous years (Damascos *et al.* 2008).

#### *Plant cover*

To assess whether the community response to simulated high summer rainfall events can be recorded at a sub-plot scale (i.e., at a scale broader than individual) we measured plant cover at the beginning (before irrigations) and at the end of the study. To accurately estimate total plant cover and cover by species, each subplot was subdivided into 400 cells of  $0.1 \times 0.1$  m (within which cover was estimated). Sampling was carried out in October 2005, at the beginning of the experiment prior to irrigations, and in December 2009, at the end of the experiment. Finally, cover difference was obtained by subtracting initial cover to final cover. This was done for total cover as well as for each species.

#### *Proxies of ecological resilience*

To assess the resilience of alternative states to weather drivers, we calculated three indices: Resistance, Elasticity and Malleability, which were adapted from Sheehan (1984), Washington-Allen *et al.* (2008), Wang *et al.* (2014) and Hoekstra *et al.* (2015). The *Resistance* is the lack of sensitivity of a system to undergo changes or persist unchanged (either to degradation or restoration processes) in response to an external driver (e.g. disturbance factor or stochastic weather events). Thus, a low speed and/or magnitude of change (e.g. degradation speed) during the occurrence of a disturbance factor or stochastic weather event, means high resistance against that disturbance and /

or external factor. Resistance index (RI) was adapted from Hoekstra *et al.* (2015) and Wang *et al.* (2014) as follows:

$$RI_{St} = (NIRR_i - IRR_i) \times (NIRR_i)^{-1}$$

This index was calculated for each state separately (St: reference state or degraded state), for a given variable (seedling density) as the difference between non-irrigated (NIRR) plots and irrigated plots (IRR) 25 days after the last irrigation of each year (i.e. 25 days after the last irrigation in 2006 and in 2007). The RI indicates the magnitude of change recorded by a given state after the occurrence of a disturbance or stochastic weather event. Values close to zero (or zero) indicate higher resistance because the system did not change after a disturbance or weather event (i.e., a lower difference between non-irrigated and irrigated plots). High absolute values (i.e. far from zero), either negative or positive indicate low resistance to restoration practices or against disturbance factors, respectively since imply a great change in response to external factors (Table C, Supplementary file).

The *Elasticity* is the recovery rate of an ecosystem after the change generated by a disturbance factor or an external driver. Elasticity index (EI) was calculated as follows:

$$EI_{St}: \sum_k^m [(NIRR_i - IRR_i) \times (NIRR_i)^{-1}]$$

This index is calculated as the addition from month *k* to month *m* (all sampling dates: April, September and December of each year) of the difference for the values of a certain variable (seedling density) between non-irrigated plots (NIRR) and irrigated (IRR) plots in year *i* (2006 or 2007). This index was calculated for each state (St: referent state or degraded state) separately. The smaller the monthly difference between non-irrigated plots and irrigated plots, the higher recovery speed to the reference values (NIRR). Values close to zero indicate higher elasticity (i.e. the system quickly returned to its original or previous "levels"). On the contrary, absolute values greater than zero, either negative or positive, indicate a low elasticity because the system does not return, or returned slowly, to its initial or original levels after the occurrence of a disturbance or a favourable event.

The *Malleability* is the difference between the final structural and/or functional level of the ecosystem and the pre-disturbance level (or the level prior to the occurrence of a favorable event). A greater difference between final- and pre-disturbance levels, for the values of the variable under study, indicates a greater malleability. If after the occurrence of a disturbance factor (or a favorable external driver), a state experiences great malleability in the medium and / or long term, this indicates that the ecosystem would have crossed (or would be crossing) a threshold to another state (degradation or restoration threshold: depending on whether the external factor is favorable or unfavorable, *sensu* Hobbs 2009). Malleability index (MI) was calculated as follows:

$$MI_{St}: (IRR_f - NIRR_i) \times (NIRR_i)^{-1}$$

This index was calculated for each state separately (St: referent state or degraded state) for a given variable (seedling density and species cover) as the difference of irrigated plots (IRR) and non-irrigated plots (NIRR) between the final study year  $f$  (2009) and the initial year  $i$  (2005 for species cover, and 2006 or 2007 for seedling density). The greater the difference between final versus initial values, the index will be higher, and thus malleability will be greater, thereby indicating that the state has less resilience to external factors or stochastic weather events. Values close to zero (or zero) indicate low (or null) malleability, that is, the ecosystem returned to pre-event or pre-disturbance structural and/or functional levels.

The three parameters would allow evaluating the resilience of each alternative state, being able to persist and/or remain in the same state after the occurrence of stochastic weather events. Specifically, a greater resistance and elasticity, implies a greater resilience of an ecosystem state (Westman, 1986, López et al. 2011, 2013; see STM concepts in Supplementary file), whereas a greater malleability indicates a lower resilience of that state due to a lower ability to recover pre-disturbance levels. The three resilience proxies are an adaptation based on indices proposed in studies such as: Sheehan (1984), Washington-Allen *et al.* (2008), Wang *et al.* (2014), Hoekstra *et al.* (2015). The main adaptation was the value used as reference. In the above-mentioned studies, pre-disturbance values were used as reference, whereas in our study we did not have this information. This is because in our study we assessed the influence of high summer rainfall events

on recruitment of new individuals of perennial species, and thus, before rainfall simulation there were no seedlings. Consequently, we used the values of the control treatments (non-irrigated plots) as reference level (except for species cover which was recorded in October 2005 previous to rainfall simulations and at the end of the study in October 2009).

### *Simulation of rain events*

Irrigations were performed during the dry season (i.e., summer) of 2006 and 2007. In the study area, water deficit is highest from December to March. During this period mean monthly rainfall is also variable, with coefficients of variation among 80 and 166% (Bustos 2006). We determined the quantity of water to be added to the system by subtracting the mean summer rainfall of the last 30 years to the historical maximum (Bustos 2006). According to these data, we added a maximum of 70 mm of water per year, by simulating several events  $\leq 10$  mm each (Coronato and Bertiller 1996; Golluscio *et al.* 1998; Oesterheld *et al.* 2001; Schwinning and Ehleringer 2001; Schwinning and Sala 2004).

For the design and implementation of the irrigation system we considered the studies of Fernández *et al.* (1992), Schwinning *et al.* (2003), Tercero-Bucardo *et al.* (2007) and Lloret *et al.* (2009). The sub-plots to be irrigated were randomly selected within each block. The simulation of rain events was done by spraying water with a perforated plastic tube (2.54 cm diameter, 4 m length, with equidistant holes). This tube allowed us to uniformly distribute the irrigation throughout each sub-plot. To avoid the 'edge effect' on soil humidity that could be caused by the dry microenvironment surrounding each sub-plot, we also irrigated a 1 m buffer belt around each sub-plot. Thus, we irrigated a total area of  $4 \times 4$  m, that included the  $2 \times 2$  m sub-plot at the center. We checked that each sub-plot received the same water amount (i.e., homogeneously distributed in space) by placing 4 beakers at the vertices of each sub-plot. Irrigations were performed on windless, and cloudy or partly cloudy days, with the aim to have environmental conditions similar to rainy days, avoiding unnecessary water losses by direct evaporation and wind-caused drifts. Abundant rain events were simulated during two consecutive years with the aim to assess the response of the

system to a potentially favorable situation. The amount of water added each year was adjusted each month, based on frequency and intensity of precipitations. Because in December 2005 and, January-February 2006 rainfall was above the historical average, we could not carry out all planned irrigations. During this period, rainfall was 100.8 mm, so the irrigated sub-plots received a total of 145.8 mm (i.e., simulated + natural rainfall, see Table 1). In contrast, for the period of December-March 2006-2007 rainfall regime was similar to the historical average, which allowed us to perform all planned irrigations. Specifically, natural rainfall was 41.4 mm, and irrigated sub-plots received a total of 111.4 mm (i.e., simulated + natural rainfall, see Table 1).

**Table 1.** Monthly rainfall and irrigations (in mm) during the period December 2005 to March 2007 (field of INTA-Pilcaniyeu, Río Negro-Argentina).

		December	January	February	March	Total
<i>Historical average</i>		6.8	4.5	13.3	17.4	42
<b>Summer 2005-2006</b>	<b>Rainfall</b>	22.6	17.4	55.2	5.6	100.8
	<b>Irrigations</b>	5.0	10.0	0.0	30.0	45.0
<hr style="border-top: 1px dashed black;"/>						
<b>Summer 2006-2007</b>	<b>Rainfall</b>	11.8	4.6	4.0	21.0	41.4
	<b>Irrigations</b>	10.0	10.0	20.0	30.0	70.0

### *Data analysis*

In order to assess the influence of abundant rainfall events on internal regulation processes we used Linear Mixed Models (LMMs). Degradation state, with two levels (reference state vs. degraded state); Irrigation, with two levels (I vs. NI); and the two-way interaction were included as predictors in the LMMs. Total density of emerged and surviving seedlings of main perennial species, seasonal growth, bud and leaf production in shrubs, leaf number, plant cover difference, and species cover difference were included as response variables in the LMMs. Block was included as a random effect in the LMMs. Degradation State and Irrigation with its two-way interaction were included as fixed effects. A split-plot design was used, with Degradation State assigned to principal plots arranged in blocks, and Irrigation assigned to sub-plots. The response variables considered in this model were:

Total density of seedlings emerged and surviving of main perennial species, seasonal growth, bud and leaf production in shrubs, leaf number, plant cover difference, and species cover difference.

With the aim to compare the response of the main grass species to high summer rainfall events, we added Species as predictor in the LMMs. Thus, Degradation state, Irrigation, Species (with two levels: *P. ligularis* vs. *P. speciosa*), and the three-way interaction were included as predictors in the LMMs. Tiller production, leaf production, the length of the longest leaf of marked and secondary tillers, and relative tiller production per sub-plot were included as response variables. Because these variables were recorded in sub-samples (i.e., four tillers within each plant, and two plants within each sub-plot), raw data were averaged to include a single value for each sub-plot in the LMMs. Block was included as a random effect in the LMMs. The structure of LMMs also accounted for the split-plot experimental design, with Species nested within Irrigation, which was nested within Degradation state. It must be clarified that response variables could not be compared between shrub species since they have different morphology and physiology.

To compare the resilience of alternative states to high summer rainfall events we again used LMMs. Degradation state was included as a fixed factor, whereas block was included as random factor. Resistance (calculated for seedling density of cohorts 2006 and 2007), elasticity (calculated for seedling density of cohorts 2006 and 2007) and malleability (calculated for seedling density of cohorts 2006 and 2007, and for cover changes at the beginning and at the end of the study) indices were included as response variables.

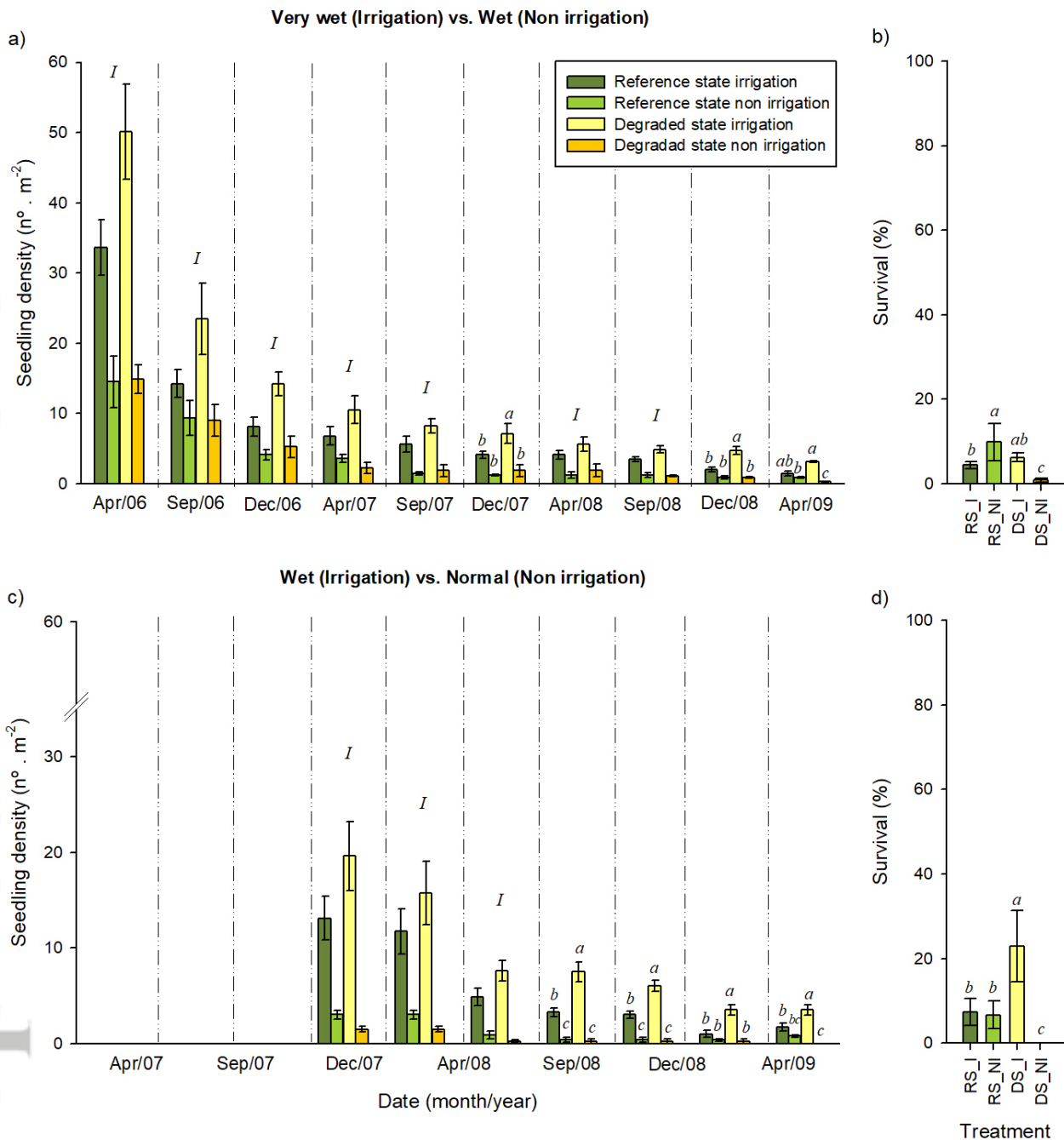
All models were implemented with the statistical software SAS (version 8). Some variables were transformed to meet normality and variance homogeneity assumptions. Specifically, cover variables were transformed with  $\arcsin(\sqrt{x})$ , and the seedling emergence and survival variables were transformed with  $\text{power } x^2$ . Significance level used in all analyzes was  $\alpha = 0.05$ . Significant interactions were evaluated using Bonferroni tests.

### 3. RESULTS

#### *Perennial species recruitment*

Seedling emergence of perennial species significantly increased in response to irrigation (Fig. 1a, c;  $p \leq 0.05$ ). Overall, forage grass species (mainly *P. speciosa*, *Bromus setifolius* and *Hordeum comosum*) accounted for more than 80% of all seedling counts, whereas shrub species (mainly *M. spinosum* and *S. filaginoides*) accounted for less than 5% of seedling counts (Fig. S2 of Supplementary materials). The response pattern of the grass species was similar to the general pattern of all perennial species (Fig. 1; and Fig. S2 of Supplementary materials). The density of seedlings emerged in 2006 was, on average, 2 times greater in irrigated sub-plots than in those non-irrigated (Fig. 1a;  $p \leq 0.05$ ). We recorded the same pattern for seedlings emerged in 2007, with mean density being 5.6 times greater in irrigated- than in non-irrigated sub-plots (Fig. 1c;  $p \leq 0.05$ ).

At the end of the experiment, the effect of irrigation on seedling survival depended irrigation and on rangeland degradation state (Fig. 1b, d;  $p < 0.05$ ). Three years after their emergence in 2006, the density of surviving seedlings was, on average, 4.2 times greater in irrigated sub-plots of degraded state than in non-irrigated sub-plots of both states (see April 2009 in Fig. 1a;  $p < 0.05$ ). However, survival percentage was greatest in non-irrigated plots of reference state, followed by irrigated plots of degraded state, and being lowest in non-irrigated plots of degraded state (Fig. 1b). Two years after emergence of 2007, the density of surviving seedlings was, at least, 4.8 times greater in irrigated plots of degraded state than in the other treatments (see April 2009 in Fig. 1c;  $p < 0.05$ ). Survival percentage showed the same pattern, being highest in irrigated plots of degraded state and null in non-irrigated plots of degraded state (Fig. 1d;  $p < 0.05$ ).



**Fig. 1.** Mean density ( $\pm$  SE) of seedlings emerged of perennial species in April 2006 (a) and 2007 (c) and mean density of surviving seedlings ( $\pm$  SE) during the subsequent years until April 2009. Mean survival percentage ( $\pm$  SE) of seedlings of perennial species at the end of the study for the cohorts 2006 (b) and 2007 (d). The graphs indicate the values for the Reference (RS) and Degraded (DS) states with- (I) and without-irrigations (NI). Significant effects for Irrigation factor in each month are shown with 'I' letter, whereas significant interaction for State and Irrigation factors are shown with lowercase letters and based on Bonferroni tests ( $p \leq 0.05$ ). Statistical analyses were done for each month separately.

### Plant growth

#### Grasses:

The influence of irrigation on grass growth depended mainly on the species, but in some cases on rangeland degradation state (Figs. 2, 3). Also, the response to abundant summer rainfall

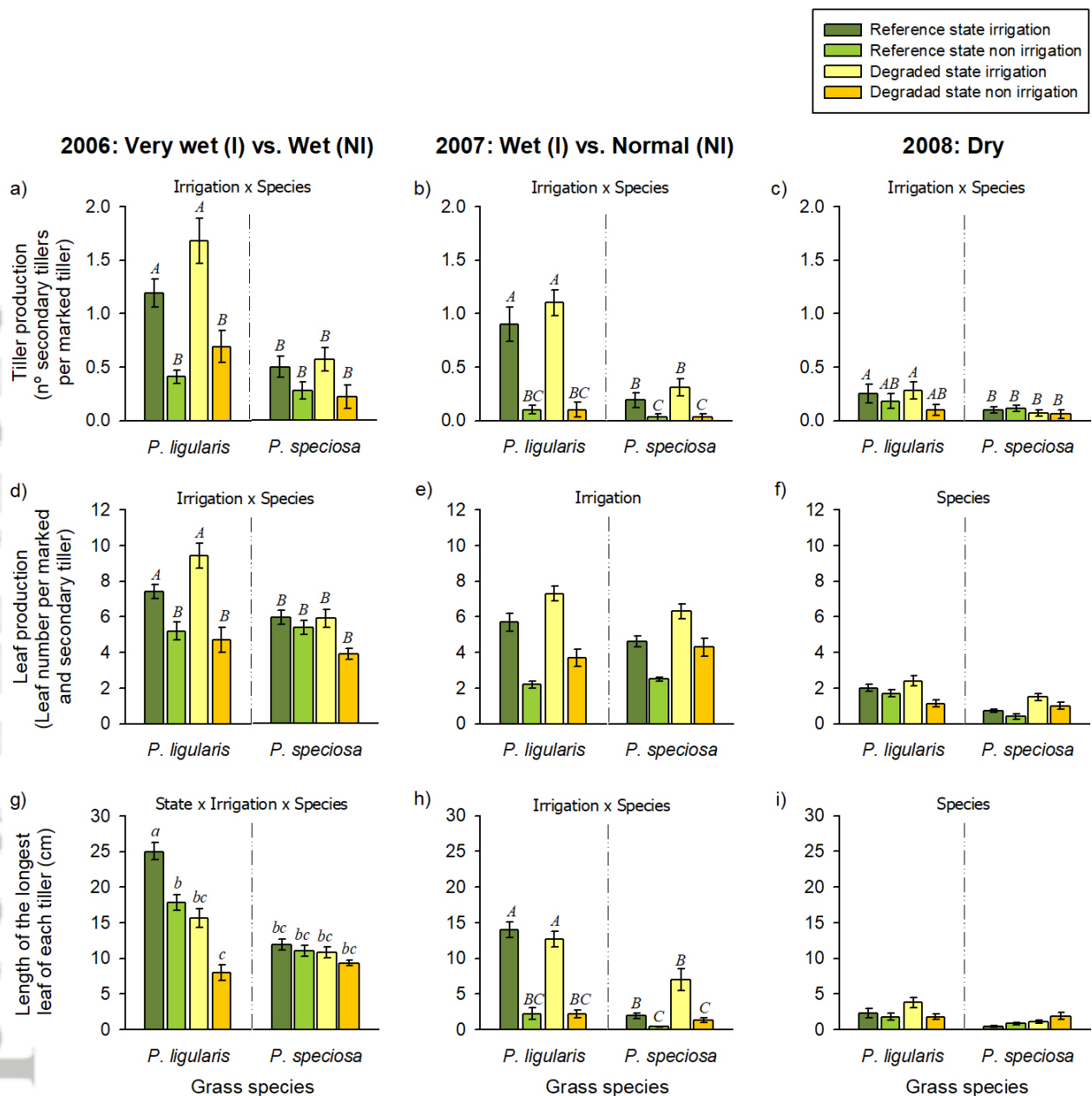


events (irrigation) depended on the scale of measurement. For variables recorded at plant level, species had a greater influence than degradation state on response to irrigation. Overall, *P. ligularis* showed a greater response to a higher water availability than *P. speciosa* (Fig. 2). In contrast, when considering the cover of each species at sub-plot level, the degradation state became more important in modulating the response to irrigation (Fig. 3). Thus, at sub-plot level, the response to irrigation was highest in *P. ligularis* individuals growing in reference state (Fig. 3).

Irrigation promoted tiller production in *P. ligularis* (Fig. 2). Specifically, in 2006 and 2007, tiller production in individuals of *P. ligularis* growing in irrigated sub-plots of both states was 60 % and 99 % higher than that recorded in the remaining treatments, respectively (Fig. 2a,b). In addition, in 2007 tiller production of *P. speciosa* was at least 80% higher in sub-plots with irrigation than in those without it (Fig. 2b). In 2008, *P. ligularis* growing in irrigated sub-plots from both states produced 69% more tillers than *P. speciosa* with and without irrigations ( $p < 0.05$ ) (Fig. 2c).

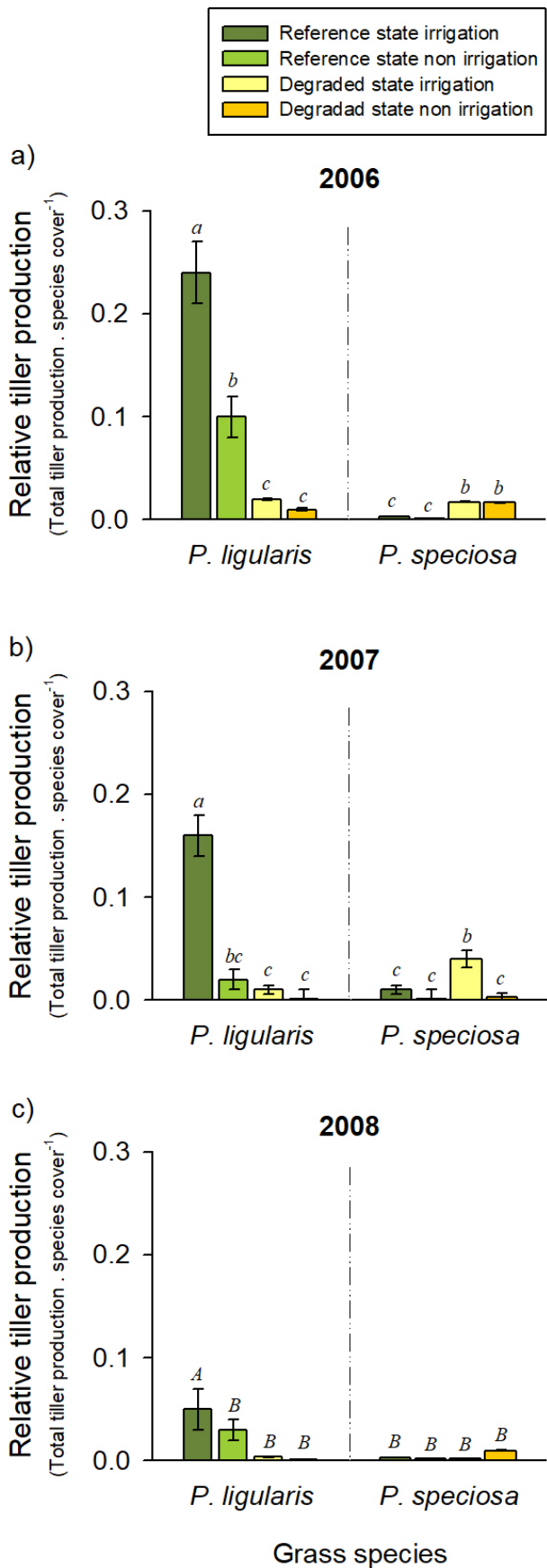
Leaf production was highest in *P. ligularis* of irrigated sub-plots from both states during the 2006 growing season, surpassing the other individuals by more than 42 % (Fig. 2d). In 2007, irrigation promoted leaf production in both states and species ( $p < 0.05$ ; Fig. 2e). Specifically, leaf production was 22 % higher in sub-plots with irrigation than in those without it. In contrast, in 2008, leaf production was different between species ( $p < 0.05$ ; Fig. 2f). The average leaf production of *P. ligularis* was twice that of *P. speciosa* ( $p \leq 0.05$ ).

The length of the longest leaf depended on degradation state, irrigation, and grass species (Fig. 2g-i). In 2006, *P. ligularis* individuals growing in irrigated sub-plots of reference state recorded the longest leaves, being, on average, 50 % longer than those of remaining treatments (Fig. 2g). In 2007, the longest leaves were recorded in *P. ligularis* of irrigated sub-plots of both states, being, on average, 80 % longer than those of the other treatments (Fig. 2h). In 2008, the length of the longest leaf was 1.3 times greater in *P. ligularis* than in *P. speciosa*, independently of degradation state and irrigation (Fig. 2i).



**Fig. 2.** Mean ( $\pm$  SE) tiller production (a-c), leaf production (d-f), and length of the longest leaf of each marked tiller for *Poa ligularis* and *Pappostipa speciosa* during the growing seasons of 2006, 2007 and 2008, in Reference and Degraded states with and without irrigation. Significant effects (for one factor or its interactions are indicated on each graph with: State, Irrigation and/or Species) are shown at the top of each sub-graph ( $p \leq 0.05$ ). Two-way interactions (Irrigation x Species) are shown with uppercase letters; three-way interactions (State x Irrigation x Species) are shown with lowercase letters; based on Bonferroni tests.

At sub-plot level, relative tiller production depended on degradation state, irrigation, and species (Fig. 3). Overall, we found the same pattern during the three years of the study. In 2006, 2007, and 2008, *P. ligularis* individuals growing in irrigated sub-plots of reference state recorded the greatest relative tiller production per sub-plot, being 78 %, 92 % and 90 % higher than that of the other treatments, respectively ( $p \leq 0.05$ ).



Grass species

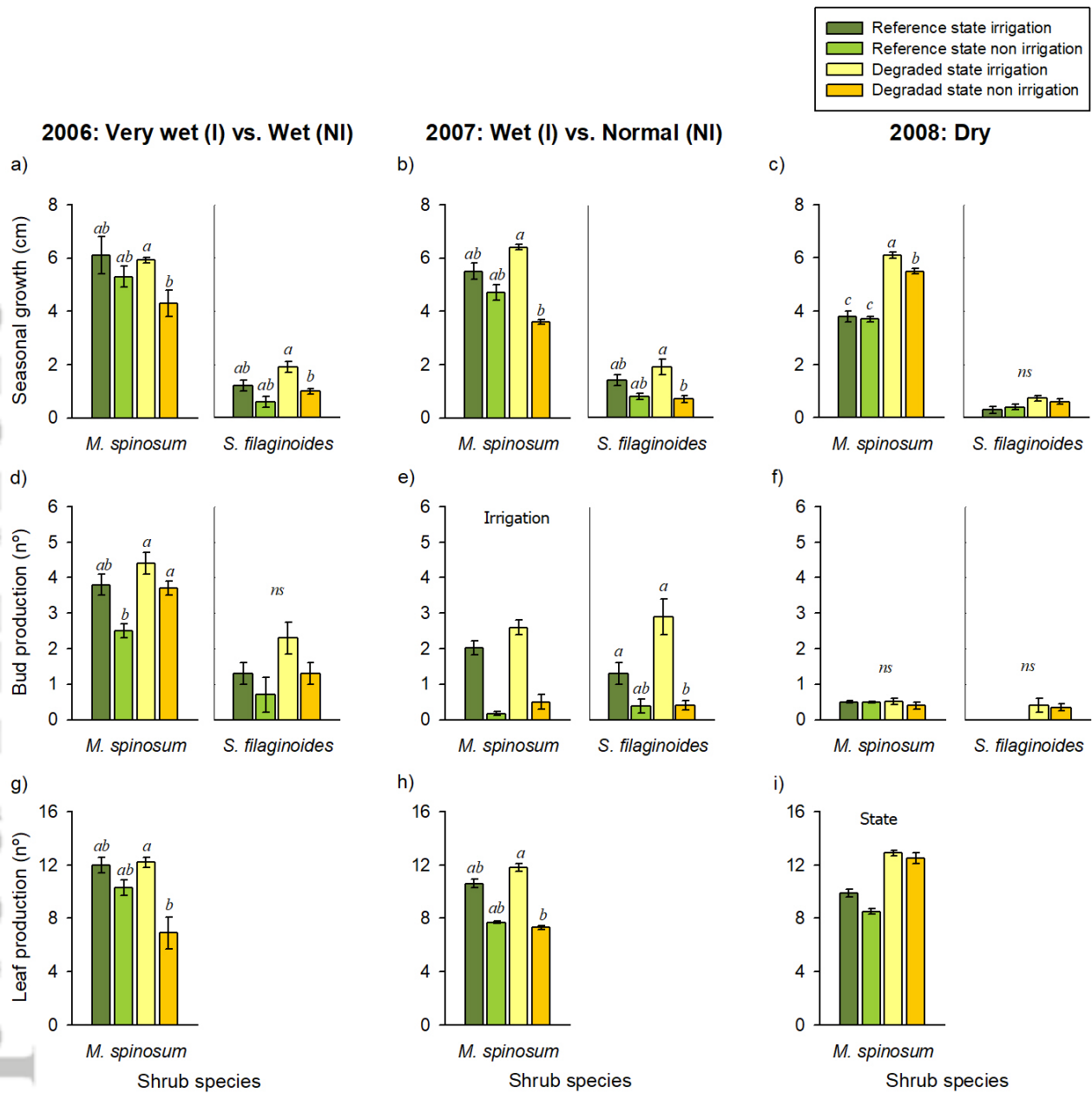
**Fig. 3.** Mean ( $\pm$  SE) relative tiller production for *Poa ligularis* and *Pappostipa speciosa* during the growing seasons of 2006 (a), 2007 (b) and 2008 (c), in Reference and Degraded states with and without irrigation. Two-way interactions (State x Species) are shown with uppercase letters; three-way interactions (State x Irrigation x Species) are shown with lowercase letters based on Bonferroni tests ( $p \leq 0.05$ ).

### Shrubs:

Seasonal growth depended on degradation state and irrigation for both shrub species (Fig. 3a-c). Specifically, irrigation only promoted seasonal growth in degraded state. This pattern was recorded during the three years of the study in *M. spinosum*, whereas during 2006 and 2007 in *S. filaginoides*. In 2008, seasonal growth of *S. filaginoides* was similar between treatments (Fig. 3a-c).

Bud production showed different patterns between years in both shrub species (Fig. 3d-f). In 2006, bud production of *M. spinosum* depended on degradation state and irrigation. Specifically, individuals in degraded state produced 69 % more buds than those in reference state without irrigation ( $p < 0.05$ ; Fig. 3d). In contrast, bud production of *S. filaginoides* was similar among treatments (Fig. 3d). In 2007, irrigation promoted bud production in *M. spinosum*, being twice in sub-plots with irrigation than in those without it ( $p < 0.05$ ; Fig. 3e). During the same year, bud production in *S. filaginoides* was at least twice in irrigated sub-plots of both states than in non-irrigated sub-plots of degraded state ( $p < 0.05$ ; Fig. 3e). Finally, in 2008 bud production was similar among treatments for both species (Fig. 3f).

During the 2006 and 2007 growing seasons, irrigation only promoted *M. spinosum*'s leaf production in degraded state (Fig. 3g, h). In contrast, in 2008 leaf production was 27 % higher in degraded than in reference state (Fig. 3i). Finally, total plant cover was similar at the beginning and at the end of the study ( $p > 0.05$ ). Considering the cover by species, *P. speciosa* was the only species that changed their cover, which increased a 4 % in irrigated sub-plots of degraded state ( $p < 0.05$ ).

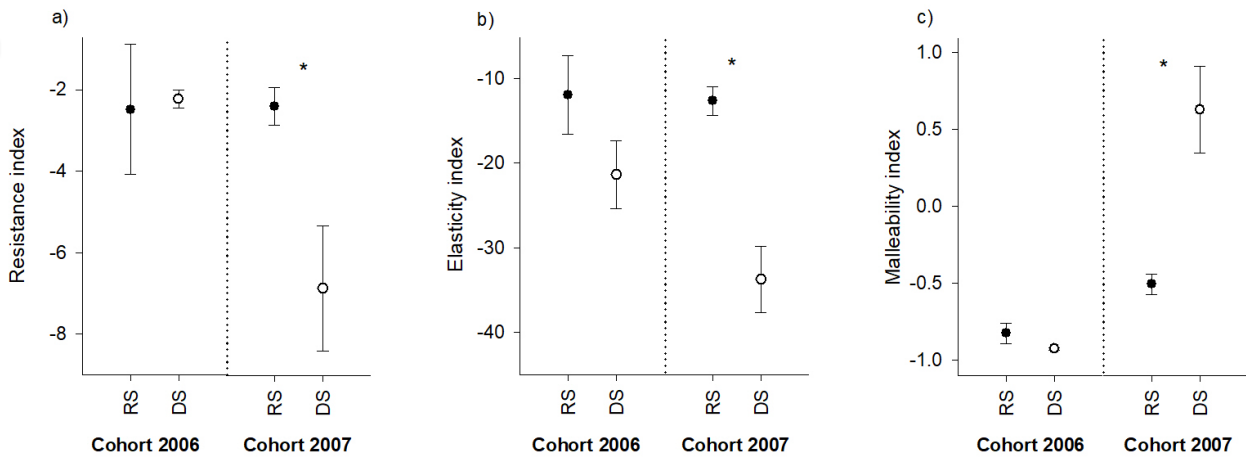


**Fig. 4.** Mean ( $\pm$  SE) seasonal growth (a-c), bud production (d-f), and leaf production (g-i) in each marked branch for *Mulinum spinosum* and *Senecio filaginoides* during the growing seasons of 2006, 2007 and 2008, in Reference and Degraded states with (I) and without irrigations (NI). Significant effects are shown at the top of each sub-graph ( $p < 0.05$ ). Two-way interactions (State x Irrigation) are shown with lowercase letters based on Bonferroni tests. Statistical analyses were done for each species separately.

## Resilience assessment

### Perennial species recruitment

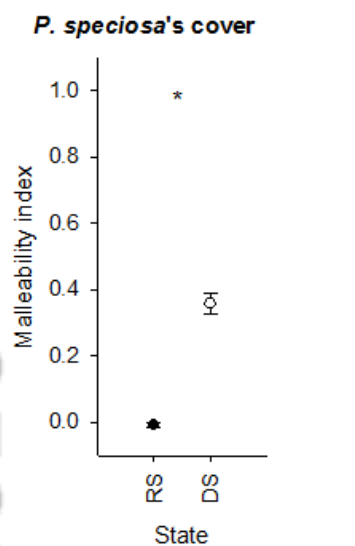
Resistance, elasticity and malleability of the cohort 2006 were similar between states (Fig. 5a, c, e). However, for the cohort 2007, the reference state had significantly greater resistance and elasticity to simulated high summer rainfall events than the degraded state (Fig. 5b, d). In contrast, malleability was significantly greater in the degraded than reference state (Fig. 5f).



**Fig. 5:** Mean ( $\pm$  SE) of Ecological Resilience proxies (adapted from Sheehan 1984; Washington-Allen *et al.* 2008; Wang *et al.* 2014 and Hoekstra *et al.* 2015) for Reference State (RS) and Degraded State (DS): Resistance index (a, b), Elasticity index (c, d) and Malleability index (e, f) in response to the simulation of high summer rainfall events, calculated for seedling density of perennial species for Cohort 2006 (a, c, e) and 2007 (b, d, f); significant differences between states are indicated by an asterisk (\*) ( $p < 0.05$ ).

### Vegetation cover

The degraded state had higher malleability than the reference state for cover of *P. speciosa*, which increased 4 % in the degraded state in response to irrigation ( $p < 0.05$ ) (Fig. 6).



**Fig. 6:** Mean ( $\pm$  SE) of *Malleability index* calculated for the change in *Pappostipa speciosa* cover; in response to the simulation of high summer rainfall events; significant differences between states are indicated by an asterisk (\*) ( $p < 0.05$ ).

#### 4. DISCUSSION

The effect of high summer rainfall events on internal regulation processes depended on the ecological state of the ecosystem. Specifically, the response to irrigation was greater in the degraded state for seedling recruitment (Fig. 1) and seasonal shrub growth (Fig. 4). In contrast, irrigation promoted grass growth in both states (degraded and reference state), with *P. ligularis* having the greatest response (Fig. 2). Nevertheless, since the cover by species is different between the alternative states, at community level, the response to irrigations also depended on the state of the ecosystem. Thus, the effect of irrigation on grass growth was greater in the reference than in the degraded state (Fig. 3). Consequently, our results suggest that degradation can influence the response of the plant community to external drivers. We partially accept the hypothesis because, contrary to our expectations, the degraded state had similar or more initial ability to respond to external environmental factors than the reference state. However, according to our expectations, the net response was lower in the reference than in the degraded state. This could be because the degraded state had a lower resistance and elasticity, and greater malleability than the reference state (Figs. 5,6 and 7).

Our study coincided with a wet period, which occurred between December 2005 and April 2006. The natural occurrence of a wet period at the beginning of the study allowed us to corroborate that the events we simulated are very likely. In fact, the amount of rainfall above the historical average during 2005-2006 growing season was similar to the event that we simulated during the subsequent growing season (Table 1). During the subsequent growing season (2007-2008), rainfall was similar to the historical average. Also, during the third year of the study (i.e., from October 2007 to April 2008), a dry period occurred in the study region (Villa-gra *et al.* 2009; Easdale and Rosso 2011). This pattern highlights that rainfall variability is the rule rather than the exception in arid and semiarid ecosystems (Ramos and-Martínez-Casasnovas 2006). Consequently, our study is representative of natural climatic cycles, and thus, our results can be applied to sustainable management of similar rangelands.

#### *Perennial species recruitment*

The simulation of high summer rainfall events increased seedling emergence and short term-survival in both states (Fig. 1). However, the final density of surviving seedlings of perennial species (i.e., in April 2009) also depended on the state of the ecosystem. Irrigation favored seedling survival in the degraded state (Fig 1b, d). In fact, seedling survival was the lowest in the degraded state without irrigations. The effect of irrigation in the degraded state was more evident when seedling density was extrapolated to the paddock-scale. Specifically, for the 2006 and 2007 cohorts, the final density of surviving seedlings was greater than 35,000 individuals per ha in irrigated plots, whereas in absence of irrigations the final density of surviving seedlings was 34 times lower (1000 individuals per ha for cohort 2006 and, null for cohort 2007). In addition, seedling recruitment recorded lower resistance and elasticity, whereas greater malleability in degraded than in reference state in response to abundant summer rainfall events (Fig. 5b, d, f). Consequently, our results indicate that rainfall variability exerted a greater influence in the degraded state than the reference state for seedling recruitment.



The greater seedling recruitment in the degraded state in response to abundant summer rainfall events could be caused by differences in the grass cover between alternative states. This is because adult grasses can outcompete recently emerged seedlings (Defossé *et al.* 1997; López and Cavallero 2017). Although the reference state can provide better micro-environmental conditions for seed germination and seedling emergence than the degraded state (López *et al.* 2013; López and Cavallero 2017); these conditions are generated by a greater soil cover (plant and litter), mainly from grass species. In fact, grasses account for more than 45 % of the soil cover in the reference state, but less than 25 % in the degraded state. Grass tussocks (i.e. individuals) have fibrous and shallow roots (mainly *P. ligularis*), and absorb water from shallow soil layers, which are also the layers occupied by seedlings' roots. This spatial overlapping of root systems increases water competition between grasses and seedlings, decreasing, in turn, seedling survival. Our results are similar to other studies that found that competition between adults and seedlings decreased the survival of younger individuals (Aguiar and Sala 1994; Defossé *et al.* 1997; López and Cavallero 2017). This fact could explain the greater resistance and elasticity of reference state in comparison with that recorded in degraded state (Fig. 5b, d). In contrast, a low grass cover in the degraded state (i.e., 21.5 % *sensu* López *et al.* 2013) would diminish water-competition between seedlings and adult grass individuals, and thus would increase state malleability in response to abundant summer rainfall events (Fig. 5f). Therefore, during wet years, the low rain use efficiency of the scarce remnant vegetation in the degraded state generates a water excess that opens a window of opportunity for the recruitment of new individuals (Aguiar and Sala 1994; Greenlee and Callaway 1996; Hunt 2001; Bisigato and Bertiller 2004, Holmgren *et al.* 2001; 2006). Also, the low seedling densities recorded in the degraded state without irrigation indicate that degradation (López *et al.* 2013) would have increased micro-environmental harshness, decreasing essential processes as seed germination and seedling emergence (López and Cavallero 2017). Consequently, the recovery of rangelands that crossed a critical threshold can only be triggered by an external resource input, such as high summer rainfall, which influences internal regulation processes such as plant recruitment (changing the competition balance between young and adult individuals).

The increase in seedling emergence in the reference state in response to irrigation suggests that this state has an annual recruitment rate that can ensure community maintenance in the long term (i.e. associated with high ecological resilience of reference state, *see Supplementary file*). The maintenance of a relatively stable annual recruitment rate is essential to withstand stochastic weather events. For example, the likelihood of adult mortality increases during droughts. Adult mortality releases space and other resources that can be used by new individuals produced by the plant community during subsequent normal or wet years (MacDonald and Watkinson 1981, Soriano *et al.* 1994; Aguiar and Sala 1999; Baskin and Baskin 2001; Bisigato and Bertiller 2004; Lloret *et al.* 2009). Therefore, in the reference state, the maintenance of an annual recruitment rate (i.e., an internal regulation process) indicates that this state has a high resilience to external factors (e.g. drought).

#### *Plant growth*

*Poa ligularis* had a great capacity to respond to abundant summer rainfall events. This species recorded the greatest seasonal growth in response to irrigations during the three years of the study in both states (Fig. 2). This result suggests that this species has a great ability to take advantage of stochastic increases in water availability (i.e., rain use efficiency) (Graff 2009). In fact, the occurrence of a very wet period (i.e., natural rainfall + irrigation during the 2006 growing season, see Table 1) promoted the growth of *P. ligularis* individuals in both states, whereas *P. speciosa* showed no response (Fig. 2a, d). Therefore, at the individual level, *P. ligularis* showed a greater capacity than *P. speciosa* to take advantage of increases in water availability in both states. This result suggests that *P. speciosa* would be more adapted than *P. ligularis* to grow in drier conditions (Fernández *et al.* 2002; Graff and Aguiar 2007; Graff 2009; López 2011). Inter-specific differences in the response to irrigation could be caused by a net photosynthetic rate in *P. speciosa* that saturates at lower levels of soil water availability than that of *P. ligularis* (Graff 2009). Therefore, *P. ligularis* and *P. speciosa* may occupy different niches in the plant community, as the former can take advantage of wet and very wet periods, while the latter is more tolerant to droughts.

The coexistence of species with decoupled spatio-temporal niches is essential for long-term community persistence in response to stochastic weather events (Chesson *et al.* 2004).

Consequently, management decisions that affect rangeland composition may also affect ecosystem resilience.

When comparing seasonal growth at community level, the response of grasses to irrigation was also modulated by the state of the ecosystem. Specifically, both grass species showed different responses. In the case of *P. ligularis*, irrigated sub-plots in reference state had the greatest relative tiller production (Fig. 3a, b). This result was mainly due to differences in species cover between alternative states. In the reference state, *P. ligularis* covered approximately a 30 % of surface; in degraded state cover was ~ 1.5 % (López *et al.* 2013). This large cover differences may have caused different relative tiller production at sub-plot level between states (Fig. 3a, b). In contrast, relative tiller production per sub-plot in *P. speciosa* was greater in degraded than in reference state; showing no response to irrigation during the wet year (i.e, 2006 growing season; Fig. 3a), but increasing relative tiller production in response to irrigation during the normal year (i.e., 2007 growing season; Fig. 3b). The greater relative tiller production of *P. speciosa* in the degraded state could also be caused by cover differences between alternative states. In the reference state, *P. speciosa* accounted for 7 % of surface cover but covers 20 % of soil in the degraded state (López *et al.* 2013). The fact that relative tiller production did not increase with irrigation during a very wet period (Fig. 3a) suggests that the net photosynthetic rate of *P. speciosa* might saturate with large increases in water availability. Consequently, in concordance with the results found at individual level, *P. ligularis* would be more efficient in taking advantage of increases in water availability during wet periods, whereas *P. speciosa* would be more drought-tolerant (Fernández *et al.* 2002; Graff and Aguiar 2007; Graff 2009).

Abundant summer rainfall events promoted seasonal shrub growth and leaf production mainly in the degraded state during the first two years of the study (i.e., summer 2006 and 2007) (Fig. 4a, b, d, g, h). The greater response of shrubs to irrigation in degraded state could be caused by a lower grass cover in that state (mainly of *P. ligularis*), which may have increased water

availability for shrubs (Fernández *et al.* 1992; Golluscio *et al.* 1998). This pattern has been observed in other ecosystems (Chesson *et al.* 2004) where the presence of species with shallower roots (like *P. ligularis* and *P. speciosa*) would decrease water availability for species with deeper roots (like *M. spinosum*) (López and Cavallero 2017).

Distinct response patterns to irrigation among the main perennial species could be caused by architectural and ecophysiological differences. On the one hand, grasses have shallow and fibrous roots (López and Cavallero 2017), being able to take advantage of even small rain events that occur during the growing season. The very shallow root system makes grasses highly competitive in terms of water use (Aguiar and Sala 1994; López and Cavallero 2017). Thus, in states with high grass cover, this functional group may outcompete shrubs and/or recently emerged seedlings. In contrast, shrubs have deeper and pivotant roots, with certain differences among species. Specifically, *M. spinosum* has deeper roots than *S. filaginoides*, which can partially overlap the roots of grasses (López and Cavallero 2017). Thus, *M. spinosum* individuals are able to take advantage of rain events that cannot be used by grasses, such as those that occur at late winter or early spring that allow water recharge of deep soil layers or those that occur during the growing season that percolate into deep soil layers (Golluscio *et al.* 1998; Paruelo *et al.* 2000; Chesson *et al.* 2004). On the other hand, distinct ecophysiological strategies for drought resistance (Chesson and Huntly 1997; Chesson *et al.* 2004) would also explain the differential response to abundant summer rainfall events for *P. ligularis* and *P. speciosa* (Fernández *et al.* 2002; Graff and Aguiar 2007; Graff 2009). Therefore, the use of soil water resources would be spatially and temporarily decoupled due to architectural and ecophysiological differences between the main perennial species. Consequently, by affecting species cover and composition (i.e., relative proportion of species with distinct architecture and ecophysiology, and thus, different abilities to cope with resource abundance/scarcity), degradation affects the ability of the plant community to respond to external drivers.

Regarding plant cover, we expected an increase in *P. ligularis* cover in the reference state in response to irrigations (i.e., since relative tiller production was highest in this treatment, Fig. 3).

Accepted Article

However, we did not detect cover differences when comparing the beginning and the end of the study. This result could be due to density-dependent tiller mortality caused by intra-specific competition, which increases in the absence of grazing pressure. Specifically, Gittins (2011) recorded a high tiller mortality in *P. ligularis* individuals growing in areas with low or null grazing pressure (i.e., with a high plant and *P. ligularis*' cover). The increase in tiller mortality in response to decreasing grazing pressure has also been recorded for several forage grasses (Lemaire *et al.* 2000). Therefore, in the reference state where grazing was excluded during at least 30 years, *P. ligularis* individuals had a high tiller production which might have been compensated by a high mortality caused by competition not only for resources allocation within each individual but also for resource acquisition between individuals. This trade-off between tiller production and mortality would maintain a relatively stable net tiller survival. Considering this, tiller mortality should decrease in the degraded state, which was heavily grazed until 2005. According to our results, tiller production was similar between alternative states (Fig. 2a, b). Therefore, the trade-off between tiller production and mortality should yield a greater net tiller survival in the degraded state in response to irrigation (because grazing was excluded since 2005). However, our results do not support this assumption because we did not measure tiller survival. Nevertheless, *P. ligularis* cover was so low in the degraded state (i.e., ~ 1.5 %) that the trade-off between tiller production and mortality could not be expressed at the community level via cover differences at the end of the study. Thus, for short term studies, plant cover might not be a sufficiently sensitive variable to document the dynamics of internal regulation processes of the plant community from arid and semi-arid areas.

A similar mechanism may have caused the increase in *P. speciosa*'s cover in response to irrigation in degraded state. In this case, *P. speciosa* is the dominant grass species in degraded state, accounting for 93 % of grass cover. In this state, tiller mortality due to resource competition at intra- and inter-individual level is expected to decrease due to high grazing pressure until 2005. Therefore, an increase in tiller production in response to irrigation, in a context of lower tiller mortality (due to grazing until 2005, and low tiller density and density-dependent competition), yielded a higher tiller survival, which, in turn, was reflected as an increase in *P. speciosa*'s cover.

Accepted Article

Finally, the lack of response for the total plant cover and of species cover (except for *P. speciosa*) can be associated with the occurrence of a drought during 2008-09, which may have caused tiller mortality, thereby affecting the final cover survey in 2009. It is likely that this drought affected the aerial cover of *P. speciosa* to a lesser extent than that of *P. ligularis* (the two main species of the community), because the former species is more tolerant to droughts than the latter.

The influence of external drivers on internal regulation processes depended on the degradation state of the ecosystem. Our results suggest that the degraded state was more sensitive and less resilient (i.e., lower resistance and elasticity, but had greater malleability) to external drivers than the reference state. Specifically, in the reference state, demographic processes such as seedling recruitment and vegetative growth might be compensated by competition and mortality maintaining stability in plant populations and indicating a greater internal regulation capacity (see between-year similarity in the values of resilience proxies; Figs. 5 and 6). Therefore, despite the greater responses to stochastic increases in water availability observed in the reference state, internal regulation processes compensated for this response, stabilizing vegetation dynamics through negative feedback mechanisms (i.e., greater resistance to change in response to weather events and elasticity to return to pre-event conditions). In contrast, the degraded state (i.e. intermediate degradation, *sensu* López *et al.* 2013) was sensitive to external drivers (i.e., greater malleability in response to increases or decreases in resource availability (i.e., wet or dry periods, respectively). This is evidenced by the increase in seedling recruitment (Fig. 1), in shrub growth (Fig. 4), and in *P. speciosa*'s relative tiller production (Fig. 3a, b) and cover in response to irrigation (Fig. 6); as well as in the low seedling emergence (Fig. 1a), null seedling survival (Fig. 1b), and low grass growth (Fig. 2c,f,i) in response to the 2007-2008 drought.

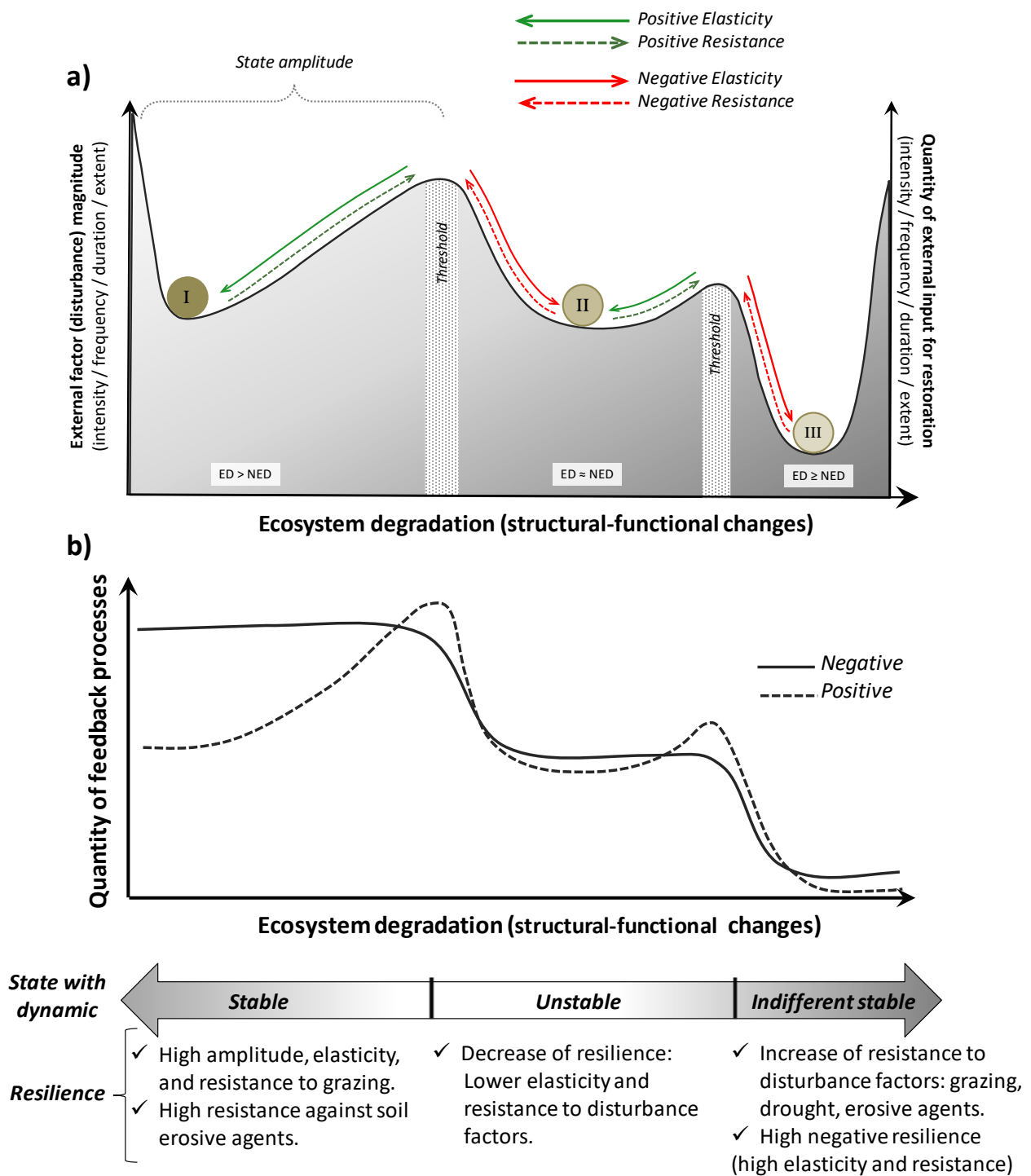
## 5. IMPLICATIONS IN RESILIENCE AND ECOSYSTEM MANAGEMENT

Degradation affects internal regulation processes and thus modifies the balance between equilibrium and non-equilibrium dynamics. Therefore, the resilience to external events and/or disturbance factors and stability of each state differ (Lake 2013; Briske 2017). Integrating our

Accepted Article

results on resistance, elasticity and malleability with a previous study about other resilience parameters (i.e. state amplitude and thresholds between alternative states) of the grass-shrubby steppes of northern Patagonia (López 2011; López *et al.* 2013), we can define the stability of three alternative states. Thus, to infer the type of stability of each ecosystem state, we take into account four resilience parameters: *amplitude* (defined by the resilience threshold of each state studied in López *et al.* 2013), *resistance* (carrying capacity and degradation rate of the system), *elasticity* (recovery speed) and *malleability* (final difference in functional-structural attributes with respect to an initial or reference state) (see the Glossary of the Supplementary file) (Fig. 5). These parameters capture different aspects of resilience of alternative states in response to external drivers and/or disturbance factors (Fig. 7).

To be able to understand the response (or lack of response) of alternative states to external factors, it is necessary to differentiate between negative or positive resilience. Positive resilience is related to the ability of each state to respond (persist and/or return) after a disturbance, maintaining its ecological integrity (i.e. without continue degrading and/or recover after the disturbance). In contrast, negative resilience is the ability to persist and/or return to the same (usually undesirable) alternative state preventing its recovery to the reference state (or a state with better structural-functional levels) in response to restoration practices or favorable weather events (Lake 2013, Standish *et al.* 2014).



**Fig. 7. (a)** Ball-cup scheme that describes the resilience of alternative degradation states of the grass-shrubby steppes of *Poa ligularis* and *Mulinum spinosum* (northern Patagonia, Argentina). State I and II are defined considering the results of our study, and State III was determined by López (2011) and López *et al.* (2013). The 'x' axis represents the ecosystem degradation (structural-functional changes) triggered by a disturbance factor (e.g. overgrazing and/or droughts). The 'y' axis represents the pressure amount necessary to drive state changes; either to cause degradation or recovery (amount of input needed to restore the ecosystem to the previous or reference state). We indicate key parameters of *resilience*: amplitude, resistance and elasticity. *State amplitude* is represented by the cup-width (defined by resilience threshold of each state); *State elasticity* is the recovery speed in absence of disturbance (associated with the recovery slope of cup); and *State resistance* is related to both, the cup-depth associated with pressure of an external factor (e.g. drought, livestock grazing, irrigation) and the degradation speed and amount (i.e. magnitude of structural-functional change: x-axis). In this scheme, the *malleability* is represented by the structural-functional differences that exist between the states when they are at the base of the cup (e.g. differences between the balls of states I, II and III in their current location). **(b)** Hypothesis about the change in the level (or quantity) of positive and



negative feedback processes in three alternative states and transitions of the ecosystem that we exemplify. The 'x' axis represents ecosystem degradation (this corresponds to the axis of figure 5a), and 'y' axis represents the amount of feedback processes (negative and positive) in each State. In this example (see **a** and **b**), State I has the greatest *amplitude*, *elasticity* and *resistance*, and thus high *stability*. In State I, equilibrium dynamics (ED) prevail over non-equilibrium dynamics (NED), because negative feedback processes prevail over positive feedback processes, which stabilize the state (Briske *et al.* 2006; Briske 2017). During state transitions, positive feedback processes (i.e., change amplification, see more in Briske *et al.* 2006) prevail over negative ones (see example of feedback processes in Fig. S1 of Supplementary file). In State II, vegetation response can be governed either by equilibrium or non-equilibrium dynamics depending on annual rainfall (normal, wet or dry years). This would be because the ecosystem is arrested in a state with a small difference between the amount of positive and negative feedback processes. Therefore, State II is *unstable*, with lower *elasticity* and *resistance* than State I (e.g. lower productivity and lower carrying capacity). In State III (i.e. state with the highest malleability with respect to state I) the level of feedback processes is too low because of the huge loss of soil and plant cover, and due to a decreased functional diversity (i.e. structural stock and processes losses). State III has a high *resistance* to droughts and grazing, as well as to soil erosion (López *et al.* 2013). State III also has low *amplitude* because its response to external drivers is scarce or null. To be able to restore the State III to States I or II, significant inputs and amounts of time are required (e.g. re-vegetation dependent on irrigation and fertilization), determining an *indifferent stability*. In degraded states, resistance and elasticity counteract restoration practices (i.e., see positive transitions on Glossary, Supplementary file) causing high negative resilience limiting restoration (*sensu* Lake 2013).

Reference states have a high resilience due to equilibrium dynamics that imparts dynamic stability, maintained through the prevalence of negative feedback mechanisms (Briske *et al.* 2005, 2006; López 2011) (Fig. 7; Fig. S1 of supplementary file). The state I (reference state) has the greatest *amplitude* because it has the maximum expression of structural attributes (plant biomass and/or soil) and the greatest functional diversity and redundancy (associated with the capacity for self-regulation). In this state, the ecosystem can lose some organic matter or plant stock without significantly affecting key ecosystem processes. This is because plant cover is greater than 60% whereas soil erosion processes are triggered when plant cover is less than 45%. Below this threshold value, the ecosystem tends to continue degrading (López *et al.* 2011, 2013). State I also has the highest *resistance* to stochastic weather events (abundant summer rainfall events and 2008-09 drought; Figs. 5a, 6), grazing, and soil erosion. State I also has the greatest carrying capacity (López 2011), due to the dominance of grass species with adaptations for grazing tolerance (e.g., apical buds hidden at the tiller base). The high soil cover and great connectivity of plant canopies protects soil from erosive agents (López *et al.* 2013). In addition, this state has the highest *elasticity* (Fig. 5b) due to its ability to recruit new individuals and vegetative growth, even after the 2007-2008 drought (Figs. 1-3), and quickly returning to its pre-event values (or 'average values') following disturbance (Fig. 5b). This state would require a high pressure of an internal (e.g.

overgrazing) or external factor (e.g. extreme and prolonged droughts) to trigger a degradation transition (see amplitude and depth of the basin in State I in Fig. 7a) to an alternative state. Consequently, state I has a malleability index close to zero and lower than more degraded states (Figs. 5c, 7), indicating that ecological process rates and stocks of state I are at their environmental potential for that 'ecological site' *sensu* Bestelmeyer *et al.* (2017).

During an ecological transition, positive feedback processes prevail over negative feedbacks (Fig. 7b; Fig. S1 of supplementary file) because the changes produced by the disturbance factor in the ecosystem are amplified. For example, overgrazing decreases plant cover and promotes soil erosion and decreases the ability of the soil to store water, which in turn, decreases plant productivity (and therefore supports less biomass or plant cover). If stocking rate remains the same, less plant productivity results in more grazing pressure (i.e.  $\text{kg animal} \times \text{kg forage}^{-1}$ ), less vegetation cover, reduced soil depth (due to greater exposure to erosive agents), less capacity of the soil to store water and less plant productivity and cover (Briske *et al.* 2005, 2006; López 2011). Thus, the effect of the disturbance factor (i.e., overgrazing) is amplified by a chain of positive feedback processes, causing a decrease in plant productivity until the ecosystem stabilizes at another structural-functional level (e.g. carbon stock, plant cover and productivity). In the new state (e.g. State II of Fig. 7a), negative feedback mechanisms prevail over positive feedback mechanisms, maintaining the ecosystem in the alternative state (Briske *et al.* 2006; Briske 2017) (Fig. 7b).

Because structural stocks and ecosystem functioning decrease with degradation (e.g. plant cover, species diversity, functional diversity and redundancy, productivity), degraded states have reduced levels of internal regulation (i.e. weakened feedback mechanisms) (López *et al.* 2011, 2013; Briske 2017) (Fig. 7b). Degraded states have a low stability due to the dominance of non-equilibrium dynamics (e.g. greater sensitivity to external factors as dry and wet years) and low resilience due to weakened feedbacks. This state with (intermediate to high levels of degradation, López *et al.* 2013) has an unstable dynamic, and it would have a lower resilience (positive and negative) than reference state. In our case study, the reduced ecological resilience of the intermediately degraded (state II) is indicated by reduced *amplitude, resistance, elasticity* but

greater malleability than the reference state (Figs. 5-7a). Specifically, degraded states tolerate a lower percentage of structural change before crossing thresholds to even more degraded states (reduced *amplitude*) (López *et al.* 2013). Degraded states have lower *resistance* to (i) grazing (because reduced productivity persists due to feedbacks, and thus their carrying capacity is reduced), (ii) erosion (because reduced plant cover and patch connectivity accelerates erosion, López *et al.* 2013), and (iii) stochastic weather events, including favorable high summer rainfall events (Fig. 5b) or unfavorable droughts (due to the null seedling recruitment and low grass growth in response to the 2007-2008 drought; Figs. 1-3; López and Cavallero 2017). Lower *elasticity* might also be associated with more xeric micro-environmental conditions, which decreased plant recruitment and vegetative growth in non-irrigated sub-plots (Figs. 1-3, 5c, d) (López 2011, López and Cavallero 2017). Finally, the greater *malleability* (Figs. 5f, 6) is reflected in observed system responses to disturbance. Therefore, this state would require lower pressure of an external factor (in comparison with reference state-I) to trigger a transition to another state (i.e., see less basin depth of state II in Fig. 7a, in comparison with the height of the second threshold).

Very degraded states would have a high stability, which has also been referred to as 'indifferent-stability' by López *et al.* (2013). In this state (III), soil depth is drastically reduced (i.e., at least, 10-15 cm less than the reference state) decreasing infiltration, water storage, and nutrient availability (López 2011, López *et al.* 2013). Such an ecosystem has crossed an 'extinction threshold' (*sensu* Briske *et al.* 2006) given by the local extinction of the main forage species (i.e., *P. ligularis*), and the increase in the abundance of drought-resistant and unpalatable species (i.e., *P. speciosa* var *major* and *Pappostipa humilis*) (López *et al.* 2013, Standish *et al.* 2014). The occurrence of this threshold is reflected in a reduction in state *amplitude* because key biophysical properties of the site have been drastically modified (e.g. soil loss, abiotic site modification, very low plant cover, and local species extinction) (Briske *et al.* 2005, Standish *et al.* 2014). The positive resilience of state III is characterized by greater *resistance* to disturbance factors (grazing, droughts, erosion) than state II for two reasons (Fig. 7a). First, the plant community is dominated by grazing- and drought-resistant species (i.e., with thorns and secondary compounds that can deter herbivores

and increase their tolerance to xeric environments) (López 2011; López and Cavallero 2017).

Second, there is less soil to be eroded because the soil has been already been lost with exposed rock on the surface (see State III in Fig. 7, evaluated by López *et al.* 2013). Also, this state has low *elasticity* (i.e., low recovery speed) after disturbances. This is because the large loss in plant cover and soil not only has significantly decreased rain use efficiency, but also increased the harshness of micro-environmental conditions (López and Cavallero 2017), decreasing in turn, the state's ability to respond to disturbances (see greater basin depth of State III in Fig. 7). In contrast, the negative resilience of this state (Fig. 7a) is reflected in high *resistance* and a high *elasticity* in response to restoration practices (Lake 2013) and/or favorable climatic events (such as high summer rainfall). Thus, negative resilience has the potential to explain the failures of restoration practices in very degraded states (Lake 2013, Standish *et al.* 2014). This negative resilience to restoration could be caused by the harsh micro-environmental conditions of this state, which would limit survival of new individuals (e.g. added to the system in revegetation), as well as the reduced growth of individuals already established (Fig. 7a).

To summarize, in reference conserved states high stability is related to high positive resilience (great amplitude, elasticity and resistance) with a great initial ability to respond to external drivers, which is compensated by internal regulation processes through negative feedback mechanisms (as recruitment and vegetative regeneration versus competition and herbivory). In contrast, in very degraded states the high stability is due to high resistance (negative and positive) due to a limited ability to respond to external drivers as well as to restoration practices, making that stability 'indifferent' (López *et al.* 2013, López y Cavallero 2017) (Fig. 7). Finally, based on our results, we can infer that states with intermediate degradation levels would be the most sensitive to stochastic weather events, and therefore, in a climate change context, these least stable states would be the most affected.

The characterization of the ecological resilience of each state through the parameters evaluated in this study has strong management implications. In well conserved states (such as the reference state and State I in Fig. 7a), the stocking rate should periodically be adjusted based on the

Accepted Article

rainfall recorded during the growing season, and on threshold indicators of the state (e.g., risk phase with > 45 % plant cover, and > 7% *P. ligularis* cover, *sensu* López *et al.* 2013). In states with intermediate degradation, our results suggest that, in absence of grazing, high summer rainfall events can trigger a positive transition (Fig. 1). This positive transition (associated with episodic windows of recovery) would increase grass cover (i.e., *P. speciosa*). However, more studies should be conducted about the long-term effects of wet periods on internal regulation processes, with the aim to determine if both the increase in water availability and grazing exclusion are enough to overcome the negative resilience of the state and allow the recovery to the reference state; or if wet periods trigger a transition to a new state dominated by *P. speciosa* and co-dominated by other species of high forage value, such as *H. comosum*. Therefore, in states with intermediate degradation grazing should be excluded during wet periods to allow recovery transitions (positive transition, see Glossary on Supplementary file) whereas during dry years, field managers should reduce grazing pressure because of the risk of further degradation. Finally, in very degraded states which have a high negative resilience (due to their high resistance to ecosystem restoration, *sensu* Lake 2013; State III, Fig. 7), rehabilitation practices promoting shrub species resistant to arid environments should be implemented (López and Cavallero 2017). Overall, to control degradation, management plans should foresee the occurrence of climatically favorable and unfavorable periods, and management decisions should consider the positive and negative effects that stochastic weather events can cause on the processes that modulate the resilience of each state.

## 7. ACKNOWLEDGEMENTS:

We thank INTA for providing the structure and logistics for this study, the project PICT-2010-1392 (FonCyT) for financial support; for contributions and conceptual suggestions or in the field work of M. Easdale, G. Siffredi, D. Bran, H. Moraga and M. Aguiar. We also thank M. Easdale for encouraging us to publish these ideas.

## 8. DATA AVAILABILITY:

Data are available at <https://repositorio.inta.gob.ar> (Institutional Repository of INTA).

## 9. REFERENCES:

- Aguiar M.R. and Sala O. (1994). Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. *OIKOS*, 70: 26-34.
- Baskin C.C. and Baskin J.M. (2001). *Ecology, biogeography and evolution of dormancy and germination*. Academic Press, Elsevier, New York.
- Bestelmeyer, B. T. (2006). Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. *Restoration Ecology*, 14: 325-329.
- Bisigato A.J. and Bertiller M.B. (2004). Temporal and micro-spatial patterning of seedling establishment. Consequences for patch dynamics in the southern Monte, Argentina. *Plant Ecology*, 174: 235-246.
- Briske D.D., Fuhlendorf S.D. and Smeins F.E. (2003). Vegetation dynamics on rangelands: a critique of the current paradigms. *Journal of Applied Ecology*, 40:601-614.
- Briske D.D., Fuhlendorf S.D. and Smeins F.E. (2005). State-and-Transition Models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management*, 58:1-10.
- Briske D. D., Fuhlendorf S. D., and Smeins F. E. (2006). A unified framework for assessment and application of ecological thresholds. *Rangeland Ecology and Management*, 59(3), 225-236.
- Briske D. D. (2017). *Rangeland systems: processes, management and challenges* (p. 661). Springer Nature.
- Bustos J.C. and Rochi V. (1993). Caracterización termopluviométrica de veinte estaciones meteorológicas de Río Negro y Neuquén. En INTA EEA Bariloche. Serie Comunicaciones técnicas Área Recursos Naturales. Agrometeorología N° 1, 43 p.
- Bustos J.C. (2006). Características climáticas del campo anexo Pilcaniyeu (Río Negro). INTA EEA Bariloche. Serie Comunicaciones Técnicas, Área Recursos Naturales. Agrometeorología N° 25.
- Chesson P. and Huntly N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist*, 150: 519-553.
- Chesson P., Gebauer R.L.E., Schwinning S., Huntly N., Wiegand K., Ernest M.S.K., Sher A., Novoplansky A. and Weltzin J.F. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141: 236-253.
- Coronato F.R. and Bertiller M.B. (1996). Precipitation and landscape related effects on soil moisture in semi-arid rangelands of Patagonia. *Journal of Arid Environments*, 34: 1-9.
- Damascos M.A., Barthélémy D., Ezcurra C., Martínez P. and Brion C. (2008). Plant phenology, shoot growth, and branching pattern in *Mulinum spinosum* (Apiaceae), a cushion shrub of the arid Patagonian steppe of Argentina. *Journal of Arid Environments*, 72: 1977-1988.
- Defossé G.E., Robberecht R. and Bertiller M.B. (1997). Seedling dynamics of *Festuca* spp. in a grassland of Patagonia, Argentina, as affected by competition, microsites and grazing. *Journal of Range Management*, 50: 73-79.
- Derry J.F. and Boone R.B. (2010). Grazing systems are a result of equilibrium and non-equilibrium dynamics. *Journal of Arid Environments*, 74: 307-309.
- Dyksterhuis E. J. (1949). Condition and management of rangeland based on quantitative ecology. *Journal of Range Management*, 2:104-115.
- Easdale M.H. and Rosso H. (2010). Dealing with drought: social implications of different smallholder survival strategies in semi-arid rangelands of Northern Patagonia, Argentina. *The Rangeland Journal*, 32: 247-255.
- Fernández-Gimenez M.E. and Allen-Diaz B. (1999). Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *Journal of Applied Ecology*, 36:36-871.
- Fernández M.E., Gyenge J.E., Dalla Salda G. and Schlichter T.M. (2002). Silvopastoral systems in northwestern Patagonia I: growth and photosynthesis of *Stipa speciosa* under different levels of *Pinus ponderosa* cover. *Agroforestry System*, 55: 27-35.
- Fernández R.J., Nuñez A.H. and Soriano A. (1992). Contrasting demography of two Patagonian shrubs under different conditions of sheep grazing and resource supply. *Oecologia*, 91:39-46.

- Gebauer R.L.E. and Ehleringer J.R. (2000). Water and nitrogen uptake patterns following moisture pulses in a cold desert community. *Ecology*, 81: 1415–1424.
- Gillespie I.G. and Loik M.E. (2004). Pulse events in Great Basin Desert shrublands: physiological responses of *Artemisia tridentata* and *Purshia tridentata* seedlings to increased summer precipitation. *Journal of Arid Environments*, 59: 41–57.
- Gittins C. (2011). Mecanismos de persistencia de *Poa ligularis* expuesta a varias frecuencias de defoliación en el noroeste de la Patagonia. Tesis de Doctorado en Biología, Escuela de Doctorado, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue.
- Golluscio R.A., Sala O.E. and Lauenroth W.K. (1998). Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonia steppe. *Oecologia*, 115:17-25.
- Graff P, Aguiar M.R. and Chaneton E.J. (2007). Shifts in positive and negative plant interactions along a grazing intensity gradient. *Ecology*, 88: 188–199.
- Graff P.B. (2009). Efecto de la competencia, la facilitación y el pastoreo sobre la estructura espacial y dinámica de la estepa patagónica. Tesis de Doctorado en Ciencias Agropecuarias, Escuela para Graduados Alberto Soriano, Facultad de Agronomía, Universidad de Buenos Aires.
- Greenlee J.T. and Callaway R.M. (1996). Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *American Naturalist*, 148: 386-396.
- Gutterman Y. (1993). Seed germination in desert plants. Springer-Verlag, Berlin, Germany.
- Hein L. (2006). The impacts of grazing and rainfall variability on the dynamics of a Sahelian rangeland. *Journal of Arid Environments*, 64:488-504.
- Holmgren M., Scheffer M., Ezcurra E, Gutiérrez J.R. and Mohren G.M.J. (2001). El Niño effects on the dynamics of terrestrial ecosystems. *TRENDS in Ecology and Evolution*, 16: 89-94.
- Holmgren M., Stapp P., Dickman C.R., Gracia C., Graham S., Gutiérrez J.R., Hice C., Jaksic F., Kelt D.A., Letnic M., Lima M., López B.C., Meserve P.L, Milstead W.B., Polis G.A., Previtali M.A., Richter M., Sabaté S. and Squeo F.A. (2006). Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment*, 4: 87-95.
- Hunt L.P. (2001). Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology*; 38: 238–252.
- Kemp P.R. (1989). Seed banks and vegetation processes in deserts. En: Leck M.A. and Parker V.T (eds.), *Ecology of Soil Seed Banks*, pag. 257–282. Academic Press, San Diego.
- Lake P.S. (2013). Resistance, resilience and restoration. *Ecological Management and Restoration*, 14: 20-24.
- León R.J.C., Bran D., Collantes M., Paruelo J. M and Soriano A., (1998). Grandes unidades de vegetación de la Patagonia extra andina. *Ecología Austral*, 8:125-144.
- Lemaire G., Hodgson J., de Moraes A., P.C. de F Carvalho and Nabinger C. (2000). *Grassland ecophysiology and grazing ecology*. CABI Publishing.
- Lloret, Peñuelas F. J., Prieto P., Llorens L. and Estiarte M. (2009). Plant community changes induced by experimental climate change: Seedling and adult species composition. *Perspective in Plant Ecology, Evolution and Systematics*, 11: 53–63.
- López, D. R. (2011). Una aproximación estructural–funcional del modelo de estados y transiciones para el estudio de la dinámica de la vegetación en estepas de Patagonia norte. Universidad Nacional del Comahue, Bariloche.
- López, D. R., Cavallero, L., Brizuela, M. A. and Aguiar, M. R. (2011). Ecosystemic structural–functional approach of the state and transition model. *Applied Vegetation Science*, 14(1): 6-16.
- López, D. R., Brizuela, M. A., Willems, P., Aguiar, M. R., Siffredi, G. and Bran, D. (2013). Linking ecosystem resistance, resilience, and stability in steppes of North Patagonia. *Ecological Indicators*, 24: 1-11.
- López, D. R. and Cavallero, L. (2017). The role of nurse functional types in seedling recruitment dynamics of alternative states in rangelands. *Acta Oecologica*, 79: 70-80.

- Ludwig J.A., Tongway D.J., Eager R.W., Williams R.J. and Cook G.D. (1999). Fine-scale vegetation patches decline in size and cover with increasing rainfall in Australian savannas. *Landscape Ecology*, 14: 557-566.
- Matos, I. S., Menor, I. O., Rifai, S. W., and Rosado, B. H. P. (2020). Deciphering the stability of grassland productivity in response to rainfall manipulation experiments. *Global Ecology and Biogeography*, 29: 558-572.
- MacDonald N. and Walkinson A.R. (1981). Models an annual plant population with a seedbank. *Journal of Theoretical Biology*, 93: 643-653.
- Noy-Meir I. (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, 4:25-51.
- Noy-Meir I. (1995). Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. *Journal of Vegetation Science*, 6:701–710.
- Novoplansky A. and Goldberg D.E. (2001). Effects of water pulsing on individual performance and competitive hierarchies in plants. *Journal of Vegetation Science* 12:199–208.
- Oesterheld M., Loreti J., Semmartin M. and Sala O.E. (2001). Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *Journal of Vegetation Science*, 12: 137-142.
- O'Reagain P.J. (1993). Plant structure and the acceptability of different grasses to sheep. *Journal of Range Management*, 46: 232-236.
- Pake C.E. and Venable D.L. (1996). Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, 77:1427–1435.
- Paruelo J. M and Sala O. E. (1992). El impacto de la desertificación sobre la capacidad de carga de las estepas patagónicas: sus consecuencias económicas. II Congreso Latinoamericano de Ecología. Caxambú. Brasil.
- Paruelo J.M., Sala O.E. and Beltrán A. (2000). Long-term dynamics of water and carbon in semi-arid ecosystems: a gradient analysis in the Patagonian steppe. *Plant Ecology*, 150: 133-143.
- Peri P.L., López D.R., Rusch V., Rusch G., Rosas Y.M., and Martínez Pastur G. (2017). State and transition model approach in native forests of Southern Patagonia (Argentina): linking ecosystem services, thresholds and resilience. *International Journal of Biodiversity Science, Ecosystem Services and Management*, 13: 105-118.
- Ramos M. C. and Martínez-Casasnovas J. A. (2006). Impact of land levelling on soil moisture and runoff variability in vineyards under different rainfall distributions in a Mediterranean climate and its influence on crop productivity. *Journal of Hydrology*, 321: 131-146.
- Retzer V. (2006). Impacts of grazing and rainfall variability on the dynamics of a Sahelian rangeland revisited (Hein, 2006)—new insights from old data. *Journal of Arid Environments*, 67: 157–164.
- SAS (1999). Version 8, SAS Institute Inc., Cary NC, USA.
- Sheehan, P. J. (1984). Effects on community and ecosystem structure and dynamics. Effects of pollutants at the ecosystem level, 51-99.
- Schwinning S. and Ehleringer J.R. (2001). Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology*, 98: 464-480.
- Schwinning S., Starr B.I. and Ehleringer J.R. (2003). Dominant cold desert plants do not partition warm season precipitation by event size. *Oecologia*, 136: 252-260.
- Schwinning S. and Sala O. (2004). Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia*, 141: 211–220.
- Soriano A., Sala O.E. and Perelman S.B. (1994). Patch structure and dynamics in a Patagonian arid steppe. *Vegetatio*, 111: 127-135.
- Standish, R. J., Hobbs, R. J., Mayfield, M. M., Bestelmeyer, B. T., Suding, K. N., Battaglia, L. L., ... and Harris, J. A. (2014). Resilience in ecology: Abstraction, distraction, or where the action is?. *Biological Conservation*, 177, 43-51.
- Steel R.G.D. and Torrie J. H. (1980). Principles and procedures of Statistics, a biometrical approach. New York, McGraw-Hill Book Company.



Tercero-Bucardo N., Kitzberger T., Veblen T. and Raffaele E. (2007). A field experiment on climatic and herbivore impacts on post-fire tree regeneration in north-western Patagonia. *Journal of Ecology*, 95: 771–779.

Villagra S., Easdale M., Giraud C., Bustos C. and Bolla D. (2009). Situación de la ganadería extensiva de la provincia de Río Negro al final del ciclo productivo 2008-2009. INTA EEA Bariloche. Serie Comunicaciones Técnicas N° 228.

Walker B. (2020). Resilience: what it is and is not. *Ecology and Society*, 25(2).

Washington-Allen R.A., Ramsey R.D., West N.E., Norton B.E. (2008). Quantification of the ecological resilience of drylands using digital remote sensing. *Ecology and Society* 13: 33. URL: <http://www.ecologyandsociety.org/vol13/iss1/art33/>

Westman W.E. (1986) Resilience: concepts and measures. In: Dell B., Hopkins A.J.M., Lamont B.B. (eds) Resilience in mediterranean-type ecosystems. Tasks for vegetation science, vol 16.

Springer, Dordrecht. [https://doi.org/10.1007/978-94-009-4822-8\\_2](https://doi.org/10.1007/978-94-009-4822-8_2). Westoby M. (1979). Draft policy position of the ESA on the relation of professional ecologists to the environmental impact assessment process. *Bulletin of Ecological Society of Australia*, 9: 3-5.

Westoby M., Walker B. and Noy-Meir I. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, 42: 266-274.

Wu J. and Loucks O.L. (1995). From balance of nature to hierarchical patch dynamics: a paradigm shifts in ecology. *The Quarterly Review of Biology*, 70: 439-466.

# Supplementary Material

The *supplementary material* contains the following information:

**Table A.** Mean annual rainfall in study site.

**Table B.** Mean summer rainfall (december-march) in study site.

**Table C.** Mean plant, litter cover, and density of individuals recorded in reference state and degraded state.

**Fig. S1.** Schematic representation of negative feedback processes (**a**) and positive feedback processes (**b**) in a rangeland ecosystem.

**Fig. S2.** Mean density of seedlings emerged of the main grass and shrub species in April 2006 and 2007, and mean density of surviving seedlings during the subsequent years.

**Fig. S3.** Seed rain of the main perennial species recorded in distinct microsites (plant patches and bare soil) in two alternative states (reference state and degraded state) of a graminous-subshrubby steppe of northwestern Patagonia (Argentina).

**Glossary:** Synthesis of the key concepts on Ecological Sites and the State and Transition Model (STM).

**Figure S3. (a)** Schematic representation of the dynamic equilibrium of a state of the study system at patch- and community-scale of the grass-shrubby steppes of *Poa ligularis* and *Mulinum spinosum* (northern Patagonia, Argentina). **(b)** Structural-Functional State and Transitions Model for the study system.